

THE ECOLOGY OF EVEN-AGED FOREST PLANTATIONS

edited by
E. D. FORD
D. C. MALCOLM
J. ATTERSON

Proceedings of the Meeting of Division 1
International Union of Forestry Research Organisations
Edinburgh, September 1978

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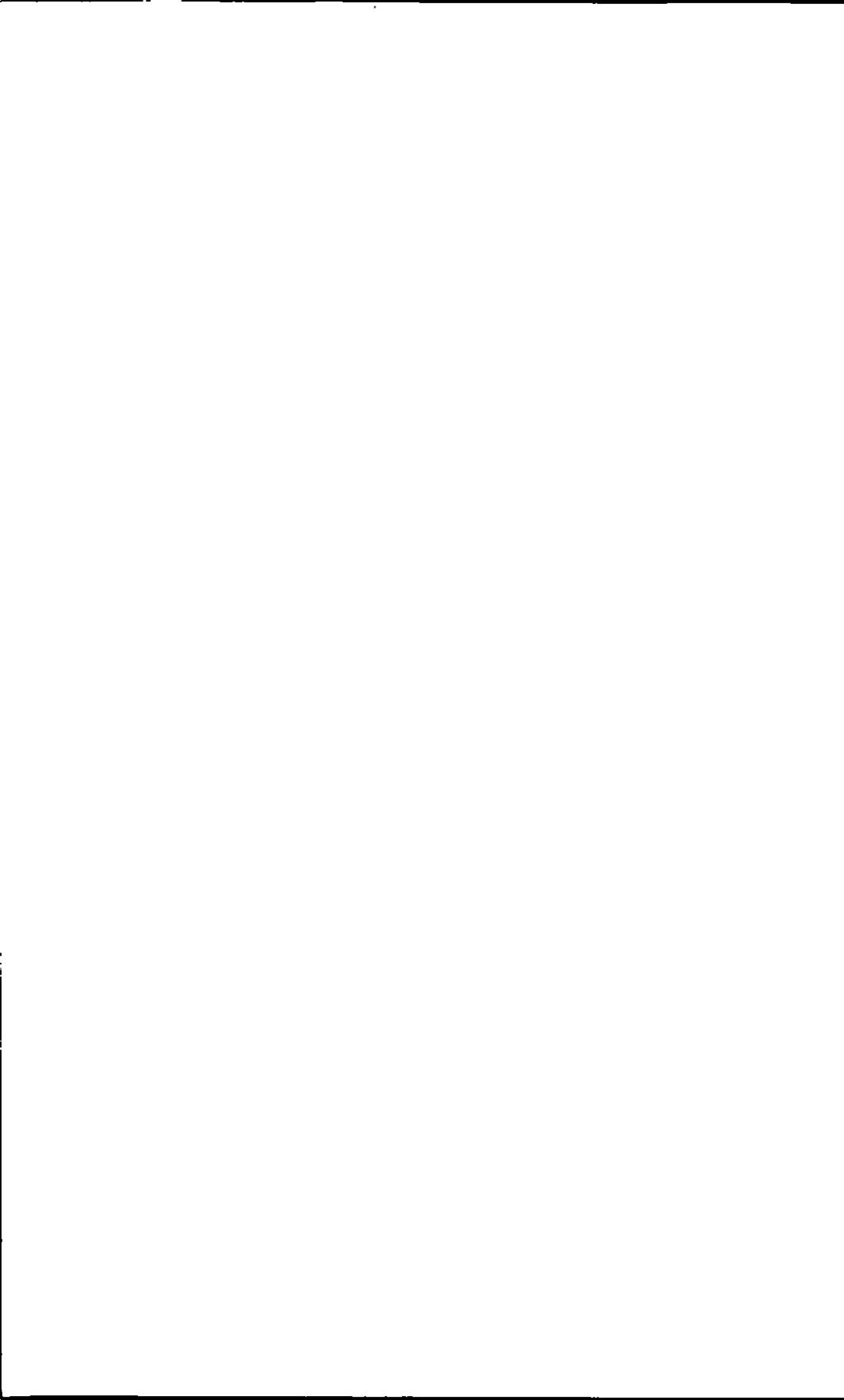
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OF

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Edited by

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and

J. ATTERSON

Forestry Commission, U.K.

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PREFACE

The initiative for Division I, 'Site and Silviculture', of the International Union of Forestry Research Organisations (I.U.F.R.O.) to hold one of its regular full divisional meetings on the ecology of even-aged plantations came from Mr. R.C. Steele, Institute of Terrestrial Ecology, in consultation with the Division Coordinator, Professor D. Mlinsek. Over the past 60 years the United Kingdom has undertaken major afforestation through plantation schemes and so was an appropriate country in which to hold such a meeting.

The organising committee for the meeting was:

Chairman Professor F.T. Last, Institute of Terrestrial Ecology
Secretary Dr. E.D. Ford, Institute of Terrestrial Ecology

Mr. J. Atterson, Forestry Commission

Dr. D.C. Malcolm, University of Edinburgh

Mr. D.T. Seal, Forestry Commission.

The programme of lectures and discussion was held at the Department of Forestry and Natural Resources, University of Edinburgh and at the University's Pollock Halls of Residence. Visits were made to Ae, Dunkeld, Eskdalemuir and Glentworth Forests by invitation of the Forestry Commission and the Economic Forestry Group. The programme incorporated the interests of the constituent Working Groups of Division I and was attended by 130 participants from 21 countries.

Further information on the activities of I.U.F.R.O. can be obtained from:

I.U.F.R.O. Secretariat,
Schönbrunn,
A-1131 Vienna,
Austria.



ACKNOWLEDGEMENTS

We are grateful to Mrs I. Bellos, Miss I. Schumacher and Miss D. Ziegler for their translations of the summaries of papers into French and German and to our colleagues in I.U.F.R.O., H. Oswald, H.W. Zöttl and G.K. Kenk for their technical comments on these translations.

We wish to thank Mr. R.H.F. Wilson who drew the figures and particularly Mrs M.F. Cannell for her painstaking work in the preparation of the typescript.

EDITORS' NOTE

This volume has been produced from camera ready copy of a typescript which itself was set by computer. The process imposed some restrictions on the use of accepted conventions for abbreviations, symbols and units of measurement. As authors did not have the opportunity of correcting proofs responsibility for errors must rest with the editors.

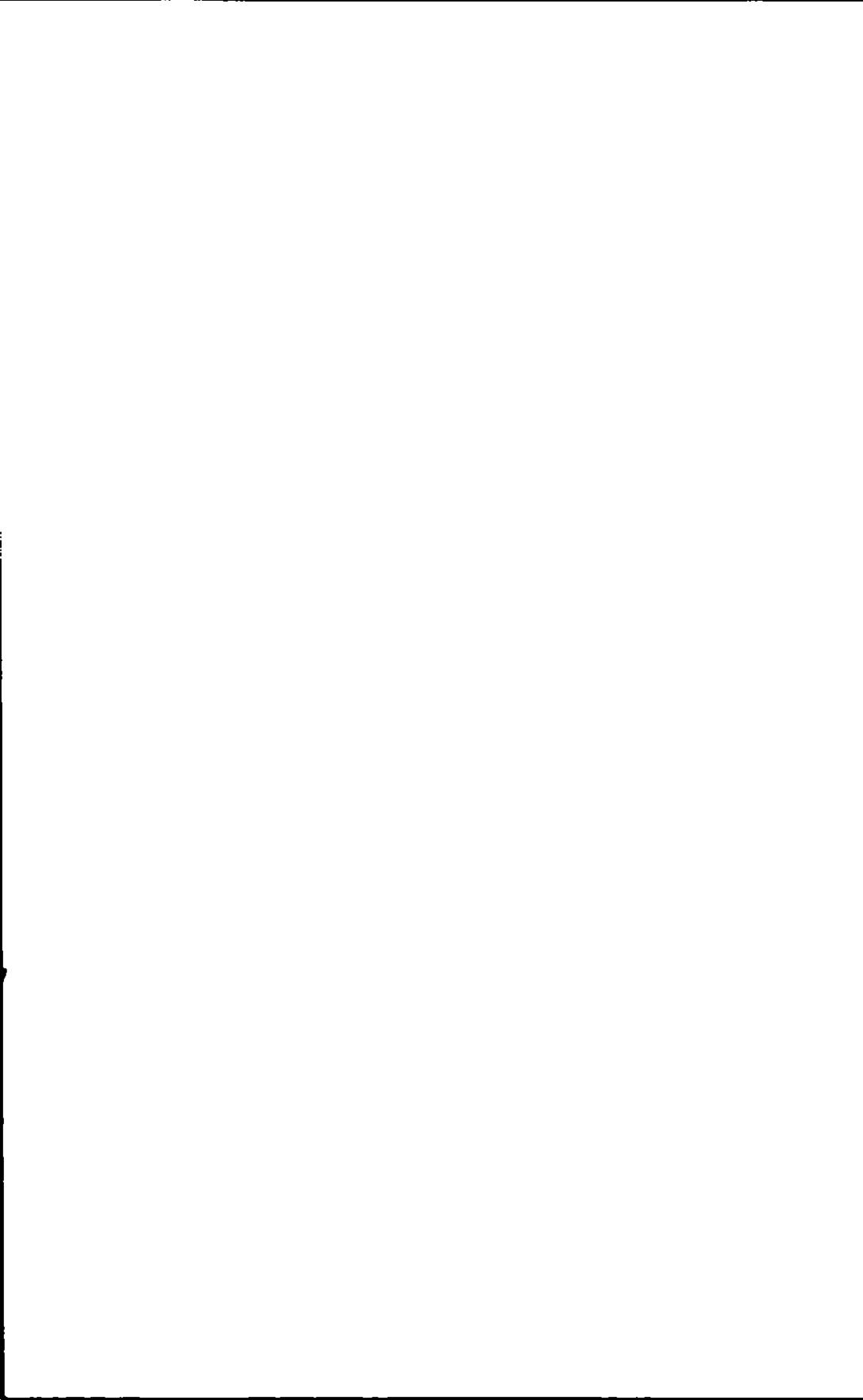


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FORESTRY IN GREAT BRITAIN

(Produced by the Forestry Commission)

FORESTRY IN GREAT BRITAIN

Conservancy Boundary

Local Authority Boundary

Conservancy Names

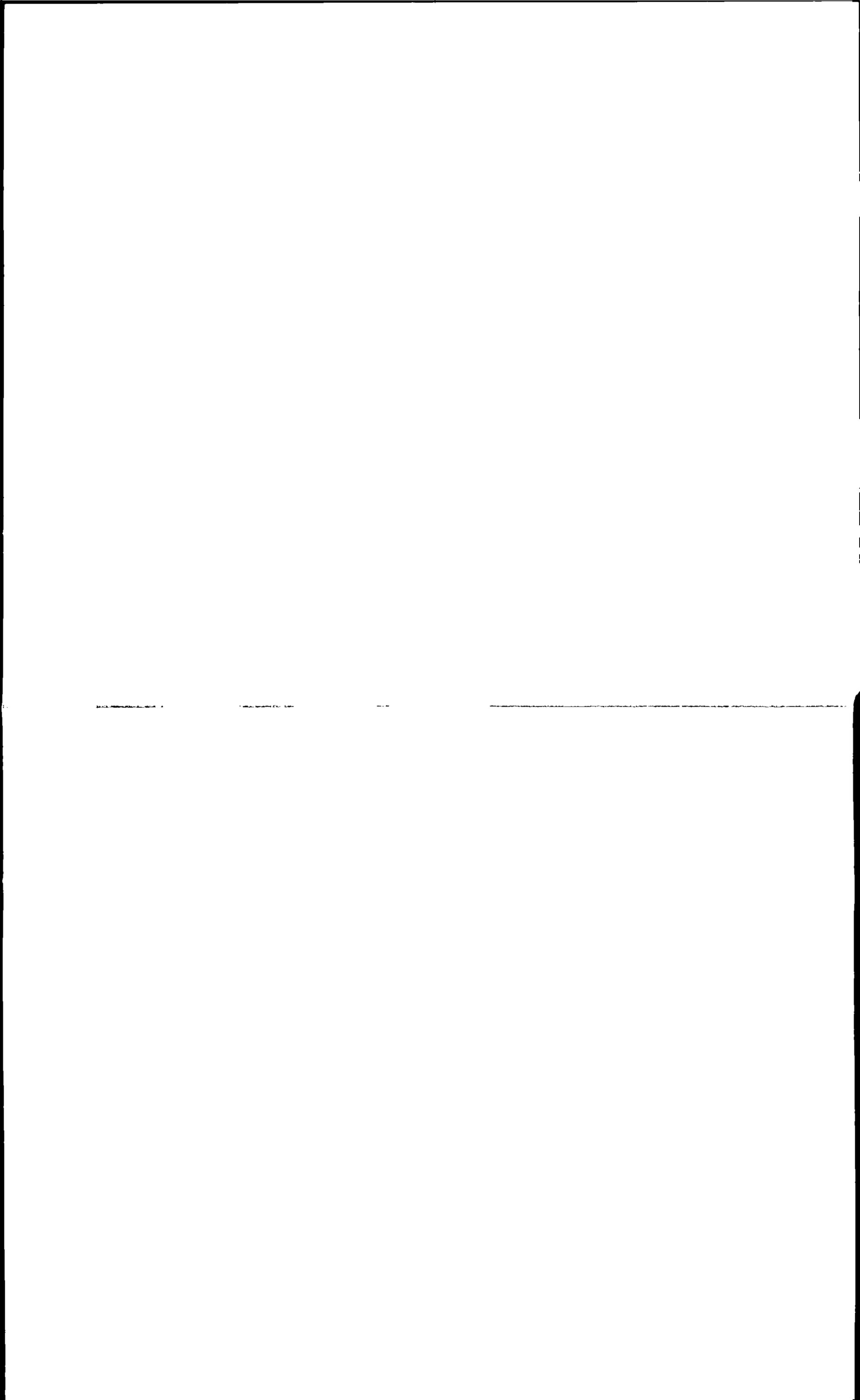
Forestry Commission Land
(including unplanted land)

Private Woodlands: Dedicated

Private Woodlands: Approved

Scale 1:1875 000





September 3, 1978

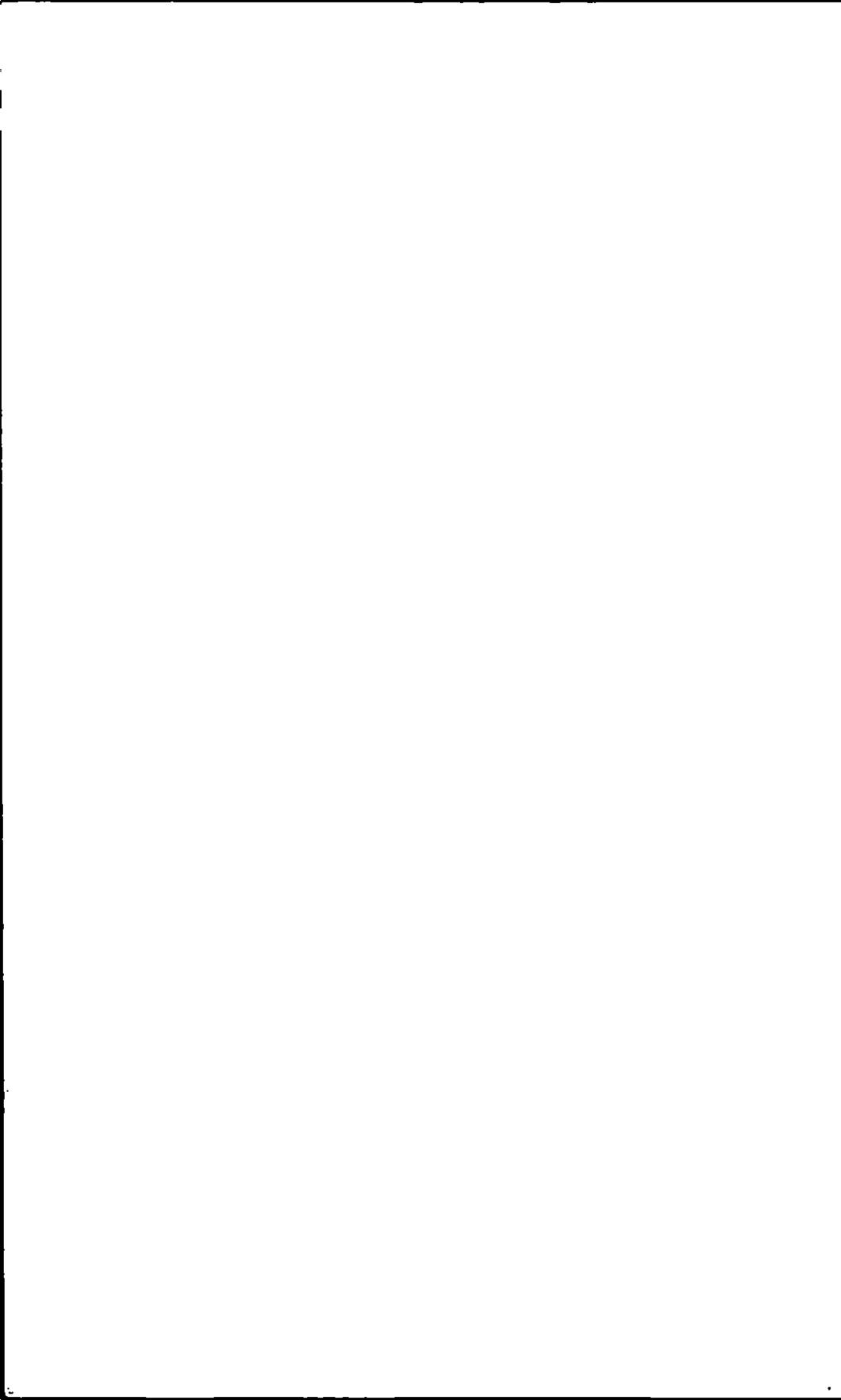
INTRODUCTION

Address by Coordinator of
Division I

D. Mlinšek

Introductory address:
An introduction to forestry
in upland Britain

G.D. Holmes



ON ECOLOGY OF EVEN-AGED MONOCULTURES

Introduction to the International Union of Forestry Research Organisations Division 1, 'Site and Silviculture' Meeting at Edinburgh, September 1978.

D. MLINŠEK

Divisional Coordinator, Biotehniška fakulteta, Krekov trg 1, 6100 Ljubljana, Jugoslavia.

At first glance the topic 'ecology of monocultures' may appear inappropriate, particularly if we recall the lengthy debates (e.g. Mitscherlich 1958; Wittish 1961) in the past about forest monocultures on the European continent. Monocultures do exist there today but often represent silvicultural formations of dubious value. At the 1975 Division I meeting in Ankara, Mr R.C. Steele proposed that we should examine this topic and particularly that our venue should be the United Kingdom. We agreed then that this would be appropriate for the regular divisional meeting in 1978. Today we are realising this idea thanks to the endeavours of Mr Steele and of the local organizing committee. On behalf of Division I, I would like to thank them all most sincerely. Particularly I would like to thank them for rendering possible continuity in the work of the Division as practised for a number of years, i.e. the holding of an annual divisional meeting.

While thinking about the 'ecology of even-aged monocultures' we find this topical area most appropriate. At our meeting we have in mind conifer monocultures in particular, yet I would like to draw your attention to the fact that an even-aged beech or oak stand, formed by a shelterwood system, also represents a monoculture and should not be excluded from our discussions.

Nowadays forest monocultures are a fact which cannot be avoided or ignored. From the historical and long-term point of view they frequently represent an obligatory, although often undesirable step in the development of a forest economy. They represent an imitation of agriculture by utilizing pioneer properties of individual tree species interesting from a narrow, short-term economic point of view. In addition monocultures are strongly favoured by modern technology. The timber-hungry countries without forests need monocultures - primarily for their wood material - regardless of the timber quality. In the given state of world economic development we

have to accept this fact. Equally, we have to take into account the fact, innate to human nature, that we do not learn anything from the experience of others, but only from our own! Here I am referring to silvicultural experience with monocultures in Central Europe.

In the history of forestry we find that the monoculture concept of wood production comes in a wave-like form and frequency which cannot be avoided. The post-war period has been characterized by a huge wave that spread over all the continents, though only in a minor form over Central Europe. In many countries establishing monocultures represents a sign of progress in forestry, a first and essential step without which not further development, characterized by stronger considerations of ecology, can take place. This means that research on monoculture has to be activated, particularly as to its future development. It is a duty of research to study forest monocultures impartially and such impartiality will be guaranteed by an ecological approach - the researcher's realization that in the case of forest formations he deals with a typical black box system. Hence the name of the sessional topic 'ecology of monocultures'

We know a lot about establishing monocultures and there has been much research on this subject. However, it is now necessary to look at the future of monocultures in forestry, and it has to be appreciated, in order to avoid any possible misunderstanding, that there are differences between the ecological and economic points of view.

I hope that our discussions will evaluate viewpoints critically without digressing from the ecosystem starting points. Here I have in mind, for example, the fact that by means of different management methods man keeps reducing biomass in various ecosystems which brings about the most unfavourable consequences. Organized accumulation of biomass is one of the prerequisites for the functioning of a forest ecosystem. From this point of view, establishing monocultures with subsequent growth and organized accumulation of biomass is partly justified. But this could not be said about the cases where we devastate natural forests with great quantities of biomass and replace them with the biomass of artificial forest monocultures.

Our efforts in establishing monocultures in areas where forests no longer exist, are positive from an ecological point of view. This holds true even more if we consider the fact that in forming forest ecosystems nature too uses various ways, even through the pioneer monoculture, with the basic starting goal to create biomass, i.e. investment. In nature this stage is followed either by a slower or faster transformation of biomass - in some cases nature stays with pure pioneers. In any case nature builds ecosystems that are more and more perfect. We, too, are facing the question

whether it is purposeful to stay, at any price, with the pure, already established monocultures. The ecology of monocultures should draw attention to the future direction of forestry in monocultures, particularly in the cases where monocultures should perform new tasks of a social and protective nature.

The great accomplishments of foresters in deforested Great Britain are admirable. They are clearly evident from the book 'Forest Service' (Ryle 1969), describing the first forty-five years of Forestry Commission work, as well as from the paper presented by Mr George Holmes. The first step was to establish the material base of the forest, i.e. to create biomass. It is possible to progress only after such a base has been created. And thus we read on p.292 of the above-mentioned book that '.... the recreational need will mean a partial breakaway from monoculture sooner or later'. This statement is particularly attractive since we already know that practical forest management methods should combine wood production with other forest functions. It has to be stressed that in such cases wood production is not diminished.

We have to ask ourselves how to shape existing monocultures in the future in order to meet the new demands of a protective and social nature. This is a question of conversion methods which should not be rigorous in their nature. The better a conversion method is adapted to normal forest management, the greater its value. This finding is of the greatest importance considering the fact that the forest ought to remain a natural counterbalance to artificial, agricultural ecosystems and industry on a local, regional and global scale. Wherever we do insist on artificial monocultures, the following questions of an ecological and economic nature arise: how and to what extent is forestry capable of maintaining artificial monocultures and what level of artificiality can forestry afford with regard to different site conditions?

Forestry certainly owes mankind help in the ecological crisis. It has been suggested that forestry will offer such help by substituting removals in natural forests by high wood production from plantations. I do not believe such theories, although they may be of local value. The task of forestry in environmental protection lies elsewhere.

The phenomenon of monocultures in forestry cannot be avoided. It is necessary, however, to search for ways of diminishing the impact caused by artificial monocultures. This is an area where ecological research can make an important contribution, although we should not search for universal prescriptions. Examples and solutions from one site, e.g. specific to Great Britain, may not be suitable for ecological, economic and social reasons elsewhere. Only general findings have universal value and our discussions should contribute to such findings.

ON ECOLOGY OF EVEN-AGED MONOCULTURES

In the changing world, artificial monocultures can be both good and evil at the same time. Quite often the character of the newly established forest is dependent primarily on the forester's goodwill, zeal and professional qualification, and only in the second place on the money available for its establishment. And as I am deeply convinced that goodwill prevails at our meeting, I have great expectations of our joint efforts in the coming days.

REFERENCES

- Mitscherlich, G. (1958). Bodenverschlechung und Düngung in ertragskundlicher Sicht. *Der Forst- und Holzwirt*, 13, 415-421.
- Ryle, G. B. (1969). *Forest Service - the first 45 years*. David and Charles, Newton Abbott, Devon, U.K.
- Wittish, W. (1961). Der Einfluss der Baumart auf den Bodenzustand. *Allgemeine Forstzeitschrift*, 16, 41-45.

THE ECOLOGY OF EVEN-AGED PLANTATIONS:
AN INTRODUCTION TO FORESTRY IN UPLAND BRITAIN

By G.D. HOLMES

Director General, Forestry Commission; 231, Corstorphine Road,
Edinburgh, United Kingdom.

SUMMARY

The need for even-aged forests.

The present structure, productivity, and history of upland forests in Britain.

Rural land use and the prospects for more afforestation.

Ecological changes affecting soil, water, flora, fauna and the forest.

Ecological problems and the reconciliation of the needs of silviculture, environmental management, and operational efficiency.

The importance of research on questions including tree health, tree stability, regeneration, soil productivity and wildlife conservation.

The need for sound knowledge of the forest ecosystem as a basis for management decisions.

The value and scope for international debate and cooperation in research.

RÉSUMÉ

Cet exposé traite des sujets suivants:

Besoin de forêts composées de peuplements équiens.

Structure actuelle, productivité et histoire des forêts des Uplands de Grande Bretagne.

Utilisation de l'espace rural et perspectives de plantations nouvelles.

Changements écologiques ayant une influence sur le sol, l'eau, la flore, la faune et la forêt.

Problèmes d'ordre écologique et réconciliation entre les besoins de la sylviculture, de la gestion de l'environnement et de l'efficacité de la mise en oeuvre.

Importance des recherches sur des questions telles que la santé et la stabilité des arbres, la régénération, la productivité du sol et la protection de la faune sauvage.

Besoin d'une connaissance solide de l'écosystème de la forêt en tant que base des décisions de gestion forestière.
Valeur et nécessité d'un débat à l'échelon international et de la collaboration sur le plan de la recherche.

ZUSAMMENFASSUNG

Die Arbeit behandelt folgende Themen:
Zweckmässigkeit gleichaltriger Wälder.
Gegenwärtige Struktur, Produktivität und Geschichte der Wälder im britischen Hochland.
Landwirtschaftliche Landnutzung und Aussichten weiterer Aufforstung.
Veränderungen von Boden, Wasserhaushalt, Flora, Fauna und ihre ökologischen Auswirkungen im Wald.
Ökologische Probleme und die Abstimmung von forstwirtschaftlichen, umweltpolitischen und betriebswirtschaftlichen Anforderungen.
Bedeutung der Forschung im Hinblick auf Forstschutz, Bestandesstabilität, Verjüngung, Bodenfruchtbarkeit und Erhaltung des Tierbestandes.
Notwendigkeit einer gründlichen Kenntnis des Waldökosystems als Grundlage forstwirtschaftlicher Entscheidungen.
Nutzen und Umfang des internationalen Erfahrungsaustausches und der Zusammenarbeit in der Forschung.

INTRODUCTION

My prime aim is to introduce you to forestry in Britain by giving a very general picture of our forests, their recent history and place in the land use scene. I also intend to say something about afforestation achievements and a selection of what I believe are the key problems requiring research attention at the present time.

I warmly welcome IUFRO's initiative in holding a full Divisional meeting on the ecology of plantations because there is clearly a need for a better understanding of man-made forests as ecosystems in order to provide a sounder foundation for future management decisions. I also welcome your meeting in Britain as I am sure that our experience of large-scale afforestation extending over a period of more than fifty years will provide a highly relevant and helpful background to your discussions. I am equally certain that your deliberations will be great value to British foresters and scientists.

THE NEED FOR EVEN-AGED PLANTATIONS

Looking for a moment at the world situation, the need for man-made plantations is increasingly more apparent. The current consumption of wood is about 2500 million cubic metres/yr which is obtained from about 2500 million ha of productive forest land. The world population is now about 3800 million and no matter how successful the world may be in controlling population growth, it seems inevitable that the population will have increased to over 5000 million by 2000 and to some 8000 million by 2025. There will, therefore, be ever increasing pressure on the land to produce both wood and food. Much of the natural forest will be cleared for agriculture or agro-forestry, and the latter is unlikely to yield large quantities of wood.

It is possible, given sufficient inputs of capital, manpower and research to increase the yield from natural forests two or threefold but man-made plantations can yield eight to ten times the current world average of 1 cubic metre/ha. Plantations can also be developed on land which is relatively poor, from the point of view of agricultural production. It seems certain, therefore, that high-yielding, even-aged plantations will provide a steadily increasing proportion of the world's growing demand for wood.

FORESTRY IN BRITAIN

The forest area of Britain per head of population is one of the lowest in Europe while the consumption of wood products is one of the highest. There is thus a very low level of self-sufficiency in wood products at about 8 per cent of consumption.

Although there have been intermittent attempts since the Middle Ages to increase timber production in Britain, a sustained national forest policy aimed at increasing the production of timber to meet the nation's needs dates only from 1919 when the Forestry Commission was set up as a Government agency with the prime task of creating a reserve of growing timber for defence reasons.

Since that time, policy has evolved by a succession of Government Reviews and the strategic reserve policy of 1919 has given way to more commercial aims based on recognition of the continuing importance of an indigenous supply of wood to industry. At the same time, present policies place much greater emphasis on the social and environmental benefits of forestry, notably employment, recreation, conservation and integration with agriculture.

Planting since 1919

The planting achievements since 1919 have been considerable. From 1919 to 1977 the area of productive forest doubled from 800,000 to 1.7 million ha, i.e. a rise from only 3.5 per cent to nearly 8 per cent of the land area of the

country. This expansion has consisted mainly of afforestation with coniferous species on bare heath land, moorland and rough pasture of low value for agriculture, particularly in the uplands of Scotland, the north of England and Wales. It is also noteworthy that this has been achieved by a combined effort of the public and private sections and that the forest estate of today is almost equally divided between the two (see Table 1). Thus, the planted area has increased by an average

Table 1. Area of productive forests in Great Britain. 1977 (000's ha)

	Conifers	Broadleaves	Total
Public (Forestry Commission)	791	50	841
Private	502	346	848
Total	1293	396	1689

of 15,000 ha/yr since 1919, but the greatest expansion has taken place over the last twenty-five years when the average rate of new planting has been about 29,000 ha/yr or nearly double the 1919-1977 average figure (see Table 2.).

Table 2. New planting - 25 years 1952-1977. (000's ha)

	Public (Forestry Commission)	Private	Total
Total area planted	425	261	686
Annual average	18	11	29

The present species and age-class structure of forest in Britain can be broadly represented as in Figs 1 and 2.

Future planting.

Today, much of the debate on forestry policy turns on the question of new planting and how much further expansion should take place. Looking to the future, and even allowing for the substantial increase of forest area in recent years, we remain a poorly forested country and it is unlikely that Britain, even by the year 2000, will be able to supply more than about 14 per cent of its needs from home sources. Such is the likely growth of demand for wood products that the country must increase its total forest area to maintain even this degree of self-sufficiency after the turn of this century. This has special implications for the country's balance of payments and we have to consider the extent to which we should use resources now to create new plantations as an insurance for the future. In an effort to throw some light on this issue, we, in this country, recently set up a working group to look into the future demand for wood on a world scale and to relate

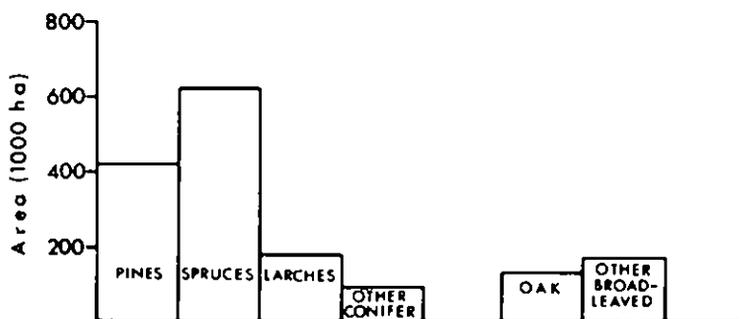


Fig. 1. Distribution of high forest species groups in Great Britain (March 1977).

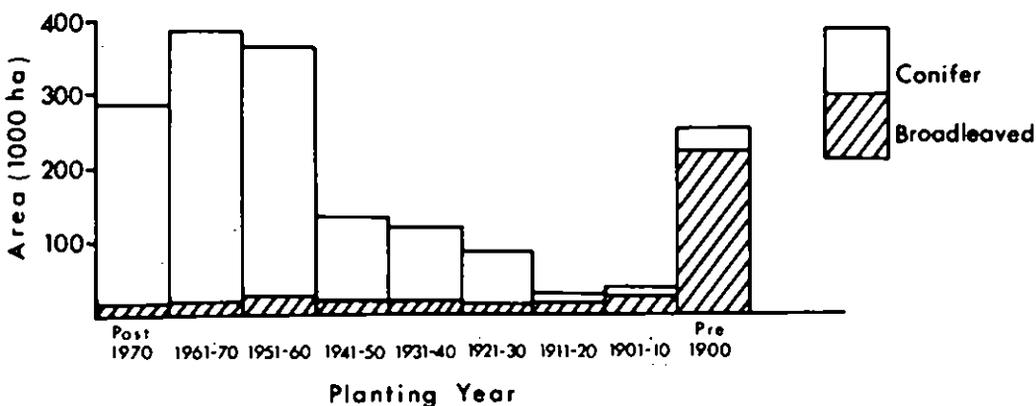


Fig. 2. Age class distribution of high forest in Great Britain (March 1977).

their findings to the British scene. The group's report was published as a consultative paper earlier this year and it is suggested that the world's forests will meet the increasing world demand for industrial wood until the turn of the century, without a serious rise in wood prices, but thereafter the continuing upward demand will result in a significant rise in the real price of wood. It is suggested that there should be a substantial continuing programme of new planting to help meet Britain's future needs.

Of course, there are technical limits to the amount of land that can be afforested in Britain. Although many soil limitations for tree growth can be ameliorated, there still remain areas which are incapable of growing economic forest crops owing to climatic conditions. Temperature, when linked with elevation, is important. Increase in elevation results in reduced temperature and increased exposure and the combination of the two quickly becomes limiting to tree growth. In the uplands, planting rarely takes place above 550m, and in the more exposed parts of the west and north the planting limit is about 300m.

As well as the physical limitations in the uplands, there are also economic limitations to the extent to which forestry can be practised in the fertile sites of the lowlands, where agriculture and urban developments have high values.

A balance has to be struck. Forestry in this country is really essentially an industry of the foothills and the uplands and this is where we must look to see any expansion.

Excluding areas with climatic conditions unfavourable to tree growth, thin soils, arable and permanent grassland, it is estimated that about 3 million ha of land in Britain could be planted with trees to produce economic crops of timber. Just over half of this (1.7 million ha) is in Scotland. In England and Wales there are some 1.3 million ha of potentially plantable land, but constraints on the amount of new planting in National Parks and in areas of outstanding natural beauty, could reduce the land available there to around 650,000 ha. Furthermore, there are considerable areas of common land in England and Wales which are not at present available for planting. Overall in Britain the main constraints on new planting are, of course, the requirements of agriculture.

Views on how much of this potential area should be planted vary from zero to over 2 million ha. There is a strong case for more planting and how much is achieved will depend in the long run on public attitudes to landscape, to rural employment and lifestyle, and to the value placed on food production in the uplands compared with wood production. It remains government policy that forestry should expand and workable procedures for consultation with agricultural and environmental and other interests exist in order to ensure that when land is proposed for afforestation, a sensible

allocation is made between the agricultural, forestry and other interests.

In the end, the aim is to achieve a pattern of land use which secures the best contribution to the welfare of the nation. This aim is simple to express but to translate it into terms of areas of land by locations is extremely difficult and could be dangerously misleading if one tried to do this precisely or by means of simplistic zoning schemes. Land can seldom, if ever, be categorised as being suitable for one and only one use. In practice, differences of interest and tradition, of aims and methods of management and of other factors play an important role in deciding which pattern of land use shall be adopted in a particular situation.

Wood production

New planting now will not affect production until the beginning of the next century and until that time output will be determined by the production goals and cutting plans for the existing forest area. Hardwood production is expected to remain at a level of about 1 million cubic metres/yr over the remainder of this century and although the value of this production is considerable, interest naturally centres on the growth of softwood production. Our latest softwood production forecasts show an overall increase of 230 per cent over the 1976 value by the turn of the century (Table 3).

The Forestry Commission will produce nearly 75 per cent of British softwoods production by the turn of the century and the rate of increase is so rapid that both the public and private sectors face a major challenge for the future if the timber becoming available is to be harvested and marketed effectively.

Some plantations will be managed on a non-thinning regime imposed by the risk of windthrow but the majority will be thinned on a cycle of four to eight years and clearfelled on a rotation of forty-five to sixty-five years. Rotations are determined largely by yield class which, expressed as maximum mean annual increment, ranges for conifers from 6 to 24 cubic metres/ha/yr, with a national average of 10 cubic metres/ha/yr.

Table 3. Softwood production in Great Britain.

	Public (Forestry Commission)	Private	Total
000,000's cu.m			
1976 actual cut	1.85	0.84	2.69
1991-96 forecast (annual average)	4.59	1.70	6.29
Increase	2.74	0.86	3.60
Factor	x 2.5	x 2	x 2.3

ECOLOGICAL CHANGE

British forests in the uplands consist in the main of pure, even-aged plantations with a preponderance of conifers and young age classes, less than twenty-five years old.

This fact conjures up a picture of a collection of dull, uniform ecosystems; a picture which is not often confirmed in practice when one examines forests on the ground. There are many reasons for this. In most areas, even though individual forests are made up of a series of even-aged stands, there is almost always a range of age classes and species, and the stands are broken up by roads and felling coupes. In practice, therefore, there is much more diversity and variation of canopy and 'edge' conditions than might at first be thought. Such diversity increases as the forest becomes older and regeneration fellings are carried out.

In establishing forests on bare upland it is hard to imagine a more dramatic change in the ecological conditions including the soil, the flora, the fauna, and not least the introduction of trees for the first time in many centuries. In general, the original site conditions were so inhospitable for the growth of trees that drastic interventions in the form of cultivation, drainage, weed control, fertilising and fencing have been necessary in order to establish productive forests.

I would like to comment on the nature of some of these ecological changes as I see them; - again in the hope that I may provide some general background to your much more detailed discussions during the next few days. At the same time, I would like to introduce the concept that when studying the ecology of plantations we are dealing with two complementary basic resources, namely:

THE PHYSICAL RESOURCE - that is the soil and its physical environment, and

THE BIOLOGICAL RESOURCE - that is the flora, fauna and the trees themselves.

We need to understand how our management affects these resources and their interactions if we are to achieve the best overall benefit to society and avoid harmful side effects.

The soil.

The soil and its physical, hydrological and chemical properties are changed by plantation forestry, either prior to planting in order to make the site more suitable for tree growth or later during the life of the crop. Many of the soils of upland Britain are initially too wet and have inadequate aeration for the growth of commercial species. Ploughs of various kinds are used to provide a planting medium and to improve the drainage either by providing channels for more rapid run-off of water or by breaking up impeded soil layers to allow better vertical percolation. Unfortunately, some ploughing systems restrict the spread of surface, buttressing roots and any gain in crop stability from increased rooting

depth may be more than cancelled out by lateral restriction to rooting. Windthrow is all too common in upland forests.

Some soils must be fertilised before tree growth is possible at all, while on many others fertilisers give worthwhile responses in yield. Phosphorous fertilisers are the most frequently used; with additional potassium, especially on peat soils. Spruces have a markedly higher need for fertilisers than pines on infertile soils.

Changes induced by the growth of the tree crop itself are becoming much better understood and in physical respects are frequently more significant than those produced by the initial ploughing. The forest canopy may intercept and evaporate up to 40 per cent of the rainfall and this important effect on water yield from forested catchments needs to be taken into account in land-use planning. In some soils with an initial excess of water, much more favourable water and aeration conditions are created. However, the wet clayey soils of the uplands are proving to be the slowest to respond in this way and the shallow rooting of spruces, especially with restricted lateral development, results in early wind damage.

The flora.

The flora has changed too. In the uplands, ploughing, draining and fencing initially encouraged plants of drier habitats and less grazing resistance. As the new forests have aged there has been a qualitative change from heath and grassland vegetation to more genuine woodland communities with ferns colonising the shaded areas and native tree species, such as rowan and birch, colonising the compartment edges. In the lowlands, changes in woodland flora have often been quantitative rather than qualitative: mature conifer crops frequently exhibit a similar range of plants to traditional broadleaf ones but with different quantities of each species. In particular, the abundant spring flora of deciduous woods is reduced in coniferous plantations but this is offset by the presence under older conifer crops of a herb flora in late summer when broadleaf shade would exclude much of it.

The fauna.

There have also been dramatic changes in the vertebrate fauna after the afforestation of bare land and wildlife management is a vital part of forestry in Britain to protect the crop, to exploit animals for recreation, sport and meat, and to conserve a balanced population of animals and birds. The variety of fauna is much influenced by the diversity of the forest, and there are marked differences between the afforestation, thicket, pole-stage and mature forest stages of development. In the 1940's and 1950's large areas of young crops predominated in many forests and such a stage is relatively sterile of fauna. However, as windthrow and regeneration fellings proceeded in the 1960's and 1970's these large areas have become a patchwork of young and older age

classes moving closer to a balanced habitat progression where birds and animals can find suitable alternative habitats within a few hundred metres as the crop changes structure.

This new habitat provides for a considerable increase in the population of the more mobile and commoner species - the less mobile and uncommon species require more active provision of suitable habitats, often more diverse in character than a plantation can provide. For example, research has shown that at least five ha of broadleaved woodland is required to sustain a bird population which differs in species composition from those found in surrounding conifer plantations.

The widespread use of exotic tree species introduces a major ecological change, and when we introduce genetically original trees into new environments, we can expect reaction from the existing inhabitants of these environments. These reactions are often of little consequence or may be favourable. Obviously also they may sometimes be damaging either to the new plantation or to the existing inhabitants themselves. Such potential 'ecological dangers' from and to the new forest tend to acquire exaggerated and sinister images because we do not fully understand them. Even so, it is clear that there are risks, especially to the new trees.

THE MANAGEMENT SYSTEM

Our forecasts are created and managed for a purpose and there are three broad aspects that have to be considered in this process:

Silviculture: to ensure the best sustained growth of trees at an economic level to produce wood of industrial quality; this implies conservation of soil productivity and of the health and stability of the trees.

Environmental management: to ensure the sustained yield at an economic level of the environmental benefits of forestry, including landscape, recreation values and conservation of flora and fauna.

Operation efficiency: to ensure that work is done in a manner that is safe and cost-effective.

In theory, the requirements of efficiency tend towards large-scale, mechanised, simple and uniform methods of management and these may conflict with the environmental values, which tend to be favoured by small, complex and diverse methods of work.

In practise, a compromise has to be struck, by choosing a management system appropriate to each region and ownership. I hope and believe that in most parts of Britain we are developing systems of forest management which are a reasonable and sensible compromise. We can measure our efficiency and product value in producing wood for the market and can even begin to measure our performance in terms of recreation

values. It is much more difficult to measure and ascribe values to the long term environmental and ecological implications of what we do for important questions such as conserving soil productivity, the vulnerability of our forests to damage by wind, pests and diseases, and the conservation of wildlife.

ECOLOGICAL PROBLEMS

I would like to refer briefly to some of the problems that arise and to some fields of current research which have a special significance for forest management in Britain today.

Tree health

Diversification of species and age classes reputedly reduces the risk of catastrophic damage from pests and diseases. Tree breeding programmes are beginning to take effect in practice and it is possible that the development of cheap ways of mass-producing genetically superior individual trees will open up the possibility of clonal forests in the fairly near future. The prospect is that through selection and breeding and improved propagation methods the genetic base of our planting stock could be rapidly reduced. The full ecological consequences of planting programmes based on highly bred planting stock can never be fully assessed. However, I think that it is so important that I hope you will find time to consider this question in the course of your discussions.

Tree stability

Windthrow is a persistent source of damage in British upland forests and current research is aimed at both prediction and reduction of likely damage. Studies are proceeding on windflows in order to permit windthrow hazard classification on species and silvicultural systems, and on cultivation and edaphic factors that limit root growth. This is such a crucial area for future management that I must commend it to your attention.

Regeneration

Clearfelling of even-aged stands can present special problems in our uplands depending on the soil and climate. On heavier soils in high rainfall areas, surface waterlogging can follow clearfelling and cause establishment problems and the presence of stumps makes remedial treatments more difficult. Basic physiological research is being done in Britain on the effect of seasonal waterlogging together with applied research on remedial soil treatments. This too represents a field of research in which international debate and sharing of experience could be particularly relevant.

Soil productivity

In most cases our upland forests have been planted on land where only very small stores of nutrients had been accumulated by natural vegetation due to various factors including burning or erosion, and foresters have had to

'recharge' the sites by manuring. Consequently forest nutrition is an active and important field of study and fertilisers are used extensively at planting in order to establish fast growing species. Much of the attention today in Britain has turned to the prospect of improving the yield of established forests by fertiliser top-dressing regimes. The question of biological and economic limits to growth is posed. In some circumstances, large returns seem achievable by such means. We need better definition of these circumstances and of the implications of such treatments. We also need to know whether greater emphasis should be given to research into species and varieties capable of reasonable growth with a minimum supply of nutrients, i.e. the whole question of 'low' input versus 'high' input forestry.

Nature conservation

Our objectives and methods of wildlife management pose important questions and I am glad to see that you have devoted a considerable part of your timetable to this subject.

CONCLUSION

It has sometimes been suggested that there is a fundamental difference in outlook on ecological matters between the foresters responsible for managing traditional, semi-natural, uneven-aged forests and those responsible for man-made plantations. I do not believe this to be so, and any differences there may be tend to reflect differences in objectives of management rather than differences to awareness or sensitivity on ecological questions.

A sound knowledge of the forest ecosystem is obviously important in all circumstances and especially so for even-aged plantations. Furthermore, it needs to be stressed that new knowledge must be translated into terms which mean something to forest managers. In particular, if there are undesirable features, the manager needs to know what these are and why they are undesirable in terms of productivity (e.g. site degradation, hazards to health, etc.), and environmental values (e.g. water, nature conservation and landscape).

In the end, the forest manager has to decide whether his objectives or methods are satisfactory or should be changed. The scientists in each country must help ensure his decisions are based on knowledge and balanced judgment rather than on folklore or prejudice.

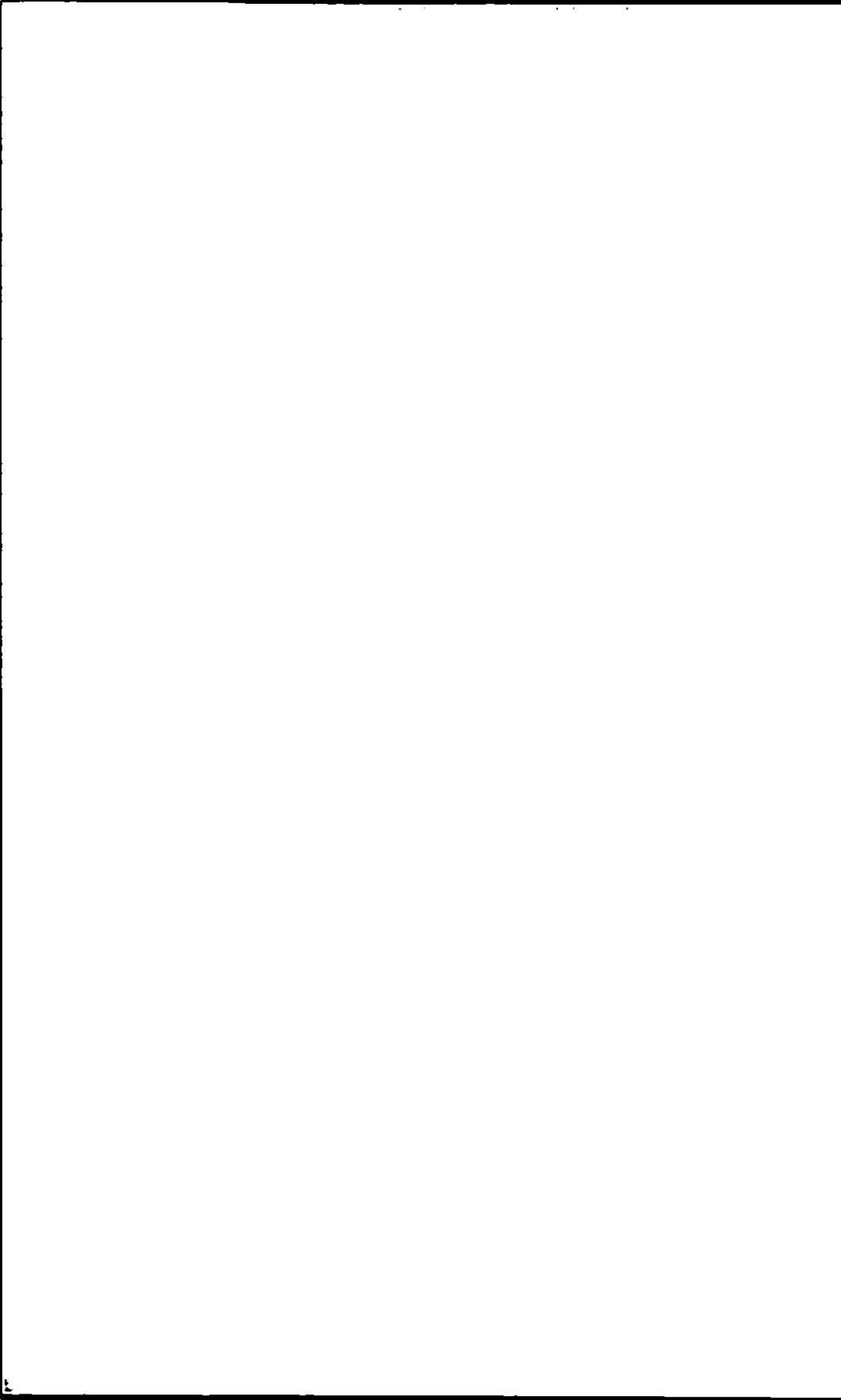
Your agenda for this week is very wide-ranging and it seems to me that some aspects of research lend themselves to international co-operation whereas others are so related to local conditions and to national policies and objectives that the scope for international co-operation is limited. In general, I think it true to say that basic biological research and non-biological basic and applied research are the most likely to benefit from international co-operation as both tend

HOLMES

not to be highly dependent on local conditions. It becomes practicable, therefore, to pool research resources and to deploy them more effectively.

It would seem that much of the agenda for the present Conference deals with aspects of research which are greatly influenced by local factors and in which the scope for international co-operation may be somewhat limited. The value of the Conference in these circumstances could lie not so much in assessing the detailed results or conclusions of research but rather in considering the concepts and methodology. But even in these areas the main speakers will suggest analogies and stimulate ideas and rewarding discussion. There is, however, a more basic element in many of the topics to be dealt with and suggestions for effective international co-operation may well emerge during the course of the meeting.

I wish your discussion every success.



September 4, 1978

THE PHYSICAL RESOURCE

Chairman: C.P. van Goor

Site classification	R.D.L. Toleman
How do physical classifications contrast with site type classifications?	K. Kreutzer
Strategies for amelioration on poor sites.	J. Päävänen



ECOLOGY OF EVEN-AGED PLANTATIONS - SITE CLASSIFICATION

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SUMMARY

If consistent and rational silvicultural decisions are to be made when establishing even-aged plantations, a site classification is essential. The classification must be readily understood and be applicable by forest managers. It should be based on soil and climatic factors which are the limitations to forest production when compared with the requirements of species. If species requirements are known, then these limitations can be ameliorated. Forecasting of yield based on site type must be imprecise where site limitations are ameliorated.

Yield forecasting is more precise on sites with few limitations to growth and on which crops have been grown to a full rotation. The ultimate objective of a site classification must be to produce a site yield guide which incorporates silvicultural proposals designed for the target yield to be achieved. Such a guide may take a considerable time to devise, as the long term effects of site modification and improvement will only be apparent over a number of rotations.

RÉSUMÉ

Si nous voulons que les décisions prises en matière de sylviculture soient logiques et rationnelles au moment de la création de peuplements équiens, il est essentiel d'établir d'abord une classification des stations. Cette classification doit être claire et capable d'être utilisée par des gestionnaires forestiers. Elle doit être basée sur des facteurs liés au sol et au climat. Certains de ces facteurs sont souvent à un niveau insuffisant, comparés aux exigences de différentes essences, et indiquent des stations

marginales. Si les exigences sont connues, une amélioration de certaines stations est possible.

La prévision de la production basée sur les différents types de stations ne peut être très précise dans le cas où l'amélioration de la station est possible et conduit à une meilleure croissance. La prévision de la production sera plus précise pour les stations ayant moins de contraintes limitatives et pour lesquelles la croissance a déjà été suivie pendant une révolution complète. L'objectif numéro un d'une classification des stations sera d'établir un guide des liaisons production - station, qui comporterait également des règles sylvicoles, conformes aux objectifs de production retenus. Le temps nécessaire à établir un tel guide sera considérable, puisque les effets à long terme de la modification et de l'amélioration d'un terrain ne seront ressentis qu'après une ou plusieurs révolutions.

ZUSAMMENFASSUNG

Wenn bei Begründung gleichaltriger Pflanzungen konsequente und rationelle waldbauliche Entscheidungen zu treffen sind, ist eine Standortklassifikation unerlässlich. Die Klassifizierung muss für den Forstmann leicht verständlich und anwendbar sein. Sie sollte auf Boden- und Klimaeigenschaften beruhen. Aus ihnen können sich oft Standortbeschränkungen ergeben, wenn man die Bedürfnisse der Baumarten berücksichtigt. Wenn die Ansprüche der Baumarten bekannt sind, kann man veränderliche Standortseigenschaften entsprechend verbessern. Ertragsvoraussagen nach dem Standortstyp sind zwangsläufig ungenau, wo wachstumsbeschränkende Faktoren verbessert und damit das Wachstum gefördert werden kann.

Die Ertragsvoraussage wird genauer sein für Standorte mit geringen Einschränkungen, und wenn die volle Umtriebszeit erreicht ist. Die Standortklassifikation sollte letztlich auf die Erstellung standortsgebundener Ertragstafeln abzielen, die auch waldbauliche Richtlinien zur Erreichung des Ertragsziels geben. Zur Ausarbeitung solcher Unterlagen ist beträchtliche Zeit erforderlich, da sich die Langzeitwirkungen von Standortveränderung und -verbesserung erst nach mehreren

Umtriebsperioden zeigen.

INTRODUCTION

The objective of this paper is to examine the requirement for a site classification in even-aged plantations, and to consider the site features that can be used. A number of existing classifications will be cited, but a comprehensive comparison is not possible due to the extensive number of systems in use. Indeed, site assessment is such a broad subject that a I.U.F.R.O. working party under Dr Burger and Dr Kreutzer is examining the different methods of classification and their various objectives.

The term 'even-aged plantation' is imprecise. It can cover the establishment of exotic or indigenous conifers and broadleaved species on bare land, abandoned scrubland with secondary regrowth, low production forest and high production forest. It also covers the regeneration of natural, uneven-aged forest, particularly where a preferred species is favoured and the re-establishment of felled, even-aged, mature plantations.

The most important requirement in establishing any of these even-aged plantations is that the preferred species must have a potential for successful growth. Where a species has a wide tolerance and where the site is relatively homogenous, the chance of successful growth will be high. If sites are diverse and species tolerances narrow, a plantation over an extensive area will produce a wide range of growth rates.

In early British plantation forestry, whenever even-aged plantations were established, a site classification was necessary, however empirical, to match the requirements of the species with characteristics of the site. The closer the species requirements were met, the greater was the potential for success on the plantation. Very often in early plantations species requirements were imperfectly known and so many were unsuccessful. A nutritional site limitation was one that showed itself early in the life of the crop, but physical or climatic limitations often appeared much later.

European foresters have long recognized the value of site classification, primarily through phyto-sociological site mapping with some pedological influence. British foresters adopted a site classification based on vegetation communities and related to it observed yields of various species (Anderson 1950). Wood (1955) examined the ecology of conifers in northwest America and related observed site conditions there to those in Britain and suggested suitable British sites based on the conditions of natural stands of our exotic plantation trees. Macdonald et al. (1957) reviewed the ecology of exotic forest trees in Britain, giving indications of suitable sites, based on site limitations.

British even-aged plantations are characterized by

establishment on bare ground, but other European, tropical, Australasian and American foresters have frequently established even-aged plantations on logged-over forest. Their objective has usually been to increase the yield of the natural forest by selecting a preferred indigenous or exotic species. The advantage of this type of even-aged plantation is that, based on the natural phyto-sociological and pedological features, the forest site type can be classified prior to establishment.

THE NEED FOR SITE CLASSIFICATION IN EVEN-AGED PLANTATIONS.

Because climate is the most dominant, single feature of site classification, as expressed by combinations of warmth and cold, a measure of growing season length, precipitation and exposure, it follows that regions of either equable or consistent climates tend to have less wide variations in site types. Regions that have an inconsistent climate tend to have wide variations of site type, which is compounded if there are also wide ranges of lithology and physiography. The latter description fits western, maritime land masses and is typified by the British uplands.

Even-aged plantations have been established using one of two broad policies. The attributes of the site were assessed, either subjectively or objectively, and species most suited to, or most tolerant of these site features were planted. Alternatively an assessment of site features which identified limitations was made. The site limitations were then ameliorated to a greater or lesser degree, depending on the relationship between cost and forest yield improvement and a single preferred species planted.

The first policy can be regarded as 'low input' and seeks to stimulate the natural forest which has a moderate range of climax species, each with its own site tolerances. This low input, multi-species, even-aged plantation will produce trees of uneven sizes, with different qualities and different potential utilization. This type of production does not easily fit current timber use requirements. Its drawback, together with the greater yield potential of single species, high input, even-aged plantations, has resulted in the dominance of the single over the multi-species afforestation.

The second policy is 'high input', where a preferred species, which must have moderately wide site tolerance, is ensured of success through the major modification of site limitations. This type of single species, even-aged plantation also seeks to be even-sized, evenly grown and hence uniformly managed, to produce an unvarying product at any particular stage of the rotation.

However, a common feature of both policies was the need to recognize the characteristics of the site and hence the limitations. In some cases a species was matched to a site,

while in others the site was adapted to the requirements of the species.

Afforestation in the British uplands in the past was traditionally of the 'low input' type, using many species, but in the last thirty years it has increasingly become 'high input', using fewer species, mainly Sitka spruce, or on the poorest sites, lodgepole pine. A major reason for this change in policy was that the British upland plantations prior to the 1930's were primarily in areas with few site limitations, i.e. sheltered valley bottoms and mid-slopes on which a wide range of species could be planted. From the 1940's onwards, more and more of the land available for afforestation was at higher elevations, which provided sites with increasing limitations to growth. Very few species could tolerate these limitations and many site features had to be ameliorated to ensure the silvicultural and commercial success of the plantation.

The objective of devising a site classification for even-aged plantations must be to aid forest managers in making rational and consistent silvicultural decisions, that will ensure the success of a crop and, if possible, indicate for a given intensity of input, what the expected yields or rate of success of the crop will be. In upland plantations it is apparent that a site classification based only on soil parameters, although facilitating rational silvicultural decisions, has been less successful in predicting yield. This is due to the dominance of the climatic element.

Prior to afforestation, the objective of a site classification is to optimize the choice of species and to ensure an acceptable growth rate. As plantations develop, crops reveal differing growth rates which can be related to site type. Gradually yield prediction based on site type becomes more reliable. After one or two rotations, in which a range of silvicultural practices has been examined for a number of species over all site types, a reliable site yield guide can be evolved. A predicted yield can then be achieved if a specific, site-related silvicultural regime is followed.

Where planting is carried out on previously forested land and where the preferred species is indigenous, a site classification will give an accurate estimate of yield. However, it is normal practice to improve the site by ameliorating site limitations and the natural forest yield of a species might be much lower than under even-aged plantation conditions. Therefore, a land capability classification for forestry based on natural forest conditions will only indicate a base level of yield. This will be subject to silvicultural improvement.

FACTORS USED IN SITE CLASSIFICATION.

A forester is primarily interested in site classification with a related yield potential as an aid to forest management.

He is not interested in the classification of soil, vegetation, or land form per se. Factors used in a site classification which is intended for a practical application by forest managers, must be readily understood and should be easy to assess. Silvicultural practices may then be related to a site classification and this will ensure that a relatively standard set of treatments will be applied to similar crops over a wide area.

Site factors fall into two groups:

Soil characteristics: nutrient availability, water availability, aeration, rootable depth, vegetation type, terrain type.

2. Climatic characteristics: warmth or coldness, wetness or dryness, exposure to wind.

Soil characteristics

Nutrient availability - The principle elements for successful tree growth are nitrogen, phosphorus and potassium (N, P and K). Although values of N, P and K can be determined in a soil, it has proved not possible to forecast either yield or the success of a crop in relation to N, P, K concentrations, except for extreme values. In upland Britain, on mineral and organo-mineral soils, there is some relationship between the soil nutrient availability and the chemical composition of the rock: quartzose and granitic rocks tend to have the lowest values. Special problems are found on other lithologies, such as low phosphorus availability in soils derived from basic igneous rocks, while high pH values are found in soils over calcareous rocks. Soils derived from stony or coarse textured glacio-fluvial or littoral deposits often have low N, P, K availability.

In organic soils, nutrient availability has been related to total content of N, P and K in the upper horizons, which itself is correlated with the bare ground vegetation. On such sites, a more consistent estimate can be made of yield, or more importantly, the nutrient input required for a successful crop. The current classification of bogs used in the Forestry Commission, is based on the bare ground vegetation, and a silvicultural policy of increasing nutrient input is applied where the vegetation type indicates low N, P, K values (Toleman 1973).

Water availability - Water availability is related to climate, lithology, soil type and depth. In a moist, maritime climate it is only in exceptional years that trees suffer visibly from drought (Burdekin 1977; Fourt & Hinson 1970), and this would usually only occur with a combination of shallow loamy soils over permeable bedrock. In drier climates water availability can become a limiting factor. It is evident in the Pacific northwest that available soil moisture plays an important part

in a yield related site classification in drier zones (Wood 1955).

Aeration - In very wet climates an excess of soil water can lead to periodic or permanent waterlogging, resulting in poor soil aeration. The intensity of anaerobic conditions in the soil is related to the precipitation and permeability of the soil and bedrock. Poorly drained or gley soils are extensive in wet, mild, maritime and cold, wet, continental climates and they frequently develop a considerable depth of surface peat.

The lack of aeration in the soil prevents deep root penetration and where this occurs in windy climates, extensive uprooting will occur. Shallow rooting in poorly drained soils does not necessarily imply a lack of soil nutrients and vigorous growth is often a feature of such sites. It has been traditional to drain waterlogged sites, but many gley soils are of a clayey texture with a very low permeability. There is an insignificant improvement in soil aeration as a result of drainage, apart from the superficial horizons, which in any case are affected by water removal by the tree crop. Gleys of a loamy texture should be separated in a classification as, with greater permeability, effective drainage and improved aeration should be possible.

Organic soils are normally waterlogged but do have varying rates of permeability. Fibrous or relatively undecomposed peats are more permeable than amorphous or well-decomposed ones, and drainage may improve peat aeration and encourage decomposition. The principle reason for attempting to improve soil aeration is to encourage deeper root penetration, so making the crop less susceptible to uprooting.

Rootable depth - Restricted rooting can occur in shallow soils over impermeable bedrock, or where there is mechanical restriction in a subsoil horizon, i.e. on indurated layers which are relict permafrost phenomena formed during the periglacial climatic conditions of the late stages of an Ice Age. Both freely drained and poorly drained soils can have a strongly indurated layer at depths of 20-50 cm from the surface. The layer may be discrete and 20-30 cm thick, but commonly it exceeds 60 cm. Roots cannot penetrate the indurated layer due to the small pore space and firmness. Induration is greatest in loamy soils, resulting in high bulk density, but decreases with increasing clay content. The identification of indurated layers and their extent is important, as the shallower, discrete type can be shattered by deep ploughing, so encouraging more extensive root penetration.

Vegetation type - Certain types of bare ground vegetation, besides indicating a site characteristic, may themselves compete with the early growth of tree crops. In upland Britain the initial competition between heather (Calluna vulgaris) and

many tree species, especially spruce, is well-known. In extreme cases spruce growth can be almost totally checked. The very lush growth of weeds on fertile lowland sites is only a limited problem, as the trees themselves are not checked and, once established, will grow rapidly.

Vegetation has been used as a means of site classification. This is based on the concept that the vegetation present is a result of prevailing environmental factors and consequently different plant associations delineate different sites. However, vegetation boundaries are not permanent and in even-aged plantation forestry, natural or semi-natural vegetation declines, until recolonization takes place after thinning and felling.

Terrain type - Features of the terrain, such as ground bearing capacity, ground roughness and slope, seldom affect the growth rate or yield of plantations, but do have an important relationship to all silvicultural harvesting operations requiring mechanization. At establishment, the type of plough and ploughing equipment selected can be influenced, and at harvesting, the type of extraction equipment.

The Forestry Commission's current classification recognizes three terrain factors, which are sub-divided into five classes (Table 1).

In dry climates, terrain can influence soil moisture and wet, receiving sites may be separated from dry, shedding ones.

Climatic characteristics

Warmth and coldness - In natural forests at high altitudes a timber line is associated with increasing climatic coldness and a reduction in growing season. Even-aged plantations are normally established well below such a timber line, as at these upper elevations yield is low. However, in wet, maritime climates and within a range of elevations in which plantations can be established, there is a strong relationship between yield and altitude (Malcolm 1971; Mayhead 1973). Also, the potential for crop response to ploughing or fertilizing is

Ground conditions (Soil bearing capacity)	Ground roughness (Presence of surface obstacles)	Slope (gradient in °)
1. very good	very even	level
2. good	slightly uneven	gentle
3. average	uneven	moderate
4. poor	rough	steep
5. very poor	very rough	very steep

Table 1. Forestry Commission terrain classification. Units of these factors and their scales are described in more detail by Rowan (1977) and are based on Scandinavian practice.

greater at lower elevations.

Wetness and dryness - Climatic dryness, i.e. potential evapotranspiration (see Jarvis & Stewart, this volume), is not a problem in wet, maritime regions, but it becomes increasingly important in warmer, continental areas, particularly those with long, dry periods. Climatic wetness is an important factor in the development of a soil from a parent material. The soil processes of organic incorporation and accumulation, clay translocation, leaching of soil nutrients, gleying, podzolization and weathering are all related to the amount of precipitation and its seasonal distribution. In climates of moderate rainfall with dry periods, where a soil potential water deficit (PWD) may develop, an established plantation can intercept and evaporate sufficient precipitation to have a marked effect on soil moisture and aeration. However, there is little effect in higher rainfall areas that do not experience a seasonal soil PWD.

Exposure to wind - Maritime climates have a high average wind speed, which at upper elevations is the major limiting factor to tree growth. It has an effect through physical uprooting and physical damage to the crown of the tree. Measurements of wind speed are difficult to make. Anemometers are expensive both to instal and maintain and are seldom installed in isolated hill areas where afforestation has been carried out. Other recording methods have been devised, though none have gained wide acceptance. Tatter flags (Lines & Howell 1963) have been used by the Forestry Commission to aid in determining upper planting limits and a method of relative topographic exposure has been devised to produce wind exposure or 'topex' maps (Pyatt, Harrison & Ford 1969). Recently an indirect technique has been developed. Models constructed on a proposed afforestation area are exposed in a wind tunnel and relative air flows over different parts of the surface measured. Although data are limited for wind flows over upland areas the Forestry Commission has used the available data to produce a wind zonation of Britain.

EXAMPLES OF SITE CLASSIFICATIONS WITH THEIR OBJECTIVES

Britain

It has been stated that the objective of a site classification must be that it aids forest managers to make rational silvicultural decisions. When the Forestry Commission adopted a site classification in 1961, it was decided to base it on soil types. Although initially this was related to the existing soil classification used by the Soil Survey of Great Britain, as more information became available, so soil attributes of silvicultural value were distinguished, e.g.

- textural class of poorly drained soils;
- depth of soil to bedrock;
- presence and depth of indurated horizons;

SITE CLASSIFICATION

- thickness of surface organic horizons;
- presence of surface rock or boulders;
- competing vegetation types;
- depth and continuity of ironpan;
- nutrient availability in deep peats as indicated by vegetation type.

Conversely soil features of only pedological differences were less important. For silvicultural considerations at a national level, the soil types are assembled into soil groups, e.g.

- | | |
|---------------------------------------|---|
| freely drained soils: | brown earths
podzols |
| imperfectly and poorly drained soils: | ironpan soils, gley
soils, bogs |
| other mineral soils: | calcareous soils
littoral soils
skeletal soils
man-made soils. |

As soil mapping extended over upland Britain, it became evident that a higher category could be introduced into the classification. This is the 'site region', which was defined as having a fairly narrow range of lithologic type within which there was a characteristic and consistent range of climate, terrain type, soil type and tree growth rate, and hence silvicultural practices could be expected to be fairly consistent. Some of the more extensive 'site regions' could be further subdivided into wetter and drier western and eastern sub-types. Contrasting examples of the differences between soil type distribution in two 'site regions' is shown when comparing the Scottish border carboniferous 'site region' with the northeast Scotland 'site region'. In the former, clayey textured gley soils and bogs account for up to 90 per cent of the soils, while in the latter there is a dominance of freely drained brown earths and podzols.

A site classification based on soil types is effective for making silvicultural decisions when establishing a plantation. For example, poorly drained mineral, organo-mineral and organic soils will require adequate cultivation and drainage. Organic soils will require varying inputs of fertilizer, dependent on the nutrient status of the peat. Indurated soils and soils with an ironpan layer will require cultivation.

To aid in forecasting crop yield and risk of uprooting, additional climatic features must be superimposed on the soil-based site classification. Since exposure to wind is difficult to measure, elevation zone has been used as a substitute. In hilly and regular terrain, e.g. mid-Wales and the southern uplands of Scotland, the topex method of exposure

assessment has been valuable. Pyatt, Harrison & Ford (1969) describe this method and relate it to the windthrow hazard that crops experience on the various site types. As crop yield is also related to elevation, an overlay of soil map, topex map and elevation zone map can give the following information:

1. Initial inputs of drainage, fertilizing and cultivation to ameliorate soil type limitations.
2. Relatively accurate estimates of yield if the inputs are at an optimum level.
3. Relatively accurate estimate of risk.

Crops on shallow or poorly drained soils at high altitudes have a higher probability of windthrow before they reach their intended final height. Windthrow is precipitated and accentuated by thinning and the Forestry Commission accepts that in such exposed sites normal thinning prescriptions (Hamilton & Christie 1971) will not be carried out and the crops will have a shorter rotation.

The windthrow hazard classification (Booth 1977) is based on four site features (Table 2). A score is given to each value and the sum of these is regarded as the score range. Windthrow hazard classes 1 to 6 are sub-divisions of the score range. The mean crop top height at the onset of windthrow is given below. Windthrow is defined as over 3 per cent of the living trees in a plantation uprooted.

Windthrow hazard class	Top height of crop at onset of windthrow (m)
1	25
2	22
3	19
4	16
5	13
6	10

At present the Forestry Commission is devising a management policy to take account of this classification. Provisionally, normal thinning will be carried out in classes 1, 2 and 3. Selective thinning will be carried out in class 4. Selective thinning will be restrictively carried out in class 5, while class 6 will have no thinning.

The Forestry Commission is at present using a provisional forest site yield guide for upland Britain (Busby 1974) in which sites are identified by elevation, wind zone and soil group. A preferred fertilizer regime is given and a yield is forecast. However, as many crops on the poorest sites have not yet been grown to final rotation and as the response to mid-rotation fertilizing has not been accurately quantified, the forecast yields remain rough estimates.

Although forest managers require a site classification on which to base silvicultural decisions, senior management and

SITE CLASSIFICATION

Table 2. Forestry Commission windthrow hazard classification (Booth 1977).

Wind Zone	Elevation above sea level (m)	Exposure, using topex scale*	Soil type
1. Consistently high wind values.	1. 0- 60	1. 0- 9	1. Rooting unrestricted.
	2. 61-140	2. 10- 15	
	3. 141-190	3. 16- 17	2. Rooting restricted at about 25-45cm.
2.	4. 191-225	4. 18- 19	
3.	5. 226-255	5. 20- 22	
4.	6. 256-285	6. 23- 24	3. Rooting very restricted
5. Consistently low wind values	7. 286-315	7. 25- 27	
	8. 316-360	8. 28- 40	less than 25cm.
A map of wind zones in Great Britain is available.	9. 361-405	9. 41- 70	
	10. 406-465	10. 71-100	
	11. 466-540	11. above 100	
	12. above 540		

*Pyatt, Harrison & Ford (1969).

research workers require to know the extent of site types, so that their national importance for research work and financial implications can be assessed.

A soil survey carried out on the Forestry Commission estate in 1971 showed the following distribution of soil groups:

- freely drained soils	28 %
- imperfectly drained soils	14 %
- poorly drained mineral and organo-mineral soils	39 %
- bogs	14 %
- others	5 %

A survey of ground awaiting planting in 1972 showed that current afforestation is on land dominated by the poorest site types and those at greatest risk to windthrow. Current and future afforestation will be of sites with major limitations that require a moderate to high cash flow for site amelioration to maintain adequate growth rates.

Canada

In the extensively forested Pacific northwest, the British Columbia Forest Service used a site classification (Spilsbury & Smith 1947) based on vegetation communities, which were indicative of soil moisture status and related to tree growth rates. However, in southeast Alaska where rainfall is higher and soil moisture is not a limiting factor, the classification was not applicable.

The Canadian Land Inventory produces a series of interpretive maps, amongst which is one on 'land capability

for forestry'. Seven classes of land are recognised each with a reducing productivity assessed from the natural forest stands. It is emphasised in the classification that productivity is based on the natural state of the land without improvements and that with site amelioration productivity will increase. The classes of land are described as having increasing limitations to the growth of commercial forests and as the limitations are identified, they can be ameliorated when even-aged plantations are established.

Subsequently the British Columbia Forest Service modified this system (Kesner 1970); first, to provide a classification and inventory of the land in terms of bedrock and surface geology, soils and vegetation and secondly, to interpret these features for land use and forest management purposes such as assessing potential productivity, species suitability, natural regeneration potential, thinning, fertilizer requirements suitability for road construction and erosion.

Hungary

During the last thirty years Hungary has embarked on a extensive afforestation and reforestation programme. A classification of forest regions and forest types has been devised and silvicultural operations have been related to them (D.G. Pyatt, personal communication). Site requirements of the major species have been determined, so not only can the correct choice of species and silvicultural method be adopted by site type, but a rational nationwide silvicultural policy can be developed.

The major site factors recognised are:

1. Climate - expressed as dryness or wetness and indicated by the mean July atmospheric humidity in four classes.
2. Topography - as an influence on soil water; there are seven classes of land, from water shedding to water receiving.

Soil - soil type identification follows accepted pedological practice, although certain features of silvicultural importance are emphasized. It includes nine groups and forty-three types.

4. Soil defects, i.e. physical limitations - features recognised are depth of soil over bedrock, depth to water table, depth to salt accumulation, extreme stoniness, high pH and subsoil compactness.

Ground vegetation - to some extent reflects soil and micro-climatic conditions and was used for site identification before being replaced by the present system.

In addition to these major site factors soil analytical data are collected:

1. pH value.
2. Hydrolytic acidity
3. Calcium carbonate content

4. Soda - alkalinity
5. Hygroscopic moisture content
6. Liquid limit
7. Capillary conductivity
8. Particle size
9. Humus content

For each of the forest regions, descriptions of geography, geology, topography, distribution of tree species, forest soils and forest types are prepared. Forest management prescriptions specific to each region are devised and yield potential is estimated from data collected from sample plots of all the major species on each site type. For each site type and based on the national silvicultural policy, a manual list suitable species with an indication of yield and rotation length.

REFERENCES

- Anderson, M.L. (1950). The selection of tree species. Oliver & Boyd, Edinburgh.
- Booth, T.C. (1977). Windthrow hazard classification. Research Information Note 22/77, Forestry Commission, Edinburgh.
- Burdekin, D.A. (1977). Dying beech. Research Information Note 31/77. Forestry Commission, Edinburgh.
- Busby, R.J.N. (1974). Forest site yield guide to upland Britain. Forestry Commission, Forestry Record #97. Her Majesty's Stationery Office, London.
- Fourt, D.F. & Hinson, W.H. (1970). Water relations of tree crops: a comparison between Corsican pine and Douglas fir in southeast England. *Journal of applied ecology*, 7, 295-309.
- Hamilton, G.J. & Christie, J.M. (1971). Forest management tables (metric). Forestry Commission Booklet #34. pp.1-201.
- Kesner, N. (1970). Mapping and interpretative system for the forested lands of British Columbia. Research notes #54, British Columbia Forest Service, Victoria, B.C., Canada.
- Lines, R. & Howell, R.S. (1963). The use of flags to estimate the relative exposure of trial plantations. Forestry Commission, Forest Record #51. Her Majesty's Stationery Office, London.
- MacDonald, J., Wood, R.F., Edwards, M.V. & Aldhous, J.R. (1957) Exotic forest trees in Britain. Forestry Commission, Bulletin #30. Her Majesty's Stationery Office, London.
- Malcolm, D.C. (1971) Site factors and growth of Sitka spruce. Ph.D. thesis, Edinburgh University.
- Mayhead, G.J. (1973). The effect of altitude above sea level on yield class of Sitka spruce. *Scottish Forestry*, 27, 231-237
- Pyatt, D.G., Harrison, D. & Ford, A.S. (1969). Guide to site types in forests of North and mid-Wales. Forestry Commission, Forestry Record #69. Her Majesty's Stationery

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Office, London. 4

- Rowan, A.A. (1977). Terrain classification. Forestry Commission, Forest Record #114. Her Majesty's Stationery Office, London.
- Spilsbury, R.H. & Smith D.S. (1947). Forest site types of the Pacific Northwest. Technical Publication #30, British Columbia Forest Service, Victoria, B.C., Canada.
- Toleman, R.D.L. (1973). A peat classification for forest use in Great Britain. Proceedings of the International peat symposium on classification of peat and peatlands. Glasgow, U.K.
- Wood, R.F. (1955). Studies of Northwest American forests in relation to silviculture of Great Britain. Forestry Commission Bulletin #25. Her Majesty's Stationery Office, London.



HOW DO PHYSICAL CLASSIFICATIONS CONTRAST WITH SITE TYPE CLASSIFICATIONS?

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SUMMARY

The different methods of site classification can be subdivided into environmental and mensurational ones.

Environmental methods.

Environmental methods characterize and classify sites primarily using the site's physical conditions such as properties of the soil, topography and climate. Vegetation is also frequently used as a supplementary indicator, in as much as it is indicating the water, temperature and nutrient supply of the site. As an additional aid the productivity of existing stands can sometimes be used. A special type of environmental method is one that uses vegetation as the only indicator of site properties.

The aims of the environmental methods are directed to provide a survey or basis for better answers to a large variety of questions concerning the site, such as choice of tree species, productive capacity, threats, pathogen attacks, erosion protection, and watershed protection.

Mensurational methods.

Mensurational or forest site type classification methods, however, characterize and classify the sites primarily using the productive capacity of the site. These methods apply suitable attributes of available stands. If the sites to be evaluated are not sufficiently stocked, productive capacity can be determined with the help of environmental features being correlated with an expression for the productive capacity.

RÉSUMÉ

Les différentes méthodes de classification des stations peuvent être divisés en deux groupes: celles qui sont liées à l'environnement physique et celles qui reposent sur la mesure de la productivité de la station.

Méthodes liées à l'environnement physique. Ces méthodes classent et caractérisent les stations en tenant compte tout d'abord des facteurs physiques, c'est à dire des propriétés du sol, de la topographie et du climat. On utilise aussi souvent la végétation comme facteur supplémentaire, dans la mesure où elle peut être un facteur indicatif du régime hydrique et thermique et de l'apport en éléments nutritifs de la station. En outre, on peut aussi utiliser la productivité des peuplements existants. Une méthode spéciale utilise exclusivement la végétation comme seul facteur indicatif des propriétés des stations. Les méthodes liées à l'environnement ont pour but d'étudier ces facteurs et d'établir une base solide qui répondra à un grand nombre de questions concernant la station, par exemple, le choix des essences, leur productivité, les dangers, les attaques pathogènes, la protection contre l'érosion et la protection des cours d'eau.

Méthodes liées à la mesure de la productivité. Par contre les méthodes liées à l'évaluation de la productivité ou méthodes de classification des types de stations classent et caractérisent celles-ci tout d'abord par leur capacité de production. Ces méthodes donnent des noms caractéristiques aux peuplements existants. Si les terrains à évaluer sont nus ou insuffisamment boisés, leur capacité de production peut être déterminée à l'aide de facteurs du milieu corrélés avec une expression de la capacité de production.

ZUSAMMENFASSUNG

Die verschiedenen Verfahren der Standortsklassifizierung lassen sich in zwei Gruppen gliedern; die eine geht aus von der Erfassung der Umweltfaktoren, die andere von der Messung der Wuchsleistung.

Standortskundliche Methoden.

Hierbei werden die Standorte vor allem durch die physischen Bedingungen, wie Bodeneigenschaften, Relief und Klima

charakterisiert und klassifiziert. Auch die Vegetation wird häufig als zusätzlicher Indikator benutzt, da sie das Wasser-, Wärme- und Nährstoffangebot des Standorts anzeigt. Als zusätzliche Hilfe kann manchmal die Wuchsleistung vorhandener Baumbestände dienen. Eine besondere Methode dieser Gruppe nimmt die Vegetation als alleinigen Indikator der Standortseigenschaften. Die Ziele der standortkundlichen Verfahren bestehen in der Schaffung einer Übersicht oder Grundlage standortkundlicher Kenntnisse zur besseren Beantwortung von Fragen im Hinblick auf Wahl der Baumarten, Produktionskapazität, drohende Gefahren, Schädlingskalamitäten, Erosionsverhinderung und Schutz von Wassereinzugsgebieten.

Wachstumskundliche Methoden.

Diese Verfahren charakterisieren und klassifizieren die Standorte vor allem an Hand der gemessenen Produktionskapazität des Standorts. Man verwendet geeignete charakteristische Merkmale vorhandener Baumbestände. Wenn die zu beurteilenden Standorte nicht oder nicht genügend bestockt sind, lässt sich die Produktionskapazität über die Beziehungen von Umweltfaktoren mit Daten der Wuchsleistung ermitteln.

DEFINITIONS

Before we examine methods of site classification in more depth, it is important to give some definitions.

Site

The term 'site' is applied with somewhat varying meanings. In older literature it was understood to mean the growing place of plants or plant communities as characterized by certain natural provisions, but today it is applied more precisely by plant ecologists. 'Site' is the totality of environmental conditions which have an effect on plants or plant communities in their growing place. 'Site' does not include the influence of competition amongst plants or temporary influences, such as a solitary fertilization which has no long-lasting effects.

In forest ecological research 'forest site' is similarly defined as in plant ecology, as the totality of environmental conditions significant for the development of forest trees and these are principally determined by topography, climate and soil.

Contrary to this environmental definition English-speaking people frequently apply the term 'forest

site' with consideration for the yield obtainable on the growing place, e.g. 'site classes' are yield classification units. Thus Gessel (1976) writes: "Most foresters understand site as an expression of the ability of forest environment to produce a given yield of species or a combination of species". In land management the meaning of the term is narrowed down even more to productivity or at least potential productivity.

These somewhat diverging opinions come together in the one point that the yield of a stand is determined by a variety of growth factors. Apart from genotype, we are interested in all factors exterior to the plant such as nutrient and water supply and temperature. In most cases we cannot make a direct, quantitative calculation of the environmental factors which determine growth and so are dependent on assessing site features indirectly.

Site factors

'Site factors' are defined as the properties of a growing place which are relevant to organisms living there. These are partly interchangeable and can be divided into the following groups:

- Climatic factors: precipitation, air temperature, solar radiation, wind patterns. Here the seasonal distribution as well as the total annual quantity is important.
- Topographical factors: elevation, orography position, steepness and form of slope, aspect.
- Edaphic factors: soil conditions which determine the water and nutrient supply, potential root depth, and soil temperature.
- Biotic factors: activity of micro-organisms, influence of pathogens, wildlife.

In their interplay site factors determine the supply of water, nutrients, warmth etc. to the growing plant and so determine the composition and growth of vegetation, the growth relations and yield capability of the tree species and the biotic and abiotic threats to stands. Moreover, site factors are related to nearly all forest management operations e.g. soil preparation, regeneration, herbicide use, thinning and harvesting techniques. Furthermore site factors influence a series of additional forestry activities which go beyond the mere production of wood, particularly those of erosion protection, water protection, landscape aesthetics and recreation. Many of these operations may themselves have an effect on 'site factors'.

Site unit

'Site unit' in environmentally based methods refers to a collection of growing places characterized by a similar combination of 'site factors', and so with a similar basis for the choice of tree species, and for assessing productive capacity and threats to the forests. 'Site units' may sometimes be subdivided into top soil or humus form

categories.

Productive capacity

'Productive capacity' of a site means the potential organic production of a distinct plant community within a distinct time span and grown over a specific rotation period. In forestry, 'productive capacity' is always related to distinct stand types and treatments. For comparisons between sites it is helpful to use the most productive stand types or, as in the case of mensurational soil site studies, at least stands of the same type and similar treatment should be used.

Site index

'Site index' is an expression of the productive capacity of the site and is derived from attributes of stands of given type and treatment. There are various site indices, e.g. top height at index age, the growth intercept, i.e. the five year height growth above breast height, mean annual height growth and maximum height of old trees. The most frequently used site index is top height at index age 50 or 100.

THE PROBLEM OF RELATING SITE INDEX TO THE PRODUCTIVE CAPACITY OF THE SITE.

This is an important problem in mensurational classification methods, and so I would like to go into it in more detail. The following questions arise:

- a) What stand types should be used?
- b) What stand treatments should be considered?
- c) What measure should be used for productive capacity and how far is it reflected by site indices?

Even-aged or nearly even-aged pure stands of the main economic tree species are suitable as indicator stands, because changes in their growth behaviour and stand parameters in relation to age are well documented and are listed in yield tables. A site index can only be determined for one species at a time; a site cannot be characterized by taking data from stands of different species. Similarly errors may also occur when there are prominent racial differences within the indicator species which influence growth. Only stands of the same race should be used. Problems may also occur in interpolating from pure to mixed stands since synergistic effects between tree species do exist to influence the yield markedly.

Different methods of thinning and stand regeneration influence the development of stand parameters and only stands which have had similar treatments should be used as indicators for different sites. However, on occasion the same stand type treated in the same way may react differently on different sites. Our knowledge is not extensive enough to consider such questions sufficiently within the framework of site evaluations and this may produce errors.

Productive capacity is usually expressed in terms of economic timber volume and excludes other components of stands such as branchwood, leaves, roots etc. Biological production would be better expressed as biomass or chemical energy content rather than timber volume but investigations into production of these quantities are too fragmentary for general application. According to our present knowledge the best measure of productive capacity is maximum mean total increment of stem volume per hectare per year. Development of mean total increment per hectare per year for Scots pine on a widespread soil type in northeastern Bavaria is shown in Fig. 1 and one can see that the maximum could be a good measure with which to evaluate site. However, these typical site and stand maxima are not directly measurable and so we have to use correlated, easily measurable attributes.

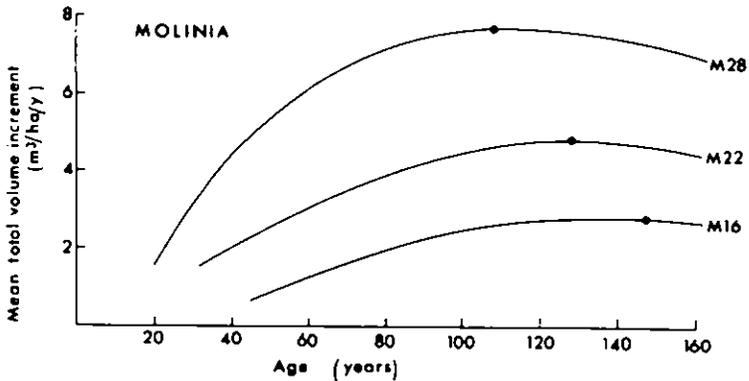


Fig. 1. Mean total volume increment of Scots pine (*Pinus sylvestris*) in northeastern Bavaria on mapping unit 'moist sands-Molinia.

Two such attributes are stand age and height. We may determine the height at distinct index ages from height growth curves (e.g. from yield tables). When taking this term as site index it should be based on the dominant, or the dominant and co-dominant trees of the stand because their heights are less influenced by the thinning processes. Furthermore, the quality and suitability of the height:age curve patterns should be critically considered (Carmean 1975). In America, harmonized yield tables often based on insufficient data have been

developed for large tracts of land and have led to serious mistakes in site evaluation. Carmean recommended the elaboration of height:age curves better suited to individual sites and suggested stem analyses and internode studies as important aids in their construction. In Europe, we have carried out similar deliberations which have led to regional and local yield tables.

But even though the site index 'top height at index age' is well derived and close to reality, we have to ask whether this site index accurately reflects the maximum mean total increment. An answer is given in Fig. 2. Using the data of the new Bavarian yield tables for spruce (Assmann & Franz 1965) the maximum mean total increment is plotted against site index, i.e. 'site class based on age 100'. Considerable variation in maximum mean total increment appears at the same site class and this is caused by differences in basal area growth. This in turn reflects differences in diameter growth and/or number of trees per unit area and as stand treatments are identical one can suppose that properties of the site are mainly responsible for this.

Such variation is not restricted to differences between regions and caused by climatic differences as earlier researchers suggested (Wiedemann 1939, 1941). Changes of the specific yield level* take place within relatively small areas because of their differing site conditions. Assmann's students have given very impressive evidence of that (Franz 1967, 1971; Schmidt 1971, 1973).

Two solutions are available to overcome this problem of evaluation. One is based on the technique of corrected or levelled yield tables (Fig. 2) (Assmann 1962, 1966; Assmann & Franz 1965; Johnston & Bradley 1963; Magin 1963, 1965; Franz 1967, 1971). To evaluate the yield capability of a stand, additional stand attributes besides stand height and age are introduced. Assmann & Franz used stand basal area and the diameter of the tree of mean basal area. New developments are underway.

The other solution is by preselection and stratification of sites. This is a particularly useful technique where physiographic site maps are available which contain site units as a mapping basis. To estimate productive capacity, separate yield studies based on these site units are carried out. The accuracy of the results depends on the quality of site

* Assmann (1966) understands yield level to be the total growth achievement depending on height development. He differentiates between the general yield level at a given height and the specific one at a given site quality as the height at a distinct age. We modified the latter definition by plotting the maximum mean total increment per hectare per year at height and age determined quality.

classification and mapping. Subjective influences may become important particularly when qualitative estimations of nutrient and water regimes are uncritical and training and education of mapping personnel is very important, as are the development of suitable methods to deduce water and nutrient supply. Despite these difficulties good results have been obtained by this technique particularly for widespread site units and this demonstrates the practical value of such yield studies (Günther 1955; Moosmayer 1955, 1957, 1960; Franz 1967; Horndasch 1969).

Similar questions arise with other site indices. The growth intercept method is particularly useful when younger stands are important as site indicators, whereas the maximum height of old trees is mainly applied in areas which are not easily accessible and yield estimations are carried out using aerial photographs. Both methods are known as substitute techniques and their accuracy is even more problematic than yield estimates through the direct assessment of height and age.

THE PROBLEM OF SITE PREDICTION

One of the main practical aims of site evaluation research is to develop suitable methods for predicting the productive capacity of growing places where indicator stands are missing. In this instance determining good correlations between productive capacity and site properties is of special importance and understanding the causal relationships does not play a primary role.

Frequently, a first objective of environmental classification is to divide the landscape into environmentally defined site units which acts as a framework for detailed yield studies. This division is not made on the basis of measured first yields. It is postulated that all growing places within the same site unit show the same or at least a similar potential yield capacity for the same tree species, whether they are stocked with this species or not. Such yield studies on individual site units enable comparisons of the productive capacity to be made between them as well as between different stand types and treatments within site units. All findings related to a site can be usefully transferred to other locations in the same unit.

Naturally problems arise when mappings are incorrect or when relevant environmental differences affecting tree growth are not taken into account. This often occurs within mapping units established purely on a vegetational basis. The reasons are obvious since the composition and vigour of plant communities are influenced by stand type and density. In most cases vegetation only indicates the relationships of a relatively shallow root zone and moreover it reacts ephemerally to short-term changes in environmental conditions.

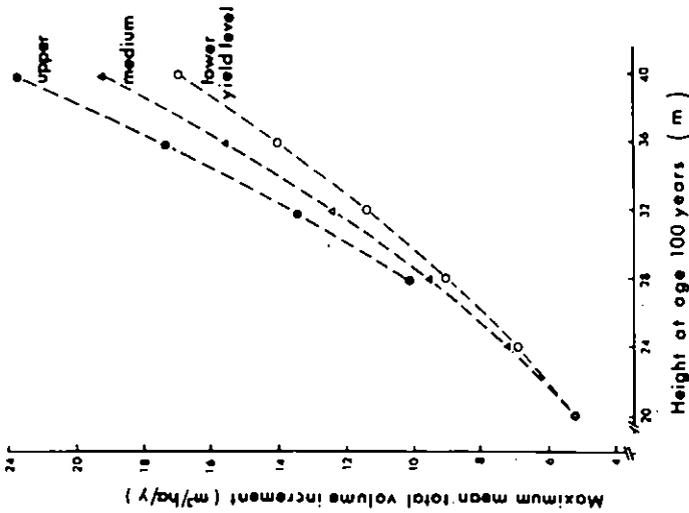


Fig. 2. Volume production of Norway spruce (*Picea abies*) in Bavaria (according to yield tables of Assmann & Franz 1965).

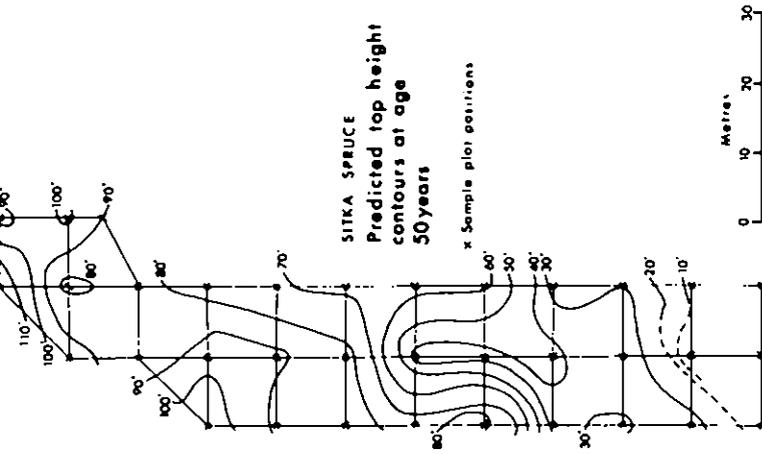


Fig. 3. Probe map of an area of Gwydyr Forest North Wales (after Page 1970). See text for details.

In southern Germany a combined, multi-level, physiographic vegetational method has proved to be quite practical. Firstly a regional classification is made and then within regions short distance differences between sites are taken into account. If necessary, these site units are further subdivided into top soil or humus type categories.

The mensurational forest site type classification methods offer another possibility of predicting the productive capacity of sites. Their development was mainly advanced in the U.S. (e.g. Carmean 1975). These methods use regression procedures in order to calculate the site index with the aid of correlated factors of soil, topography and climate. They are based on intensive field research of site factors and yield parameters on suitable stands from sample plots which are equally distributed to represent the various relationships within a defined research area. Multiple regression equations mostly include site index as a dependent variable, and a series of site factors are included as independent variables. Nowadays computer techniques provide the derivation of well suited equations for such purposes, but equations should be proved at a series of test stands before they are used in practice.

An equation of Page (1970) for Sitka spruce in a Welsh research area can be taken as an example:

$$Y = 119.82 - 0.042X_1 + 4.28X_2 + 3.92X_3 + 2.62X_4 - 0.13X_5 - 59.83X_6 + 27.04X_7$$

where Y = top height at 50 years

X₁ = elevation (ft)

X₂ = shape of slope (numerically converted)

X₃ = shape of contours (numerically converted)

X₄ = 'hue' of soil at 6'' depth (according to the Munsell colour notation)

X₅ = percentage moisture content of soil at 6'' depth (soil at field capacity, dried for 24 h at 105°C)

X₆ = bulk density of soil at 6'' depth

X₇ = bulk density of soil at 12'' depth.

This equation explains a great part of the total variation of the site index within the study area at a high statistical significance.

Equations of this kind are not only used for identifying site quality and predicting yield at certain growing places, but also serve as a basis for classification and mapping of the landscape into units representing different site classes. Using the above equation, site index maps were constructed for Sitka spruce in Gwydyr forest (Fig. 3). Site factors contained in the equation as independent variables were registered every 10 m, site indices were calculated, plotted and then isohypes of site indices were drawn.

If corresponding equations have been derived, maps can be made in the same area for different tree species, and yields compared on the same sites. The accuracy of these maps depends on:

1. How far the site index represents the real productive capacity. Sometimes from a pragmatic point of view it is said that the time spent on a very exact estimation of productive capacity is not worth the benefit of a very precise yield prediction.
2. The practicability of the method is decisively determined by how easily the independent variables can be identified in the field. Here there is also a pragmatic consideration; possibly in order to have a quicker process in the field, a less accurate estimation of the site index is accepted using only equations which contain easily identifiable site factors.
3. The application of yield prediction equations is only sensible when certain restrictions are accepted. These are:
 - that sites should fall within the environmental boundary conditions of the study area, and that values of site properties should fall within the ranges used in establishing the relationships.

ESTIMATION OF CAUSAL RELATIONSHIPS BETWEEN THE ENVIRONMENT AND THE PRODUCTIVE CAPACITY OF THE SITE.

This problem is significant for both scientific research and for practical forestry. Relevant questions are:

- What changes in yield are to be expected when the supply of certain nutrients is improved, for example by fertilization?
What changes in productive capacity result when new harvesting methods such as complete tree utilisation decrease the nutrient storage?
How does lowering the ground water level, or, conversely, irrigation affect the productive capacity?

Strictly, neither environmental nor mensurational methods can give exact evidence of causal relationships. However, these methods are suitable for developing better insights and working hypotheses which in some cases these can even stand up to experimental arguments.

Mensurational forest site type studies can be developed to investigate causal relationships by including a wide range of variables which can improve interpretation of variation in yield. Amongst these may be the contents of distinct nutrients in the soil volume of certain horizons, the C/N ratios in the litter or distinct humus layers and the nutrient contents in the needles.

The development of computer techniques has aided research into causal factors. Besides simple correlation matrices connected with association analysis and clustering techniques, stepwise and full regression models and more complex techniques such as factor and principal component analysis, are available. The latter in particular opens new ways for causal research, because "a large quantity of data can be reduced to comprehensible proportions without disturbing any of the relationships involved and by examining the vectors that are heavily loaded on the components, it may be possible to interpret the latter in an ecologically meaningful way" (Malcolm 1976). Additionally, the single components can be used as regressor variables with productivity as the dependent

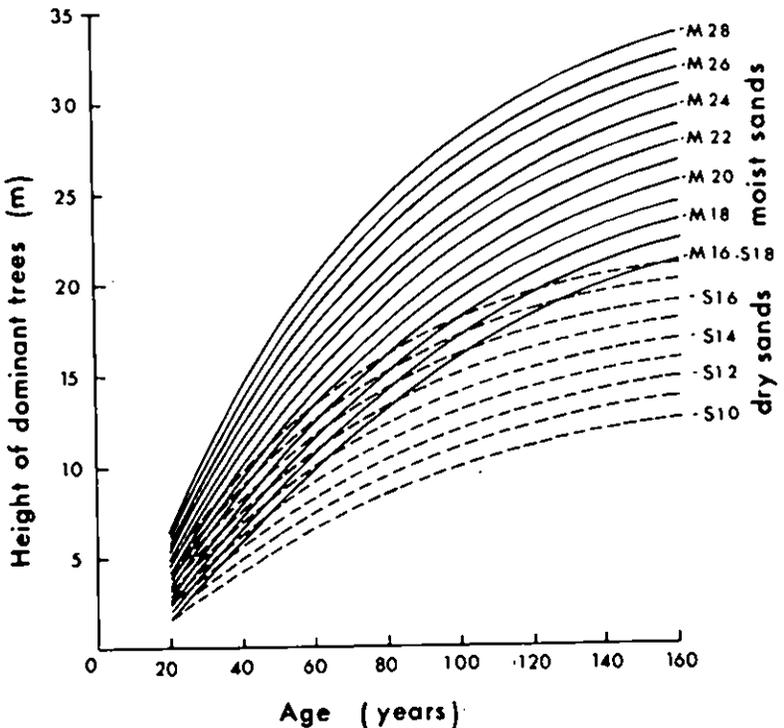


Fig. 4. Height growth curves of Scots pine (*Pinus sylvestris*) on two mapping units in northeastern Bavaria.

variable.

Present computer techniques make it promising to create and validate complicated models of ecosystems, so that simulation techniques can be used for causal research. Such studies are underway for instance at the Institute of Soil Science and Forest Nutrition in Goettingen and at the Institute of Forest Ecology in Stockholm.

Causal research can be aided by environmental site survey methods too. An example is given by Schmidt (1971). He studied the yield relationships of Scots pine in a northeast Bavarian region, where the climatic conditions are rather uniform. His studies were based on site maps, whose mapping units used substrate type and water regime. To that a study of the pines' nutrition conditions were added, using needle analysis and an investigation of soil physical conditions.

Fig. 4 shows the pattern of the height growth curves on the 'dry sands' (dotted line) and on the 'moist Molinia sands' (continuous lines) whose rooted zone is influenced by capillary water ascending from ground water level. Each mapping unit is characterized by a particular fan of the height age curves. The curves of the 'dry sands' approach a maximum early in the life of the stand, whereas those of the 'moist Molinia sands' approach a maximum later. Each single curve, equidistant within its fan, represents a site quality curve, with the height at age 100 as site index. There is a recognizable variation within the same mapping unit, the causes of which are currently under investigation. Some preliminary results are shown in Fig. 5. Site quality is recorded on the abscissa and the maximum mean total increment on the ordinate. The lines represent single mapping units, including the two extreme examples used in Fig. 4. For the same value of site quality i.e. height at index age, the maximum mean total increment of the Scots pine stands is higher on the sites with a worse water supply than on those with a better one, i.e. for the same site quality class stands with worse water supply had a higher basal area increment. To a large extent the needle analyses explained this phenomena, nitrogen nutrition conditions, were mainly responsible for site quality class variation within the same mapping unit. No influence of other nutrients was found. Those quantitative relations between growth and nitrogen nutrition, as well as those between growth and water supply can be considered to be causative for volume increment within the boundary conditions of the other factors.

Obviously water supply considerably determines the shape of height growth curves and hence also determines tree form. On sites where there is a water deficit trees diminish their height growth earlier than on sites well-supplied with water possibly because the hydraulic gradient between root space and crown influences the potential maximum height: Nutrient supply

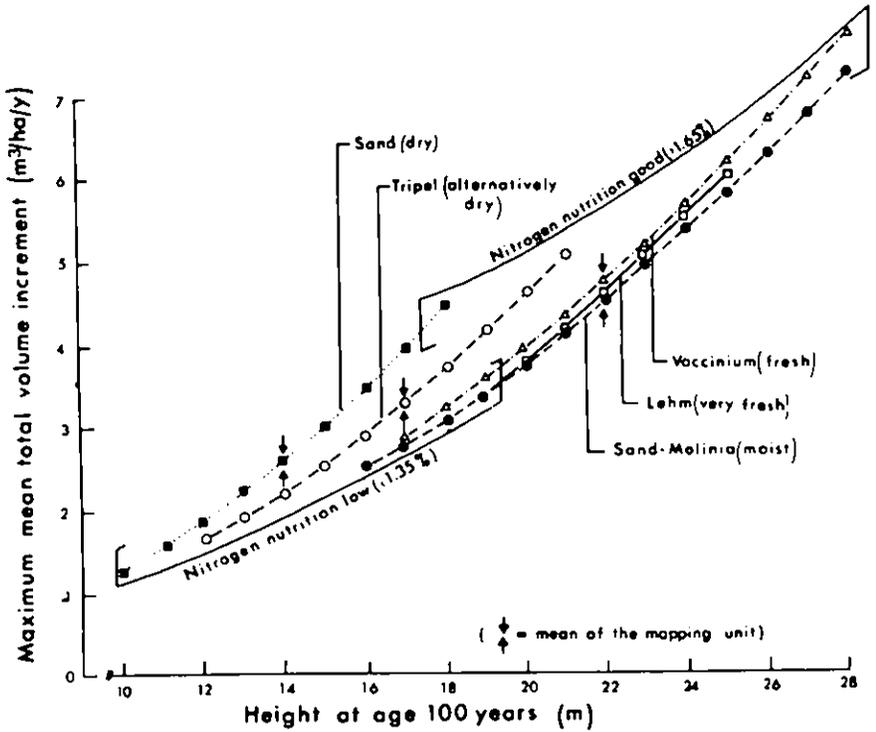


Fig. 5. Volume production of Scots pine (*Pinus sylvestris*) in northeastern Bavaria on different mapping units.

seems to have less effect on the shape of the height growth curves, its variation mainly opens the fan.

These relationships still need to be examined further, but the results of Franz (1971) and Moosmayer (1960) from south German spruce stands can be explained in a similar manner.

CONCLUSIONS

The two methods of site classification are different in approach but may lead to similar results with regard to yield prediction, site mapping and suggestions as to which are the basic requirements for tree growth. The methods are complementary rather than contradictory.

Environmental methods are based on extensive pre-selections and stratifications of the landscape into site

units and site phases with similar environmental conditions. They may be used to investigate the influence of site on productive capacity and the relative performance of different species. Environmentally based site classifications are also of relevance in assessing erosion hazards, harvesting methods, disease threats, etc. The main problems of environmental classifications are:

- i They must be related to forest management and silviculture. Though many environmental surveys from soil scientists or plant sociologists produce important subdivisions of the landscape and contain valuable information, they are often overcharged with specific academic objectives and do not meet the utilitarian requirements of foresters.
- ii Their mapping units must be sufficiently precise to define areas that comprise forest sites with similar potential for tree growth, forest yield capabilities and susceptibility to hazard. But in order to remain practical the definitions should not be too narrow.
- iii Maps must be constructed to a scale and based on a sampling that enables different site types to be shown as distinct units.

These problems may be overcome by coordinated teamwork of soil scientists, ecologists, plant sociologists and foresters. Environmentally based classification and mapping can be of value to a large variety of empirical studies and comparisons as well as permitting the extrapolation of results found at one point to other locations of the site unit.

The problems associated with mensurationally based classifications are:

- i The site indices used are based on data from even-aged pure stands. Any increase in yield in mixed stands caused by synergistic effects between tree species are not predictable.
- ii For even-aged pure stands site indices should reflect the real productive capacity as timber volume and including the yield effects of different site-typical growth curves.
- iii The varying effects of different stand treatments should be excluded, for they introduce inaccuracies into the yield prediction equations.
- iv The site properties must be quantified and sometimes only numerical conversions can be used.
- v Yield prediction equations have to combine precision and practicability.

Preselections and stratifications of stands and sites are often required to resolve these problems. This may be considered to be an approach towards environmental methods, for sites are stratified with regard to distinct site features and corresponding yield prediction equations are established.

SITE CLASSIFICATION METHODS

The main advantage of the mensurational site studies, or soil site studies as they frequently are called, are:

- i They show, a priori, the economic value of the sites or mapping units.
- ii They point out various environmental features which are closely related to the yield capability of the stands.
- iii They make evident the magnitude of yield potential associated with each significant environmental feature.

Application of these methods is valuable in areas where site evaluation is focussed on the yield of even-aged pure stands. However, mapping units defined by site indices alone are not satisfactory in all respects, because they are an expression of the integration of environmental features of the site. The same site index can be the result of a very different interplay of site factors and therefore it is unfit for expressing the variety of silvicultural possibilities and constraints existing of the sites of the mapping unit. We have to consider that the ecological amplitudes of different tree species are different with respect to the various combinations of site factors. Furthermore, it is of importance to know which growth factors within a distinct mapping unit are limiting growth and which can be improved.

Certainly such shortcomings may be resolved by using significant environmental features from yield prediction equations and introducing them into the definitions of mapping units. However, this may also be considered as an approach towards environmental methods.

Mensurational site type methods are of value when attempting an environmentally based classification:

- i As a preliminary to environmental classifications, they can provide additional information in defining mapping units;
- ii subsequent to environmental mappings they may give evidence of site index variations within and between mapping units.

Further applications of mensurational methods in forest practice could be:

- i To achieve preliminary reviews of correlations between productivity and site conditions especially in remote regions, where forest experience is rather limited. Aerial photography may be used, possibly together with preceding geological, climatic or other environmental stratifications if such data bases are available.
- ii To gain better insights into causal relations. Here many possibilities of combinations with environmental methods exist for forest practice as well as for forest research.

REFERENCES

- Assmann, E. (1962). Die Fortentwicklung unserer Ertragstafeln. *Allgemeine Forstzeitschrift*, 17, 817-820; 839-41.
- Assmann, E. (1966). Die Schätzung jetziger und künftiger Ertragsleistung. *Forstwissenschaftliches Centralblatt*, 85, 355-371.
- Assmann, E. & Franz, F. (1965). Vorläufige Fichtenertragstafel für Bayern 1963. *Forstwissenschaftliches Centralblatt*, 84, 13-43.
- Carmean, W.H. (1975). Forest site quality evaluation in the United States. *Advances in Agronomy*, 27, 209-269.
- Fourt, D.F., Donald, D.G.M., Jeffers, J.N.R. & Binns, W.O. (1971). Corsican pine in southern Britain. *Forestry*, 44, 189-207.
- Franz, F. (1967). Ertragsniveau-Schätzverfahren für die Fichte an Hand einmalig erhobener Bestandesgrößen. *Forstwissenschaftliches Centralblatt*, 86, 98-125.
- Franz, F. (1971). Grundlagen und Verfahren standortsbezogener Leistungsschätzung. *Forschungsberichte forstliche Forschungsanstalt*, 2, 384 pp. (incl. 68 pp of tables).
- Gessel, St. (1976). Site in relationship to forest tending. Paper at I.U.F.R.O. meeting in Ossiach, Austria, 1977.
- Günther, M. (1955). Untersuchungen über das Ertragsvermögen der Hauptholzarten im Bereich verschiedener Standortseinheiten des Württembergischen Neckarlandes. *Mitteilungen des Vereins für forstliche Standortskartierung*, 4, 5-31.
- Horndasch, M. (1969). Die Standortserkundung und ihre Fortentwicklung. *Annual Report of the Bayerischen Forstvereins*, pp. 40-68.
- Johnston, D.R. & Bradley, R.T. (1963). Forest management tables. *Commonwealth Forestry Review*, 42, 217-227.
- Magin, R. (1963). Standortsgerechte Ertragsermittlung als Teil der Forsteinrichtung. *Allgemeine Forstzeitschrift*, 18, 128-130.
- Magin, R. (1965). Zustandserfassung und Ertragsregelung im Rahmen einer zeitgemässen Forsteinrichtung. *Allgemeine Forstzeitschrift*, 20, 781-784.
- Malcolm, D.C. (1976). Site factors and the growth of Sitka spruce. *Proceedings Section 21 of the 15th IUFRO Congress, Gainesville, Florida. Published in Wageningen*. pp. 269-83.
- Moosmayer, H.U. (1955). Die Wuchsleistung der Fichte und Buche auf den wichtigsten Standortseinheiten im Forstamt Königsbrunn. *Mitteilungen des Vereins für forstliche Standortskartierung*, 4, 52-60.
- Moosmayer, H.U. (1957). Zur ertragskundlichen Auswertung der Standortsgliederung im Ostteil der Schwäbischen Alb. *Mitteilungen des Vereins für forstliche Standortskartierung*, 7, 1-42.

- Moosmayer, H.U. (1960). Die ertragskundliche Auswertung der Standortskarten im Hinblick auf die praktische Forsteinrichtung. Mitteilungen des Vereins für forstliche Standortskartierung, 10, 13-24.
- Page, G. (1970). Quantitative site assessment: some practical applications in British forestry. Forestry, 43, 45-56.
- Schlenker, G. & Kreuzer, K. (1976). Vergleich von Klassifikationssystemen für forstliche Standortskartierungen. Proceedings IUFRO World Congress, Division I, Oslo. pp. 219-37.
- Schmidt, A. (1971). Wachstum und Ertrag der Kiefer auf wirtschaftlich wichtigen Standortseinheiten der Oberpfalz. Forschungsberichte forstliche Forschungsanstalt, 1, 245 pp. (including 58 pp of tables).
- Schmidt, A. (1973). Ertragsniveau und Standort dargestellt am Beispiel der Kiefer. Forstwissenschaftliches Centralblatt, 92, 268-274.
- Wiedemann, E. (1939). Untersuchungen der Preussischen Versuchsanstalt über Ertragstafelfragen. Mitteilungen aus Forstwirtschaft und Forstwissenschaft, 4, 1-40.
- Wiedemann, E. (1941). Vorschläge für einheitliche Ertragsklassen. Der Deutsche Forstwirt, 33/34, 313-317.

STRATEGIES FOR AMELIORATION ON POOR SITES

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SUMMARY

Site preparation is an action taken for the primary purpose of improving the survival and growth rate of a new stand. It includes prescribed burning, herbicide application, and various mechanical treatments. Amelioration measures, such as cultivation in particular, but also drainage and fertilization, can be said to 'prepare' the site where a new stand is to be established. Cultivation is the use of equipment to loosen and mix the soil in order to improve its structure and thus the overall growing conditions for trees. The purpose of drainage is to remove excess water from sites and so enhance the survival and growth of forest crops and fertilizers are applied to the forest stands for the purpose of accelerating their growth rate.

This paper deals with amelioration including drainage, cultivation and fertilization both on mineral and organic soils, mainly for stand establishment. It concentrates on results gained from research and practice in Northern Europe and, in particular, Finland.

RÉSUMÉ

La préparation d'un terrain c'est d'abord, essayer d'améliorer le taux de survie et de croissance d'une nouvelle plantation. Cela comprend le brûlage contrôlé, l'application d'herbicides et divers traitements mécaniques. Des mesures d'amélioration, tels que le labour en particulier, mais aussi la fertilisation et l'assainissement, forment en quelque sorte la préparation du terrain avant l'établissement d'une nouvelle plantation. Le labour consiste en l'utilisation d'un certain équipement pour défoncer et mélanger le sol afin d'en améliorer la structure et par là les conditions générales pour la croissance des arbres. La raison du

travail d'assainissement est d'éliminer l'excédent d'eau du terrain et, par là, d'améliorer la survie et la croissance de la forêt. Les engrais sont utilisés afin d'accélérer le taux de croissance d'une plantation.

Dans cet exposé on traite de ces améliorations - assainissement, labour, fertilisation - que ce soit sur sols minéraux ou organiques, en vue de l'établissement d'une plantation. On examine les résultats de recherches et la pratique en Europe septentrionale et en particulier en Finlande.

ZUSAMMENFASSUNG

Die Vorbereitung der Kulturflächen dient in erster Linie zur Verbesserung der Überlebens- und Wachstumsrate des neuen Bestandes. Das schliesst ein kontrolliertes Brennen, Anwendung von Herbiziden und verschiedene Arten mechanischer Bodenbearbeitung. Bodenbearbeitungsmassnahmen, wie vor allem Pflügen, aber auch die Drainage und Düngung, sind als 'Vorbereitung' des Standorts für den neuen Bestand anzusehen. Beim Pflügen wird der Boden durch verschiedene Geräte gelockert und durchmischt, was seine Struktur und die Wachstumsbedingungen insgesamt verbessert. Durch die Drainierung soll Überschusswasser dem Standort entzogen und damit die Überlebens- und Wachstumsrate der Bäume vergrössert werden. Düngemittel wiederum sollen das Wachstum des Bestandes beschleunigen.

Diese Arbeit befasst sich mit Standortsmeliorationsmassnahmen, einschliesslich Drainierung, Pflügen und Düngung auf Mineralböden und organischen Böden zur Bestandesbegründung. Im Mittelpunkt stehen Ergebnisse aus Forschung und Praxis, die in Nordeuropa, insbesondere in Finnland, gewonnen wurden.

DRAINAGE

Water relations of poorly drained soils

All water present in the soil, at water contents between saturation and permanent wilting point, is available to plants; it is not prevented from being taken up by the plants due to being chemically or physically bound to the soil matrix. Superfluous water in the soil may, however, impair

aeration to such an extent that low oxygen and high carbon dioxide concentrations inhibit growth. In the case of undrained peatlands and water-logged mineral soils, the ground water table is frequently located at, or very close to, the ground surface and in such cases the pore space of the soil is completely filled with water. If water moves very slowly then anaerobic conditions may prevail in the soil. Root development may be limited by factors other than the lack of aeration, particularly in the case of saturated organic soils, eg. due to the development of toxic concentrations of ferrous iron, sulphides and manganese.

There is little general information available concerning the minimum air space required by the roots of trees growing on peat. Paavilainen (1967) found that roots of pine trees growing on pine swamps did not penetrate to a depth greater than that at which the air space of the peat dropped below 10 per cent and this value is used as the upper limit of available water (Päivänen 1973). It is of course open to adjustment because of the lack of information on the minimum air space required by the roots of other tree species growing on peat. The water content corresponding to pF 4.2, which has usually been considered as being the permanent wilting point, is used as the lower limit of available water.

The quantity of water available to plants growing in peats with different bulk densities is shown in Fig. 1 for different hypothetical equilibria of soil water. In interpreting Fig. 1 it must be kept in mind that soil water under field conditions will rarely reach a static equilibrium; there is continuous movement of water in one direction or another.

In undecomposed peat the minimum air space is obtained at a matric suction below pF 1, the corresponding value being pF 1.5 for peats at an advanced stage of decomposition. For the latter peat and at equilibrium conditions, the ground water table should be some 32 cm below the layer of observation. All the water which enters this minimum air space is superfluous.

A number of studies have been carried out to solve the question of the optimum drainage for forestry purposes (e.g. Heikurainen, Päivänen & Sarasto 1964). However, this probably varies with the size and the stage of development of the tree e.g. germinating seed, seedling, young tree, mature tree etc. It is not exactly clear how close a relationship there is between tree growth and soil water tension but somewhat above pF 2 can be considered to be optimum for tree growth (Heikurainen 1967). An average drainage depth of some 45 cm may provide the best growing conditions for tree roots.

The most important task of drainage is to adjust the water content of the soil to a level which ensures sufficient aeration. Studies carried out in Finland have indicated that there is no risk of overdrainage in forests grown on peatlands (Päivänen 1973), at least not without fertilizer application

Drainage techniques

Recommendations for ditch depth and spacing at present in use for different sites in Finland are:

Site	Spacing m	Drainage ditch		
		Density m/ha	Depth m	Size cu.m/m
<u>Tree-covered peatlands</u>				
shallow peat soils (and wet mineral soils)	50	200	0.65	0.55
deep-peat soils of good quality	40	250	0.75	0.70
deep-peat soils of poor quality	30	333	0.75	0.70
<u>Open peatlands</u>				
fens	30	333	0.80	0.75
bogs	25	400	0.80	0.75

(Huikari & Paarlahti 1967).

On open peatlands water furrows are also used. Drainage ditches are spaced 25-40 m apart, and the furrows are placed perpendicularly to them at 3-5 m spacing. The furrows are 25-50 cm deep and are made by rotary ditchers or planting ploughs. Water furrows shorten the duration of high ground water and contribute to the lowering of the water table particularly at wide drainage-ditch spacings (Päivänen 1974). Since precipitation, the hydraulic conductivity of peat, and the tree stands on the area to be drained vary within wide limits, the combinations of ditch spacing and ditch depth used are different in different parts of the world.

Forest ditches in Finland were dug manually until 1953 when mechanized forest drainage commenced with the introduction of forest ditch ploughs. A standard ditch may be ploughed into firm peat soil at the rate of 500-600 m per hour.

The relative length of ditches made by ploughing has decreased during the last decade and the most common machine at present in use is a tractor digger or backhoe (Fig. 2) which has a work output of 70-90 m forest ditch per hour. About 90 per cent of all forest ditches dug annually are made with tractor diggers, and the total number of units working in forest drainage is about 700.

During the past few years rotary ditchers have been used though only for furrowing and site preparation prior to afforestation on deep peat sites. Some of these machines are capable of making either vertical-walled, narrow ditches or ordinary open ditches. In open peatlands standard forest ditches can be dug by rotary ditchers at a rate of 60-200 m per hour.

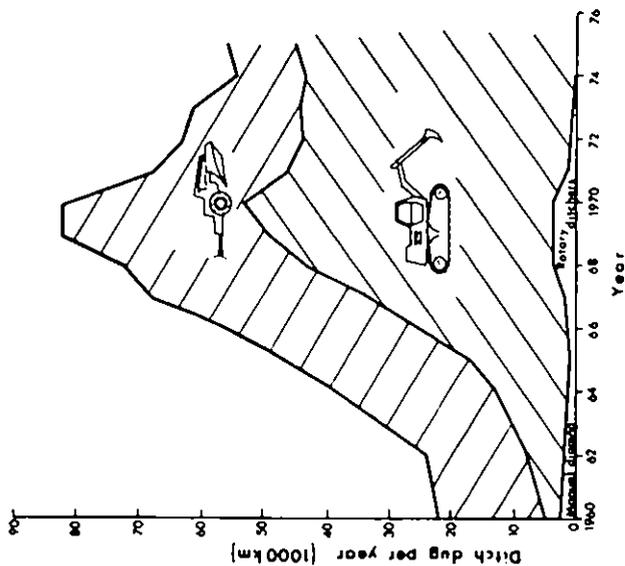


Fig. 2. Digging methods used in forest drainage in Finland during the period 1960-75

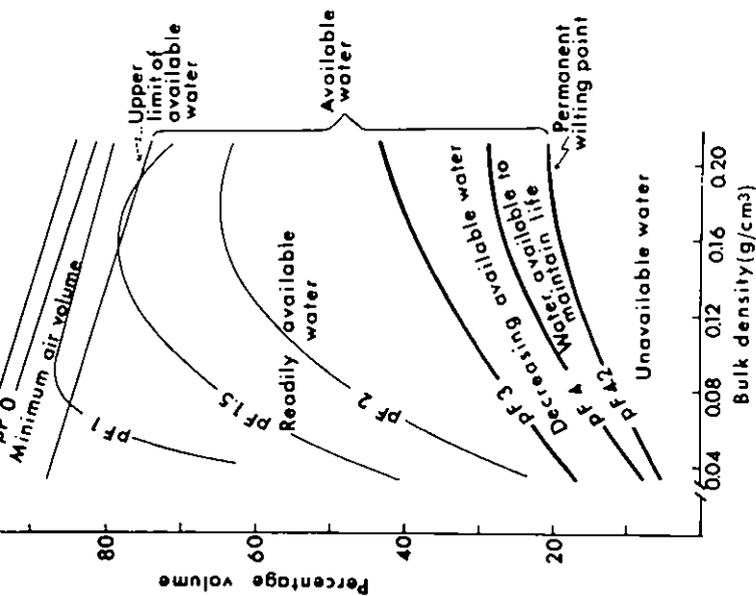


Fig. 1. Volumes of solid material and minimum air space as well as of water available and unavailable to plants in peats with different bulk density. The thin lines show the quantities of water retained in the peat at pF 0, 1, 1.5 and 2

Effect of drainage on tree growth

Several studies have shown the response of trees to drainage (see e.g. Heikurainen 1964). Continuation of the post-drainage effect on growth has been studied on naturally tree covered peatlands (Seppälä 1969; Heikurainen & Seppälä 1973). Growth seems to increase gradually even after the immediate effect obtained following drainage and we can be sure that during the first rotation drainage will be adequate. Altogether we have enough data to calculate the suitability of various peatlands for forest drainage (Heikurainen 1973)

Because there are numerous naturally tree-covered peatlands in Finland, it has not been as important to study the afforestation of peatlands, as the effect of drainage on the growth of tree stands already growing on the site at the time of draining. However, afforestation problems and the early growth of seedlings and transplants have been studied to some extent (Kaunisto 1972, 1975). It is concluded that afforestation of open peatlands is not a biological problem, since it is quite possible for young trees to grow well on peat, but rather a question of economics as is discussed later. In other countries more has been published about tree planting on peat (Zehetmayer 1954; Braekke 1974; Savill, Dickson & Wilson 1974; Thomson 1974).

CULTIVATION

Necessity for cultivation

Very often the main purpose of cultivation has been to aid the work of afforestation. After cultivation the work output in planting is twice as high as without site preparation. The other objective of cultivation has been to improve survival and early growth of a new stand. From the point of view of soil improvement the ultimate aim is, however, to reach long-term favourable effects but the factors associated with cultivation are numerous and complex (Fig 3.) (Mälkönen 1976).

In northern countries low soil temperature is one of the limiting factors to the early growth of trees through its effect in reducing root development and the activity of soil organisms (Söderström 1975). By cultivation, the humus layer is removed from the planting position or is mixed into the mineral soil and the temperature of the soil can be increased. However, extreme temperature fluctuations, i.e. a high maximum during the day and low minimum at night ought to be avoided.

The humus layer on mineral soil reduces fluctuations in the water content of the soil, and on coarse mineral soils lack of water is a limiting factor for the early growth of trees, so that on such sites only a light scarification is recommended.

Lack of water may also be the principal limiting factor for transplants on other sites. During transportation from

nursery to planting sites the roots may be damaged and the general physiological condition of transplants may be lowered. This, together with a dry spell, may be fatal for the newly planted trees. The water retention capacity of the soil is greater, the finer the texture or the poorer the structure of the soil. Cultivation tries to improve soil structure by increasing the total pore space and particularly the air space of the soil. This is known to be favourable for root development and to increase the growth of the established stand later on. So there is an obvious contradiction between the requirements for soil aeration and for soil moisture.

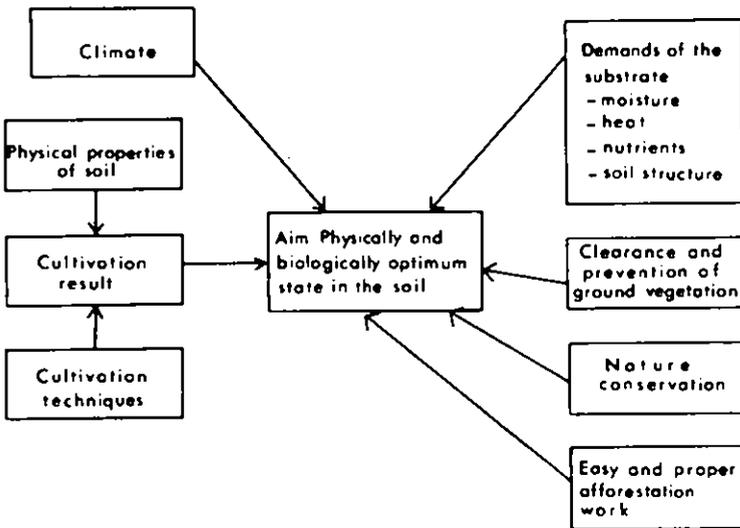


Fig. 3. Factors associated with cultivation
(after Mälkönen 1976).

This can be avoided by developing cultivation methods that satisfy both these needs. Mixing the humus layer and the underlying mineral soil, and then ridging and compressing the mixture is one such method. The organic matter increases the water retention capacity and, when mixed with the mineral soil, improves the structure and so the aeration. Another method could be based on intensive cultivation where a thick enough layer of mineral soil is ploughed over so that logging

slash from the previous rotation will be buried underneath. However, at present, suitable cultivation equipment for this technique is not available.

In addition to the above-mentioned, the following goals can be considered for cultivation:

- to reduce competition from ground vegetation
- to prevent damage from insects, and
- to increase the release of nutrients confined to the organic matter.

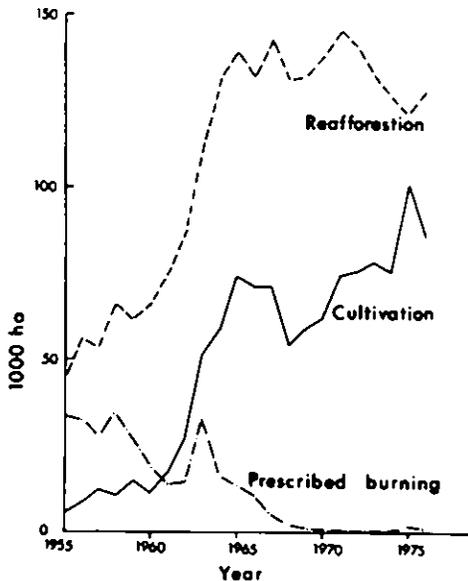


Fig. 4. Reforestation, cultivation and prescribed burning in Finland during the period 1955-76.

Cultivation techniques

As a site preparation technique, cultivation has increased remarkably in Finland over the last two decades (Fig. 4), whilst prescribed burning has diminished and is now almost non-existent. There are several reasons for this. Prescribed burning is a labour-intensive operation and one which fire laws and insurance requirements do not favour. At the same time, technical developments have made it possible to mechanize site preparation work. Until the middle 1960's, scarification was the most commonly used technique. The action of scarifiers is confined to exposing the mineral soil underlying the humus layer. In Sweden, scarifiers have been

developed to cultivate and shape the scarified spot, whilst in Finland they have been replaced by forest disc ploughs which make two continuous mineral soil furrows. Reforestation ploughs are used particularly in northern Finland where, because evapotranspiration rates are never very high, even in summer, and are exceeded by precipitation, the soil needs draining. Trees are either planted in the exposed mineral soil on both sides of the furrow or, on wetter sites, in the furrow slice. Disc ploughs and afforestation ploughs are drawn by wheeled tractors, though, to a small extent, afforestation ploughs are also drawn by crawler - tractors. The work output of disc ploughs and afforestation ploughs is about 0.9 and 0.5 ha per hour, respectively.

On open-drained peatlands rotary ditchers are used which are operated on the chain, disc cutter or spiral principles.

Effect of cultivation on tree growth

Cultivation costs can often be recovered at the time of planting as a result of reduced planting costs. Also the effect of appropriate soil preparation on survival and early growth of planted trees is evident (Mälkönen 1972; Thomson & Neustein 1973; Pohtila 1977). Not only does cultivation lead to an amelioration of soil structure but nutrients available to the trees are increased due to an increase in organic matter decomposition. Whilst there are too few experiments old enough with which to assess the long-term effects of cultivation, we can assume that, at least with intensive treatments, prolonged advantageous results can be expected.

FERTILIZATION

On mineral soils, the lack of nutrients is not usually a limiting factor for stand establishment (Leikola & Rikala 1974). On clearfelled areas nutrients in the waste wood are returned to the nutrient cycle, and the nutrient status of the soil may be better than it ever was during the whole rotation (Kubin 1977). If whole tree harvesting methods become general the situation may change.

Open peatlands may be poor in nutrients. On a practical scale, the drainage and afforestation of open peatlands has been small in Finland. However, numerous experiments have been laid out in order to ascertain the best method of fertilizer application when fertilizing is carried out in connection with stand establishment. When directly sown, seedlings of Pinus sylvestris respond best if the topmost peat layer is rotavated and fertilizers are worked into the shredded peat (Kaunisto 1972). When planting pine seedlings on poor organic soils raw phosphate can be applied into the planting hole (Paavilainen 1966). Only small quantities of a mixed NPK fertilizer ought to be used and the fertilizer should not be thrown very near the transplant (Seppälä 1971). Large quantities of fertilizer broadcast at the time of planting increase mortality

(Heikurainen & Laine 1976). The duration of the initial fertilization effect after afforestation is only 5-7 years. Refertilization with nitrogen alone is not recommended for Scots pine on oligotrophic peatlands (Kaunisto & Paavilainen 1977).

Afforestation experiments on open peatlands are still too young to allow conclusions on the profitability of this kind of activity. Compared with other amelioration techniques the afforestation of open, nutrient poor peatland is likely to be unprofitable even with the help of draining and prolonged fertilization.

DISCUSSION

A range of site preparation methods is in general use for improving survival and growth rate of the stand to be established. By cultivation we hope to maximize both advantages at the time of planting or direct seeding, as well as to secure a good start for the seedlings and to ameliorate soil properties over the long-term. The aims are similar for drainage and fertilization but until now only short-term advantages have been shown conclusively. However, with drainage on naturally tree-covered peatlands long-term effects have been demonstrated. Long-term effects of cultivation, fertilization and refertilization are likely, although as yet not proved.

REFERENCES

- Braekke, F.H. (1974). The effect of fertilization and drainage intensity on height growth of Scots pine and Norway spruce in north Norway. Proceedings of the International Symposium on Forest Drainage, Jyväskylä-Oula, Finland. pp.207-18.
- Heikurainen, L. (1964). Improvement of forest growth on poorly drained peat soils. International Review on Forest Research, 1, 39-113.
- Heikurainen, L. (1967). On the possibilities of optimum drainage in peat lands. Proceedings XIV Congress IUFRO Section 23, pp.264-77.
- Heikurainen, L. (1973). A method for calculation of the suitability of peatlands for forest drainage. Acta forestalia fennica, 131, 1-35. (In Finnish with English summary).
- Heikurainen, L. & Laine, J. (1976). Effect of fertilization, drainage, and temperature conditions on the development of planted and natural seedlings on pine swamps. Acta forestalia fennica, 150, 1-38. (In Finnish with English summary).
- Heikurainen, L. & Seppälä, K. (1973). Regionality and continuity of stand growth in old forest drainage areas. Acta forestalia fennica, 132, 1-36. (In Finnish with English summary).

summary).

- Heikurainen, L., Päivänen, J. & Sarasto, J. (1964). Ground water table and water content in peat soil. *Acta forestalia fennica*, 77.1, 1-18.
- Huikari, O. & Paarlahti, K. (1967). Results of field experiments on the ecology of pine, spruce and birch. *Communicationes Instituti Forestalis Fenniae*, 64.1, 1-135.
- Kaunisto, S. (1972). Effect of soil preparation and fertilization on the growth of young pine plantations on peat. *Proceedings 4th International Peat Congress, Volume III*, pp. 501-508.
- Kaunisto, S. (1975). Rotavation and fertilizer placement in connection with direct seeding of Scots pine on peat. Greenhouse experiments. *Communicationes Instituti Forestalis Fenniae*, 85.4, 1-58. (In Finnish with English summary).
- Kaunisto, S. & Paavilainen, E. (1977). Response of Scots pine plants to nitrogen refertilization on oligotrophic peat. *Communicationes Instituti Forestalis Fenniae*, 92.1, 1-54.
- Kubin, E. (1977). The effect of clear cutting upon the nutrient status of a spruce forest in northern Finland (64°28' N). *Acta forestalia fennica*, 155, 1-40.
- Leikola, M. & Rikala, R. (1974). The effect of fertilization on the initial development of pine and spruce on mineral soils. *Folia forestalia*, 201, 1-19. (In Finnish with English summary).
- Mälkönen, E. (1972). Some aspects concerning cultivation of forest soil. *Folia forestalia*, 137, 1-11. (In Finnish with English summary).
- Mälkönen, E. (1976). Markberedningens ekologi och inverkan på planteringsresultatet. *Forskningsstiftelsen Skogsarbeten, Redogörelse 6*, 11-15.
- Paavilainen, E. (1966). Initial development of root systems of Scots pine transplants in *Eriophorum vaginatum* swamp. *Communicationes Instituti Forestalis Fenniae*, 61.6, 1-17. (In Finnish with English summary).
- Paavilainen, E. (1967). Relationship between the root system of Scots pine and the air content of peat. *Communicationes Instituti Forestalis Fenniae*, 63.6, 1-21. (In Finnish with English summary).
- Päivänen, J. (1973). Hydraulic conductivity and water retention in peat spoils. *Acta forestalia fennica*, 129, 1-70.
- Päivänen, J. (1974). The effect of ditch spacing and furrowing on the depth of the ground water table and on the development of a Scots pine plantation on small-sedge bog. *Silva fennica*, 8, 215-224.
- Pohtila, E. (1977). Reforestation of ploughed sites in Finnish Lapland. *Communicationes Instituti Forestalis Fenniae*, 91.4, 1-98.

- Savill, P.S., Dickson, D.A. & Wilson, W.T. (1974). Effects of ploughing and drainage on growth and root development of Sitka spruce on deep peat in Northern Ireland. Proceedings of the International Symposium on Forest Drainage, Jyväskylä-Oulu, Finland. pp.241-252.
- Seppälä, K. (1969). Post-drainage growth rate of Norway spruce and Scots pine on peat. Acta forestalia fennica, 93, 1-89. (In Finnish with English summary).
- Seppälä, K. (1971). On the quantity of fertilizer and application methods used in afforestation of open bogs. Silva fennica, 5, 61-69.
- Söderström, V. (1975). Ecological effects of ploughing mineral soil before planting on clearfelled areas. Sveriges Skogsvårdsförbunds Tidskrift, 73, 443-472. (In Swedish with English summary).
- Thompson, D.A. (1974). A brief review of drainage in deep peat in the Forestry Commission. Proceedings of the International Symposium on Forest Drainage, Jyväskylä-Oulu, Finland. pp.253-259.
- Thomson, J.H. & Neustein, S.A. (1973). An experiment in intensive cultivation of an upland heath. Scottish Forestry, 27, 211-221.
- Zehetmayer, J.W.L. (1954). Experiments in tree planting on peat. Forestry Commission Bulletin 22.

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THE BIOLOGICAL RESOURCE

Chairman: L. Roche

Variation between and within
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The exploitation of genetic
variation by selection and
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VARIATION BETWEEN AND WITHIN TREE SPECIES

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SUMMARY

Genetic variation in forest trees has three primary components: among populations, among individuals within populations and among species. Variation among populations has been widely studied. Much variation is apparently adaptive with some traits, such as phenology, temperature optima for photosynthesis, seed weight, DNA content, and drought resistance, varying with climatic clines in photoperiod, temperature and rainfall. Clinal variation may be environmentally correlated in quite localized areas, i.e. up a single mountain slope or from one aspect to another. Nonclinal variation also occurs, most commonly in response to edaphic factors. Considerable variation among populations is not obviously correlated with environmental factors. Much of this may be due to historical factors producing isolation and drift.

Recent studies have found considerable genetic variation within populations. The indications, but without solid evidence, are that at least a portion of this may be adaptive, especially with respect to pest resistance and competition avoidance. On the other hand, effective pollen dispersal is apparently highly localized, suggesting that isolation and drift produce at least some of this variability.

Differences among species are well known and impossible to detail here. A major segregating factor has been adaptive strategy as manifested in successional status, leading to differences in silviculturally significant traits such as shade tolerance, efficiency of nutrient cycling and possibly pest resistance.

Ample genetic variation exists, or may be created through newly developing technologies,

to yield significant genetic gains in individual tree growth. Possible approaches include selection for temperature optima, efficiency of water and nutrient utilization, optimal mesophyll density, crowns that efficiently gather light, lower light respiration, and phenologies that fully utilize the growing season.

Because foresters probably will never deal with cultivated systems in the agricultural sense, it seems prudent not to decrease the natural buffering capacity of forests through drastic reductions in genetic diversity. Therefore, I suggest that genetic manipulation should focus both on individuals and communities. Much more study of ecosystem dynamics is needed but perhaps communities which are properly designed mixtures of genotypes can be both stable and productive.

RÉSUMÉ

Les variations génétiques des arbres forestiers peuvent être primitivement classées en trois composantes: variation entre populations, variation entre individus au sein d'une population et variation entre espèces. Nombreuses ont été les études sur les variations entre les populations. Apparemment, les variations sont en grande partie du genre adaptatif avec certains traits, tels que phénologie, température optimale de photosynthèse, poids des graines, contenu en DNA et résistance à la sécheresse variant avec les gradients climatiques, la température et la pluie. Les variations clinales peuvent être corrélées avec des facteurs du milieu dans certaines zones limitées par exemple le long d'un versant, ou d'un versant à l'autre. Les variations qui ne sont pas clinales sont liées, le plus souvent, à des facteurs édaphiques. Mais une grande partie des variations entre populations n'est manifestement pas liée à des facteurs du milieu. Elle serait plutôt liée à des facteurs historiques qui produisent soit un isolement, soit une dérive.

Des études récentes ont montré qu'il y avait au sein des peuplements des variations génétiques considérables. Elles ont indiqué, mais sans preuves solides, qu'au moins une partie de cette variation avait un caractère adaptatif,

surtout la résistance aux parasites et l'aptitude à éviter la compétition entre espèces. D'un autre côté, la dispersion effective du pollen est très localisée. Cela suggérerait que l'isolement et la dérive seraient au moins une source partielle de cette variation.

Les différences entre les espèces sont bien connues et il est impossible de les énumérer ici. Un des facteurs de différenciation les plus importants est la stratégie d'adaptation qui s'est manifestée dans la succession des peuplements amenant des différences significatives dans le comportement sylvicole, tel que la tolérance d'ombre, l'efficacité du cycle des éléments nutritifs et peut-être la résistance aux parasites.

Il existe une vaste variation génétique, ou du moins celle-ci peut être créée par des technologies nouvelles, qui amèneraient des apports génétiques significatifs pour la croissance d'un individu. Les approches possibles comporteraient une sélection pour des températures optimales spécifiques de certaines stations, pour l'utilisation efficace de l'eau et des éléments nutritifs, pour une densité du mésophylle optimale, pour des cimes qui recueillent avec efficacité la lumière, pour une photorespiration plus basse et pour des phénologies qui utilisent pleinement la saison de végétation.

Bien que les forestiers ne seront jamais amenés à traiter des systèmes culturaux au sens agricole du terme, il serait prudent de ne pas diminuer la capacité de régulateur naturel des forêts qui est due, en large partie, à la diversité génétique. Par conséquent, je suggère que les manipulations génétiques portent aussi bien sur les individus que sur les populations. Une étude plus approfondie de la dynamique des écosystèmes serait certes utile mais il se pourrait aussi que les peuplements issus d'un choix efficace d'essences différentes puissent être à la fois stables et productifs.

ZUSAMMENFASSUNG

Genetische Verschiedenartigkeit bei Waldbäumen hat drei Hauptkomponenten: die zwischen Populationen, die zwischen Einzelexemplaren innerhalb von Populationen und die zwischen

Baumarten.

Die Verschiedenartigkeit zwischen Populationen ist gründlich erforscht worden. Häufig ist die Verschiedenartigkeit offenbar das Resultat einer Anpassung an bestimmte Gegebenheiten, wie beispielsweise Phänologie, Temperaturoptimum für Photosynthese, Saatgewicht, DNA-Gehalt and Dürresistenz, die sich mit den klimatischen Abstufungen in der Photoperiode, der Temperatur und dem Niederschlag ändern. Stufenweise Unterschiede mögen sogar in engem Raum von der Umwelt abhängig sein, wie zum Beispiel auf einem einzigen Berghang oder von einer Exposition zur anderen. Es gibt auch nicht-abgestufte Unterschiede, meist als Reaktion auf edaphische Faktoren. Vieles in der Verschiedenartigkeit innerhalb von Populationen ist nicht offensichtlich von Umweltfaktoren abhängig. Das ist zum grossen Teil auf historische Gegebenheiten zurückzuführen, die Isolierung und Abwanderung verursachen.

Jüngere Studien haben eine beträchtliche genetische Verschiedenartigkeit innerhalb von Populationen festgestellt. Auch wenn es keine handfesten Beweise gibt, sprechen doch die Anzeichen dafür, dass zumindest ein Teil davon Ergebnis einer Anpassung ist, besonders im Hinblick auf die Schädlingsresistenz und die Vermeidung von Konkurrenz. Andererseits ist eine effektive Pollenverbreitung weitgehend räumlich begrenzt. Dies lässt vermuten, dass Isolierung und Abwanderung wenigstens in einem gewissen Mass die Variabilität erzeugen.

Unterschiede zwischen Baumarten sind hinreichend bekannt und es ist hier nicht möglich, darauf im einzelnen einzugehen. Ein wichtiger trennender Faktor ist die Anpassungsstrategie gewesen, die sich im Sukzessionsstand manifestiert. Dies führte zu Unterschieden in waldbaulich bedeutenden Eigenschaften, wie beispielsweise Schattentoleranz, Wirksamkeit des Nährstoffumsatzes und möglicherweise Schädlingsresistenz.

Entweder ist reichlich genetische Verschiedenartigkeit vorhanden, oder sie kann durch neu entwickelte Techniken geschaffen werden, um signifikante genetische Gewinne für das Wachstum des Einzelbaumes zu erzielen. Mögliche Ansätze schliessen eine Selektion ein,

die abzielt auf bestimmte standortspezifische Temperaturoptima, wirksame Wasser- und Nährstoffverwertung, optimale Mesophyllidichte, Kronen mit wirksamer Lichtausnutzung, geringere Respiration bei Tageslicht und Phänologien die die Wachstumsperiode voll ausnutzen. Da man es in der Forstwirtschaft wahrscheinlich nie mit Kultivierungssystemen im landwirtschaftlichen Sinn zu tun hat, scheint Vorsicht angebracht, damit die natürliche, vor allem durch genetische Verschiedenartigkeit bedingte Pufferwirkung von Wäldern nicht abnimmt. Deshalb schlage ich vor, genetische Manipulationen sowohl auf Individuen als auch auf Gemeinschaften auszurichten. Die Dynamik des Ökosystems ist noch sehr viel gründlicher zu erforschen, aber vielleicht können Gemeinschaften aus richtig zusammengestellten Mischungen von Baumarten stabil und gleichzeitig auch produktiv sein.

INTRODUCTION

This brief review of genetic differences in trees discusses some ways these differences might affect future silviculture. Fifteen years ago Allard & Bradshaw (1964) suggested that no one had the competence to review all published information on plant genotype-environment interactions. Even narrowing the field from all plants to just trees, I am quite willing to take refuge in that statement today. The unfortunate consequence of this is, that this review will not mention many pertinent papers. This is my error, and in no way reflects on the quality of uncited work. Any apparent bias towards North American conifers should be considered, I hope charitably, as random drift introduced by choosing a reviewer from a small, isolated population.

Perhaps I should warn of another bias. I am an ecologist, not a plant breeder. Therefore, to me, two questions must be asked about manipulation of forest gene pools. How much can we change? And, more importantly, how much should we change? Unfortunately very little research is available to guide us in answering the latter question and discussing it can be frustrating. It is a question, however, that must be addressed.

My argument is developed in two phases: (i) a summary of what is known about genetic variation in forest trees, starting with differences among populations, then moving to within-population variability, and finally some brief statements about variation among species; (ii) a discussion of ways in which forest yield may be improved through genetic selection at both the organism and community level.

VARIATION WITHIN SPECIES: AMONG POPULATIONS

Patterns of variation correlated with environment

Stern & Roche (1974) and Wright (1976) summarized information concerning clinal variation in forest tree species. Clines generally occur along the three primary axes of latitude, longitude and elevation, reflecting various changes in photoperiod, thermoperiod and precipitation. The adaptive characteristics of a single population result from a complex combination of those factors, and other influences not so easily measured.

Adaptation to climatic variation appears to be accomplished primarily through the developmental cycle of a plant (Heslop-Harrison 1964). One of the central problems of provenance transfer, especially in high latitudes, is synchronization of development with the seasonal cycle (Langlet 1967; Campbell 1974a). Discussing British Columbia spruces, Roche (1969) wrote:

'In so far as there is a difference in the photothermal regime between any two regions, the genetic constitution of the populations occupying those regions will differ, and one of the most important external manifestations of this difference is the time of cessation of growth and initiation of dormancy'.

Both latitude and elevation correlate with critical daylength for growth cessation in Norway spruce (Heide 1974). Phenological clines have been demonstrated in a number of other species: latitudinal in the genus Populus (Pauley & Perry 1954; Hoffman 1953), Scots pine (Sarvas 1969), Jack pine (Giertych & Farrar 1962; Mergen, Warren & Furnival 1967), lodgepole pine (Cannell 1976), ponderosa pine (Madsen & Blake 1977), Sitka spruce (Falkenhagen 1977), and red oak (Kreikel et al. 1976); elevational in western white pine (Barnes 1967) and lodgepole pine (Hagner 1970a); and elevational-longitudinal in Douglas fir (Irgens-Möller 1968; Campbell & Sorensen 1978).

Most, if not all, wide ranging plant species are probably differentiated along climatic clines (cf. Hiesey & Milner 1965) but this is sometimes difficult to demonstrate. Local climates may not correlate smoothly with easily measured variables such as latitude or elevation and other complicating factors, which I will detail later, may come into play.

Vaartaja (1959) studied photoperiodic adaptation in eighteen tree species from nine genera, finding latitudinal differentiation in only eight species. Intergenetic differences were pronounced. Three of five species of spruce, but none of five pine species, showed photoperiodic differentiation. Vaartaja's results with certain species conflict with findings of his own and of other researchers, indicating the difficulties involved in generalizing about these phenomena.

Between-population variation may differ considerably from one part of a species range to another. Reck (1973) investigated the phenology and growth patterns of forty-two Douglas fir provenances. Inland sources were clearly differentiated, whereas provenances from the Pacific coast, an area of relatively uniform climate, were not. Similarly, Squillace & Silen (1962) found latitudinal clines among inland populations of ponderosa pine, but not among coastal populations. The correlation between the weight of ponderosa pine seed and climatic factors differs strikingly among regions (Wells 1964). These patterns may simply be artifacts of low sampling intensity rather than real biological phenomena.

Many traits, other than those related to phenology, show patterns of clinal variation. For yellow birch, Wearstler & Barnes (1977) found strong south-north clines of decreasing height, increasing seed weight, earlier initial germination and increasing total germination. In other species, seed weight seems to be negatively correlated with moisture supply and length of growing season (e.g. Wells 1964, Perry & Lotan 1978), which probably is an adaptation for producing large seedlings in a relatively short time.

Differences have been found among populations within various species in drought resistance (Ferrell & Woodard 1966), Bilan, Hogan & Carter 1977; Eickmeir, Adams & Lester 1975; Dijkstra 1974; Kreikel et al. 1976); frost resistance (Illingworth 1975; Van den Driessche 1977; Langlet 1967); optimum temperature for photosynthesis (Slatyer & Ferrar 1977) and characteristics of bark reflectance (Covington 1975). Gerhold (1959) and May & Means (1977) found that chloroplast structure differed along elevational gradients.

In a classic experiment, Thoday & Boam (1959) showed that strong selection would maintain genetic differences between populations of *Drosophila* despite intense gene flow. This result seems to apply equally well to trees. Non-clinal transitions between soil types, to be discussed later, are well known. However, populations may vary over short gradients in elevation and abrupt changes in aspect as well. The most striking example was given by Fryer & Ledig (1972) who found that the optimum temperature for photosynthesis in Balsam fir over an elevational gradient varied closely with the adiabatic lapse rate. Growth and phenology of Douglas fir were shown to differ significantly among populations 150 m apart (vertical) along an elevational transect (Hermann & Lavender 1968). Douglas fir on south slopes are, in some cases, more drought resistant than those on neighbouring north slopes (Ferrell & Woodard 1966). Later, however, I will discuss findings by Rehfeldt (1974) that urge caution in extrapolating these results.

The adaptive benefit for some traits that vary clinally

is obscure. For example, Douglas fir populations vary latitudinally in mycorrhizal formation (Wright & Ching 1962). DNA content and nuclear volume of cells varies latitudinally in several coniferous species (Miksche 1967; Sziklai, El-Lakany & De-Vescovi 1976). Wareing & Matthews (1971) suggested that greater production of enzymes compensates for lower rates of enzyme action at low temperatures.

Stern & Roche (1974, p.117 ff) discuss discontinuous, also termed ecotypic or racial variation in plants, most of which relates to edaphic factors. Differential ability to extract nutrients, or tolerance of low availability has been found between populations on granitic and ultramafic soils (Jenkinson 1974), calcareous and acidic sites (Ladiges & Ashton 1977; Holst 1974), and swampy and upland sites (Musselman, Lester & Adams 1975; Sannikov, Sannikov & Grishina 1976). Not surprisingly, rooting characteristics seem to play a role in edaphic adaptation (Schmidt-Vogt 1971; Ladiges & Ashton 1977). Provenance differences in needle nutrient concentration (Van den Driessche & Webber 1975; Woessner et al. 1975; Falkenhagen 1976) and fertilizer response (Bramlett & Belanger 1976) may represent adaptation to edaphic factors (Giertych (1969) reviewed earlier publications).

Patterns of variation without obvious environmental correlation

Much variation among populations cannot be attributed easily to differential selection along environmental gradients. This often appears as 'noise' superimposed upon broad environmentally related trends. For example, Wells (1964) found that 32 per cent of progeny:environment correlations in ponderosa pine were significant when calculated with data from an entire region, but only 3 per cent when data from separate ecotypes within regions were used. Small-scale stochasticity in population traits was also noted by Rehfeldt (1974), who found patterns of differentiation in Rocky Mountain Douglas fir to be essentially random with respect to topography. Sampling error may account for some of this. Other explanations include:

- (1) Some phenotypic traits in a population may exist independently of natural selection (Stern & Roche 1974). Others may not be influenced by the environmental gradient that was studied. For example, growth rate is an often studied trait which, in many cases, may have little bearing on a plant's ability to survive and reproduce, particularly in harsh environments (Namkoong 1969).
- (2) In species that pioneer disturbed sites, founder effects (random shifts in genetic composition due to establishment of a population by only a few parents) may produce differences between populations.
- (3) Major periods of selection occur infrequently in pioneers suggesting that some populations may be adapted to

weather conditions which have since changed.

- (4) Past glaciation led to large scale biological migration, so many populations may now exist on sites to which they have yet not fully adapted (Wright 1973).
- (5) Historical factors may result in isolation and drift, leading to rapid differentiation. Comparing the Rocky Mountain and Pacific Coast varieties of ponderosa pine, Wells (1964) wrote

"..... differences between the two varieties stem from more ancient causes that are not reflected in ... weather records of the past seventy years".

 For a discussion of the possible relation between diastrophism and episodes of evolution see Axelrod (1967).
- (6) Populations may adapt to environmental differences in diverse, but equally effective ways (Heslop-Harrison (1964).
- (7) Adaptation occurs in response to a set of environmental factors, and the adaptive significance of a character may become evident only when the full set of relevant niche parameters is considered (Stern & Roche 1974).
- (8) Some important environmental factors may be normally overlooked. For example, Elliot (1974) found that predation by squirrels living in stands of lodgepole pine has selected for certain seed and cone characteristics. Factors affecting squirrel populations may then be reflected in tree phenotypes.

Some traits that seem to vary randomly have clear selective advantage. Pest resistance differs widely within species. For example, Scots pine varies in its resistance to Zimmerman pine moth (Wright, Wilson & Bright 1975), loblolly pine to rust (Wells 1966), European larch to various insect pests (Sindelar & Hochmut 1972) and lodgepole pine to Crumenula sororia (Hayes 1975). Provenance or clonal differences in resistance to pollutants have been found in lodgepole pine (Lang, Neumann & Schutt 1971), Japanese larch (Vogl, Schönbach & Hadicke 1968), Norway spruce (Braunn 1977a,b) and trembling aspen (Karnosky 1977).

Terpene content varies considerably among populations of some conifers (Van Rudloff 1972; Thielges 1972; Gansel & Squillance 1977; Faulkner et al. 1977). The adaptive value of differing terpenes is not apparent and much of the variation may be due to gene flow between species (eg. Zavarin, Critchfield & Snajberk 1969). However, terpenes probably play an important role in interaction with pests. Faulkner et al. (1977) found Fomes annosus to be absent from most Sitka spruce in which alpha-pinene formed at least 35 per cent of the root resin. The role of chemicals as mediators of ecosystem structure and dynamics is virtually unknown, although interesting work is in progress (eg. Meinwald et al. 1978).

Hendry (1976) hypothesized that dietary chemicals may substructure insect populations in ecological and evolutionary time, although Miller et al. (1976) offered a counter argument. Other subtle ecosystem interactions are mediated by chemical factors as well - see the discussions by Smith (1976) and Karimbayeva & Sizova (1977) on the role of root exudates in rhizosphere ecology.

One of the most interesting phenomena of forest genetics is the fact that local populations, especially those on severe sites, are often not optimal either in growth, which may not be a trait selected for, or other adaptive characteristics (Namkoong 1969; Campbell 1974a). Similarly, many populations have superior growth characteristics even when transferred far from their native location (eg. Giertych 1976; Illingworth 1975). Height of five year old lodgepole pine at two different planting sites, one of which was quite severe, was highly correlated ($r^2 = 0.88$ and 0.92) with the site index of the parent stand, even though the sampled provenances spanned about 1500 km (Perry & Lotan 1978; Perry & Steinhoff, unpublished data). In that study, height was also correlated closely with length of the growing season at the native location, suggesting that favourable environments may permit the evolution of genotypes which are vigorous and which are also highly buffered against environmental change.

VARIATION WITHIN SPECIES: WITHIN POPULATIONS

One of the most critical yet least understood questions in population genetics relates to the adaptive nature of variability within populations (cf Simpson 1975). Electrophoretic studies have revealed large amounts of enzyme polymorphism within populations of most studied organisms; whether this variability is selectively neutral or not, is vigorously debated (Gillespie & Langley 1974; Nei, Fuerst & Chakraborty 1976; Gilpin et al. 1976).

Saki & Park (1971) found isozyme differences between groups of trees separated by only a few hundred meters and with no obvious environmental gradient included, which they attributed to isolation and drift, i.e. pollen dispersal was very localized. Significant variation within populations has been found in the growth characteristics of several species (Hagner 1970b; Clausen 1975; Wells & Snyder 1976; Dietrichson 1969; Eriksson et al. 1976; Ledig & Clark 1977; Perry & Lotan 1978). Family differences have also been shown in stress response (Perry et al. 1978) and nutrient relations (Burdon 1971).

Variability in growth characteristics within populations occurs primarily in young seedlings, tending to disappear with time (Namkoong, Usanis & Silen 1972; Namkoong & Conkle 1976; Perry & Lotan 1978). Namkoong et al. (1972) suggested that this is due to the relatively large micro-environmental

diversity encountered by young seedlings, with a consequent selective premium for differential growth strategy. As trees grow and micro-environments become less important, diversity in growth strategy also becomes less important. Among lodgepole pine populations, family related phenotypic variance correlates closely with differential family response to changing environments, suggesting that variability has an adaptive component (Perry & Lotan 1978). Families may also follow differing growth patterns as a mechanism for dividing resources in time (Perry 1978).

Despite much speculation little is actually known about the role of genetic diversity in ecosystem regulation. Mono-specific forests are more susceptible to pest outbreaks than diverse ones (Vouté 1964) and in an elegant laboratory experiment, Pimentel & Bellotti (1976) demonstrated that diversity is indeed an important pest regulator. Intraspecific as well as interspecific diversity probably play important regulatory roles. Shaw & Little (1977) found that foliar components of dietary importance to spruce budworm varied locally in balsam fir, Hunt & Von Rudloff (1977) showed that leaf - oil - terpene variation was greater within than between populations of western white pine. Observations of this type do not, of course, prove a regulatory function. However, recent studies investigating both insect and tree hosts suggest a great deal of genotype : specific interaction (Claridge & Wilson 1978; Edmunds & Alstad 1978). Levin (1975) concluded that pest pressures have played a large role in maintaining open recombination systems in climax species.

Indirect evidence suggests that within-species diversity varies inversely with between species diversity. Levins (1968) predicted on theoretical grounds that increasingly uncertain environments would result in broader niches, one component of which could be genetic diversity within species, with consequent decrease in between-species diversity. That species diversity decreased with increasing site severity, within certain limits, has been demonstrated both for animals (MacArthur 1975) and forest plants (Brünig 1973; Glenn-Lewin 1977), although this is not always the case (eg. Zobel et al. 1976). Factors such as rapid crown closure on good sites (del Moral 1972) may confound matters by introducing a time dimension.

Little work has been done on within-population variability as a function of environment, although Heslop-Harrison (1964) felt that it should be greater at the margin of the species distribution because of low inter-specific competition. May & Means (1977) reported that the variability of Englemann spruce chloroplasts increased up an elevational gradient. Clausen & Hiesey (1958) found a similar relationship in the height variability of Achillea spp. I have found a close correspondence between phenological

variability within lodgepole pine populations and the elevation of their native habitat, although these stands spanned a considerable latitudinal gradient, with consequent confounding effect on the climate-elevation relation. On the other hand, Stern & Roche (1964) concluded that the studies they cited indicate greater variability in central rather than marginal populations; they argue that inter-specific competition produces variability. These two viewpoints may be compatible. Where physical factors are highly variable and dominate the selection regime, certain sets of adaptive traits will be diversified. As biological factors become increasingly important (in relatively benign habitats), diversifying selection acts on other sets of traits. For example, the greatest diversity of genes for pest resistance are usually found in the centre of the species range (Levin 1975). Links between enzyme and phenotypic variability are not well established (see, however, Mitton 1978), but Tigerstedt (1973) did find that differences in isozyme variability between central and marginal populations of Norway spruce depend on the enzyme pattern studied.

Do we then expect populations from harsh sites to be the most highly buffered against physical factors of the environment? This may often be the case, and prudent management demands that, in the absence of specific evidence to the contrary, we assume that it is (Morgenstern & Roche 1969). However, some data do not fit the model. Relative growth of Norway spruce provenances is highly consistent across a wide variety of environments, with non-local sources out-performing locals on many harsh sites (Giertych 1976). I have seen similar trends in lodgepole pine, although the seedlings are too young to draw conclusions. Clearly much still must be learned about the population ecology, but current evidence suggests that certain populations, often from the center of the species range, are genetically superior not only in growth, but also in overall buffering capacity. On the other hand, fitness for a given site may ultimately be determined by the ability of a genotype to survive infrequent climatic events, and short term studies tell us little about this.

VARIATION BETWEEN SPECIES

Rather than review the information about differences between tree species, I will briefly and generally discuss broad differences in adaptive strategies as they relate to silviculture, focussing more on what is not known than what is.

Temperate and boreal forests have evolved under an environmental regime of periodic disturbance. Thus time has produced a rough dichotomy in adaptive strategy, distinguished in forestry as pioneer and climax species and in current

ecological theory as r and K selected species (Stearns (1976) reviewed life history tactics). Two distinguishing characteristics of these groups are especially pertinent here: (1) genetic systems or devices for regulating variability (Darlington 1939) and (2) a degree of adaptation to physical factors on the one hand and biotic factors on the other.

Adaptive strategies form a continuum between the ephemeral pioneer and climax species, with pioneer tree species falling somewhere in between. Thus applying theoretical results directly to trees is misleading although some generalizations seem possible. At least three arguments can be made that greater genetic diversity occurs in long-lived pioneers relative to climax species:

- (1) Because of low interspecific competition, pioneers can tolerate more genetic deaths and, therefore, can afford to produce more variability (Grant 1963).
- (2) Because of low interspecific competition, pioneers occupy relatively broad niches, mediated by both genetic diversity and phenotype plasticity (Levins 1968).
- (3) Because major episodes of selection may occur decades apart in pioneers, i.e. at the time of seedling establishment, they must maintain the ability to cope with relatively large changes in climate.

On the other hand, sound arguments support less recombination in pioneer species (e.g. Pickett 1976). Resolution of these two lines of argument may lie in the organisation of variation within populations, with climax species tending toward individual buffering and pioneers toward populational buffering, thereby preserving homozygosity in individuals without foregoing diversity in the population. From a practical standpoint, these questions bear directly on the potential for gains through selection and the degree to which a given gene pool should be narrowed. However, I am aware of little research to assess the validity of these speculations.

The genetic systems of species differ, although why is not always clear. Red pine, for example, is genetically quite uniform, which Fowler & Morris (1977) attributed to historical factors. Wright (1976) discussed the considerable differences among pine species in the effectiveness of mass selection techniques. Trends within species might tell us something about differences between species. Lotan and I compared variabilities between open- and closed-cone progeny of lodgepole pine, which probably evolved in very different environments, and among populations from relatively severe and benign habitats (Perry & Lotan 1978). We found differences, but they were inconsistent so we could not draw conclusions about causal factors. Considerable work is needed before we understand the forces that shape the genetic systems of species.

Odum (1969) discussed numerous functional and structural differences between developmental stages and mature ecosystems. Many of these may be important to silviculture but here I will mention one in particular which I will discuss in more detail in the next section. Pioneer species generally occupy habitats with, at least in the beginning, greater resource availability (Gadgil & Bossert 1970) and less interspecific variability, thus they are often poor competitors. Some coniferous species, as a means of indirect competition, may in fact have evolved mechanisms for retarding decomposition of organic material and consequent release of nutrients (first suggested to me by Don Despain, a biologist at Yellowstone National Park). In contrast, angiosperms seem to cycle nutrients very rapidly. Later I discuss how this might be used to silvicultural advantage.

Pest resistance is another difference between pioneer and climax species which may have silvicultural importance. Pioneer species persist because of periodic disasters, and thus have little evolutionary incentive to develop resistance to epidemic pest outbreaks, in fact, they may have evolved to encourage them. For obvious reasons climax species must develop a greater degree of pest resistance. Grant (1963) suggested that much diversity in tropical forests was due to selection for pest resistance.

UTILIZATION OF GENETIC DIVERSITY

Crop breeders speak in terms of ideotypes, idealized plant models with optimum potential for growth under a given set of environmental conditions (e.g. Donald 1968; Frey 1970). Within the context of the physiological basis of yield, this is a sensible approach and one which, as long as we understand its limitations, has much to offer forest tree breeders. Several authors have recently discussed plant factors most amenable to genetic manipulation for increased yield (Wareing & Matthews 1971; Gordon 1975; Nasyrov 1978). At its first level, the model is very simple: yield is a function of photosynthesis, less respiration, integrated over a growing season. Let us consider each of these separately.

(1) Photosynthesis Improving the quantum yield of photosynthesis would have enormous payoff, but seems rather remote at this time (Gordon 1975). However, differing chloroplast structure among genotypes of a species suggests that such an advance is not out of the question. Alternatively, several indirect approaches seem feasible to increase gross carbon fixation. First, genetic variation for process-oriented traits, e.g. temperature optima, efficiency of mineral or water utilization and decreased mesophyll resistance might be exploited within populations to narrow the range of 'maladapted' individuals on a given site. Wareing &

Mathews (1971) suggested breeding for individuals with optimal intercellular space distribution within the mesophyll, high rates of enzyme activity and the ability to maintain high rates of photosynthesis at low temperatures. Secondly, structural characteristics determining the number and orientation of leaves could be important targets of selection, i.e. canopies should be designed as optical systems (Nasyrov 1978; Horn 1971; numerous references cited by Monsi, Uchiuima & Oikawa 1973). Wareing & Matthews (1971) pointed out that species in genera such as Abies, Thuja and Tsuga, with long crowns, dense foliage and low light compensation points, are highly productive, both as single trees and in dense stands. For example, on the Oregon Coast a twenty-six year old stand of western hemlock is producing dry matter at a rate of 36 metric tons ha/yr (Fujimori 1971). Within-species variability in crown structure (see Stern & Roche 1974) provides an additional source of raw material. Finally, leaf senescence is important in the loss of photosynthetic capacity and, though poorly understood, is amenable to genetic modification. Nasyrov (1978) produced a mutant of cotton in which leaf senescence was delayed with consequent increase in productivity. Kim (1976) attributed the high productivity of an F1 hybrid of loblolly and pitch pine to increased photosynthetic life of needles.

- (2) Respiration "Perhaps the most promising basic modification of the photosynthetic process is the suppression of respiration in the light" (Gordon 1975; see also Marx 1973). Differences in C4 and C3 plants are well known. More relevant to forestry is the possibility of differing rates of photorespiration among C3 genotypes. Wilson (1972) did, in fact, find genetic variation in photorespiration within Lolium sp, suggesting that similar searches within, or among, tree species may be productive.
- (3) Full utilization of the growing season. Substantial gains seem possible here, both by selection within populations and by transfer across clines. In several species of pines, genotypes moved north of their native location outgrew local provenances (Wells & Wakely 1970a, 1970b; Morgenstern & Teich 1969). However, experience with Scots pine in Sweden has been the opposite, with greatest volume gains made by moving provenances southward and down in elevation (Eriksson et al. 1976). This is primarily due to increased survival, reflecting the fact that large numbers of individuals within provenances are apparently unfit for the climate at their home location (Hagner 1970b). Wareing & Matthews (1971) suggested an

actuarial approach to provenance transfer, using weather records to balance gains in productivity against the probability of loss due to early or late frost. Campbell (1974b) used predictions of timing of vegetative bud burst to examine response of seedlings to seed transfer. He concluded that east-west transfers were likely to be more maladaptive than north-south transfers. The Swedish experience suggests that intra-population variability should be included in analyses such as these.

Radiation and chemicals have been extensively used to induce mutants in crop breeding (see Frey 1970 for a review), and powerful new techniques are being developed for genetic manipulation (eg. Hoskins et al. 1977; Carlson & Polacco 1975). We may be standing on the threshold of a quantum leap in our ability to shape the genetic system of the organisms which serve us, a power that carries considerable risk.

At this juncture it is appropriate to ask if, in forestry, we wish to follow in the footsteps of crop geneticists. I suggest that we do not and that, while the concept of the organismic idotype can be used advantageously, our primary focus should be on the ideotypic community. The reason for this is simple. We deal with ecological systems, of which autecological considerations form only one component. In traditional agriculture, high inputs of cultural energy maintain a simplified system state dominated by autecological factors. The system has no internal buffering, and it is stable only as long as the external energy source, based on fossil fuel, lasts. Even if high levels of cultural input became feasible in forestry an unlikely eventuality, commitment to genetic 'uniformity' seems unwise to me for two basic reasons. First, cultural treatments are poorly suited to protect populations against unpredictable, e.g. temporal environmental variation (Allard & Bradshaw 1964). Second, the track record of pest control in forests through approaches such as spraying, has not been good.

The relation between stability and diversity of ecosystems is a subject of considerable debate (see Goodman 1975 for a review), much of which stems from an inadequate definition of both diversity and stability. If we define buffering capacity, like Allard & Bradshaw (1964), as 'stability in those aspects of phenotype, especially yield and quality, that are important economically', the role of genetic diversity seems incontrovertible (Allard & Bradshaw 1964; Edmunds & Alstad 1978; Schaal & Levin 1976; Clausen & Hiesy 1958; Mitton 1978).

Populations may be buffered in two ways, individually and as a population. In the former, buffering is a property of individual organisms, whereas population buffering 'arises in interactions among different coexisting genotypes' (Allard & Bradshaw 1964). To the extent that population buffering is important, any factor which narrows the genetic base of a

population carries with it the risk of decreasing that population's ability to absorb environmental change. Very little research among tree species bears on this question. Owino (1977) concluded that eleven sets of loblolly pine families were average to below average in genotypic stability, i.e. buffering capacity. Significantly, the study showed no difference in the buffering capacity of wide and local crosses, suggesting that heterozygosity did not influence genotypic stability. I found fifty lodgepole pine families from five populations to vary considerably in genotypic stability (unpublished data) and in stress resistance (Perry et al. 1978), suggesting that population buffering may be important in this species.

Does a commitment to genetic diversity in forest stands necessarily imply losses in yield? I think not. Growth in the ideotypic community might be enhanced through three modes: structure in space, structure in time and what I will call 'process complementation'. Gordon (1975) suggested that 'efficient occupancy of space allocated to each individual in a stand becomes the criterion by which genotypes should be chosen for intensive culture'. Mixtures including at least one shade-tolerant species hold promise. Alan B. Berg (School of Forestry, Oregon State University, Corvallis 1978, personal communication) planted western hemlock beneath a thinned stand of fifty-year-old Douglas fir; the hemlock is growing rapidly and growth of the Douglas fir has not decreased detectably. Niche separation in the rooting zone has been found in successional annuals (Parrish & Bazzaz 1976), and it may play a role in decreasing competition among tree genotypes as well.

Resources can be partitioned in time as well as space. This should manifest itself as a differential growth pattern either in one growing season or across a span of several years. Seasonal phenology shows considerable genetic variation, both between species which occupy the same site (Marks 1976; Parrish & Bazzaz 1976) and at the family level within populations (Kaufman 1977; Perry 1978); however, it has not been established as representing competition avoidance. Delayed bud set, especially at high elevations or latitudes obviously carries risk. However, individuals native to severe climates may have considerable frost tolerance, even during periods of active growth. I have seen actively growing lodgepole pine seedlings unaffected by temperatures well below freezing. In any event, evolution has certainly used the actuarial approach of Wareing & Matthews (1971), balancing risk of loss against potential gain. In at least some species, families vary in long-term growth patterns (Namkoong & Conkle 1976; Perry 1978). As in the case of seasonal variation, however, any selective advantage this might confer through competition avoidance is yet to be demonstrated.

Process complementation is the enhancement of some rate

limiting step or process within ecosystems. The most pertinent example is nutrient cycling. Many ecologists believe that mixed forests maintain a higher soil fertility than monocultures (cf. Powers 1974). Conifers and other species, e.g. buckwheat, which exude relatively large amounts of acids, are apparently able to obtain nutrients unavailable to other species (Fisher & Stone 1969; McLachlan 1976; Graustein, Cromack & Sollins 1977). Nutrient cycling, however, is generally more efficient in deciduous communities. Mixtures of hardwoods and conifers cycle nutrients more quickly than coniferous monocultures, thereby improving stand productivity (Tappeiner & Alm 1975; Rakhtsyeyenka & Kabashnikana 1975). Thus, the ideotypic community may develop a synergism in nutrient relations, conifers improving the 'pumping' step and angiosperms the cycling, with benefit to both components.

Incorporating nitrogen-fixing species within forest ecosystems will become increasingly important. In Washington, a mixed stand of red alder and Douglas fir had twice the biomass of adjacent Douglas fir monocultures (Miller & Murray 1977). Berg & Doerksen (1975) found that red alder that seeded into a thinned stand of Douglas fir added from 200 to 800 kg/ha N in seventeen years. In our laboratory, we are attempting to select nitrogen-fixing genotypes suited for interplanting in young, pre-commercially thinned conifer stands.

The silvicultural potential of genetically diverse forests as opposed to monocultures will undoubtedly vary with site conditions. That potential cannot be adequately assessed until we have a much fuller understanding of the structure and functions of forest communities. However, it seems likely that, given silviculturalists with knowledge and imagination, the ideotypic community has much to offer forestry.

REFERENCES

- Allard, R.W. & Bradshaw, A.D. (1964). Implications of genotype - environment interactions in applied plant breeding. *Crop Science*, 4, 503-8.
- Axelrod, D.I. (1967). Drought, diastrophism and quantum evolution. *Evolution*, 21, 201-209.
- Barnes, B.V. (1967). Phenotypic variation associated with elevation in western white pine. *Forest Science*, 13, 357-364.
- Berg, A.B. & Soerksen, A. (1975). Natural fertilization of a heavily thinned Douglas fir stand by understory red alder. Oregon State University, Forest Research Laboratory, Corvallis. Research Note 56. 3 pp.
- Bilan, M.V., Hogan, C.T. & Carter, H.B. (1977). Stomatal opening, transpiration and needle moisture of loblolly pine seedlings from Texas seed sources. *Forest Science*, 23, 457-462.

- Bramlett, D.L. & Belanger, R.P. (1976). Fertilizer and phenotypic selection increase growth and flowering of young Virginia pine. *Forest Science*, 22, 461-467.
- Braun, G. (1977a). Causes and criteria of resistance to air pollution in Norway spruce. 2. Reflexive resistance. *European Journal of Forest Pathology*, 7, 129-151.
- Braun, G. (1977b). Causes and criteria of resistance to air pollution in Norway spruce (*Picea abies*). 3. Tolerance of toxic materials (internal resistance). *European Journal of Forest Pathology*, 7, 236-249.
- Brüning, E.F. (1973). Species richness and stand diversity in relation to site and succession of forests in Sarawak and Brunei (Borneo). *Amazoniana*, 4, 293-320.
- Burdon, R.D. (1971). Clonal repeatabilities and clone:site interactions in *Pinus radiata*. *Silvae Genetica*, 20, 33-38.
- Campbell, R.K. (1974a). A provenance-transfer model for boreal regions. Reports of the Norwegian Forest Research Institute, 31, 541-566.
- Campbell, R.K. (1974b). Use of phenology for examining provenance transfers in reforestation of Douglas fir. *Journal of Applied Ecology*, 11, 1069-1080.
- Campbell, R.K. & Sorensen, F.C. (1978). Effect of test environment on expression of clines and on delimitation of seed zones in Douglas fir. *Theoretical and Applied Genetics*, 51, 233-246.
- Cannell, M.G.R. (1976). Shoot apical growth cataphyll initiation rates in provenances of *Pinus contorta* in Scotland. *Canadian Journal of Forest Research*, 6, 539-556.
- Carlson, P.S. & Polacco, J.C. (1975). Plant cell culture techniques and genetic aspects of crop improvement. *Science*, 188, 622-625.
- Claridge, M.F. & Wilson, M.R. (1978). British insects and trees: a study in island biogeography or insect/plant coevolution? *American Naturalist*, 112, 417-456.
- Clausen, J. & Hiesey, W.M. (1958). Experimental studies on the nature of species. IV. Genetic structure of ecological races. Carnegie Institute, Washington D.C. Publication #615. 321 pp.
- Clausen, K.E. (1975). Early results of a yellow birch progeny test. Proceedings IUFRO working party on progeny testing, November 1974. pp. 16-23. Southeastern Forestry Experiment Station, Asheville, North Carolina.
- Covington, W.W. (1975). Altitudinal variation of chlorophyll concentration and reflectance of the bark of *Populus tremuloides*. *Ecology*, 56, 715-720.
- Darlington, C.D. (1939). The evolution of genetic systems. Cambridge University Press, Cambridge. 265 pp.
- Dietrichson, J. (1969). Growth rhythm and yield as related to provenance, progeny and environment. Second World

- Consultation on Forest Tree Breeding, Section 2/3, IUFRO and FAO, Rome.
- Donald, C.M. (1968). The breeding of crop ideotypes. *Euphytica*, 17, 385-403.
- Dykstra, G.F. (1974). Drought resistance of lodgepole pine seedlings in relation to provenance and tree water potential. British Columbian Forest Service, Research Note 62. 9 pp.
- Edmunds, G.F., Jr. & Alstad, D.N. (1978). Coevolution in insect herbivores and conifers. *Science*, 199, 941-945.
- Eickmeier, W., Adams, M. & Lester, D. (1975). Two physiological races of *Tsuga canadensis* in Wisconsin. *Canadian Journal of Botany*, 53, 940-950.
- Elliot, P.F. (1974). Evolutionary responses of plants to seed eaters. Pine squirrel predation on lodgepole pine. *Evolution*, 28, 221-231.
- Eriksson, G., Anderson, S., Eiche, V. & Persson, A. (1976). Variation between and within populations in a provenance trial of *Pinus sylvestris* at Nordanas, lat. 64° 19', long. 18° 09', alt. 400 m. *Studia Forestalia Suecica*, 133, 1-46.
- Falkenhagen, E.R. (1976). Variation in foliar macronutrients of one-year-old Sitka spruce seedlings of ten provenances. *Northwest Science*, 50, 209-212.
- Falkenhagen, E.R. (1977). Genetic variations in 38 provenances of Sitka spruce. *Silvae Genetica*, 26, 67-75.
- Faulkner, R., Fletcher, A.M., Johnstone, R.C.B. & Forest, G.I. (1977). Report on forest research. British Forestry Commission, London. 27 pp.
- Ferrell, W.K. & Woodard, E.S. (1966). Effect of seed origin in drought resistance of Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco). *Ecology*, 47, 499-503.
- Fisher, R.F. & Stone, E.L. (1969). Increased availability of nitrogen and phosphorus in the root zone of conifers. *Soil Science Society of America Proceedings*, 33, 955-961.
- Fowler, D.P. & Morris, R.W. (1977). Genetic diversity in red pine: evidence for low genic heterozygosity. *Canadian Journal of Forest Research*, 7, 343-347.
- Frey, K.J. (1970). Improving crop yields through plant breeding. 'Moving off the yield plateau'. (Ed. by R. Munson) pp. 15-58. Special Publication #20 American Society of Agronomy Madison, Wisconsin.
- Fryer, J.H. & Ledig, F.T. (1972). Micro-evolution of the photosynthetic temperature optimum in relation to the elevational complex gradient. *Canadian Journal of Botany*, 50, 1231-1235.
- Fujimori, T. (1971). Primary productivity of a young *Tsuga heterophylla* stand and some speculations about biomass of forest communities on the Oregon Coast. U.S. Forest Service, Pacific Northwest Forest and Range Experiment

- Station, Portland, Oregon. Research Paper PNW-123. 11 pp.
- Gadgil, M. & Bossert, W.H. (1970). Life historical consequences of natural selection. *American Naturalist*, 104, 1-24.
- Gansel, C.R. & Squillace, A.E. (1977). Geographic variation of monoterpene in cortical oleoresin of slash pine. *Silvae Genetica*, 25, 150-153.
- Gerhold, H.D. (1959). Seasonal variation of chloroplast pigments and nutrient elements in needles of geographic races of scotch pine. *Silvae Genetica*, 8, 105-132.
- Giertych, M.M. (1969). Growth as related to nutrition and competition. Second World Consultation on Forest Tree Breeding, Section 2/4, IUFRO and FAO, Rome.
- Giertych, M.M. (1976). Summary results of the IUFRO 1938 Norway Spruce (*Picea abies* (L.) Karst)) provenance experiment height growth. *Silvae Genetica*, 25, 154-163.
- Giertych, M.M. & Farrar, J.L. (1962). A provenance study of jack pine seedlings. *Silvae Genetica*, 11, 111-114.
- Gillespie, J.H. & Langley, C.H. (1974). A general model to account for enzyme variation in natural populations. *Genetics*, 76, 837-884.
- Gilpin, M., Soule, M., Ondricek, A. & Gilpin, E.A. (1976). Over-dominance and U-shaped gene frequency distributions. *Nature*, 263, 497-499.
- Glenn-Lewin, D.C. (1977). Species diversity in North American temperate forests. *Vegetatio*, 33, 153-162.
- Goodman, D. (1975). The theory of diversity. Stability relationships in ecology. *Quarterly Review of Biology*, 50, 237-266.
- Gordon, J.C. (1975). The productive potential of woody plants. *Iowa State Journal of Research*, 49, 267-274.
- Grant, V. (1963). The origin of adaptations. Columbia University Press, New York.
- Graustein, W., Cromack, K.Jr. & Sollins, P. (1977). Calcium oxalate: occurrence in soils and effect on nutrient and geochemical cycles. *Science*, 198, 1252-1254.
- Hagner, M. (1970a). A genealogical investigation of the annual rhythm of *Pinus contorta* Dougl. and a comparison with *Pinus sylvestris* L. *Studia Forestalia Suecica*, 81, 26 pp.
- Hagner, M. (1970b). The intra-provenance correlation between annual rhythm and growth of single trees of *Pinus sylvestris* L. *Studia Forestalia Suecica*, 82, 34pp.
- Hayes, A.J. (1975). The mode of infection of lodgepole pine by *Crumenula sororia* Karst. and the susceptibility of different provenances to attack. *Forestry*, 48, 99-113.
- Heide, O.M. (1974). Growth and dormancy in Norway spruce ecotypes (*Picea abies*). I. Interaction of photoperiod and temperatures. *Physiologia Plantarum*, 30, 1-12.
- Hendry, L.B. (1976). Insect pheromones: Diet related? *Science*, 192, 143-145.
- Hermann, R.K. & Lavender, D.P. (1968). Early growth of Douglas

- fir from various altitudes and aspects in Oregon. *Silvae Genetica*, 17, 143-151.
- Heslop-Harrison, J. (1964). Forty years of geneecology. *Advances in Ecological Research*, 2, 159-247.
- Hiesey, W.H. & Milner, H.W. (1965). Physiology of ecological races and species. *Annual Review of Plant Physiology*, 16, 203-216.
- Hoffman, D. (1953). Photoperiodism in tree breeding. *Zeitschrift für Forstgenetik und Forstpflanzenzuchtung*, 2, 44-47.
- Holst, M.J. (1974). Performance of Japanese larch and the Dunkeld hybrid larch at Petawawa Forest Experiment Station. *Forestry Chronicle*, 50, 109-110.
- Horn, H.S. (1971). The adaptive geometry of trees. Princeton University Press, Princeton, New Jersey, U.S.A. 144 pp.
- Hoskins, B.B., O'Connor, J.T., Shannon, T.A., Widdus, R. & Danielli, J.F. (1977). Application of genetic and cellular manipulations to agricultural and industrial problems. *BioScience*, 27, 188-191.
- Hunt, R.S. & von Rudloff, E. (1977). Leaf-oil-terpene variation in western white pine populations of the Pacific Northwest. *Forest Science*, 23, 507-516.
- Illingworth, K. (1975). Lodgepole pine provenance research and breeding in British Columbia. *Proceedings of a Symposium on management of lodgepole pine ecosystems*, pp. 47-67. Washington State University Press.
- Irgens-Møller, H. (1968). Geographical variation in growth patterns of Douglas fir. *Silvae Genetica*, 17, 106-110.
- Jenkinson, J.L. (1974). Ponderosa pine progenies: differential response to ultraspecific and granitic soils. U.S. Forest Service, Pacific Southwest Forest and Range Experiment Station, Research Paper PSW-101. 14 pp.
- Karimbayeva, L.Y. & Sizova, T.P. (1977). Effects of root exudates of pine and spruce seedlings on developing mycoflora in rhizosphere of the conifers. *Mikologija i Fitopatologija*, 11, 191-198.
- Karnosky, D.F. (1977). Evidence for genetic control of response to sulfur dioxide and ozone in *Populus tremuloides*. *Canadian Journal of Forest Research*, 7, 437-440.
- Kaufman, C.M. (1977). Growth of young slash pine. *Forest Science*, 23, 217-226.
- Kim, J.H. (1976). Studies on the productivity and the productive structure of the forests: II. Comparison between the productivity of *Pinus rigida* and of *Pinus rigitaeda* plantation. *Korean Journal of Botany*, 19, 85-91.
- Kreikel, H.B., Bagley, W.T., Deneke, F.J., Funseh, R.W., Roth, P., Jokela, J.J., Merritt, C., Wright, J.W. & Williams, R.D. (1976). Geographic variations in *Quercus rubra* in north central U.S. plantations. *Silvae Genetica*, 25, 118-122.
- Ladiges, P.Y. & Ashton, D.H. (1977). A comparison of some populations of *Eucalyptus viminalis* Labill. growing on

- calcareous and acid soils in Victoria, Australia. *Australian Journal of Ecology*, 2, 161-178.
- Lang, K.J., Neumann, P. & Schutt, P. (1971). The effect of seed source and fertilizing on SO₂-sensitivity of *Pinus contorta* seedlings. *Flora*, 160, 1-9.
- Langlet, O. (1967). Regional intra-specific variousness. *Proceedings 14th IUFRO Congress Division III, Section 22-AG22/24*. pp. 423-58. Munich.
- Ledig, F.T. & Clark, J.G. (1977). Photosynthesis in a half-sib family experiment in pitch pine. *Canadian Journal of Forest Research*, 7, 510-514.
- Levin, D.A. (1975). Pest pressure recombination systems in plants. *American Naturalist*, 109, 437-451.
- Levins, R.A. (1968). *Evolution in changing environments*. Princeton University Press, Princeton, New Jersey. 120 pp.
- MacArthur, J.W. (1975). Environmental fluctuations and species diversity. 'Ecology and evolution of communities'. (Ed. by M.L. Cody and J.M. Diamond), pp. 74-80. Belknap Press, Cambridge, Massachusetts.
- Madsen, J.L. & Blake, G.M. (1977). Ecological genetics of ponderosa pine in the northern Rocky Mountains. *Silvae Genetica*, 26, 1-8.
- Marks, P.L. (1976). On the relation between extension growth and successional status of deciduous trees of the northeastern U.S. *Bulletin of the Torrey Botanical Club*, 102, 172-177.
- Marx, J.L. (1973). Photorespiration; key to increasing plant productivity? *Science*, 179, 365-367.
- May, D.S. & Means, K.S. (1977). Chloroplast pigments as units of selection in *Picea engelmannii*. *American Midland Naturalist*, 98, 283-295.
- McLachlan, K.D. (1976). Comparative phosphorus responses in plants to a range of available phosphorus situations. *Australian Journal of Agricultural Research*, 27, 323-341.
- Meinwald, J., Prestwich, G.D., Nakanishi, K. & Kuko, I. (1978). Chemical ecology; studies from East Africa. *Science*, 199, 1167-1173.
- Mergen, F., Worrall, J. & Furnival, G.M. (1967). Genotype environment interactions in 50 sources of jack pine seedlings. *Proceedings 14th Congress IUFRO Division III, Section 22*, pp. 459-466. Munich.
- Miksche, J.P. (1967). Variation in DNA content of several gymnosperms. *Canadian Journal of Genetics and Cytology*, 9, 712-722.
- Miller, J.R., Baker, T.C., Carde, R.T. & Roelefs, W.L. (1976). Re-investigation of oak leaf roller sex pheromone components and the hypothesis that they vary with diet. *Science* 192, 140-143.
- Miller, R.E. & Murray, M.D. (1977). The effects of red alder on

- growth of Douglas fir. U.S. Forest Service. Pacific Northwest Forest and Range Experiment Station, Olympia, Washington, Unpublished manuscript.
- Mitton, J.B. (1978). Relationship between heterozygosity for enzyme loci and variation of morphological characters in natural populations. *Nature*, 273, 661-662.
- Monsi, M., Uchiuima, Z. & Oikawa, T. (1973). Structure of foliage canopies and photosynthesis. *Annual Review of Ecology and Systematics*, 4, 301-327.
- Moral, R. del (1972). Diversity patterns in forest vegetation of the Wenatchee Mountains, Washington. *Bulletin Torrey Botanical Club*, 99, 57-64.
- Morgenstern, E.K. & Roche, L. (1969). Using concepts of selection to delimit seed zones. 2nd World Consultation of Forest Tree Breeding, Section 2/16 IUFRO, August 7-16, Washington, D.C.
- Morgenstern, E.K. & Teich, A.H. (1969). Phenotypic stability of height growth of jack pine provenances. *Canadian Journal of Genetics and Cytology*, 11, 110-117.
- Musselman, R.C., Lester, D.T. & Adams, M.S. (1975). Localized ecotypes of *Thuja occidentalis* L. in Wisconsin. *Ecology*, 56, 647-655.
- Namkoong, G. (1969). Nonoptimal local races. *Proceedings 10th Southern Conference on Forest Tree Improvement*, pp. 149-153. Texas A & M University, College Station, Texas.
- Namkoong, G. & Conkle, M.T. (1976). Time trends in genetic control of height growth in ponderosa pine. *Forest Science*, 22, 2-12.
- Namkoong, G., Usanis, R.A. & Silen, R.R. (1972). Age selected variation in genetic control of height growth in Douglas fir. *Theoretical and Applied Genetics*, 42, 151-159.
- Nasyrov, Y.S. (1978). Genetic control of photosynthesis and improving of crop productivity. *Annual Review of Plant Physiology*, 29, 215-237.
- Nei, M., Fuerst, P.A. & Chakraborty, R. (1976). Testing the neutral mutation hypothesis by distribution of single locus heterozygosity. *Nature*, 262, 491-493.
- Odum, E.P. (1969). The strategy of ecosystem development. *Science*, 164, 262-270.
- Owino, F. (1977). Genotype X environment interaction and genotypic stability in loblolly pine. 2 Genotypic stability comparisons. *Silvae Genetica*, 26, 21-24.
- Parrish, J.A.D. & Bazzaz, F.A. (1976). Underground niche separation in successional plants. *Ecology*, 57, 1281-1288.
- Pauley, S.S. & Perry, T.O. (1954). Ecotypic variation of the photoperiodic in *Populus*. *Journal of the Arnold Arboretum*, 35, 167-188.
- Perry, D.A. (1978). Minimization of intraspecific competition through differential growth patterns in trees.

- Proceedings 8th World Forestry Congress, Jakarta, Indonesia. In Press.
- Perry, D.A. & Lotan, J.E. (1978). Variation in lodgepole pine (*Pinus contorta* var. *latifolia*): Greenhouse response of wind-pollinated families from five populations to daylength and temperature-soil. *Canadian Journal of Forest Research* 8, 81-89.
- Perry, D.A. Lotan, J.E., Hinz, P. & Hamilton, M.A. (1978). Variation in lodgepole pine: family response to stress induced by polyethylene glycol 6000. *Forest Science*. In press.
- Pickett, S.T.A. (1976). Succession: an evolutionary interpretation. *American Naturalist*, 110, 107-119.
- Pimentel, D. & Bellotti, A.C. (1976). Parasite-host population systems and genetic stability. *American Naturalist*, 110, 877-888.
- Powers, R.F. (1974). Mineral cycling in temperate forest eco-systems. Proceedings Northern California Section of the Society of American Foresters. Nov. 7-8, Redding, California and Feb. 20-22, Eureka, California.
- Rakhtseenka, I.N. & Kabashnikava, H.I. (1975). Biological activity of soils under pure and mixed stands of pine and birch during the growing season. *English Abstract in Forestry Abstracts*, 38, 4005. Abstract #3999. 1977.
- Reck, S. (1973). Differences in growth behaviour between Douglas fir provenances. *Forst- und Holzwirt*, 28, 334-6.
- Rechfeldt, G.E. (1974). Local differentiation of populations of Rocky Mountain Douglas fir. *Canadian Journal of Forest Research*, 4, 399-406.
- Roche, L. (1969). A genealogical study of the genus *Picea* in British Columbia. *New Phytologist*, 68, 505-554.
- Rudloff, E. von (1972). Chemosystematic studies in the genus *Pseudotsuga*. I. Leaf oil analysis of the coastal and Rocky Mountain varieties of the Douglas fir. *Canadian Journal of Botany*, 50, 1025-1050.
- Saki, K.I. & Park, Y.G. (1971) Genetic studies on natural populations of forest trees. III. Genetic differentiation within a forest of *Cryptomeria japonica*. *Theoretical and Applied Genetics*, 41, 13-17.
- Sannikov, S.N., Sannikov, N.S. & Grishina, I.V. (1976) Population structure of *Pinus sylvestris* in the Transurals. *Lesovedenie*, 1, 76-81. In Russian. English abstract in *Forestry Abstracts*, 37, 445. Abstract #4952.
- Sarvas, R. (1969). Genetical adaptation of forest trees to the heat factor of the climate. Second World Consultation of Forest Tree Breeding, Section 2/15 August 7-16, Washington D.C. FAO & IUFRO, Rome.
- Schaal, B.A. & Levin, D.A. (1976). The demographic genetics of *Liatris cylindracea* Michx. (Compositae). *American Naturalist*, 110, 191-206.

- Schmidt-Vogt, H. (1971). Wachstum und Wurzelentwicklung von Schwarzerlen verschiedener Herkunft. Allgemeine Forst- und Jagdzeitung, 142, 149-155.
- Shaw, G.C. & Little, C.H.A. (1977). Natural variation in balsam fir foliar components of dietary importance to spruce budworms. Canadian Journal of Forest Research, 7, 47-53.
- Simpson, G.C. (1975). Review of A.V. Yaklovov. Variability of mammals. Science, 189, 987-988.
- Sindelar, J. & Hochmut, R. (1972). Variability in the occurrence of some insect pests on various provenances of European larch (Larix decidua Mill). Silvae Genetica, 21, 86-93.
- Slatyer, R.O. & Ferrar, P.J. (1977). Altitudinal variation in the photosynthetic characteristics of snow gum, Eucalyptus pauciflora Sieb. ex Spreng. III. Effects of growth temperatures under controlled conditions. Australian Journal of Plant Physiology, 4, 289-299.
- Smith, W.H. (1976). Character and significance of forest tree root exudates. Ecology, 57, 324-331.
- Squillace, A.E. & Silen, R.R. (1962). Racial variation in ponderosa pine. Forest Science Monographs, 2, 27.
- Stearns, S.C. (1976). Life history tactics: a review of the ideas. Quarterly Review of Biology, 51, 3-47.
- Stern, K. & Roche, L. (1974). Genetics of forest ecosystems. Springer Verlag, New York. 330 pp.
- Sziklai, O., El-Lakany, M.H. & De-Vescovi, M.A. (1976). On the clinal variability in nuclear characteristics of Douglas fir, its possible causes and applications. Egyptian Journal of Genetics and Cytology, 5, 146-152.
- Tappeiner, J.C. & Alm, A.A. (1975). Undergrowth vegetation effects on the nutrient content of litterfall and soils in red pine and birch stands in northern Minnesota. Ecology, 56, 1193-1200.
- Thielges, B.A. (1972). Intraspecific variation in foliage polyphenols of Pinus (subsection sylvestris). Silvae Genetica, 21, 114-119.
- Thoday, J.M. & Boam, T.B. (1959). Effects of disruptive selection. II. Polymorphism and divergence without isolation. Heredity, 13, 205-218.
- Tigerstedt, P. (1973). Studies of isoenzyme variation in marginal and central populations of Picea abies. Hereditas, 75, 47-60.
- Vaartaja, O. (1959). Evidence of photoperiodic ecotypes in trees. Ecological Monographs, 29, 92-111.
- Van den Driessche, R. (1977). Survival of coastal and interior Douglas fir seedlings after storage at different temperatures, and effectiveness of cold storage in satisfying chilling requirements. Canadian Journal of Forest Research, 7, 125-131.
- Van den Driessche, R. & Webber, J.E. (1975). Total and soluble nitrogen in Douglas fir in relation to plant nitrogen

- status. Canadian Journal of Forest Research, 5, 580-585.
- Vogl, M., Schönbach, H. & Hadicke, E. (1968). Experimentelle Untersuchungen für relative Rauchharte im Rahmen eines Provenienzversuchs mit der japanischen Larche. Archiv für Forstwesen, 17, 101-115.
- Voute, A.D. (1964). Harmonious control of forest insects. International review of forest research I (Ed. by J.A. Romberger and P. Mikola). pp. 325-83. Academic Press, New York.
- Wareing, P.F. & Matthews, J.D. (1971). Physiological and genetical factors determining productivity of species. Proceedings 15th IUFRO Congress, Gainesville, Florida. pp. 136-43.
- Wearstler, K.A. & Barnes, B.V. (1977). Genetic diversity of yellow birch seedlings in Michigan. Canadian Journal of Botany, 55, 2778-2788.
- Wells, O.O. (1964). Geographic variation in ponderosa pine. II. Correlations between progeny performance and characteristics of the native habitat. Silvae Genetica, 13, 125-132.
- Wells, O.O. (1966). Variation in rust resistance among pine seed sources and species in a Mississippi planting. Forest Science, 12, 461-463.
- Wells, O.O. & Snyder, E.B. (1976). Longleaf pine half-sib progeny test. Forest Science, 22, 404-406.
- Wells, O.O. & Wakely, P.C. (1970a). Variation in long leaf pine from several geographic sources. Forest Science, 16, 28-42.
- Wells, O.O. & Wakely, P.C. (1970b). Variation in shortleaf pine from several geographic sources. Forest Science, 16, 415-423.
- Wilson, D. (1972). Variation in photorespiration in Lolium. Journal of Experimental Botany, 23, 517-524.
- Woessner, R.A., Davey, C.B., Crabtree, B.E. & Gregory, J.C. (1975). Nutrient content of the above-ground tissue of 12-week old loblolly pine intraprovenance and interprovenance crosses. Canadian Journal of Forest Research, 5, 592-598.
- Wright, E. & Ching, K.K. (1962). Effect of seed source on mycorrhizal formation on Douglas fir. Northwest Science, 36, 1-6.
- Wright, J.W. (1973). Genotype-environment interaction in north-central U.S. Forest Science, 19, 113-124.
- Wright, J.W. (1976). Introduction to forest genetics. Academic Press, New York. 463 pp.
- Wright, J.W., Wilson, L.F. & Bright, J.N. (1975). Genetic variation in resistance of Scotch pine to Zimmerman pine moth. Great Lakes Entomologist, 8, 231-236.
- Zavarin, E., Critchfield, W.B. & Snajberk, K.L. (1969). Turpentine composition of Pinus contorta x Pinus banksiana hybrids and hybrid derivatives. Canadian Journal of Botany, 47,

1443-1453.

Zobel, D.B., McKee, A., Hawk, G.M. & Dyrness, C.T. (1976). Relationships of environment to composition, structure, and diversity of forest communities of the central western Cascades of Oregon. *Ecological Monographs*, 46, 135-156.

THE EXPLOITATION OF GENETIC VARIATION BY SELECTION AND BREEDING.

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SUMMARY

A brief historical review is provided of factors leading to the plus tree concept; this is based on observations on crown and stem-form characters. Most breeding programmes are concerned with wood production in which volume, stem-form, branching and wood density are the most important traits. Problems of multiple-trait selection and selection indices are discussed against the background problems of time, physical available resource and breeding strategy. Methods of indirect selection are unsuitable for plus tree selection.

Heritability values for specified traits and species and their limitations are discussed together with some of the main reasons why responses to phenotypic selection have been low in the past. Response to genotypic selection, based on sexually and asexually produced planting material is generally high for form but not vigour.

Reliable juvenile-mature correlations in progenies are of great potential value to the breeder who seeks to maximize gain per unit of time. At present there are very few progeny tests old enough to enable the breeder to do this and most evidence on timber volume production is based on provenance test data. Some of the dangers to be expected in predicting future volume production are highlighted and the value of data obtained from seedling plants raised under controlled or semi-controlled environments will be mainly related to factors such as early-frost susceptibility and the ability to develop, and amounts of, free growth.

The value, use and problems associated with the

production of inter- and intra-specific hybrids are discussed in addition to a brief reference to the commercial production of seed from orchards.

The value and uses of vegetatively produced planting material are described and attention is drawn to the problems of selecting young plant material and predicting performance from the aspects of plant shape and vigour. Mixed-cloned families based on recreated hybrids from single-pair matings with known superior performance values are likely to provide a satisfactory way of getting genetic improvement quickly into the forest.

RÉSUMÉ

Bref historique des facteurs qui ont amené le concept de 'l'arbre plus'; celui-ci est basé sur l'observation des caractéristiques de la cime et de la forme du tronc. La plupart des programmes d'amélioration concernent la production du bois, dont les caractères les plus importants sont le volume, la forme du tronc, l'aspect des branches et la densité du bois. Les problèmes de sélection selon plusieurs caractéristiques et les indices de sélection sont discutés en tenant compte des problèmes de temps, des ressources physiques disponibles et des stratégies d'amélioration. Des méthodes de sélection indirecte ne conviennent pas à la sélection 'd'arbres plus'. L'exposé traite aussi de l'hérédité de certains caractères et de certaines espèces et leurs limitations, ainsi que certaines des raisons principales qui expliquent les déboires dans le passé d'une sélection phénotypique. Les résultats d'une sélection génotypique, basée sur des individus produits de façon sexuée et asexuée sont, en général, favorables quant à la forme, mais mauvais quant à la vigueur de l'individu.

Des bonnes corrélations entre les stades juvéniles et adultes sont d'une importance capitale pour celui qui cherche à améliorer le rendement par unité de temps. En ce moment il y a encore très peu de tests juvéniles ayant assez de recul et qui permettraient à l'améliorateur d'établir ces relations, et la plupart des résultats sur la production en volume est actuellement basée sur les résultats

des tests juvéniles. Certains des dangers auxquels on peut s'attendre dans la prédiction de la production sont mentionnés. Les résultats obtenus avec des plants cultivés en milieu contrôlé ou semi-contrôlé portent essentiellement sur la résistance vis à vis des gelées précoces et sur les facultés de développement et quantité de la croissance libre.

On traite aussi de l'usage et des problèmes associés à la production des hybrides inter- et intra-spécifiques. On se réfère aussi, brièvement, à la production commerciale de graines provenant des vergers à graines.

On décrit aussi la valeur et l'utilité des individus produits végétativement et l'on fera remarquer les problèmes de sélection des jeunes individus et la prédiction de leur performance en tenant compte de la forme et de la vigueur des plants. Des peuplements formés d'un mélange de clones de familles basés sur des hybrides créés à partir de croisements entre couples de performances supérieures connues, seront certainement à même d'apporter à la forêt une amélioration génétique rapide.

ZUSAMMENFASSUNG

Es soll hier, basierend auf Kronen- und Stammformcharakteristiken, ein kurzer historischer Abriss über die Faktoren gegeben werden, die zur 'Plus-Baum'-Idee geführt haben. Die meisten Zuchtprogramme befassen sich mit der Holzproduktion, wobei Volumen, Stammform, Astigkeit und Holzdichte die wichtigsten Merkmale sind. Die Probleme, die in Bezug auf die Auswahlkriterien bei der Auswahl nach mehreren Merkmalen entstehen, sollen vor dem Hintergrund solcher Probleme wie Zeit, verfügbare Mittel und Anzuchtverfahren diskutiert werden. Methoden der indirekten Auswahl sind für die 'Plus-Baum'-Auswahl ungeeignet.

Zur Diskussion gestellt werden 'Vererbungswerte' für verschiedene Merkmale und Baumarten und die Grenzen ihrer Aussage, sowie einige der Hauptgründe, warum die Wirkung der Auswahl von Phänotypen bisher so gering war. Die Wirkung der Auswahl von Genotypen, die aus sexuell und asexuell produziertem Pflanzenmaterial stammen, ist im allgemeinen

sehr gut, wenn es um die Bauform und weniger gut, wenn es um die Wüchsigkeit geht. Zuverlässige Daten über die Jugend-Reife Verhältnisse bei der Nachkommenschaft sind von grossem potentiellen Wert für den Züchter, der eine zeitliche Gewinnmaximierung anstrebt. Gegenwärtig gibt es nur wenige, genügend alte Nachkommenschaftsprüfungen, die das dem Züchter ermöglichen könnten. Die meisten Zahlen über die Masse der Holzproduktion stützen sich auf Werte, die von Provenienzprüfungen abgeleitet werden. Es wird auf die Gefahren hingewiesen, die die Voraussage zukünftiger Wuchsleistung beinhaltet. Fraglich ist vor allem, inwieweit Daten zuverlässig sind, die von Sämlingen aus geschützter oder halbwegs geschützter Umgebung stammen. Dies ist problematisch vor allem im Hinblick auf Frühfrostempfindlichkeit und in Bezug auf die Fähigkeit für 'freies Wachstum' (oder Johannistriebbildung) und dessen Quantität.

Diskutiert werden auch Wert, Nutzen und Probleme in Zusammenhang mit der Erzeugung von inter- und intraspezifischen Hybriden. Darüberhinaus wird auf die kommerzielle Produktion von Samen aus Baumpflanzungen kurz hingewiesen.

Der Wert und die verschiedenen Verwendungsmöglichkeiten von vegetativ produziertem Pflanzenmaterial wird diskutiert unter besonderer Berücksichtigung der Probleme, die bei der Auswahl jungen Pflanzenmaterials entstehen, und wie aufgrund von Form und Wüchsigkeit der Pflanzen ihr späteres Verhalten vorausgesagt werden kann. Mit Hilfe gemischt-klonischer Familien aus neu gezüchteten Hybriden, die aus Einzelpaaren hervorgegangen sind und die hervorragende Verhaltenseigenschaften aufweisen; sollte es möglich sein, schnell eine genetische Verbesserung des Waldes zu erreichen.

INTRODUCTION

Selection and breeding of individual forest trees on a scientific basis began in 1924 and lagged behind similar work on many other crop plants. For example, rice was in cultivation and influenced by selection for over 5000 years and has been systematically bred since 1905. Undoubtedly the delay to the start of tree breeding was due to the long breeding cycle of most tree species, physical difficulties of

artificially pollinating flowers borne high above the ground or, in some cases working with small hermaphrodite flowers, e.g. Eucalyptus spp., and difficulties of cheaply and reliably propagating old trees by rooting cuttings or other methods of vegetative propagation. Where vegetative propagation is easy, it has been exploited and used to advantage, for example extensive clonal plantation forests were begun with vegetatively reproduced Cryptomeria japonica in Japan over 400 years ago (Toda 1974).

THE PLUS TREE CONCEPT

Opperman (1908) published his findings that undesirable shape in stem- and crown-form is inherited and Nicolai (1932) suggested the selection of special seed trees in Pinus sylvestris, which he termed 'elite', from which separate seed collections should be made and later progeny performances recorded. One year later Bornebusch (1933), writing on beech breeding, recommended one-parent progeny-tests to estimate breeding values and Larsen (1934) introduced the concept of the clonal seed orchard thus: "I strongly urge therefore, taking up vegetative propagation and in conjunction with experiments on artificial pollination, the establishment of seed plantations for the supply of seed for practical use".

The term 'plus tree' appears to have been introduced first around 1950 by the Royal Board of Private Forestry of Sweden (Anon.1951). Before this elite tree was used as a synonym, a fact which has led to much confusions in the literature. Currently accepted definitions of these terms are:

Plus tree: a phenotype judged (but not proved by tests) to be unusually superior in some quality or qualities, e.g. exceptional growth rate relative to site, desirable growth habit, high wood quality, exceptional apparent resistance to disease, insect attack or other adverse locality factors.

Elite tree: one that has been shown by testing to be capable of producing progeny with superior qualities and is, therefore, of superior genotype (Anon. 1971).

In a later publication, reporting on some early progeny test results, Larsen (1947) suggested that tree phenotypes are more environmentally conditioned than those of other crop plants, and also, because trees are cross-pollinated and are highly heterozygous, progeny testing would be essential to estimate the genotype for certain characters. Undoubtedly he had been convinced from observation that some characters, for example, crown-shape and stem-form, were highly inherited and that grafted trees would give an indication of genotype but not necessarily enough to form definite opinions of an individual's suitability for breeding. Lindquist (1948) supported Larsen's proposal and recommended that mother trees for use in elite seed plantations (seed orchards) should be

the "most extreme plus tree variations", which he suggested should be trees with an acceptable type of branching and crown and superior stem-diameter, height growth and flower production. The criteria for selection were described for several species, and for Scots pine he suggested that selected trees should contain fifty percent more volume than their three nearest dominant trees.

In the period 1950-1970 many countries began tree breeding programmes. Most had the main objective of increased yields of high-quality wood through multiple-trait selection as described by e.g. Stonecypher (1970) and Dorman (1976). Others were specifically aimed at improvement in yield or quality of other products, for example, pine resin yields in southeastern U.S.A. (Squillace & Dorman 1961). Plus tree selection, which is a form of mass selection, was an important aspect of these programmes and the criteria for selection varied according to species, age of crop, objectives of the breeding work and available resources (Mathews & McLean 1957; Mitchell 1956; Vidakovic 1966; Squillace 1968; Morgenstern et al. 1975). It soon was realized, that a high selection-intensity for several traits was rarely feasible, particularly when traits were independently inherited, or negatively correlated and, which was often the case, controlled by several gene-pairs (Mergen 1959; Campbell 1964).

PLUS TREE SELECTION CRITERIA

Problems arise in describing the characteristics of plus trees which are usually related to growth rate and wood quality, and in establishing a classification system in which points are awarded for the degree of excellence of each trait in the plus tree. Traits are weighted according to their economic importance (Anderson 1966). Independent culling levels are often chosen in which a level of merit for each trait is established. Individuals falling below this level are excluded regardless of their superiority in other traits. Cech (1959) investigated five methods of selection used in the southern U.S.A. and formed the opinion that the estimator is more important than the method and, as might be expected, that numerical scoring systems are more effective than subjective, descriptive systems. In even-aged plantations the candidate plus tree is often compared with neighbouring dominants for superiority by measurements or by scoring (Fletcher & Faulkner 1972). In natural forests, where age and espacement between trees may be quite variable and where there may be family relationships and risks of inbreeding between candidate and adjacent comparison trees, such comparisons are less valuable. For this reason Ledig (1974) suggests that in wild populations there may be more gain from individual tree selection than from comparative methods.

In many animal and plant breeding programmes selection

indices have been widely used to determine the economic value of a new cultivar. The procedure entails the combination of the economic values of each trait, their heritabilities and correlations with other traits of economic importance (Stern 1964). This is relatively easy for those agricultural crops about which much is known of their genetic and economic attributes. But for the tree breeder, with limited and not very reliable information on genetic parameters, the problem will remain largely academic, the more so when coupled to the problem of giving probable economic weightings for material to be marketed twenty-five to seventy-five years ahead. Attempts to use selection indices for tree species have been made (van Buijtenen & Horne 1960; Baradat et al. 1970; Bunn 1975). The technique may, in the course of time and in some circumstances (Namkoong 1976), replace the method of independent culling levels currently practised by most breeders but this replacement will depend on the accuracy of estimates of genetic variance and covariance matrices (Williams 1962). Tandem-selection, in which selection is practised on one trait per generation, followed by selection of all traits over several further generations, is impracticable for forest trees because of the time element.

If they can be established, strong phenotypic correlations between traits can be useful, particularly when one trait is easy to assess and the other difficult. However, phenotypic correlations are a function of genetic and environmental correlations and the strength of narrow-sense heritabilities obviously plays an important interactive role. Since estimates of genetic correlations between characters in older trees can only be established on the basis of growing families of known origin to near-rotation age, it is unlikely to feature in breeding programmes for all but the fastest growing species. Of particular interest to breeders are phenotypic correlations between stem volume and branching characteristics, such as numbers per whorl and their diameter, as investigated in Pseudotsuga menziesii by Campbell (1961, 1963).

Maximum genetic gain per unit of time is a primary objective of most breeding projects. It is dependent upon the genetic variance, estimated breeding values as expressed by the heritability, the selection differential i.e. the difference between the population mean and the average of the selected individuals (Stern 1964), and the length of breeding cycle and time at which future progeny performances can be reliably predicted. Burdon & Shelbourne (1972) pointed out that for a given investment in a breeding programme, selection differentials must be maximized in order to maximize genetic gain. They showed that selection differential increases curvilinearly with the ratio of individuals screened to those selected. Thus the increase in selection differential falls

rapidly in relation to the additional effort required. An accurate appraisal of breeding strategies depends on detailed calculations of the expected gain for varying proportions of the population selected for traits, each of which has different heritabilities. At present few breeders have sufficiently accurate information on the selection intensities used in their programmes on which to base estimates of genetic gain.

Selection on the basis of factors influencing growth, such as photosynthetic rate, particularly at low temperatures, higher enzyme activity, leaf-area index, dormancy control mechanisms, seasonal patterns of extension and radial growth, and ageing is complex (Wareing 1964; Wareing & Matthews 1971) and cannot be directly practised in plus tree selection. In future such criteria may play a useful role in the selection of families in the seedling and juvenile stages of growth (Richardson 1960; Ledig 1975, 1976; Cannell, Thompson & Lines 1976).

RESPONSE TO PHENOTYPIC SELECTION.

Response to phenotypic selection can only be determined from progeny or clonal tests from which estimates of the heritabilities of the characters under selection can be obtained. Heritability values are not constant for a given character since they are the ratio of additive genetic variance V_{AG} to total variance, i.e. environmental variance V_E , non-additive genetic variance V_{NA} and V_{AG} itself.

$$\text{Heritability} = \frac{V_{AG}}{V_E + V_{NA} + V_{AG}}$$

For this reason heritability values may vary mainly according to the site conditions under which a progeny test is conducted, within-plot competition and ability to compete between trees and the age of the material under test.

The value of phenotypic selection to a breeder is greatest when a trait is under the control of a single or very few genes and when heritability of the traits to be improved is moderate to high and persists from youth through to the end of the crop rotation. This has been shown to be generally the case in numerous conifers for tree-form characters such as stem straightness, branch angle and length, and wood characters such as tracheid length, cell wall thickness and spiral grain (Ehrenberg 1970; Faulkner 1969; Harris 1970). In contrast, tree vigour, expressed by stem diameter and height growth, generally has a low, narrow-sense heritability indicating polygenic control of the trait or that environmental factors may play an over-riding role in tree growth rate. Forest sites are intrinsically variable and before 1945 were seldom ameliorated by treatments such as drainage, deep cultivation and fertilization. For this reason

plus tree selection in old crops, even when very high selection intensities were practised, often proved unrewarding. Where difficult site conditions have been ameliorated or where sites are inherently more uniform, selection for vigour offers higher prospects for success. For these reasons it can be assumed that as improved silvicultural techniques for the rapid establishment of plantations are developed and put into practice, so heritability values will be raised.

From 5-10% of plus trees selected in even-aged plantations frequently show height gains of about 15% in progeny tests. Somewhat lower height gains are reported from plus trees selected in older crops. This may be due to the fact that they were established on variable sites and raised under silvicultural regimes very different from those currently practised or, alternatively, that inaccurate age determinations were made on plus trees in natural stands, perhaps compounded by microsite variation which favoured the rapid establishment and fast development of certain individuals.

A further complication affecting plus tree selection can be the year when flowering begins and the periodicity and amount of flowering thereafter. It is well-known that heavy seed and pollen production adversely affects diameter growth and that trees which grow extremely well to normal rotation age with moderate flower crops, may later fail to meet selection standards if they produce bountiful and regular seed crops in relation to their neighbours when approaching senescence. For this reason plus trees should only be selected in crops up to but not beyond the expected rotation age, when grown in plantations under current silvicultural practices.

Finally, plus trees should only be selected in large plantations derived from extensive seed collections involving many parents. This minimizes the risk of relatedness and the undesirable consequences of inbreeding which may only become manifest in subsequent generations.

RESPONSE TO GENOTYPIC SELECTION

The majority of well-designed progeny tests have been established since 1960 and reliable information on heritability values for some characters is now beginning to emerge. Most relates to characters which are easily assessed in young trees, such as height and diameter growth, frost-hardiness, resistance to certain pests and diseases, stem form and branching characters (Illy 1966; Ehrenberg 1963, 1966). Regression of parent tree/family data has been attempted by only a few workers, e.g. Illy (1967). Strong correlations for vigour between parent tree and progeny are unlikely and are rarely strictly comparable because of ageing and local differences in competition and site treatments.

Similarly crown-shape is strongly influenced by competition and stand management treatments, but stem and branch straightness have been strongly correlated in young progeny material.

Several workers have established correlations between the performances of vegetatively propagated ramets, both grafts and rooted cuttings, of plus trees and their parents but these are unlikely to be of much practical value since age of parent, method of raising cuttings, origins of the scionwood or cuttings on the parent tree, precocity in flowering, ease of rooting and grafting and speed of asserting apical dominance in the ramet can all have a profound influence on the shape of the propagated material and its growth performance. Wellendorf (1970) attempted to establish parent/graft correlation for Pinus sylvestris and established a relationship for height.

JUVENILE-MATURE CORRELATIONS

To maximize genetic gain per unit of time tree breeders have to shorten the generation cycle and, therefore, reliable predictions of future performances of individuals, families and clones are essential (Squillace & Gansell 1974). Theoretical ways for making predictions have been suggested by Nanson (1967, 1976).

Due to the long rotation of most forest crops there are very few published data on juvenile-adult correlations for many commercially important characters: most information has been gathered for tree height and wood quality characters from provenance experiments rather than progeny tests. Western European provenance experience shows that height 5-10 years after planting, when trees are about 1.5 m tall and have recovered from planting shock and are not affected by weed competition, is strongly correlated with total wood volume production and height at 25-60 years (Nanson 1976). Selection of 'super seedlings' with very high selection intensities (1 in 200,000) is not a reliable method for predicting future height growth in pines (Ellestein 1955; Callaham & Duffield 1962) and may be more closely linked with initial seed size and very rapid germination. In Britain, glasshouse-grown two-year-old Picea sitchensis seedlings provided correlations of $r=0.5$ to $r=0.6$ with forest-grown plants, one to four years after planting. In a typical Pinus sylvestris progeny test consisting of sixty-one open-pollinated progenies, the correlation coefficient matrix for height was:

	1st yr				
1st yr	1.000	3rd yr			
3rd	0.832	1.000	6th yr		
6th	0.543	0.849	1.000	10th yr	
10th	0.506	0.755	0.962	1.000	15th yr
15th	0.409	0.671	0.860	0.942	1.000

Toda (1974) struck a note of caution in predicting longterm future performances from young plant material and cited a commercially used Cryptomeria clone in Japan which grew very rapidly for only the first twenty years, after which growth declined. He also reported that stem diameter is a better predictor of volume performance than height growth for pine, spruce and larch up to 30-40 years old. Namkoong & Conkle (1976) reported good height growth correlations between ages three and twenty-nine for seven provenances of Pinus ponderosa in a twenty-nine year experiment. Family variances within provenances were often smaller than environmental variances; differences were not well correlated between earlier and later phases of growth and sometimes correlations were negative. Typical sigmoid curves were reported, indicating exponential growth after planting followed by constant growth and then declining growth towards maturity - probably due to more intense competition or perhaps the onset of heavy seed production. Family average growth curves were fairly close up to twenty years, indicating that family differences during the adolescent stage are not accumulated and for this reason Namkoong suggested that changes in growth rate may be better selection criteria than total size.

Early test on which to base height growth predictions are of course less reliable for crops grown on sites subjected to episodic or unpredictably extreme climatic conditions, for example conditions favouring heavy accumulations of wet snow leading to branch breakage, exceptional drought, frosts, hurricanes, hailstorms, disease and insect attacks or various combinations of these hazards. Results from early tests on first rotation crops of exotic species and of indigenous species with origins other than local ones, must always carry a greater risk of unreliability than tests based on indigenous materials of local origin.

Zobel & Rhodes (1956) working with individual trees of Pinus taeda established highly significant correlations between wood specific gravity of the juvenile core (first eight rings around the pith core) and mature tree wood; and between wood specific gravity of stem sections and adjacent branch sections. This suggests that estimates of young trees could be obtained from a tree branch - an obvious advantage in progeny test work where trees cannot be sacrificed. By predicting potential rate of cambial activity from mean tracheid diameters and leaf characters together with ring widths in first year conifer seedlings, Denne (1976) suggested that rate of wood production could be separated from length of growing-season. Wedel, Zobel & Shelbourne (1967) investigating knot-wood in 7-8 year old Pinus taeda, reported high uniformity in branch diameter, number of branches per whorl, branch angle and knot volume percent within open-pollinated

families and also significant correlations between branch-diameter, bole diameter and the number of branches, and branch diameter and branch angle. Branch diameter increased with increasing bole diameter, steeper branch angles and a decreasing number of branches.

The use of fully or partially controlled glasshouses is valuable for raising young plants of species which show responses to photoperiod. Such plants can be periodically measured to assess growth responses to varying daylengths from which plant susceptibility to early and late frosts can be predicted (Ekberg et al. 1976). In pines, patterns of shoot growth and their adaptive roles have been described by Lanner (1976), who mentions that 'free' growth, the precocious expansion of new buds or the supplementary initiation and emergence of foliage after the spring flush, beyond the seedling stage is related to mildness of climate; for obvious reasons flexibility in shoot growth behaviour can allow great gains in growth rate. In young plants of some *Picea* species 'free' growth after the spring flush contributes to total height; it is affected by photosynthesis and temperature and decreases with age (Pollard & Logan 1976). Different combinations of these variables in different years and localities could account for some of the more variable results between years for some progeny performances and so reduce the value of early testing for some species.

Branch angle, stem circularity, stem straightness and branch numbers per whorl are all tedious to assess and few research workers have made repeated assessments of these characters over a period of time. Ehrenberg (1970) reports fairly good correlations of stem and branching characters in young and older pines.

In clonal material correlations between stock plant and ramet for stem and crown characters are normally very good, as evidenced by the ease of early visual recognition of some poplar clones and of conifer garden 'cultivars' when grown on a wide variety of sites.

Reliable early tests for disease resistance have not been developed on any scale, except for resistance to *Cronartium fusiforme* in *Pinus elliottii* and *P. taeda*, which can be tested by using 3-5 year old seedlings (Griggs & Dinus 1977); *Ceratocystis ulmi* on elms and resistance to *Aplano bacterium populi* in poplars. It seems probable that biochemical methods are likely to be used to a greater extent in the future for predicting resistance to certain insects and diseases.

THE PRODUCTION OF HYBRIDS

Most countries include a hybridization programme in their breeding strategies. This is often at the inter-specific level, for example *Larix kaempferi* x *L. decidua* and between *Populus* species in many European and American countries;

Eucalyptus species in Australia; Pinus rigida x P. taeda in Korea; and between five-needled pines in America. F1 hybrid vigour is a frequent but rarely attained objective and resistance to diseases or climatic injury is often a more important reason. Other programmes are based on intra-specific (provenance) hybridization. In Scandinavia there is much interest in the production of hybrids between Scandinavian and eastern European sources of Picea abies and in Britain between coastal and inland origins of Pinus contorta in order to develop varieties which are both vigorous and stable under infertile and exposed situations. In the course of time it is expected that outstanding hybrids derived from single pair matings will be used commercially, as is already the case with poplars. When vegetative propagation presents few difficulties, the mass production of hybrids is easy. Most F1 hybrid seed has to be obtained by artificial pollination due to poorly matched flowering times of the parent species. Quite often the seed has a low percentage germination due to a low seed set, or physiological barriers associated with fertilization, adverse effects of pollen handling and storage methods, pollination techniques and unsuitable methods of isolating the female flowers before and after pollination. In conifers seed production from artificial pollinations is usually between ten and fifty percent of that obtained by wind pollination under normal forest or seed orchard conditions.

SEXUALLY DERIVED PLANTING MATERIAL

In the majority of cases forest planting stock is obtained from seed. Before 1940 most forest enterprises used seed from unselected sources, but since then the importance of seed origin (provenance) has been recognized and seed from selected stands of superior phenotype has been more widely used. As a consequence both national and international seed and plant certification schemes have been developed for marketing purposes (Barber 1975).

By combining performance information from progeny tests and information on amount, periodicity sex ratio and dates of flowering of plus and elite parent trees, the tree breeder can design and plan a programme of clonal or seedling orchards for the mass production of seed of improved genetic quality for a variety of planting regions (Weir & Zobel 1975).

VEGETATIVELY DERIVED PLANTING MATERIAL

Vegetatively produced planting stock used either as single or mixed clones, offers a fast method of introducing material of the highest genetic quality into commerce. It has been extensively used for many years for the establishment of poplar plantations throughout the world, for Cryptomeria in Japan (Toda 1974) and on a more limited scale for Pinus radiata in the southern hemisphere. More recently,

vegetatively produced planting stock has been used for Picea abies in West Germany and there are plans to use vegetatively produced, intra-specific hybrids of P. abies more extensively in Scandinavian countries. In Britain Larix x eurolepis hybrids are being produced vegetatively and are likely to be used commercially within the next five years. Grafts are too expensive to produce for use as normal planting stock and current and projected schemes are based on rooted cuttings. Active research and development programmes for micro-propagation, using cell- and tissue- cultures, are to be found in many countries, notably in the U.S.A. and France (Boulay 1977).

Until well-designed long-term tests have been carried out to compare the behaviour of clonal and seedling conifer material, there will always be doubt about the real value and role of vegetatively propagated stock.

In the Pinaceae rootability of cuttings declines rapidly on plants over five years old. Therefore, a decision to accept a parent for clonal work must be made on evidence derived from early tests. As stated earlier, good correlations with future performance on the basis of height growth are seldom attainable until the plant is 5-7 years old, at a time when rootability declines rapidly. This provides an obvious dilemma for the breeder wishing to introduce into commerce large stocks of material from a few, highly selected clones, produced from selected phenotypes in his best families. Furthermore, cuttings satisfactorily rooted from older and therefore larger plants, as in the case of larch (John 1977), will probably behave differently when taken from different parts of the tree due to topophytic (positional and may be irreversible) and cyclophytic (ageing) effects. Both phenomena can result in different degrees of plagiotropic growth, the times taken to achieve orthotropism, earlier seed production and consequent loss of volume growth. In a five-year-old P. radiata experiment, comparing seedlings with cuttings, Sweet & Wells (1974) showed that seedling relative growth rate values, corrected for co-variance on plant size, were higher than those for cuttings. Shelbourne & Thulin (1974) have reported poor repeatability between tests of the same clonal material at the same age.

Kleinschmidt (1974) described a commercial programme for the propagation of Picea abies based on cuttings from a mixture of over 1000 clones. These were derived from selected, open-pollinated families from stands or clonal orchards or from controlled crosses. His predicted gains are suspect, however, on the grounds that selections are made on young families grown in nurseries, where selection may favour trees which are tallest on account of late growth in autumn, original seed size and strong growth responses to favourable nursery conditions. To avoid this problem and to obtain

maximum gain, it is necessary to first test numerous single pair matings and when satisfied as to which are the best combinations, repeat the crosses to provide enough plants for adequate multiplication by vegetative means. Plant mixtures of twenty or more 'cloned families' would be genetically heterogeneous as a mixed population and would produce a more stable output in a range of environments. Such variation should enable trees of different genetic constitution to use the agglomeration of ecological niches effectively on many sites with a lower probability of risk from episodic harmful events.

REFERENCES

- Anderson, E. (1966). The selection of plus trees in Sweden. *Sumarski List*, 1-2, 21-37.
- Anon (1951). Directions for seed collecting and trading in forest seeds and plants. Issued in 1950 by the Royal Board of Private Forestry in Sweden. David Broberg. Stockholm.
- Anon (1971). "Terminology of forest science, technology, practice and products". (Ed. by F.C. Ford-Robertson). Society of American Foresters, Washington D.C.
- Baradat, Ph., Illy, G., Maugé, J.P. & Mendibourne, P. (1970). Sélection pour plusieurs caractères sur indice programmes de calcul. Application à la conduite de verger à graines test de descendance. Compte rendu d'activaté 1970 de l'Association Forêt-Cellulose, 46-69.
- Barber, J.C. (1975). Seed certification. "Seed orchards". (Ed. by R. Faulkner), pp. 143-148. Forestry Commission, London. Bulletin #54.
- Bornebusch, C.H. (1933). Dedanske Bøge Foraedling. Dansk Skovforeningens Tidsskrift, 292-295.
- Boulay, M. (1977). Recherches sur la propagation du Douglas par culture en vitro. Annales de Recherches Sylvicoles 1976. Association Forêt-Cellulose, 83-145.
- Buijtenen, J.P. van & Horne, W.M. (1960). A selection index for aspen based on genetic principles. Progress Report #6. Lake States aspen genetic and tree improvement group meeting, Appleton, Wisconsin, U.S.A.
- Bunn, E.H. (1975). Genetics and tree improvements. Report Forest Research Institute, New Zealand Forest Service 1974. pp. 12-15.
- Burdon, R.D. & Shelbourne, C.J.A. (1972). Breeding populations for recurrent selection: conflicts and possible solutions. *New Zealand Journal of Forestry Science*, 1, 124-193.
- Callaham, R.Z. & Duffield J.W. (1962) Height of selected Ponderosa pine seedlings during 20 years. Proceedings Forest genetics workshop, Macon, Georgia. pp. 11-13.
- Campbell, R.K. (1961). Phenotypic variation and some estimates of repeatability in branching characteristics of Douglas

- fir. *Silvae Genetica*, 10, 109-118.
- Campbell, R.K. (1963). Phenotypic correlation among branch and upper crown attributes in Douglas fir. *Forest Science*, 9, 444-451.
- Campbell, R.K. (1964). Recommended traits to be improved in a breeding program for Douglas fir. Forest Research Note #57. Weyerhaeuer Co., Centralia, Washington, U.S.A.
- Cannell, M.G.R., Thompson, S. & Lines, R. (1976). An analysis of inherent differences in shoot growth within some north temperate conifers. "Tree physiology and yield improvement". (Ed. by M.G.R. Cannell and F.T. Last), pp. 171-205. Academic Press, London and New York.
- Cech, F.C. (1959). Superior tree selection. A comparison of grading systems. Proceedings 5th Southern forest tree improvement conference. pp. 49-52.
- Denne, M.P. (1976). Predicting differences in potential wood production from tracheid diameters and leaf cell dimensions in conifer seedlings. "Tree physiology and yield improvement". (Ed. by M.G.R. Cannell and F.T. Last), pp 283-289. Academic Press, London and New York.
- Dorman, K. (1976). The genetics and breeding of southern pines U.S. Department of Agriculture Forest Service. *Agriculture Handbook*, 471, 339-351.
- Ehrenberg, C.E. (1963). Genetic variation in progeny tests of Scots pine. *Studia Forestalia Suecica*, 10.
- Ehrenberg, C.E. (1966). Parent-progeny relationship in Scots pine (*Pinus sylvestris*). *Studia Forestalia Suecica*, 40.
- Ehrenberg, C.E. (1970) Breeding for stem quality. *Unasylva*, 24, 23-31.
- Ekberg, I., Dormling, I., Erikson, G. & Wettstein, D. von (1976). Inheritance of the photoperiodic response in forest trees. "Tree physiology and yield improvement", (Ed. by M.G.R. Cannell and F.T. Last), pp 207-21. Academic Press, London and New York.
- Ellerstein, B.W. (1955) Selection of pine super seedlings an exploratory study. *Forest Science*, 1, 111-114.
- Faulkner, R. (1969) Some characters of secondary importance to stem straightness in the breeding of conifers. Proceedings 2nd World consultation of forest tree breeding, Washington D.C., 1, 269-283.
- Fletcher, A.M. & Faulkner R. (1972) A plan for the improvement of Sitka spruce by selection and breeding. Research and Development Paper #85. Forestry Commission, London.
- Griggs, M.M. & Dinus, R.J. (1977). Patterns of fusiform rust increase and their implications for selection and breeding. Proceedings 14th Southern Forest tree improvement conference, 43-52.
- Harris, J.M. (1970) Breeding to improve wood quality. *Unasylva*, 24, 32-36.
- Illy, G. (1967). Recherches sur l'amélioration génétique du

- pin maritime. *Annales des Sciences Forestières*, 23, 771-948.
- John, A. (1977). Vegetative propagation of hybrid larch in Scotland. Symposium on Vegetative propagation of forest trees - physiology and practice. Institute for Forest Improvement, Stockholm. pp. 129-136.
- Kleinschmidt, J. (1974) A programme for large scale cutting propagation of Norway spruce. *New Zealand Journal of Forestry Science*, 4, 359-366.
- Lanner, R.M. (1976) Patterns of shoot development in *Pinus* and their relationship to growth potential. "Tree physiology and yield improvement". (Ed. by M.G.R. Cannell and F.T. Last), pp. 245-251. Academic Press, London and New York.
- Larsen, C.S. (1934). Forest tree breeding. Royal Veterinary and Agricultural College Yearbook for 1934, Copenhagen, p. 112.
- Larsen, C.S. (1947). Estimation of the genotype in forest trees. Royal Veterinary and Agricultural Yearbook for 1947, Copenhagen. pp. 87-128.
- Ledig, F.T. (1974). An analysis of methods for the selection of trees in wild stands. *Forest Science*, 20, 2-16.
- Ledig, F.T. (1975). Increasing the productivity of forest trees. "Forest tree improvement - the third decade". Proceedings 24th Annual Forestry Symposium, pp. 189-208. Louisiana State University, Division of Continuing Education, Baton Rouge, U.S.A.
- Ledig, F.T. (1976). Physiological genetics, photosynthesis and growth models. "Tree physiology and yield improvement". (Ed. by M.G.R. Cannell and F.T. Last), pp. 21-54. Academic Press, London and New York.
- Lindquist, B. (1948). Genetics in Swedish forestry. Svenska Skogsvarvdsföreningens Forlag, Stockholm.
- Matthews, J.D. & McLean, C. (1957) Improvement of Scots pine in Britain by selection and breeding. Paper 7th British Commonwealth Forestry Conference, Australia and New Zealand. pp 1-13.
- Mergen, F. (1959). Forest tree breeding research. *Unasylyva*, 13, 129-37.
- Mitchell, A.F. (1956). The selection of plus European larch trees. *Scottish Forestry*, 10, 68-80.
- Morgenstern, E.K., Holst, M.J., Trich, A.H. & Yeatman, C.W. (1975). Plus tree selection. Review and outlook. Department of the Environment, Canadian Forest Service, Publication #1347.
- Namkoong, G. (1976). A multiple index selection strategy. *Silvae Genetica*, 25, 192-199.
- Namkoong, G. & Conkle, M.T. (1976). Time trends in genetic control of height growth in ponderosa pine. *Forest Science*, 22, 1-12.

- Nanson, A. (1967). Modèle théorique pour l'étude des tests précoces. *Biométrie-Praximétrie*, 8, 84-107.
- Nanson, A. (1976). Juvenile-mature relationships mainly in provenance and progeny tests. Proceedings I.U.F.R.O. joint meeting on advanced generation breeding, Bordeaux 1976, pp.99-119. Institut national de la Recherche Agronomique, France.
- Nicolai, F. (1932). Anregung zur Individual- und Rassenzucht. Bericht des Westpreussischen botanisch-zoologischen Vereins, 54, 1-12.
- Opperman, A. (1908). In: Det forstlige forsøgsvæsen i Danmark 2, 29-256.
- Pollard, D.F.W. & Logan, K.T. (1976). Inherent variation in free growth in relation to numbers of needles produced by provenances of *Pinus mariana*. "Tree Physiology and yield improvement". (Ed. by M.G.R. Cannell and F.T. Last), pp. 245-251. Academic Press, London and New York.
- Richardson, S.D. (1960). The role of physiology in forest-tree improvement. Paper at the 5th world Forestry Congress Seattle 1960. New Zealand Forest Service Reprint #23.
- Shelbourne, C.J.A. & Thulin, I.J. (1974). Early results from a clonal selection and testing programme with radiata pine. *New Zealand Journal of Forestry Science* 4, 387-398.
- Squillace, A.E. (1968). Selection of superior trees. Proceedings 9th Southern conference on tree improvement, pp. 7-9. U.S. Department of Agriculture Forest Service.
- Squillace, A.E. & Dorman, K.W. (1961). Selective breeding of slash pine for high oleoresin yield and other characters. Recent advances in Botany, 2, 1616-1621.
- Squillace, A.E. & Gansell, C.R. (1974). Juvenile : mature correlations in slash pine. *Forest Science*, 20, 225-229.
- Stern, K. (1964). Population genetics as a basis for selection. *Unasylva*, 18, 21-9.
- Stonecypher, R.L. (1970). Multiple trait breeding. *Unasylva*, 24, 48-51.
- Sweet, G.B. & Wells, L.G. (1974). Comparisons of the growth of vegetative propagules and seedlings of *Pinus radiata*. *New Zealand Journal of Forestry Research*, 4, 399-409.
- Toda, R. (1974). Vegetative propagation in relation to Japanese forest tree improvement. *New Zealand Journal of Forest Science*, 4, 410-417.
- Vidacovic, M. (1966). Selection of plus trees. *Sumarski List*, 1-2, 7-13.
- Wareing, P.F. (1964). Tree physiology in relation to genetics and breeding. *Unasylva* 18, 61-70.
- Wareing, P.F. & Matthews, J.D. (1971). Physiological and genetical factors determining productivity of species. Proceedings 15th I.U.F.R.O. Congress, Gainesville, Florida, pp. 136-143. I.U.F.R.O. Munich.

- Wedel, K.W. von, Zobel, B.J. & Shelbourne, C.J. (1967). Knotwood in loblolly pine. North Carolina State University Cooperative tree improvement program. Technical Report #36.
- Weir, R.J. & Zobel, B.J. (1975). Advanced generation seed orchards. "Seed orchards". (Ed. by R. Faulkner), pp. 118-216. Forestry Commission, London. Bulletin #54.
- Wellendorf, H. (1970). Resemblance in height growth between original trees and clones of Scots pine. Forest tree Improvement, 1, 25-45.
- Williams, J.S. (1962). The evaluation of the selection index. Biometrics, 18, 375-93.
- Zobel, B.J. & Rhodes, L.R. (1956). Specific gravity estimations of mature loblolly pine from juvenile wood and seedling limb sections. Forest Science, 2, 107-12.



BIOLOGICAL OPPORTUNITIES FOR GENETIC IMPROVEMENT IN FOREST PRODUCTIVITY.

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SUMMARY

The genetically variable attributes that influence forest productivity can be divided into three groups.

First, there are attributes which can be, and are being, improved, normally as the unplanned consequence of selection for genotypes which produce the largest, highest-quality individuals in the shortest time. These include adaptive traits, enabling trees to more fully exploit available growing seasons, and more effectively deal with or endure adverse features of the environment (especially water stress). These adaptive traits are becoming understood from studies on provenances, and could be used as early selection criteria. Individual tree 'vigour' and, in a sense, gigantism, are being favoured, by selecting for rapid establishment, rapid individual tree crown development, root regeneration and 'site capture', possibly favouring competitive types and enhancing early sawlog production. And, most of all, stem quality defects are being minimized or eliminated.

Secondly, there are attributes which could be improved, but which are not being fully exploited. It is often considered too costly, too risky or potentially counterproductive to attempt to tailor genetically more uniform populations to particular sites or cultural environments. These judgements need to be regularly reviewed. Opportunities for genetic improvement in biomass yields may be particularly large under intensive culture, because of lessened need for mutually-depressing competitive traits, and smaller investment of assimilates in

non-harvested branches and roots. More attention might also be given to selection for delayed ageing, avoiding early flowering genotypes, and employing new technologies to induce parent trees to flower.

Thirdly, there are attributes which do not seem readily amenable to genetic improvement, even though attempts may be made to improve them. Foremost among these attributes may be fundamental changes in the potential radiant energy conversion efficiencies of well-adapted closed forest stands. It is pointed out that (a) in temperate regions, natural, coniferous forest stands are potentially already among the most productive biomass producers of all terrestrial crops, (b) contrary to common belief there are few precedents in agriculture for substantial genetic improvements in yield resulting from selection for greater photosynthetic efficiency of crop stands, including vegetative crops like grasses (Alberda 1971), and (c) it may be particularly difficult to improve the per hectare biomass productivities of forest stands as long as we need to select for rapidly growing competitive individuals, because compromises have to be made between traits desired for rapid site capture and competitiveness, and traits desired for maximum community productivity after full site capture.

RÉSUMÉ

Les attributs variables sur le plan génétique qui influencent la productivité de la forêt peuvent se diviser en trois groupes:

Premièrement, il existe des attributs qui peuvent être, et sont, améliorés; en général, ces améliorations sont la conséquence, non planifiée, d'une sélection de génotypes qui produisent, dans le temps le plus court des individus les meilleurs en qualité et en dimension. Ces attributs comprennent les facteurs d'adaptation, qui permettent aux arbres d'exploiter au maximum les saisons de végétation et de lutter le plus efficacement possible contre les facteurs adverses de la nature (surtout contre le manque d'eau). La connaissance que l'on a des facteurs d'adaptation provient des études des provenances et peuvent être utilisés comme

premiers critères de sélection. La 'vigueur' d'un arbre, et dans un certain sens, le gigantisme, sont favorisés par la sélection pour une reprise rapide, un développement rapide de la cime de l'arbre, une régénération rapide des racines et une exploitation rapide du potentiel de la station, favorisant éventuellement le pouvoir compétitif et arrivant ainsi rapidement à produire des bois de sciages. Et surtout les défauts de qualité du tronc sont minimisés, ou même éliminés. Deuxièmement, il y a les attributs qui seraient à même d'être améliorés mais qui n'ont pas encore été complètement exploités. On a souvent pensé qu'essayer de créer des peuplements génétiquement plus uniformes pour des stations ou des milieux particuliers, était un procédé trop coûteux et trop risqué, qui irait même à l'encontre du résultat désiré. On se doit de réviser ce jugement régulièrement. Les possibilités permettant une amélioration génétique du rendement en biomasse peuvent être très importantes dans le cadre d'une culture intensive parce que la compétition entre individus est moins grande et l'investissement en produits de photosynthèse dans les branches et les racines non récoltées est plus faible. On devrait aussi porter plus d'attention à la sélection portant sur un vieillissement retardé et éliminer les génotypes qui fleurissent trop tôt et sur l'utilisation de techniques nouvelles pour induire la floraison chez des arbres-mères.

Troisièmement, il existe des attributs qui ne semblent pas être améliorables, bien que l'on ait essayé. L'attribut le plus important parmi ceux-ci est celui qui amènerait un changement fondamental dans l'efficacité de la conversion potentielle de l'énergie de radiation dans des peuplements fermés et bien adaptés. Il faut remarquer que (a) dans les régions tempérées les peuplements naturels de résineux sont déjà parmi les meilleurs producteurs de biomasse de toutes les productions terrestres, (b) contrairement à l'opinion commune, il y a peu de précédents en agriculture qui montrent une amélioration génétique importante du rendement, qui résulterait d'une sélection basée sur une plus grande efficacité de la photosynthèse dans les peuplements, y compris les prairies

(Alberda 1971) et, (c) il serait particulièrement difficile d'améliorer la productivité de biomasse par hectare dans les peuplements forestiers si l'on continue à choisir des essences à croissance rapide et compétitive, car on doit trouver un compromis entre, d'une part, l'utilisation plus rapide du potentiel de la station et une certaine compétition, et d'autre part une productivité maximale de l'ensemble du peuplement après une occupation complète de la station.

ZUSAMMENFASSUNG

Die genetischen Eigenschaften, welche die Produktivität eines Waldes beeinflussen, lassen sich in drei Gruppen gliedern.

Erstens gibt es Eigenschaften, die sich verbessern lassen und die auch wirklich verbessert werden. Normalerweise geschieht das als ungeplante Folge der Selektion von Genotypen, die in der kürzesten Zeit die grössten und qualitativ besten Einzel Exemplare hervorbringen. Zu diesen Eigenschaften gehört auch die Fähigkeit der Anpassung, aufgrund derer die Bäume die Wachstumsperioden intensiver nutzen und widrigen Umweltbedingungen (besonders Wasserknappheit) standhalten können. Diese Merkmale der Anpassungsfähigkeit werden aus Provenienzstudien klar ersichtlich und könnten als erste Selektionskriterien dienen. In der Selektion auf raschen Bestandesschluss, rasche individuelle Entwicklung der Baumkronen, Regenerationsfähigkeit der Wurzeln und 'Eroberung des Standorts' hin werden die Wuchskraft von Baumindividuen und in gewissem Sinn auch Riesenwuchs bevorzugt. Man versucht nach Möglichkeit, wettbewerbsaktive Typen besonders zu fördern und damit eine frühe Sägeholzproduktion zu steigern. Vor allem aber werden Qualitätsmängel bei den Baumstämmen auf ein Minimum reduziert oder sogar ganz verhindert.

An zweiter Stelle stehen Eigenschaften, die zwar verbesserungsfähig sind, aber nicht voll genutzt werden. Es gilt häufig als zu kostspielig, zu riskant oder der Produktivität möglicherweise abträglich, wenn man versucht, genetisch gleichformigere Populationen für bestimmte Standorte oder Umweltbedingungen zu

schaffen. Solche Ansichten sollten in regelmässigen Abständen neu überdacht werden. Bei intensiver Bewirtschaftung gibt es besonders viele Möglichkeiten genetischer Verbesserung der Biomasseerträge, da weniger Bedarf besteht für gegenseitig unterdrückende und rivalisierende Eigenschaften und somit weniger Assimilate den nicht genutzten Zweigen und Wurzeln zugeführt werden. Man könnte auch der Selektion im Hinblick auf eine Verzögerung des Alterns mehr Aufmerksamkeit schenken, indem man frühblühende Genotypen vermeidet und neue Methoden anwendet, um die Mutterbäume zum Blühen zu bringen.

Drittens gibt es Eigenschaften, die nicht ohne weiteres genetisch zu verbessern zu sein scheinen. Dennoch könnten entsprechende Versuche unternommen werden. Grundsätzliche Veränderungen in der potentiellen Fähigkeit von gut angepassten, geschlossenen Waldbeständen, den Ausnutzungsgrad der Strahlungsenergie zu steigern, können an erster Stelle in der Reihe dieser Eigenschaften stehen.

Es wird darauf hingewiesen, dass (a) in gemässigten Zonen natürliche Nadelwaldbestände heute schon potentiell zu den produktivsten Erzeugern von Biomasse unter allen Landpflanzen gehören; (b) im Gegensatz zur allgemeinen Auffassung es in der Landwirtschaft nur wenige Beispiele für substantielle genetische Verbesserungen des Ertrags gibt, die durch die Selektion im Hinblick auf grössere photosynthetische Effizienz von Pflanzenbeständen, einschliesslich vegetativ vermehrter Pflanzen, wie Gräser (Alberda 1971), erzielt wurden; und (c) es sich als besonders schwierig erweisen kann, den Biomasseertrag der Waldbestände pro Hektar zu verbessern, so lange wir nach rasch wachsenden resistenten Einzelpflanzen selektieren müssen, weil Kompromisse nötig sind zwischen Merkmalen, die wegen rascher Standorteroberung und Resistenz erwünscht sind und Merkmalen, die wegen ihrer optimalen allgemeinen Produktivität nach der vollen Eroberung des Standorts wünschenswert sind.

INTRODUCTION

The yields of modern varieties of most field and horticultural crops are several-fold those of their wild

progenitors, partly as a result of selection and breeding. Could the growth rates and yields of forest plantations be increased similarly by breeding, bearing in mind that forest trees are only at the threshold of domestication? What are the biological constraints and limits on forest productivity set by their physiology and the way they are grown?

This contribution gives some personal viewpoints on these questions based on considerations of (a) the physiological basis of yield of forest trees - their strengths and weaknesses as productive systems, and (b) the yield-determining processes that have been improved by selection and breeding in field crops (Wallace, Ozburn & Munger 1972; Ivins 1973; Evans 1975).

To provide a framework I shall examine four broad categories of attributes which have to be improved in order to increase forest productivities - attributes affecting

- (a) adaptation,
- (b) the speed of 'site capture' to full canopy cover after planting and each thinning,
- (c) the efficiency of 'site utilization' in terms of dry matter productivity per hectare per year after full site capture, and
- (d) the proportion and value of the dry matter that is harvested.

ADAPTATION

The biological potential for improving forest yields by selecting species and provenances which are better adapted for volume growth than local populations is well-known. Many locally native forest populations, like primitive cereals and maize (Evans & Dunstone 1970; Mangelsdorf, MacNeish & Galinat 1964) seem to exploit environmental resources rather conservatively, sacrificing rapid growth for long-term stress tolerance, ensuring survival over an evolutionary time scale, always in the face of competition from other species. Similarly, native provenances of trees often appear to under-utilize the growing season available to them in their localities, or they may seem to be 'over-sensitive' to mild levels of water stress. These may have been desirable strategies during their evolutionary history, but during the 20-30 years history of provenance research they have seemed over-cautious. There is a prodigious literature on the benefits of provenance transfer from long-season, wet or otherwise favourable climates, to shorter-season, less-favourable climates (e.g. Wright 1976; Farmer 1976). The fastest growing provenances are often from areas with somewhat longer seasonal periods of shoot, bud or cambial growth or, in the case of Pinus taeda, for instance, are from areas with more frequent or reliable summer rainfall (Wells 1969).

But all individuals within a forest population are not

equally well-adapted. Progenies selected within provenances differ in their abilities to endure or exploit particular environmental conditions. Kleinschmit & Sauer (1976) found more variation in shoot growth phenology among clones within provenances of *Picea abies* than between provenances, and van Buijtenen, Bilan & Zimmerman (1976) found considerable variation in drought resistance among families belonging to certain provenances of *Pinus taeda*. Thus, during the early generations of recurrent selection, there is considerable scope to improve the adaptive traits of the best provenances. This selection could be done most effectively, and perhaps at an early age, if we gained and used information on the physiological and morphological basis of provenance differences.

Provenance differences in phenology can be traced to particular temperature and photoperiodic thresholds for budburst budset and bud development (e.g. Campbell 1974; Ekberg et al. 1976). Desirable genotypes may have enhanced temperature or photoperiodic sensitivities at particular thresholds or may be indifferent to photoperiod. In fact, the shoot apices of *Picea* spp. may already be indifferent to photoperiod during bud development (Pollard & Logan 1977), in which case temperature thresholds for growth and frost hardiness may be all important. It is noteworthy that the photoperiodic requirements of maize, soybean, potato and some rice varieties have been relaxed during selection to enable them to utilize the full growing seasons at temperate latitudes. In these, and many other annual field crops, temperature thresholds for vegetative growth seems to limit yields (Monteith & Elston 1971).

Provenance differences in crown form can be traced to a few rules governing the branching patterns (Cannell 1974; Cochrane & Ford 1978). Differences in drought resistance can be traced to particular avoidance or tolerance mechanisms, and so on.

The biological potentials for forest productivity are set not only by how well the trees are adapted to particular natural environments, but also how well they are adapted to the management system under which they will be grown. Most tree breeders select genotypes which will grow well in a range of climates, at various nutrient levels and with current site preparation and forest management. This may be wise, but the history of agriculture suggests that we could be missing large and perhaps profitable opportunities for genetic improvement if we do not explore the potential genetic gains under intensive culture, ignoring, for the moment, the high costs of support energy. The outstanding feature of many field crop improvement programmes has been the synergism between new varieties, fertilizers, weed control and an increase in planting density. The prime achievements of cereal breeding

have been adaptations to fertilizers and close spacing. Without them, genetic improvement by selection would probably have been small. Indeed, Zohary (1969) reported that the grain yield from mixed stands of the wild progenitors of wheat, barley and oats in the Middle East were similar to the yields of wheat in England, and rice in Japan, during the Middle Ages, that is, before the age of artificial fertilizers. A few researchers who are examining biomass and pulp production by trees with intensive culture, report very high yield of particular genotypes using high rates of fertilizers and close spacing (Schultz 1975; Anon 1976).

Unfortunately, the information on exploitable interactions between tree genotypes and their cultural environments is scanty. Researchers are only just beginning to explore the responses of large single-family blocks to various management regimes (Bridgwater & Stonecypher 1978). There is, however, evidence that phosphate-responsive varieties of Pinus taeda and Pinus elliottii could be developed for phosphate-deficient sites, and certain specific crosses within these species are exceptionally responsive to nitrogen fertilizers (Goddard, Zobel & Hollis 1976). Campbell & Wilson (1973) found no full-sib x spacing interactions among young Pseudotsuga menziesii, but Snyder & Allen (1971) and Adams, Roberds & Zobel (1973) found evidence that competitive ability had a genetic component in Pinus elliottii and Pinus taeda, respectively.

An important trait which could be regarded as adaptive, is the length of the life cycle. Different species, families and even clones mature at different ages, which partly determines the shapes of their height : age progress curves and times of maximum current annual increment (Muckadell 1959; Wareing & Matthews 1973). The onset of these genetically determined ageing processes (inheritance studied in fruit trees, e.g. Visser 1976) is usually signalled by increased cone production and a loss of apical dominance. Some species (e.g. Pinus virginiana) and some provenances (e.g. Lulu Island, B.C. Pinus contorta growing in Britain) are undesirable because of early ageing. Less obvious family differences in ageing may not become apparent for many years, and should, where possible, be observed on their parents. There could be dangers in selecting heavily flowering plus trees, particularly if they are not very old.

How far it is wise to go in fine-tuning the adaptive traits of forest trees, is a matter of judgement. Improvements in the fitness of varieties to particular natural or man-modified environments carry with them deteriorations in their abilities to cope with spatial and temporal variations: adaptation and adaptability are antagonistic (Simmonds 1962; Tigerstedt 1974). Most tree breeders prefer to breed for widely adapted types which are genetically heterogeneous and

physiologically adaptable. These types will perform as expected in a wide range of niches and environments and will exercise least selection pressure on potential pests and pathogens. Risks and breeding costs will be modest, but there will inevitably be sacrifices in potential genetic gains as long as some genotypes remain poorly adapted. The traditional approach of foresters is, in many respects, like that of subsistence farmers: aimed at some yield in most years on most sites, and satisfied with a modest overall optimum yield rather than striving for the maximum possible. A modest step towards adaptive fine-tuning, involving little further breeding costs, would be to assign single families to uniform sites and cultural treatments to which they respond (Bridgwater & Stonecypher 1978). Further steps would be to grow single blocks of full-sib families or clone mixtures. These steps should not be rejected for reasonably uniform sites, bearing in mind that even single clones can be phenotypically plastic (Bradshaw 1965). Thus, some tree genotypes can acclimatize more readily than others to changes in temperature and light intensity (Ledig 1976; Ledig, Clark & Drew 1977). A few potato clones are highly adaptable, and growers of tea and rubber have managed extensive areas with genetically homogeneous perennial crops for many years. We should also be aware, however, that many studies have shown that cereal cultivar mixtures slightly outyield completely pure stands (Simmonds 1962) and that coffee (an inbreeding species), which is genetically homogeneous, was wiped out of Sri Lanka by leaf rust.

SITE CAPTURE

A coniferous forest crop may spend half the total rotation 'capturing' and 'recapturing' the site, that is, exploring the soil profile and building up a full foliage canopy after planting and after each thinning. Consequently, forests, like annual crops, probably assimilate carbon and accumulate dry matter at rates which are proportional to the amount of intercepted radiation over the life of the crop (Monteith 1977). It is important, therefore, to increase the speed of 'site capture'. On fertile, lowland sites hardwoods will restore their foliage canopies rapidly, and if they are coppiced their soil environments are explored almost continuously. With conifers, however, we must endure the prolonged period of early crown development of new saplings, and accept that the soil profile has to be re-explored with new roots when a tree is felled.

It is important to realize that the biological attributes which limit the speed of site capture are those which limit the growth rates of trees as individuals. Many of these attributes are different from those influencing the per hectare productivity of closed forest stands (Cannell 1978).

It is equally important to realize that almost all forest tree breeders evaluate the growth of genotypes on the basis of the mean sizes of individuals, normally in rows, before or after canopy closure. They do not, and cannot, evaluate families on a per hectare basis in blocks large enough to allow the spatial processes of competition to operate (Ford 1975), because of the cost and the environmental heterogeneity of forest sites. Because they select for rapid individual tree growth, tree breeders are successfully improving many attributes favouring rapid site capture, involving rapid exploration of surrounding environmental resources, and increased competitive ability. These improvements will be inevitable consequences of selecting for fast-growing individuals, and will be highly desirable for half the rotation. During the other half, when the sites are fully captured, intensified inter-tree competition could have two effects. On the negative side, it could conceivably depress per hectare productivity (Fig. 1). This is because, to maximize volume production per hectare, a large proportion of the trees should produce large volumes per year by using environmental resources efficiently, and not by robbing them from their neighbours (Donald 1968; Ford 1976; Cannell 1978). On the positive side, intensified inter-tree competition may spread tree size frequency distributions (producing some large dominants) and so enhance the chances of producing some large trees of high value early in the rotation (Fig. 1). According to Schwanitz (1966) one of the important steps in the evolution of crop plants has been a transition to gigantism, often involving hybridization or an increase in ploidy. Large cereal grains, maize cobs, beans and beets, like large trees, are more valuable than small ones. Selection for gigantism in trees may be a worthwhile pursuit in itself, irrespective of its possible negative effect on per hectare volume productivity.

What are the biological attributes which regulate the speed of site capture? First, they will include the size of the embryonic capital and other factors which influence seedling size in the nursery and after outplanting (e.g. Sweet & Wareing 1966; Perry 1976). The value of \bar{W} in the equation $W = W_0 e^{rt}$ depends on the starting value W_0 , as well as the relative growth rate, r , and time, t . So-called 'superseedlings' of *Pinus taeda*, *P. elliottii* and *P. echinata*, selected in the nursery, can be 20-200 per cent greater in individual-tree volume at age ten than trees grown from average-sized seedlings (Zarger 1965), and differences in the initial size of *Pinus radiata* cuttings can lead to 4-5-fold overestimates of genetic gain at age four (Burdon & Sweet 1976). Maternal, seed size, nursery and 'C' effects could be exploited to speed the rate of site capture.

Cereals and Grasses

Small 'crop'
ideotypeHigh yield per
hectare at
close spacingsLarge 'isolation/
competition'
ideotypeLow yield per
hectare at
any spacing

Trees

Small 'crop'
ideotypeHigh productivity
per hectare :
inter-tree
competition
delayed and
reducedLarge isolation/
competition'
ideotypeLow productivity
per hectare :
competition
early and
intenseSelection here will
favour 'isolation/
competition' ideotype

Fig. 1. Possible differences in the performance of various ideal plant types (ideotypes) as spaced individuals (centre), in mixtures (left) and in stands (right) (after Donald 1968; Donald & Hamblin 1976). Note that (a) relationships between individual plant performances and per hectare productivity after canopy closure can be negative (Hamblin & Powell 1975), (b) 'isolation/competition' ideotypes may tend to be selected if the criterion is plant size, and (c) selection for 'isolation/competition' ideotypes may lead to a desirable early spread in tree size frequency distributions.

Secondly, among the factors influencing r in the above equation, is the rate of leaf area expansion. In general, plants which invest a large proportion of their dry matter in photosynthetic tissue and distribute that tissue over a large surface area (often producing 'thin' leaves) to increase light interception, tend to succeed as individuals (Jackson 1963; Potter & Jones 1977). Relative leaf growth rates are important determinants of the time taken to develop fully light-intercepting crop canopies. Within conifer species there are striking differences in branching and crown form which influence the rate of build-up in photosynthetic tissue after planting and thinning. The components have been considered (Campbell 1963; Miller 1965; Cannell 1974) and are contained in crown expansion factors in single-tree computer models (Arney 1972; Mitchell 1975). Unfortunately, we cannot select rigorously for rapid crown development because of its undesirable impacts on stem knot size, wind stability and resistance to snow breakage. Very coarsely-branched, wide-crowned trees are rejected in favour of trees with moderately full crowns of fine branches, recognizing that there is a strong relationship between bole size and crown size (e.g. Waring et al. 1977). Also, genotypes which display current-year needles as late summer flushes may be superior on favourable sites to genotypes which store all their needle primordia in buds until the following year.

Thirdly, inherent differences in root morphology and mycorrhizal development may be important. In droughty or competitive situations early growth after transplanting may be limited by the speed of access to water and nutrients, rather than the speed of radiant energy capture. In these situations, breeders, selecting fast-growing progenies, may be selecting for increased root growth (e.g. *Pinus taeda*, Cannell, Bridgwater & Greenwood 1978). If so, this seems somewhat wasteful because trees, like land races of field crops (Jennings 1976) may already invest heavily in roots as a survival strategy in competitive habitats. Young conifers send up to 50 per cent of their fixed carbon below ground (Webb 1977). It would be better if some of this dry matter were employed in shoot growth, but apparently this is not possible as long as there is a need for rapid root regeneration after transplanting. It would be interesting to know whether known genetic differences in root : shoot relative growth rates (Ledig & Perry 1965) could bring about interactions between genotypes and planting techniques or environments. If so, this would be another instance where genetic improvements were conditional upon improvements in tree culture.

So far, I have spoken of attributes which influence light, nutrient and water 'capture'. To these must be added attributes which improve the efficiency with which light is intercepted, carbon fixed and water and nutrients used,

remembering that we are considering these traits for individuals and not for forest stands. The ideal light interception characteristics of isolated plant canopies (Charles-Edwards & Thornley 1963) are different from those of crop canopies (Duncan et al. 1967). High rates of light-saturated photosynthesis which are desirable for isolated plants may be less important in crop stands because most leaves are then shaded. And we should be aware that light-saturated photosynthetic rates, or net assimilation rates, have not been improved much during the evolution of many field crops (Evans 1976 and see below), possibly because high photosynthetic rates are associated with small mesophyll cells, small leaves and slow leaf relative growth rates which mean slow rates of 'site capture' (Charles-Edwards 1978).

Nevertheless, potential genetic improvements in the growth rates of individual trees, resulting from improvements in rates of site capture combined with better adaptation, appear to be considerable. Widely spaced trees of some new poplar clones grow twice as rapidly as old ones (van Goor & Koster 1969). And many conifer breeders confidently predict 50 per cent genetic gains over 2-4 generations of recurrent selection for individual-tree heights and bole volumes, attainable without intensive culture or intensive exploitation of genotypes x environment interactions. However, such figures for gains in yield may apply in full, as gains per hectare, only during the periods of site capture, and they are, of course, modest compared with the several-fold genetic gains in, for instance, wheat and rubber yields since their domestication (rubber: Ferwerda 1969).

SITE UTILIZATION

Once the site has been fully captured the productivity of a forest depends on how effectively finite resources of light, water and nutrients are utilized by the community. As mentioned above, whilst it is desirable to have some vigorous, competitive individuals to rapidly produce some large high-value stems, intense competition throughout even-aged stands could well depress per hectare productivity of dry matter and wood volume (Fig.1). The need to compromise between vigorous, competitive, pioneer-like individuals, and those which contribute to high per hectare productivities after full site capture, could severely limit potential genetic gains in per hectare volume production averaged over complete rotations.

This dilemma becomes clearer when we consider the traits that need to be compromised. First, there is the compromise between reasonably wide, spreading crowns giving rapid site capture and tall, narrow crowns which apparently intercept light most effectively in closed canopies (Jahnke & Lawrence 1965) and produce the greatest stem volume per unit of crown

volume or surface area (Assman 1970; Hamilton 1969). Secondly, there is the compromise between characteristics giving maximum photosynthetic rates at light-saturation, desirable on open-grown trees, and maximum shade adaptation, light absorptivity and photochemical efficiency, more important for shaded needles in conifer stands with leaf area indices often greater than ten (see Cannell 1978). Thirdly, there could be compromises between below-ground nutrient-capture and drought-avoidance mechanisms desirable for open-grown individuals, and adaptive traits needed to utilize, mobilize and recycle nutrients effectively, and contend with water stress, in forest stands. In general, the compromises are between traits ideally expressed by what Donald & Hamblin (1976) called 'isolation/competition' ideotypes and 'crop' ideotypes. The 'isolation/competition' ideotype for cereals is a lax, free-tillering, leafy plant, able to explore its environment as extensively as possible, whereas the 'crop' cereal ideotype is small, with few, erect leaves, minimum leaf display and few tillers (Fig. 1). In conifers the differences between ideotypes may be more subtle, but the effect on genetic advance may be the same. That is, selection for fast-growing individuals may not increase stand productivity during the years when the site is fully captured. Selection for yield on the basis of spaced plant performance is believed by some agricultural crop breeders to be an ineffective way of increasing yields (e.g. grasses, Lazenby & Rogers 1960-65; cereals, Syme 1972; Fischer & Kertesz 1976; beans, Hamblin & Evans 1976). Similarly, selection of high-yielding competitive individuals in mixed-genotype stands can favour genotypes which perform poorly in pure stands (Fig. 1; Hamblin & Rowell 1975).

However, we should not be complacent about genetically improving the potential per hectare dry matter productivities of closed forest stands. Plantations of well-adapted, but genetically unimproved temperate-zone forests, especially conifers, which are well-supplied with nutrients and water, are already physiologically capable of producing as much dry matter as any highly-bred annual or perennial field crop employing C3 photosynthesis at the same latitude (Fig. 2). In north-temperate regions this is 30-40 Mt/ha/yr or above-ground dry matter - equal to C4 crops in these regions. In certain sub-tropical regions the maximum for forests may be nearer 50 Mt/ha/yr - less than C4 tropical grasses (Dawkins 1963; Bevege 1976; Fig. 2). Reviews by Westlake (1963), Art & Marks (1971), Loomis & Gerakis (1975), Gordon (1975), Kira (1975), and computer models of de Wit (1968) and Monteith (1977), all lead to the conclusion that unimproved coniferous forest canopies are very effective solar energy converters (Cannell 1978). An optimistic interpretation of these figures would be that the potential productivity of genetically improved coniferous

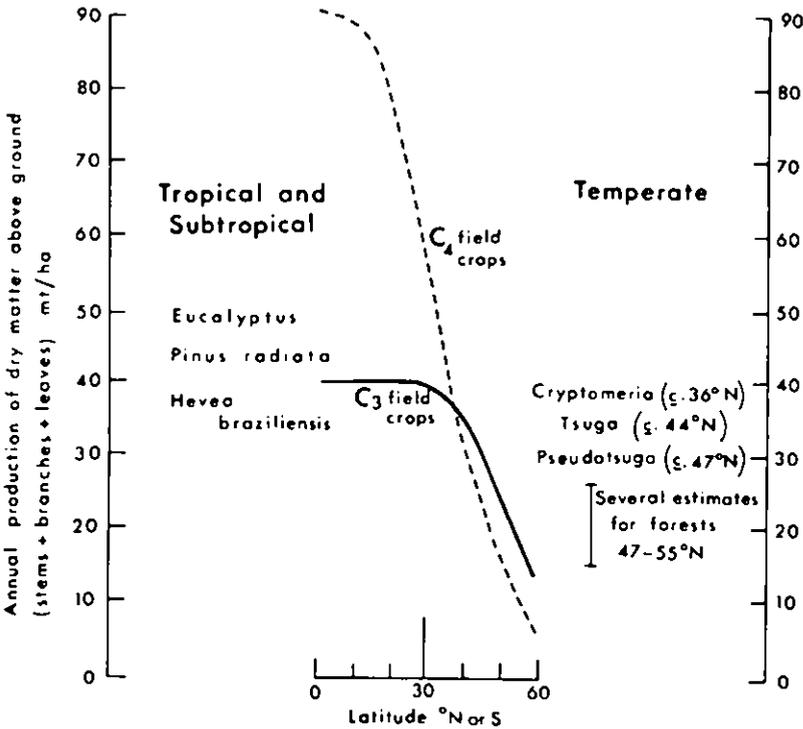


Fig. 2. Maximum annual total above-ground dry matter production recorded for field crops (including perennials) with C₃ and C₄ photosynthesis (after Loomis & Gerakis 1975), compared with maximum recorded for forest plantations (estimated or taken from Dawkins 1964; Templeton 1968; Westlake 1963; Kira 1975; Cannell 1978). Maximum productivities of temperate hardwoods are less than those of conifers (Day & Monk 1977).

forests may be much greater than that of other C3 crops because of their high capacities for winter photosynthesis (Fry & Phillips 1977), their high leaf area indices (e.g. Grier & Running 1977), high energy conversion efficiencies of shaded foliage, and large cambial sink capacities. On the other hand, attempts to genetically improve the photosynthetic efficiency of field crops in a fundamental sense have been singularly unrewarding (Evans 1975). Computer models constructed by Monteith (1977) and Charles-Edwards (1978) for field crop stands indicate that it would need about a 4- to 5-fold increase in light-saturated photosynthetic rates to bring about a 50 per cent increase in annual dry matter productivity. Genetic variation in photosynthetic rates per unit leaf area within crop species has rarely been positively correlated with productivity, and these rates, or relative growth and/or net assimilation rates, have been negatively correlated with yields among evolutionary races or among modern varieties of wheat (Evans & Dunstone 1970), maize (Duncan & Hesketh 1968), sorghum (Downes 1971), sugar beet (Watson & Witts 1959), sugar cane (Bull 1971), ryegrass (Rhodes 1972), tomatoes and cotton (Evans 1975). The maximum crop growth rates, and radiant energy conversion efficiencies, are remarkably similar for a wide range of C3 crops in Britain and the Netherlands (Greenwood et al. 1977; Sibma 1968; Monteith 1977). It may be very difficult to achieve, say, a 50 per cent improvement in the potential dry matter productivity of well-adapted forest stands in the present-day CO₂ environment by selection within the natural pool of variation in C3 photosynthesis.

I specify the present-day CO₂ environment because global atmospheric CO₂ concentrations are increasing by about 1 ppm/yr, which, according to Monteith (1977) could produce an 11 per cent increase in crop growth rates by the end of the century, without any credit to forest researchers! I also specify the natural pool of variation. According to Charles-Edwards (1978) there is no compelling evidence that crop growth rates can be increased in Britain by selection within the existing genetic variation in leaf photosynthetic characteristics. On the other hand, there could be fundamental biochemical weaknesses universally limiting energy conversion by C3 photosynthesis and existing mitochondrial respiration, which could conceivably be overcome by genetic or chemical modification (Oliver & Zelitch 1977; Day 1977; Radner & Kok 1977). Lastly, I specify C3 photosynthesis because all forest trees examined so far are C3 plants (except mangrove, Schaedle 1975; and possibly larch, Fry & Phillips 1976), and in tropical regions potential productivities are greatest with C4 photosynthesis. Crops with C4 photosynthesis can make use of high irradiances, at high temperatures (PEP carboxylase has a temperature optimum exceeding 30°C) and have high water use

efficiencies. In temperate regions, however, C4 photosynthesis is at a premium only in summer (Monteith 1978). Over the whole year, especially for crops with high leaf area indices and substantial winter photosynthesis, C3 crops are often more productive than C4 crops (Loomis & Gerakis 1975; Gifford 1974; Moore 1974).

Let me make clear that most closed forest plantations are not producing to the limits of their photosynthetic potential (perhaps 30-40 Mt/ha/yr of above-ground dry matter, about 2.5 per cent solar energy conversion, in north-temperate regions) and selection and hybridization can produce better-adapted genotypes which are more likely to approach this potential especially with inputs of support energy. My point is that we should not be complacent about the prospects of genetically improving this potential energy conversion efficiency of forest stands, particularly if we need to select for big trees.

PROPORTION AND VALUE OF THE DRY MATTER THAT IS HARVESTED.

Diversion of assimilates to the harvested sink (grain, tuber etc.) has been a highly significant feature in field crop improvement. Evans (1976) stated that "the evolution of crop plants has been primarily the evolution of the sink organs". Donald & Hamblin (1976) concluded that "most of the progress in breeding high-yielding cereal cultivars seems to be related to higher harvest indices (HI, the proportion of the aboveground dry matter that is harvested) with little change in biological yield (total dry matter produced)". In the early 1900's the HI of wheat varieties was 32 per cent, whereas for current dwarf wheats it is 49 per cent (Wallace, Ozburn & Munger 1972), Phaseolus bean varieties have HI's ranging from 55 to 67 per cent (Wallace, Ozburn & Munger 1972), potatoes from less than 50 per cent for wild progenitors to 84 per cent for modern varieties (Watson 1971), and rubber clones from 3 per cent to 11 per cent (Templeton 1968), and oil palm progenies from 25 per cent to 55 per cent (Corley, Hardon & Tan 1971). Thus, by changing the HI alone it has been possible to increase crop yields by between 20 and 250 per cent!

Ovington's (1957) study of Pinus sylvestris in England showed that about 40 per cent of the net total dry matter (including needles) produced above-ground by a forest crop is accumulated in the boles and somewhat less than 40 per cent will be recovered and converted into marketable products. If this index could be increased to 50 per cent, this could represent a 25 per cent increase in yield without any increase in total biomass production.

There are certainly considerable genetic differences in dry matter distribution within tree species - in root-shoot allometry (Ledig & Perry 1965; Cannell, Bridgwater & Greenwood

1978) in stem-branch, and bole-crown ratios (Matthews et al. 1975; Thompson 1974) - large enough to increase the above-ground harvest index of individual trees to maybe 50-60 per cent. However, this potential cannot be fully exploited to increase forest yields as long as these depend greatly on the speed of site capture. As mentioned above, with current forestry practice, it is important to maintain, even enhance, the capacity for rapid crown and root development after transplanting and thinning. Consequently, there is unlikely to be much improvement in bole yields over entire rotations resulting from decreased investment in other tree parts.

One could, however, envisage carefully-planted, regularly thinned, closely-planted plantations, where there was a lesser need for rapid crown development, with inputs of fossil fuels permitting reduced investment in roots and reserves. Under these circumstances, genetic selection for higher harvest indices could increase stem pulpwood yields very considerably, both directly, and maybe indirectly, because the boles require less respiratory maintenance than do additional roots, branches and leaves. It is noteworthy that stem wood production per unit of foliage increases anyway after canopy closure (Mitchell 1975, his p.9 and Fig. 7), either because the trees become photosynthetically more efficient and/or because an increased proportion of the annual dry matter increment goes to the boles (Cannell 1978).

An obvious way to increase the harvest indices of forests is to include the branches, stumps and even structural roots in the harvest (Young 1973; Eskilsson 1974) or improve the technology of harvesting and utilization (e.g. King & Smith 1974). These approaches need not be discussed here.

Fielding (1960) stressed that up to 16 per cent of the above-ground dry matter produced by 7-year-old Pinus radiata can be used to produce strobili, seeds and pollen, and other workers have recorded decreased stem girth increment in heavy-coning years (Rohmeder 1951). However, provided there is some effort to avoid very precocious or fecund genotypes (Gerhold 1966), it would be misleading to exaggerate the potential for genetic gain in stem yields by selecting for reduced use of assimilates in flowering and opposed to selection for delayed ageing. If 15 per cent of the annual dry matter increment were taken by cones over one third of the rotation, this would average out as a reduction in vegetative growth of only 5 per cent, even if we assume that the cones are non-photosynthetic and have the same respiratory losses per unit weight as new vegetative tissues. But we know that green fruits, cereal ears, cotton bolls and sexual structures on other plants fix considerable amounts of external and respiratory CO_2 , and that the presence of fruit sinks often enhances photosynthetic rates. In my view, in trees, the association between flowering and ageing is likely to be more

important in breeding programmes than the direct impact of flowering on the harvest index.

By far the most important gains in harvest index resulting from current tree improvement programmes will be gains in the proportion of stem wood which has a high merchantable value. Glästone (1975) and Matthews (1975) elaborated the dramatic gains to be made by diminishing crook, sweep, taper, knot sizes, spiral grain and other quality defects. There may not be much room for altering the proportion of stem to bark, at least in *P. taeda* (Matziris & Zobel 1973), but most other wood quality characteristics are genetically variable and usually highly heritable. First-generation seed-orchard progenies should contain a much smaller proportion of defective genotypes than unimproved stock. Selection for plant form in field crops (e.g. in brassicas) and elimination of defects (e.g. shattering cereal inflorescences) has been very successful during their domestication (Evans 1976) and will undoubtedly be one of the success stories of forest tree breeding, particularly with pines.

REFERENCES

- Adams, W.T., Roberds, J.H. & Zobel, B.J. (1973). Intergenotypic interactions among families of loblolly pine (*Pinus taeda* L.). *Theoretical and Applied Genetics*, 43, 319-322.
- Alberda, T. (1971). Potential production of grassland. "Potential crop production". (Ed. by P.F. Wareing and J.P. Cooper), pp.159-171. Heinemann, London.
- Anon. (1976). Intensive plantation culture. U.S. Department of Agriculture Forest Service. General Technical Report NC-21. Northeast Central Forest Experimental Station, St. Paul, Minnesota.
- Arney, J.F. (1972). Computer simulation of Douglas fir tree and stand growth. Unpublished Ph.D. thesis. Oregon State University, and Canadian Forest Service, Victoria. Internal Report BC-27.
- Art, H.W. & Marks, P.L. (1971). A summary table of biomass and net annual primary production in forest ecosystems of the world. "Forest biomass studies". Life Sciences and Agricultural Experiment Station, University of Maine and Orono, U.S.A. Miscellaneous Publications, 132, 6-32.
- Assman, E. (1970). The principles of forest yield study. Pergamon Press, Oxford.
- Bevege, D.I. (1976). A green revolution in the high yield forest: rational silviculture or new technology? *Australian Forestry*, 39, 40-50.
- Bradshaw, A.D. (1965). Evolutionary significance of phenotypic plasticity in plants. *Advances in Genetics*, 13, 115-155.
- Bridgwater, F.E. & Stonecypher, R.W. (1978). Genotype x environment interaction: implications in tree breeding

- programs. Proceedings of 5th North American forest biology workshop, University of Florida, Gainesville. (in press)
- Buijtenen, van J.P., Bilan, M.V. & Zimmerman, R.H. (1976). Morpho-physiological characteristics related to drought resistance in Pinus taeda. "Tree physiology and yield improvement". (Ed. by M.G.R. Cannell and F.T. Last), pp.349-359. Academic Press, London and New York.
- Bull, T.A. (1971). The C4 pathway related to growth rates in sugar cane. "Photosynthesis and photorespiration". (Ed. by M.D. Hatch, C.B. Osmond and R.O. Slatyer), pp.68-75. Wiley, New York.
- Burdon, R.D. & Sweet, G.B. (1976). The problem of interpreting inherent differences in tree growth shortly after planting. "Tree physiology and yield improvement". (Ed. by M.G.R. Cannell and F.T. Last), pp.483-502. Academic Press, London and New York.
- Campbell, R.K. (1963). Phenotypic correlations among branch and upper-crown stem attributes in Douglas fir. Forest Science, 9, 444-451.
- Campbell, R.K. (1974). Use of phenology for examining provenance transfer in reforestation of Douglas fir. Journal of Applied Ecology, 11, 1069-1080.
- Campbell, R.K. & Wilson, B.C. (1973). Spacing-genotype interaction in Douglas fir. Silvae Genetica, 22, 15-20.
- Cannell, M.G.R. (1974). Production of branches and foliage by young trees of Pinus contorta and Picea sitchensis: provenance differences and their simulation. Journal of Applied Ecology, 11, 1091-1115.
- Cannell, M.G.R. (1978). Improving per hectare forest productivity. Proceedings of 5th North American forest biology workshop. University of Florida, Gainesville, U.S.A. (in press).
- Cannell, M.G.R., Bridgwater, F.E. & Greenwood, M.S. (1978). Seedling growth rates, water stress responses and root-shoot relationships related to eight-year volumes among families of Pinus taeda L. Silvae Genetica (in litt.).
- Charles-Edwards, D.A. (1978). An analysis of the photosynthesis and productivity of vegetative crops in the United Kingdom. Annals of Botany, 42, 717-731.
- Charles-Edwards, D.A. & Thornley, J.H.M. (1973). Light interception by an isolated plant. A simple model. Annals of Botany, 37, 919-928.
- Cochrane, L.A. & Ford, E.D. (1978). Growth of a Sitka spruce plantation: analysis and stochastic description of the development of the branching structure. Journal of Applied Ecology, 15, 227-244.
- Corley, R.H.V., Hardon, J.J. & Tan, G.Y. (1971). Analysis of growth of oil palm (Elaeis guineensis Jacq.). 1.

- Estimation of growth parameters and application in breeding. *Euphytica*, 20, 304-315.
- Dawkins, H.C. (1963). The productivity of tropical high-forest trees and their reaction to controllable environment. Unpublished Ph.D. thesis. Commonwealth Forestry Institute, Oxford, England.
- Day, F.P. & Monk, C.D. (1977). Net primary production and phenology on a southern Appalachian watershed. *American Journal of Botany*, 64, 1117-1125.
- Day, P.R. (1977). Plant genetics: increasing crop yield. *Science*, 197, 1334-1339.
- Donald, C.M. (1968). The breeding of crop ideotypes. *Euphytica*, 17, 385-403.
- Donald, C.M. & Hamblin, J. (1976). The biological yield and harvest index of cereals as agronomic and plant breeding criteria. *Advances in Agronomy*, 28, 361-405.
- Downes, R.W. (1971). Relationship between evolutionary adaptation and gas exchange characteristics of diverse *Sorghum* taxa. *Australian Journal of Biological Sciences*, 24, 843-852.
- Duncan, W.G. & Hesketh, J.D. (1968). Net photosynthetic rates, relative leaf growth rates, and leaf numbers of 22 races of maize grown at eight temperatures. *Crop Science*, 8, 670-674.
- Duncan, W.G., Loomis, R.S., Williams, W.A. & Hanau, R. (1967). A model for simulating photosynthesis in plant communities. *Hilgardia*, 38, 181-205.
- Ekberg, I., Dormling, I., Eriksson, G. & Wettstein, von D. (1976). Inheritance of the photoperiodic response in forest trees. "Tree physiology and yield improvement". (Ed. by M.G.R. Cannell and F.T. Last), pp. 207-221. Academic Press, London and New York.
- Eskilsson, S. (1974). Whole tree pulping. 3. Pulp properties. *Svenska Papperstidning*, 77, 165-174.
- Evans, L.T. (1975). *Crop physiology, some case histories*. Cambridge University Press, London and New York.
- Evans, L.T. (1976). Physiological adaptation to performance as crop plants. *Philosophical Transactions of the Royal Society, London*, B.275, 71-83.
- Evans, L.T. & Dunstone, R.L. (1970). Some physiological aspects of evolution in wheat. *Australian Journal of Biological Sciences*, 23, 725-741.
- Farmer, R.E. (1976). Relationships between genetic difference in yield of deciduous tree species and variation in canopy size, structure and duration. "Tree physiology and yield improvement". (Ed. by M.G.R. Cannell and F.T. Last), pp. 119-137. Academic Press, London and New York.
- Ferwerda, F.P. (1969). Rubber (*Hevea brasiliensis* (Wild.) Mull. Arg.). "Outlines of perennial crop breeding in the tropics". (Ed. by F.P. Ferwerda and F. Wit), pp. 427-458.

- Miscellaneous Papers #4. Agricultural University, Wageningen, Netherlands.
- Fieldings, J.M. (1960). Branching and flowering characteristics of Monterey pine. Bulletin #37. Forestry and Timber Bureau, Australia.
- Fisher, R.A. & Kertesz, Z. (1976). Harvest index in spaced populations and grain weight in microplots as indicators of yielding ability in spring wheat. *Crop Science*, 16, 55-59.
- Ford, E.D. (1975). Competition and stand structure in some even-aged plant monocultures. *Journal of Ecology*, 63, 311-333.
- Ford, E.D. (1976). Competition, genetic systems and improvement of forest yield. "Tree physiology and yield improvement". (Ed. by M.G.R. Cannell and F.T. Last), pp. 463-472. Academic Press, London and New York.
- Fry, D.J. & Phillips, I.D.J. (1976). Photosynthesis of conifers in relation to annual growth cycles and dry matter production. I. Some C₄ characteristics in photosynthesis of Japanese larch (Larix leptolepis). *Physiologia Plantarum*, 37, 185-190.
- Fry, D.J. & Phillips, I.D.J. (1977). Photosynthesis of conifers in relation to annual growth cycles and dry matter production. II. *Physiologia Plantarum*, 40, 300-306.
- Gerhold, H.D. (1966). Selection for precocious flowering in Pinus sylvestris. U.S. Department of Agriculture Forest Service, Research Paper NC-6.
- Gifford, R.M. (1974). A comparison of potential photosynthesis, productivity and yield of plant species with differing photosynthetic metabolism. *Australian Journal of Plant Physiology*, 1, 107-117.
- Gladstone, W.T. (1975). Tree improvement programs of forest industries. "Forest tree improvement - the third decade". (Ed. by B.A. Thielges), pp. 65-71. 24th Forestry Symposium, Louisiana State University, Baton Rouge, U.S.A.
- Goddard, R.E., Zobel, B.J. & Hollis, C.A. (1976). Responses of Pinus taeda and Pinus elliottii to varied nutrition. "Tree physiology and yield improvement". (Ed. by M.G.R. Cannell and F.T. Last), pp. 449-462. Academic Press, London and New York.
- Goor, C.P. van & Koster, R. (1969). New poplar clones. *Populier*, 6, 43-47.
- Gordon, J.C. (1975). The productive potential of woody plants. *Iowa State Journal of Research*, 49, 267-274.
- Greenwood, D.J., Cleaver, T.J., Loquens, S.M.H. & Niendorf, K.B. (1977). Relationship between plant weight and growing period for vegetable crops in the U.K. *Annals of Botany*, 41, 987-997.
- Grier, C.C. & Running, S.W. (1977). Leaf area of mature

- northwestern coniferous forests: relation to site water balance. *Ecology*, 58, 893-899.
- Hamblin, J. & Evans, E.M. (1976). The estimation of cross yield using early generation and parental yields in dry beans (*Phaseolus vulgaris* L.). *Euphytica*, 25, 515-520.
- Hamblin, J. & Rowell, J.G. (1975). Breeding implications of the relationship between competitive ability and grain yield in a barley cross. *Euphytica*, 23, 535-542.
- Hamilton, C.J. (1969). The dependence of volume increment of individual trees on dominance, crown dimensions and competition. *Forestry*, 42, 133-144.
- Ivins, J.D. (1973). Increasing productivity. Crop physiology and nutrition. *Philosophical Transactions of the Royal Society, London*, B.267, 81-91.
- Jackson, J.E. (1963). The relationship of relative leaf growth rate to net assimilation rate and its relevance to the physiological analysis of plant growth. *Nature, London*, 200, 909.
- Jahnke, L.S. & Lawrence, D.B. (1965). Influence of photosynthetic crown structure on potential productivity of vegetation, based primarily on mathematical models. *Ecology*, 46, 319-326.
- Jennings, P.R. (1976). The amplification of agricultural production. *Scientific American*, 235, 181-194.
- King, N.J. & Smith, C.A. (1974). Problems of wood waste. *Forest and Home grown Timber*, 3, 46-48.
- Kira, T. (1975). Primary productivity of forests. "Photosynthesis and productivity in different environments". (Ed. by J.P. Cooper), pp. 5-40. Cambridge University Press, London.
- Kleinschmit, J. & Sauer, A. (1976). Variation in morphology, phenology and nutrient content among *Picea abies* clones and provenances, and its implications for tree improvement. "Tree physiology and yield improvement". (Ed. by M.G.R. Cannell and F.T. Last), pp. 503-517. Academic Press, London and New York.
- Lazenby, A. & Rogers, H.H. (1960-65). Selection criteria in grass breeding. Parts I-IV. *Journal of Agricultural Science*, 59, 51-66; 62, 282-298; 65, 65-78 and 79-89.
- Ledig, F.T. (1976). Physiological genetics, photosynthesis and growth models. "Tree physiology and yield improvement". (Ed. by M.G.R. Cannell and F.T. Last), pp. 21-54. Academic Press, London and New York.
- Ledig, F.T. & Perry, T.O. (1965). Physiological genetics of the shoot-root ratio. *Proceedings of the Society of American Foresters, Detroit, Michigan*. pp. 39-43.
- Ledig, F.T., Clark, J.G. & Drew, A.P. (1977). The effects of temperature treatment on photosynthesis of pitch pine from northern and southern latitudes. *Botanical Gazette*, 138, 7-12.

- Loomis, R.S. & Gerakis, P.A. (1975). Productivity of agricultural ecosystems. "Photosynthesis and productivity in different environments". (Ed. by J.P. Cooper). Cambridge University Press, London.
- Mangelsdorf, P.C., MacNeish, R.S. & Galinat, W.C. (1964). Domestication of corn. *Science*, 143, 538-545.
- Matthews, J.A., Feret, P.P., Madgewick, H.A.I. & Bramlett, D.L. (1975). Genetic control of dry matter distribution in twenty half-sib families of Virginia pine. Proceedings 13th Southern forestry tree improvement conference. pp.234-241.
- Matthews, J.D. (1975). Prospects for improvement by site amelioration, breeding and protection. *Philosophical Transactions of the Royal Society, London*, B.271, 115-138.
- Matziris, D.I. & Zobel, B.J. (1973). Inheritance and correlation of juvenile characteristics in loblolly pine (*Pinus taeda* L.). *Silvae Genetica*, 22, 38-45.
- Miller, W.E. (1965). Number of branchlets on red pine in young plantations. *Forest Science*, 11, 42-49.
- Mitchell, K.J. (1975). Dynamics and simulated yield of Douglas fir. Supplement to *Forest Science* 21. Monograph 17.
- Monteith, J.L. (1977). Climate and the efficiency of crop production in Britain. *Philosophical Transactions of the Royal Society, London*, B 281, 277-294.
- Monteith, J.L. (1978). Reassessment of maximum growth rates for C3 and C4 crops. *Experimental Agriculture*, 14, 1-5.
- Monteith, J.L. & Elston, J.F. (1971). Microclimatology and crop production. "Potential crop production". (Ed. by P.F. Wareing and J.P. Cooper). Heineman, London.
- Moore, P.D. (1974). Misunderstandings over C4 carbon fixation. *Nature, London* 252, 438-439.
- Muckadell, M.S. de (1959). Investigations on aging of apical meristems in woody plants and its importance in silviculture. *Forstlige Forsogsvaesen I., Denmark*, 25, 309-455.
- Oliver, D.J. & Zelitch, I. (1977). Increasing photosynthesis by inhibiting photorespiration with glyoxylate. *Science*, 196, 1450-1451.
- Ovington, J.D. (1957). Dry matter production by *Pinus sylvestris* L. *Annals of Botany*, 21, 287-316.
- Perry, T.O. (1976). Maternal effects on the early performance of tree progenies. "Tree physiology and yield improvement". (Ed. by M.G.R. Cannell and F.T. Last), pp.473-481. Academic Press, London and New York.
- Pollard, D.F.W. & Logan, K.T. (1977). The effects of light intensity, photoperiod, soil moisture potential and temperature on bud morphogenesis in *Picea* species. *Canadian Journal of Forest Research*, 7, 415-421.
- Potter, J.F. & Jones, J.W. (1977). Leaf area partitioning as an

- important factor in growth. *Plant Physiology*, 59, 10-14.
- Radner, R. & Kok, B. (1977). Photosynthesis: limited yields, unlimited dreams. *Bioscience*, 27, 599-605.
- Rhodes, I. (1972). Yield, leaf area index and photosynthetic rate in some perennial ryegrass (*Lolium perenne* L.) selections. *Journal of Agricultural Science, Cambridge*, 78, 509-511.
- Rohmeder, E. (1951). *Beitrage zur Keimungsphysiologie der Forstpflanzen*. Bayerischer Landwirtschaftsverlag, München.
- Schaedle, M. (1975). Tree photosynthesis. *Annual Review of Plant Physiology*, 26, 101-115.
- Schultz, R.P. (1975). Intensive culture of southern pines: maximum yields on short rotations. *Iowa State Journal of Research*, 49, 325-337.
- Schwanitz, F. (1966). *The origin of cultivated plants*. Harvard University, Cambridge, Massachusetts, U.S.A.
- Sibma, L. (1968). Growth of a closed green surface in the Netherlands. *Netherlands Journal of Agricultural Science*, 16, 211-216.
- Simmonds, N.W. (1962). Variability in crop plants, its use and conservation. *Biological Review*, 37, 442-465.
- Snyder, E.B. & Allen, R.M. (1971). Competitive ability of slash pine analysed by genotype x environment stability method. *Proceedings 11th Southern forest tree improvement conference*. pp.142-147.
- Sweet, G.B. & Wareing, P.F. (1966). The relative growth rates of large and small seedlings in forest tree species. *Supplement to Forestry*. pp.110-117.
- Syme, J.R. (1972). Single-plant characters as a measure of field plot performance of wheat cultivars. *Australian Journal of Agricultural Research*, 23, 753-760.
- Templeton, J.K. (1968). Partition of assimilates. *Proceedings Natural Rubber Conference, Kuala Lumpur, Malaysia*. pp. 1-4.
- Thompson, S. (1974). Shoot growth and dry matter production in two contrasting provenances of *Pinus contorta* Dougl. Unpublished Ph.D. thesis, University of Aberdeen, Scotland.
- Tigerstedt, P.M.A. (1974). The application of ecological genetics principles to forest tree breeding. *Silvae Genetica*, 23, 62-66.
- Visser, T. (1976). A comparison of apple and pear seedlings with reference to the juvenile period. II. Mode of inheritance. *Euphytica*, 25, 339-342.
- Wallace, D.H., Ozburn, J.L. & Munger, H.M. (1972). Physiological genetics of crop yield. *Advances in Agronomy*, 24, 97-146.
- Wareing, P.F. & Matthews, J.D. (1973). Physiological and genetic factors determining productivity in species of forest trees. *Proceedings of 15th Congress of I.U.F.R.O.*,

- Gainesville, Florida, U.S.A. pp.136-143.
- Waring, R.H., Gholz, H.L. Grier, C.C. & Plummer, M.L. (1977). Evaluating stem conducting tissue as an estimator of leaf area in four woody angiosperms. *Canadian Journal of Botany*, 55, 1474-1477.
- Watson, D.J. (1971). Size, structure and activity of the productive systems of crops. "Potential crop production". (Ed. by P.F. Wareing and J.P. Cooper), pp.76-88. Heineman, London.
- Watson, J.D. & Witts, K.J. (1959). The net assimilation rates of wild and cultivated beets. *Annals of Botany*, 23, 431-439.
- Webb, W.L. (1977). Seasonal allocation of photoassimilated carbon in Douglas fir seedlings. *Plant Physiology*, 60, 320-322.
- Wells, O.O. (1969). Results of the southwide pine seed source study through 1968-9. Proceedings 10th Southern forestry tree improvement conference, Houston, Texas. pp. 117-129.
- Westlake, D.F. (1963). Comparisons of plant productivity. *Biological Review*, 38, 385-425.
- Wit, C.T. de (1968). Plant production. "Agricultural sciences and world food supply". (Ed. by S.J. Wellensiek). *Miscellaneous Publications #3*. Landbouwhogeschool, Wageningen, Netherlands.
- Wright, J.W. (1976). Introduction to forest genetics. Academic Press, London and New York.
- Young, H.E. (1973). Biomass nutrient elements harvesting and chipping in the complete tree concept. 10th Research conference, A.P.I.-T.A.P.P.I., College Relations Group, Point Clear, Alabama. 20 pp.
- Zarger, T.F. (1965). Performance of loblolly, shortleaf and eastern white pine superseedlings. *Silvae Genetica*, 14, 177-208.
- Zohary, D. (1969). The progenitors of wheat and barley in relation to domestication and agricultural dispersal in the Old World. "The domestication and exploitation of plants and animals". (Ed. by P.J. Ucko and G.W. Dimbleby), pp.47-66. Duckworth, London.

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THE GROWTH OF PLANTATION FORESTS

Chairman: R.C. Steele

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AN ECOLOGICAL BASIS FOR PREDICTING
THE GROWTH AND STABILITY OF PLANTATION FORESTS.

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SUMMARY

The widespread establishment of even-aged forests is one further stage in the intensification of forest management which has taken place in response to a continuous increase in the demand for forest products. Two problems are foreseen in the future management of these plantations which will require further evolution in silvicultural techniques.

(1) The growth rate of plantations must be increased and accurate predictions made of likely timber yield. Where the crop cycle is long this has to be achieved against a background of continuous variation in the conditions of growth and in the response of trees. The variation due to (i) long and short term cycles in the weather; (ii) the changing response of trees with different age at different levels of amelioration, is discussed. Classical yield table techniques are not suitable as a basis for predicting plantation growth under more intensive management systems. The potential of individual tree models to predict both the total yield of the forest and the distribution of different sizes of tree within it are examined.

(2) As plantations age, the standing yield of timber is increasingly at risk from such hazards as fire and windthrow. These are not to be seen as inevitable 'catastrophies'. Their incidence is a function of species, site and silvicultural system. The potential for developing a model of the ecological basis of windthrow is examined.

It is suggested that whilst there is considerable research into the component processes of forest growth and tree:site interactions, there are few investigations into the design of new silvicultural systems for

high production or the avoidance of hazards to production

RÉSUMÉ

La création de plus en plus étendue de forêts équiennes n'est qu'une étape dans l'intensification de la gestion forestière, due à la demande accrue de produits forestiers. La gestion future de ces plantations fera face à deux problèmes qui nécessiteront un développement plus grand des techniques sylvicoles.

(1) Le taux de croissance des plantations doit être augmenté et la prévision des productions doit devenir plus exacte: dans le cas d'une longue révolution il faudra tenir compte des variations continues des conditions de croissance des arbres et de leurs réactions. Nous traitons dans notre exposé des variations dues (i) aux cycles climatiques longs et courts, (ii) aux changements de réactions des arbres selon l'âge et les différents niveaux d'amélioration. Les tables de production classiques sont mal appropriées à la prévision de la production d'une plantation gérée intensivement. Nous examinons la possibilité d'établir des modèles-arbres permettant de prévoir la production totale du peuplement ainsi que les tailles des différents arbres qui la composent.

(2) A mesure que la forêt vieillit, le bois sur pied doit lutter de plus en plus contre les risques d'incendie et les chablis, qu'on ne doit pas considérer comme des 'catastrophes'. Ces incidents sont fonction à la fois des espèces, des stations et des systèmes sylvicoles. Nous indiquons la possibilité de développer un modèle basé sur le phénomène écologique du chablis.

Nous suggérons que, malgré des études considérables sur les divers procédés de la croissance d'une forêt et les interactions arbre/station, il y a un manque de recherches dans le domaine des modèles de sylviculture centrés sur une haute production ou sur les manières d'éviter les risques pour la production.

ZUSAMMENFASSUNG

Als Reaktion auf die ständige Zunahme der

Nachfrage nach Waldprodukten ist die verbreitete Begründung gleichaltriger Bestände eine weitere Phase in dem Entwicklungsprozess zu einer intensiveren Waldbewirtschaftung.

In der zukünftigen Bewirtschaftung dieser Bestände lassen sich zwei Probleme voraussehen, die eine weitere Entwicklung von Techniken in der Forstkultur erfordern:

(1) Man muss das Wachstum von Beständen beschleunigen und genaue Voraussagen der wahrscheinlichen Holzerträge machen. Das hat bei langen Umtriebszeiten unter Berücksichtigung eines ständigen Wechsels in den Wachstumsbedingungen und des Wachstums selbst zu geschehen. Hier wird der Wechsel diskutiert, der bedingt ist (i) durch lang- und kurzfristige Witterungsperioden und (ii) durch die mit Alter und Genotyp wechselnden Reaktionen.

Konventionelle Ertragstafeltechniken eignen sich nicht als Grundlage für die Prognose des Bestandeswachstums unter intensiveren Bewirtschaftungssystemen. Wir erfassen den Wuchsverlauf von Einzelbäumen als Modell, um sowohl den Gesamtertrag eines Waldes als auch die Ertragsverteilung in Abhängigkeit von der Baumhöhe zu erfassen.

(2) Mit zunehmendem Alter der Bestände ist die nutzbare Holzmasse immer mehr Risiken wie Feuer und Windbruch ausgesetzt. Diese werden nicht als unvermeidliche 'Katastrophen' betrachtet. Ihr Auftreten ist eine Funktion der Baumart, des Standorts und der waldbaulichen Situation. Wir untersuchen die Möglichkeit, auf ökologischer Basis ein Modell für Windbruch zu entwickeln.

Wir behaupten, dass es nur wenige Untersuchungen für die Entwicklung neuer waldbaulicher Systeme zur Ertragssteigerung oder zur Vermeidung von Produktionsrisiken gibt, während die Faktoren des Wachstumsprozesses von Beständen und die Wechselbeziehung Raum-Standort gründlich erforscht sind.

INTRODUCTION

Increase in the demand for timber and timber products is not a new phenomenon, neither is the evolution of silvicultural systems designed to meet this demand. Fifty years ago silviculturalists felt the pressure for more wood threatened the destruction of forests and sought ways of

managing them to cope with this.

"Forestry is now passing through a critical stage. The depletion of natural forests that has taken place during the past hundred years in many parts of the world gives genuine cause for alarm ... if the problem of future timber supplies is to be solved, it is (also) of the utmost importance that the reduced forest area now available should be treated in such a way as to produce the highest possible sustained yield of timber ..." (Troup 1928). Also, in 1928, Toumey put forward a basic concept which he considered should be followed in silvicultural practice. "Forest vegetation is composed of plant communities or units of vegetation developed and arranged in accordance with definite biological laws and is not an aggregation of trees and other plants brought together by chance" (in Toumey & Korstian 1947). Toumey's view of the forest as an ecological entity was strongly felt and he considered that his text on the foundations of silviculture "is not an outgrowth of plant ecology but rather plant ecology is an outgrowth of it".

The silvicultural systems of Troup and Toumey have their origins in tending natural forest to produce a sustained yield without destroying the forest itself. Their considered "ecological" basis is that yield is in balance with the site without recourse to large scale amelioration of site conditions. Since 1928 the demand for timber has continued to increase. This, combined with the worldwide reduction in areas of accessible natural forest, has led to the establishment of substantial areas of plantations in a wide variety of climates and frequently on land not previously forested. "Plantation forestry is subject to stringent demands requiring intervention during the growth of the crop to maintain or increase growth rates or to adjust the proportions of different timber sizes to be produced. This requires a further development in silvicultural systems which itself demands more detailed understanding of ecological processes underlying the growth and development of forests.

PROBLEMS OF GROWTH RATE AND THE DEVELOPMENT OF FOREST STRUCTURE IN A PLANTATION ENTERPRISE.

The culture of forest plantations involves more than just careful management of an existing ecosystem on conservative ecological principles - it is an extensive investment exercise with the following characteristics.

- (i) Plantations are frequently restricted to marginal lands with soils and climates which are poorer and more variable than those used for agriculture - these environments do not automatically support high yields and may present hazards such as windthrow, frosts etc.
- (ii) Timber is a bulky product, so that a large proportion of the cost of producing it is incurred in its transport to

processing mills. The plantation enterprise should be concentrated to minimize transport and investment costs, but yet must generate sufficient production to sustain the development of an industrial infra-structure (Boardman, this volume).

In commercial plantation forests with these characteristics there are three closely related problems of forest growth and development.

Achieving a predictable, high growth rate

Plantations are costly to establish in terms of land, roads and fencing, and so generally the higher the yield/area obtained, the greater the profitability. High growth rates also mean that processing plant can be supported from a smaller area of land, again minimizing costs. However, almost as important as achieving high growth rates, is the need to predict the yield of timber which will be obtained in order to develop the associated forest industry efficiently.

Protecting the forest against hazards and predicting risk

In many cases an even-aged plantation produces a forest structure which is at risk to destruction by strong winds, fire, animals (Crooke; König; Cooper & Mutch, this volume) and pathogens (Murray, this volume). Since the incidence of such hazards is related to the structure of the forest, attempts can be made to assess risk and devise silvicultural systems to minimize it.

The development of a balanced forest structure

Conflicting requirements can arise in relation to the optimum size and spatial distribution of stands of different species and age within a forest. This topic is dealt with in some detail by Malcolm and Davies in this volume. Management options in forest design are critically affected by the capacity to increase and secure production which themselves are influenced by variations in site and topography.

ACHIEVING A PREDICTABLE, HIGH GROWTH RATE.

Traditional methods of predicting forest yields require no detailed understanding of which factors control growth rates. A 'site index' is used to classify the productive capacity of each stand based on some aspect of the growth made up to the time of observation, most frequently height (Kreutzer, this volume). Future growth is predicted from a set of empirically constructed yield tables on two assumptions, (i) the productive capacity of the stand will not change, i.e. growth will follow a pattern established from previous stands which have been similarly classified, and (ii) a particular, prescribed silviculture is followed, which determines the frequency, severity and type of thinning during the course of growth. This technique of yield prediction originates largely from the work of German foresters of the nineteenth century in long-established forests (Assmann 1970) and is based on the

precept that the removal of a timber harvest should be in balance with the 'site'.

Over the years refinements have been made in the parameters used to measure site indices so that they relate more closely to productive capacity, e.g. in Britain production classes used in conjunction with general yield classes, to incorporate a measure of stand basal area as well as height (Hamilton & Christie 1971). Another development has been to stratify forest sites in relation to physiography and various measurable site factors before constructing yield tables. However, as Kreuzer (this volume) has pointed out, whilst this approach has made predictions more accurate, it has also raised many questions about the relationships between various environmental factors and forest growth. One needs to know which variables to choose when making yield class stratifications. These are exactly the questions that we must answer to understand how to increase the growth rate of established stands.

The stage has now been reached where we should question the extent to which this yield table technique is an appropriate model for yield prediction in plantation forestry.

Neither of the two assumptions under which yield tables are constructed, are applicable to modern plantation silviculture! Plantations do not grow under uniform conditions and intervention may be required to accelerate (Davies, this volume) or maintain (Boardman, this volume) timber production. The removal of yield as thinnings has now become a more variable operation in response to the advent of new machinery (Hamilton 1976a), fluctuations in the demand for timber of different sizes, or the development of systems with no-thinning (Godwin 1968) or pre-commercial thinning (Fenton & Sutton 1968) silvicultures. We need to consider how these characteristics of plantation forestry may be incorporated into techniques for predicting yield.

Changes in 'site' conditions and tree response during the plantation cycle

Plant growth is regulated by the amounts of radiation, water and nutrients received or available and by conditions of temperature and humidity. These are not constant over the plantation cycle, neither is the level or type of tree response. There are three sources of variation (i) long and short term changes in weather patterns, (ii) continuous developments in stand microclimate and (iii) differences in response to environmental variation as the trees age or as the conditions for growth alter greatly. Let us consider these three sources of variation in turn.

(i) Changes in weather patterns. In extreme climates the width of tree rings may be very closely related to variation in a single environmental factor e.g. annual precipitation in arid zones (Fritts 1965). In more temperate regions, climatic

variation may not be so dramatic but still has a major influence on tree growth. Over twenty-eight sites in Colorado, Fritts et al. (1971) found that on average some 60-65 per cent of the variation in tree ring widths of three species was related to variables representing the seasonal march of climate. Different environmental variables were important on different sites, and whilst 20 per cent of the sites showed less than 50 per cent of the variation related to these variables, another 20 per cent showed more than 80 per cent of the variation so related.

Climatic cycles can have a substantial effect on growth. In a mature plantation of *Pinus sylvestris*, Miller, Miller & Binns (1977) showed that rings had varied from 0.5 mm to 1.25 mm in a regular way between the seventy-fourth and eighty-ninth year. They detected three significant cyclical patterns with periods of 42.0, 23.0 and 4.4 years. Fertilization increased the amplitude of the variation associated with these cycles.

The influence of short term, i.e. daily or weekly changes in the environment on tree growth has been largely ignored. Physiologists have tended to stress either the influence which conditions in one year may have on a subsequent year's growth (Kozlowski, Torrie & Marshall 1973), or the importance of trends in the development of trees during a season (Denne 1976).

'Carry over' effects from one year to the next are well-known in agricultural experimentation and must be taken into account when assessing the yields of crops under different treatments over a series of years (Patterson & Lowe 1970). In forests such evidence as exists suggests that these effects can be small compared with the effects of current season's weather. Over the twenty-eight Colorado sites investigated by Fritts et al (1971) only 15 per cent of the variation in ring width was 'explained' by correlation with the previous year's ring width, compared to 60-65 per cent variation 'explained' by current weather. For trees it has yet to be proved that there is a direct physiological influence on yield by one season's conditions on the next year's yield. The influence which variation in weather in one year has on growth in the next, seems most likely to be restricted to aspects of shoot elongation where bud development takes place a year in advance of extension. This may determine the number of needles which will be produced in the following year (Cannell, Thompson & Lines 1976), but both the size of needles and the total length of shoot on which they are carried are influenced by the amount of photosynthesis made during the year of growth itself (Little 1974).

Factors controlling the duration of the growth period are important, particularly with regard to bud development and shoot elongation. Variation in response to these factors is a

major source of exploitable genetic variation in growth (Perry, Cannell, this volume). However, within the limits set by the seasonal period of development, growth fluctuates in response to changes in the environment. In a plantation of Sitka spruce in the Scottish uplands, cell production by the cambium during the production of early wood varied between zero and twelve cells per radial file of tracheids per day, being greatest on days with high solar radiation (Ford, Robards & Piney 1978). In the same forest, the population of fine roots was found to decrease by up to 50 per cent over a fifteen-day period with no rain, but after heavy rainfall the population increased almost to its original size within five days (Deans in press). The magnitude of these effects varied between soil horizons and depended upon their particular microclimates. These results suggest that fast growth requires alternation of sunny and wet periods each with a duration of no more than a few days. Whilst cambial activity may respond to individual days of high radiation, long uninterrupted sequences will lead to the development of high moisture tension within the tree which checks cambial activity (Little 1975). The amplitude and frequency of weather changes may be as important to the achievement of high growth rates as the mean conditions and may explain some of the very high growth rates in mild, temperate climates (e.g. Tottenham & Joyce 1975).

(ii) Development of stand microclimate. The extent to which plantation growth is sensitive to changes in the environment, will depend upon its size and structure since this has a large influence on the microclimate of the stand. In a young plantation height increments were found to increase slowly until the branches from neighbouring trees overlapped. Increments then increased rapidly from year to year until competition between trees started (Cochrane & Ford 1978) from which time annual height increments oscillated around a mean. The precise environmental changes, which cause the acceleration of height increment and those which determine the limit of mean annual height increment are not known for this forest. The environmental factors which determine the size a forest canopy can attain and the size at which competition becomes important, have been variously specified as a balance between temperature and solar radiation (Nomoto 1964) and the ratio between incoming rain and potential transpiration (Grier & Running 1977). Whilst such combinations of factors may be predominant at the extremes of wet or dry climates, some more complex balance may be struck in intermediate zones between water balance, temperature and nutrition (Waring et al. 1978). Factors controlling maximum growth rate and the canopy size at which this maximum is achieved, are important areas for future research, since microclimate, e.g. increasing 'interception loss' with increasing forest size, is strongly implicated and

may possibly be manipulated through silvicultural techniques. Boardman (this volume) has pointed out that little opportunity may exist for rapid acceleration of growth rate once canopy closure has occurred. Silvicultures which depend largely on maintaining a closed canopy for long periods of time and taking a substantial proportion of their yield as thinnings, i.e. anticipating mortality, may not prove as flexible as those in which the rotation is short and final yield is a large proportion of total yield.

(iii) Differences in tree response. Alterations in the physiological characteristics of trees as they age, are well-known (Moorby & Waering 1963). Many of these are easy to predict and can be counted as intrinsic properties of the crop. Such ageing effects are likely to become important to strategies of increasing and predicting yield where differences are known to exist between and particularly within species. In a progeny trial with Ponderosa pine, Namkoong & Conkle (1976) found indications of trends in height growth which differed between the phases of plantation growth, planting site and family. More research on such differences is required to determine whether they are directly due to differences in genotype or indirectly due to differences in stand structure and therefore in microclimate.

A major consequence of accelerating growth rates through a treatment such as fertilization, is the production of wide growth rings (Davies, this volume) and a possible change in wood properties. Generally, sale of timber for structural purposes is more profitable than sale for pulp and industrial processing, but such timber must meet certain specifications of strength. This is determined by the properties of knottiness, wood density, grain angle and the incidence of compression wood. Tree spacing, thinning and pruning can all influence these properties (Brazier 1977) but the silvicultural technique of most interest for its effects on quality is fertilization, since this has the general effect of increasing total growth. Little is known of the effects of fertilizing on knottiness, grain angle and the incidence of compression wood and more research is required on these aspects of growth and their importance in determining wood strength (Brazier 1977).

Brazier (1977) reviewed a number of reports indicating that fertilization decreased wood density, which, by implication, would be expected to decrease timber strength. Exceptions to this are very slow growing trees which were initially producing 'starvation wood'. Fertilization increases the proportion of early wood, the cells of which have a high lumen area:wall thickness ratio. Smith, Wellwood & Elliot (1977) also reported this general result but suggested that climatic differences were important and could interact with fertilization to affect wood density. They also reported

differences in response to fertilization between trees. Finally, fertilization sometimes alters the form of trunks and hence the 'form factor' used in prediction (Flewelling & Yong 1976).

This examination of 'site' conditions and tree response leads to the following conclusions:

- (i) Trees respond to variation in weather over a range of frequencies and ameliorative treatments may amplify the effects of such variation.
- (ii) In temperate regions, unless irrigation is used or large reservoirs of soil moisture exist, the highest growth rates are likely to be achieved in conditions where there are rapid short term fluctuations in the weather.
- (iii) Where the growth process is largely controlled by the supply of a necessary resource, e.g. water, radiation, or nutrients, then forest growth rates will change markedly with age as the stand structure influences the microclimate. Ameliorative treatments, such as fertilization or drainage may accelerate these effects.
- (iv) Low input silvicultural systems, may neither respond adequately to 'ameliorative' treatments or if they do, may not produce timber of the same quality as originally intended.

The essential character of forest growth is that it is variable and intensification of management is likely to make it more so. Current mensurational techniques for predicting yield assume that the largest part of variation can be expressed in terms of a growth curve, either empirically constructed from the growth records of previous stands (Hamilton & Christie 1974a) or by attempting to fit various types of growth curves, e.g. logarithmic (Kilpatrick 1978) or the Richards growth function (Rawat & Franz 1974). Variation is treated as error. Neither approach provides a satisfactory basis for yield prediction of intensively managed plantation. Rather we should consider forest growth as being produced by a series of impulses under changing conditions and the appropriate mathematical structure for this is multivariate time series analysis (e.g. Box & Jenkins 1970). Growth can be analysed by time series techniques (Ford & Robbards 1976; Ford, Robbards & Piney 1978) and models for prediction using such techniques are increasingly in use in economics.

Manipulating and predicting the distribution of yield by adjusting stand structure

The distribution of yield from a plantation, both in time and in terms of the assortments of stem sizes, can be influenced by initial spacing (Hamilton & Christie 1974b) and by the thinning regime adopted (Assmann 1970). When yield tables are constructed by an empirical site index technique,

e.g. Hamilton & Christie (1974a), it is necessary to specify quite closely the particular thinning regime to be used and most frequently this has been some form of selective thinning. However, increasing interest in mechanical thinning (Hamilton 1976a), no-thinning (Godwin 1968), often combined with more intensive forest management and a range of harvesting techniques, have together stimulated attempts to model the competition process between individual trees with the object of providing more flexible predictions of growth and yield (Arney 1974; Munro 1974).

A number of curve fitting techniques have been applied to provide descriptions of stem size distributions in even-aged plantations, e.g. Baily & Dell (1973). However, a more fundamental approach, modelling the influence that a tree's neighbours may have on its growth, has recently been quite widely adapted. By concentrating on the growth of the individual, this approach offers a framework whereby all the major direct influences on growth may ultimately be incorporated into one model. It is intended that individual tree models which simulate the mechanisms of growth and competition will provide flexible predictive models, beyond the scope of conventional yield tables (Munro 1974).

Competition occurs for the resources used in growth and can be defined as a process. "When the immediate supply of a single factor necessary (for growth) falls below the combined demands of the individual plants, competition begins" (Clements quoted in Donald 1963). These resources, viz. light, water and nutrients, exist in finite concentrations so competition is a spatial process and its onset in a plant community depends upon the relative growth rates of the plants themselves. Thus, fertilization increases growth and accelerates the competition process (Yoda et al. 1963). The competition process has five characteristics which must be considered when a model is being constructed.

(i) Two plants of the same size may not have the same status in a community. If one has bigger neighbours than itself, whilst the other has smaller neighbours, the two individuals would not be expected to achieve the same growth in future. 'Success' in competition is a matter of probabilities - it depends upon the relative sizes of neighbours - so competition should be regarded as a stochastic process.

(ii) Competition in a plant monoculture can only be assessed by observing the distribution of relative growth rates, RGR, e.g. for basal area, square cm/square cm/yr. We must ask: "Has there been a change in the efficiency at which the growth machinery of the individual plant operates?" Little can be judged from the distribution of plant size in a community. This can take many forms (Ford 1975; Diggle & Ford, unpublished) as a community ages.

Absolute growth rate, e.g. for basal area, square centimeters/year, may not be a sensitive indicator of competition since it is greatly influenced by plant size. The necessity for observing RGR was illustrated by examining growth rates and RGRs of individual trees in a young Sitka spruce plantation in Scotland just reaching the stage when its annual production of needles was constant (Fig. 1). Ninety percent of the trees, i.e. those with basal area between 53 and 240 square centimeters, had the same relative growth rates, although there were considerable differences between them in size and in growth rate. Only the smallest 4 per cent and the largest 6 per cent had substantially different RGRs and showed the effects of competition. In an unthinned plantation, differences in mean RGR between size classes accentuated as the stand grew (Ford 1975).

(iii) The intensity of competition changes as a stand develops. In its simplest form this can be seen in differences found between young and old stands in calculated competition coefficients. These coefficients decrease with increasing age (Thomas & Stevens 1977).

(iv) The importance of competition in determining the distribution of final plant size may depend on the degree of site heterogeneity (Cannell et al. 1977) and genetic variability (Diggle & Ford unpublished).

(v) The competition process can influence the total amount of growth that a stand makes. Differences exist between trees within a stand in the amount of timber produced per unit of crown volume or crown surface area. In general, dominants and sub-dominants are more efficient than dominants, e.g. Hamilton (1969). But there are some suggestions that the largest trees in a stand can be less efficient than those slightly smaller. Some indication of this effect can be seen in Fig. 1 where the mean RGR of trees in the category of second largest basal area is higher than those of the largest basal area. Similar effects can be seen in some older unthinned plantations (Ford 1975). Differences in crown efficiency can also be produced by thinning treatments. In a series of experiments where selective thinning was maintained to remove increasing numbers of small trees (Krammer 1966), the mean individual crown volume was largest in the most severely thinned stands but timber production per unit of crown volume was lowest.

Competition models for even-aged forest stands are at an early stage of development. There are two important problems which must be faced, (i) relative tree status must be represented accurately and (ii) descriptions of the total amount of growth to be 'shared' amongst trees must be made flexible if the effects of different environmental factors are to be assessed.

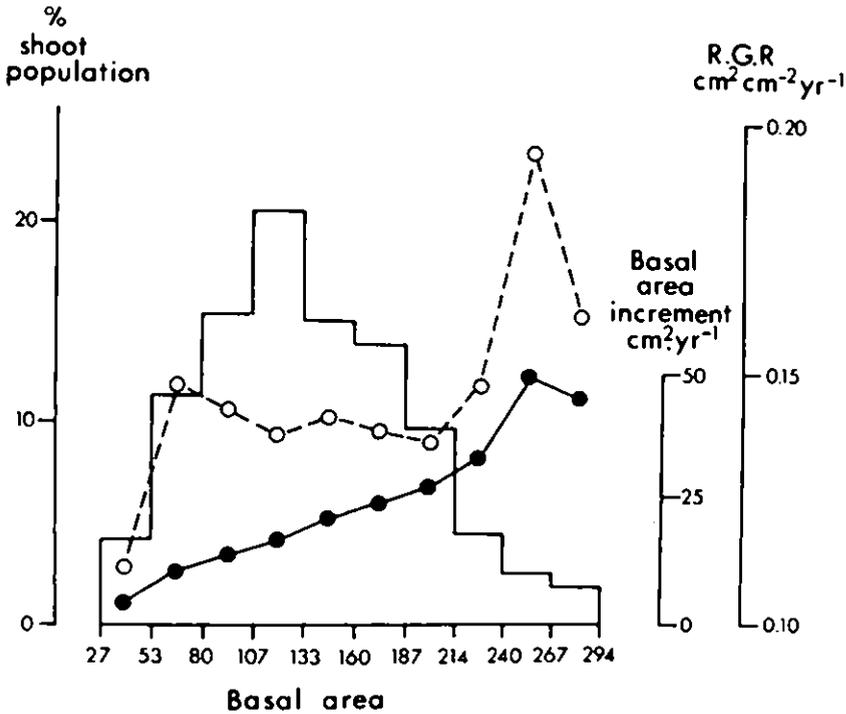


Fig. 1. Frequency distribution of trees by basal area and the mean basal area growth rate (closed circles) and basal area relative growth rate (open circles) for each basal area category in a 14yr plantation of Sitka spruce.

Some techniques for describing relative tree status are described in Fig. 2, but rarely has more than 60 per cent of the variation in growth between individuals been accounted for. Parameters are required to express the degree of influence which a plant may have on its neighbours. In some models a zone of influence is estimated for each tree as a function of its diameter (Bella 1971; Hegyi 1974) and interaction with other trees is calculated either as a function of the distance between neighbours or by estimating a zone of influence and calculating interaction as the summation of intersections, with a weighted influence in favour of large trees (Bella 1971) (Fig. 2). Neither tree diameter nor basal area are sufficiently accurate representations of tree size to

be used in competition models. They are integrated values of all growth made by the tree over the history of the stand and can only describe general differences between individuals; a more suitable measure would be basal area increment over the last year as this would give a better indication of the changing status of individuals. Basal area or diameter can not be directly related to the competition process as can measures such as height or crown size.

More functional measures of tree status have been used in stand simulations. Newnham & Smith (1964) modelled competition as the extent to which a tree crown was intersected by neighbours; Ek & Monserud (1974) used tree height in conjunction with an estimated crown radius (Fig. 2), whilst Mitchell (1969) simulated crown development directly as dependent upon branch growth which was in turn related to the proximity of neighbouring crowns. However, these three models, in common with many others, use the form and size of open grown trees as a base line for estimating growth and development. They do not simulate competition at the process level in terms of the relative distribution of resources for growth and this they would have to do in order to predict the effects of treatments such as fertilization on the distribution of tree sizes within the stand.

A strategy for modelling forest growth

Difficulties have been encountered with models designed to predict both the distribution of yield and growth in relation to site factors. Frequently this has been because the requirements of management have been kept too closely in view when formulating model structures. Accuracy requires an effective simulation of physiological and ecological processes but for ease of use, models must not be too complicated. I suggest a three level modelling strategy for producing a more reliable yield prediction technique for forest plantations.

(1) Basic growth models

Two are required, a physiologically based model of plant response to environmental variation and a population dynamics model of the competition process. The former should be modelled at the level of carbohydrate, water and nutrient balance of trees and should be able to predict the factors limiting growth as conditions vary. It should provide information on growth rate to a population model describing competition as a stochastic process. This second model should determine the rate of change of competition intensity as stands develop and the extent to which relative growth rates are determined by factors other than competition, particularly genetic variation.

(2) Growth-yield Linking models

Two models are required to link simulated growth of processes with yield prediction techniques. One to describe the distribution of yield over individual trees and how this

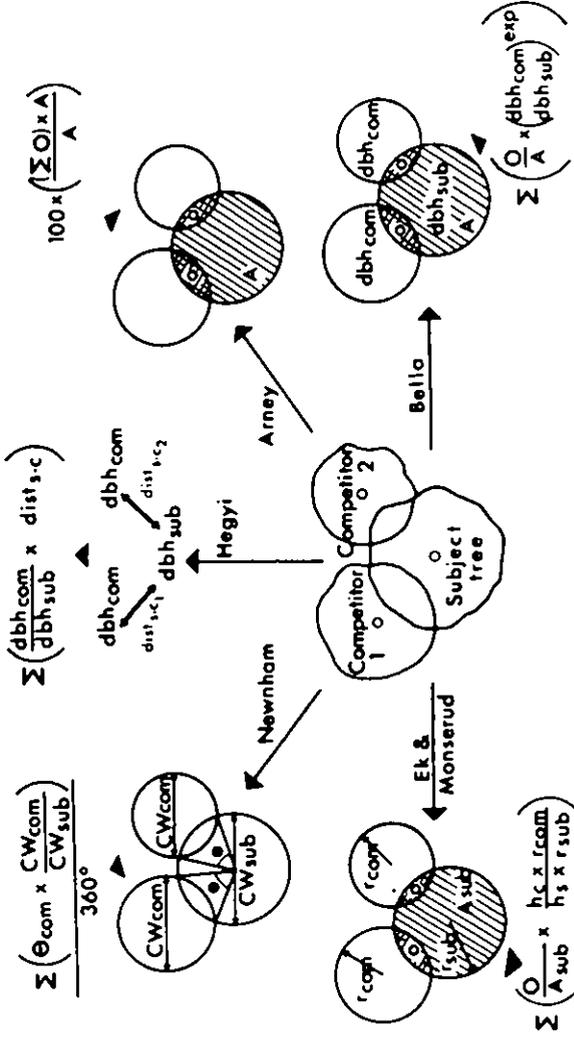


Fig. 2. Techniques for calculating relative tree status or competition coefficient suggested by various workers (references in text).

Subscripts: sub or s = subject tree, com or c = competitor tree.
 Area A = crown size estimated from open grown trees of same trunk size
 O = area of overlapping crowns, θ = angle of crown intersections
 CW = crown width, r = crown radius
 dbh = diameter at breast height, h = tree height

may vary under a range of conditions. Such a model would link physiological and competition models with the actual production of timber in terms of both total yield and quality. The second to describe the changes which can occur in stand microclimate as stand structure is manipulated. The object of this would be to provide the link between proposed silvicultural treatments and their effect on growth. Models in this category are the most neglected aspect of the science of yield prediction.

(3) Yield models

The prime object of these should be to estimate the 'error' in prediction. They should be capable of examining the likely fate of a proposed silvicultural treatment under a range of future weather patterns and management options.

HAZARDS TO PLANTATION DEVELOPMENT.

The fate of many forests is regeneration through destruction, by wind or fire (Malcolm; Adlard, this volume). When such a process occurs in a plantation it is considered to be a catastrophe and whilst this is certainly so as far as management is concerned, such catastrophes have ecological reasons and are not purely random events. The study of their ecology can provide insight leading to both control and prediction. Fire is a major hazard in dry climates, and attempts have been made to predict its occurrence in both scrub, e.g. Rothermel (1972) and forest, e.g. Davis & Irwin (1976), Cunningham & Martel (1973). Windthrow is a major hazard to plantation development in the United Kingdom (James & Dier 1968), the Irish Republic (Gallagher 1974), New Zealand (Irvine 1970; Wilson 1976), Australia (Cremer et al. 1978) and Germany (Hutte 1968).

Three groups of factors influence the occurrence of windthrow:

- (i) the frequency and strength of the wind,
- (ii) the interception of wind by the tree crown to create a drag force,
- (iii) the resistance to windthrow offered by soil and roots.

Our knowledge of how these interact is limited. Published studies have either analysed either a single factor, for example, resistance offered to windthrow by soil and roots (Fraser & Gardiner 1967) or the incidence of windthrow over a forest in relation to site and management factors after a gale has taken place. Unfortunately the latter type of analysis is complicated by methodological problems. In most plantations the distribution of species and soil types are confounded and certainly in the British Isles, soil type is confounded with topography. Most important of all, the cultural techniques used during establishment are confounded with age of crop. Consequently, the analysis of gale damage can be of very

limited value, even to predict future windthrow, let alone advance understanding of the mechanism itself. A further drawback is that the conditions which operate in major gales may not be closely related to those which are important in smaller but more frequent storms. The latter may cause substantial loss of timber (Gallagher 1974; Irvine 1970) and it is protection against them which is more frequently sought by forest managers (Booth 1974b).

(i) The frequency and strength of the wind

The arrival of wind storms cannot be predicted accurately, but, like other weather phenomena, must be treated as a stochastic process. However, wind has a complex structure (Allen 1968; Meroney 1968) and we need to know more about the combinations of factors which produce windthrow, such as the relationship between the duration of high mean wind speeds and the incidence of strong gusts and between wind speed and rainfall. Without this information detailed analysis of wind as a stochastic process in an attempt to predict risk may not be fruitful.

Hutte (1968), Irvine (1970) and O Cinneide (1974) have all suggested that storm damage is greatest in places where turbulence and wind speed are increased by relief, particularly on lee slopes. Measurements of variation in wind speed over a landscape were made with anemometers and were found to be related to topographic features (Hutte 1968). However, it is difficult to characterize the components of topography which effect wind microclimates. Flow round many regular objects can be predicted mathematically (Schlichting 1968), but flow over a specific natural topography cannot. In the U.K. attempts have been made to assess variations in wind speed in relation to topography by (a) using simple integrated measurements of wind run, e.g. tatter flags, (b) calculating 'topographic shelter', the sum of the horizon angles to the eight major compass points (Howell & Neustein 1966), and (c) constructing models of forest topography for use in wind tunnels. However, Booth (1974a) concluded that a combination of these techniques had not been proved helpful in stability zoning although recent work has proved more encouraging (Booth, personal communication). Measurements of wind speed at different points over model forests in wind tunnels have correlated well with anemometer data from the forest itself, although tatter flags and anemometer data did not correlate. The scale models incorporated either an exaggeration of vertical height or a roughened surface.

(ii) The interaction of wind with tree crowns

Susceptibility to windthrow has been related to increase in tree height (e.g. O Cinneide 1974) and, under U.K. silviculture, to increased thinning intensity (e.g. Booth 1974b). However, some evidence (Irvine 1970; O Cinneide 1974) suggests that windthrow risk peaks in plantations of middle

age when thinnings are frequent and that older stands are more stable. The disruption which thinning causes to the surface of the crop is generally considered to produce an uneven distribution of drag forces between the crowns (Mitcherlich 1974; Cremer et al. 1978). Two silvicultural techniques have been suggested to combat this problem and to produce a plantation with an undisturbed canopy as crop height approaches that of greatest windthrow risk. (a) No thinning throughout the life of the crop (Godwin 1968) combined with an early final felling; (b) early non-commercial thinning, designed to produce a short rotation crop which has an undisturbed canopy as the 'critical height' approaches and produces a final yield of sawlogs (Fenton & Sutton 1968 as applied in Irvine 1970; Moore 1976). Neither technique is fully tested and there is need for fundamental studies on these systems of the relationship between stand structure, the distribution of drag forces and windthrow.

Over the past decade a number of micrometeorologists have measured wind profiles over and within forest canopies (Jarvis, James & Landsberg 1976). Most usually their objective has been to assess the importance of ventilation of the canopy in the transfer of heat, water vapour and carbon dioxide between the atmosphere and the crop. The logarithmic wind speed profile has usually been assumed, which for tall vegetation is

$$U(z) = \frac{U_*}{k} \ln \frac{z-d}{z_0}$$

where $U(z)$ is the wind speed at height z ,

U_* is the 'friction' velocity or 'eddy' velocity and represents the rapidity with which momentum finds its way to the surface.

k is a constant

d is the zero plane displacement

z_0 is the 'roughness length' of the surface.

d and z_0 are parameters which give some indication of the aerodynamic characteristics of a surface. d indicates the mean level of action at which momentum is absorbed by the individual elements of the plant community: the level of action of the bulk aerodynamic drag on the community. The size of z_0 specifies the bulk effectiveness of the canopy as a momentum absorber.

However, although variation in d/h and z_0/h have been found for crops with different structures, the potential of such parameters for analysing susceptibility to windthrow seems limited for the following reasons. (a) Large uniform areas of forest are required to determine z_0 and d accurately. (b) d and z_0 can be determined only for wind profiles obtained under the limited conditions of no exchange of heat between the canopy and the atmosphere (but see Jarvis,

James & Landsberg 1976). (c) The use of the logarithmic profile to describe momentum exchange for vegetation greater than 2m high is being increasingly questioned. The three-dimensional structure of tall crops (Ford 1976) may influence momentum transfer (Mulhearn & Finnigan 1978). From a theoretical analysis, Perrier et al. (1972) considered that the logarithmic profile could only be applied to a tall row crop when the inter-row cavities were completely filled with foliage. For other crop structures they described the wind profile in terms of the different degrees of mixing of the wakes and vortices which develop behind individual roughness elements.

Papesch (1974) emphasised that more attention must be paid to the structure of the wind when considering the forces which act to produce windthrow. Wind does not provide a constant force but one which occurs in gusts. A wind can be described in terms of its turbulence structure, i.e. the relative amounts of energy which it contains as little gusts, high frequency energy, and large gusts, low frequency energy. Observations made across a forest edge showed a reduction in total energy as the wind passed from a grassland over the forest, but a relative concentration of energy at higher frequencies close to the natural sway period of the trees. This was due to interaction with the tree crowns.

Papesch (1974) developed a mathematical formulation for the relationship between the wind, tree crown and the movement of the tree combining both static parameters, such as mean wind speed, and dynamic description, such as the oscillation in wind amplitude. One interesting prediction from calculations with this model was that, under the same general conditions, when edge trees required a mean wind speed of 80 mph to blow them down, trees within the forest required a mean wind speed of only 62 mph. It is indeed a common occurrence that edge trees are the only ones left standing after windblow. A greater fluctuation of the forces acting on trees just behind the forest edge was predicted from wind tunnel studies with static forest models by Fraser (1964).

Testing the analysis developed by Papesch requires (a) more comprehensive measurements of the frequency distribution of wind energy over forest canopies of different types (Bull & Reynolds 1968), (b) more detailed analyses of the dynamic response of tree crowns to increase in wind speed (Mayhead 1973), and (c) the development of methods to describe the configuration of the canopy surface (Ford 1976) and to apply these to the changes in shape which occur as the wind blows. With this information experiments to investigate the distribution of drag forces could be conducted in windtunnels (see Marshall 1971 for an agricultural application) with more 'realistic' forests than have been used to-date.

(iii) The resistance to windthrow produced by soil and roots

Early studies in the plantations of upland Britain indicated that windthrow occurred principally on shallow rooted crops growing in soils with impeded drainage, most typically peaty gleys (Fraser & Gardiner 1967; Pyatt 1968). On gleyed soils closely spaced deep ditches were ploughed to dry the soil and enhance transplant growth (Taylor 1970). This technique has now been revised since tree pulling experiments on gleyed soils indicated that lateral spread of roots between widely spaced ploughing ditches (4.27 m) was more effective in promoting stability than the small increase in rooting depth which could be achieved with closely spaced (1.22 m) ploughing ditches (Booth 1974b).

The relationship between root growth, soil conditions and stability is complex. Cremer et al. (1978) measured soil shear strength on well-drained and poorly drained soils in a Pinus radiata plantation near Canberra, Australia, shortly after a destructive gale. The mean relative shear strength of the undisturbed poorly drained soils was 1.0 compared with 2.0 for undisturbed well-drained soils. However, within the root balls of blown trees the relative shear strengths were respectively 5.3 and 3.2 for poorly and well-drained sites. On the intrinsically mechanically weaker soils the root balls had grown firmer and to a larger diameter with better lateral attachment but poorer vertical hold. Cremer et al. (1978) did not identify the mechanically weaker soil as being more prone to windthrow.

Shallow root growth is frequently attributed to the occurrence of some impenetrable zone in the soil or to waterlogging. However, concentration of roots at the surface of forest soils is the rule rather than the exception (e.g. Eis 1974). Following a destructive gale in New Zealand, Irvine (1970) concluded that shallow rooting was prevalent among uprooted Pinus radiata but that this was a response to the distribution of nutrients in the soil since these were located in the surface soil horizons. Ford & Deans (1977) analysed the growth of fine roots in an eleven year old plantation of Picea sitchensis on a peaty gley in Scotland. A distinctive and more active root population was found in the surface soil and those soil horizons formed beneath turf upturned during ploughing. Most fine roots were found in soil with the largest concentrations of available nutrients. The importance of the upturned turf ribbon as a source of nutrients on gleyed sites and its role in root development has also been stressed by Savill (1976). Increasing the available nutrient to a stand by fertilizing increases the total amount of root (Paavilainen 1967) and root thickening is also increased by increased nutrient concentration (Coutts & Phillipson (1976). Further work is required to determine the effect which cultural techniques may have on the mineralisation process and how this

may vary with soils of different basic nutrient status and physical characteristics.

Mineralization requires specific physical conditions (Heal, this volume) and may not proceed at a uniform rate in all parts of the forest soil and this could affect the distribution of root growth. Deans (in press) has shown that in a young plantation of *Picea sitchensis* in the southern uplands of Scotland with an annual rainfall 1800 mm/yr, root mortality can occur during the summer months and is associated with drying out of the soil. The distribution of water to the soil of this plantation is very localized, some 40 percent of water received during the summer months flows down stems (Ford & Deans 1978), a phenomenon which may have a direct influence on root growth and may also influence the mineralization process in the soil. McColl (1973) has demonstrated that mineralization is enhanced by the passage of a wetting front through a soil horizon.

Before a silviculture can be specifically designed for windy areas, further research is necessary into all three of these factors:

- (i) to define the frequency and spatial variability of risk,
- (ii) to search for variability which may exist between canopies of different structure in the dissipation of momentum,
- (iii) to formulate the relative importance of soil moisture, nutrient concentration and physical impediment to the lateral and vertical spread of roots and to examine more precisely the influence which different root structures may have on stability.

Some interesting silvicultures for windy areas have been proposed. From different regions both Irvine (1970) in New Zealand and Moore (1976) in Ireland have suggested that widely spaced crops could be grown over short rotations without production thinning. Mitcherlich (1974) has suggested that on gentle terrain planting in strips with the youngest trees up-wind can improve stability and both Fraser (1964) and Mitcherlich (1974) have suggested high pruning or early thinning of edge trees to reduce turbulence above the canopy just interior to the edge. Hengst & Schulz (1976) have suggested that specific silvicultures be applied to match topography in a wind damaged forest, including the creation of a new network of forest roads with specially structured stand margins and conversion of uniform stands to mosaics of different species and ages. Following a comprehensive description of the linked catastrophies of windthrow and fire which occur in Lower Saxony Otto (1976) described silvicultures for a range of soil types which would minimize risk. He particular stressed the advantages of wide spacing and species mixtures.

CONCLUSIONS

The intensification of forest management with a general trend towards higher growth rates and realisation of yield, secure against wind and other hazards, have continuously produced research problems. In some cases the solutions to a number of these problems imply a need to change the silvicultural system. For instance, a suggestion has been made in both the British Isles and New Zealand to increase spacing, shorten the rotation and abandon commercial thinning in conifer plantations. This silvicultural system has been proposed both to minimize risk from windthrow and to shorten the time in which saw timber can be obtained. In implementation it is not a single alternative to high density crops which require thinning; interactions between spacing, quality of planting stock and pre-commercial thinnings must all be considered (Bunn 1974).

When such radical proposals are made, it is profitable to consider them as a 'new' silviculture and to question other aspects of the cultural technique. Dawson (1975) emphasized that "intensive culture is concerned with a number of culture treatments applied to the same stand, not just one or two practices as generally in 'timber stand improvement'". The large gains made in agricultural productivity have been through the application of not one, but a number of improvements working together. In this respect it is important to appreciate that from the economic viewpoint "the extremes of intense culture are quite expensive and are, in this sense, high risk" (Bentley 1975). This makes it all the more important to define the objectives of a plantation enterprise more closely than 'maximum sustained yield' (Elliott 1977). The opportunities for devising high yield silvicultures are greater when a range of specific objectives can be given rather than one general objective. Not only can the physiologist, breeder and ecologist work towards more closely defined endpoints, but particular advantage can be taken of natural variations which occur both in the biological and the physical resources (Patterson 1975). Attempts to design silvicultures to meet specific management objectives in specific climates and on specific soils would provide a stimulus to the further incorporation of plant physiological and ecological knowledge into the forest industry.

REFERENCES

- Allen, L.H. (1968). Turbulence and wind spectre within a Japanese larch plantation. *Journal of Applied Meteorology*, 7, 73-78.
- Arney, J.D. (1974). An individual tree model for stand simulation in Douglas fir. "Growth models for tree and stand simulation" (Ed. by J. Fries), pp. 38-46. Research Notes #30, Department of Forest Yield Research, Royal

College of Forestry, Stockholm.

- Assman, E. (1970). *The principles of forest yield study*. Pergamon Press, Oxford.
- Bailey, R.L. & Dell, T.R. (1973). Quantifying diameter distributions with the Weibull function. *Forest Science*, 19, 97-104.
- Bella, I.E. (1971). A new competition model for individual trees. *Forest Science*, 17, 364-372.
- Bentley, W.R. (1975). Economic environment of intensive culture. *Iowa State Journal of Research*, 49, 275-277.
- Booth, T.C. (1974a). Topography and wind risk. *Irish Forestry*, 31, 130-134.
- Booth, T.C. (1974b). Silviculture and management of high-risk forests in Great Britain. *Irish Forestry*, 31, 145-153.
- Box, G.E.P. & Jenkins, G.M. (1970). *Time series analysis forecasting and control*. Holden-Day, San Francisco.
- Brazier, J.D. (1977). The effect of forest practices on quality of the harvested crop. *Forestry*, 50, 49-66.
- Bull, G.A.D. & Reynolds, E.R.G. (1968). Wind turbulence generated by vegetation and its implications. *Supplement to Forestry*, pp.28-37.
- Bunn, E.M. (1974). Production forestry in the 1980s. *New Zealand Journal of Forestry*, 19, 181-190.
- Cannell, M.G.R., Thompson, S. & Lines, R. (1976). An analysis of inherent differences in shoot growth within some north temperate conifers. "Tree Physiology and Yield Improvement" (Ed. by M.G.R. Cannell and F.T. Last) pp.173-205. Academic Press, London and New York.
- Cochrane, L.A. & Ford, E.D. (1978). Growth of a Sitka spruce plantation: analysis and stochastic description of the development of the branching structure. *Journal of Applied Ecology*, 15, 227-244.
- Coutts, M.P. & Philipson, J.J. (1976). The influence of mineral nutrition on the root development of trees. I. The growth of Sitka spruce with divided root systems. *Journal of Experimental Botany*, 27, 1102-1111.
- Cremer, K.W., Myers, B.J., Duys, F.P. van der & Craig, I.E. (1977). Silvicultural lessons from the 1974 windthrow in radiata pine plantations near Canberra. *Australian Forestry*, 40, 274-292.
- Cunningham, A.A. & Mortel, D.L. (1973). A stochastic model for the occurrence of man-caused fires. *Canadian Journal of Forest Science*, 3, 282-287.
- Davis, J.B. & Irwin, R.L. (1976). FOCUS: a computerized approach to fire management planning. *Journal of Forestry*, 74, 615-618.
- Dawson, D.H. (1975). Are cultural methods available to maximize yields? *Iowa State Journal of Research*, 49, 279-280.
- Deans, J.D. (in press). Fluctuations of the soil environment and fine root growth in a young Sitka spruce plantation.

Plant and Soil.

- Denne, M.P. (1976). Effects of environmental change on wood production and wood structure in Picea sitchensis seedlings. *Annals of Botany*, 40, 1017-1028.
- Diggle, P.J. & Ford, E.D. Competition in plant monocultures as a spatial stochastic process. Unpublished manuscript. Institute of Terrestrial Ecology, U.K.
- Donald, C.M. (1963). Competition among crop and pasture plants. *Advances in Agronomy*, 15, 1-118.
- Eis, S. (1974). Root system morphology of western hemlock, western red cedar and Douglas fir. *Canadian Journal of Forestry Research*, 4, 28-38.
- Ek, A.R. & Monserad, R.A. (1974). Trials with program FOREST: growth and reproduction simulation for mixed species even- or uneven-aged forest stands. "Growth models for tree and stand simulation" (Ed. by J. Fries) pp.56-73. *Research Notes #30*, Department of Forest Yield Research, Royal College of Forestry, Stockholm.
- Elliott, D.A. (1977). Plantation forestry: the future - a state forester's viewpoint. *New Zealand Journal of Forestry*, 22, 229-232.
- Fenton, R.T. & Sutton, W.R. (1968). Silvicultural proposals for radiata pine on high quality sites. *New Zealand Journal of Forestry*, 13, 220-228.
- Flewelling, J.W. & Yong, Y.C. (1976). Tree volume table growth relationships possibly affected by fertilization. *Forest Science*, 22, 58-60.
- Ford, E.D. (1975). Competition and stand structure in some even-aged plant monocultures. *Journal of Ecology*, 63, 311-333.
- Ford, E.D. (1976). The canopy of a Scots pine forest: description of a surface of complex roughness. *Agricultural Meteorology*, 17, 9-32.
- Ford, E.D. & Deans, J.D. (1977). Growth of a Sitka spruce plantation: spatial distribution and seasonal fluctuations of lengths, weights and carbohydrate concentrations of fine roots. *Plant and Soil*, 47, 463-485.
- Ford, E.D. & Deans, J.D. (1978). The influence of canopy structure on the pattern of rainfall distribution to the floor of a Sitka spruce plantation. *Journal of Applied Ecology*, 15, 807-819.
- Ford, E.D. & Robards, A.W. (1976). Short term variation in tracheid development in the early wood of Picea sitchensis. "Wood structure in biological and technical research" (Ed. by A.J. Bolton, D.M. Catlin and P. Baas), pp.212-221. Leiden University Press, Netherlands.
- Ford, E.D., Robards, A.W. & Piney, M.D. (1978). Influence of environmental factors on cell production and differentiation in the early wood of Picea sitchensis.

- Annals of Botany, 42, 683-692.
- Fraser, A.I. (1964). Wind tunnel and other related studies on coniferous trees and other crops. *Scottish Forestry*, 18, 84-92.
- Fraser, A.I. & Gardiner, J.B.H. (1967). Rooting and stability in Sitka spruce. *Bulletin of the Forestry Commission* #40.
- Fritts, H.C. (1965). Tree-ring evidence for climatic changes in western North America. *Monthly Weather Review*, 93, 421-443.
- Fritts, H.C., Blasing, T.J., Hayden, B.B. & Kutzbach, J.E. (1971). Multivariate techniques for specifying tree growth and climate relations and for reconstructing anomalies in paleoclimate. *Journal of Applied Meteorology*, 10, 845-864.
- Gallagher, G.J. (1974). Windthrow in state forests of the Republic of Ireland. *Irish Forestry*, 31, 154-167.
- Godwin, G.E. (1968). The influence of wind on forest management and planning. *Supplement to Forestry*, pp.60-6.
- Grier, G.C. & Running, S.W. (1977). Leaf area of mature northwestern coniferous forests: relation to site water balance. *Ecology*, 58, 893-899.
- Hamilton, G.J. (1969). The dependence of volume increment of individual trees on dominance, crown dimensions and competition. *Forestry*, 42, 133-144.
- Hamilton, G.J. (1976a). Different thinning methods and their influence on yield. *Proceedings 16th I.U.F.R.O. Congress Oslo, Division IV*. pp.324-32.
- Hamilton, G.J. (Ed.) (1976b). *Aspects of thinning*. *Forestry Commission Bulletin #55*. Her Majesty's Stationery Office, London.
- Hamilton, G.J. & Christie, J.M. (1971). *Forest Management Tables (metric)*. *Forestry Commission Booklet #34*. Her Majesty's Stationery Office, London.
- Hamilton, G.J. & Christie, J.M. (1974a). Construction and application of stand yield models. "Growth models for tree and stand simulation" (Ed. by J.Fries), pp.222-239. *Research Notes #30*, Department of Forest Yield Research, Royal College of Forestry, Stockholm.
- Hamilton, G.J. & Christie, J.M. (1974b). Influence of spacing on crop characteristics and yield. *Forestry Commission Bulletin #52*. Her Majesty's Stationery Office, London.
- Hegyí, F. (1974). A simulation model for managing jack pine stands. "Growth models for tree and stand simulation" (Ed. by J.Fries), pp.74-90. *Research Notes #30*, Department of Forest Yield Research, Royal College of Forestry, Stockholm.
- Hengst, E. & Schulz, W. (1976). Beispiele zur Herstellung der räumlichen Ordnung als Massnahme für eine Erhöhung der Betriebssicherheit im Fichtenwald (Informationsartikel mit Depotangabe). *Wissenschaftliche Zeitschrift der*

- Technischen Universität Dresden, 25, 313-314.
- Howell, R. & Neustein, S.A. (1966). The influence of geomorphic shelter on exposure to wind in northern Britain. Report of Forestry Research 1965, Forestry Commission, Her Majesty's Stationery Office, London.
- Hutte, P. (1968). Experiments of windflow and wind damage in Germany; site and susceptibility of spruce forests to storm damage. Supplement to Forestry, pp.20-27.
- Irvine, R.E. (1970). The significance of windthrow for Pinus radiata management in the Nelson district. New Zealand Journal of Forestry, 15, 57-68.
- James, J.E. & Dier, H.V.S. (1968). Wind damage in Forestry Commission forests and its influence on management. Supplement to Forestry, pp.78-83.
- Jarvis, P.G., James, G.B. & Landsberg, J.J. (1976). Coniferous forest. "Vegetation and atmosphere" Volume 2. (Ed. by J.L. Monteith), pp.171-240. Academic Press, London and New York.
- Kilpatrick, D.J. (1978). Growth models for unthinned stands of Sitka spruce in Northern Ireland. Forestry, 51, 47-56.
- Kozłowski, T.T., Torrie, J.H. & Marshall, P.E. (1973). Predictability of shoot length from bud size in Pinus resinosa Ait. Canadian Journal of Forest Research, 3, 34-38.
- Krammer, H. (1966). Crown development in conifer stands in Scotland as influenced by initial spacing and subsequent thinning treatment. Forestry, 39, 40-58.
- Little, C.H.A. (1974). Relationship between the starch level at bud break and current shoot growth in Abies balsamea. Canadian Journal of Forest Research, 4, 268-273.
- Little, C.H.A. (1975). Inhibition of cambial activity in Abies balsamea by internal water stress: role of abscisic acid. Canadian Journal of Botany, 53, 3041-3050.
- Marshall, J.K. (1971). Drag measurements in roughness arrays of varying density and distribution. Agricultural Meteorology, 8, 269-292.
- Mayhead, G.J. (1973). Some drag coefficients for British forest trees derived from wind tunnel studies. Agricultural Meteorology, 12, 123-130.
- McCull, J.G. (1973). Environmental factors influencing ion transport in a Douglas fir forest soil in western Washington. Journal of Ecology, 61, 71-83.
- Meroney, R.N. (1968). Characteristics of wind and turbulence in and above model forests. Journal of Applied Meteorology, 7, 780-788.
- Miller, H.G., Miller, J.D. & Binns, W.O. (1977). Growth of Scots pine under nutritional and climatic stress. Plant and Soil, 48, 103-114.
- Mitchell, K.J. (1969). Simulation of the growth of even-aged stands of white spruce. Bulletin #75, School of Forestry,

Yale University. 48pp.

- Mitcherlich, G. (1974). Sturmgefahr und Sturmsicherung. Schweizerische Zeitschrift für Forstwesen, 125, 199-216.
- Moorby, J. & Waring, P.F. (1963). Ageing in woody plants. Annals of Botany, 27, 291-308.
- Moore, D.G. (1976). The oceanic forest. Irish Forestry, 33, 4-15.
- Mulhearn, P.J. & Finnigan, J.J. (1978). Turbulent flow over a very rough, random surface. Boundary-Layer Meteorology, 15, 109-132.
- Munro, D.D. (1974). Forest growth models - a prognosis. "Growth models for tree and stand simulation" (Ed. by J.Fries), pp.7-21. Research Notes #30, Department of Forest Yield Research, Royal College of Forestry, Stockholm.
- Namkoong, G. & Congle, M.T. (1976). Time trends in genetic control of height growth in ponderosa pine. Forest Science, 22, 2-12.
- Newnham, R.M. & Smith, J.H.G. (1964). Development and testing of stand models for Douglas fir and lodgepole pine. Forest Chronicle, 40, 494-502.
- Nomoto, N. (1964). Primary productivity of beech forest in Japan. Japanese Journal of Botany, 18, 385-421.
- O Cinneide, M.S. (1974). Quantitative assessment of the relative importance and cooperative effects of factors influencing forest instability. Irish Forestry, 31, 135-144.
- Otto, H.-J. (1976). Forstliche Erfahrung und Folgerungen aus den Waldkatastrophen in Niedersachsen. Forst- und Holzwirt, 31, 285-295.
- Paavilainen, E. (1967). The effect of fertilization on the root systems of swamp pine stands. Folia Forestalia Fennica, 31, 1-9.
- Papesch, A.J.G. (1974). A simplified theoretical analysis of the factors that influence windthrow of trees. Proceedings of the 5th Australasian Conference on Hydraulics and Fluid Mechanics. University of Canterbury, Christchurch, New Zealand. pp.235-42.
- Patterson, D.B. (1975). Silvicultural practices on extensive areas of complex sites. Scottish Forestry, 29, 140-144.
- Patterson, H.D. & Lowe, B.I. (1970). The errors of long-term experiments. Journal of Agricultural Science, 74, 53-60.
- Perrier, E.R., Robertson, J.M., Millington, R.J. & Peters, D.B. (1972). Spatial and temporal variation of wind above and within a soyabean canopy. Agricultural Meteorology, 10, 443-465.
- Pyatt, D.G. (1968). Forest management surveys in forests affected by wind. Supplement to Forestry, pp.67-77.
- Rawat, A.S. & Franz, F. (1974). Detailed non-linear asymptotic regression studies on tree and stand growth with particular reference to forest yield research in Bavaria (Federal Republic of Germany) and India. "Growth Models

- for Tree and Stand Simulation" (Ed. by J.Fries), pp.180-221. Research Notes #30, Department of Forest Yield Research, Royal College of Forestry, Stockholm.
- Rothermel;R.C.(1972). A mathematical model for predicting fire spread in wildland fuels. U.S. Department of Agriculture Forest Service Research Paper INT.115. Intermountain Forest and Range Experimental Station, Ogden, Utah, U.S.A.
- Savill,P.S.(1976). The effect of drainage and ploughing of surface water gleys on rooting and windthrow of Sitka spruce in Northern Ireland. *Forestry*, 49, 133-141.
- Schlichting,H.(1968). Boundary layer theory. McGraw-Hill, London (6th ed.). 747pp.
- Smith,C.J., Wellwood,R.W. & Elliot,G.K.(1977). Effects of nitrogen fertilizer and current climate on wood properties of Corsican pine (*Pinus nigra* var. *maritima* (Ait.) Melv.). *Forestry*, 50, 117-138.
- Taylor,G.G.M.(1970). Ploughing practice in the Forestry Commission. Forest Record #73, Her Majesty's Stationery Office, London.
- Thom,A.S.(1975). Momentum, mass and heat exchange of plant communities. "Vegetation and atmosphere" Volume 1. (Ed. by J.L.Monteith), pp.57-109.
- Thomas,C.A. & Stevens,R.D.(1977). The influence of competition from nearby trees on the selection of western hemlock plus trees. Final Report Contract OSS7-02040, Science Sector, Science Procurement Branch. Supply and Services Branch, Government of Canada.
- Tottenham,R. & Joyce,P.M. (1975). Sitka spruce yield class 500! *Irish Forestry*, 32, 30-33.
- Toumey,J.W. & Korstian,C.F.(1947). Foundations of silviculture. John Wiley & Sons, New York.
- Troup,R.S.(1928). Silvicultural systems. Oxford University Press.
- Wareing,R.H., Emmingham,W.H., Grolz,H.L. & Grier,C.C.(1978). Variation in maximum leaf area of coniferous forests in Oregon and its ecological significance. *Forest Science*, 214, 131-40.
- Wilson,H.H.(1976). The effect of the gale of August 1975 on forests in Canterbury. *New Zealand Journal of Forestry*, 21, 133-140.
- Yoda,K., Kira,T., Ogawa,H. & Hozumi,H.(1963). Self-thinning in overcrowded pure stands under cultivated and natural conditions. *Journal of the Institute of Polytechniques, Osaka City University Series D*, 14, 107-129.

THE DEVELOPMENT OF A FLORA IN EVEN-AGED PLANTATIONS

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SUMMARY

When a conifer plantation is established there is a big change in the ground flora as the canopy closes. Under crops of Abies spp, Picea spp and Tsuga* spp, which generate heavy shade, vascular plants are largely eliminated during the thicket stage, and at least with the short rotations that are necessary in most of upland Britain, do not reappear in quantity before clearfelling. Bryophytes often increase, though under very dense canopies even these may be absent. Under the lighter canopies of Larix spp and Pinus spp a larger flora persists and there may often be an almost complete cover of vascular plants in the later stages of the rotation. The flora in western European conifer plantations is intermediate in composition between that of boreal forest and that of deciduous woodland. The fern Dryopteris dilatata* is a particularly characteristic feature. On clearfelling there is often a rapid increase of vascular plants. The composition of the reappearing flora and the speed of its re-establishment depend on the amounts of seed present in the soil and on the vegetation present on the site at the time of clearfelling. In many plantations there are large populations of viable seeds in the surface layers of the soil, densities of 1000-5000 seeds per sq.m being typical, though those in peat are much lower. Seeds of plants with wind dispersal seldom survive in the soil, and have to be replenished each year. Many plant species survive in marginal habitats in

*Nomenclature follows Clapham, Tutin & Warburg (1962), Dallimore & Jackson (1974), and Smith (1978).

forests, notably on roadsides and beside streams. A moderate to large number of lowland species immigrate on roadsides, thereby diversifying the flora of upland areas in Britain. However, many plants of marshes and bogs are eliminated in afforested areas, so that on balance there is little change in the number of species present.

RÉSUMÉ

L'établissement d'une plantation de conifères amène un changement important de la végétation (au niveau du sol) à mesure que la voûte des arbres se reforme. Dans le cas des essences (tels que Picea, Tsuga* et Abies) qui produisent beaucoup d'ombre, les plantes vasculaires sont largement éliminées au stade de fourré, et à cause des courtes révolutions, souvent nécessaires dans les régions élevées de Grande Bretagne, elles ne réapparaissent pas en quantité avant la coupe à blanc. Le nombre des bryophytes augmente souvent mais si le couvert est très épais, ils peuvent même être absents. Sous le couvert plus léger des Larix et des Pinus, la végétation persiste d'une manière plus importante et on peut souvent trouver une couverture presque complète de plantes vasculaires vers la fin de la révolution.

La composition de la flore des peuplements de conifères d'Europe occidentale est comprise entre celle des forêts boréales et celle des forêts de feuillus: la fougère Dryopteris dilatata* y est très caractéristique. Les coupes à blanc sont suivies d'un accroissement rapide de plantes vasculaires. La composition de cette flore et la rapidité de sa réinstallation dépendent de la quantité de graines présentes dans le sol et de la végétation existante au moment des coupes à blanc. On peut trouver dans de nombreux peuplements un grand nombre de graines viables dans les couches superficielles du sol, des densités de 1000-5000 graines/m.carré étant typiques, mais elles sont plus faibles dans les sols tourbeux. Les graines des plantes qui sont disséminées par le vent ne survivent que rarement dans le sol et doivent être réapportées chaque année. Beaucoup d'espèces survivent dans des stations marginales en forêt, surtout au bord des routes et des cours

d'eau. Un grand nombre d'espèces provenant de la plaine émigrent vers le bord des routes, amenant ainsi une certaine diversification de la flore de montagne en Grande Bretagne. Cependant de nombreuses espèces provenant de stations marécageuses sont éliminées dans les reboisements, ce qui nous montre qu'en fait, il n'y a pas de grand changement dans le nombre des espèces présentes.

ZUSAMMENFASSUNG

Eine Nadelbaumpflanzung führt zu einem grossen Wandel in der Bodenflora, sobald sich das Kronendach schliesst. Abies spp, Picea spp und Tsuga* spp beschatten so stark, dass Gefässpflanzen während des Dickungsstadiums weitgehend eliminiert werden und, zumindest bei den kurzen Umtriebszeiten, die fast überall im britischen Hochland nötig sind, auch bis zum Kahlschlag nicht mehr in nennenswertem Umfang auftauchen. Bryophyten breiten sich oft stärker aus, aber unter sehr dichtem Kronendach können sogar sie fehlen. Unter dem lichterem Kronendach von Larix spp und Pinus spp hält sich eine umfangreichere Flora. In späteren Stadien der Umtriebszeit bildet sich oft eine fast geschlossene Decke von Gefässpflanzen aus. Die Flora westeuropäischer Nadelbaumpflanzungen liegt in ihrer Zusammensetzung zwischen der eines borealen Nadelwaldes und der von Laubwäldern. Ein besonders charakteristisches Merkmal ist der Farn Dryopteris dilatata*. Nach dem Kahlschlag kommt es oft zu einer raschen Vermehrung der Gefässpflanzen. Die Zusammensetzung der wieder auftauchenden Flora und die Geschwindigkeit ihrer Ausbreitung sind abhängig von der Menge noch im Boden lagernder Samen und der Vegetation, die zur Zeit des Kahlschlags am Standort wächst. In vielen Pflanzungen liegen grosse Mengen lebensfähiger Samen in den obersten Bodenschichten. Dabie sind 1000-5000 Samen pro Quadratmeter durchaus typisch. In Torfböden liegt die Zahl allerdings niedriger. Vom Wind verbreitete Samen überleben selten im Boden und müssen jedes Jahr neu anfliegen.

Viele Pflanzenarten überleben in den Randgebieten der Wälder, hauptsächlich an Strassenrändern und an Flüssen. Eine mittlere bis grosse Zahl von Tieflandarten wandert

entlang der Strassenränder ein und bringt so Abwechslung in die Flora des britischen Hochlandes. Viele Marsch- und Moorpflanzen sind jedoch in Aufforstungsgebieten ausgestorben, so dass sich insgesamt die Artenzahl wenig ändert.

VASCULAR PLANTS AND BRYOPHYTES IN PLANTATIONS OF DIFFERENT TREE SPECIES.

In British plantations, the heaviest shade is cast by the canopy of Western hemlock (Tsuga heterophylla). There is virtually no ground flora, except perhaps in very old stands after heavy thinning; even bryophytes are excluded. Under hemlock, therefore, the development of the ground flora is restricted to the establishing phase before canopy closure.

Sitka spruce (Picea sitchensis) casts a shade that is less dark, and although vascular plants are normally scarce or absent, a bryophyte cover of perhaps 5-10 per cent is usual (Fig. 1). After planting, higher plants decline rapidly as the canopy closes (ten to fifteen years); there is little regrowth later. During establishment of the second rotation, higher plants are generally less abundant than they were at the same stage in the first rotation. The difference is due in part to ineffective recolonization of bare ground and in part to the presence of slash which suppresses the growth of most vegetation. Sprawling plants such as Rubus fruticosus and Corydalis claviculata can sometimes cover larger areas of slash effectively, but these plants are absent on the peatier soils where Sitka spruce is often planted.

The development of a bryophyte flora follows a totally different pattern. Bryophytes, mostly mosses, increase from the first, and may continue to increase after canopy closure. There is, however, much variation in the pattern of bryophyte development, depending on the condition of the crop and the dampness of the ground. Generally, the more successful the crop and the drier the ground, the fewer are the bryophytes. During establishment of the second rotation, perhaps because of reduced competition from higher plants, bryophytes are distinctly more numerous than at the same stage in the first rotation.

Norway spruce (Picea abies) casts a slightly less dense shade than Sitka spruce, with the result that there is a more abundant ground flora. Bråkenhielm (1977), working in Småland, South Sweden, followed the development of the ground flora in even-aged plantations of Norway spruce on abandoned arable land over a period of ten years. The general pattern was similar to that under Sitka spruce in Britain, with higher plants decreasing and bryophytes increasing during the first ten years, followed by a rapid decline of higher plants as the canopy closed, and somewhat inconsistent changes in the bryophytes. There were, however, marked differences later. In

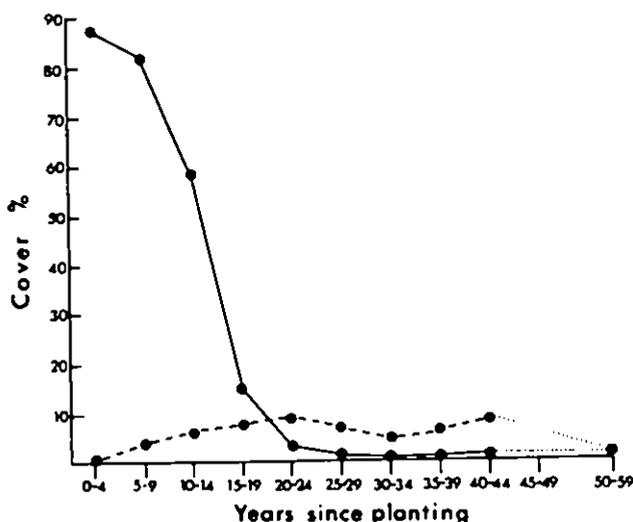


Fig. 1. Cover of vascular plants (solid line) and bryophytes (dotted line) in relation to age of crop in plantations of *Picea sitchensis* in upland Britain.

particular, a woodland flora including some vascular plants began to establish itself when the crop was cleaned by felling of hardwoods and subordinate spruce at about twenty years. The vascular plants increased appreciably at the time of first thinning, about thirty years, but as the canopy reclosed they decreased again. Woodland bryophytes, on the other hand, also increased at this time, but did not die back as the canopy reclosed.

Pines (*Pinus* spp) and larches (*Larix* spp) cast a lighter shade than spruces, so that a larger ground flora is normally present through the rotation (Fig. 2). The cover of bryophytes is similar to that found under spruces. Unlike the pattern under spruces, there is a large increase in the cover of the ground flora towards the end of the rotation.

The flora of broad-leaved plantations will not be considered here, except to remark that although vernal species such as *Anemone nemorosa* and *Endymion nonscriptus* may become abundant on better soils in lowland areas, these plants do not generally increase under broad-leaved crops on the peatier soils of upland Britain. For example, the ground flora was examined in a Forestry Commission experiment at Clocaenog Forest, North Wales, where forty-three year-old stands of

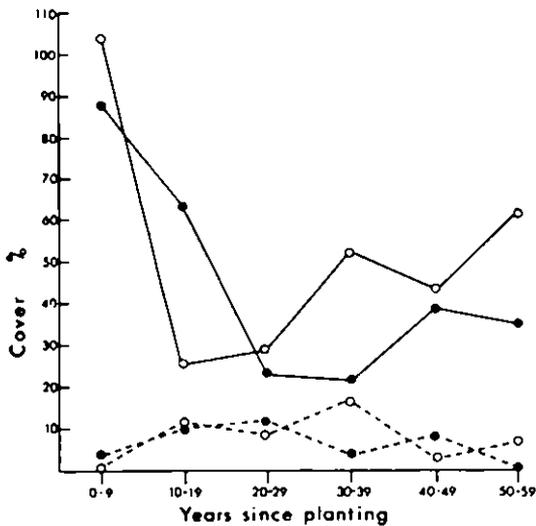


Fig. 2. Cover of vascular plants (solid lines) and bryophytes (dotted lines) in relation to age of crop in plantations of Pinus spp (closed circles) and Larix leptolepis (open circles) in upland Britain. There is some irregularity in these curves due to random variation in a rather small sample of observations.

Pinus contorta and Betula spp could be compared. Both the ground flora species present and their cover were similar. The soil was a peaty gley intergrading with a brown earth.

COMPOSITION OF THE FLORA

On the geographical scale the composition of the flora under planted conifers depends both on climate and on the species available in the surrounding area to imigrate. On a local scale it depends on soil, species planted, stage of the rotation, and on the past history of the site.

The climate determines not only which plants can grow on the forest floor, but also which tree species are suitable for planting as crops in the first place. It is, however, worth noting some differences between northwest Europe and more continental regions further east. Heather (Calluna vulgaris) and ferns (especially Dryopteris dilatata) are perhaps the most characteristics species in many forest of northwest Europe. Heather is not shade-tolerant, but is common in plantation forests before closure of the canopy, reappearing from seed when the crop is clearfelled. The fern Dryopteris

dilatata is often the only vascular plant to achieve appreciable cover in British conifer plantations, and it has been noted as a characteristic plant of Douglas fir (Pseudotsuga menziesii) plantations in Holland (Sissingh 1975).

Further to the east, as for example in Bråkenhielm's Swedish plantations, heather and ferns are less prominent or absent, but a wider variety of typical woodland plants occur. Bråkenhielm (1977) noted that Luzula pilosa, Melampyrum sylvaticum, Oxalis acetosella and Viola riviniana soon established themselves after the crop was cleaned or thinned. To some extent this difference reflects not only the climate, but also the availability of a suitable local flora to occupy the ground and a soil that was relatively good after years of agricultural use. The area of Sweden in which Bråkenhielm made his observations is very diverse, with fields, meadows, lakes and woodland forming an intimate and complex mosaic of habitats. Consequently there is a large available flora in the immediate vicinity of the plantations, and, in particular, a woodland flora that has not been eliminated by years of grazing as in so much of upland Britain.

In accordance with the greater cover of plants under pines and larches than under spruces, there is also a greater variety of species. Vascular plants that are particularly characteristic of pine and larch plantations on more fertile soils in Britain are bramble (Rubus fruticosus) and bracken (Pteridium aquilinum). These species are almost totally eliminated by Sitka spruce once it has closed its canopy. Bracken seldom reappears even after thinning. On heathier soils the grass Deschampsia flexuosa and bilberry (Vaccinium myrtillus) prevail and may survive in very small quantities even under Sitka spruce; though really successful thickets will eliminate them.

Both the overall cover of bryophytes and the diversity of species are similar under spruces and pines. There are, however, a few bryophytes that do not normally survive under Sitka spruce in Britain though they are frequent under those crop species with lighter canopies. Of these the most notable are Hylocomium splendens and Pleurozium schreberi, large pleurocarpous mosses that are often abundant in the boreal forest, and which are common before afforestation in the British uplands (Hill & Jones 1978). This is in contrast to Bråkenhielm's Norway spruce plantations in Sweden, where Pleurozium schreberi was one of the woodland plants that invaded after the crop was thinned.

The soil is one of the biggest influences on the composition of the flora. Where it is initially acid and infertile, few species of vascular plants occur. In Britain, the almost ubiquitous Deschampsia flexuosa, Dryopteris dilatata and Vaccinium myrtillus would often be the only

vascular plant species present. On more fertile soils there is a much richer flora, and a greater variety of woodland plants may invade, including Oxalis acetosella, Rubus fruticosus and Sorbus aucuparia. Bryophytes, however, which grow mainly on the litter and stumps, are less affected by soil quality than by available moisture. They are not notably more plentiful on damp soils and on northfacing slopes than on dry soils and on south-facing slopes.

INFLUENCE OF THE DEVELOPING PLANTATION ON GROUND VEGETATION

The strongest influence of all on the composition of the ground flora is the crop. Before the canopy closes, light-demanding plants including weeds and pasture species can thrive. After the canopy has closed, only the most shade-tolerant species can survive under spruces. Even under pines and larches many formerly abundant plants such as Calluna vulgaris and most grasses other than Deschampsia flexuosa vanish.

While light intensity is clearly the strongest single influence on the ground flora, its effects are difficult to separate from other influences correlated with the density of the canopy. In particular where the canopy is denser, less rain can penetrate, and there is a greater fall of litter. Root competition can also be expected to be greater. In a series of experiments to assess the effects of tree-root competition and of litter in a Pinus strobus forest in New Hampshire, Toumey (1929) severed the roots round some experimental plots, and removed the litter from a part of them. Removal of litter led to a large increase of vascular plants. Severing the roots led to a large increase of soil moisture during the summer, and to an appreciable increase of vascular plants.

Toumey concluded that light was not the factor controlling the entrance of natural vegetation under his experimental conditions. This conclusion, somewhat polemical at the time, is of course unjustified. No factor can be said to be ineffective unless it has been varied under controlled conditions. Nevertheless, his experiments aptly illustrate the combination of adverse influences that the ground vegetation in a conifer forest has to contend with. The full combination of adverse influences is often necessary for suppression of the ground vegetation. If any one of them is relaxed, the vegetation can develop. Bryophytes often show this clearly, growing vigorously on stumps that are left after thinning of the crop, but being almost totally absent on the forest floor where they are smothered by accumulating litter. The effect of root competition is probably less in wet regions such as the British uplands than in Toumey's experimental plots. Drought can be appreciable even in the west of Britain, but is certainly not as severe as in more continental regions.

Competition for mineral nutrients is presumably the main influence of root competition in wetter climates.

Because of the other influences of the crop it is unrealistic to speak of a unique critical value for the intensity of light below which vegetation will not grow. In addition various authors' thresholds for the cover of vegetation below which plants may be considered to be 'absent' have rarely been stated precisely. Measurements of relative illumination have varied, some authors making their observations on sunny days, and others on days when the sky is overcast. In general, the grey-day relative illumination is to be recommended as a measure of shade, as it depends little on the angle of the sun; for a comparison of the relative illumination under spruce with and without an overcast sky; see Eber (1972).

Even if authors had been consistent, and even if other environmental condition were comparable, the relation between relative illumination and the cover of the ground flora would not be exact, as the flora is seldom in equilibrium with the canopy. In Bråkenhielm's (1977) observation of Norway spruce plantations in South Sweden there was an increase in the ground flora after thinning, and a subsequent decrease as the canopy reclosed. Both during the expansion and during the subsequent die-back there would be a lag, so that the cover of the ground flora would depend on the previous few years of illumination as well as on current illumination.

In spite of these sources of variation, and in spite of possible differences in thresholds below which species are considered to be absent, the observation of various European authors are broadly consistent (Table 1). Vascular plants do not occur below about 10-20 per cent relative illumination. On a proportional basis the lower limit of illumination for bryophytes varies more widely, between 2 per cent and 9 per cent. The reason for the greater variability of the bryophyte threshold is the greater sensitivity of bryophytes to local influences, notably the accumulation of litter and the effects of desiccation. The most discordant value in Table 1 is due to Eber (1972). Here, the anomaly may be due to a difference of soil and slope, as Eber was working on steeply sloping, calcareous ground, whereas the other observations relate to acid or neutral soils on more level ground where litter would accumulate more thickly.

At all events, whether the main limiting factor is light, moisture or smothering by litter, the broad empirical relation between relative illumination and the ground flora can explain the differences found between spruces on the one hand, with Abies spp and Pseudotsuga menziesii resembling spruces in this respect, and pines and larches on the other. In spruce plantations the relative illumination is normally between 1 per cent and 10 per cent until they are over sixty years of

Table 1. Minimum relative illumination (grey-day) for growth of vascular plants and bryophytes under conifers. (Values are drawn from observations in the literature. Values for Clocaenog Forest in North Wales are based on my own observations).

Author	Crop	Minimum relative illumination for vascular plants	Minimum relative illumination for bryophytes
Cousens (1974)	<i>Pinus sylvestris</i>	17%	9%
Eber (1972)	<i>Picea abies</i>	6%	?
Koie (1938)	<i>Pinus</i> spp	10%	2%
Rheinheimer (1957)	<i>Picea abies</i>	20%	5-7%
Rheinheimer (1959)	<i>Picea abies</i>	?	7%
Schluter (1966)	<i>Picea abies</i>	12-15%	?
(Clocaenog Forest)	<i>Picea</i> and <i>Pinus</i>	12-13%	2-8%

age; whereas in pine and larch plantations after thinning, values between 10 per cent and 40 per cent are typical.

DIFFERENCES BETWEEN CONIFER PLANTATIONS AND NATURAL WOODLAND

Most conifer plantations in western Europe are in the climatic zone that would naturally support broad-leaved forest. As a result, their ground vegetation consists largely of species that also occur in nearby broad-leaved woodland. For example, in a detailed study of changes resulting from afforestation of some rough grazings in South Wales, Hill & Jones (1978) found only two species occurring in plantations that were not present in nearby oak (*Quercus petraea*) woods. Both were bryophytes that produce abundant spores, *Plagiothecium curvifolium* and *Polytrichum longisetum*, and presumably could have reached the area from considerable distances. Otherwise the origin of the flora was clearly local.

From the point of view of the wild flora, plantation forests differ from natural woodland in two major respects: the uniformity of the thicket stage and shortness of the rotation. When a crop reaches the thicket stage simultaneously over a wide area, species may be eliminated completely that would otherwise re-occupy the ground during later stages of the rotation. This means that opportunities for true woodland species in plantations are much reduced, as they lack suitable refuges during the establishment and thicket stages. There is perhaps more resemblance to a fire-succession. But in regions such as western North America where fire-successions have been extensively studied, the trees often reach ages of eighty to

Table 2. Commonest plants of coniferous plantations in upland Britain.

Data for this Table are derived from an unpublished report submitted by the Institute of Terrestrial Ecology to the Nature Conservancy Council. The two categories do not correspond to precise levels of frequency, but the plants in Category A have frequency approximately 40-100% in 200 sq.m, and plants in Category B have frequency approximately 20-40%. The establishment stage (0-20 years) of the first rotation has been excluded, but the establishment stage of the second rotation is included, this being regarded as a closer approximation to what will be present in a normal forest. Equal representation has been given to each of the age-classes 0-20 years, 20-40 years and 40-60 years.

A. Almost ubiquitous

<i>Deschampsia flexuosa</i>	<i>Hypnum jutlandicum</i>
<i>Dryopteris dilatata</i>	<i>Plagiothecium undulatum</i>
<i>Vaccinium myrtillus</i>	<i>Lophocolea cuspidata</i>
<i>Dicranum scoparium</i>	

B. Other very common plants

<i>Calluna vulgaris</i>	<i>Campylopus paradoxus</i>
<i>Chamaenerion angustifolium</i>	<i>Dicranella heteromalla</i>
<i>Galium saxatile</i>	<i>Eurhynchium praelongum</i>
<i>Molinia caerulea</i>	<i>Mnium hornum</i>
<i>Rubus fruticosus</i>	<i>Pleurozium schreberi</i>
<i>Sorbus aucuparia</i>	<i>Hypogymnia physodes</i>

V. vitis-idaea and *Deschampsia flexuosa* constant and sometimes co-dominant. Otherwise the commonest flowering plants are *Linnaea borealis*, *Luzula pilosa*, *Melampyrum pratense* and *Trientalis europaea*. On clearfelling, *Deschampsia flexuosa* becomes dominant, with abundant *Epilobium angustifolium*, *Luzula pilosa* and *Rubus idaeus*.

100 years or more. By that age most spruce plantations in the British uplands would have been windblown. The crop cannot be harvested at much more than fifty years of age and this short rotation is highly inimical to the establishment of a true woodland flora.

In spite of these differences there are marked resemblances between the flora of conifer plantations in the northern deciduous zone of Europe and that found in the boreal forest. The commoner species in British upland forests (Table 2) include two, *Dryopteris dilatata* and *Hypnum jutlandicum*, that are largely absent from the North European boreal forest; but the other species are all frequent or common there.

According to Sjörs (1965) Vaccinium myrtillus is dominant in the field layer under Norway spruce in the boreal forest of Sweden, with

REGENERATION OF THE GROUND FLORA FOLLOWING CLEARFELLING

Because of poor development of the ground flora in many plantation forests, the revegetation of sites that have been clearfelled is particularly dependent on seed surviving in the soil, and on the few vascular plants that may have survived the rotation. Woodland plants normally die back. In Britain this usually means Dryopteris dilatata, which often does not actually die but merely survives unhealthily without increasing, and several species of woodland bryophytes. The moss Plagiothecium undulatum is not very tolerant of desiccation, but Hypnum jutlandicum, which is also very common in mature plantations, can grow equally happily on dry heathland and is not adversely affected by removal of the tree canopy.

After clearfelling there are four main sources of the regenerating flora: viable seed surviving buried in the soil; seed entering the area after clearance; seed distributed by plants surviving on the site, and vegetative spread of the surviving green plants. Where there has been a successful crop of a dense-canopied species such as Sitka spruce, seed surviving in the soil is generally the main source of propagules for the regenerating flora, at least away from the edges of felled compartments. Near the edges, many relatively light-demanding plants such as bracken (Pteridium aquilinum) may survive, so that in the season after clearance the centre of the compartment can be almost bare, while there is a dense growth of vegetation round the edge. Pteridium is almost totally dependent on vegetative spread, and does not reappear in areas from which it has been eliminated.

Some of the viable seed present in the soil at the time of clearfellings is of recent origin; some, often the majority, has survived for many years in the soil. These two categories can usually be told apart by the fact that the recently arrived seeds are mainly in the litter, while the seeds that have been present for longer are mainly in lower horizons. Peter (1893, 1894) working in the vicinity of Gottingen, was the first to demonstrate the remarkable longevity of seeds in forest soils although there had been several earlier, anecdotal reports. Using a simple technique of germinating seeds from boxes of soil in the greenhouse, he found that where plantations had been established on old arable or pasture land, the seeds of arable or pasture weeds remained abundant in the soil for up to fifty years. In plantations established for more than 100 years the flora of the previous land-use was largely eliminated though there was sometimes a small population of weed species in the surface

layers of the soil. These he attributed to the use of the woodland by local farmers for sheltering livestock. Some small-seeded plants, chiefly of the genera Hypericum and Juncus, were present in the deeper layers of the soil, and these had perhaps survived for much longer. The seeds of true woodland species were very poorly represented in the soils, with the result that densities of viable seeds were much less in old plantations and ancient woodlands than in plantations established within the previous fifty years.

Peter's experiments were conducted with a care and thoroughness that have not been surpassed, and his conclusions have been amply confirmed by subsequent observers. My colleague P.A. Stevens, using essentially the same technique, has examined soil seed populations in British upland forests on several types of soil. He found seed densities typically in the range 1000-5000 seeds/sq.m on brown earths and peaty gleys, but much lower, typically 40-100 seeds per sq.m, on deep peat (P.A. Stevens, personal communication). Seeds of many species survived readily through the dark stage of the rotation, i.e. for about thirty-five years; but tree seeds (Betula, Picea and Pseudotsuga) appeared always to be of recent origin. In general the larger seeds survived less well than smaller seeds, and many grasses were scarcely represented in samples taken from older plantings. In particular, Deschampsia flexuosa did not appear to survive for long as soil seed, so that when it invades a clearfelled area, it has to do so from plants surviving on the site. Under larch and pine it is usually present before clearfelling, but it may be largely eliminated by well-grown Sitka spruce.

Among the small-seeded plants that showed good survival as soil seed, the most notable were Calluna vulgaris, generally in large numbers, Carex spp, Digitalis purpurea, Erica tetralix, Galium saxatile, Juncus spp, Luzula spp and Potentilla erecta. The reappearance of these species on clearfelled areas, is therefore often to be expected. Also, the grasses Agrostis canina, A. tenuis and Deschampsia cespitosa often reappear after clearfelling, and their seeds probably survive considerable periods of burial.

In addition to plants whose seeds survive on the site, certain plants with airborne seeds are capable of colonizing the area from outside. In Britain these are mainly Epilobium spp and Compositae; in many parts of North America and the Soviet Union, grasses of the genus Calamagrostis are often abundant. Chamaenerion angustifolium is generally the most plentiful windborne colonist of clearcut areas in Britain, though it often grows poorly and fails to become abundant on the poorer peaty soils. Plants with windborne seeds are particularly characteristic of fire-successions elsewhere, as some individuals are able to disperse over long distances, and are, therefore, at an advantage where seeds buried in the

surface soil have been destroyed.

Dispersal of berries by birds is undoubtedly responsible for some regeneration of Rubus spp, Sorbus aucuparia and Vaccinium myrtillus. However, the seeds of these plants are often buried in the mineral soil, and clearly have considerable longevity. Where seeds are introduced from outside this is most probably by roosting birds while the crop is still standing. It is quite possible that birds serve mainly to introduce these species in the first place, but that the bulk of their regeneration is from plants already present in the soil before the crop closed its canopy.

Depending on the species of crop and on its management there may be an appreciable flora already present on the site to serve as a source of seedlings after clearfelling. Deschampsia flexuosa is markedly affected in this way, frequently being the most abundant plant of clearcut areas which had supported a final crop with a canopy broken by endemic windthrow, disease, etc. Grasses such as Agrostis spp and Molinia caerulea may spread vigorously from a few existing plants and brambles (Rubus fruticosus) and bracken (Pteridium aquilinum) may spread vegetatively.

OUTLOOK FOR THE GROUND FLORA IN FUTURE ROTATIONS

In Britain, most plantation forests are still in their first rotation; large areas still remain to be planted in Scotland. Moreover, methods of silviculture and the choice of crop species have changed so much in the past fifty years that it is not possible to be sure what will happen in future rotations from a knowledge of what has happened to-date. Least known are the changes that may take place in populations of buried viable seeds. Existing populations of buried seeds were mostly derived from the flora that preceded afforestation. At the end of the next rotation the original seeds will almost all be dead, and numbers may not be replenished during the open phase before closure of the canopy of the second crop. If so, then the seed population may gradually drop, so that successive crops may be progressively more free of weeds.

This, however, is certainly not the outlook for the more fertile soils. One of the sites where the buried seed population was examined by P.A. Stevens, was on a brown earth in Gwydyr Forest, North Wales, on a site that had always been woodland. The buried seed population was here exceptionally large, about 5000 seeds/sq.m, of which 4000 seeds/sq.m were of Digitalis purpurea. After clearfelling, Digitalis germinated abundantly, and will evidently leave a vast population of buried seeds to appear when the next crop is clearfelled. Digitalis is a species that can be expected to increase in future rotations, extending to areas that were formerly grassland as well as occurring in old woodland sites.

On peats, however, few seeds survive in the soil.

Deschampsia flexuosa is normally the principal colonist after clearfelling though if it has been largely eliminated by the previous crop, and has not already colonized windthrown areas, it may perhaps fail to establish a large population before the next crop closes its canopy. If so, then the ground flora on peats may eventually be very sparse.

There is much uncertainty in this prediction. Windthrow is proving to be more of a problem in Britain than had been anticipated. Patches of windthrow allow populations of mature plants to develop in planted blocks towards the end of the rotation and may eventually result in a more fine-grained pattern of age-classes than we have at present. If so, then a large ground flora may survive even on peats.

REGENERATION OF TREES FROM SEED

An important category of windborne seeds not mentioned above is tree seeds. In British forests this usually means the seeds of birches (Betula pendula and B. pubescens) and conifers. As with windborne seeds of herbaceous species, tree seeds do not survive for long in the soil, and are mostly replenished each year. They regenerate more readily in mineral soils than on peats, especially if there has been some disturbance.

Available data on the regeneration of conifers in Britain are rather scattered, and there are still many gaps in our knowledge. The subject has been ably reviewed by Brown & Neustein (1972), who draw attention to the role of small mammals in destroying the seeds. However, much of our knowledge is still anecdotal, and the effect of other vegetation on regenerating trees is little understood. Grasses and heather are considered to have an adverse effect on regeneration, whilst Polytrichum and Vaccinium are reputed to make a good seed bed (Robertson 1976). The factors controlling natural regeneration require further study.

FLORA OF MARGINAL HABITATS IN PLANTED FORESTS

There has been a widespread fear among nature conservationists in Britain that the extensive new plantations would impoverish the flora of the uplands, and it is true of course that much of the existing vegetation is destroyed when a forest is established. Although many species survive in the soil as seed, and although a small number immigrate, nevertheless if only the planted blocks themselves were considered, there would be an appreciable loss of species diversity in planted forests.

But, in addition to destroying existing habitats, afforestation also creates new ones, notably the rides and roads. Rides in my experience are rather a poor habitat for plants, as they are not disturbed enough to keep the vegetation open, with the result that they are normally

dominated by a thick mat of coarse-growing plants such as Agrostis canina, Calluna vulgaris, Holcus mollis or Molinia caerulea. The coarse-growing dominant plant then excludes smaller plants, preventing establishment of a diverse flora. It is possible that rides have not yet had enough time for a characteristic flora to develop. In particular, until clearfelling of the first rotation, they may experience very little disturbance. After disturbance a characteristic flora may begin to immigrate, though completion of the process could take several rotations.

Roadsides, on the other hand, are disturbed from the first, and are normally kept open by various management practices such as mowing. They are colonized by a wide variety of plants, including many that are scarce or absent in upland areas before afforestation (D.F.Evans, personal communication) but mainly those characteristic of roadsides and hayfields in the lowlands. In Dalby Forest, North Yorkshire, where the roads are surfaced with limestone, the flora of the verges is particularly rich and includes a wide variety of immigrating species.

The flora of streamsides in forests varies greatly, depending on the size of the stream and the closeness of planting. At one end of the scale, small streams are commonly canalized and trees planted right up to their edge. Their flora is largely obliterated. Large streams and rivers often have roads running alongside them and have a flora effectively unmodified by afforestation.

The habitats that are worst affected by afforestation are marshes and bogs. Not only are they commonly drained for planting but many species of base-rich marshes are low-growing and dependent on heavy grazing for their survival. When the grazing animal is excluded many small plants such as Drosera rotundifolia, Pinguicula spp, Valeriana dioica and numerous bryophytes are more or less eliminated. Some may survive here and there on damp verges beside forest roads, but in general they die out.

The result of these various influences, some leading to an increase of the flora, others to a decrease, is that the overall effect of afforestation on the number of species present in an area is small. However, marshes and bogs are interesting habitats; and in areas where extensive afforestation is taking place it would be advisable to exercise restraint in planting them up. In that way, it should be possible to maintain the diversity of flora and habitat that many of us value.

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REFERENCES

- Bråkenhielm, S. (1977). Vegetation dynamics of afforested farmland in a district of southeastern Sweden. *Acta Phytogeographica Suecica*, 63, 1-106.
- Brown, J.M.B. & Neustein, S.A. (1972). Natural regeneration of conifers in the British Isles. "Conifers in the British Isles". Proceedings Royal Horticultural Society 3rd Conifer Conference, London, 1970. pp.29-39. Royal Horticultural Society, London.
- Clapham, A.R., Tutin, T.G. & Warburg, E.F. (1962). *Flora of the British Isles*. 2nd edition. Cambridge University Press, London.
- Cousens, J. (1974). *An introduction to woodland ecology*. Oliver & Boyd, Edinburgh.
- Dallimore, W. & Jackson, A.B. (1974). *A handbook of Coniferae and Ginkgoaceae*. Revised by S.G. Harrison. Edward Arnold, London.
- Eber, W. (1972). Ueber das Lichtklima von Waldern bei Göttingen und seinen Einfluss auf die Bodenvegetation. *Scripta Geobotanica*, 3, 1-150.
- Hill, M.O. & Jones, E.W. (1978). Vegetation changes resulting from afforestation of rough grazings in Caeo Forest, south Wales. *Journal of Ecology*, 66, 433-456.
- Kjæie, M. (1938). The soil vegetation of the Danish conifer plantation and its ecology. *Danske Videnskabskaernes Selskabsskrifter, Series 9*, 7, 1-85.
- Peter, A. (1893). Kulturversuche mit 'ruhenden' Samen. *Nachrichten von der königlichen Gesellschaft der Wissenschaften zu Göttingen*, 17, 673-691.
- Peter, A. (1894). Kulturversuche mit 'ruhenden' Samen. II. Mittheilung. *Nachrichten der königlichen Gesellschaft der Wissenschaften zu Göttingen, Mathematische-Physische Klasse*, 4, 373-393.
- Rheinheimer, G. (1957). Ueber die Standorte der Moosvegetation in Nadelholzforsten bei Hamburg. *Mitteilungen der Staatsinstitut für allgemeine Botanik*, 11, 89-136.
- Rheinheimer, G. (1959). Veränderungen der relativen Beleuchtungsstärke und der Bodenvegetation in einem Fichtenforst. *Bericht der Deutschen botanischen Gesellschaft*, 72, 246-250.
- Robertson, S.U. (1976). The possible role of natural regeneration in Scottish forestry. *Scottish Forestry*, 30, 134-142.
- Schlüter, H. (1966). Licht- und Temperaturmessungen an den Vegetationszonen einer Lichtung im Fichtenforst. *Flora, Abteilung B*, 156, 133-154.

- Sissingh, G. (1975). Niederländische Nadelforsten und ihr Humus als Substrat für ihre Vegetation. "Vegetation und Substrat". (Ed. by H. Dierschke), pp. 317-41. J. Cramer, Vaduz.
- Sjörs, H. (1965). Forest regions. Acta Phytogeographica Suecica, 50, 48-63.
- Smith, A. J. E. (1978). The moss flora of Britain and Ireland. Cambridge University Press, London.
- Toumey, J. T. (1929). The vegetation of the forest floor; light versus soil moisture. Proceedings 4th International congress of plant sciences, Ithaca, 1926. (Ed. by B. M. Duggar), Vol. 1, pp. 575-590. George Banta, Menasha, Wisconsin, U.S.A.

THE DEVELOPMENT OF POPULATIONS OF PESTS AND PATHOGENS IN
EVEN-AGED PLANTATIONS - FUNGI

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SUMMARY

From the point of view of establishment and persistence of pathogenic fungi in even-aged plantations, it is convenient to divide the rotation into four stages: establishment, thicket, pole stage and mature.

In the establishment stage, the pathogens may be derived from the nursery and be taken into the field with the planting stock. Many common nursery pathogens can continue their attacks in this way, some being important only on the young stages. For this reason disease control in the stand may begin with disease control in the nursery or stoolbed. Plantations established by direct seeding are affected mainly by pathogens existing in the field.

In the thicket stage, microclimatic conditions favour external pathogen activity such as spore casting, germination and possibly primary infection. The intense competition between trees which develops during this stage favours pathogens which can attack stressed trees. Thus diseases of the foliage and bark are common in the thicket stage.

In later stages competition between trees is relieved by thinning and the better ventilated canopy offers a less favourable environment to foliage diseases. However, the more numerous interventions by the forester during the last two stages may greatly affect the disease situation and result in an increasing importance of root fungi and decay with age.

Throughout the rotation pathogen establishment and activity is affected mainly by the following groups of factors:

- past history of the site and former crop residues;

- pathogens carried on nursery stock;
- changing microclimatic of the stand during the rotation;
- activity by man, including management decisions and silvicultural operations.

Thus, a considerable part of the background to the disease situation is under the control of the forester. The extent to which he would be prepared to manipulate it, depends on how far such actions would compromise other objectives of management.

RÉSUMÉ

Si on examine l'apparition et le maintien des champignons pathogènes dans les peuplements équiens, il est souvent pratique de diviser la révolution en quatre étapes: stade de fourré, stade de gaulis, stade de perchis et stade de futaie.

Pendant le stade de fourré, les pathogènes, issus des pépinières, peuvent être transportés sur le terrain au moment de la plantation. Un grand nombre de pathogènes usuels peuvent, de cette manière, continuer leurs attaques, certains n'étant dangereux que chez des arbres très jeunes. Par conséquent, le contrôle des infections dans les plantations doit débuter dans les pépinières. Les plantations établies par semis à la volée sont surtout affectées par des pathogènes existant déjà dans le terrain.

Pendant le stade de gaulis, les conditions du microclimat existant favorisent l'activité pathogène externe telle que l'expulsion des spores, la germination et peut-être les infections primaires. La compétition très intense entre les arbres à ce stade, favorise les pathogènes qui peuvent attaquer les arbres affaiblis. Ainsi des infections du feuillage et de l'écorce sont habituelles pendant le stade de gaulis.

Pendant les stades subséquents la compétition entre les arbres est amoindrie par les éclaircies et un couvert plus aéré offre aux infections du feuillage un milieu moins favorable. Cependant les interventions de plus en plus nombreuses du forestier pendant ces deux derniers stades peuvent avoir une influence considérable sur l'état des infections et peuvent amener avec l'âge l'importance des champignons de racines et de

la pourriture du tronc.

Tout au long de la révolution, l'établissement et l'activité des pathogènes sont affectées par les groupes de facteurs suivants:

- passé du terrain et résidus des anciens peuplements,
- pathogènes accompagnant les stocks de pépinières,
- changement du microclimat pendant la révolution
- activité de l'homme gestion et sylviculture,

Ainsi, une part importante des facteurs d'infection est sous le contrôle du forestier. Il pourra en tenir compte dans la mesure où ils n'entreront pas en conflit avec d'autres objectifs de gestion.

ZUSAMMENFASSUNG

Bei der Betrachtung des Aufkommens und Überdauerns pathogener Pilze in gleichaltrigen Pflanzungen ist es zweckmässig vier Altersstufen zu unterscheiden: Kulturstadium, Dichtung, Stangenholz und Altbestand.

Im Kulturstadium können die Pilze aus dem Pflanzgarten stammen und mit dem Pflanzmaterial in die Kultur gelangt sein. Viele verbreitete Pflanzgartenschädlinge setzen so ihren Befall fort, wobei einige nur im jüngsten Kulturstadium von Bedeutung sind. Die Infektionskontrolle des Bestandes sollte daher schon im Pflanzgarten oder Saatbeet beginnen. Pflanzungen, die durch direkte Aussaat begründet wurden, werden hauptsächlich von in der Schonung vorkommenden Schadpilzen betroffen.

Im Dichtungsstadium fördern die mikroklimatischen Bedingungen die externe Infektionsaktivität, wie Sporenverbreitung, Keimung und unter Umständen primäre Infektion. Der in diesem Stadium harte Konkurrenzkampf unter den Bäumen begünstigt den Befall der unterdrückten Bäume. Krankheiten der Blätter und der Rinde sind daher im Dichtungsstadium verbreitet.

Im späteren Bestandesleben wird der Konkurrenzkampf unter den Bäumen infolge Durchforstung gemildert, und der besser belüftete Kronenraum ist Blattinfektionen weniger förderlich.

Andererseits jedoch kann es durch die häufigeren forstlichen Eingriffe während der beiden letzten Bestandesphasen vermehrt zu Wurzelinfektionen und Holzerstörung mit zunehmendem Alter der Bäume kommen.

Während des Bestandeslebens werden Eintritt und Aktivität der Infektionen hauptsächlich von folgenden Faktorengruppen beeinflusst:

- Vorgeschichte des Standorts und Rückstände des Vorbestands,
- Infektionen mit dem Pflanzmaterial,
- Änderung des Bestandesmikroklimas während der Umtriebszeit,
- menschliche Eingriffe einschliesslich betriebswirtschaftlicher Entscheidungen und waldbaulicher Massnahmen.

Die Vorgeschichte einer Pilzinfektion unterliegt also zu einem beträchtlichen Teil der Kontrolle des Forstmannes. In welchem Umfang er hier Einfluss ausüben kann, hängt vor allem davon ab, inwieweit solche Massnahmen mit anderen Zielsetzungen in Einklang zu bringen sind.

INTRODUCTION

The establishment and persistence of pathogenic fungi in even-aged plantations and the damage they cause, depend on several factors. Some of these are associated with particular stages of growth of plantations as shown in Table 1. The stage of growth may also modify the local environment within the canopy and affect pathogen development. It may also affect the physiology of the trees and their predisposition to attack. A particular pathogen may depend on a special living or non-living factor that is itself dependent on the stage of growth of the crop. And, lastly, stages of growth are often associated with silvicultural operations which can affect tree susceptibility.

Age related liability to infection	Structure of canopy	Silvicultural operations
	Environmental factors: -humidity -temperature -shade.	Competition within the crop. Predisposition.

Table 1. Stage of growth of plantations.

Thus, where land is to be under continuous forestry, it may be convenient to regard the successive rotations as long cycles during each of which a changing picture of pathology is presented. Table 2 portrays a rotation with some of the important influences which can affect the course of pathology during it. From this point of view it may be convenient to divide the rotation into four stages of growth: establishment, thicket, pole and mature, and consider examples of disease associated with each stage.

THE ESTABLISHMENT STAGE

Even-aged plantations may be established by direct seeding, or, more commonly, by planting rooted stock. Certain pathogens are known to be specially damaging on young crops during and shortly after the establishment stage. The longer such pathogens can be excluded from the crop, therefore, the less damage they may eventually cause. An important factor in this consideration is the source of the inoculum. There are three main sources: presence on the planting stock, presence on the site and incoming to the site.

Some pathogens may be present in the nursery and be taken into the field on the planting stock. Many of the familiar nursery diseases in Britain are in this category, Meria laricis Vuill. on larch; Didymascella thujina (Durand) Maire on Thuja; Microsphaera alphitoides Griff. and Maubl. on oak, and Phytophthora spp. on various hosts. Some of these, such as M. laricis and D. thujina are much more damaging in the early stages of plantation growth and cause only little damage in the later stages. They are especially damaging on trees recovering from the shock of transplanting into the field.

Recently, Skilling (1977) stated that in the case of Scleroderris lagerbergii Crem. in red and jack pine plantations in northern U.S.A. and Canada, damage was limited almost exclusively to trees less than ten years old and that most of the originally affected plantations were infected by nursery stock.

Therefore, where establishment is by nursery plants, control of disease in the plantation begins in the nursery and measures aimed at preventing losses in the nursery may have a bonus in also reducing them in the plantation. Particularly important among such control measures are those which aim at disease avoidance either by siting nurseries remote from inoculum sources or by avoiding continuous raising of stock in the same nursery so that pathogens are annually transferred from older to younger stock. Such avoidance measures are particularly important in the case of host-limited pathogens.

Most of the above cases concern nursery stock raised from seed, but infected, vegetatively produced stock might be used as well. Such stock, rooted and unrooted sets, may often suffer small wounds from pruning or accidental damage when

CROP STAGE	ESTABLISHMENT	THICKET	POLE	MATURE
Silvicultural operations	Direct seeding Planting Weed control Cleaning		Racking Pruning Thinning Roading	Clearfelling
Factors involved	Transplanting shock. Competition with ground flora. Alteration in ground flora.	Increasing crop competition. Increasing humidity decreasing light, more stable temperature		Crop competition relieved. Higher transpiration rates. Increasing root spread and contacts. Provision of stumps. Increasing injury rate to trees.
Pathological consequences	Introduction of nursery pathogens. Effect on alternate hosts of rusts. Young plants may be susceptible to pathogens present on the site.	Facultative bark parasites favoured. Environment favours foliage and bark pathogens.		Establishment of stump inhabiting pathogens. Spread of root attacking fungi. Establishment of decay.

being moved to the planting site. The shock of transplanting often leads to a reduction of the moisture content of the bark, allowing facultative parasites to use the wounds as entries and to kill areas of bark. Cytospora chrysosperma (Pers.) Fr. and Dothichiza populea Sacc. and Briard. have both been recorded attacking poplar sets in this way. Another example is the use of sets of Salix alba as planting stock. The stool beds used may be infected with Erwini salicis (Day) Chester, causing water mark disease, so that the pathogen may be introduced into a plantation which might otherwise have remained free of it (Gremmen 1977).

In this respect, pathogens which are present in the host for some time before causing obvious symptoms are especially dangerous since infected plants may not be culled in the nursery. Cronartium ribicola Fisch. which causes blister rust of five-needled pines, is especially prevalent on young stock from one-year old seedlings upwards. Typically it invades needles on which few symptoms appear and takes some time to grow down to the shoots. Use of such infected stock for establishing plantations has led both to early losses and introduction of the pathogen to new areas. Work on Lophodermium (Millar, personal communication) has shown that apparently healthy individual needles of Scots pine nursery stock can contain mycelia of up to three Lophodermium species differing in their pathogenicity. The physiological effect of planting out stock carrying such latent infection is not known but it has been surmised that the consequent stress may favour the more pathogenic forms of Lophodermium present in the needles and lead to the frequent epidemics reported at establishment stage.

When plantation establishment is by direct seeding such nursery originated diseases are for the main part avoided. Reported pathogens conveyed on or in the seed are few. Geniculodendron pyriforme Salt. may kill seed of Sitka spruce especially at temperatures around 10°C and Ciberia batschiana (Zopf) Buchwald may kill acorns. The former is an example of a pathogen of apparently limited distribution in the world which could be farther spread by direct seeding and the latter one of general occurrence in oak woods in Europe. Certain seed-borne pathogens may attack other parts of the tree as, for example Gloeosporium quercinum Westd. which can attack acorns and also cause leaf spots on oak. The ability to attack other parts of the tree increases the risk of persistence in plantations of such seed-introduced pathogens.

Where the pathogen is not carried on the planting stock, it may still infect the young stages if it is present on the planting site or possesses a stage in its life history allowing it to be easily vectored from a remote source.

Residues of previous crops, especially stumps and root systems, may carry pathogenic root fungi. This residue, which

may persist for some considerable time, can be a serious cause of loss both where plantation follows plantation and where plantations replace existing natural forest. Modern site preparation practices which remove such residues or bring them up to the surface may be important in breaking the chain of persistence in this class of disease because very often the fungi involved cannot survive in the soil without such woody masses.

Older, lightly infected trees may be the source of inoculum, which can produce a serious and sometimes lethal infection of the young plants. Scirrhia acicola (Dearn.) Sigg., the brown spot fungus, is a good example of this. It is widely distributed in pine stands in the south and west U.S.A. where it can cause mortality and loss of growth of the young stages, but declines in importance as the plantations age. Another example is Nectria ditissima Tul. which causes canker on young beech raised under the uniform system and where the sources of infection are branch cankers on the older trees (Perrin 1975). The regularly distributed mother trees are ideally placed to distribute infection to the young stands, and the first step advocated by Perrin in control of the canker is the elimination of such cankered adult trees.

Many foliage pathogens show a similar behaviour, damaging mainly young stages. Basset & Gadgil (1975) describe the relationship between damage of Pinus radiata due to Dohiostroma pini Hulb. and age of crop in New Zealand. The 1-10 year age classes are mainly affected, with some stands up to fifteen years also attacked, very occasionally trees up to twenty-two years are infected and trees older than this are entirely resistant. The authors emphasize that controls of D. pini by spraying in the plantations is economic by virtue mainly of two features: the efficiency and persistent effect of a well-timed spray and the short period during the rotation when the spraying is required. Since not all pine species in New Zealand show increasing resistance with age to D. pini this factor is tending to reduce the acreage of them planted in favour of P. radiata.

In many cases the reasons for a relationship between age of crop and disease intensity are not known, especially where changes in the physiology of the host with age are concerned. In some cases, however, the reason is obvious. The snow moulds typified by Herpotrichia nigra Hartig. are dependent on snow cover, which must often be relatively deep. Apart from the lower branches of larger trees, these moulds are most damaging at the young stages of the plantation when trees can be covered for some time and are unimportant beyond the thicket stage. Rhizina undulata Fr. may kill young stock shortly after planting out on areas which have been burned during site preparation (Seaby 1977).

A silvicultural operation may affect the probability and

scale of disease attack. Moriondo (1975) showed that severe attacks by Cronartium flaccidum (Alb. and Schw.) Wint. on pine plantations in Italy may be due in part to the presence of the alternate host, Vincetoxicum officinale, necessary for the maintenance of the disease cycle, in the vicinity of the affected plantations. He further showed that V. officinale could act as a pioneer species well able to colonize sites where the ground was prepared for planting. In Italy, the natural distribution of pine species Pinus pinaster, P. pinea, P. nigra and P. sylvestris is outside of the natural distribution of V. officinale. The management decision to greatly extend the area of pine plantations into regions where V. officinale was present and the silvicultural decision to prepare planting sites have resulted in severe losses due to the rust with intensities as high as 50-100 per cent for plantations in every zone between the Appenines and the eastern seaboard.

In another case, Miller (1972) working with fusiform rust, (Cronartium fusiforme Hedg. and Hunt.) on Pinus eliottii showed that the degree of preparation before planting significantly increased liability to individual tree infection, number of lethal galls and number of galls per tree. His site preparation involved different grades of ploughing and harrowing before planting.

THE THICKET STAGE

This stage of growth is a period when competition between trees is intensifying and when canopy closure and density greatly affect the microclimate of the stand. The humidity in particular tends to increase and remain at high levels for considerable periods consequent on reduced wind speeds, increased interception of rain and exclusion of insolation. The increasing competition may result in a proportion of the crop being predisposed to infection by certain pathogens. Competition for water may result in the more suppressed individuals having low bark moisture contents and being liable to infection by bark facultative pathogens. Bier (1959) showed that for a number of host - parasite combinations a threshold value existed of about 80 per cent for bark turgidity, below which certain facultative bark pathogens extended and above which they did not. Further work by Bloomberg (1962) reinforced the importance of bark moisture in this respect.

During the thicket and on into the young pole stages light intensity within the stand decreases. Anderson (1972) showed experimentally that cankers developed and enlarged more rapidly on stems of quaking aspen, Populus tremuloides, when they were shaded although the basis of the association is not known. The results fit well with observations associating high canker intensities with dense stands, and by inference with stages in the rotation when light values are low.

Other workers have recorded high incidence of particular diseases in the thicket and young pole stages. Hopkins (1963), in a survey of cankers caused by Atropellis piniphila (Weir) Lohm. on lodgepole pine in Alberta, showed a peak for initiation of cankers on stem tissues in the 10-14 year age class. He showed that the pathogen could enter undamaged stem bark directly. He postulated that during the course of forest development, stem tissue changed in its likelihood of infection: an initial period of low likelihood being followed by a period of high likelihood succeeded by one of low likelihood. He suggested that the first period of low likelihood in the upper crown could be due to the microclimate associated with that region and that the low likelihood of the third period was associated with host resistance resulting from the thick bark. The high humidities associated with the thicket and young pole stages would explain why disease figures became high at that stage.

THE POLE STAGE

At the pole stage in crop development the crop has passed through a long period when the forester may have intervened little in its development apart from carrying out cleanings for density and mixture regulation. At the pole stage when the crop is about 10 m in height, the forester starts to carry out a series of operations which may comprise creating racks, brashing, thinning and pruning. These operations, together with changes in microclimate and crop physiology, may affect the likelihood of disease incidence.

As the canopy grows upwards and lower branches die, the increasing exposure of foliage in the wind results in lower humidities in the crown and shorter periods when leaf and bark surfaces remain wet. This would be expected to be unfavourable to the germination and infection stages of many pathogens. Castellani (1966) has shown that heavy attacks by Marssonina brunnea (E. & E.) Sacc. on poplar in Italy are associated with climatic conditions which result in a water film on leaf surfaces lasting for a certain time and that the distribution of serious attacks by the disease is associated with weather patterns involving rainfall, temperature and humidity. Similarly, Cronartium ribicola has been reported by Boyce (1961) to need forty-eight hours of saturated air and temperatures of not over 18° C for the processes involving production of promycelia, casting, germination of sporidia and penetration of the pine needle. Such requirements also dictate the pattern of spread of the rust in western North America. The changes in microclimate associated with the more exposed, elevated canopy of the pole stage would be expected to be unfavourable to pathogens with such demands. The further opening of the canopy following thinnings would intensify such microclimatic effects.

Increasing size of trees is associated with extending root systems and may involve root contacts and root grafting, especially in pure stands. This favours those root diseases transmissible by direct contact or grafting and is particularly important where the root fungus finds difficulty in surviving in unsterilized soils. In spreading patches of such root attack there is usually one clone of the fungus associated with each patch. According to Childs (1963) Portia weirii (Murr.) Murr. spreads mainly by root contact when attacking Douglas fir in western North America, though actual root grafting is not necessary, and experiments have shown that P. weirii cannot survive in unsterilized soil. Many other root pathogens show a similar life history.

Bakshi, Reddy & Singh (1976) have described the same life history of Ganoderma lucidum (Leyss.) Karst. in plantations in India stressing that the spread is greatly slowed down or stopped in natural forests where there is a mixture of resistant and susceptible hosts and the continuity of the susceptible root mat is broken. Severe damage has occurred in pure plantations of susceptible species, especially where they have replaced natural forests where the pathogen was present in the root systems. The importance of the developing root mat is exemplified also where Armillaria mellea Vahl ex. Fr. is unable to form rhizomorphs in certain soils and is dependent for spread on a continuous root system in the plantation. Wilt fungi may also be transmitted through root grafts. This method of spread is well-known for oak wilt, Ceratocystis fagacearum (Br etz) Hunt., in North America and for Dutch elm disease due to Ceratocystis ulmi (Buism.) C. Mor.

The silvicultural operations carried out from the pole stage onwards may affect the disease situation. Brushing may cause wounds and encourage bark pathogens. Van Vloten (1952) showed experimentally that large annual cankers on stems of Japanese larch were caused by the invasion of brushing wounds made in winter by Phomopsis pseudotsugae (Phacidiopycnis pseudotsugae (Wils.) Hahn.) and similar damage may follow removal of branches of Douglas fir in winter (Zycha 1962).. In New Zealand, Gilmour (1964) carried out four surveys of Diplodia pinea (Desm.) Kickx. infection of bark of Pinus radiata termed Diplodia whorl canker and showed it could be initiated by green pruning wounds. In this case, unlike Phacidiopycnis, the damage was independent of season of pruning. An added consequence of the Diplodia infection was the entry of decay through the lesions.

During thinning operations workers tend to be in the woods for prolonged periods and the ground is often open enough in the later pole stages for lunchtime fires to be lit. Such fire sites may be colonized by Rhizina undulata which may then cause dying of groups of trees in plantations of susceptible conifers (Murray & Young 1961). This is analogous

to the killing of newly planted stock emanating from burned areas at the time of site preparation already referred to and represents the second phase in the rotation when such activity by Rhizina is possible. The activity is enhanced by the provision of stumps as food sources at the same time.

The pole stage with its repeated thinning operations and provision of stumps is especially significant in the entry of root and decay fungi to the stand. The importance of the conifer stump as an entry for Fomes annosus (Fr.) Cje., especially on first rotation sites, is well-known and protection of such stumps against Fomes has dominated much of the recent research work on this pathogen. It is likely that provision of stumps is generally favourable to the whole class of root and butt rot fungi which can exploit their parasitic ability in colonizing a still living stump in advance of saprophytic competitors and then lead a saprophytic existence in the large mass of woody material provided. Such stumps offer both points of colonization and means of persistence to these organisms.

Where thinning operations are neglected and intense competition develops in the stands, a disease problem may arise subsequent to insect attack. Gilmour (1964) has described attacks by Sirex noctilia F. on stands of various conifers in New Zealand. In pine species particularly and especially Pinus radiata, the less dominant trees in unthinned stands were badly affected by the Amylostereum sp. carried by Sirex and injected by it when ovipositing. The fungus causes a crown wilt and in inconspicuous white decay of the timber.

At the pole stage the proportion of heart wood in stem and root becomes significant and this combined with the increasing number of injuries to trees from operations in the forests, may affect the incidence of decay fungi in the trees. The thinning stages represent the first time during the rotation that butts and root systems may be significantly mechanically damaged. The injuries depend on many factors but in general greater and heavier mechanization of harvesting has resulted in deeper wounding of butts and surface root systems. Many studies, especially in countries with older coniferous plantations than Britain, have shown that a wide variety of decay fungi can enter such wounds. In Britain, Pawsey & Gladman (1965) analysed a large number of such wounds in spruce plantations and demonstrated the importance of these as entries for a number of decay fungi of which Stereum sanguinolentum Alb. and Schw. ex Fr., was the most important. S. sanguinolentum has been described as a primary colonizer of wounds, being able to tolerate the inhibitory conditions associated with freshly exposed wood, especially heart wood, but being unable to compete with organisms established on older wounds. Thus species such as S. sanguinolentum are early colonizers of wounds. This is important where rotations are

short, as in many coniferous crops. With other decay fungi there may be various intervals between provision of a wound entry and its colonization. Lavallie (1965) showed that on Picea mariana, Fomes pini (Thore) Lloyd infected wounds that had been exposed for at least a year and possibly longer. Various writers have described the late entry of Fomes ignarius (L. ex Fr.) Kickx. into wounds. In a case described by Etheridge (1961) investigating the succession of organisms in Populus tremuloides the fungus was not isolated until nineteen years and longer after the wound was available.

In the above cases there is often a simple and obvious relationship between disease incidence and stage of the crop. In other cases the relationship is obscure. Murray, Millar & van der Kamp (1969) showed that Peridermium pini (Pers.) Lev. in northeast Scotland was extremely rare in plantations below ten years of age but that the incidence rose as the crop attained the pole stage. The reason for the pole stage being so badly affected is not known and in this respect the rust differs from other species such as Cronartium ribicola where losses in young stages due to juvenile susceptibility are severe.

THE MATURE STAGE

In the fourth stage of the rotation the trees reach a degree of maturity in which height and diameter growth decreases, crowns broaden and branches become stouter. In regularly thinned plantations the canopy is high with spaces between adjoining crowns. At this stage the well-ventilated environment in the crown is not generally favourable to leaf and needle infecting pathogens and their attacks are more dependent on fluctuating climatic conditions than at earlier stages. However, infections especially by obligate or strong parasites, do occur. Mycosphaerella alphitoides often defoliates relatively old oak plantations in Europe and this may be associated with the high water content of the conidia of mildews, in general enabling them to germinate and invade tissue at lower humidities than many other pathogens. Lophodermella sulcigena (Rostr.) v.Hohn., again an obligate parasite, may cause conspicuous browning of older trees of Pinus nigra and similarly Rhabdocline pseudotsugae Syd. may cause thinning of crowns of Douglas fir but such attacks on the older stages are more sporadic than on thicket stages.

Diseases of the bark may be found in the older stages, especially where trees are damaged or predisposed by other agencies. Possibly the best known in Britain is beech bark disease. Parker (1974) describes it occurring in stands from twenty-five years of age upwards but some of its worst effects are in older woods. The disease is a good example of the syndromic type of injury often suffered by the older stages. The main fungus involved, Nectria coccinea Pers. ex Fr.,

invades bark damaged by the scale insect Cryptococcus fagi Baer. and is itself followed by a variety of organisms including ambrosia beetles and decay fungi with Bjerkandera adusta (Willd. ex Fr.) Karst. a very common species. In the worst cases the trees die and remain standing or are snapped off where decay has developed in the stem. In the last decade the increasing incidence of beech bark disease has affected the management of large areas of beech forest in northern France raised under the uniform system.

In the older stages of plantation growth, the trees are likely to have suffered many types of wounds. Some are due to natural causes but, due to the many harvesting and extraction operations carried out since the start of the pole stage, many are caused by man. Snow and wind breakage of crowns, death of branches by shading, especially in shade intolerant species such as oak, fire and animal damage, felling grazes to stems and wounds on butts and root systems following harvesting and road making operations, all offer avenues of infection for decay fungi which probably constitute the most important group of damaging fungi at this stage. A factor of importance is the date when the injuries were caused. The earlier the rotation the injury and the more pioneer the decay fungus, the greater the damage. The shorter rotations now favoured for many coniferous rotations have tended to reduce such decay losses which are possibly more serious in broadleaved plantations with their longer rotations than in coniferous ones.

CONCLUSION

A large proportion of the factors controlling the incidence and impact of pathogenic fungi is concerned with the particular stage of the rotation. This relationship is probably best seen in even-aged plantations. In uneven-aged plantations and in natural regeneration stands raised by a relatively long regeneration period, the more complex canopy development would tend to obscure the relation between disease incidence and stage of growth.

Because of this, even-aged plantations are likely to present simpler problems in understanding disease initiation and development than other types of forest stand. But even in this situation, although something may be known about the more obvious causes and pathological effects associated with the different stages of plantation development, a great deal of the more subtle and indirect relationships remain to be discovered.

Many of the controlling factors are affected by management decisions and silvicultural measures. It is probably no exaggeration to say that every managerial decision has an effect on the disease situation. Such decisions begin with the choice of site to be planted and the provision of

planting stock and continue until the end of the rotation. There is no doubt that a proportion of disease control lies within the hands of the forest manager, although occasions arise when there is a conflict of interest between disease control and some other desirable objective.

Because of the association between crop development and disease and the relatively simple situation in even-aged stands, the latter seem to offer the best situation for management to take a part in disease control.

REFERENCES

- Anderson, G.W. (1972). Development of Hypoxyylon mammatum cankers on artificially shaded aspen stems. Forest Science, 18, 316-318.
- Bakshi, B.K., Reddy, M.A.R. & Singh, S. (1976). Canoderma root rot mortality in Khair in reforested stands. European Journal of Forest Pathology, 6, 30-38.
- Bassett, C. & Gadgil, P.D. (1975). Control of Dothistroma needle blight in New Zealand. Second World Technical Consultation on forest diseases in insects. New Delhi. pp. 1-9.
- Bier, J.E. (1959). The relation of bark moisture to the development of canker diseases caused by native facultative parasites. Canadian Journal of Botany, 37, 781-788.
- Bloomberg, W.J. (1962). Cytospora canker of poplars: Factors influencing the development of the disease. Canadian Journal of Botany, 40, 1271-1280.
- Boyce, J.S. (1961). Forest pathology. McGraw-Hill, New York.
- Castellani, E. (1966). Report on two little-known poplar diseases. "Breeding pest resistant trees" (Ed. by H.D. Gerhold, E.J. Schreiner, R.E. McDermatt and J.A. Winieski), pp 89-96. Pergamon Press, Oxford.
- Childs, T.W. (1963). Poria weirii root rot. Phytopathology, 53, 1120-1136.
- Etheridge, D.E. (1961). Conditions affecting branch infection in aspen. Canadian Journal of Botany, 39, 799-816.
- Gilmour, J.W. (1964). Survey of Diplodia whorl canker in Pinus radiata. Research leaflet #5 New Zealand Forest Service, pp. 1-4.
- Gremmen, J. (1977). The benefit of silvicultural measures to prevent damage and disease in forest trees. European Journal of Forest Pathology, 7, 158-164.
- Hopkins, J.C. (1963). Atropellis canker of lodgepole: etiology symptoms, and canker development rates. Canadian Journal of Botany, 41, 1535-1545.
- Lavallie, A. (1965). Modes d'entrée des caries du tronc de l'épinette, naira. Phytoprotection, 46, 163-168.
- Miller, T. (1972). Fusiform rust in planted slash pines: influence of site preparation and spacing. Forest

- Science, 18, 70-75.
- Moriondo, F. (1975). Some features of pine blister rust Cronartium flaccidum (Alb. and Schw.) Wint. in Italy. Second World Technical Consultation on forest diseases and insects. New Delhi. pp.1-13.
- Murray, J.S., Millar, C.S. & Kamp, B.J. van der (1969). Incidence and importance of Peridermium pini (Pers.) Lev. in Northeast Scotland. Forestry, 42, 166-184.
- Murray, J.S. & Young, C.W.T. (1961). Group dying of conifers. Forest Record #46, Forestry Commission, U.K.
- Parker, E.J. (1974). Beech bark disease. Forest Record #96, Forestry Commission, U.K.
- Pawsey, R.G. & Gladman, R.J. (1965). Decay in standing conifers developing from extraction damage. Forestry Commission Forest Record No. 54. Her Majesty's Stationery Office. 25pp.
- Perrin, R. (1975). Le chancre du hêtre à Nectria ditissima. Rapport annuel, Laboratoire de pathologie forestière, INRA-CNRF, France. pp7-8.
- Skilling, D.D. (1977). The development of a more virulent strain of Scleroderris lagerbergii in New York State. European Journal of Forest Pathology, 7, 297-302.
- Vloten, H. van (1952). Evidence of host-parasite relations by experiments with Phomopsis pseudotsugae Wilson. Scottish Forestry, 6, 38-46.
- Zycha, G. (1962). Zur Astung der Douglasie bei Schmuckreisegewinnung. Forstarchiv, 33, 78.

THE DEVELOPMENT OF POPULATIONS OF INSECTS

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SUMMARY

This paper considers the succession of different pests which may occur during the various growth stages of even-aged coniferous plantation crops. Only the temperate regions are considered and most of the specific examples quoted are British. The main conclusion reached is that the different growth stages do indeed have characteristic species or groups of pests which are likely to give most trouble. Sometimes, however, a completely unexpected and unpredictable outbreak may occur. Other time scales apart from the rotation length itself, the creation of the total plantation resource and the rise and fall of the individual infestation, are briefly mentioned.

RÉSUMÉ

Dans cet article nous considérons la succession des différents effectifs de nuisibles qui affectent et accompagnent les différentes stades de croissance des forêts résineuses équiennes. Les exemples donnés appartiennent à la région tempérée et la plupart sont typiquement britanniques. Nous arrivons à la conclusion suivante, à savoir que des espèces ou groupes de nuisibles sont caractéristiques des différentes stades de l'évolution des peuplements. Pourtant, il se peut qu'une affection entièrement imprévisible et inattendue se développe. Nous mentionnons brièvement d'autres échelles du temps, qui ne sont pas directement liées à la longueur de la révolution, à l'importance des plantations et aux gradations de certaines attaques individuelles.

ZUSAMMENFASSUNG

Dieser Beitrag befasst sich mit der Sukzession verschiedener Schaderreger, die in entsprechenden Altersklassen gleichalter Nadelwälder auftreten können. Berücksichtigt wird nur die gemässigte Klimazone und die Mehrzahl der Beispiele bezieht sich auf Britannien. Die wichtigste Schlussfolgerung ist, dass die verschiedenen Altersklassen tatsächlich unter charakteristischen Schädlingen oder Schädlingsgruppen leiden. Gelegentlich kommt es jedoch zu völlig unerwarteten Gradationen. Neben der Umtriebszeit sind andere Zeiteinheiten erwähnt, (die Einfluss auf die Schädlingspopulation haben mögen), wie die Gesamtdauer einer Massenvermehrung und die Verjüngungsperiode eines Bestandes.

INTRODUCTION

This paper deals with the development of populations of forest insects in even-aged plantations. It is restricted to consideration of such population changes amongst pest species in conifer crops in the temperate zone with most of the examples being drawn from the United Kingdom scene with which the author is most familiar. It is clear that such plantations have a likelihood of supporting epidemic numbers and of being damaged by certain characteristic groups or species of pests at different times and stages of growth during the rotation. It is equally clear that any individual plantation may suffer damage from only a few, or one, or none, of the various groups or species of insects which can in succession erupt at different times during the existence of such a crop. It is highly probable that an analogous situation exists with respect to other phytophagous insects associated with other types of trees in different climatic regions, but this is not examined. There will, of course, be changes too in the densities of other groups such as parasites, predators and soil insects during the course of the rotation but these aspects are also omitted from consideration.

ESTABLISHMENT

The dominant factor influencing the level of insect damage in newly established crops is whether or not the area has recently carried a previous tree crop. In afforestation areas where there is no such recent history of tree cover the probability of insect damage to the newly planted crop is very low, in fact, almost non-existent, even though Chrystal (1937) does record instances where, in the Welsh border counties, the species Aphelia viburnana F. and Eupithecia nanata Hubn.

having almost totally destroyed their normal food supplies of bilberry (Vaccinium myrtillus L.) inflicted considerable damage to young European and Japanese larches (Larix decidua Mill. and L. L. kaempferi (Lamb.) Carr), Douglas firs (Pseudotsuga menziesii (Mirb.) Franco), and Scots pines (Pinus sylvestris L.) There are similar records from Germany (Gauss 1960). In restocking areas, on the other hand, high populations of such damaging insects as Hylobius abietis L. and Hylastes spp. inevitably arise where the felling of the previous crop results in an abundance of stumps and slash providing breeding sites. In such situations damage can be intense and because epidemics are such a regular feature, the plants used for restocking Britain are routinely protected by being dipped in insecticide. According to King & Scott (1975), restocking of coniferous forests by the Forestry Commission covers 3600 ha/yr and this figure will double by 1990. The use of insecticidally dipped plants on such large areas could be avoided by delaying replanting, since the pest population naturally declines three or four years after the felling of the previous crop. Such an approach is undesirable, however, because it not only lengthens the rotation but also creates weeding problems.

THICKET

In the thicket stage a variety of pests begin to make their appearance with sap-sucking insects, defoliators and shoot border probably the most prominent.

Of the sap-suckers, the Adelgids are the most common and although the results of their activities are obvious as with for example, the discolouration and deformation of Douglas fir needles, caused by Adelges cooleyi Gill., the practical effect of their attacks is typically of little importance. A major exception to this is A. nordmannianae (Eck.) which so cripples the European silver fir, Abies alba Mill., in its young stages of growth that the cultivation of this tree has been almost totally discontinued in Britain despite the fact that it has many desirable silvicultural characteristics (Varty 1956). Another sucking insect which becomes common in thicket stage crops, in this stage of Sitka spruce, Picea sitchensis (Bong) Carr., is the green spruce aphid, Elatobium abietinum Walk. which causes marked loss of older needles. Populations of both E. abietinum and Adelges spp. persist into stages of plantation development later than the thicket one.

Most species of defoliators are of limited importance at this stage in the growth of the crop, but here again there is one major exception namely, the pine sawfly, Neodiprion sertifer Geoffr., which produces very noticeable needle loss from Scots and more particularly lodgepole pine (Pinus contorta Dougl.) crops of about 2 to 3m in height. Theregarious caterpillars concentrate their attack on the older

needles and in severe attacks the whole of the inner crown is stripped. Control has been achieved here and elsewhere (e.g. Bird 1953) by introducing a virus disease which brings about a population collapse, accelerating the natural decline in numbers which occurs after a few years of high density.

The attack of shoot borers often becomes apparent during the thicket stage. For example, the dead twigs produced by the feeding of the larvae of Argyresthia laevigatella (H.-S.) on Larix spp. may be numerous and conspicuous but the economic importance of this type of damage is slight. On Pinus spp., however, the pine shoot moth, Rhyacionia buoliana Schiff., is a major pest producing various types of main stem distortion including forking and posthorn deformations. There have been recent heavy attacks in Eire, whilst in Canada Scots pine being grown for Christmas trees and P. resinosa have suffered damage. Where attacks are repeated over a number of years very few leaders escape undamaged (Scott 1972).

POLE AND THINNING

During this phase of growth the predominant entomological possibility, now being increasingly realised in Britain, is that of large scale attacks by defoliators. These outbreaks may be caused by either introduced or native pests and it is somewhat surprisingly, the latter which have so far inflicted most damage.

Commencing in the 1950's the pine looper, Bupalus piniarius L., has erupted on a number of occasions in different parts of the country and has had to be controlled with various insecticidal treatments (Crooke 1959; Bevan 1961). It is possible to predict the likelihood of epidemics by monitoring the numbers of overwintering pupae in the soil and, if required, of the egg state in the pine crowns, so that treatments can usually be applied before serious damage is inflicted on the affected crop. The pupal indices derived from annual surveys are of interest in revealing population trends in relation to time and Table 1 shows sequences of pupal counts from three forest areas.

The counts for Elveden, Thetford Forest, East Anglia, exemplify a situation where the population levels have been consistently low for some twenty years. The counts for Rendlesham, Thetford Forest, East Anglia, also have been low for most of that time but they did peak to 41.8/sq.m in 1959 before dropping back to more normal levels. The population collapse that occurred in 1960 was due to a combination of an abnormally low field fecundity on the part of the moth and a very high level of parasitism of those eggs which were laid. The figures for Cannock Chase, Staffordshire, demonstrate a much more volatile situation where on average the densities have exceeded normal, endemic levels and where on two occasions in 1954 and in 1963, insecticidal intervention was

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Table 1. Annual pupal indices for *B. piniarius*.

Year	No. of pupae/sq.m. Mean for highest compartment		
	Elveden	Rendlesham	Cannock
1954		4.4	281.9*
1955		3.2	1.6
1956		8.2	0.6
1957		6.4	3.2
1958	-	6.6	2.6
1959	1.8	41.8	6.8
1960	0.6	0.6	34.6
1961	0.6	0.4	25.4
1962	0.8	1.2	22.4
1963	1.2	3.2	81.2*
1964	2.4	10.0	4.8
1965	1.2	3.6	2.0
1966	0.8	0.8	1.2
1967	0.8	0.4	5.2
1968	2.8	4.0	12.4
1969	3.2	2.4	18.8
1970	2.4	2.8	9.6
1971	0.8	0.4	2.8
1972	0.0	0.4	11.2
1973	0.8	0.4	44.8
1974	-	0.8	18.0
1975	1.2	0.4	5.6
1976	0.4	2.4	10.0
1977	0.0	4.0	17.2
1978	0.8	3.6	34.8

* Insecticidal treatment applied.

Figures for earlier years are number of pupae/sq.yard which, at lower population levels, do not differ appreciably from number of pupae/sq.m.

required to reduce population numbers to acceptable levels. These sequences of figures show the short term and erratic fluctuations in pest population densities which may occur at any time during the approximately forty year period when the crops are in a vulnerable stage. The fact, however, that population trends of *B. piniarius* move in the same direction in the same year in forests in a given region or even throughout most of Britain, suggests that the underlying factors influencing population change are climatic, e.g. in 1959 virtually all forests in Britain recorded an increase in

population density. These may operate either directly by providing favourable conditions e.g. for adult flight and oviposition or larval feeding (Hussey 1957), or indirectly through mediation of the physiological condition of the host plant (White 1974).

The larch feeding sawfly, Anoplonyx destructor Bens., is a common and sometimes spectacular defoliator in thinning stage stands (Crooke 1953). Much of the larval feeding, however occurs very late in the growing season and has no effect on tree health or timber increment. The species is mentioned here, not because it is of any forest importance but because it illustrates rather well the change of status that may occur consequent upon the introduction of an insect to a region outwith its natural range. When Benson (1952) described the species from British material he stated that it was a rare insect on the continent of Europe being known only from Finland, its native home. Thus, managerial practices in Britain have not prevented A. destructor from becoming endemic. This is true of other sawfly pests such as Gilpinia hercyniae Htg. on spruce and Cephalcia alpina Klug. on larch, which have reached damaging numbers on thinning stage stands, mainly in Wales (Billany, Borden & Brown 1978; Brown & Billany 1977). It seems clear therefore, that these types of incidents have become more frequent in the fairly recent past and may be expected to recur in the future in thinning stage plantations.

During pole and thinning stages bark beetles become more common. The introduction of thinning operations and the fact that increasing tree height predisposes to wind damage provide favourable breeding conditions. Unless there is a natural catastrophe on a large scale, e.g. the storm damage to woodlands in Scotland caused by the gale of 31 January 1953, it is usually possible to restrict bark beetle damage to low levels by sensible management practices. The situation may, however, be complicated with species such as Ips cembrae Heer. which is associated with larch and which can disseminate various fungi capable of causing dieback and death of affected trees.

FINAL FELLING

Most plantations in Britain are regenerated by clear felling followed by replanting and not by any system of natural regeneration. The production of much felled timber can favour the multiplication of bark beetles and of timber borers such as Trypodendron lineatum (Oliv.) and Hylecoetus dermestoides (L.) (Bletchly & White 1962) but if the felled material is removed from the forest quickly these problems can be avoided. Sometimes, however, because of marketing hold-ups this cannot be done and it may be necessary to resort to chemical protection of the logs (Bevan 1962) Also of course, as mentioned earlier, the final felling of the mature crop provides favourable breeding conditions in stumps for pests

which can affect the young trees used for replanting.

THE UNEXPECTED

Despite the fact that there is a more or less clearly defined and well-established succession of different types of insect attack affecting plantations at different stages of growth, the possibility nevertheless exists of some unexpected and unforeseeable infestation taking place. This possibility has recently been demonstrated in a most remarkable way by the outbreak of the pine beauty moth, Panolis flammea (D.+S.), on lodgepole pine crops in the north of Scotland. This outbreak which necessitated insecticidal treatment of some 4600 ha in 1978 appears to have had its observable origins in 1973 when larvae of this species were common in plantations of the Forestry Commission's Shin, Rumster and Naver forests (Stoakley 1977). The pine beauty is a well-known defoliator of Scots pine crops, usually of more than twenty-five years of age in Central Europe. In the Scottish outbreak the attack was on a different species of host tree, occurred at an unusually early stage in the growth of the crop, took place near the northerly limit of the insect's range, and developed in a location where soil and climatic conditions are very different to those of areas where previous infestations have been recorded. The combination of all these abnormal factors made the incident entirely unpredictable. Another remarkable feature is the relative rapidity with which the situation developed. The first plantings of lodgepole pine in the area in question took place in 1958. It is possible, but not definitely established, that the pine beauty was present prior to 1958 in very small numbers on the few Scots pine which grow in Caithness and Sutherland. Thus the whole course of the establishment of the pest in the plantations and its increase in numbers to damaging levels was compressed into a brief period of time: the first planting in 1958, first larvae found quite commonly in 1973, some defoliation in 1974, no reports for 1975, defoliation apparent in June 1976, control unsuccessfully attempted in 1977 with a Bacillus thuringiensis preparation applied over 540 ha, and insecticidal treatment of 4600 ha in 1978 (results not yet known).

CONCLUSION

Three time scales operate in respect of the development of insect populations in plantations. The first and longest is that of the creation and maturation of the total plantation estate. During this usually long and rather ill-defined period opportunities arise, first, for the introduction of non-indigenous pest species and, second, for the dissemination of both native and exotic pests. Accompanying these processes in time is the establishment of increasingly large areas of plantations which potentially can support epidemics of

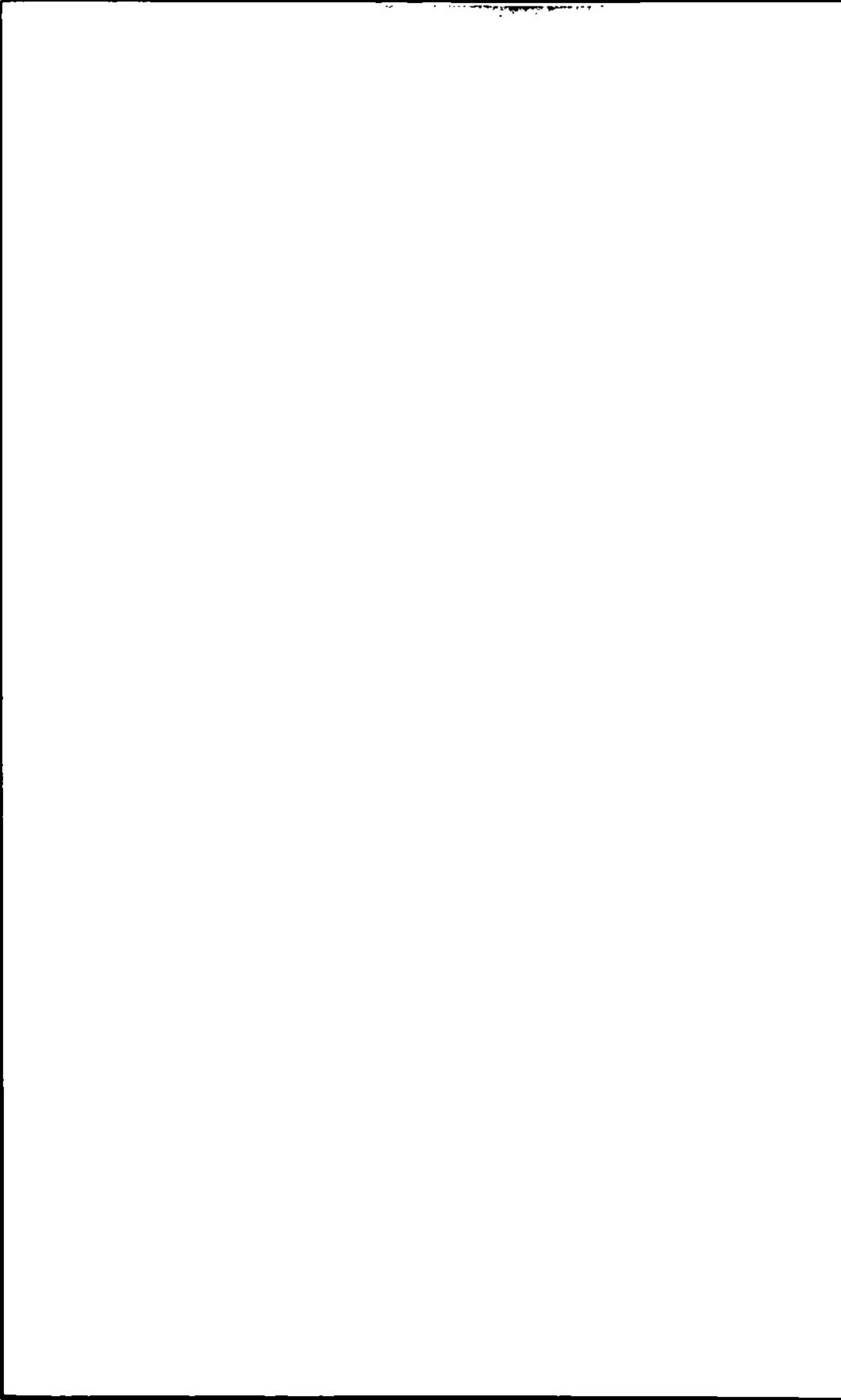
different types of pests as the crops successively reach ages favourable to these pests. In Britain it is convenient to think of the start of this period as being around 1920. Before then there had of course been much plantation establishment using mainly either the native Scots pine or trees introduced from elsewhere in Europe and this had had its effects upon the establishment and spread of the forest insect fauna (e.g. Crooke 1957). The end of the First World War however, saw the introduction of the major planting programmes to recreate forests felled for wartime timber requirements. These programmes have continued up until the present and have become increasingly dependent on conifers introduced from North America. Against this time scale and keeping in mind the essential features of forestry practice, it was possible to make some guesses or predictions about future development in the pattern of forest insect damage in the country as a whole (Crooke 1958) and in the main it appears that these have been realised.

The second time scale is the life of the individual plantation itself and it is this aspect of the subject which has formed the main content of this paper. The third time scale, which has been hinted at but not explored, is that concerned with the beginning and end of the single epidemic. In some cases the ecological factors contributing to the 'graduation' are obvious and well understood (e.g. *H. abietis*); in other cases the changes in insect density during the course of the infestation can readily be recorded but are only imperfectly accounted for by ecological explanation (e.g. *B. piniarius*); and in yet others the ecological underlying influences operating on the arisal and termination of the outbreak are little if at all appreciated (e.g. *P. flammca*). It is in this epidemiological area that much future research will have to be conducted.

REFERENCES

- Benson, R.B. (1952). A new *Anoplonyx* destructive to larch in Britain. *Bulletin of Entomological Research*, **43**, 543-547.
- Bevan, D. (1961). Insecticidal control of the pine looper in Britain. II Population assessment and fogging. *Forestry*, **34**, 14-24.
- Bevan, D. (1962). The ambrosia beetle or pinhole borer, *Trypodendron lineatum* Ol. *Scottish Forestry*, **16**, 94-99.
- Billany, D.J., Borden, J.H. & Brown, R.M. (1978). Distribution of *Gilpinia hercyniae* (Hymenoptera, Diprionidae) eggs within Sitka spruce trees. *Forestry*, **51**, 67-72.
- Bird, F.T. (1953). The use of a virus disease in the biological control of the European pine sawfly. *Canadian Entomologist*, **85**, 437-446.
- Bletchly, J.D. & White, M.G. (1962). Significance and control of attack by the ambrosia beetle *Trypodendron lineatum*

- (Oliv.) (Col. Scolytidae) in Argyllshire forests. Forestry, 35, 139-163.
- Brown, R.M. & Billany, D.J. (1977). The web spinning larch sawfly Cephalcia lariciphila Wachtl. (= C. alpina Klug.). Report on Forest Research, London, pp. 35.
- Chrystal, R.N. (1937). Insects of the British Woodlands. Frederick Warne + Co. Ltd., London and New York.
- Crooke, M. (1953). Some notes on Anoplonyx destructor Bens. Bulletin of Entomological Research, 44, 77-81.
- Crooke, M. (1957). A brief review of the conifer feeding sawflies. Zeitschrift für angewandte Entomologie, 41, 179-183.
- Crooke, M. (1958). Some aspects of forest entomology in Britain. Proceedings 10th International Congress on Entomology (1956), 4, 233-239.
- Crooke, M. (1959). Insecticidal control of the pine looper in Great Britain. I. Aerial spraying. Forestry, 32, 166-196.
- Gauss, R. (1960). Tortrix viburnana F. erneut als Forstschädling. Zeitschrift für angewandte Entomologie, 47, 46-51.
- Hussey, N.W. (1957). Effects of the physical environment on the development of the pine looper, Bupalus piniarius. Report on Forest Research, London, pp. 111-128.
- King, C.J. & Scott, T.M. (1975). Control of the large pine weevil and bark beetles of the genus Hylastes. Forestry, 48, 87-97.
- Scott, T.M. (1972). The pine shoot moth and related species. Forestry Commission Record, 83.
- Stoakley, J.T. (1977). A severe outbreak of the pine beauty moth on lodgepole pine in Sutherland. Scottish Forestry, 31, 113-125.
- Varty, I.W. (1956). Adelges insects of silver firs. Forestry Commission Bulletin 26. Edinburgh.
- White, T.C.R. (1974). A hypothesis to explain outbreaks of looper caterpillars with special reference to populations of Selidosema suavis in a plantation of Pinus radiata in New Zealand. Oecologia, 16, 279-301.



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NUTRITION

Chairman: K. Parkin

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Decomposition and nutrient release in even-aged plantations.	O.W. Heal
Biological means of improving nutrient uptake in trees.	P.P. Kormanik
Current fertilizer use in plantations.	J. Atterson



THE NUTRIENT BUDGETS OF EVEN-AGED FORESTS

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SUMMARY

Nutrients are introduced to a forest in rainwater, by the trapping on tree surfaces of aerosols and dust, through adsorption of gases and by nitrogen fixation. The input from sources other than rainfall is difficult to assess but for some elements may be as large as that in rainwater, and it is probable that the total input from all sources is sufficient to compensate for losses through harvesting. Irrespective of the mode of introduction, nutrients are very efficiently retained within forests, to the extent that, provided sensible management practices are followed, high inputs in fertilizer or in sewage effluent are unlikely to contaminate neighbouring waterways. However, this same ability could mean that forest are peculiarly susceptible to air-borne pollutants.

Within the ecosystem nutrients are taken up and released by the trees, the rate of transfer varying greatly with species, growth rate and size of the crop. Nutrients become progressively immobilized both in the trees and in the humus, and immobilization of nitrogen may even reach such proportions that growth declines. In general it seems that, provided the nutrient capital of the site is sufficient to enable establishment, nutrient deficiencies later in the rotation result from changes in the ability of the soil to supply nutrients, rather than from changes in demand by the crops.

Nutrients move within the tree as a result of (i) current nutrient uptake, (ii) the moving into temporary storage of recent uptake and its subsequent mobilization during the growing season, (iii) the withdrawal from ageing

tissues, and (iv) should there be an insufficient supply from the first three sources, the mobilization of nutrients accumulated during previous years. This latter may represent use of stored excess nutrient, or may result in the sacrifice of older tissues.

RÉSUMÉ

Les éléments nutritifs sont introduits dans la forêt par l'eau de pluie; les cimes des arbres arrêtent les aérosols et les poussières, absorbent les gaz et les arbres fixent l'azote. L'apport d'éléments nutritifs provenant des sources autres que les chutes de pluie est difficile à évaluer mais dans certains cas il peut être aussi important que celui de l'eau de pluie et il est probable que l'apport total, provenant de toutes les sources, suffirait à compenser les pertes dues aux coupes. Quelque soit le mode d'introduction de ces éléments nutritifs, ceux-ci sont retenus d'une manière très efficace par la forêt au point que, si l'on maintient une forme d'exploitation raisonnable, l'apport d'engrais ou d'eaux résiduelles ne serait pas une source de contamination des cours d'eaux avoisinants. Cependant le processus décrit plus haut rendrait les forêts particulièrement susceptibles aux polluants portés par l'air.

Au sein de l'écosystème, les éléments nutritifs sont absorbés et relibérés par les arbres. Le taux de transfert varie beaucoup entre les différentes essences et l'âge des peuplements. Les éléments nutritifs sont progressivement immobilisés par les arbres et par l'humus; l'immobilisation de l'azote peut atteindre de telles proportions, qu'elle entraîne un déclin de la croissance. En général, il semble que, si le capital d'éléments nutritifs de la station suffit à assurer la reprise à la plantation, les carences nutritives qui apparaissent plus tard résultent plutôt de l'incapacité du sol à fournir les éléments nutritifs, que des besoins accrus du peuplement.

Le mouvement des éléments nutritifs dans l'arbre est le résultat des cas suivants: (1) l'absorption courant d'éléments nutritifs, (2) le stockage temporaire des éléments nutritifs et leur mobilisation pendant la période de croissance, (3) le retrait d'éléments nutritifs

de tissus âgés et, (4) au cas où ces trois premières sources seraient insuffisantes, la mobilisation des éléments nutritifs accumulés antérieurement. Dans ce dernier cas il peut s'agir soit de l'utilisation d'un excédent d'éléments nutritifs, soit du sacrifice de tissus plus âgés.

ZUSAMMENFASSUNG

Nährstoffe gelangen in den Wald im Regenwasser, durch Auskämmen von Aerosolen und Staub, durch Adsorption von Gasen und Bindung von Stickstoff. Es ist schwierig, den Nährstoffeintrag durch Gase, Aerosole und Staub abzuschätzen. Er dürfte jedoch bei manchen Elementen in ähnlicher Höhe wie der durch Regenwasser liegen. Insgesamt sind die Gewinne aus allen Quellen wohl ausreichend, um die Verluste durch Ernte auszugleichen. Nährstoffe werden, unabhängig von der Art ihrer Zufuhr, in den Wäldern sehr wirkungsvoll gespeichert. Daher sind bei richtiger Handhabung selbst hohe Zufuhren von Düngemitteln oder Abwasser möglich ohne Beeinträchtigung benachbarter Gewässer. Aus dem gleichen Grund ist jedoch denkbar, dass der Wald besonders für Verschmutzung durch die Luft anfällig ist.

Innerhalb des Ökosystems werden die Nährstoffe von den Bäumen aufgenommen und abgegeben. Die Umsatzrate ist abhängig von Art, Wachstumsleistung und Alter der Bäume. Die Nährstoffe werden in zunehmender Masse sowohl in den Bäumen als auch im Humus festgelegt; dabei kann die Fixierung von Stickstoff solches Ausmass erreichen, dass das Wachstum zurückgeht. Im allgemeinen wird bei ausreichend hohen Nährstoffvorräten des Standorts Nährstoffmangel während der Umtriebszeit eher infolge Veränderung in der Nährstoffnachlieferung des Bodens auftreten als durch Veränderungen im Bedarf der Pflanzen.

Die Nährstoffbewegung im Baum ist bedingt durch 1) laufende Nährstoffaufnahme, 2) vorübergehende Speicherung und nachfolgende Mobilisierung während der Wachstumsperiode, 3) Rückzug aus alternden Geweben und 4) Mobilisierung von in früheren Jahren gespeicherten Nährstoffen im Falle ungenügenden Angebots nach 1)-3). Letzteres kann bedeuten, dass gespeicherte Überschussmengen aufgebraucht oder aber ältere Gewebe geopfert werden.

INTRODUCTION

The fact that tree growth can be reduced if there is an insufficient supply of any of at least twelve essential nutrient elements was clearly demonstrated by early studies using pot culture (e.g. Aldrich-Blake 1930; Addoms 1937; Mitchell 1939; Ludbrook 1940; Smith 1943) and deficiencies of certain of these elements were subsequently identified under field conditions (see reviews of Tamm 1964; Mustanoja & Leaf 1965; Stone 1968; Baule & Fricker 1970). The available literature on forest studies, however, is largely based on results from extensive fertilizer trials and contains confusing contradictions. In seeking to find some order, or framework, on which to build hypotheses, the published work on nutrient dynamics within forests, particularly studies of the full nutrient-cycle (e.g. Remezov 1956; Ehwald 1957; Ovington 1959 and 1962; Will 1959 and 1964; Smith, Nelson & Switzer 1963; Miller 1963) has had to be studied. This, in turn, has led to a new generation of experiments, established mainly during the 1960's, that were designed to investigate, inter alia, the effect of management practices on nutrient cycles and their controlling influence on tree growth. Such studies have considered the effects of fertilizer applications - either alone (e.g. Wittwer, Leaf & Bickelhaupt 1975; Miller, Miller & Pauline 1976; Turner 1977; Stone & Kszystniak 1977) or combined with thinning treatments (e.g. Weetman 1962 and 1967) - the replacement of tree species (e.g. Ulrich et al. 1976; Nihlgard 1971), the effects of harvesting (e.g. Weetman & Webber 1972; Mälkönen 1974 and 1977), the effects of burning (e.g. Kimmins & Feller 1976) and, more recently, the effects on, or of pollution (e.g. Tamm 1973, 1976 and 1977).

Although definitive results have still to appear from some of the more ambitious studies started in recent years, a considerable amount of information has become available over the past decade. This is, therefore, a convenient point at which to review our knowledge of nutrient cycles in forests and to consider (a) whether it can provide a framework within which to assess the significance of results from other studies on limited parts of the system and (b) whether the picture that is emerging will give any practical assistance to the forest manager.

Nutrient cycles occur at three interrelated levels: (i) the geochemical cycle, which contributes nutrients to and removes them from the forest site, (ii) the cycle transferring nutrients between zones of accumulation within the ecosystem and (iii) the physiological cycle within the tree.

GEOCHEMICAL CYCLE

Nutrient elements enter a forest site in rainwater, by the trapping on tree surfaces of aerosols and insoluble dust, through adsorption of such gases as sulphur dioxide, ammonia

Table 1. Weights of sodium, calcium and potassium (kg/ha/yr) in rainfall at two coastal and two inland sites in Scotland during 1977 (author's data).

Element	West Coast	Inland	Inland	East Coast
Na	41	23	21	45
Ca	10	9	8	10
K	1	4	2	2
Rainfall (mm)	1530	1620	1020	1120

and oxides of nitrogen and by biological fixation of nitrogen.

Input in rainwater has attracted attention for many years (e.g. Miller 1905; Freeman 1924; Ingham 1950; Madgwick & Ovington 1959; Miller 1961; Attiwill 1966; Dovland, Joranger & Semb 1976). Values range widely, reflecting factors such as the amount of rainwater received and distance from the sea or from possible terrestrial sources of contamination (Table 1). A variety of evidence points to the sea as the main source of most elements in rainwater and amounts generally decrease on moving inland (O'Carroll & McCarthy 1973; Turner & Kelly 1973; Probert 1976; Hingston & Gailitis 1976). The sea is probably also the main source of soluble salts in trapped aerosols (Yaalon & Lomas 1970; Hitchcock 1976) and rate of input of these to the forest varies not only with concentration in the air, but also with the nature and spatial arrangement of the receiving surfaces (Chamberlain 1975). Placing an inert wind-filter over a rain gauge results in an increase in the concentration of many elements in the collected rainwater (Nihlgard 1970; Clayton 1972; Azevedo & Morgan 1974; Schlesinger & Reiners 1974), the effect varying with location of the gauge (Table 2). This aerosol contribution is difficult to assess, but recent studies in pole-stage in Germany and Scotland (Table 3) suggest it is of comparable magnitude to the amount introduced in rainwater.

Over land masses and at a height of more than 2 km over oceans aerosols mainly consist of insoluble mineral (Rodhe, Persson & Akesson 1972; Gether, Lunde & Markali 1976) and organic particles (Gether, Gjos & Lunde 1976; Lunde et al. 1976) of continental origin (Delany, Pollock & Shedlovsky 1973). A dramatic example of long distance transfer is the Sahara derived dust that has fallen as 'red rain' as far north as the Isle of Skye (Pitty 1968; Bain & Tait 1977). In addition, there is a short-range transport of dust (Tamm & Troedsson 1955; Miller & Williams 1977) that is again almost entirely soil-derived. Virtually no information exists on the quality of nutrients introduced in dust from all sources, but certainly the amount of dry particles trapped by trees is

Table 2. Weights of sodium, calcium and potassium collected in rain gauges beneath inert wind-filters polyethylene-coated wire mesh expressed as a percent of the weights of these elements collected in standard rain gauges. Results are taken from the four sites shown in Tables 1 and over the same year (author's data).

Element	West Coast	Inland	Inland	East Coast
Na	425	185	100	445
Ca	190	115	150	225
K	465	110	200	500

Table 3. Inputs (Kg/ha/yr) in rainwater and in aerosols estimated for a beech stand in central Germany (Mayer & Ulrich 1974) and for a coastal stand of Corsican pine in Scotland (Miller, Cooper & Miller 1976).

	Na	Ca	K	Mg
Germany				
Rainwater	7	13	4	3
Aerosol	3	6		
Scotland				
Rainwater	25	3		
Aerosol	15	4	7	2

greater than that deposited on open ground (Chamberlain 1975; Slinn 1977). Tamm (1958) has suggested that dust may be an important source of phosphorus which, although initially insoluble, can be mobilized by weathering.

Turbulent transfer to and impaction of gases on forest vegetation is now the object of a considerable amount of investigation in relation to the input of pollutant gases. Direct measurement of the input of gaseous compounds is very difficult. Deposition is usually assumed to be proportional to the concentration of the gas in the surrounding atmosphere, the constant of proportionality being called the 'deposition velocity'. Values for the deposition velocity of sulphur dioxide are around 0.4 to 0.8 cm/s (Fowler & Unsworth 1974; Bache 1977; Garland 1977), which is a magnitude greater than the estimated deposition velocities of typical atmospheric particles in dry air (Chamberlain 1975). Sulphur dioxide and gaseous ammonia may also be absorbed directly by the soil (Hall & Miller 1911; Ingham 1950; Allison 1955; Paul 1976). Furthermore, Tamm (1953) has pointed out that the acid moss

Table 4. Concentrations (mg/l) of elements in rainwater, soil leachates and drain-water collected over three months beneath a crop of Sitka spruce in east Scotland (author's data).

	N	P	K	Ca	Mg	Na	S	Cl
Throughfall and stemflow	8.0	0.235	5.7	7.4	2.2	9.6	8.0	22
Leachate								
-below humus	3.1	0.044	2.3	5.3	0.8	7.0	5.1	7
-below root zone	1.1	0.004	1.3	3.7	1.2	44.7	19.9	15
Water draining from the site	1.6	0.003	0.8	6.6	2.6	13.9	1.3	13

flora of coniferous forests absorbs ammonia from the atmosphere, and as nitrogen in mosses is relatively readily mineralized on decomposition (Zöttl 1960) this may be an important source for tree growth in boreal forests (Weetman 1967).

There is also an accretion of nitrogen through biological fixation. The presence in a forest of leguminous or other nodulated species, such as *Casuarina* (Bond 1957) or *Podocarpus* (Becking 1965), has long been known to be beneficial (Tarrant & Miller 1963; Richards & Bevege 1967; Gadgil 1971 and 1977), and large accretions of nitrogen have been recorded beneath pure stands of black locust (Ike & Stone 1958) and red alder (Turner, Cole & Gessel 1976). Moreover, Richards (1964) has pointed to many examples of nitrogen accretion in coniferous forests containing no nodulated species. Suggestions that this fixation may be associated with mycorrhizae are probably unfounded (Richards & Voigt 1963; Harley 1969) and it seems to result from free-living organisms within the soil (Reddy & Knowles 1965; Roskoski 1975) and, perhaps, in the phyllosphere (Jones 1970). By extrapolation from laboratory studies Knowles (1965) estimated annual rates of nitrogen fixation of from 5-35 kg/ha, although more recent studies under field conditions seem to be suggesting that the lower figure is the more likely (see also Kormanik, this volume).

The forest floor and surface soil horizons are remarkably effective at retaining nutrients received in rainwater (Table 4). Comparisons of water reaching the forest floor with that of drainage from the bottom of the profile suggest a net retention of nitrogen and phosphorus within the soil (Cole & Ballard 1970; Grier & Cole 1972; Fredrikson 1972; Gessel, Cole & Steinbrenner 1973; Nishimura 1973; Mayer & Ulrich 1974; Heinrichs & Mayer 1977; Likens et al. 1977; Staaf & Berg 1977; Feller 1977) and although the soil may show a net loss of many cation species, Mayer & Ulrich (1977) have calculated that,

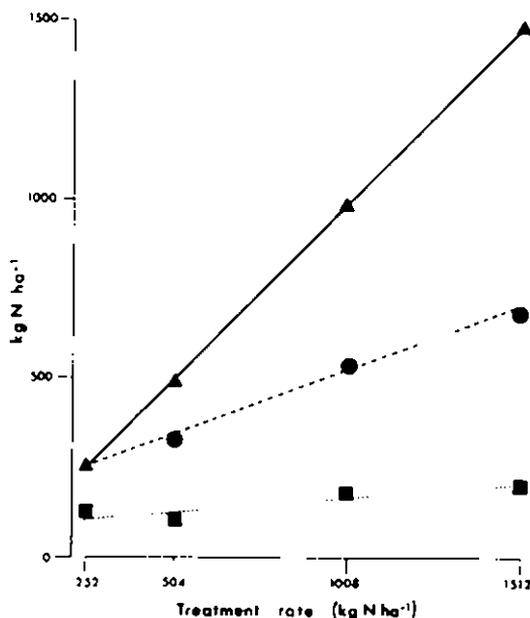


Fig. 1. Retention of fertilizer nitrogen within a crop of Corsican pine (●) and retention in the associated soil organic layers (■) in comparison to the weight of nitrogen applied (▲). (Miller, Miller & Pauline 1976).

when account is taken of increasing accumulation within the tree crop, only sodium of those elements shown in Table 4 decreases in the ecosystem. In this respect forestry seems to be more effective than other forms of land use (Dillon & Kirchner 1975). Forests also have the ability to retain large amounts of fertilizer applied nutrients. Studies with ¹⁵N suggest total recovery of nitrogen when applied at standard rates to raw humus (Overrein 1970), and repeated sampling in a Corsican pine plantation before and after a three-year period of a nitrogen fertilizer application revealed very high retention rates (Fig. 1). Similar results have been quoted by Morrison & Foster (1977) for urea fertilized jack pine. However, if a large amount of nitrate is applied, leaching losses may occur (Kreutzer & Weiger 1974). Fertilizer phosphorus is also retained efficiently by most forests, although there is some recent evidence of leaching of this element in drained peat (Malcolm et al. 1977; Cuttle & Malcolm, personal communication; see also Fig. 2), and potassium, although very mobile, is efficiently retained by

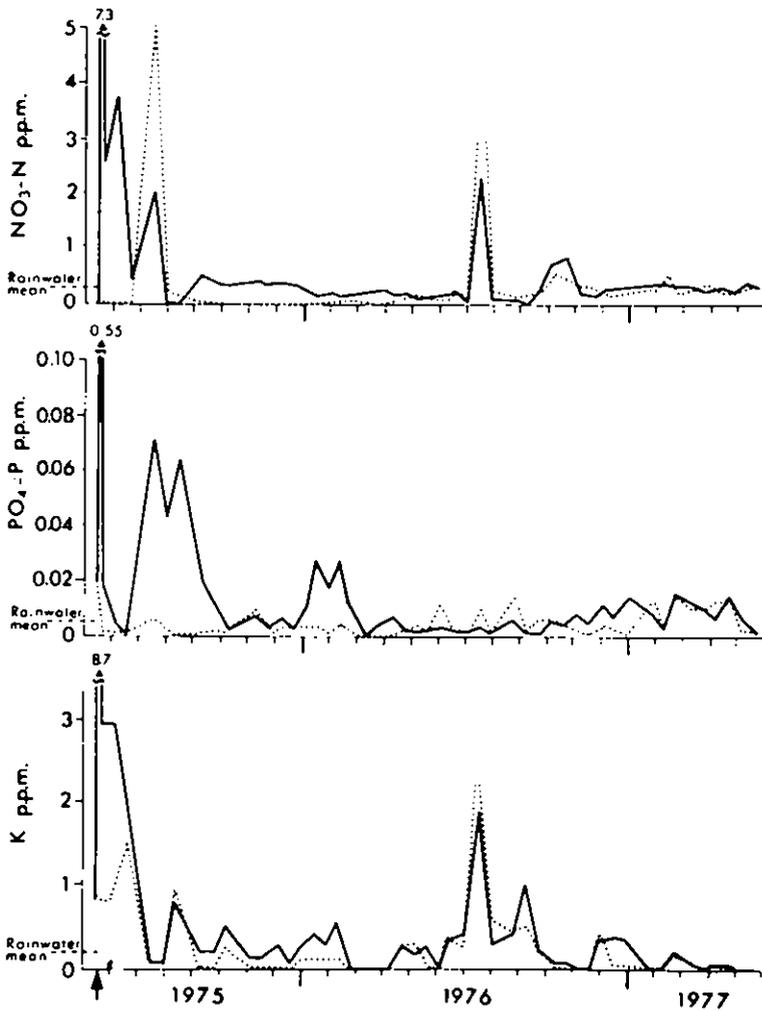


Fig. 2. Comparison of levels of nitrate, phosphate and potassium in ditch water on entering (.....) and leaving (—) a Sitka spruce plantation (25 yr, top height 11.5m) to which ammonium nitrate, rock phosphate and potassium chloride were applied at the outset of period (vertical arrow). Soil: peaty-gley. (The W.H.O. suggests that nitrate in drinking water should not exceed 11.3 ppm as nitrogen.)

incorporation into the rapid cycle of this element (Miller et al. in press; Stone & Kszystniak 1977).

Practical significance

In 1955 Rennie calculated that the nutrient drain associated with timber harvesting in managed plantations would lead to "soil degradation and seriously reduce production" (Rennie 1955). Subsequently Ovington (1962) pointed out that the mean annual removal in tree trunks is largely balanced, at least for elements other than nitrogen and phosphorus, by the nutrient input in precipitation - an observation that has since been amply confirmed using more precise data (e.g. Weetman & Webber 1972; Foster & Morrison 1976). Whether the further drain associated with practices such as slash burning (Harwood & Jackson 1975; Kimmins & Feller 1976; McColl & Grigal 1977) and complete- or whole-tree utilization (Keays & Hatton 1976) would then be balanced by the inputs through impaction of aerosols and gases and through nitrogen fixation, remains an open question. Burning, which mainly releases nitrogen (Robertson & Davies 1965; Kimmins & Feller 1976), is thought not to cause irreparable loss if properly managed (DeBell & Ralston 1970; Wollum & Davy 1975; Klemmedson 1976). Although there is less agreement about the consequences of harvesting the tree crowns as well as stems, recent data does confirm that this practice results in a marked increase in nutrient removal (Table 5), and it has been suggested that on sites of low fertility it may be necessary to balance the loss by fertilizer application (Weetman & Webber 1972; White, E. 1974; Mälkönen 1974 and 1976; Wells & Jorgensen 1977). However, there is still too little information on the input of nutrients, other than that in direct precipitation, to obtain a clear picture.

Management practices, in particular clearfelling, may result in increased leaching of many nutrients (Cole & Gessel 1965; Fredriksen, Moore & Norris 1975; Popovic 1975; Nykvist 1977). In the mixed hardwoods of New England it has been shown that, whereas in the undistributed stand nutrients were conserved and losses to lower soil layers were minimized, clearfelling was followed by a marked increase in the leaching of most elements. The reappearance of forest vegetation, however, was followed by rapid stabilizing of the nutrient cycles, leaching returning almost to pre-treatment rates (Likens et al. 1977; Borrmann, Likens & Melillo 1977; Likens et al. 1978). An essentially similar pattern can occur following application of fertilizer, for although there is an overall high retention of applied nutrients, concentrations in water leaving the site may increase for a period after application, largely as a result of the fertilizer that falls directly into the drainage ditches (Fig. 2). The most important effect of this is probably the pollution caused in neighbouring waterways (Tamm & Wiklander 1972; Tamm 1973; Kreutzer & Weiger

Table 5. Comparison of the nutrient removal resulting from harvesting stem alone, with that resulting from removal of all above-ground components of tree for both Corsican pine and Sitka spruce growing in Scotland (author's data).

Kg element per M³ of stem wood and bark

	Pine			Spruce		
	N	P	P	N	P	K
Stem alone	0.46	0.04	0.19	0.52	0.05	0.22
Whole Tree	1.38	0.12	0.62	2.17	0.23	0.78

1974; Bengston & Kilmer 1975).

Recently the ability of forest soils to retain chemical elements, and so purify the water passing through them, has been exploited as a means of sewage effluent disposal (Sopper 1975). However, the obverse of this ability is that forests are peculiarly susceptible to atmospheric pollution, and there is now considerable concern about the effects of increasing inputs of sulphur and nitrogen to forests (e.g. Likens & Bormann 1974; Dovland et al. 1976). Sulphur, as sulphates and sulphites in acid rain, may have a direct effect on trees (Tamm & Cowling 1977) or an indirect effect through inducing changes in the soil (Ulrich 1975; Abrahamsen et al. 1976; Tamm 1976) - although there is, as yet, very little definitive information on either. Certainly large amounts of sulphur can be introduced into forests (Ulrich et al. 1976), but this has to be viewed against the normal rate at which sulphur cycles within the ecosystem and also the complex interactions that contribute to the buffering characteristics of a soil. Claims that tree growth has been reduced through acid rain (Jonsson & Sundberg 1972) are difficult to confirm (Abrahamsen et al. 1976) and may have been confused with variations in growth in response to regular variations in climatic factors (Miller & Cooper 1976). Indeed it is easier to substantiate suggestions that trees show a positive growth response to enhanced inputs of nitrogen pollutants from the atmosphere (Ulrich 1975). However, the proven ability of forests to retain most chemical elements means that pollution-derived inputs be viewed with concern, and their effects investigated.

CYCLES WITHIN THE ECOSYSTEM

Within the ecosystem, nutrients move between the three zones of accumulation represented by the living vegetation, the soil organic layers and the lower soil horizons.

Since rate of nutrient uptake by trees differs with species and soil conditions (Table 6), and even within species shows a considerable variation both with growth rate and

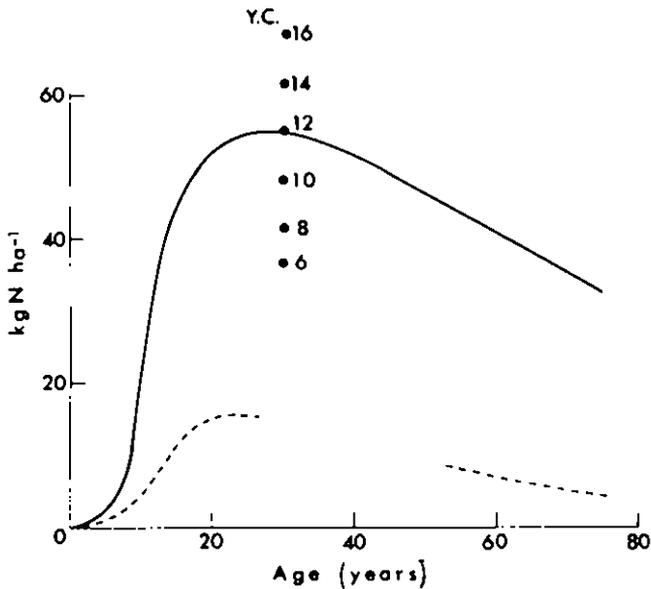


Fig. 3. Variation in nitrogen uptake with growth rate (Y.C.= yield class, Hamilton & Christie 1971) and age for one growth rate; broken line shows rate of net increase in accumulation of nitrogen at this growth rate. Values predicted by models derived for Corsican pine (Miller, Miller, & Pauline 1976, together with unpub. results.)

developmental stage of the crop (Fig. 3), values of uptake, taken alone, have little meaning. As trees simultaneously release nutrients, the net proportion of the uptake that remains to accumulate within the crop is low and generally ranges from 8 to 38 per cent (Mälkönen 1974, 1977; Miller, Miller & Pauline 1976). Despite this, the amount of nutrient, particularly nitrogen, that eventually accumulates within trees can be large, and on poor sites may represent a significant fraction of the total capital of the site.

Nutrients are released by trees through litter fall, crown leaching, root death and root exudation. Litter fall is composed predominantly of dead leaves, the amount of which is broadly proportional to growth rate (Bray & Gorham 1964; Miller, Cooper & Miller 1976). Presumably the release of organic matter and associated nutrients by root systems is also proportional to growth rate, but little information exists. Orlov (1955) considered that in young coniferous crops organic matter turn-over below ground is about half of that above ground. More recently it has been suggested that the

Table 6. Recent estimates of nutrient uptake in even-aged forests, kg/ha/yr.

Genera and location			Mg	Reference
<u>Fagus</u>				
Germany	72	46	33	J Ulrich & Mayer 1972
S. Sweden				
(3 site types)	50-113	34-49	63-107	5-12 Nihlgard & Lindgren 1977
<u>Quercus</u>				
Belgium	92	7	69	201 Duvigneaud & Denaeyer 1970
England (2 sites)	44-85	3-6	30-60	40-111 Brown 1974
Oklahoma				
(mixed species)	101	11	80	300 Johnson & Risser 1974
Missouri				
(mixed species)	54	29	82	7 Rochow 1975
<u>Pinus</u>				
S. Finland				
(3 site types)	19-39	2-4	10-15	11-19 Mätkönen 1974
N. Ontario	26	2	15	19 3 Foster & Morrison 1976
Central Sweden	6.5	0.6	3.5	6.9 1.1 Bringmark 1977
Scotland				
-nitrogen deficient	17	4	14	36 Miller, Miller & Pauline
-at maximum growth	69	28	34	11 1976

ratio of release of an element to total weight accumulated is similar for the root system and the shoot system (Newbould 1968; Andersson 1970; Whittaker & Woodell 1971; Whittaker et al. 1974). Whether this also accounts for release in root exudates is not clear, but certainly, root exudation can release appreciable quantities of nutrients, in particular potassium and calcium (Smith 1976).

Table 7. Release in litter fall and through crown leaching measured in Corsican pine, Kg/ha/yr (Miller, Cooper & Miller 1976).

	N	P	K	Ca	Mg
Litter fall	35	3	8	18	3
Crown leaching	trace	trace	6	2	3

For some elements, release through crown leaching can be as important as that through litter fall (Table 7). Rate of crown leaching varies with season, with the amount, nature and acidity of the incident precipitation, with element concentrations in the tree foliage and with species (Miller 1963; Eaton, Likens & Bormann 1973; Mahendrappa & Ogden 1973; Päivänen 1974; Fairfax & Lepp 1975; Wood & Bormann 1975; Abrahamsen et al. 1976; Miller, Cooper & Miller 1976). Moreover, the relative magnitude of the leaching of different elements changes with species. Thus, Nihlgard (1970) found that whereas phosphorus and sulphur are not readily leached from beech, these elements are among the most easily removed from a Norway spruce canopy; a similar difference by the leaching of phosphorus has been noted between Corsican pine and Sitka spruce (Miller & Williams 1973).

Accumulation of nutrients, particularly of nitrogen and phosphorus in the soil organic layers beneath many coniferous species can be comparable to, or even exceed, that accumulated within the trees themselves. Organic matter builds up very rapidly while the crop is young, probably reaching a maximum by the middle of the rotation (Page 1968). However, there are suggestions that there might be a continuing accretion of nitrogen long after organic matter accumulation has stabilized (Foster & Morrison 1976). This immobilized nitrogen may be regarded, in the short-term, as an effective removal of nitrogen from the cycle within the forest and can cause the gradual development of deficiency conditions on sites already low in this nutrient, as has been shown in Germany (Zöttl 1960; Rehfuss 1968), Sweden (Tamm, Carbonnier & Hagberg 1960), Finland (Siren 1955; Viro 1967), eastern Canada (Weetman 1962), Washington (Heilmann & Gessel 1963; Turner 1977) and Scotland (Miller 1969; Miller & Cooper 1973; Miller, Miller & Binns 1977). Indeed, Heilmann (1966) has suggested that the reduction in the availability of nitrogen beneath

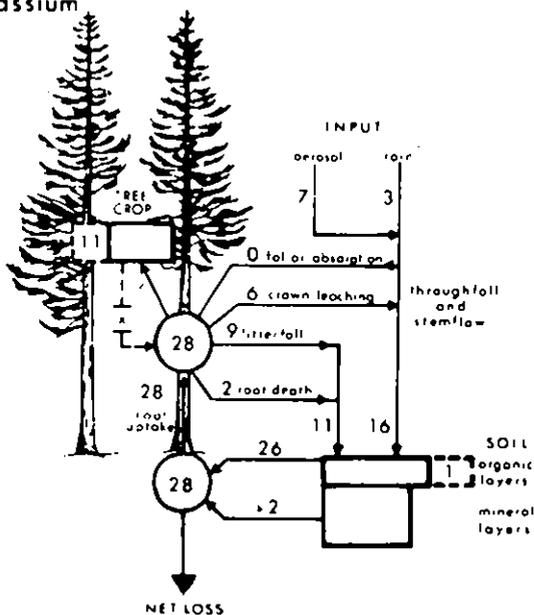
black spruce in Alaska has led to accumulation of a thick moss layer and eventual deterioration to a sphagnum bog.

The accumulation of organic matter on the forest floor may also play a positive role (a) by acting as a reservoir of nutrients that will buffer the system against disturbances promoting loss of nutrients (Gosz, Likens & Bormann 1976) and (b) as pointed out above, by retaining much of the nutrient input to the ecosystem.

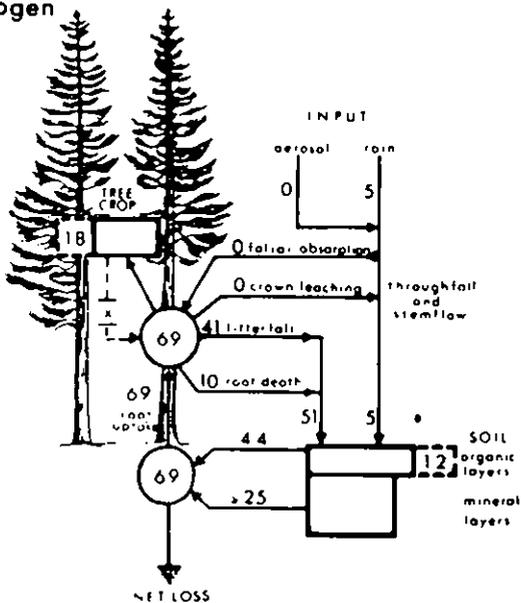
During the early years of a plantation, much of the nutrient taken up is supplied from the mineral soil. With time, however, a cycle becomes established between the tree and soil organic horizons that, together with enhanced input through aerosol capture, reduces the dependence of the trees on nutrients from the lower soil horizons. Indeed, recent models of nutrient cycling in Corsican pine (Miller et al. in press) suggest that for potassium, which cycles rapidly and which is immobilized at a rate sufficiently low to be compensated for by atmospheric input, the mineral soil may supply only 7 per cent of the trees' uptake (Fig. 4). A similar situation exists for magnesium. For nitrogen, however, the trees have to make continuing demands on soil reserves throughout the rotation (Fig. 4) and this also seems to apply for phosphorus and calcium. Although in most soils the amount of potentially 'available' nutrients is relatively large compared with the amount accumulated in the tree crop (Weetman & Webber 1972; Foster & Morrison 1976), and although trees are able to obtain nutrients from fairly intractable soil sources (Voigt 1965; Harley 1969), there are many soils, such as the peats of Britain and Ireland (Binns 1962; O'Carroll 1966) and the sandy outwash soils in New York State (Heilberg & White 1950), in which one or more nutrient is in such low supply that fertilizers have to be applied if trees are to be established.

Once established, trees interact with the soil, producing changes that probably vary with species. The effects induced by many broadleaved species are notably different to those induced by coniferous species, the latter tending to lead to the development of a pronounced organic layer, and increased acidity and podzolization. Beneath spruce as compared to beneath adjacent beech, exchangeable cation contents in the surface horizons are usually lower, phosphate, aluminium and exchangeable hydrogen contents higher, while the rate of nitrification is depressed (Nihlgard 1971; Ulrich, Ahrens & Ulrich 1971). There may also be a difference in soil structure; whilst roots of some coniferous species promote an increase in large soil pores, the removal of sesquioxides associated with podzolization may lead to a loss of aggregate stability (Grieve 1978). However, the very variable nature of soil, even within a crop of the same species, means that it is difficult to make a precise assessment of the effects of a

Potassium



Nitrogen



change of tree species; indeed, Anderson (1976) has recently suggested that, despite initial differences noticed in the soil beneath a range of coniferous trees, subsequent development indicates convergence towards a uniform soil type. Although soils, beneath different tree species have been compared, there have been few opportunities to monitor the changes following afforestation of bare ground. Several authors have reported marked drying and physical changes in peat beneath planted lodgepole pine (Binns 1962; Pyatt 1975; Boggie & Miller 1976). Williams, Cooper & Pyatt (1978) have shown that in such peat there is a decrease in exchangeable calcium, magnesium and potassium, presumably associated with tree uptake, and an increase both in exchange capacity and amount of exchangeable sodium, reflecting greater decomposition and catch of sea-derived aerosols beneath the trees.

Practical significance

Knowledge of the accumulation of nutrients in the tree, humus and soil is necessary to understand the significance of the input and loss of nutrients from the ecosystems. Attempts to balance atmospheric input against nutrient drain on harvesting require information on the amount of nutrients accumulated in different organs at different stages of growth. Similarly, studies of the nutrient supplying ability of a soil can only be assessed against the known demands of a tree crop.

The pattern of nutrient demand by a tree crop can now be established with reasonable certainty (Fig. 3). Although it reaches its peak at, or just before, the time of maximum current annual increment, deficiencies either appear soon after planting or in middle-age suggesting that, provided the nutrient capital of the site is such that trees can become established, variation in uptake is less significant than is variation in supply. Beneath many coniferous crops the nutrient supplying ability of the soil, particularly for nitrogen and phosphorus, appears to alter as the trees age. This is probably due to immobilization in living vegetation and soil organic layers, although the possibility of a build-up of a harmful microbial population cannot be discounted (Florence 1967).

Fig. 4. Calculated annual fluxes and rates of accumulation of K and N (kg/ha/yr) required to maintain maximum growth rate (20 cu.m/ha/yr) of 40 yr Corsican pine in Scotland. Zones of accumulation are shown by rectangles the annual rate of new accumulation being represented by the dashed portion. Mobile pools are depicted by circles. Link x between accumulation and mobile pool in the tree represents potential mobilization from second level sources (see text).

The deleterious effect of accumulation of a deep mor-humus layer has attracted the attention of silviculturalists since the outset of systematic forest management. Countermeasures include soil disturbance, increasing penetration of sunlight, liming, fertilization and burning. Because the feeding roots of most conifers are shallow, soil cultivation can only be used at the end of the rotation (Rehfuess & Schmidt 1971; Ford & Deans 1977) when nitrogen mineralization is, in any case, fairly rapid (Popovic 1975). The amount of sunlight reaching the soil, on the other hand, can be altered during the rotation by changing the thinning intensity and the advantages of this are probably worth more critical examination. Although lime will increase both the rate of organic matter decomposition and nitrogen mineralization (Williams 1972; Adams & Dickson 1973; Adams & Cornforth 1973), few positive effects on tree growth have been observed in recent experiments (Adams et al. 1978), despite claims for such an effect in older literature (Baule & Fricker 1970), an exception being a response to heavy rates of lime when rotovated into the surface layers of deep oligotrophic peat (Dickson 1977). It has also been suggested that application of nitrogen increases mineralization of native organic nitrogen (Chu & Knowles 1966; Williams 1972) but the response is short-lived, as is that to added phosphate (Williams 1972). Fire or heat sterilization has frequently been reported to increase the availability of nitrogen (e.g. Siren 1955; Weetman & Nykvist 1963) and this does appear to be a useful treatment. It is interesting to note that the three 'catastrophic' factors of burning, reduction in canopy cover and soil disturbance, such as that resulting from wind-blow, appear to be most effective at mobilizing humus nitrogen.

CYCLES WITHIN THE TREE

Trees can move nutrients from one organ to another, the best documented example being the withdrawal of nutrients from old foliage prior to abscission. Viro (1955) estimated that about 85 per cent of the nitrogen, phosphorus and potassium in old needles of Scots pine can be retranslocated into living tissues during senescence. Presumably the tree similarly conserves nutrients during the death of other tissues; indeed, Merrill & Cowling (1966) considered that the progressive decrease in nitrogen content of annual xylem increments on passing from the cambium to the heartwood was associated with the withdrawal of nitrogen from parenchyma cells prior to death.

Most retranslocation, however, is not associated with death of tissues, but represents the accumulation of nutrients during dormant periods and their subsequent mobilization for use, often in a different part of the tree, during active growth. Studies with nitrogen (David & David 1966; Durzan

1963; Tromp & Ovaas 1971) which is stored as protein but translocated as soluble amino acids, indicate considerable movement with a marked conversion into mobile forms just prior to bud-break. The appearance and disappearance of mobile nitrogen in the tree is even reflected in variations in the amount of mineral nitrogen lost through crown leaching during a year (Miller, Cooper & Miller 1976).

Thus, there is a marked seasonal pattern of translocation between different organs of the tree that, together with uptake during the growth period, would normally account for all the nutrient required for new growth. Should these supplies, which Miller et al. (in press) have termed supplies from 'first level sources', be insufficient, either through low availability in the soil or through some abnormal demand, such as for heavy coning (Rehfuss 1970), then the tree will utilize nitrogen accumulated during previous growing seasons. This mobilization from 'second level sources' (Fig. 4) usually occurs at sub-optimum levels of nutrition and is at the expense of the proper functioning, or even continued existence, of older tree tissues - a sacrifice that is inevitably accompanied by a reduction in growth. For example, it has frequently been observed that nitrogen deficiency reduces the age at which needles senesce (e.g. Heilman & Gessel 1963b; Miller & Miller 1976a; Turner & Olson 1976). Mobilization from second level sources of a nutrient previously accumulated in excess of the then requirements for growth is less usual but this can happen following heavy fertilizer application. Indeed this is sufficient to explain alone the continuation of growth response in the years after fertilizers were last applied (Miller, Miller & Pauline 1976).

Following fertilizer application all living components of the tree show an increased concentration of that nutrient (Table 8). The largest proportional increase occurs in lateral roots and foliage, but significant increases also occur in stem wood and stump. Accumulation even within the heartwood

Table 8. Changes in amount of accumulated nitrogen following application of nitrogen fertilizer (504 kg N ha/yr for these years) to 40-year-old Corsican pine (author's data).

Tree component	%increase in N concentration	Increased weight (kg/ha) of N
Foliage	280	250
Branches	210	45
Stem bark	225	55
Stem wood	185	45
Stump	190	10
Lateral roots	295	90

has been revealed by electron probe microanalysis of the medullary rays taken from deep inside Sitka spruce stems, which have shown higher phosphorus and potassium contents following application of rock phosphate and potassium chloride (J.D. Miller & A.C. Birnie, pers. comm.). The increased accumulation of nitrogen in fertilized Corsican pine (Table 8) can be regarded as an increase in the potential supply of this nutrient from second level sources, for it can be utilized at least until the concentration values fall back to pre-treatment levels. Clearly, as most of this accumulated nitrogen is located in the foliage and lateral roots, anything promoting premature death of these organs, such as drought or pollution will, apart from the obvious consequence, reduce the 'store' of nutrients available for subsequent growth. This danger is most severe early in the rotation when foliage, and to a lesser extent lateral roots, represent a large proportion of the total weight of the crop and the amount of available nutrient that can be accumulated in the relatively small quantity of woody tissue is significant in relation to the requirements for new growth.

Practical significance

Recent problems with certain species in diagnosing nutrient deficiencies from analysis of top-whorl foliage (e.g. Miller & Williams 1972), coupled with the difficulty of obtaining foliage from this position on any regular basis, has encouraged investigations into the pattern of accumulation in other organs of the tree. A clear understanding of the sink-source relationships within the tree should enable identification of the organ, time of sampling, and type of analysis that most accurately reflects the nutrient status (Van den Driessche 1974). Thus Florence & Chuong (1974) suggested that even when nitrogen and phosphorus deficiencies are not indicated in top-whorl foliage, they are reflected by a gradient of these elements across age categories of needles - a result of more pronounced withdrawal of nutrients from older needles on deficient trees. Similarly Lamb (1975) has shown that withdrawal of nitrogen and phosphorus from ageing green needles is more marked on poor than on fertile sites. In some studies foliage from the lower crown, despite the difficulty of giving this a standard physiological identity, has proved to be a better indicator of nutrient status than has top-whorl foliage (Carey, pers. comm.). Considerable success at diagnosing nitrogen deficiency has recently been achieved using analysis of newly fallen needle-litter (Mahendrapa & Weetman 1973; Miller & Miller 1976b), and as litter nitrogen levels may in turn be reflected by the levels in the accumulated humus, this might be a suitable material to analyse (Malm, Möller & Nömmik 1974; Adams 1974; Miller et al. 1977; Van den Driessche & Webber 1977 and 1978). Other organs attracting attention include surface roots (Van den Driessche

& Webber 1978), outer sapwood (Alcubilla, Aufsess & Rehfuess 1976) and, because of its successful use in rubber tree plantations (Bolle-Jones 1957), inner-bark (White, Alexander & Clark 1972; Alcubilla & Rehfuess 1975; Alcubilla et al 1976; Van den Driessche & Webber 1977 and 1978).

With coniferous species, foliage samples are usually taken early in the dormancy period, simply because at this time the concentration of nutrients in foliage remains fairly constant over a few months (White 1954). However, nutrient stress in tissues may be more marked during the growing season, when demands by the new growth are large (Smith, Switzer & Nelson 1970; Waring & Youngberg 1972). It has also been suggested that levels of total soluble nitrogen, monosubstituted guanidino compounds, arginine or proline may give the best indication of any disturbances in nitrogen metabolism (Durzan 1974; Van den Driessche & Webber 1975, 1977 and 1978). However, routine sampling either during the growing season or for such transient substances as free amino acids, would need careful control and standardization. Although these approaches probably justify more attention, they require a clearer understanding of the cycling of such components within the tree.

There is a growing awareness that changes or imbalances in tree nutrition can be reflected in pathological disturbances other than those produced directly by nutrient deficiencies. Thus, White (1969, 1974) has postulated that changes, resulting from moisture stress, in the pattern of accumulation of free amino acids in foliage can explain sudden increase in numbers of defoliating caterpillars, and Parry (1977) has shown that seasonal variations in populations of the aphid Elatobium abietinum on spruce closely paralleled changes in the amount of free amino acids. Similar explanations have been offered for attacks by the spruce budworm (Durzan 1968) and for some fungal diseases (Baule & Fricker 1970; Baule 1973). Furthermore, there is the possibility that an insufficient supply of trace elements at critical periods of the year can predispose the tree to damage by inorganic agencies, such as frost, and it is now known that a deficiency of potassium can adversely affect the water economy of the tree (Bradbury & Malcolm 1977).

CONCLUSIONS

There can be little doubt that integrated research on nutrient cycles within forest ecosystems is leading to an appreciation of nutrition as a system of functional processes. As a result it is now possible to generate and test the hypotheses that are basic to a proper understanding of tree nutrition and the time is foreseen when the manager will be in a position to deduce, from fundamental principles, the

nutritional consequence of any proposed action.

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REFERENCES

- Abrahamsen, G., Bjor, K., Horntvedt, R. & Tveite, B. (1976). Effects of acid precipitation on coniferous forest. "Impact of acid precipitation on forest and freshwater ecosystems in Norway." (Ed. by F.H. Braekke), pp. 37-63. Sur Nedbørs Virkning på skog og Fisk Fagrapport FR 6/76, Oslo-Ås.
- Adams, S.N. (1974). Some relations between forest litter and growth of Sitka spruce on poorly drained soils. *Journal of Applied Ecology*, 11, 761-765.
- Adams, S.N. & Cornforth, I.S. (1973). Some short-term effects of lime and fertilizers on a Sitka spruce plantation. II. Laboratory studies on litter decomposition and nitrogen mineralization. *Forestry*, 46, 39-47.
- Adams, S.N. & Dickson, D.A. (1973). Some short-term effects of lime and fertilizers on a Sitka spruce plantation. I. Field studies on the forest litter and the uptake of nutrients by the trees. *Forestry*, 46, 31-37.
- Adams, S.N., Cooper, J.E., Dickson, D.A., Dickson, E.L. & Seaby, D.A. (1978). Some effects of lime and fertilizer on a Sitka spruce plantation. *Forestry*, 51, 57-65.
- Addoms, R.M. (1937). Nutritional studies on loblolly pine. *Plant Physiology*, 12, 199-205.
- Alcubilla, M. & Rehfuess, K.E. (1975). Voruntersuchungen über die Eignung Bastanalyse zur Beurteilung des Ernährungszustandes von Fichten (*Picea abies* Karst.). *Forstwissenschaftliches Centralblatt*, 94, 344-351.
- Alcubilla, M., Aufsess, H. & Rehfuess, K.E. (1976). Stickstoffdüngungsversuche in einer Fichtenwachsstockung (*Picea abies* Karst.) auf devastierter Kalkmerger-rendzina: Wirkungen auf die Nährelementgehalte der Fichtengewebe und den Hohenzuwachs. *Forstwissenschaftliches Centralblatt*, 95, 306-323.
- Aldrich-Blake, R.N. (1930). The plasticity of the root systems of Corsican pine in early life. *Oxford Forestry Memoirs* #12.
- Allison, F.E. (1955). The enigma of soil nitrogen balance sheets. *Advances in Agronomy*, 7, 213-250.
- Anderson, M.A. (1976). Effect of trees on soil. Report on Forest Research London, 1976. pp.22.
- Anderson, F. (1970). Ecological studies in Scanian woodland and meadow area, southern Sweden. II. Plant biomass, primary production and turnover of organic matter. *Botaniska*

- notiser, 123, 8-51.
- Attiwill, P.M. (1966). The chemical composition of rainwater in relation to cycling of nutrients in mature eucalyptus forest. *Plant and Soil*, 24, 390-406.
- Azevedo, J. & Morgan, D.L. (1974). Fog precipitation in coastal California forests. *Ecology*, 55, 1135-1141.
- Bache, D.H. (1977). Sulphur dioxide uptake and the leaching of sulphates from a pine forest. *Journal of Applied Ecology*, 14, 881-895.
- Bain, D.C. & Tait, J.M. (1977). Mineralogy and origin of dust fall on Skye. *Clay Minerals*, 12, 253-255.
- Baule, H. (1973). Effect of fertilizers on resistance to adverse agencies. *Proceedings F.A.O./I.U.F.R.O. International Symposium on forest fertilization, Paris 1973*, pp. 181-214. Ministère de l'Agriculture, Paris.
- Baule, H. & Fricker, C. (1970). The fertilizer treatment of forest soils. (Translated by C.L. Whittles). B.L.V. Verlagsgesellschaft m.b.H., München.
- Becking, J.H. (1965). Nitrogen fixation and mycorrhiza in *Podocarpus* root modules. *Plant and Soil*, 23, 213-226.
- Bengston, G.W. & Kilmer, V.J. (1975). Fertilizer use and water quality: considerations for agriculture and forestry. "Forest soils and forest land management". *Proceeding 4th North American forest soils conference* (Ed. by B. Bernier and C.H. Winget), pp. 245-265. Les Presses de l'Université Laval, Quebec.
- Binns, W.O. (1962). Some aspects of peat as a substrate for tree growth. *Irish Forestry*, 19, 32-35.
- Boggie, R. & Miller, H.G. (1976). Growth of *Pinus contorta* at different water-table levels in deep blanket peat. *Forestry*, 49, 123-131.
- Bolle-Jones, E.W. (1957). Foliar diagnosis of mineral status of *Hevea* in relation to bark analysis. *Journal of the Rubber Research Institute of Malaya*, 15, 109-127.
- Bond, G. (1957). The development and significance of root modules of *Casuarina*. *Annals of Botany n.s.* 21, 373-380.
- Bormann, F.H., Likens, G.F. & Melillo, J.M. (1977). Nitrogen budget for an aggrading northern hardwood forest ecosystem. *Science*, 196, 981-983.
- Bradbury, I.K. & Malcolm, D.C. (1977). The effect of phosphorus and potassium on transpiration, leaf diffusive resistance and water-use efficiency in Sitka spruce (*Picea sitchensis*) seedlings. *Journal of Applied Ecology*, 14, 631-641.
- Bray, J.R. & Gorham, E. (1964). Litter production in forests of the world. *Advances in Ecological Research*, 2, 100-157.
- Bringmark, L. (1977). A bio-element budget of an old Scots pine forest in central Sweden. *Silva Fennica*, 11, 201-209.
- Brown, A.H.F. (1974). Nutrient cycles in oakwood ecosystems in N.W. England. "The British Oak" (Ed. by M.G. Morris and

- F.H. Perring), pp.141-161. E.W. Classey, Berkshire, for The Botanical Society of the British Isles.
- Chamberlain, A.C. (1975). The movement of particles in plant communities. "Vegetation and the atmosphere. Volume 1, Principles." (Ed. by J.L. Monteith). Academic Press, London.
- Chu, J.P.H. & Knowles, R. (1966). Mineralization and immobilization of nitrogen in bacterial cells and in soil organic fractions. Soil Science Society of America Proceedings, 30, 210-213.
- Clayton, J.L. (1972). Salt spray and mineral cycling in two California coastal ecosystems. Ecology, 53, 74-81.
- Cole, D.W. & Ballard, T.M. (1970). Mineral and gas transfer in a forest floor - a phase model approach. "Tree growth and forest soils". Proceedings 3rd North American forest soils conference, Raleigh, N. Carolina, (Ed. by C.T. Youngberg and C.B. Davey), pp. 347-358. Oregon State University Press, Corvallis.
- Cole, D.W. & Gessel, S.P. (1965). Movement of elements through a forest soil as influenced by tree removal and fertilizer additions. "Forest soil relationships in North America". Proceedings 2nd North American forest soils conference. Oregon State University, Corvallis, (Ed. by G.T. Youngberg), pp.95-104. Oregon State University Press, Corvallis.
- David, R. & David, H. (1966). Teneur en azotes protéiques et solubles des bourgeons et phénomènes de migration des composés azotes se produisant dans les rameaux du pin maritime. Compte rendu de l'Académie des sciences, Paris, Série D, 18, 1945-1948.
- DeBell, D.S. & Ralston, C.W. (1970). Release of nitrogen by burning light forest fuels. Soil Science Society of America Proceedings, 34, 936-938.
- Delany, A.C., Pollock, W.H. & Shedlovsky, J.P. (1973). Tropospheric aerosol; the relative contribution of marine and continental components. Journal of Geophysical Research, 78, 6249-6265.
- Dickson, D.A. (1977). Nutrition of Sitka spruce on peat problems and speculations. Irish Forestry, 34, 31-39.
- Dillon, P.J. & Kirchner, W.B. (1975). The effects of geology and land use on the export of phosphorus from water sheds. Water Research, 9, 135-148.
- Dovland, H., Joranger, E. & Semb, A. (1976). Deposition of air pollutants in Norway. "Impact of acid precipitation on forest and freshwater ecosystems in Norway" (Ed. by F.H. Braekke), pp.15-35. Sur Nedbørs Virkning på Skog og Fisk Fagrapport FR 6/76, Oslo-Ås.
- Durzan, D.J. (1968). Nitrogen metabolism of Picea glauca. I. Seasonal changes of free amino acids in buds, shoot apices and leaves, and the metabolism of uniformly

- labelled 14 C-L-arginine by buds during the onset of dormancy. *Canadian Journal of Botany*, 46, 909-919.
- Durzan, D.J. (1974). Nutrition and water relations of forest trees: a biochemical approach. Proceedings 3rd North American forest biology workshop, September 1974 (Ed. by C.P.R. Reid and C.H. Fechner), pp.15-63. Colorado State University.
- Duvigneaud, P. & Denaeyer-De Smet, S. (1970). Biological cycling of minerals in temperate deciduous forests. "Analysis of temperate forest ecosystems. Ecological studies 1" (Ed. by D.E. Reichle), pp.199-225. Chapman & Hall, London.
- Eaton, J.S., Likens, G.E. & Bormann, F.H. (1973). Throughfall and stemflow chemistry in a northern hardwood forest. *Journal of Ecology*, 61, 495-508.
- Ehwald, E. (1957). Ueber den Nährstoffkreislauf des Waldes. Sitzungsberichte der Deutschen Akademie der Landwirtschaftswissenschaften, 6. 56pp.
- Fairfax, J.A.W. & Lepp, N.W. (1975). Effect of simulated 'acid rain' on cation loss from leaves. *Nature*, Lond. 255, 324-325.
- Feller, M.C. (1977). Nutrient movement through western hemlock - western red cedar ecosystems in British Columbia. *Ecology*, 58, 1269-1283.
- Florence, R.G. (1967). Factors that may have a bearing upon the decline of productivity under forest monoculture. *Australian Forestry*, 31, 50-71.
- Florence, R.G. & Chuong, P.H. (1974). The influence of soil type on foliar nutrients in *Pinus radiata* plantations. *Australian Forest Research*, 6, 1-8.
- Ford, E.D. & Deans, J.D. (1977). Growth of a Sitka spruce plantation; spatial distribution and seasonal fluctuations of lengths, weights and carbohydrate concentrations of fine roots. *Plant and Soil*, 47, 463-485.
- Foster, N.W. & Morrison, I.K. (1976). Distribution and cycling of nutrients in a natural *Pinus banksiana* ecosystems. *Ecology*, 57, 110-120.
- Fowler, D. & Unsworth, M.H. (1974). Dry deposition of sulphur dioxide on wheat. *Nature*, 249, 389-390.
- Fredriksen, R.L. (1972). Nutrient budget of a Douglas fir forest on an experimental watershed in western Oregon. "Research on coniferous forest ecosystems", Proceedings of the Bellingham, Washington, Symposium (Ed. by J.F. Franklin, L.J. Dempster and R.H. Waring), pp.115-131. U.S. Department of Agriculture Forest Service, Portland, Oregon.
- Fredriksen, R.L., Moore, D.G. & Norris, L.A. (1975). The impact of timber harvest, fertilization and herbicide treatment on streamwater quality in western Oregon and Washington. "Forest soils and forest land management". Proceedings

- 4th North American forest soils conference (Ed. by B. Bernier and C.H. Winget), pp.283-313. Les Presses de l'Université Laval, Quebec.
- Freeman, J.F.(1924). Nitrogen in the rainwater at different points in Kentucky. *Journal of the American Society of Agronomy*, 16, 356-358.
- Gadgil, R.L.(1971). The nutritional role of *Lupinus arboreus* in coastal sand dune forestry, 1, 2 and 3. *Plant and Soil*, 34, 357-367; 35, 113-126.
- Gadgil, R.L.(1977). Alternatives to the use of fertilizers. 'Use of fertilizers in New Zealand forestry'. Proceedings Forest Research Institute Symposium #19 (compiled by R. Ballard), pp.83-94. New Zealand Forest Service Forest Research Institute, Rotorua.
- Garland, J.A.(1977). The dry deposition of sulphur dioxide to land and water surfaces. Proceedings of the Royal Society, London A, 354, 245-268.
- Gessel, S.P., Cole, D.W. & Steinbrenner, E.C.(1973). Nitrogen balances in forest ecosystems of the Pacific Northwest. *Soil Biology and Biochemistry*, 5, 19-34.
- Gether, J., Gjøvs, N. & Lunde, G.(1976). Isolation and characterization in precipitation of organic micropollutants associated with long-range transport in air. *Sur Nedbørs Virkning på Skog og Fosk Fagrapport FR 8/78*, Oslo-Ås.
- Gether, J., Lunde, G. & Markali, J.(1976). Particulate material in atmospheric fall-out and precipitation over the south of Norway. *Sur Nedbørs Virkning på Skog og Fisk Fagrapport FR 7/76*, Oslo-Ås.
- Gosz, J.R., Likens, G.E. & Bormann, F.H.(1976). Organic matter and nutrient dynamics of the forest and forest floor in the Hubbard Brook Forest. *Oecologia*, 22, 305-320.
- Grier, C.C. & Cole, D.W.(1972). Elemental transport changes occurring during development of a second-growth Douglas fir ecosystems. "Research on coniferous forest ecosystems". Proceedings of the Bellingham, Washington Symposium (Ed. by J.F. Franklin, L.J. Dempster and R.H. Waring), pp.103-113. U.S. Department of Agriculture Forest Service, Portland, Oregon.
- Grieve, I.C.(1978). Some effects of the plantation of conifers on a freely drained lowland soil, Forest of Dean, U.K. *Forestry*, 51, 21-28.
- Hall, A.D. & Miller, N.H.J.(1911). On the absorption of ammonia from the atmosphere. *Journal of Agricultural Science*, 4, 1911-1912.
- Hamilton, G.J. & Christie, J.M.(1971). Forest management tables (metric), Forestry Commission London, Booklet #34.
- Harley, J.L.(1969). The biology of mycorrhiza (2nd edition). *Plant Science Monographs* (Ed. by N. Polunin). Leonard Hill, London.

- Harwood, C.E. & Jackson, W.D. (1975). Atmospheric losses of four plant nutrients during a forest fire. *Australian Forestry*, 38, 92-99.
- Heiberg, S.O. & White, D.P. (1950). Potassium deficiency in reforested pine and spruce stands in northern New York. *Soil Science Society of America Proceedings*, 15, 369-376.
- Heilman, P.W. (1966). Changes in distribution and availability of nitrogen with forest succession on northern slopes in interior Alaska. *Ecology*, 47, 825-831.
- Heilman, P.E. & Gessel, S.P. (1963a). Nitrogen requirements and the biological cycling of nitrogen in Douglas fir stands in relationship to the effects of nitrogen fertilization. *Plant and Soil*, 18, 386-402.
- Heilman, P.W. & Gessel, S.P. (1963b). The effect of nitrogen on the concentration and weight of nitrogen, phosphorus and potassium in Douglas fir trees. *Soil Science Society of America Proceedings*, 27, 102-105.
- Heinrichs, H. & Mayer, R. (1977). Distribution and cycling of major and trace elements in two central European forest ecosystems. *Journal of Environmental Quality*, 6, 402-407.
- Hingston, F.J. & Gailitis, V. (1976). The geographic variation of salt precipitated over Western Australia. *Australian Journal of Soil Research*, 14, 319-335.
- Hitchcock, D.R. (1976). Microbiological contribution to the atmospheric load of particulate sulfate. "Environmental Biogeochemistry, Volume 1, Carbon, nitrogen, phosphorus, sulfur and selenium cycles" (Ed. by J.O. Nriagu), pp. 351-367. Ann Arbor Science, Ann Arbor, Michigan.
- Ike, A.F. & Stone, E.L. (1958). Soil nitrogen accumulation under black locust. *Soil Science Society of America Proceedings*, 4, 346-349.
- Ingham, G. (1950). Effect of materials absorbed from the atmosphere in maintaining soil fertility. *Soil Science*, 70, 205-212.
- Johnson, F.L. & Risser, P.G. (1974). Biomass, annual net primary production and dynamics of six mineral elements in a post-oak-blackjack oak forest. *Ecology*, 55, 1246-1258.
- Jones, K. (1970). Nitrogen fixation in the phytosphere of the Douglas fir, *Pseudotsuga douglasii*. *Annals of Botany*, 34, 239-244.
- Jonsson, B. & Sundberg, R. (1972). Has the acidification by atmospheric pollution caused a growth reduction in Swedish forests? *Rapporter och Uppsatser, Institutionen for Skogsproduktion, Skogshogskolan*, 20.
- Keays, J.L. & Hatton, J.V. (1976). The implication of full-forest utilization on worldwide supplies of wood by the year 2000. *World Wood*, 17, 12-15.
- Kimmins, J.P. & Feller, M.C. (1976). Effect of clearcutting and broadcast slashburning on nutrient budgets, streamwater chemistry and productivity in western Canada. *Proceedings*

- XVI I.U.F.R.O. Congress, Division I, Oslo, Norway. pp. 186-197.
- Klemmedson, J.O. (1976). Effect on thinning and slash burning on nitrogen and carbon in ecosystems of young dense Ponderosa pine. *Forest Science*, 22, 45-53.
- Knowles, R. (1965). The significance of nonsymbiotic nitrogen fixation. *Soil Science Society of America Proceedings*, 29, 223.
- Kreutzer, K. & Weiger, H. (1974). Untersuchungen über den Einfluss forstlicher Düngungsmassnahmen auf den Nitratgehalt des Sickerwassers im Wald. *Forstwissenschaftliches Centralblatt*, 93, 57-74.
- Lamb, D. (1975). Patterns of nitrogen mineralization in the forest floor of stands of *Pinus radiata* on different soils. *Journal of Ecology*, 63, 615-625.
- Likens, G.E. & Bormann, F.H. (1974). Acid rain: a serious regional environmental problem. *Science*, 184, 1176-1179.
- Likens, G.E., Bormann, F.H., Pierce, R.S. & Reiner, W.A. (1978). Recovery of a deforested ecosystem. *Science*, 199, 492-496.
- Likens, G.E., Bormann, F.H., Pierce, R.S., Eaton, J.S. & Johnson, N.M. (1977). The biogeochemistry of a forested ecosystem. Springer Verlag, New York.
- Ludbrook, W.V. (1940). Boron deficiency symptoms on pine seedlings in water culture. *Journal of the Council for Scientific and Industrial Research in Australia*, 13, 186-190.
- Lunde, G., Gether, J., Gjøs, N. & Lande, M.B.S. (1976). Organic micropollutants in precipitation in Norway. *Sur Nedbørs Virkning på Skog og Fisk Fagrapport FR 9/76*, Oslo-Ås.
- Madgwick, H.A.I. & Ovington, J.D. (1959). The chemical composition of precipitation in adjacent forest and open plots. *Forestry*, 32, 14-22.
- Mahendrappa, M.K. & Ogdén, E.D. (1973). Effects of fertilization of a black spruce stand on nitrogen contents of stemflow, throughfall and litterfall. *Canadian Journal of Forest Research*, 3, 54-60.
- Mahendrappa, M.K. & Weetman, G.F. (1973). Nitrogen concentrations in the current foliage and in fresh litter of fertilized black spruce stands. *Canadian Journal of Forest Research*, 3, 333-337.
- Malcolm, D.C., Bradbury, I.K. & Freezallah, B.C.Y. (1977). The loss of nutrients from fertilized peat in an artificial system in the field. *Forest Ecology and Management*, 1, 109-118.
- Mätkönen, E. (1974). Annual primary production and nutrient cycle in some Scots pine stands. *Communicationses Instituti Forestalis Fenniae*, 84.5. 87 pp.
- Mätkönen, E. (1976). Effect of whole-tree harvesting on soil fertility. *Silva Fennica*, 10, 157-164.

- Mätkönen, E. (1977). Annual primary production and nutrient cycle in a birch stand. *Communicationes Instituti Forestalis Fenniae*, 91.5. 35 pp.
- Malm, D., Möller, G. & Nömmik, H. (1974). Gödslingseffektens samband med växträringsinnehåll; mark och barr. Föreningen Skogsträisförädling och Institut för Skogsförbättring. Årsbok 1973. pp.48-75.
- Mayer, R. & Ulrich, B. (1974). Conclusions on the filtering action of forests from ecosystem analysis. *Oecologia Plantarum*, 9, 157-168.
- Mayer, R. & Ulrich, B. (1977). Acidity of precipitation as influenced by the filtering of atmospheric sulphur and nitrogen compounds - its role in the element balance and effect on soil. *Water, Air and Soil Pollution*, 7, 409-416.
- McCull, J.G. & Grigal, D.F. (1977). Nutrient changes following a forest wildfire in Minnesota: effects in watersheds with differing soils. *Oikos*, 28, 105-112.
- Merrill, W. & Cowling, E.B. (1966). Role of nitrogen in wood deterioration: amounts and distribution of nitrogen in tree stems. *Canadian Journal of Botany*, 44, 1555-1580.
- Miller, H.G. (1969). Nitrogen nutrition of pines on the sands of Culbin forest, Morayshire. *Journal of the Sciences of Food and Agriculture*, 20, 417-419.
- Miller, H.G. & Cooper, J.M. (1973). Changes in amount and distribution of stem growth in pole-stage Corsican pine following application of nitrogen fertilizer. *Forestry*, 46, 157-190.
- Miller, H.G. & Cooper, J.M. (1976). Tree growth and climatic cycles in the rain shadow of the Grampian mountains. *Nature London*, 260, 697-698.
- Miller, H.G. & Miller, J.D. (1976a). Effect of nitrogen supply on net primary production in Corsican pine. *Journal of Applied Ecology*, 13, 249-256.
- Miller, H.G. & Miller, J.D. (1976b). Analysis of needle fall as a means of assessing nitrogen status in pine. *Forestry*, 49, 57-61.
- Miller, H.G. & Williams, B.L. (1972). Research on forest soils and tree nutrition. Report on Forest Research, London 1972, 143-147.
- Miller, H.G. & Williams, B.L. (1973). Research on forest soils and tree nutrition. Report on Forest Research, London 1973, 145-147.
- Miller, H.G. & Williams, B.L. (1977). Nutrition and forest soils. Report on Forest Research, London 1977, 51-52.
- Miller, H.G., Cooper, J.M. & Miller, J.D. (1976). Effect of nitrogen supply on nutrients in litter fall and crown leaching in a stand of Corsican pine. *Journal of Applied Ecology*, 13, 233-248.
- Miller, H.G., Miller, J.D. & Binns, W.O. (1977). Growth of Scots

- pine under nutritional and climatic stress. *Plant and Soil*, 48, 103-114.
- Miller, H.G., Miller, J.D. & Pauline, O.J.L. (1976). Effect of nitrogen supply on nutrient uptake in Corsican pine. *Journal of Applied Ecology*, 13, 955-966.
- Miller, H.G., Cooper, J.M., Miller, J.D. & Pauline, O.J.L. (in press). Nutrient cycles in pine: their adaptation to poor soils. *Canadian Journal of Forest Research*.
- Miller, H.G., Williams, B.L., Miller, C.S. & Warin, T.R. (1977). Ground vegetation and humus nitrogen levels as indicators of nitrogen status in an established sand-dune forest. *Forestry*, 50, 96-101.
- Miller, N.H.J. (1905). The amounts of nitrogen as ammonia and nitric acid, and of chlorine in the rainwater collected at Rothamstead. *Journal of Agricultural Science, Cambridge*, 1, 280-303.
- Miller, R.B. (1961). The chemical composition of rainwater at Taita, New Zealand, 1956-58. *New Zealand Journal of Science*, 4, 844-853.
- Miller, R.B. (1963). Plant nutrients in hard beech. III. The cycle of nutrients. *New Zealand Journal of Science*, 6, 388-413.
- Orlov, A.J. (1955). The role of feeding roots of forest vegetation in enriching soil with organic matter. *Pochvovedenie*, 6, 14-20.
- Overrein, L.N. (1970). Tracer studies on nitrogen immobilization-mineralization relationships in forest raw humus. *Plant and Soil*, 32, 478-500.
- Ovington, J.D. (1957). The volatile matter, organic carbon and nitrogen contents of tree species grown in close stands. *New Phytologist*, 56, 1-11.
- Ovington, J.D. (1959). The circulation of minerals in plantations of *Pinus silvestris* L. *Annals of Botany n.s.*, 23, 230-239.
- Ovington, J.D. (1962). Quantitative ecology and the woodland ecosystem concept. *Advances in Ecological Research*, 1, 103-192.
- Page, G. (1968). Some effects of conifer crops on soil properties. *Commonwealth Forestry Review*, 47, 52-62.
- Päivänen, J. (1974). Nutrient removal from Scots pine canopy on drained peatland by rain. *Acta forestalia fennica*, 139, 19pp.
- Parry, W.H. (1977). The effects of nutrition and density on the production of alate *Elatobium abietinum* on Sitka spruce. *Oecologia*, 30, 637-375.
- Paul, E.A. (1976). Nitrogen cycling in terrestrial ecosystems. "Environmental Biochemistry. Volume 1. Carbon, nitrogen, phosphorous, sulfur and selenium cycles" (Ed. by J.O. Nriagu) pp. 225-243. *Ann Arbor Science, Ann Arbor, Michigan*.

- Pitty, A.F. (1968). Particle size of the Sahara dust which fell in Britain in July 1968. *Nature London*, 220, 364-365.
- Popovic, B. (1975). Kalhuggningens inverkan på markens kvavemineralsisering speciellt nitratbildningen. Institutionen för Skogsproduktion, Avdelning för skogsekologi, Skogshögskolan. Rapporter och Uppsatser #24.
- Probert, M.E. (1976). The composition of rainwater at two sites near Townsville, Queensland. *Australian Journal of Soil Research*, 14, 397-402.
- Pyatt, D.G. (1975). Classification and improvement of upland soils. Report on Forest Research, London 1975, 25-26.
- Reddy, T.K.R. & Knowles, R. (1965). The fungal flora of a boreal forest raw humus. *Canadian Journal of Microbiology*, 11, 837-843.
- Rehfuess, K.E. (1968). Zusammenhänge zwischen dem Ernährungs-zustand und der Bonität Nordostbayerischer Tannenbestände (*Abies alba* Mill.). Forstwissenschaftliches Centralblatt, 87, 276-296.
- Rehfuess, K.E. (1970). Vergleich zwischen nadelanalytischen Merkmalen von Weisstannen (*Abies alba* Mill.) mit und ohne Zapfenbehang. Zeitschrift für Pflanzenernährung und Bodenkunde, 127, 75-84.
- Rehfuess, K.E. & Schmidt, A. (1971). Die Wirkung von Lupinenunterbau und Kalkammonsalpeterdüngung auf den Ernährungszustand und den Zuwachs alterer Kiefernbestände in der Oberpfalz. Forstwissenschaftliches Centralblatt, 90, 237-259.
- Remezov, N.P. (1956). The role of the biological circulation of the elements in soils formation under forests. 6th International Congress on Soil Science, Paris, E. pp.269-274.
- Rennie, P.J. (1955). The uptake of nutrients by mature forest growth. *Plant and Soil*, 7, 49-95.
- Richards, B.N. (1964). Fixation of atmospheric nitrogen in coniferous forests. *Australian Forestry*, 28, 68-74.
- Richards, B.N. & Bevege, D.I. (1967). The productivity and nitrogen economy of artificial ecosystems comprising various combinations of perennial legumes and coniferous tree species. *Australian Journal of Botany*, 15, 467-480.
- Richards, B.N. & Voigt, G.K. (1963). Nitrogen accretion in coniferous forest ecosystems. "Forest soil relationships in North America" (Ed by C.T. Youngberg), pp.105-116. Oregon State University Press, Corvallis.
- Robertson, R.A. & Davies, C.E. (1965). Quantities of plant nutrient in heather ecosystems. *Journal of Applied Ecology*, 2, 211-219.
- Rochow, J.J. (1975). Mineral nutrient pool and cycling in a Missouri forest, *Journal of Ecology*, 63, 985-994.
- Rodhe, H., Persson, C. & Akesson, O. (1972). An investigation into regional transport of soot and sulfate aerosols.

- Atmospheric Environment, 6, 675-693.
- Roskoski, J.P. (1975). Differential nitrogen fixation in wood litter. Bulletin of the Ecological Society of America, 56, 12.
- Schlesinger, W.H. & Reiners, W.A. (1974). Deposition of water and cations of artificial foliar collectors in fur krummholz of New England mountains. Ecology, 55, 378-386.
- Siren, G. (1955). The development of spruce forests on raw humus sites in northern Finland and its ecology. Acta forestalia fennica, 62, 1-363.
- Slinn, W.G.N. (1977). Some approximations for the wet and dry removal of particles and gases from the atmosphere. Water, Air and Soil Pollution, 7, 513-543.
- Smith, M.E. (1943). Micronutrients essential for the growth of Pinus radiata. Australian Forestry, 7, 22-27.
- Smith, W.H. (1976). Character and significance of forest tree root exudates. Ecology, 57, 324-331.
- Smith, W.H., Nelson, L.E. & Switzer, G.L. (1963). The characterization of dry matter and nitrogen accumulation by loblolly pine (Pinus taeda L.) on poor soils. Soil Science Society of America Proceedings, 27, 475-478.
- Smith, W.H., Switzer, G.L. & Nelson, L.E. (1970). Development of the shoot system of young loblolly pine. L. Apical growth and nitrogen concentration. Forest Science, 16, 483-490.
- Sopper, W.E. (1975). Wastewater recycling on forest lands. "Forest soils and forest land management". Proceedings 4th North American forest soils conference, Quebec 1973 (Ed. by B. Bernier and C.H. Winget) pp. 227-243. Les presses de L'Université Laval, Quebec.
- Staafl, H. & Berg B. (1977). Mobilization of plant nutrients in a Scots pine forest mor in central Sweden. Silva Fennica, 11, 210-217.
- Stone, E.L. (1968). Micro-element nutrition of forest trees: a review, "Forest fertilization - theory and practice". Proceedings Symposium of forest fertilization, Gainesville Florida, 1967, pp. 132-175. Tennessee Valley Authority. National Fertilizer Development Center, Muscle Shoals, Alabama.
- Stone, E.L. & Kszystniak, R. (1977). Conservation of potassium in the Pinus resinosa ecosystem Science 198, 192-194.
- Tamm, C.O. (1953). Growth, yield and nutrition in carpets of a forest moss (Hylocomium splendens). Meddelanden fran Statens Skgskforskningsinstitut #43.
- Tamm, C.O. (1958). The atmosphere. "Encyclopaedia of plant physiology. Volume IV. Mineral nutrition of plants" (Ed. by W. Ruhland) pp. 233-242. Springer Verlag, Berlin.
- Tamm, C.O. (1964). Determination of nutrient requirements of forest stands. International review of forestry research #1 (Ed. by J.A. Romberger and P. Mikola), pp. 115-170.
- Tamm, C.O. (1973). Effects of fertilizers on the environment.

- Proceedings F.A.O./I.U.F.R.O. International Symposium on forest fertilization, Paris 1973. pp229-317. Ministère de l'Agriculture, Paris.
- Tamm, C.O. (1976). Acid precipitation: biological effects in soil and on forest vegetation. *Ambio*, 5, 235-238.
- Tamm, C.O. & Cowling, E.B. (1977). Acidic precipitation and forest vegetation. *Water, Air and Soil Pollution*, 7, 503-511.
- Tamm, C.O. & Troedsson, T. (1955). An example of the amount of plant nutrients supplied to the ground in road dust. *Oikos*, 6.
- Tamm, C.O. & Wilkander, G. (1972). Kvavehalten i grundvattnet oakr vid skogsgodsling och kalhuggning. *Forskning och Framsteg*, 7, 27-9.
- Tamm, C.O. & Hagberg, N. (1960). Recent results of fertilizer experiments in Swedish forests. *Proceedings 5th World Forestry Congress*, 1, 558-561.
- Tarrant, R.F. & Miller, R.E. (1963). Accumulation of organic matter and soil nitrogen beneath a plantation of red alder and Douglas fir. *Soil Science Society of America Proceedings*, 27, 231-234.
- Tromp, J. & Ovaa, J.F. (1971). Spring mobilization of storage nitrogen in isolated shoot sections of apple. *Physiologia Plantarum*, 25, 16-22.
- Turner, J. (1977). Effect of nitrogen availability on nitrogen cycling in a Douglas fir stand. *Forest Science*, 23, 307-316.
- Turner, J. & Kelly, J. (1963). Foliar chloride levels in some south eastern Australian plantations forests. *Soil Science Society of America Proceedings*, 37, 443-445.
- Turner, J. & Olsen, P.R. (1976). Nitrogen relations in a Douglas fir plantation. *Annals of Botany*, 40, 1185-1193.
- Turner, J., Cole, D.W. & Gessel, S.P. (1976). Mineral nutrient accumulation and cycling in a stand of red alder (*Alnus rubra*). *Journal of Ecology*, 64, 965-974.
- Ulrich, B. (1975). Die Umweltbeeinflussung des Nährstoffhaushaltes eines bodensäuren Buchenwaldes. *Forstwissenschaftliches Centralblatt*, 94, 280-287.
- Ulrich, B. & Mayer, R. (1972). Systems analysis of mineral cycling in forest ecosystems. "Isotopes and radiation in soil-plant relationships including forestry", *Proceedings I.A.E.A./F.A.O. Vienna Symposium, December 1971*. pp. 329-39. International Atomic Energy Agency, Vienna.
- Ulrich, B., Ahrens, E. & Ulrich, M. (1971). Soil chemical differences beneath beech and spruce sites - an example of the methods used. "Ecological studies. Analysis and synthesis" (Ed. by H. Ellenberg), 2, 171-190.
- Ulrich, B., Mayer, R., Khanna, P.K., Seekamp, G. & Fassbender, H.W. (1976). Input, output und interner Umsatz von chemischen Elementen bei einem Buchen- und einem Fichtenbestand.

- Berichte der Gesellschaft für Ökologie, Göttingen, September 1976, pp 17-28.
- van den Driessche, R. (1974). Prediction of mineral nutrient status of trees by foliar analysis. *Botanical Review*, 40, 347-394.
- van den Driessche, R. & Webber J.F. (1975). Total and soluble nitrogen in Douglas fir in relation to plant nitrogen status. *Canadian Journal of Forest Research*, 5, 580-585.
- van den Driessche, R. & Webber, J.E. (1977). Variation in total and soluble nitrogen concentrations in response to fertilization of Douglas fir. *Forest Science*, 23, 134-142.
- van den Driessche, R. & Webber J.F. (1978). Seasonal variations in a Douglas fir stand in total and soluble nitrogen in inner bark and root and in total and mineralizable nitrogen in soil. *Canadian Journal of Forest Research*, 7, 641-647.
- Viro, P.J. (1955). Investigations on forest litter. *Metsatie-teellison tutkimuslaitoksen julkaisu*, 45, 1-65.
- Viro, P.J. (1967). Forest manuring on mineral soils. *Meddelelser fra det Norske skogforsøksvesen*, 23, 113-136.
- Voigt, C.K. (1965). Biological mobilization of potassium from primary minerals. "Forest soil relationships in North America" Proceedings 2nd North American forest soils conference Corvallis 1963 (Ed. by C.T. Youngberg), pp. 33-46. Oregon State University Press, Corvallis.
- Waring, R.H. & Youngberg C.T. (1972). Evaluating forest sites for potential growth response of trees to fertilizer. *Northwest Science*, 46, 67-75.
- Weetman, G.F. (1962). Establishment report on a humus decomposition experiment. *Woodlands Research Index #134*, Pulp and Paper Research Institute of Canada, Montreal.
- Weetman, G.F. (1967). Nitrogen deficient black spruce on raw humus soils in northern Quebec - response to thinning and urea treatment. *Proceedings 14th I.U.F.R.O. Congress*, Munchen, 4, 608-618.
- Weetman, G.F. & Nykvist, N.B. (1973). Some mor-humus, regeneration and nutrition problems and practice in north Sweden. *Woodlands Research Index #139*, Pulp and Paper Research Institute of Canada, Montreal.
- Weetman, G.F. & Webber, B. (1972). The influence of wood harvesting on the nutrient status of two spruce stands. *Canadian Journal of Forest Research*, 2, 351-369.
- Wells, C.G. & Jorgensen, J.E. (1977). Nutrient cycling in loblolly pine - silvicultural implications. *Proceedings 1977 Forest biology wood chemistry conference*, Madison, Wisconsin, pp. 89-93. Technical Association Pulp and Paper Industry, Atlanta, Georgia.
- White, D.P. (1954). Variation in the nitrogen, phosphorus and

- potassium contents of pine needles with season, crown position and sample treatment. Soil Science Society of America Proceedings, 18, 326-330.
- White, E.H. (1974). Whole-tree harvesting depletes soil nutrients. Canadian Journal of Forest Research, 4, 530-535.
- White, J.D., Alexander, L.T. & Clark, E.W. (1972). Fluctuations in the inorganic constituents of inner bark of loblolly pine with season and soil series. Canadian Journal of Botany, 50, 1287-93.
- White, T.C.R. (1969). An index to measure weather induced stress of trees associated with outbreaks of psyllids in Australia. Ecology, 50, 905-909.
- White, T.C.R. (1974). A hypothesis to explain outbreaks of looper caterpillars with special reference to populations of Selidosema suavis in a plantation of Pinus radiata in New Zealand. Oecologia, 16, 279-301.
- Whittaker, R.H. & Woodell, G.M. (1971). Measurement of net primary production of forests. "Productivity of forest ecosystems". Proceedings Brussels Symposium 1969 on Ecology and conservation (Ed. by P. Duvigneaud), pp.191-205. U.N.E.S.C.O., Paris.
- Whittaker, R.H., Bormann, F.H., Likens, G.E. & Siccama, T.G. (1974). The Hubbard Brook ecosystem study: forest biomass and production. Ecological Monographs, 44, 233-252.
- Will, G.M. (1959). Nutrient return in litter and rainfall under some exotic conifer stands in New Zealand. New Zealand Journal of Agricultural Research, 2, 719-734.
- Will, G.M. (1964). Dry matter production and nutrient uptake by Pinus radiata in New Zealand. Commonwealth Forestry Review, 43, 57-70.
- Williams, B.L. (1972). Nitrogen mineralization and organic matter decomposition in Scots pine humus. Forestry, 45, 177-188.
- Williams, B.L., Cooper, J.M. & Pyatt, D.G. (1978). Effects of afforestation with Pinus contorta on nutrient content, acidity and exchangeable cations in peat. Forestry, 51, 29-35.
- Wittwer, R.F., Leaf, A.L. & Bickelhaupt, D.H. (1975). Biomass and chemical composition of fertilized and/or irrigated Pinus resinosa plantations. Plant and Soil, 42, 629-651.
- Wollum, A.G. & Davey, C.B. (1975). Nitrogen accumulation, transformation and transport in forest soils. "Forest soils and forest management". Proceedings 4th North American forest soils conference, Quebec 1973. (Ed. by B. Bernier and C.H. Winget), pp.67-106. Les Presses de l'Université Laval, Quebec.
- Wood, T. & Bormann, F.H. (1975). Increases in foliar leaching caused by acidification of an artificial mist. Ambio, 4,

169-171.

- Yaalon, D.H. & Lomas, J. (1970). Factors controlling the supply and the chemical composition of aerosols in a near shore and coastal environment. *Agricultural Meteorology*, 7, 433-454.
- Zöttl, H. (1960). Dynamik der Stickstoffmineralisation im organischen Waldbodenmaterial. II. Einfluss des Stickstoffgehaltes auf die Mineralstickstoffnachlieferung. *Plant and Soil*, 13, 183-206.

DECOMPOSITION AND NUTRIENT RELEASE IN EVEN-AGED PLANTATIONS

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SUMMARY

The decomposition sub-system is a complex interacting set of organisms and processes whose activities are central to the availability of nutrients to plants and to the maintenance of the nutrient capital of the ecosystem. Information on decomposition and nutrient release in plantations is sparse and much is inferred from accumulation patterns on the forest floor. This paper describes the general principles of the control of decomposition and nutrient release, and examines their application and implications to even-aged plantations.

Decomposition comprises katabolism, comminution and leaching, commonly measured by weight loss and respiration which are correlated with rates of nutrient release with an approximate release sequence $K > Mg > Ca > Mn > C > P > N > S$.

Decomposition is a function of three factors: climate, soil and resource quality, acting through the heterotrophic organisms. The broad limits to decomposition, set by site conditions, are modified by management and forest development.

Decomposition of different litters is related to the proportions of ethanol soluble and ethanol insoluble fractions and in some cases to initial nitrogen concentration. Two exponential curves provide a reasonable representation of the main phase of decomposition, followed by long-term decomposition of resistant humus fractions.

During decomposition nutrients are 'immobilized' in micro-organisms and faunal tissues, but the concept of immobilization, with mineralization at critical C:nutrient

ratios, masks the short-term recycling of nutrients through microbial turnover.

The temporal pattern of decomposition and nutrient release includes pedogenetic trends over millenia, successional changes over decades or centuries, and seasonal and diurnal rhythms. In plantations the successional sequence is very distinct with additional pulses introduced by management.

There is little evidence of the variation in nutrient release during a crop rotation but phases of nutrient supply and demand are apparently not synchronized as closely as in mixed-aged stands. The proportion of the ecosystem nutrients retained in the forest floor and the turnover time increases with latitude. The organic accumulation, while acting as a stabilizing influence in high latitudes, reduces nutrient flow to the trees. A manipulated increase in rate of turnover is expected to increase primary production.

RÉSUMÉ

Le sous-système de la décomposition est un système interactif d'organismes et de processus dont l'activité est indispensable à la disponibilité et au capital d'éléments nutritifs de l'écosystème. Les renseignements que l'on possède à présent sur la décomposition et la libération d'éléments nutritifs dans les plantations sont minces et nous basons nos connaissances sur les types d'accumulation trouvés dans les sols des forêts. Notre exposé décrit les principes généraux du contrôle de la décomposition et de la libération d'éléments nutritifs et nous examinons leur application et les conclusions que l'on peut en tirer dans le cas de forêts équienues.

La décomposition comprend le katabolisme, le broyage et le lessivage qui se mesurent habituellement par la perte de poids et la respiration, qui sont corrélées avec le taux d'éléments nutritifs libérés, selon l'ordre-type suivant: K>Mg>Ca>Mn>C>P>N>S.

La décomposition dépend de trois facteurs, climat, sol et qualité en ressources, qui agissent par l'intermédiaire d'organismes hétérotrophiques. Les limites générales de la décomposition, dictées par les conditions de la station, sont modifiées par la gestion et le

développement des forêts.

La décomposition de litières différentes est proportionnelle à des fractions solubles et insolubles dans l'éthanol et dans certains cas à la concentration initiale d'azote. La phase principale de décomposition, suivie de la longue décomposition de fractions d'humus plus résistant, peut être représentées par deux courbes exponentielles.

Pendant la décomposition, les éléments nutritifs sont 'immobilisés' dans des micro-organismes et des tissus de la microfaune mais le concept même d'immobilisation, avec une minéralisation à des rapports critiques de C:éléments nutritifs, masque le recyclage à court terme des éléments nutritifs par l'intermédiaire du cycle microbien.

Du point de vue temporel, la décomposition et la libération des éléments nutritifs présentent des tendances pédogénétiques sur une période de mille ans, des changements de succession sur des décennies ou des siècles et des rythmes saisonniers et diurnes. Dans les plantations, l'ordre des successions est très distinct, montrant des pulsations supplémentaires dûe à la gestion.

Il n'est pas évident que la libération d'éléments nutritifs varie pendant une révolution mais on peut dire que les phases d'offre et de demande d'éléments nutritifs ne sont pas aussi étroitement synchronisées que dans les peuplements d'âge mixte. La proportion d'éléments nutritifs de l'écosystème retenus au sol de la forêt et la durée du recyclage augmentent avec la latitude. L'accumulation organique qui a un effet stabilisateur à des latitudes élevées réduit le flux d'éléments nutritifs vers l'arbre. Une augmentation de la rapidité du cycle - amenée artificiellement pourrait augmenter la production primaire.

ZUSAMMENFASSUNG

Das Subsystem der Verwesung besteht aus einem komplexen Zusammenwirken von Organismen und Prozessen, deren Wirken von zentraler Bedeutung für die Pflanzenverfügbarkeit von Nährstoffen und für die Aufrechterhaltung des Nährstoffvorrats im Ökosystem ist. Kenntnisse über Verwesung und Freisetzung von Nährstoffen in Forstpflanzungen sind spärlich und vieles

muss man aus Anhäufungsmustern auf dem Waldboden ableiten. Dieser Beitrag beschreibt die Gesetzmässigkeiten, denen Verwesung und Freisetzung von Nährstoffen unterliegen und untersucht ihre Übertragbarkeit auf gleichaltrige Pflanzungen.

Verwesung umfasst Katabolismus, Zerkleinerung und Auswaschung. Man misst sie üblicherweise am Gewichtsverlust und der Atmung. Diese Grössen sind korreliert mit den Nährstoff-Freisetzungsraten (ungefähre Reihenfolge $K > Mg > Ca > Mn > C > P > N > S$).

Verwesung ist eine Funktion der drei Faktoren Klima, Boden und Angreifbarkeit für heterotrophe Organismen. Die durch Standortbedingungen gesetzten Grenzen der Verwesung werden durch Bewirtschaftung und Waldentwicklung modifiziert.

Die Verwesung verschiedener Streuarten ist abhängig vom Anteil der Äthanol-löslichen und Äthanol-unlöslichen Fraktionen; in einigen Fällen auch vom ursprünglichen Stickstoffgehalt. Zwei Exponentialkurven geben eine zutreffende Darstellung der Hauptphase der Zersetzung, auf die dann der langfristige Abbau resistenter Humusfraktionen folgt.

Während der Verwesung werden Nährstoffe in Mikroorganismen und tierischen Geweben 'immobilisiert'. Das Konzept der Immobilisierung, mit einer Mineralisierung bei kritischen Kohlenstoff : Nährstoff Verhältnissen, verdeckt jedoch das kurzfristige Recycling von Nährstoffen durch mikrobiellen Umsatz.

Das Zeitschema der Verwesung und der Freisetzung von Nährstoffen schliesst ein die pedogenetischen Tendenzen über Jahrtausende, Sukzessionswechsel über Jahrzehnte oder Jahrhunderte sowie jahreszeitliche und tägliche Rhythmen. In Pflanzungen sind Sukzessionsfolgen sehr ausgeprägt; sie sind zusätzlich beeinflusst durch Bewirtschaftungsmassnahmen.

Es gibt wenig Anhaltspunkte für die Schwankungen in der Freisetzung von Nährstoffen während der Umtriebszeit. Phasen der Nährstoffanlieferung und des Nährstoffbedarfs sind jedoch offensichtlich nicht so gut aufeinander abgestimmt wie in verschiedenaltigen Beständen. Der Anteil der Nährstoffe des Ökosystems, die im Auflagehumus

enthalten sind, und die Umsatzzeit nehmen mit dem Breitengrad zu. Die Anhäufung in organischer Form, die in hohen Breitengraden einen stabilisierenden Einfluss ausübt, reduziert gleichzeitig die Nährstoffzufuhr zu den Bäumen. Es ist zu erwarten, dass eine gesteuerte Zunahme der Umsatzrate die Primärproduktion steigert.

INTRODUCTION

The decomposition sub-system in forests, as in other ecosystems, is not just a 'black-box', best left unopened and considered as a component which accepts and releases elements. It is Pandora's box containing a complex interacting set of organisms and processes whose activities are central to the availability of nutrients to plants and to the maintenance of the nutrient capital of the ecosystem. The sub-system, therefore, demands our understanding, on the assumption that better understanding will lead to better management, although much of the experience in agriculture suggests that a pragmatic approach to management can be very successful. Forestry, however, has not had the benefit of centuries of experience from trial and error and of a century of intensive soil research. Thus management of nutrient processes in forests has the opportunity, and the need, to use the research tool more directly than has agriculture and also to make use of the understanding from research in agriculture and from basic science.

The information on decomposition and nutrient release in forest plantations is sparse and scattered. Therefore, I have adopted the approach of describing first the general principles of decomposition, then of examining their application to even-aged forests in order to describe the pattern of processes during a rotation, and finally of discussing some implications, including comparisons with other systems. The emphasis throughout is on the organic horizons of the forest floor and on coniferous plantations.

DECOMPOSITION

The term decomposition has been used in a wide variety of senses, but here it is used to include three main processes: katabolism, comminution and leaching. Katabolism, the disruptive processes of chemical change by organisms, involving the breakdown of carbohydrates, proteins and other organic compounds for heterotrophic anabolism with the associated release of simpler, insoluble, soluble or gaseous compounds or elements. Thus the katabolism of organic compounds by heterotrophic organisms results in the incorporation of elements into their tissues, i.e. immobilization, and release of elements into the soil and

aerial environment, i.e. mineralization. However, it must be emphasized that the tissues of the heterotrophs are themselves subject to decomposition with subsequent mineralization of elements. Comminution is the reduction in particle size by a combination of biological and physical mechanisms and results in redistribution of organic matter in the soil. Leaching is the physical process of transport of water-soluble or fine particulate material from organic matter. The combination of the processes of katabolism, comminution and leaching results in measurable parameters of weight loss, change in chemical composition and release of gaseous and water-soluble material from the organic matter but the component processes are often indistinguishable.

Weight loss is a common measure of decomposition which combines all losses and is biased towards the major organic substrates which constitute most of the organic matter. Respiration provides a direct measure of carbon katabolism which usually correlates well with weight loss and with the rate of release of nutrient elements, although each element has a different pattern and rate of release. Potassium is not organically bound and is released rapidly through leaching. Calcium and magnesium are mainly contained in plant structural components, are released more slowly and accumulate in fungi and fauna (Cromack et al. 1977). Phosphorus, nitrogen and sulphur are mobilized during katabolism, but, because their concentration in microbial tissue is higher than that in plant tissues, they tend to be retained within the microbial population and released slowly. Thus the release sequence tends to be $K > Mg > Ca > Mn > C > P > N > S$, largely reflecting the demand by decomposers but with some variation in different litters, depending on the relative concentration of the elements (Will 1967; Attiwell 1968; Wood 1974; Toth, Papp & Lenkey 1975; Gosz, Likens & Bormann 1973).

FACTORS CONTROLLING DECOMPOSITION

Although there is a wide variety of types of organic matter decomposing in various environments, within any ecosystem, the rate of decomposition is basically a function of three groups of factors: climate, soil and resource quality, the term 'resource' being used for organic matter composed of a number of chemical compounds, while the term 'substrate' is used in the biochemical sense of a chemical entity that reacts in a specific manner with an enzyme. These factors control the activities of the heterotrophic microflora and fauna and can be represented as a module (Fig. 1) which is repeated for different types of resource, e.g. needle, leaf, stem or root within an ecosystem and in different ecosystems (Bunnell & Tait 1975; Swift, Heal & Anderson, in press). The rate of decomposition in planted forests is determined by:

- (1) The microclimate of the forest floor, which is basically

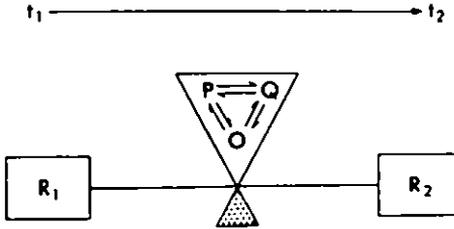


Fig. 1. Module of decomposition of organic matter. The decomposition of a resource from state R_1 to R_2 over time t_1 to t_2 is controlled by physico-chemical (P) factors of the environment and resource quality (Q) acting through heterotrophic organisms (O). (From Swift, Heal & Anderson in press).

that of the local climate modified by the vegetation canopy, which varies with tree species, planting density, growth rate and management.

- (2) The soil on which the forest floor develops, the degree of soil influence itself depends on the extent of site preparation and exposure of the mineral soil.
- (3) The chemical and physical composition i.e. resource quality of the organic matter input to the forest floor which is dependent on the initial vegetation, the type of tree and the associated management.

The rate of decomposition will vary, therefore, during a forest rotation because the forest and its management modify the controlling factors and the amount of organic matter available for decomposition.

Climate

Although there are no detailed studies of the influence of climate on decomposition through the cycle of an even-aged forest, a general picture can be drawn from the scattered data and from results in other systems. The model of the influence of temperature and moisture on microbial respiration by Bunnell et al. (1977) has proved reasonably applicable to a range of litters, including aspen and dwarf shrub, in tundra, boreal forests and temperate bogs. It provides a succinct statement of the effect of the major climatic variables, with respiration rate of the litter ($R(T,M)$) in $\mu\text{l O}_2/\text{g}$ expressed as:

$$R(T, M) = \frac{M}{a_1 + M} \times \frac{a_2}{a_2 + M} \times a_3 \times a_4^{((T-10)/10)}$$

where T is temperature in °C; M is moisture in per cent dry weight; a_1 is the percentage moisture at which activity is at half its optimal value, thus representing availability of water for metabolism by decomposer organisms; a_2 is the percentage moisture at which gas exchange is limited to half its optimal value, thus representing the decreasing oxygen supply to organisms with increasing water content; a_3 represents the effect of substrate composition as the respiration rate in $\mu\text{l O}_2/\text{g/hr}$ at 10 C, when neither moisture nor oxygen are limiting; a_4 is the Q10 coefficient determining the respiration response to temperature.

The model has been fitted to data from the litter, fermentation and humus layers of an aspen (Populus tremuloides) forest (Fig. 2). The calculated response surfaces show the retarding effect of both low and high moisture levels and also the decrease in respiration rate which occurs as the organic matter ages. Respiration rate of the three organic layers, measured seasonally, was influenced more strongly by temperature than by moisture, with the importance of temperature increasing with depth as the variability in moisture decreased (Van Cleve & Sprague 1971). The site studied, a fifty year-old stand in central Alaska, is a silt loam in a cold, dry climate in which moisture levels are moderate to low, but in forests on poorly drained soils and wet climates, the respiration rates will be inhibited by high moisture levels which retard oxygen diffusion. The principles of oxygen depletion in mineral soils (Greenwood 1968) probably apply to organic matter with the additional emphasis that the development of anaerobic microsites is related to the respiration rate and is, therefore, likely to be greatest in fresh and rapidly decomposing organic matter and to be temperature dependent. Thus respiration rates, commonly measured as oxygen uptake or carbon dioxide output, may omit a significant katabolic component of anaerobic respiration.

The rate of respiration by the microflora, although usually taken as a measure of carbon release, is also directly related to mineralization of the physiologically active plant nutrients (Witkamp 1966; Attiwell 1968; Wollum & Davey 1975). The reduction - oxidation state of the elements, however, depends on the degree of oxygen depletion which is dependent not only on moisture content but also on microbial activity (Fig. 3).

The rate of decomposition of organic matter in the cycle of an even-aged plantation will, therefore, vary with the changing temperature and moisture regimes. The forest floor temperature will follow air temperature but show reduced

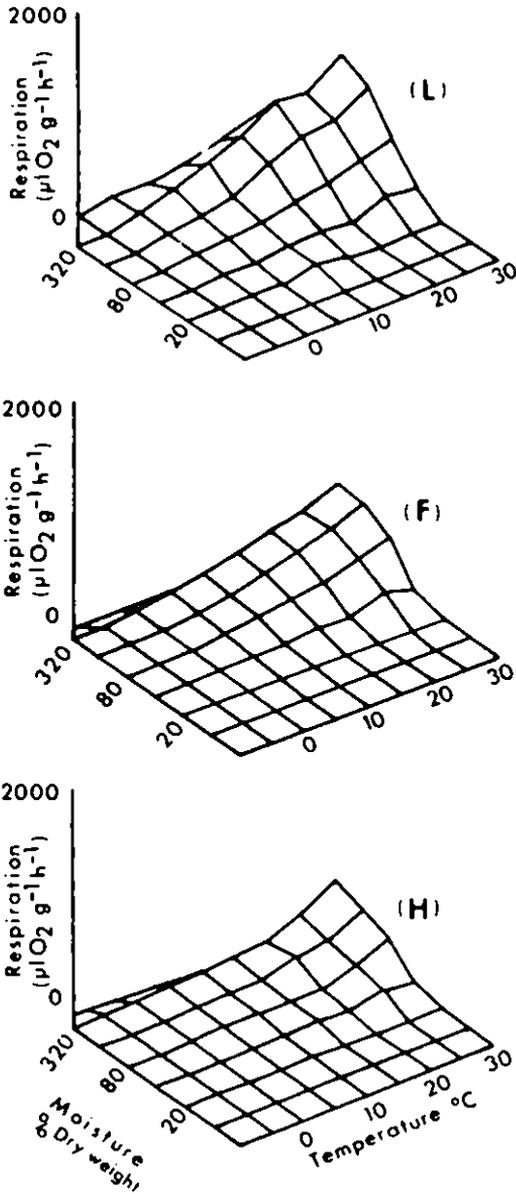


Fig. 2. Respiration rates of litter (L), fermentation (F) and humus (H) layers of aspen (*Populus tremuloides*) forest floor in Alaska, in relation to temperature and moisture. (From Bunnell et al. 1977).

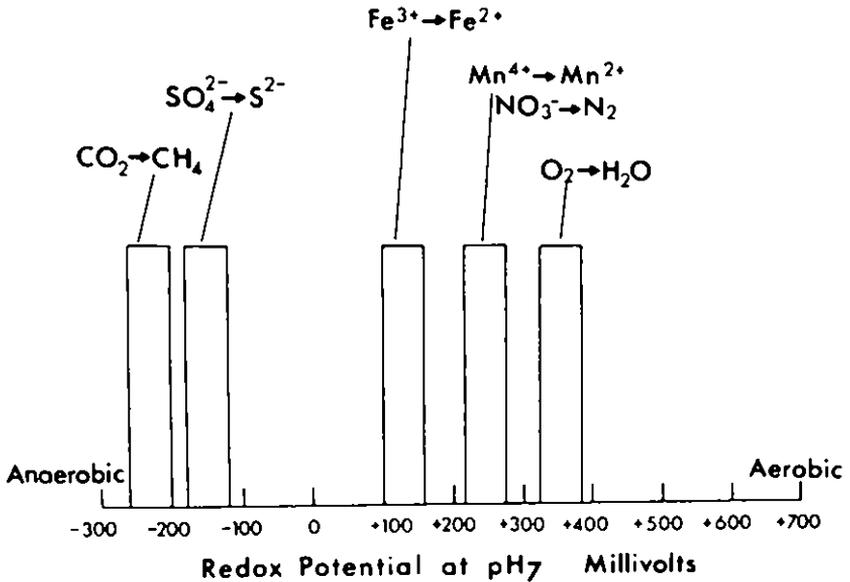


Fig. 3. Approximate critical redox potentials at which various redox systems are reduced. (From Patric 1978).

diurnal and seasonal maxima and minima as the stand ages and canopy closes, although fluctuation will be increased at thinning (Hansen 1937; Odin 1974; Edgerton & McConnell 1976; Piene & Van Cleve 1978). On mineral soils development of the organic layers will also reduce fluctuation because of their low thermal and water conductivity resulting from their low bulk density. The higher temperature minima and resulting longer decomposer season which occur as the forest develops will not compensate fully for the higher temperature maxima in unforested areas because the relationship of microbial respiration to temperature is basically exponential. In addition, freeze-thaw cycles which include nutrient release will also be depressed in the forest (Birch 1964; Witkamp 1969). The principle of reduced temperature fluctuations is reasonable but direct evidence is very limited. Piene & Van Cleve (1978) found that thinning in a *Picea glauca* forest in Alaska increased the rate of litter decomposition as a result of higher temperatures and more favourable moisture conditions. However, Brown (1976) found no detectable difference in surface temperatures in cut and uncut strips of black spruce (*Picea mariana*) on a peat bog in Minnesota. He concluded that temperature related microbial activity was not

expected to vary as a result of felling.

The varying effect of moisture during a forest cycle is more complex than that of temperature, as well as interacting with it, because of the balance between aerobiosis and anaerobiosis. The increase in evapotranspiration and canopy interception as the forest develops will reduce water input to the litter surface and moisture levels in the soil. The degree of soil drying will vary with tree species, soil type, cultural technique and thinning (Hansen 1937; Lull & Axley 1958; Haberland & Wilde 1961; Binns 1968; Read, Armstrong & Weatherall 1973; Pyatt 1973; Helvey 1975; Williams, Cooper & Pyatt 1978). Moisture content and temperature will also vary spatially within a plantation, especially in the pre-thicket stage, where ploughing has occurred, with greater temperature variation and lower moisture levels on ridges than in furrows. The changes in moisture content in organic horizons are reasonably predictable, but they are associated with more complex changes in other factors both in the organic and mineral horizons. Over the longer term, bulk density tends to increase as a result of decreasing moisture which causes a partially reversible compaction, especially in soils with a high organic content, while pH tends to fall and is related to alteration in the exchange capacity (e.g. Wilde 1964; Hamilton 1965; Pyatt 1973; Grieve 1978; Williams, Cooper & Pyatt 1978).

Thus during the development of a forest the change in physical and chemical factors outlined above is expected to cause the following changes in the rates of decomposition and release of minerals:

- (1) a gradual decrease at moist and dry sites because of decreasing fluctuation in temperature and decreasing moisture content as the canopy develops, reaching a constant level after canopy closure. At thinning, decomposition and release will increase for a few years with increased temperature and moisture and at felling the rate will rise considerably through the canopy removal.
- (2) In wet sites either an increase or a decrease with tree growth, depending on the balance between the retarding effect of reduced amplitude of temperature variation and the stimulating effect of increased aeration through lower moisture levels.

Soil factors

The initial soil conditions, like climate, set broad limits to the rate of decomposition with a direct relationship to soil pH and concentration of minerals. Such a simplistic statement is inadequate, but there are surprisingly few studies which have examined decomposition in a wide range of soils and determined the influence of specific edaphic factors (Williams & Gray 1974; Dickinson 1974). One reason for the lack of information is that many factors are correlated and it

is virtually impossible to modify individual variables. In addition there is a strong interaction between climatic and soil factors which confounds analysis of decomposition in field conditions (Heal & French 1974).

Comparative studies have shown that decomposition of litter on the surface is correlated with pH, phosphorus and calcium concentrations and is higher in soils with mull humus than in those with moder, mor or peat (Bocock & Gilbert 1957; Witkamp & Van der Drift 1961; Frankland 1966; Heal & French 1974). Such studies correspond with results from research on particular processes such as cellulose decomposition, organic phosphate mineralization and nitrification (Alexander 1977). The chemical characteristics of the soil are intimately linked with physical characteristics, particularly texture and particle size, which have a great influence on adsorption characteristics, exchange capacity and pH. The chemical and physical characteristics influence decomposition by their effects on the organisms and on the rate of enzyme activity, but they also affect retention of nutrients in the soil and their availability to decomposers. Because clay particles have a high ion exchange capacity, retention of nutrients is particularly related to the amount and composition of the clay fraction (e.g. Kolenbrander 1971). The soil moisture regime is closely related to soil structure (Salter, Berry & Williams 1966) through its associated aeration characteristics, the microsite phenomenon being applicable to pH and other physical factors as well as oxygen. The complex combination of soil factors which influence nutrient movements under varying soil conditions are well described by Nye & Tinker (1977) and the dynamics of nutrients within ecosystems are defined in various computer simulations (Beek & Frissel 1973; Innis 1978; Tanji & Gupta 1978).

There is a vast literature on nutrient transformations in soils, especially nitrogen and phosphorus in agricultural soils (Frissel & Damen 1977), but the pattern of variation in decomposition and mineral release as related to different soils in forests is poorly documented. During the cycle of a conifer stand there is an accumulation of organic matter on the forest floor which reaches a maximum and may then decline in older stands (Ovington 1959; Page 1968, 1974; Kholopova 1972; Jorgensen, Wells & Metz 1975). This accumulation, representing the balance between input and loss, is greater than under comparable deciduous stands and tends to have lower pH, lower nitrogen content and a different balance of exchangeable nutrients (Ovington 1953, 1954; Nihlgard 1971; Tappeiner & Alm 1975). The changes in composition of the forest floor result in alterations to the lower horizons but the direction, degree, time-scale and consequences of such alterations are the subject of considerable debate (Stone 1975). The arguments will not be repeated here except to say

that soil properties are affected by the chemical and physical composition of the incoming organic matter and its decomposition characteristics. Although not proven because of technical difficulties, such as accumulated sampling errors, comparability of sites and the range of variables to be measured, the theoretical and practical evidence indicates that conifers will cause soil changes which tend to reduce the rate of decomposition and nutrient release as compared with deciduous species.

Resource quality

It is obvious that different resources, e.g. deciduous or coniferous leaf litter or wood, have different rates of decomposition. Such variations occur between species, between different parts of the same plant, within the same species grown under differing soil conditions, and within the same plant as it matures and senesces. Thus, while it is convenient to define the resource as Pinus contorta needles or Pseudotsuga menziesii branches, such names are insufficient to describe the important physico-chemical characteristics which determine the rate of decomposition of that resource. Although our current understanding of the control of decomposition by resource factors is poor, four factors, which are often inter-correlated, are recognized:

- (1) Carbon sources - a range of organic substrates act as carbon and energy sources for micro-organisms and their chemical composition controls their susceptibility to katabolism, e.g. Minderman (1968). The combination of carbon substrates within a resource modifies its rate of decomposition (Fig. 4). Although many substrates are involved, the decomposition rate is largely determined by, or at least correlated with, the percentage of lignin (Van Cleve 1974). Bunnell, Tait & Flanagan (1977) developed these principles and found that ethanol soluble components were katabolized at 5-10 times the rate of ethanol insoluble components. From this they showed that a double exponential model, expressing both rapid and slow decomposing constituents, defined by the proportion of ethanol soluble and non-soluble fractions, provided a good fit between observed and predicted loss rates for a number of different litter types.
- (2) Nutrient sources - the chemical elements of importance in plant growth are also important in microbial and faunal growth, and are provided by katabolism of organic matter. The concentration of nutrient elements in fresh organic matter is generally related directly to the rate of decomposition and mineral release as shown by the strong positive correlation between weight loss and initial nitrogen concentration (e.g. Witkamp 1966; Jensen 1974; Van Cleve 1974). There is, however, an opposing trend, that during decomposition, the rate of decomposition

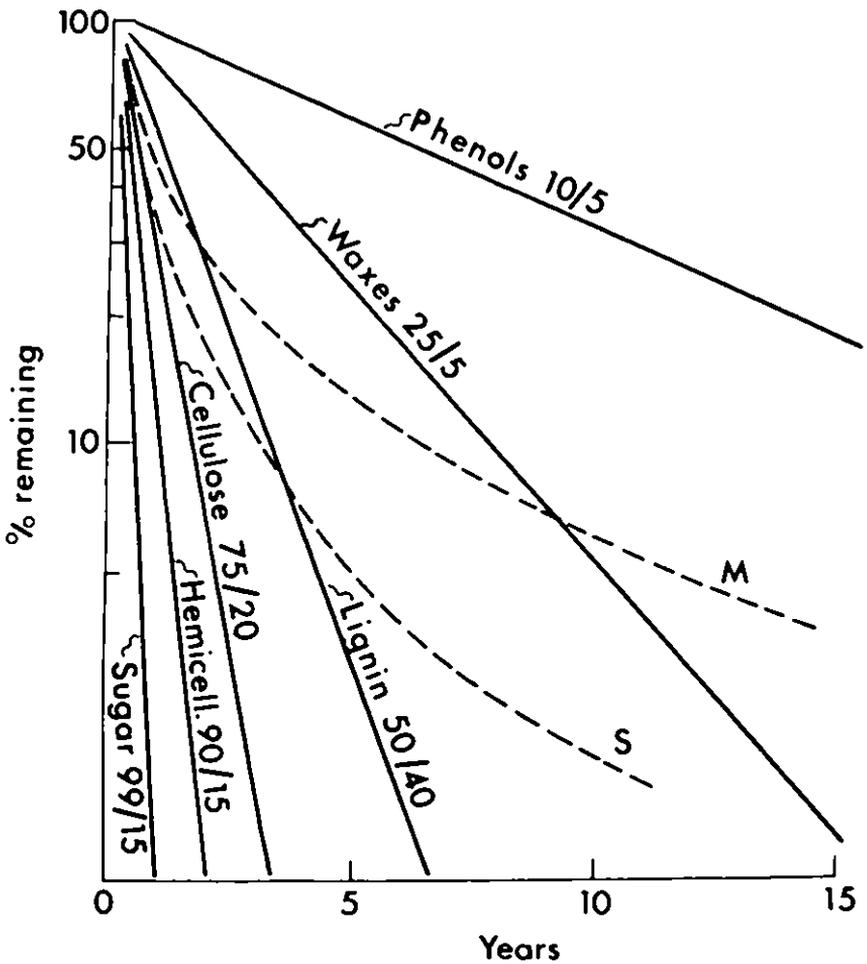


Fig. 4. Decomposition curves of substrates which constitute woodland litter. For each substrate the first number indicates the percentage of the substrate lost in one year, the second number is the approximate percentage in weight of the original litter. The curve S is the annual summation of the residual amounts of substrates remaining. The curve M is the approximate course of decomposition based on observed values. (From Minderman 1968).

declines while the nutrient concentration often increases as a result of loss of gaseous carbon and immobilization of nutrients by the microbial population. The lowest rates of decomposition are found in 'humus' which has a high nutrient concentration, but the nutrients are combined in complex organic molecules which are the result of decomposition.

- (3) Modifiers - chemical compounds, either present in the initial litter or produced by micro-organisms, whose presence in organic matter retards or stimulates microbial and faunal activity. A wide variety of compounds are involved but for technical reasons they have not been measured in comprehensive studies of decomposition. Their presence probably accounts for much of the variation in decomposition which is not explained by the composition of carbon and nutrient sources. Phenolic and quinonic compounds and tropolones extracted from conifer wood have been shown to be toxic to fungi (Scheffer & Cowling 1966); polyphenols retard leaf litter decomposition and inhibit earthworm feeding (King & Heath 1967; Satchell & Lowe 1967) and may cause low rates of decomposition of roots (Sinha 1972); and of course Handley (1954) developed the hypothesis of the role of phenol tanned proteins in mull and mor formation. No general relationship between decomposition rate and concentration of modifier compounds has been described, but evidence suggests that conifers tend to have evolved these inhibiting compounds to a greater extent than many other plants (e.g. Bauzon, van den Driessche & Dommergues 1969). Variation in decomposition of the same litter from different sites and ages may be attributed to nutritionally induced differences in polyphenol complexing of litter materials, as in Pinus radiata needles (Lamb 1976).
- (4) Physical factors - the surface properties, toughness, particle size and other physical properties of the organic matter influence their rate of decomposition, particularly through their influence on moisture uptake and retention and on the resistance to attack by micro-organisms and fauna. The main feature is the physical character of coniferous forest litter with its hydrophobic surface and small surface area to volume. Thus, in comparison with most deciduous leaf litter, they tend to have a low uptake but high retention of moisture, and retain their physical shape until late in the process of decomposition. These needle characteristics result in a lower leaching loss of soluble organic compounds and nutrients than in deciduous litters. Water soluble organic compounds thus decompose to a greater extent inside needles than inside leaf litter (Nykvist 1963).

The four groups of factors which constitute resource quality combine to determine the relative rate of decomposition and nutrient release from different litters at a given site, with the environmental factors determining the absolute rate at different microsites. Although examples are cited in which a correlation exists between decomposition rate and concentrations of organic fractions or nutrients, there are many examples in which correlations were not detected (e.g. Melin 1930; Mikola 1955; Daubenmire & Prusso 1963). Much depends on the range of resource quality which is examined, the range of chemical components determined and the extent to which interactions between factors are expressed.

The variation in rate of decomposition of different litters, as expressed by weight loss, has been determined in many comparative studies. These show a general pattern of decreasing rate over the series:

herb leaves > grass leaves > deciduous tree leaves >
 conifer needles > moss > deciduous wood > conifer wood,
 (Mikola 1955; Daubenmire & Prusso 1963; Bocock 1964; Voigt 1965; Manganot 1966; Witkamp 1966; Satchell & Lowe 1967; Kira & Shidei 1967; Attiwell 1968; Mommaerts-Billiet 1971; Gosz, Likens & Bormann 1973; Dickinson & Pugh 1974; Heal & French 1974; Swift et al. 1976; Heal, Latter & Howson 1978). Rates of loss have usually been measured for only the first year or two of decomposition but within this period the fastest rates are about ten times those of the slowest. There is considerable overlap between loss rates of the groups identified and it is particularly difficult to isolate the relative importance of different chemical and physical characteristics within groups. The initial state of the litter influences its subsequent decay rate, with faster rates recorded for green litter from which soluble fractions have not been resorbed before death - a factor relevant to the decomposition of brush. The decomposition of wood is also dependent on the proportions of bark, sapwood and heartwood, which vary considerably in chemical and physical composition and in decomposition rate (Gosz, Likens & Bormann 1973; Kaarik 1974).

The data on rate of decomposition of roots are very few but indicate slower rates than for leaf material of the same species (Jenkinson 1965; Smith 1966; Malone & Reichle 1973; Sinha 1972). The results are mainly for agricultural crops but are probably similar in non-cultivated species, with tree and shrub roots having rates comparable with those of above-ground wood (Kaarik 1974; Waid 1974; Heal & French 1974). Root exudates constitute a very variable fraction of the total plant production, mainly as organic acids, sugars and amino acids whose rate of decomposition is probably high compared with other inputs (Smith 1969, 1970; Nye & Tinker 1977).

Thus, during the life of an even-aged plantation there is a changing pattern of quality of organic matter input, and

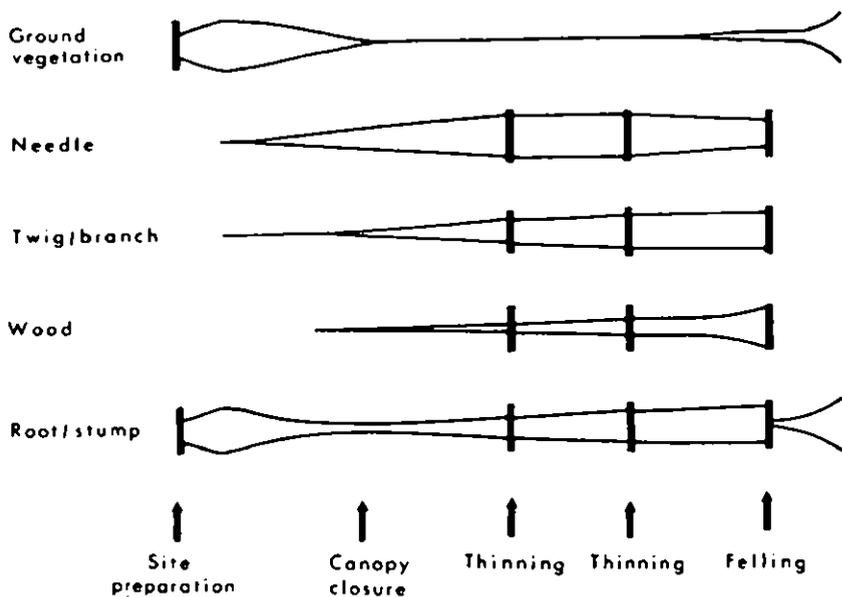


Fig. 5. Schematic input of various resources to the forest floor during a rotation. Bars represent major inputs of fresh material with relatively high soluble organic and nutrient content.

therefore, a changing rate of decomposition. The general phases of input are a gradual reduction in ground flora components compensated by needles and by twigs and branches as the forest matures. The production of dead roots probably increases with time but data are very sparse. A series of inputs result from management practices with the particular characteristic that they usually comprise fresh plant material, needles, wood and roots, from which soluble organic material and nutrients have not been resorbed by the plant. At planting, fresh ground vegetation may be killed as a result of sward inversion; brushing adds dead twigs and branches; thinning contributes green needles, fresh twigs, branches, stumps and roots, with a similar major input at final felling. Felling is followed by a period of negligible input until the ground flora redevelops, this being characterized by fast growing species whose litter probably has a high decay rate. The general sequence of events, represented in Fig. 5, is recognized from well-documented, quantitative measurements of

above-ground input in plantations at varying stages of development (Bray & Gorham 1964; Turner 1975; Miller, Cooper & Miller 1976; Carey & Farrell 1978), and occasionally for a complete age sequence for a species, e.g. Pinus sylvestris (Ovington 1959), P. radiata (Will 1964; Florence & Lamb 1974).

The varying types of organic matter decompose at differing initial rates, but the composition changes with time as material is concentrated in microflora or converted to humus. The rate of decomposition of some of these residual fractions is very slow and as a result there are pools of organic matter and nutrients with different turnover rates. This is clearly expressed in the model developed by Jenkinson & Rayner (1977) based on data from the Rothamsted field experiments and on measured organic matter fractions and rates of decomposition. The input (1 tC/ha/yr) is separated into two fractions: 'decomposable plant material' and 'resistant plant material' in proportions 0.837 and 0.163, respectively. Each of these fractions decomposes to produce 'soil biomass', 'physically stabilized organic matter' and 'chemically stabilized organic matter' in proportions of 0.076, 0.125 and 0.0035, respectively, with the release of carbon dioxide. These three fractions are repeatedly decomposed, yielding the same fractions at each step. The estimated half life of the fractions varied considerably and the predicted accumulation of the fraction when the model was run to 10,000 years assuming steady state (Table 1) was acceptably close to measured accumulations. The model indicates that small changes in input to the residual fractions, or changes in their turnover time, can cause large changes in the amounts of accumulated organic matter, and nutrients.

A change in rate of decomposition and accumulation can result from input of residues which tend to produce more or less of specific humus fractions. Alternatively, a change in the aerobic / anaerobic balance during the forest development can modify the production of such compounds. For example, Sinha (1972) showed that anaerobic decomposition of oat roots produced more fulvic acid and less humic acid and humins than did aerobic decomposition, the rate of decomposition of these fractions being in the sequence: fulvic acid > humic acid > humins (Campbell et al 1967).

IMMOBILIZATION AND RELEASE

The pool of organic matter with high rate of turnover may be small but provides a rapid supply of recycled nutrients, while the larger pools of resistant organic matter with slow turnover provide a continuous supply of nutrients. The supply from the resistant organic matter, although representing a very small contribution from each year's input, represents a considerable accumulated release in any one year. The turnover of the microbial and faunal biomass are key factors in the

Table 1. Turnover (half-life) and accumulation of fine fractions of organic matter in a cropped agricultural system at steady state (from Jenkinson & Rayner 1977).

Fraction	Half-life (years)	Accumulation (tC/ha)
Decomposable plant material	0.165	0.01
Resistant plant material	2.31	0.47
Soil biomass	1.69	0.28
Physically stabilized o.m.	49.5	11.3
Chemically stabilized o.m.	1980	12.2

mobilization of nutrients in the pools. The concentration of many elements in the decomposer organisms (Table 2) is much higher than in plant residues. As the carbon compounds are used as energy sources by the microflora, carbon is released as carbon dioxide or as anaerobic respiratory products, and only a small fraction is converted into microbial tissue. In contrast nutrients are first mineralized from the plant residue, absorbed and converted into microbial tissue. The transfer of nutrients from plant to microbial compounds, commonly referred to as immobilization, results in the well-known fall in the C:N or C:element ratio. The decline in the ratio is considered to continue until it approximates to that of microbial tissue, at which stage the nutrient concentration is in excess of that required by the microflora and therefore the excess becomes available for plant uptake.

The changing concentration or ratios of elements indicate the stage at which there is net release of the element from the intimate mixture of plant residue and microbial population. Critical levels approximate to 2 per cent for nitrogen (C:N c.25:1), 0.1 per cent for phosphorus (C:P c.500:1), 0.20 per cent for sulphur (C:S c.250:1) and 0.10 per cent for potassium (C:K c.500:1) (Gosz, Likens & Bormann 1973; Dowding 1974; Toth, Papp & Lenkey 1975). Such generalizations are dangerous, however, because there is considerable variation between types of resource and in methods of analysis and release is inferred, not measured. The expression of concentration or ratio also ignores the state of the element, thus release will depend on the availability of the element, including carbon, to micro-organisms, and also on the availability of other elements.

The concepts of immobilization and critical concentrations or ratios provide a convenient outline of the main sequence of events during decomposition and of differences between resources, but they mask the dynamic nature of the processes, particularly those involving the

Microflora	Mg				Source
Fungal mycelium	1.74	0.48	0.33	4.28	
mean	0.23-4.31	0.02-1.31	0.16-0.61	0.68-9.50	Swift (1977)
range	(30)	(19)	(19)	(18)	
(n)					
Fungal mycelium	2.80	0.24	0.12	-	
Fungal fruit bodies	4.40	1.00	4.90	-	Ausmus, Edwards & Witkamp (1976)
Fungal rhizomorphs	4.13	0.93	3.16		
Bacteria	4.00	0.91	1.50		
Actinomycetes	4.20	1.00	4.00		
Fauna					
Oligochaeta	10.5	1.1	0.5	0.3	Allen et al. (1974).
Diplopoda	5.8	1.9	0.5	14.0	McBrayer et al. (1974).
Insecta	8.5	6.9	0.7	0.3	
Detritivores	7.74	0.80	0.13	10.30	
Fungivores	7.74	1.39	0.40	3.95	Allen et al. (1974)

Table 2. Nutrient concentration (% dry weight) of microflora and soil fauna.

microflora. Measurements of the standing crop of microflora in various resources have been used, in conjunction with nutrient concentrations of the microflora, to calculate the quantities of nutrients immobilized. The calculated percentage of the total nutrient which is immobilized varies greatly, e.g. 2-3 per cent for nitrogen and phosphorus in the forest floor of black spruce (*Picea mariana*) in Alaska (Flanagan & Van Cleve 1977), but more than 100 per cent for some nutrients in the litter of *Liriodendron tulipifera* forest in Tennessee (Ausmus, Edwards & Witkamp 1976). Methodological problems make accurate measurements very difficult, but these two studies show that nutrients are rapidly circulated through the microbial population which has generation times in days. Death and decomposition may be balanced by growth to give a fairly constant standing crop, but the nutrients are being circulated through inorganic pools which are capable of being utilized by fine plant roots permeating the litter. Both studies also show marked growth in microbial populations and immobilization of nutrients in spring and early summer, with a decline and presumably a release of nutrients in late summer. The extent to which nutrients are retained in dead microbial cells and mycelium is unknown and the presence of dark, apparently empty hyphae in acid organic soils argues for slow decomposition of at least the chitinous cell walls which have a high nitrogen content. However, Flanagan & Van Cleve (1977) estimated that as a result of a decrease in microbial biomass, 90 per cent of which was fungal, there was a net release of 0.24 g N/sq.m and 0.025 g P/sq.m. within the forest floor in an eleven day period in summer. Ausmus, Edwards & Witkamp (1976) showed similar fluctuations in the L, F and H layers.

The immobilization of nutrients by the microflora and possibly the mechanism of release is shown in the analysis of wood decomposition, for example (Ausmus (1977) and Swift (1977)). Most nutrients in wood are gradually concentrated by fungi until 30-50 per cent of the total calcium, magnesium and potassium, and 90-100 per cent of the nitrogen and phosphorus are contained in mycelium (Fig. 6). Potassium, unlike other elements, shows a large initial decrease in concentration in wood as in other litters through leaching, while other elements are retained by the microflora. An increase in quantity of nutrient may result from nitrogen fixation or from import by fungi. Colonization by a sequence of fauna occurs after there has been considerable decomposition by fungi and is probably influenced by the concentration of nutrients in the microflora, which provide a more accessible nutrient source than the wood itself. Feeding by fauna then results in a net loss of nutrients from the wood, probably by a combination of leaching, movement of animals and comminution, which causes loss of fragments which are rich in nutrients. During the feeding by animals nutrients are ingested,

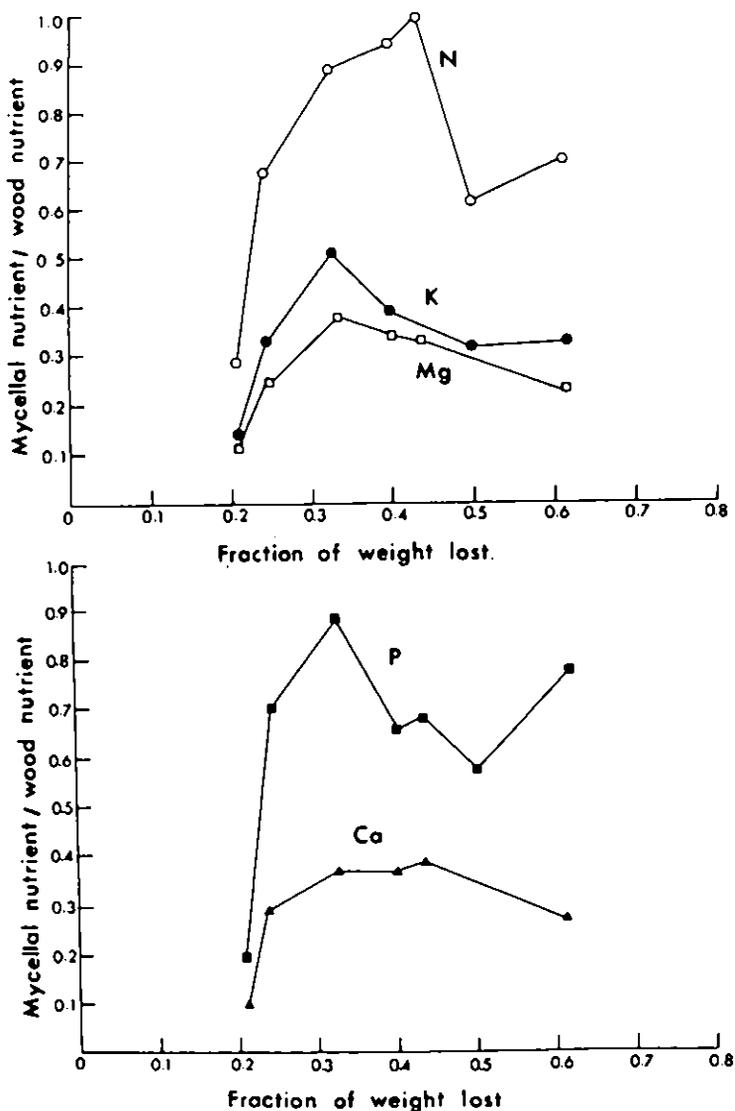


Fig. 6. The pattern of immobilisation of branch-wood nutrients by mycelium of the white rot basidiomycete *Stereum hirsutum* in relation to state of decomposition. Mycelial nutrient is calculated from mycelial standing crop multiplied by mycelium nutrient concentration and is expressed as a proportion of the branch-wood nutrient. (From Swift 1977.)

mineralized and excreted as well as being incorporated into tissue. Thus, there is a continual turnover of the inorganic and organic nutrient pools within the wood. The presence of plant roots within wood after faunal colonization, indicates that the nutrients are utilized by the vegetation and probably contribute to their net loss - at a time when the nitrogen concentration is about 0.5 per cent (C:N 100:1).

The release of nutrients from microflora results from excretion, autolysis, decomposition by other microflora and grazing by fauna on both live and dead cells and hyphae. There is considerable evidence that suppression or elimination of fauna retards the rate of decomposition, directly through consumption and respiration and indirectly through reduced microbial activity (Edwards, Reichle & Crossley 1970; Dickinson & Pugh 1974). Grazing on the microflora by protozoa and by nematodes decreases the microbial biomass but increases the rate of organic matter decomposition and the release of phosphorus and nitrogen in terrestrial and aquatic systems (Johannes 1965; Barsdate, Fenchel & Prentki 1974; Fenchel & Harrison 1976; Coleman et al. 1977), although interpretation of experimental results on phosphorus release may be conflicting (Fenchel & Harrison 1976).

Within an even-aged plantation, especially with conifers, changes in the physico-chemical conditions and in resource quality will influence faunal populations. Increase in acidity and of input of conifer litter will reduce earthworm populations if they were present initially, and the forest floor decomposition is usually dominated by micro-arthropods and enchytraeids and by fungi. The reduction in moisture level is likely to encourage faunal activity by increasing aeration on wet sites, but if waterlogging occurs as a result of felling, anaerobic conditions will again reduce the fauna. Although protozoa can modify bacterial populations and processes, their influence on fungi is probably much more limited as few species are known to be fungivorous (Stout 1974) and their participation in nutrient cycling is likely to decline during the development of a conifer plantation. Interaction within the microflora occurs and the most relevant aspect is the inhibition of litter decomposition by mycorrhizae. Gadgil & Gadgil (1975) showed that the weight loss of Pinus radiata needles without plants or with non-mycorrhizal plants was significantly higher (44 per cent after six months) than in the presence of mycorrhizal plants (39 per cent). The difference is difficult to interpret but may result from the production of antibiotics which inhibit the growth of saprophytes or the greater competitive ability of mycorrhizal fungi, whose nutrient uptake is not dependent on an associated energy source. Thus, organic matter decomposition may be retarded by the spread of mycorrhizas in the development of a plantation, while the mobilization of

nutrients is maintained by the mycorrhizas.

PATTERN AND IMPLICATIONS

Decomposition and nutrient release comprise a complex series of interacting processes controlled by the physico-chemical environment and resource quality and quantity. The balance between these processes and the input of organic matter determines the rates of accumulation of organic matter and nutrients in and beneath the forest floor. In most ecosystems there are a series of trends occurring over different time scales - a pedogenic trend over millenia, on which is superimposed a successional sequence which may be repeated over decades or centuries, and a seasonal and even diurnal rhythm. In even-aged plantations the successional sequence is much more distinct than in mixed-aged situations, with the additional effect of distinct pulses introduced by management activities like brashing, thinning and felling.

The hypothesis, based on the review given in this paper, is that the general sequence of decomposition in conifer plantations will be:

- (1) an initial pulse as a result of death of ground vegetation and site preparation;
- (2) a gradual decline as input from ground vegetation declines and conifer litter increases, and as soil temperature variation and moisture content decline as the canopy closes;
- (3) a pulse as a result of input of green needles, fresh wood and roots at thinning with associated short-term increases in temperature variation and moisture;
- (4) a further decline as the proportion of wood input increases with stand age;
- (5) a final pulse, greater than that at thinning, when felling provides a major input of fresh material and there is increased temperature and moisture response;
- (6) the effect of the final pulse may be sustained by input from regrowth of ground vegetation into a favourable microclimate, until forest cover redevelops in a subsequent generation of trees.

Such a sequence is described in relation to specific management practices by Bunn & Will (1974) and Wollum & Davey (1975). However, there is no direct evidence for or against the suggested sequence of events in terms of measured rates of decomposition and nutrient release over a rotation. The main corroborative evidence comes from the observed amounts of organic matter and nutrients accumulated over time or in response to particular practices. This evidence allows some inferences of rates of decomposition processes, particularly loss of carbon, but gives little indication of the actual pattern of mineralization or of supply of nutrients to the trees.

The studies on effects of clearfelling appear to provide direct evidence with marked increases in nitrate output in stream water from felled, compared with unfelled, areas, additional variation being related to management of the forest waste and forestry practice (Pierce et al. 1972; Verry 1972; Brown, Gahler & Marston 1973; Likens & Bormann 1974; Wiklander 1974; Fredriksen, Moore & Norris 1975; Snyder, Haupt & Belt 1975; Neary 1977). Although there are major variations in concentration, many of these studies show an increase in nitrate output of about an order of magnitude after felling, with a return to base-line concentrations when ground vegetation is redeveloped. Actual changes within the forest floor and soil have received little attention, but Popovic (1974) showed an increased nitrification in soils as a result of felling, the rate being greatest in soils with pH above about 4.3 and C:N below about 30:1. Tamm et al. (1974) point out that the change in nitrogen release is the result of loss of nutrient uptake by the trees which allows temporary accumulation of ammonia, providing the necessary substrate for nitrification. Unless inhibited by soil conditions, there will be an increase in nitrification and, in the absence of uptake by vegetation, the nitrate produced will be readily leached. Thus, there is a change in the product of nitrogen mineralization rather than a change in rate. The amount which is available for mineralization will, however, depend on the amount of organic residues from felling.

Loss of nitrate, and to a lesser extent phosphate, after felling is related to the change in demand, analogous to nutrient leaching under fallow conditions in agriculture. This raises the question of the synchronization of nutrient release from the forest floor and the nutrient demand by the growing crop. The apparent pattern of increasing accumulation of organic matter and nutrients in the forest floor as the forest develops, implies decreasing release of nutrients, although some of the change is probably a redistribution of material within the soil profile rather than a change in absolute amount. The sequence of management practices from site preparation to felling results in a series of pulses of nutrient release. The initial pulse coincides with a small, localized demand by the establishing forest; at thinning the pulse of nutrients from the forest floor probably accounts for some of the increased crop growth at a time when nutrient demand is maximal; at felling there is a release which does not coincide with forest demand. Thus, in even-aged plantations, both supply and demand are phased, but these two major cogs in the nutrient cycle are apparently not fully synchronized. In contrast, the mixed-aged forest has a spatial mosaic which allows greater opportunity for trees and other vegetation to benefit from phases of nutrient input and release associated with individual trees. The mosaic in a

mixed-aged forest will include seasonal variation in input and release when a range of species are involved.

The importance of synchrony of nutrient supply and demand is only theoretical, and probably varies in different climatic regimes. In tropical regions a major proportion of the nutrient capital is maintained in the forest biomass, with a small proportion in the forest floor which has a very short turnover time. With increasing latitude the balance changes, and an increasing proportion of the ecosystem nutrients are retained in the forest floor, until in boreal forests there is a long turnover time (Olsen 1963; Duvigneaud & Denayer-DeSmet 1969; Witkamp & Ausmus 1976). The forest floor, acting as both nutrient sink and source, provides a stability in high latitude forests which makes them less liable than tropical forests to suffer nutrient loss through man's activity. However, while acting as a stabilizing influence, the forest floor reduces the flow of nutrients to the trees, and any increase in the rate of nutrient turnover is expected to increase primary production. Fertilizers give some increase in growth, but efficiency of uptake is low compared with agricultural systems, partly because of the slow response rate of trees. Grazing is an alternative practice which has the potential to increase the rate of nutrient turnover in the forest floor, and by maintaining a vegetation cover can retain nutrients during management disturbances. Some of the positive responses of trees to experimental grazing (Hedrick & Keniston 1966) may result from increased nutrient availability despite potential competition between trees and ground flora. Although current evidence of the value of grazing in forests is inconclusive (Adams 1975), there are logical reasons for examining this, and other alternatives to current management practices, which can increase and control nutrient circulation through the forest floor.

REFERENCES

- Adams, S.N. (1975). Sheep and cattle grazing in forests: a review. *Journal of Applied Ecology*, 12, 143-152.
- Allen, S.E., Grimshaw, H.M., Parkinson, J.A. & Quarmby, C. (1974). *Chemical analysis of ecological materials*. Blackwell, Oxford.
- Alexander, M. (1977). *Introduction to soil microbiology*. Wiley, New York.
- Attiwell, P.M. (1968). The loss of elements from decomposing litter. *Ecology*, 49, 142-145.
- Ausmus, B.S. (1977). Regulation of wood decomposition rates by arthropod and annelid populations. "Soil organisms as components of ecosystems." (Ed. by U. Lohm and T. Persson), pp. 180-192. *Ecological Bulletin*, Swedish Natural Science Research Council, 25.

- Ausmus, B.S., Edwards, N.T. & Witkamp, M. (1976). Microbial immobilization of carbon, nitrogen, phosphorus and potassium: implications for forest ecosystems processes. "The role of terrestrial and aquatic organisms in decomposition processes." (Ed. by J.M. Anderson and A. Macfadyen), pp.397-416. Blackwell, Oxford.
- Barsdate, R.J., Fenchel, T. & Prentki, R.T. (1974). Phosphorus cycle of model ecosystems: significance for decomposer food chains and effect of bacterial grazers. *Oikos*, 25, 239-251.
- Bauzon, D., Van den Driessche, R. & Dommergues, Y. (1969). L'effet litière. I. Influence en situ des litières forestières sur quelques caractéristiques biologiques de sols. *Oecologia plantarum*, 4, 99-122.
- Beek, J. & Frissel, M.J. (1973). Simulation of nitrogen behaviour in soils. Pudoc, Wageningen.
- Binns, W.O. (1968). Some effects of tree growth on peat. Proceedings 3rd International Peat Congress, Quebec 1968.
- Birch, H.F. (1964). Mineralization of plant nitrogen following alternate wet and dry conditions. *Plant and Soil*, 20, 43-50.
- Bocock, K.L. (1964). Changes in the amounts of dry matter, nitrogen, carbon and energy in decomposing woodland leaf litter in relation to the activities of the soil fauna. *Journal of Ecology*, 52, 273-284.
- Bocock, K.L. & Gilbert, O.J.W. (1957). The disappearance of leaf litter under different woodland conditions. *Plant and Soil*, 9, 179-185.
- Bray, J.R. & Gorham, E. (1964). Litter production in forests of the world. *Advances in Ecological Research*, 2, 101-157.
- Brown, G.W., Gahler, A.R. & Marston, R.B. (1973). Nutrient losses after clearcut logging and slash burning in the Oregon Coast Range. *Water Resources Research*, 9, 1450-1453.
- Brown, J.M. (1976). Peat temperature regime of a Minnesota bog and the effect of canopy removal. *Journal of Applied Ecology*, 13, 189-194.
- Bunn, E.H. & Will, C.M. (1974). Management operations affecting nutrient cycling and fertilizer response in forest stands. Proceedings F.A.O./ I.U.F.R.O. International Symposium on Forest Fertilization, Paris. pp.33-53.
- Bunnell, F.L. & Tait, D.E.N. (1975). Mathematical simulation models of decomposition processes. "Soil organisms and decomposition in tundra." (Ed. by A.J. Holding, O.W. Heal, S.F. MacLean and P.W. Flanagan), pp.207-225. Tundra Biome Steering Committee, Stockholm.
- Bunnell, F.L., Tait, D.E.N. & Flanagan, P.W. (1977). Microbial respiration and substrate weight loss. II. A model of the influences of chemical composition. *Soil Biology and Biochemistry*, 9, 41-47.
- Bunnell, F.L., Tait, D.E.N., Flanagan, P.W. & Van Cleve, K. (1977).

- Microbial respiration and substrate weight loss. I. A general model of the influences of abiotic variables. *Soil Biology & Biochemistry*, 9, 33-40.
- Campbell, C.A., Paul, E.A., Rennie, D.A. & McCallum, K.J. (1967). Applicability of the carbon-dating method of analysis to soil humus studies. *Soil Science*, 104, 217-224.
- Carey, M.L. & Farrell, E.P. (1978). Production, accumulation and nutrient content of Sitka spruce litterfall. *Irish Forestry*, 35, 35-44.
- Coleman, D.C., Cole, C.V., Anderson, R.V., Campion, M.K., Clarholm, M., Elliot, E.T., Hunt, H.W., Schaefer, B. & Sinclair, J. (1977). An analysis of rhizosphere - saprophage interactions in terrestrial ecosystems. "Soil organisms as components of ecosystems." (Ed. by U. Lohm and T. Persson), pp. 299-309. *Ecological Bulletin, Swedish Natural Science Research Council*, 25.
- Cromack, K., Sollins, P., Todd, R.L., Fogel, R., Todd, A.W., Fender, W.M., Crossley, M.E. & Crossley, D.A. (1977). The role of oxalic acid and bicarbonate in calcium cycling by fungi and bacteria: some possible implications for soil animals. "Soil organisms as components of ecosystems." (Ed. by U. Lohm and T. Persson), pp. 246-252. *Ecological Bulletin, Swedish Natural Science Research Council*, 25.
- Daubenmire, R. & Prusso, D.C. (1963). Studies of the decomposition rates of tree litter. *Ecology*, 44, 589-592.
- Dickinson, C.H. (1974). Decomposition of litter in soil. "Biology of plant litter decomposition." (Ed. by C.H. Dickinson and G.J.F. Pugh), pp. 633-658. Academic Press, London.
- Dickinson, C.H. & Pugh, G.J.F. (1974). Biology of plant litter decomposition. Academic Press, London.
- Dowding, P. (1974). Nutrient losses from litter on I.B.P. tundra sites. "Soil organisms and decomposition in tundra." (Ed. by A.J. Holding, O.W. Heal, S.F. MacLean and P.W. Flanagan), pp. 363-373. Tundra Biome Steering Committee, Stockholm.
- Duvigneaud, P. & Denayer-DeSmet, S. (1969). Biological cycling of minerals in temperate deciduous forest. "Analysis of temperate forest ecosystems" (Ed. by D.E. Reichle), pp. 199-225. Springer Verlag, New York.
- Edgerton, P.J. & McConnell (1976). Diurnal temperature regimes of logged and unlogged mixed conifer stands on elk summer range. U.S. Department of Agriculture Forest Service Research Note, PNW-277.
- Edwards, C.A., Reichle, D.E. & Crossley, D.A. (1970). The role of soil invertebrates in turnover of organic matter and nutrients. "Analysis of temperate forest ecosystems." (Ed. by D.E. Reichle), pp. 147-172. Springer Verlag, New York.
- Fenchel, T. & Harrison, P. (1976). The significance of bacterial grazing and mineral cycling for the decomposition of

- particulate detritus. "The role of terrestrial and aquatic organisms in decomposition processes." (Ed. by J.M.Anderson and A.Macfadyen), pp.285-299. Blackwell, Oxford.
- Flanagan,P.W. & Van Cleve,K.(1977). Microbial biomass, respiration and nutrient cycling in a black spruce taiga ecosystem. "Soil organisms as components of ecosystems." (Ed. by U.Lohm and T.Persson), pp.261-273. Ecological Bulletin, Swedish Natural Science Research Council, 25.
- Florence,R.G., & Lamb,D.(1974). Influence of stand and site on radiata pine litter in South Australia. New Zealand Journal of Forestry Science, 4, 502-510.
- Frankland,J.C.(1966). Succession of fungi on decaying petioles of Pteridium aquilinum. Journal of Ecology, 54, 41-63.
- Fredriksen,R.L., Moore,D.G. & Norris,L.A.(1975). The impact of timber harvest, fertilization and herbicide treatment on streamwater quality in western Oregon and Washington. "Forest soils and forest land management." Proceedings 4th North American Forestry Soils Conference, Quebec. (Ed. by B.Bernier and E.H.Winget), pp.283-313. University of Laval Press, Quebec.
- Frissel,M.J. & Damen,J.P.N.(1977)(Eds) Cycling of mineral nutrients in agricultural ecosystems. Agro-Ecosystems, 1 and 2.
- Gadgil,R.L. & Gadgil,P.D.(1975). Suppression of litter decomposition by mycorrhizal roots of Pinus radiata. New Zealand Journal of Forestry Science, 5, 33-41.
- Gosz,J.R., Likens,G.E. & Bormann,F.H.(1973). Nutrient release from decomposing leaf and branch litter in the Hubbard Brook Forest, New Hampshire. Ecological Monographs, 43, 173-191.
- Greenwood,D.J.(1968). Measurement of microbial metabolism in soil. "Ecology of soil bacteria." (Ed. by T.R.Gray and O.Parkinson), pp.138-151. Liverpool University Press, Liverpool.
- Grieve,I.C.(1978). Some effects of the plantation of conifers on a freely drained lowland soil, Forest of Dean, U.K. Forestry, 51, 21-28.
- Haberland,F.P. & Wilde,S.W.(1961). Influence of thinning of red pine plantation on soil. Ecology, 42, 584-586.
- Hamilton,C.D.(1965). Changes in the soil under Pinus radiata. Australian Forestry, 29, 275-289.
- Handley,W.R.C.(1954). Mull and mor formation in relation to forest soils. Forestry Commission Bulletin #23.
- Hansen,T.S.(1937). Ecological changes due to thinning jack pine. University of Minnesota, Technical Bulletin, 124, 1-77.
- Heal,O.W. & French,D.D.(1974). Decomposition of organic matter in tundra. "Soil organisms and decomposition in tundra." (Ed. by A.J.Holding, O.W.Heal, S.F.MacLean and

- P.W.Flanagan), pp.279-309. Tundra Biome Steering Committee, Stockholm.
- Heal, O.W., Latter, P.M. & Howson, G. (1978). A study of the rates of decomposition of organic matter. "Production ecology of British moors and montane grasslands." (Ed. by O.W.Heal and D.F.Perkins), pp.136-159. Springer Verlag, Berlin.
- Hedrick, D.M. & Keniston, R.F. (1966). Grazing and Douglas fir growth in the Oregon white oak type forest. *Journal of Forestry*, 64, 735-738.
- Helvey, J.D. (1975). Soil moisture depletion and growth rates after thinning ponderosa pine. U.S. Department of Agriculture Forest Service Research Note, PNW-243.
- Innis, G.S. (1978). Grassland simulation model. Springer Verlag, Berlin.
- Jenkinson, D.S. (1965). Studies on the decomposition of plant material in soil. I. Losses of carbon from ^{14}C labelled ryegrass incubated with soil in the field. *Journal of Soil Science*, 16, 104-115.
- Jenkinson, D.S. & Rayner, J.H. (1977). The turnover of soil organic matter in some of the Rothamsted classical experiments. *Soil Science*, 123, 298-305.
- Jensen, V. (1974). Decomposition of angiosperm tree leaf litter. "Biology of plant litter decomposition." (Ed. by C.H.Dickinson and G.J.F.Pugh), pp.69-104. Academic Press, London.
- Johannes, R.E. (1965). Influence of marine protozoa on nutrient regeneration. *Limnology and Oceanography*, 10, 434-442.
- Jorgensen, J.R., Wells, C.G. & Metz, L.J. (1975). The nutrient cycle: key to continuous forest production. *Journal of Forestry*, 73, 400-403.
- Kaarik, A.A. (1974). Decomposition of wood. "Biology of plant litter decomposition." (Ed. by C.H. Dickinson and G.J.F.Pugh), pp.129-174. Academic Press, London.
- Kholopova, L.B. (1972). Variation in some physical and chemical soil properties with age of pine plantations. *Lesovadenie* 1972, pp.38-48.
- King, H.G.C. & Heath, G.W. (1967). The chemical analysis of small samples of leaf material and the relationship between the disappearance and composition of leaves. *Pedobiologia*, 7, 192-197.
- Kira, T. & Shidei, T. (1967). Primary production and turnover of organic matter in different forest ecosystems of the western Pacific. *Japanese Journal of Ecology*, 17, 70-87.
- Kolenbrander, G.J. (1971). Contribution of agriculture to eutrophication of surface waters with nitrogen and phosphorus in the Netherlands. Institute of Soil Fertility, Haren, Groningen.
- Lamb, D. (1976). Decomposition of organic matter on the forest floor of Pinus radiata plantations. *Journal of Soil*

- Science, 27, 206-217.
- Likens, G.E. & Bormann, F.H. (1974). Effects of forest clearing on the northern hardwood forest ecosystem and its biogeochemistry. Proceedings 1st International Congress on Ecology, The Hague, Netherlands. pp.330-335.
- Lull, H.W. & Axley, J.H. (1958). Forest soil moisture relations in the coastal plain sands of southern New Jersey. *Forest Science*, 4, 2-19.
- McBrayer, J.F., Reichle, D.E. & Witkamp, M. (1974). Energy flow and nutrient cycling in a cryptozoan foodweb. Oak Ridge National Laboratory, Oak Ridge.
- Malone, C.R. & Reichle, D.E. (1973). Chemical manipulation of soil biota in a fescue meadow. *Soil Biology and Biochemistry*, 5, 629-639.
- Melin, E. (1930). Biological decomposition of some types of litter from North American forests. *Ecology*, 11, 72-101.
- Mikola, P. (1955). Experiments on the rate of decomposition of forest litter. *Communicationes Instituti Forestalis Fenniae*, 43, 1-50.
- Miller, H.G., Cooper, J.M. & Miller, J.D. (1976). Effect of nitrogen supply on nutrients in litter fall and crown leaching in a stand of Corsican pine. *Journal of Applied Ecology*, 13, 233-248.
- Minderman, G. (1968). Addition, decomposition and accumulation of organic matter in forests. *Journal of Ecology*, 56, 355-362.
- Mommaerts-Billiet, F. (1971). Aspects dynamiques de la disparition de la litière de feuilles. *Bulletin Société royale de botanique de Belgique*, 104, 181-195.
- Neary, D.A. (1977). Impact of timber harvesting on nutrient losses in stream flow. *New Zealand Journal of Forestry*, 22, 53-63.
- Nihlgård, B. (1971). Pedological influence of spruce planted on former beech forest soils in Scania, South Sweden. *Oikos*, 22, 302-314.
- Nye, P.H. & Tinker, P.B. (1977). Solute movement in the soil-root system. Blackwell, Oxford.
- Nykvist, N. (1963). Leaching and decomposition of water-soluble organic substances from different types of leaf and needle litter. *Studia Forestalia Suecica*, 3, 1-31.
- Odin, M. (1974). Some meteorological effects of clearfelling. *Sveriges Skogsvårdsförbunds Tidskrift*, 1, 60-65.
- Olson, J.S. (1963). Energy storage and the balance of producers and decomposers in ecological systems. *Ecology*, 44, 322-331.
- Ovington, J.D. (1953). Studies of the development of woodland conditions under different trees. I. Soil pH. *Journal of Ecology*, 41, 31-34.
- Ovington, J.D. (1954). Studies of the development of woodland conditions under different trees. II. The forest floor.

- Journal of Ecology, 42, 71-80.
- Ovington, J.D. (1959). The circulation of minerals in plantations of Pinus sylvestris L. Annals of Botany, 23, 229-239.
- Page, G. (1968). The effects of conifer crops on soil properties. Commonwealth Forestry Review, 47, 52-62.
- Page, G. (1974). The effect of forest cover on the properties of some Newfoundland forest soils. Canadian Forest Service Publication #1332.
- Patrick, W.H. (1978). Measurement and predication of anaerobiosis in soils. "Nitrogen in the environment. I. Nitrogen behaviour in field soil." Academic Press, London.
- Pienc, H. & Van Cleve, K. (1978). Weight loss of litter and cellulose bags in a thinned white spruce forest in interior Alaska. Canadian Journal of Forest Research, 8, 42-46.
- Pierce, R.S., Martin, C.W., Reeves, C.C., Likens, G.E. & Bormann, F.H. (1972). Nutrient loss from clearcuttings in New Hampshire. Proceedings of the symposium on watersheds in transition. American Water Resources Association, Urbana. pp.285-295.
- Popovic, B. (1974). The effect of clearfelling on soil nitrogen transformation. Sveriges Skogsvarvsforbunds Tidskrift, 1, 80-85.
- Pyatt, G. (1973). Physical and mechanical properties of soil types. Report on Forest Research, London. 1973. pp.62-66.
- Read, D.J., Armstrong, W. & Weatherall, J. (1973). The effects of cultivation treatment on water potential and soil aeration in wet heathland with special reference to afforestation. Journal of Applied Ecology, 10, 479-487.
- Salter, P.J., Berry, G. & Williams, J.B. (1966). The influence of texture on the moisture characteristics of soils. III. Quantitative relationships between particle size, composition and available water capacity. Journal of Soil Science, 17, 93-98.
- Satchell, J.E. & Lowe, D.G. (1967). Selection of leaf litter by Lumbricus terrestris. "Progress in soil biology." (Ed. by O. Graff and J.E. Satchell), pp.102-118. North Holland Publishing Co., Amsterdam.
- Scheffer, T.C. & Cowling, E.B. (1966). Natural resistance of wood to microbial deterioration. Annual Review of Phytopathology, 4, 147-170.
- Sinha, M.K. (1972). Organic matter transformation in soils. I. Humification of C¹⁴-tagged oat roots. Plant and Soil, 36, 283-293.
- Smith, J.H. (1966). The use of isotopes in soil organic matter studies. Pergamon Press, Oxford. pp.223-224.
- Smith, W.H. (1969). Release of organic materials from the roots of tree seedlings. Forest Science, 15, 138-143.

- Smith, W.H. (1970). Root exudates of seedling and mature sugar maple. *Phytopathology*, 60, 701-703.
- Snyder, G.G., Haupt, H.F. & Belt, G.H. (1975). Clearcutting and burning slash alter quality of stream water in northern Idaho. U.S. Department of Agriculture Forest Service Research Paper INT-168. Intermountain Forest Range Experimental Station.
- Stone, E.L. (1975). Effects of species on nutrient cycles and soil change. *Philosophical Transactions of the Royal Society, London B*, 271, 149-162.
- Stout, J.D. (1964). Protozoa. "Biology of plant litter decomposition". (Ed. by C.H. Dickinson and G.J.F. Pugh), pp.385-420. Academic Press, London.
- Swift, M.J. (1977). The roles of fungi and animals in the immobilization and release of nutrient elements from decomposing branchwood. "Soil organisms as components of ecosystems." (Ed. by U.Lohm and T.Persson), pp.193-202. *Ecological Bulletin, Swedish Natural Science Research Council*, 25.
- Swift, M.J., Heal, O.W. & Anderson, J.M. (in press). Decomposition in terrestrial ecosystems. Blackwell, Oxford.
- Swift, M.J., Healey, I.N., Hibberd, J.K., Sykes, J.M., Bampeo, V. & Nesbitt, M.E. (1976). The decomposition of branchwood in the canopy and floor of a mixed deciduous woodland. *Oecologia*, 26, 139-149.
- Tamm, C.O., Holmen, H., Popovic, B. & Wiklander, G. (1974). Leaching of plant nutrients from soils as a consequence of forestry operations. *Ambio*, 3, 211-221.
- Tanji, K.K. & Gupta, S.K. (1978). Computer simulation modelling for nitrogen in irrigated croplands. "Nitrogen in the environment. I. Nitrogen behaviour in field soils." (Ed. by D.R. Nielsen and J.G. MacDonald), pp.79-130. Academic Press, New York.
- Tappeiner, J.C. & Alm, A.A. (1975). Undergrowth vegetation effects on the nutrient content of litterfall and soils in red pine and birch stands in northern Minnesota. *Ecology*, 56, 1193-1200.
- Toth, J.A., Papp, L.B. & Lenkey, B. (1975). Litter decomposition in an oak forest ecosystem (*Quercetum petraeae cerris*) of northern Hungary studied in the framework of the 'Sikfokut project'. "Biodégradation et Humification." (Ed. by G.Kilbertus, O.Reisinger, A.Mourey and J.A.Cancela Da Fonseca), pp.41-58. Université de Nancy.
- Turner, J. (1975). Nutrient cycling in a Douglas fir ecosystem with respect to age and nutrient status. *Forestry Abstracts*, 37, 6003.
- Van Cleve, K. (1974). Organic matter quality in relation to decomposition. "Soil organisms and decomposition in tundra." (Ed. by A.J.Holding, O.W.Heal, S.F.MacLean and

- P.W.Flanagan), pp.311-324. Tundra Biome Steering Committee, Stockholm.
- Van Cleve, K. & Sprague, O. (1971). Respiration rates in the forest floor of birch and aspen stands in interior Alaska. *Arctic and Alpine Research*, 3, 17-26.
- Verry, E.S. (1972). Effect of an aspen clearcutting on water yield and quality in northern Minnesota. Proceedings Symposium on Watersheds in Transition, Fort Collins. American Water Resources Association, Urbana.
- Voigt, G.K. (1965). Nitrogen recovery from decomposing tree leaf tissue and forest humus. Soil Science Society of America Proceedings, 29, 756-759.
- Waid, J.S. (1974). Decomposition of roots. "Biology of plant litter decomposition." (Ed. by C.H.Dickinson and G.J.F.Pugh), pp.175-211. Academic Press, London.
- Wiklander, G. (1974). Effect of clearfelling on the content of nutrients in surface and ground water. *Sveriges Skogsvarvsforbunds Tidskrift*, 1, 86-90.
- Wilde, S.A. (1964). Changes in soil productivity induced by pine plantations. *Soil Science*, 97, 276-278.
- Will, G.M. (1964). Dry matter production and nutrient uptake by Pinus radiata in New Zealand. *Commonwealth Forestry Review*, 43, 57-70.
- Will, G.M. (1967). Decomposition of Pinus radiata litter on the forest floor. I. Changes in dry matter and nutrient content. *New Zealand Journal of Forestry Science*, 10, 1030-1044.
- Williams, B.L., Cooper, J.M. & Pyatt, D.G. (1978). Effects of afforestation with Pinus contorta on nutrient content, acidity and exchangeable cations in peat. *Forestry*, 51, 29-35.
- Williams, S.T. & Gray, T.R.G. (1974). Decomposition of litter on the soil surface. "Biology of plant litter decomposition." (Ed. by C.H.Dickinson and G.J.F.Pugh), pp.611-632. Academic Press, London.
- Witkamp, M. (1966). Decomposition of leaf litter in relation to environment, microflora and microbial respiration. *Ecology*, 47, 194-201.
- Witkamp, M. (1969). Environmental effects on microbial turnover of some mineral elements. I. Abiotic factors. *Soil Biology and Biochemistry*, 1, 167-176.
- Witkamp, M. & Ausmus, B.S. (1976). Processes in decomposition and nutrient transfer in forest systems. "The role of terrestrial and aquatic organisms in decomposition processes." (Ed. by J.M.Anderson and A.Macfadyen), pp.375-396. Blackwell, Oxford.
- Witkamp, M. & Drift, J.van der (1961). Breakdown of forest litter in relation to environmental factors. *Plant and Soil*, 15, 295-311.
- Wollum, A.G. & Davey, C.B. (1975). Nitrogen accumulation,

transformation and transport in forest soils. "Forest soils and land management." (Ed. by B. Bernier and C.H. Winget), pp.67-106. Université de Laval Press, Quebec.

Wood, T.G. (1974). Field investigations on the decomposition of leaves of Eucalyptus delegatensis in relation to environmental factors. Pedobiologia, 14, 343-371.



BIOLOGICAL MEANS OF IMPROVING NUTRIENT UPTAKE IN TREES

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SUMMARY

Nitrogen-fixing micro-organisms and mycorrhizal fungi play important roles in nutrient relationships in present-day natural forest stands and undoubtedly they will play significant roles in even-aged plantations in the future. Nodulated non-legumes, shrubs, also can be important on forestry sites, which frequently have soil conditions not suitable for long-term development of herbaceous legumes. Free-living, nitrogen-fixing organisms require abundant organic substrate and good soil moisture conditions, and nitrogen from them only becomes available after the organisms decay. These organisms exhibit a preference for mineralized nitrogen over atmospheric nitrogen, factors which limit their importance in agricultural soils but should not be a drawback in forest soils. Both groups of organisms working together may provide significant amounts of nitrogen for tree growth and stand development.

The importance of mycorrhizae as absorbing structures may not yet be fully appreciated, but they are indispensable to many forest trees for P uptake. The availability of this element is normally too low in forest soils to support growth of trees lacking mycorrhizae. The methodology, however, for studying the mycorrhizal contribution in biological nutrient uptake in the forest ecosystem has not been perfected. Because of the complex relationship among tree mixtures, fungal symbionts, and soil types, the techniques will be difficult to develop. Evidence on the importance of

mycorrhizae in nutrient absorption by many agronomic plants is overwhelming and this uptake function by mycorrhizae on trees in forests will probably prove to be even more important than on plants growing in heavily fertilized agronomic soils. Forest soils that contain sufficient available P to permit suitable growth of trees lacking mycorrhizae are rare.

The greatest immediate impact of mycorrhizal technology will be in nursery seedling production, plantation establishment and tree improvement programs, all three of these areas are closely integrated. There is mounting evidence that planted seedlings with heavily mycorrhizal root systems survive and grow significantly better than seedlings with few or no mycorrhizae.

RÉSUMÉ

Les microorganismes qui fixent l'azote et les mycorrhizes jouent un rôle important dans les cycles d'éléments nutritifs des forêts naturelles actuelles et continueront sans doute ce rôle dans les forêts équiennes de l'avenir. Les non-légumineuses à nodule sont des arbustes. Elles peuvent être importantes dans les stations forestières qui ont souvent des sols mal adaptés au développement à long terme des légumineuses herbacées. Les organismes libres et fixateurs d'azote demandent des sous-sols organiques riches et des conditions d'humidité favorables. L'azote qu'ils libèrent n'est disponible que lorsque ces organismes se décomposent. Ces organismes préfèrent l'azote minéralisé à celui de l'atmosphère, ce qui limite leur importance dans les sols agricoles mais ne devrait pas être un inconvénient dans les sols forestiers. Ces deux groupes d'organismes devraient pouvoir travailler de concert pour produire la quantité appréciable d'azote utile à la croissance de l'arbre et au développement du peuplement.

Il se peut que nous ne comprenions pas bien l'importance des mycorrhizes en tant que structures absorbantes, mais nous savons qu'elles sont indispensables à l'apport de P dans beaucoup d'arbres forestiers. Le taux de P disponible est normalement trop bas dans les sols forestiers pour aider à la croissance

d'arbres manquant de mycorrhizes. Cependant, les méthodes qui étudient la contribution des mycorrhizes dans le cycle des éléments nutritifs de l'écosystème - forêt ne sont pas très perfectionnées. Les techniques seront difficiles à développer à cause des relations complexes entre mélanges d'arbres, symbiotes et types de sols. Nous savons l'importance des mycorrhizes dans l'absorption d'éléments nutritifs de nombreuses plantes agronomiques et le rôle des mycorrhizes dans l'arbre forestier s'avérera encore plus important que chez les plantes poussant dans des sols agricoles très riches en engrais. Les sols forestiers qui comportent suffisamment de P disponible pour permettre une croissance favorable des arbres et qui manquent de mycorrhizes sont rares. Là où la technologie liée aux mycorrhizes aura la plus grande influence sera dans les pépinières, la création de plantations et les programmes d'amélioration des arbres - ces trois champs d'utilisation étant étroitement liés. Il devient de plus en plus évident et significatif que les plantes ayant des racines comprenant des mycorrhizes survivent et poussent plus favorablement que ceux qui n'ont peu ou pas de mycorrhizes.

ZUSAMMENFASSUNG

Stickstoffbindende Mikroorganismen und Mykorrhizen spielen eine bedeutende Rolle in bezug auf die Nährstoffbeziehungen heutiger Naturwaldbestände und werden zweifelsohne auch in zukünftigen gleichaltrigen Pflanzungen von Bedeutung sein.

Nichtleguminosen mit Knöllchenbakterien sind Sträucher. Sie können auf Waldstandorten wichtig sein, wo die Bodenbedingungen oft nicht für eine langzeitliche Entwicklung krautiger Leguminosen geeignet sind.

Freilebende stickstoffbindende Organismen benötigen Substrate mit hohem organischen Anteil und gute Bodenfeuchtigkeitsbedingungen. Erst bei der Zersetzung der Organismen wird ihr Stickstoff frei. Diese Organismen bevorzugen Mineralstickstoff gegenüber Luftstickstoff, was ihre Bedeutung für landwirtschaftliche Böden einschränkt, aber für Waldboden kein Nachteil sein sollte.

Wenn beide Organismengruppen zusammenarbeiten,

können sie bedeutende Stickstoffmengen für das Wachstum der Bäume und die Entwicklung des Bestandes anliefern.

Die Bedeutung von Mykorrhizen für die Nährstoffaufnahme wird vielleicht noch nicht genügend geschätzt, aber ohne sie wäre eine Phosphoraufnahme bei vielen Waldbäumen unmöglich. Die Verfügbarkeit dieses Elements ist im Waldboden normalerweise zu niedrig für ausreichendes Wachstum von Bäumen ohne Mykorrhizen. Eine Methodik, mit der man der Beitrag der Mykorrhizen zur biologischen Nährstoffaufnahme in Waldökosystemen bestimmen könnte, steht noch nicht zur Verfügung. Wegen der komplexen Beziehung zwischen verschiedenen Bäumen, Pilzsymbionten und Bodentypen wird es schwierig sein, entsprechende Verfahren zu entwickeln.

Es gibt überwältigendes Beweismaterial für die Wichtigkeit von Mykorrhizen bei der Nährstoffaufnahme vieler landwirtschaftlicher Nutzpflanzen, und diese Aufnahmefunktion wird sich wahrscheinlich für Waldbäume als noch viel wichtiger erweisen als für Pflanzen in stark gedüngten landwirtschaftlichen Böden. Waldböden, die genügend verfügbaren Phosphor für ein normales Wachstum von Bäumen ohne Mykorrhizen aufweisen, sind selten.

Die grössten unmittelbaren Effekte wird die Mykorrhiza haben in der Sämlingsproduktion im Pflanzgarten, bei der Begründung der Pflanzungen und bei der Zuwachssteigerung von Beständen, wobei diese drei Gebiete alle eng miteinander verbunden sind. Es gibt umfangreiche Hinweise dafür, dass ausgepflanzte Sämlinge mit starkem Mykorrhizabesatz weitaus besser überleben und wachsen als Sämlinge mit wenig oder ohne Mykorrhizen.

INTRODUCTION

The most important organisms for biologically improving nutrient relationships in plant communities are the nitrogen-fixing organisms and the mycorrhizal fungi. There is universal agreement on the importance of nitrogen fixers in the nutritional balance of plants, regardless of site. Nitrogen fixation is seen as the key to increasing the productivity of the biosphere. The absorption capacity of mycorrhizae, with many plants, surely must be ranked second in biological importance. However, universal agreement is lacking on the importance of mycorrhizal fungi because many scientists

view them as extraneous organisms whose importance to trees is limited to soils low in available nutrients.

Great emphasis has been placed on increasing agricultural productivity to sustain the world's increasing population. In comparison, little has been done to increase productivity on forested lands. Increased agricultural productivity can be attributed to greater mechanization and the development of superior hybrids and varieties coupled with increased use of fertilization and inoculation with nitrogen-fixing bacteria. Most of the world's important food and grain crops are hosts for mycorrhizal fungi and significantly benefit from mycorrhizae in terms of both nutrient and water uptake (Nicolson 1967; Gerdemann 1968; Smith 1974; Safir, Bayer & Gerdeman 1971, 1972). Unfortunately, breeding programs seem to select against this important mycorrhizal symbiotic relationship that has been with plants since they evolved from their water habitat (Pirozynski & Malloch 1975). Before a specific hybrid or variety is released, it is normally tested under quite favourable water and fertility regimes for plant development but are artificial environmental conditions not conducive to optimum mycorrhizal development?

Throughout the world, foresters are gathering superior trees to be included in seed orchards and, in many cases, they have seed orchards well established. From these orchards will come seed for the plantations of the future. I think we should include in our selection criteria tests to identify those mother trees whose progeny derive the greatest benefit from the mycorrhizal symbiosis and, thus, have an added advantage in biological nutrient uptake.

NITROGEN-FIXING ORGANISMS

It has been estimated that almost 100 million tons (about 10 kg/ha/yr) of nitrogen are fixed annually by natural processes worldwide in comparison to 25 million tons fixed by industrial methods (Noggle & Fritz 1976) and it is agreed that industrial production could never sustain the world's requirements to maintain present levels of plant production.

Rhizobium symbiosis with herbaceous legumes is of primary importance to agriculture. However, it is responsible for only about 0.5 kg/ha/yr of the nitrogen fixed at the earth's surface. Lichens and free-living heterotrophic bacteria account for about 3.5 kg/ha/yr. The rest of the total is about equally divided between blue-green algae and nodulated non-legumes and woody legumes (Richards 1974).

At present it seems likely that nitrogen fixation via Rhizobium will play only a minor role in forest plantation nutrition although it may be important on some of the more fertile forested sites where legumes could be planted between the rows in young plantations to help control weeds and at the same time contribute significant amounts of nitrogen for

several years. Haines, Haines and White (1978) reported encouraging results in a young sycamore (Pseudoplatanus occidentalis) plantation in northern Alabama. After four years with a clover cover crop, Trifolium spp, the volume of a six-year old plantation was 52/cu.m./ha, without clover it was 14/cu.m./ha. It may also be feasible to introduce woody legumes into plantations to enhance nitrogen fixation. This approach may gain in importance if management is directed more towards total fibre yield rather than fibre yield for specific products such as paper.

Nodulated non-legumes (acinomycete symbiosis) have been reported in at least thirteen plant genera (Richards 1974) and may prove to be more significant than Rhizobium in plantations and forests of the future. These genera have a worldwide distribution and are represented by at least 300 species, about 100 of which have been examined and found to develop nodules. Most of these nodulated plants are trees and shrubs which often grow on the relatively infertile sites usually available to forestry and their contribution to nitrogen fixation can be significant. For instance, in acid peat bogs Gale palustris fixes about 9 kg/ha/yr, but in artificial culture may greatly surpass the fixation by either red clover or other legumes. Alnus crispa has been shown to fix between 62 and 164 kg N/ha/yr. In Africa, Casuarina equisetifolia has been reported to fix up to 58 kg N/ha/yr (Richards 1974).

Many nodulated non-legumes are woody shrubs that probably only compete with trees in young plantations. However, research is needed to determine if there are any biological advantages in encouraging their growth in the understory of plantations to take advantage of their ability to fix atmospheric nitrogen.

Nitrogen fixing nodules can fix 100 to 200 times more nitrogen than the free-living micro-organisms per unit of cell material. Asymbiotic organisms are limited in agricultural soils because they require an abundant supply of organic substrate and a good moisture supply. They also have a high affinity for mineralized nitrogen, such as ammonium, which they utilize in preference to molecular nitrogen (Noggle & Fritz 1976). In agricultural soils these requirements may limit their importance, but in forest soils they may not be critical. Jorgensen (1975) reported favourable fixation rates in coastal plain soils in South Carolina in conjunction with controlled burning experiments. From samples collected in June, before burning, he reported fixation rates of approximately 3 kg/ha/yr in mineral upland soils and 30 kg/ha/yr in swamp soils. Little if any of this activity could be attributed to blue-green algae. Jorgensen also reported that there is still no realistic assessment of the importance of anaerobic N_2 fixation in practical forestry. Switzer & Nelson (1972) found that during the first twenty years of a

Pinus taeda plantation total nitrogen on site increased from 75 kg/ha before planting to 298 kg/ha at age 20. The N_2 fixation rates reported by Jorgensen (1975) could easily be sufficient to meet the stand's need, and even lower fixation rates would be of considerable significance in the nitrogen cycle.

Non-symbiotic fixation by blue-green algae may be significant in the world nitrogen balance but may only be significant in forest plantations under specific conditions. It is generally assumed that a combination of low light intensity, less than optimum soil moisture and temperature, and low pH in forest soils minimize the significance of these organisms in nitrogen fixation (Jurgensen & Davey 1968). These authors, working with acid forest soils in both the Appalachian Mountains and the Atlantic Coastal Plain, reported a general absence of nitrogen-fixing algae. However, on wetter sites or desert areas where the pH is higher than six, blue-green algae may assume considerable local biological importance.

In North Carolina, Meyer (1977) studied nitrogen fixation on leaves and bark of a mature oak-hickory (Quercus-Carya) forest and on the needles of a Pinus strobus stand. In the oak-hickory, fixation by bark and stem lichens was 1.9 kg N/ha/yr while the phyllosphere fixed 0.16 kg N/ha/yr and these above-ground epiphytes contributed approximately 16 per cent of the annual nitrogen fixation in this forest. It was calculated that the white pine epiphytes fixed 0.92 kg N/ha/yr.

Lichens may play a role in biological nitrogen nutrition in plantations in tropical and subtropical forests where they are particularly abundant in those environments. For example, Harrelson (1969) reported nitrogen fixation rates by lichens in a Puerto Rican forest of 25 to 75 kg/ha/yr, and Forman (1975) reported 1 to 8 kg/ha/yr in a Colombian rain forest. Further research is required to assess the contribution of lichens to the total nitrogen in the soil, both in tropical and subtropical forests as well as in other climatic zones.

MYCORRHIZAE

Most higher plants in nature develop mycorrhizae to varying degrees (Fig. 1). Wilhelm (1966) states that under field conditions plants do not, strictly speaking, have roots, they have mycorrhizae. Although much of the original basic mycorrhizal research has been done with agronomic plants, a significant portion of the recent awareness of the practical importance of mycorrhizae to plant growth and productivity can be traced to the application of the mycorrhizal technology in forestry (Marks & Kozlowski 1973; Kormanik, Bryan & Schultz 1977a, b; Marx 1975, 1977). Many professional foresters and scientists do not grasp the importance of this symbiotic

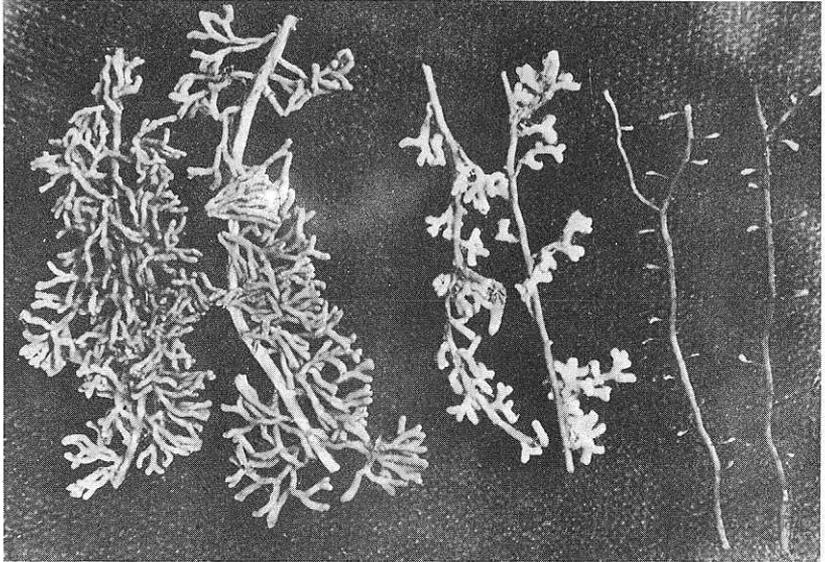


Fig. 1. Infection of a seedling pine root system by Pisolithus tinctorius (left), Thelephora terrestris (centre) and no mycorrhizal fungus (right).

relationship to trees. It is really not a question of how much better would the trees in the forest grow with mycorrhizae, but rather, would the forest exist at all without the mycorrhizae. Forest managers must become as aware of the importance of mycorrhizal symbiotic relationships as they are of photosynthesis. Photosynthesis may convert solar energy into chemical energy, but even the most photosynthetically efficient tree would not be self-supporting in a natural environment without the contribution of mycorrhizae.

In forestry, the two major types of mycorrhizae are ectomycorrhizae and endomycorrhizae. A third type, ectendomycorrhizae, is less frequently encountered, more poorly understood, and is currently considered of less ecological importance than the other two. Several general articles provide an understanding of these organisms (Nicolson 1967; Smith 1974; Marx 1975).

Ectomyorrhizae

The major distinguishing feature of ectomycorrhizae is the intercellular development of hyphae in the cortex resulting in the Hartig-net. Externally, ectomycorrhizae may appear as simple unforked roots, bifurcate roots, multi-forked (coralloid) roots, or even nodular-like roots that are readily visible to the naked eye. Most fungi that form ectomycorrhizae with forest trees are Basidiomycetes, which produce mushrooms or puffballs as reproductive structures. Certain of the Ascomycetes, such as truffles, are also

symbiotic. The fruiting bodies of these fungi produce millions of spores which are readily and widely disseminated by wind and water.

Ectomycorrhizae occur naturally on many of the important forest tree species of the world. All members of the gymnosperm family Pinaceae, i.e. Pinus (pine), Picea (spruce), Abies (fir), Larix (larch), Tsuga (hemlock), and Pseudotsuga (Douglas-fir), as well as certain angiosperms, such as Salix (willow), Populus (aspen), Carya (hickory and pecan), Quercus (oak), and Fagus (beech), are ectomycorrhizal.

Endomycorrhizae

One major subtype of endomycorrhizae is commonly referred to as the vesicular-arbuscular or VA mycorrhizae. The vesicles and arbuscules are quite distinctive in the cortical zone of roots. Arbuscules consist of dense clusters of very fine dichotomously branched filaments which may occupy the entire lumen of a cortical cell. Vesicles develop later and appear as terminal swellings either within or between cells. No characteristic external changes in morphology occur in roots infected with endomycorrhizal fungi.

The fungi which form endomycorrhizae are mainly Phycmycetes which do not produce large, above-ground fruiting bodies or wind-disseminated spores. They are spread in the soil by root contact, moving water and animals. The spores are able to survive for many years in the soil when a suitable host is not present.

Many of the important angiosperm forest trees in the United States, such as Liquidambar (sweetgum), Platanus (sycamore), Ulmus (elm), Juglans (walnut), Fraxinus (ash), Liriodendron (poplar), Acer (maple), and perhaps Alnus (alder) normally form endomycorrhizae.

Ectendomycorrhizae

This type of mycorrhizae has the features of both ecto- and endomycorrhizae. Ectendomycorrhizae have a limited occurrence and are found primarily on roots of forest trees that are normally ectomycorrhizal. Since little research has been done on these fungi, very little is known about the species of fungi involved or their importance to growth of trees.

Influence of mycorrhizae on plant nutrition

The role of mycorrhizae in plant development which has received the greatest attention is that relating to mineral nutrition, particularly phosphorus uptake. This interest in phosphates is justified both from the viewpoint of the fungi and the plants. High levels of soluble phosphates in the soil seemingly depress mycorrhizal development, and low levels adversely affect plant growth. When referring to 'high' or 'low' levels of soil phosphate we must begin to specify for what plant. Readily available soil P of 100 ppm may significantly reduce or almost eliminate endomycorrhizae synthesis on one plant species but another species may be readily infected by the same symbiont at 200 ppm or higher.

However, it is unlikely that soluble phosphorus concentrations in any natural forest soils would ever be large enough to interfere with mycorrhizal synthesis of forest trees and thereby deter plantation establishment.

Greater soil exploitation by mycorrhizal roots as a means of increasing phosphate uptake is well established for both ecto- and endomycorrhizae. Current estimates place the normal phosphate depletion zone around non-mycorrhizal roots at between 1 and 2 mm. Working with plants grown in containers, Pearson & Tinker (1975) and Rhodes & Gerdemann (1975) demonstrated that an endomycorrhizal root symbiont increased this zone to 7-20 mm.

The main question is not whether mycorrhizae are involved and effective in phosphorus uptake, but whether this efficiency is due to exploitation of soil phosphates unavailable to non-mycorrhizal roots or simply greater efficiency in capturing the available soluble phosphates. There is still no clear-cut answer to this question. Several investigators (Hayman & Mosse 1972; Sanders & Tinker 1971) report no difference in capacity to solubilize phosphate. Contrary to speculation (Noggle & Fritz 1976), these fungi have not been reported to digest plant litter in significant amounts and so feed back minerals to their hosts.

Results from studies on increased uptake of the other major and minor elements by mycorrhizal plants have been even more variable than those concerning phosphates. Sometimes the elements N, K, Ca, Mg, Fe, Cu, Mn, Na, Si, Zn, Al and B are present in greater concentrations in mycorrhizal plants than in non-mycorrhizal plants. In other cases, the concentrations of these same elements are higher in non-mycorrhizal plants, and sometimes no significant difference in concentrations between the two groups of plants is observed. The differential uptake of these elements, however, is not normally reflected in plant growth (Gray & Gerdemann 1973). Characteristically, if mycorrhizal infection causes striking growth increases, the total amounts of all elements will be greater in the mycorrhizal plants, and the elements whose concentrations are affected most by mycorrhizal infection are very likely to be those limiting growth (Kleinschmidt & Gerdemann 1972).

Methodology must be developed for systematic study of mycorrhizae in older stands and plantations before quantitative data on nutrient cycling can be obtained; this will be extremely difficult, and such an effort has not yet been started. At present we must assume that nutrient and even water uptake of forest trees is at least enhanced by mycorrhizae.

It is in the nursery phase and early plantation establishment where the greatest practical application of mycorrhizal technology may occur. In fact, the only quantitative data we have with forest trees involves nursery

studies and outplanting trials that are less than five years old.

Such nursery work must be complemented by carefully designed outplanting experiments on specific sites if in the future we hope to be able to write regeneration prescriptions instead of just compiling case histories. Much of the initial work at the U.S. Forest Service Institute for Mycorrhizal Research and Development, Athens, Georgia, indicated an advantage from inoculating seedlings with a specific symbiont in the nursery for planting on adverse sites such as mining spoils and borrow pits. We thought at first that our results would be applied only on such sites. With considerable justification, we have gradually altered our thinking on this matter. Any area harvested by clearcutting is at least temporarily adverse for seedling growth. This adversity can be measured in terms of high temperature, altered moisture regimes, excessive competition, etc. A seedling should be developed in the nursery that is very competitive during the critical early years of stand establishment. We feel that a heavily infected mycorrhizal root system provides that competitive edge.

Nursery application

Periodic soil fumigation is desirable, if not essential, in a forest tree nursery. Effective fumigation eliminates destructive root pathogens and competing weeds, but it also eliminates mycorrhizal inoculum. The loss of ectomycorrhizal inoculum can be rectified early in the growing season if sufficient wind-disseminated spores are naturally available. Sufficient spores are usually available in the southeastern United States, but may not be in other parts of the world. To hasten this seedbed inoculation or to reinfest beds with specific ectomycorrhizal fungi, either spores or vegetative inoculum can be incorporated into the nursery beds. Both techniques have been used successfully (Theodorou 1967; Marx & Bryan 1970; Marx 1977).

Nursery beds are reinfected more slowly by endomycorrhizal fungi since the spores are not wind-disseminated nor can vegetative inoculum be produced in aseptic culture. The seedling roots must penetrate below the zone of effective fumigation where they come in contact with spores or infected root fragments. This is a slow process and too frequently results in inferior seedling production during the year of fumigation. Cover crops can be grown during the season of fumigation to build up endomycorrhizal inoculum but selected herbicides that will not destroy the inoculum in subsequent years must be used in place of annual fumigation. This cover crop rotation is being explored at the Mycorrhizal Institute in Athens, Georgia.

Seedling quality can be significantly improved by assuring early season development of mycorrhizae. It has been

repeatedly demonstrated that specific combinations of host and ectomycorrhizal fungus can result in seedlings with significantly improved growth and survival not only on adverse mining spoils, but also on the more typical forested sites (Marx 1977). In one nursery in North Carolina, Marx, Bryan & Cordell (1976) obtained growth increases of 100 to 150 per cent after one growing season with seedlings of Pinus taeda, P. strobus, and P. virginiana following soil infestation and ectomycorrhizal development by Pisolithus tinctorius. In another test Marx & Artman (1978), introduced vegetative mycelial inocula of P. tinctorius and Thelephora terrestris into fumigated soils in two nurseries in two different physiographic regions in Virginia. After one growing season, Pinus taeda seedlings with Pisolithus and Thelephora ectomycorrhizae had 57 and 31 per cent greater fresh weights in the coastal plain nursery and 40 and 20 per cent greater weights in the mountain nursery, respectively, than control seedlings. Soil inoculation with either fungus in both nurseries increased ectomycorrhizal development approximately 50 per cent over control seedlings.

Nursery inoculations with ectomycorrhizal symbionts has been tested extensively and the use of specific root symbionts for specific problem sites, as well as for routine reforestation, seems quite practical. Practical application of ectomycorrhizal fungi to nursery management is well advanced and should be put into practice as soon as the reliability of commercial inoculum is substantiated. Over 75,000 seedlings have been planted out at the Mycorrhizal Institute since 1974, and results encourage such practices for a wide range of sites (Marx 1977).

For example, on strip-mined lands trees frequently do poorly because the soil pH is usually low and soil temperatures high. However, use of Pisolithus tinctorius as the primary root symbiont instead of the naturally occurring Thelephora terrestris has been successful on several such sites with pH's ranging from 3.4 to 3.9.

In one test on a coal spoil (pH 3.8) Pinus virginiana seedlings were first grown with either Pisolithus tinctorius or Thelephora terrestris ectomycorrhizae in our experimental nursery in Athens, Georgia. (Marx & Bryan 1975). After two years only one percent on the Thelephora seedlings survived against 49 per cent of the Pisolithus seedlings, which also showed greater growth (Table 1).

There are numerous other examples of species of ectomycorrhizal fungi which have been shown to be quite beneficial under specific site or environmental conditions (Marx 1978).

As a silviculturist, I believe that nursery management practices that favour optimum root colonization by ectomycorrhizal fungi are a prerequisite to successful

Table 1. Survival and growth of mycorrhizal *Pinus virginiana* seedlings after two years on coal spoil in the Southeastern United States.

Mycorrhizal condition at planting	Percent survival	Height (cm)	Stem diameter (cm)	Seedling volume (cu.cm)**
Pisolithus	49*	49*	1.6*	130*
Thelephora	1	19	0.4	3

* Denotes significant differences ($P=0.05$) between means for mycorrhizal treatments.

** Seedling volume (cu.cm) = (stem diameter) x height.

plantation establishment. In my opinion, and one that is shared by many foresters, careless planting and inferior root systems of pine seedlings are the leading causes of early plantation failure or poor development. Excessive nursery fertilization resulting in large top : root ratios and poorly developed ectomycorrhizal root systems should be discouraged. To-date the world fibre industry has been geared for softwood utilization, and until recently few hardwood plantations of endomycorrhizal host species were being established in the United States or other countries. Planting patterns have changed dramatically in the United States in the past decade because of technological changes in milling. Large acreages of hardwood plantations are being established, and many of these hardwoods are endomycorrhizal host species. This trend of increasing hardwood utilization will probably be accelerated as other industrial uses of wood fibre compete with the paper industries.

In the past, hardwood plantations of species that are endomycorrhizal hosts have often been unsuccessful. Quality planting stock has been difficult to obtain, and poor stock probably was the cause of poor, early (during the first 3-5 years) growth of many plantations. Essential nursery soil fumigation probably played a major role in this because of the long delay before endomycorrhizal inocula returns to fumigated soil. After effective fumigation the newly developed seedling root of an endomycorrhizal species must grow through 15 to 20cm of soil before coming into contact with viable inoculum, either infected root fragments or spores. Spore density at these depths is probably much less than it would be higher in the profile in the major root zone. It is our experience that until infection occurs, the roots of most endomycorrhizal tree hosts grow very poorly at the low

phosphorus levels which do not have an adverse effect on the symbiont. Thus, the seedling may appear chlorotic and stunted and remain a few centimeters tall until late in the summer when mycorrhizae form. By this time, 50 to 80 per cent of the effective growing season has passed, and the resulting seedlings are substandard for planting out the following year as is the usual practice.

Much of our endomycorrhizal research in Athens has been with Liquidambar styraciflua, but we have also run fertilizer/mycorrhizal interaction tests with Prunus serotina, Acer rubrum, Acer saccharum, Acer negundo, Juglans nigra, Fraxinus pennsylvanica, and Platanus occidentalis. Most of our experimentally grown seedlings have been destructively sampled, and only two rather small outplanting trials have been installed. We have fertilized all species with rates of from 140 kg/ha to 1120 kg/ha of a commercial 10-10-10 fertilizer (10 per cent each for total N, available P_2O_5 and water soluble K_2O) plus top dressing during the growing season of 1680 kg/ha of NH_4NO_3 (Bryan & Kormanik 1977; Kormanik et al 1977 a,b,c). At the highest fertilizer rate the soils have approximately 50 to 60 ppm of available P, amounts six to ten times higher than normally occur in our forest soils of the southeastern United States. The seedlings normally grow from sixteen to eighteen weeks before harvest.

Under these conditions non-mycorrhizal sweetgum seedlings had an average height of 50 mm, against 340 to 400 mm for mycorrhizal seedlings, and this regardless of fertilizer applied. The mycorrhizal seedlings have been rather consistently seventy to eighty times heavier in total biomass than the non-mycorrhizal ones. Mycorrhizal seedlings of the other seven test species have been thirty to sixty times heavier than their non-mycorrhizal counterparts, and height differences are comparable to those with Liquidambar styraciflua. Analyses of the responses of the seven species have not been completed.

Thus far we have not picked up fertilizer effect in any of our experiments, but we have detected in each significant mother tree responses. The progeny from all mother trees we have tested consistently fail to develop when available soil P in sterile soils is less than 60 ppm, yet all develop well with adequate soil infestation at these levels. However, in all of our experiments thus far analyzed, we have measured significant family responses in seedling biomass. Thus, while the great majority of all seedlings from all mother trees are reaching plantable size even in our shorter growing season, the progeny from specific mother trees produce a greater percentage of seedlings in the larger sizes. With Liquidambar styraciflua, as well as with most other hardwoods, seedling size has been positively correlated with field performance. We feel that standard tests could be developed to select superior

trees on the basis of progeny performance in nursery beds if the level of P was <15 ppm, a typical amount found under field conditions.

No direct assessments have been reported of the relative growth of outplanted endomycorrhizal and non-mycorrhizal seedlings. However, we observed dramatic differences in the degree of root infection in Liquidambar styraciflua depending on the level of available P in the nursery bed. With available P <60ppm, 75 per cent or more of L. styraciflua seedling roots become infected, but at >60 ppm infection rate drops rapidly to an average of 15 per cent or less. Many forest tree nurseries have available P levels of >120 ppm and this may result in the production of acceptable Liquidambar styraciflua seedling production without mycorrhizae. This may be one reason for the poor early development of this species in plantations.

As with ectomycorrhizae, the greatest immediate benefit from endomycorrhizae in even-aged plantation management will come in early establishment by providing the seedlings with competitive root systems. There is little published information on field performance of seedlings whose endomycorrhizal condition was known, but I feel no hesitation in stating my belief that endomycorrhizae are indispensable to those tree hosts which enter into a symbiotic relationship with them; endomycorrhizae are indispensable as absorbing organs in natural forested soil.

CONCLUSION

One cannot overemphasize the importance of nitrogen-fixing organisms in the nutrition of even-aged stands. Except perhaps in early stand establishment, it would appear to be economically impractical to apply nitrogen as a standard silvicultural treatment in any of its manufactured forms on forest lands. In even-aged stands we may see the growing importance of nodulated non-legumes and free-living nitrogen-fixing organisms because forest conditions provide a good environment for them. Harvest methods should provide an adequate substrate in forest soils so that temporary nitrogen tie-ups by free-living organisms are of no disadvantage. Lichens and phyllosphere organisms will contribute significant amounts of nitrogen under special conditions. Considerable work remains to be done to quantify the contribution of these sources of nitrogen fixation in the forest. Recent work indicates higher nitrogen contributions by lichens and non-symbiotic free-living organisms than has previously been reported for non-forested situations.

Second in importance only to nitrogen-fixing organisms in the biological nutrient relationships of even-aged stands are the mycorrhizae. Plant scientists in general want to relegate these organisms as significant only in ecosystems where soils

are low in available nutrients but they are equally important on our most fertile forested sites. For most host trees which form endomycorrhizae, it would probably take available elemental P in excess of 60 ppm to result in tree growth without these important root symbionts and I question the existence of such P levels in forest soils anywhere in the world. It is well-known that non-mycorrhizal plants grow well when supplied with inorganic mineral salts in soil or in hydroponics or sand cultures. But what is the relevance of these findings to forested situations? There is now ample evidence that forest tree seedlings require mycorrhizae to function at P levels most frequently found in natural soils. There is no scientific basis for assuming this requirement diminishes with tree age.

Developing a practical mycorrhizal technology on a worldwide basis offers no panacea for even-aged management now or in the foreseeable future. Trees will not grow better simply because of what we are learning about this symbiotic relationship; they have always possessed and utilized mycorrhizae. However, mycorrhizal technology in the nursery can help to provide more competitive seedlings for outplanting on a variety of sites. Marx's extensive work with Pisolithus tinctorius certainly indicates that root systems can be 'tailored' with an aggressive fungus in nursery beds to meet specific outplanting conditions.

Unfortunately a great many plant scientists still resist exploring Harley's sound observation which I will quote from a conclusion by Voight (1971).

"One is forced to accept the fact that in a great many species of plants they (mycorrhizal roots) are the main organs of contact with the soil. In short, mycorrhizae have been selected in evolution against uninfected root systems in a large number of species. Viewed in this way the original question of whether mycorrhizal infection is beneficial becomes secondary to the question of how these composite organs work and how they differ in any of their functions from uninfected roots."

REFERENCES

- Bryan, W.C. & Kormanik, P.P. (1977). Mycorrhizae benefit survival and growth of sweetgum seedlings in the nursery. *Southern Journal of Applied Forestry*, 1, 21-23.
- Forman, R.T.T. (1975). Canopy lichens with blue-green algae: A nitrogen source in a Columbian rain forest. *Ecology*, 56, 1176-1184.
- Gerdeman, J.W. (1968). Vesicular-arbuscular mycorrhiza and plant growth. *Annual Review of Phytopathology*, 6, 397-418.
- Gray, L.E. & Gerdemann, J.W. (1973). Uptake of sulphur-35 by vesicular arbuscular mycorrhizae. *Plant and Soil*, 39, 687-689.

- Haines, S.G., Haines, L.W. & White, G. (1978). Leguminous plants increase sycamore growth in northern Alabama. *Soil Science Society of America Journal*, 42, 130-132.
- Harrelson, M.A. (1969). Tropical epiphyllae and nitrogen fixation. Ph.D. Dissertation, University of Georgia, Athens. 103pp.
- Hayman, D.S. & Mosse, Barbara (1972). Plant growth responses to vesicular-arbuscular mycorrhiza. III Increased uptake of labile P from soil. *New Phytologist*, 71, 41-47.
- Jorgensen, J.R. (1975). Nitrogen fixation in forested coastal plain soils. U.S. Department of Agriculture Forest Service Research Note SE-130, 16pp.
- Jurgensen, M.F. & Davey, C.B. (1968). Nitrogen-fixing blue-green algae in acid forest and nursery soils. *Canadian Journal of Microbiology*, 14, 1179-1181.
- Kleinschmidt, G.D. & Gerdemann, J.W. (1972). Stunting of citrus seedlings in fumigated nursery soils related to absence of endomycorrhizae. *Phytopathology*, 62, 1447-1453.
- Kormanik, P.P., Bryan, W.C. & Schultz, R.C. (1977a). Endomycorrhizae: their importance in nursery production of hardwood seedlings. Proceedings 1976 SE Area Nurserymen's Conference, pp.16-21. Eastern session, Charleston, South Carolina, August 3-5, 1976.
- Kormanik, P.P., Bryan, W.C. & Schultz, R.C. (1977b). Influence of endomycorrhizae on growth of sweetgum seedlings from eight mother trees. *Forest Science*, 23, 500-509.
- Kormanik, P.P., Bryan, W.C. & Schultz, R.C. (1977c). Quality hardwood seedlings require early mycorrhizal development in nursery beds. Proceedings 14th Southern Forest Tree Improvement Conference, Gainesville, Florida. pp.289-293.
- Marks, G.C. & Kozlowski, T.T. (eds) (1973). *Ectomycorrhizae: their ecology and physiology*. Academic Press, New York 444pp.
- Marx, D.H. (1975). Mycorrhizae and establishments of trees on strip-mined land. *The Ohio Journal of Science*, 75, 288-297.
- Marx, D.H. (1977). The role of mycorrhizae in forest production. Tappi Conference papers. Annual meeting, February 14-16, 1977, Atlanta, Georgia. pp 151-161.
- Marx, D.H. (1978). Ectomycorrhizal fungus inoculations: a tool for improving forestation practices. International Workshop on Tropical Mycorrhiza Research, Forest Products Research Institute, 28 August - 6 September, 1978, Kumasi, Ghana.
- Marx, D.H. & Artman, J.D. (1978). Growth and ectomycorrhizal development of loblolly pine seedlings in nursery soil infested with Pisolithus tinctorius and Thelephora terrestris in Virginia. U.S. Department of Agriculture Forest Service Research Note. SE-256 6pp.
- Marx, D.H. & Bryan, W.C. (1970). Pure culture synthesis of ectomycorrhizae by Thelephora terrestris and Pisolithus

- tinctorius on different conifer hosts. Canadian Journal of Botany, 48, 639-643.
- Marx, D.H. & Bryan, W.C. (1975). Growth and ectomycorrhizal development of loblolly pine seedlings in fumigated soil infested with the fungal symbiont Pisolithus tinctorius. Forest Science, 21, 245-254.
- Marx, D.H., Bryan, W.C. & Cordell, C.E. (1976). Growth and ectomycorrhizal development of pine seedlings in nursery soils infested with the fungal symbiont Pisolithus tinctorius. Forest Science, 22, 91-100.
- Meyer, R.D. (1977). Nitrogen fixation by epiphytes of an oak-hickory and a white pine forest. Master's Thesis University of Georgia, Athens. 67 pp.
- Nicolson, T.H. (1967). Vesicular arbuscular mycorrhiza - a universal plant symbiosis. Science Progress, 55, 561-581.
- Noggle, G.R. & Fritz, G.J. (1976). Introductory plant physiology. Prentice-Hall, Englewood Cliffs, New Jersey, xiv + 688pp.
- Pearson, V. & Tinker, P.B. (1975). Measurement of phosphorus fluxes in external hyphae of endomycorrhizas. "Endomycorrhizas" Academic Press, London + New York. 626pp.
- Pirozynski, K.A. & Maslock, D.W. (1975). The origin of land plants: a matter of mycotropism. BioSystems, 6, 153-164.
- Rhodes, L.H. & Gerdemann, J.W. (1975). Phosphate uptake zones of mycorrhizal and non-mycorrhizal onions. New Phytologist, 75, 555-561.
- Richards, B.N. (1974). Introduction to soil ecosystems. Longman Group Ltd., Essex, Harlow and Burnt Mill. 266pp.
- Safir, G.R., Boyer, J.S. & Gerdemann, J.W. (1971). Mycorrhizal enhancement of water transport in soybean. Science, 171, 581-583.
- Safir, G.R., Boyer, J.S., & Gerdemann, J.W. (1972). Nutrients status and mycorrhizal enhancement of water transport in soybean. Plant Physiology, 49, 700-703.
- Sanders, F.E. & Tinker, P.B. (1971). Mechanisms of absorption of phosphate from soil by endogone mycorrhizas. Nature, 233, 278-279.
- Smith, S.E. (1974). Mycorrhizal fungi. CRC Critical Reviews in Microbiology, January. pp.273-313.
- Switzer, G.L. & Nelson, L.E. (1972). Nutrient accumulation and cycling in loblolly pine (Pinus taeda L.) plantation ecosystems: The first twenty years. Soil Science Society of America Proceedings, 36, 143-147.
- Theodorou, C. (1967). Inoculation with pure cultures of mycorrhizal fungi of Radiata pine growing in partially sterilized soil. Australian Forestry, 31, 303-309.
- Voight, G.K. (1971). Mycorrhizae and nutrient mobilization. "Mycorrhizae" (Ed by E. Hacskaýlo). Proceedings First North American Conference on Mycorrhizae, U.S. Department of Agriculture Forest Service Miscellaneous Publications

1189. 255pp.

Wilhelm, S. (1976). Chemical treatments and inoculum potential of soils. Annual Review of Phytopathology, 4, 53-78.



CURRENT FERTILIZER USE IN PLANTATIONS

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SUMMARY

The following subjects are dealt with: the most frequently found nutrient deficiencies, the rates and types of fertilizer currently in use and their time and methods of application, species' responses, the economics of fertilizers use, advisory work and fertilizer supply to the forest industry.

Nitrogen (N) and phosphorus (P) are the two main nutrients used in forestry throughout the world, typically at rates of 150 kg N and 50 kg P element per hectare. Artificially produced N compounds such as urea and ammonium nitrate usually are favoured because of their high N content, while crushed phosphate rock is a common type of P applied because of its low cost.

Some species can be 'nutrient demanding', such as Sitka spruce, while others, such as lodgepole pine, are tolerant of low nutrient status of a site. The question of 'high input - high yield' versus 'low input - low yield' is raised. In the long term research on species, varieties and clones which can grow satisfactorily with low nutrient levels is required.

The economics of fertilizer use in plantation forestry are complex, and efficient and effective advice is essential. Methods of application can influence the cost and the effectiveness of the fertilization and more work is required to improve these. The relative costs of N and P fertilizers are likely to rise, making accurate advice on response and on the economics even more essential.

RÉSUMÉ

Nous traitons des sujets suivants: éléments nutritifs normalement insuffisants, types d'engrais utilisés et la quantité appliquée, temps et méthodes d'utilisation, réactions des espèces, dynamique économique de l'utilisation des engrais et travaux consultatifs et finalement fourniture d'engrais.

L'azote et le phosphore sont les deux éléments nutritifs communs, utilisés en forêt dans le monde entier, avec environ 150 kg de N et 50 kg de P par hectare. Les composés artificiels d'azote tels que l'urée et l'ammoniaque sont les plus courants à cause de leur taux élevé d'azote, tandis que le phosphate de roche broyé est le type normal de phosphore utilisé à cause de son prix modique.

Certaines essences demandent beaucoup d'éléments nutritifs, comme l'épicéa de Sitka tandis que d'autres, tel le lodgepole pin se contentent de stations à taux d'éléments nutritifs peu élevé. Nous posons la question de 'taux élevé - rendement élevé', contre 'taux bas - rendement bas'. Nous prônons des recherches à long terme sur des essences, des variétés et des clones qui se contenteraient d'un niveau d'éléments nutritifs peu élevé.

La dynamique économique de l'usage d'engrais dans une plantation est complexe: un service consultatif efficace et compétent est nécessaire. Les méthodes d'utilisation peuvent influencer sur le coût et l'efficacité d'application et il reste encore beaucoup de chemin à parcourir avant de parvenir à un perfectionnement. Le coût relatif d'engrais à base de N et de P augmentera sans aucun doute soulignant ainsi le besoin d'un système consultatif perfectionné en ce qui concerne les réactions à la fertilisation et sa rentabilité.

ZUSAMMENFASSUNG

Folgende Themen werden behandelt: an welchen Nährstoffen fehlt es normalerweise, welche Düngemittel und -mengen werden verwendet, wann und wie geschieht die Ausbringung, welche Reaktion zeigen die Baumarten, wie verhält es sich mit dem wirtschaftlichen Nutzen der Düngeranwendung, der Beratungsarbeit und schliesslich der Versorgung mit Düngemitteln. Stickstoff und Phosphor sind die zwei

Hauptnährstoffe, die überall auf der Welt im Forst in Mengen von etwa 150 kg Stickstoff und 50 kg Phosphor pro Hektar verwendet werden. Unter den Stickstoffdüngern werden gewöhnlich synthetische Stickstoffverbindungen wie Harnstoff und Ammoniumnitrat wegen ihres hohen N-Gehalts bevorzugt, während unter den Phosphordüngern gemahlene Rohphosphate wegen ihres niedrigen Preises zur Anwendung kommen. Einige Baumarten, wie z.B. die Sitkafichte, können hohen Nährstoffbedarf haben, während andere, wie die Murray-Kiefer, mit niedrigem Nährstoffangebot eines Standorts auskommen. Es erhebt sich die Frage, in wie weit die Regel gilt: 'hohe Zufuhr - hoher Gewinn' oder 'geringe Zufuhr - geringer Gewinn'. Langzeitversuche sind erforderlich mit Arten, Varietäten und Klonen, die einen geringen Nährstoffbedarf haben.

Die wirtschaftlichen Aspekte der Düngieranwendung in Forstpflanzungen sind komplex; fachmännische und effektive Beratung ist daher sehr wichtig. Die jeweiligen Anwendungsmethoden können die Kosten und die Wirksamkeit der Düngung beeinflussen. Zu ihrer Verbesserung ist noch einige Arbeit notwendig. Die relativen Kosten von Stickstoff- und Phosphordüngern werden wohl eine genaue Beratung über die Auswirkungen und Wirtschaftlichkeit noch wichtiger machen.

INTRODUCTION

Fertilizers are now required on a large scale in forestry throughout the world, in cold and hot climates, and in high and low rainfall areas. Table 1 gives a few of the more recent publications and indicates the widespread use of fertilizers in forestry.

Initially, slow-growing stands were selected for trials where a nutrient deficiency was the likely cause of the slow growth (Zehetmayer 1954; Guinaudeau 1945). Later many workers started looking for responses in faster-growing areas (Gustavsen & Lipas 1975). There can be few areas of plantation forestry anywhere in the world where fertilizers have not now been tried.

NUTRIENTS

An analysis of 'Forestry Abstracts' shows nitrogen as the nutrient most reported with phosphorus second. With the exception of decomposing organic soils, nitrogen is the only major nutrient which cannot be supplied directly by the soil.

Table 1. Recent publications concerning fertilizer use in forestry in various countries.

Country	Authors
Britain	Mayhead 1976
Canada	Weetman, Krause & Koller 1978
Denmark	Anon. 1976
East Germany	Fiedler 1975
France	Barneoud & Bonduelle 1973
Ireland	Farrell 1976
Korea	Chung 1977
New Guinea	Lamb 1977
New Zealand	Kirkland 1977
Russia	Sudnitsyna 1976
Sweden	Holmen 1978
Switzerland	Baule 1977
Tropics and subtropics	Schutz 1976
U.S.A.-Florida	Anon. 1978a

It is obtained from atmospheric nitrogen through fixation by soil and symbiotic organisms and by the oxidation of atmospheric nitrogen by lightning, the oxide subsequently being brought to earth by rain. If neither of these processes supplies sufficient nitrogen, then the application of nitrogen compounds would be likely to improve growth.

Nutrients other than nitrogen are obtained from soil minerals and from rainfall. The amount of phosphorus in rainfall, however, is much lower relative to the other major nutrients (Allen et al. 1968) and if the minerals in the soil are low in phosphorus, which is frequently the case, responses to added phosphorus would be likely. Most rocks in Britain are deficient in phosphorus and consequently agricultural crops and trees on almost all soils in this country respond when this nutrient is added.

Potassium (K) can be limiting to tree growth but less frequently than nitrogen and phosphorus. However, the application of additional nitrogen and/or phosphorus can increase the N/K and P/K ratios in trees, indicating an imbalance which is often revealed by K deficiency symptoms. Responses to potassium on such sites would not have been obtained without the added nitrogen and/or phosphorus.

Calcium deficiency is uncommon in conifer plantations, although the addition of calcium as lime has been tried in order to decrease litter acidity, increase litter breakdown and thereby release nutrients and improve tree growth. This technique has sometimes worked but can lead to other problems such as an increase in butt-rot. Bonneman (1970) found that liming of Norway spruce stands on pseudogleys had little effect on the growth of trees, the ground flora or the soil.

With species other than conifers, calcium can be limiting. Eucalyptus grandis, which has a high calcium and low phosphorus requirement, has been found to respond to lime (Schutz 1976).

Magnesium deficiency can occur on certain soil types such as some in New Zealand (Will 1966) where it is normally corrected using magnesium salts or magnesium limestone.

Minor nutrients can cause deficiencies in specific areas, for example boron and copper in New Zealand (Will 1971, 1972), boron in Tanzania (Procter 1967), copper both in Holland (Oldenkamp & Smilde 1966) and in France (Bonneau 1972) and manganese in South Africa (Donald 1977). Fortunately most of these deficiencies can be corrected by the application of relatively low rates of element per hectare. Sometimes soil fixation problems arise necessitating the use of chelates or foliar sprays, e.g. iron deficiency on soils high in calcium (Karschon 1958).

RATES OF APPLICATION

Rates of application used in experiments vary depending on the site and species being treated, but those most frequently recommended are around 150 kg N, 50 Kg P and 100 kg K element per hectare per application. Frequency of application can vary widely from one at the start of a rotation for phosphate on a site not too deficient in phosphorus, to every four years for nitrogen on infertile sands or inhospitable peats.

The standard rate used in British forests on any unimproved soil is 50 kg P per hectare as unground rock phosphate. This rate was found by experimentation over many years, on numerous site types and with many species (Zehetmayr 1954, 1960; Mayhead 1979), to give a long lasting response on the better sites and a reasonable response, say for six years, on the worst sites, e.g. unflushed acid peats. Applying rates higher than this gave no added yield on the better sites, while on the poorer sites other nutrients, most frequently potassium, had to be added later and could conveniently be mixed with phosphate rock for easier and more uniform application. The cost of a heavy, initial dressing of phosphorus would also have attracted more compound interest.

TYPES OF FERTILIZER

The types of compound in use vary from crushed rock and natural organic materials to manufactured chemical compounds and mixtures and 'man-made' organic materials such as plastics, refuse and sewage. The best type is one which produces the largest response per unit cost in materials, transportation and application. In forestry fast-acting materials are not required and in many cases are undesirable as they can be lost through leaching or fixation or cause

burning of plant tissue, Slower acting materials can be used and are frequently cheaper, e.g. crushed rock, industrial by-products, refuse or sewage.

An exception is N, where the high concentration of NH_4NO_3 and urea result in transportation and application economics. The lower N concentration of industrial by-products, sewage, sludge etc. means that to achieve the usual application rates would require the transportation of bulky materials not readily distributed from the air. Urea has been widely used but under some conditions can be volatile, producing ammonium and nitrate radicals which can be lost from the site. This is a particular problem where the species being grown cannot absorb the ammonium radical directly. On the other hand Bhure (1970) has shown in laboratory tests that when urea is applied to forest soils and litter, only small losses occur by volatilization. In Finland urea was found to be less effective than ammonium compounds (Gustaven & Lipas 1975).

Types of phosphate rock can vary greatly in their total and citric-soluble phosphorus content; from less than 5 per cent P to almost 14 per cent total P with the citric-soluble fraction being from less than 10 per cent to almost 40 per cent of the total P. Mayhead (in press) has shown that when the total phosphorus applied to stands of both lodgepole pine and Sitka spruce was equal but different rocks were used, then height growth was correlated with amount of phosphorus in the citric-soluble fraction of the rock. Particle size of rocks did not influence height growth within the range used, i.e. from crude Gafsa rock of which only 2 per cent passed through a 0.075 mm aperture sieve, to finely ground Kola and Nauru rocks, where 50 per cent passed through the same sieve. It would appear that in the acid soil conditions of these experimental sites, as long as the phosphate rock is not too coarse, phosphorus becomes available.

TIME OF APPLICATION

Many trees respond to fertilizer applied at time of planting. Later applications to established stands have been shown to be profitable in many countries. In Britain, some stands which were not given phosphorus at planting responded dramatically to applications of this element (Dannatt, Davies & McTavish 1971).

The season of application of phosphorus, when applied as phosphate rock is unimportant, except perhaps where algal blooms could occur in reservoirs or waters used for fishing. In such areas application in the autumn may be best. On a deficient site, delay of phosphorus application results in slow growth which is never made up after application and phosphorus should always be applied before or in the year of planting.

METHODS OF APPLICATION

Before the 1960's most fertilizers were applied by hand, either as spot treatments to individual trees or broadcast, and improved and cheaper methods for hand application have been devised over the years using for example, knapsack spreaders.

Mechanical methods were developed during the 60's and 70's using tracked or wheeled vehicles with mounted or towed spinners and blowers, and aircraft, both fixed-wing and helicopters. Machines on the ground are at a disadvantage in established plantations because of difficulty of access and are mainly used well before canopy closure. Other problems arise with them in effecting uniformity of spread which necessitates application in narrow swaths which increased cost per unit area (Attersson & Davies 1967; Ballard & Will 1971; Virtanen 1975).

SPECIES RESPONSE

Frequently a choice of tree species is available for a given site in plantation forestry and if such a site has low levels of one or more nutrients, most tree species would respond to nutrient application. However, some may not, while of those which do, some will respond more in volume than others because of their inherently higher growth potential. In other words, some species appear to be more 'demanding' regarding nutrients e.g. Sitka spruce is more 'demanding' than lodgepole pine, which will produce more timber on poor sites than spruce (Zehetmayr 1954), but given sufficient fertilizer the spruce is capable of producing a larger volume than the pine. Several recent experiments in Scotland indicate this, although results are not available as yet for a full rotation. In one experiment in Shin, Sutherland, lodgepole pine planted in 1969 is compared with Sitka spruce on unflushed hill peat with a vegetation of cotton grass (Eriophorum), deer grass (Trichophorum), heather (Calluna) and peat moss (Spagnum). In this experiment all plots were treated with phosphorus and potassium at 50 kg P per hectare and 95 kg K per hectare, broadcast before planting. After six years the height of the trees indicated that the pine were on the yield class (YC) 13 curve, whereas the spruce were on the YC 15 curve and where the vegetation had been killed prior to planting, the pine did not respond but the spruce were on the YC 17 curve. There is no reason to suppose that such differences cannot be maintained throughout the rotation if the trees are kept healthy by subsequent fertilizer applications.

ECONOMICS

The fact that species response differs, leads on to the economics of fertilizer use and whether low-input, low-output species are more economic than high-input, high-output species

on the poorer sites. Such a calculation obviously differs depending on the site/species combination being considered and on the relative costs of fertilizer and timber. The economics of fertilizer application to forest plantations is a complex subject because of the relatively long time scale between expenditure and harvesting and because there are in many cases intermediate returns from thinnings (Edwards 1974; Gagnon, Conway & Swan 1976). The return from fertilizing can be from thinning heavier than normal, from a higher total volume from thinning plus clearfelling, or from an earlier final felling resulting in a lower total compound interest (Everard 1974). As such operations take place over many years and as compound interest has to be taken into account, such calculations can be misleading unless all the factors are known when comparing one set of calculations with another. The use of fertilizers in forestry should be considered nationally as part of the total energy of a nation because the continued provision of wood as a renewable basic resource is important to the economic well-being of many essential industries.

ADVICE TO MANAGERS

Fertilizer application can be recommended following successful experimentation either where it is essential for growth or to enhance growth. The economic justification of the former is simple but for the latter much more detailed and accurate estimates of volume production with and without fertilizer are essential. The most cost effective methods of estimating volume increment in fertilizer experiments are being investigated in several countries, including Britain. Once fertilizer needs have been established for given site/species combinations, recommendations can either be as regimes based on a series of long-term experiments, or as individual prescriptions for given sites based on foliage appearance, recent height and/or diameter growth, chemical analysis of tree tissue, usually foliage, and a knowledge of likely responses for similar site/species combinations. The regime-type recommendations require a series of experiments which cover all major site/species combinations and run for a whole rotation, while the latter system requires a high input of advisor hours and a source of experienced advisors. In Britain at present both systems operate: regimes are being recommended for the site-species combinations with the most predictable responses (Busby 1974), with an advisory service for other sites. The improvement of foliage sampling techniques and the search for alternative tissues to foliage for chemical analysis, are subjects of current interest in Britain and several other countries.

FERTILIZER SUPPLY

Finally, the question of the availability of fertilizer

to the forest industry should be considered. Nitrogen should always be available, albeit at a price, due either to high transportation cost of low N organic materials, such as industrial by-products, refuse or sewage, or high energy requirement when artificial nitrogen compounds are produced from atmospheric nitrogen. As the relative price of nitrogen fertilizer is likely to rise because energy costs will rise, research into nitrogen fixation and low nitrogen-demanding species, varieties and clones will be important in the long term. World rock phosphorus could be used up within 400 years according to data published by the Centre for Agricultural Strategy (Anon 1978b). Before this stage is reached and also because of the uneven world distribution of phosphate rock, the relative cost of phosphorus will undoubtedly rise considerably. As with nitrogen, low-phosphorus demanding species, varieties and clones should be investigated and developed. Nutrients other than nitrogen and phosphorus are not required in such large quantities throughout the world and should be available for use in forestry.

CONCLUSIONS

In the short term, a great deal of research is still required in most countries to determine optimum fertilizer rates and regimes. Improved methods of volume estimation are necessary to quantify such work.

Fertilizer application to forest plantations is and will continue to be an accepted practice for a wide range of site/species combinations. However, because of a likely rise in the cost of fertilizers relative to the price of wood, research effort should be increased to find species, varieties and clones or inter- or intra-specific hybrids which will grow with no or minimal fertilizer applications.

REFERENCES

- Allen, S.E., Carlisle, A., White, E.J. & Evans, C.C. (1968). The plant nutrient content of rainwater. *Journal of Ecology*, 56, 497-504.
- Anon (1976). Report of the fertilizing of Norway spruce etc. *Dansk Skovforeningens Tidsskrift*, 61, 167-253.
- Anon (1978a). Annual Report for 1977 of cooperative research in forest fertilization - programme summary. University of Florida, U.S.A.
- Anon (1978b). Phosphorus: a resource for U.K. agriculture. Centre for Agricultural Strategy Report #2.64pp.
- Atterson, J. (1966). Fertilizers in coniferous forests. *Forestry and home grown timber*. Supplement to *Timber Trades Journal* October 1966, pp. 39-41.
- Atterson, J. & Davies E.J.M. (1967). Fertilizers - their use and methods of application in British Forestry. *Scottish Forestry*, 21, 222-228.

- Ballard, R. & Will, G.M. (1971). Distribution of aerially applied fertilizer in New Zealand forests. *New Zealand Journal of Forest Science*, 1, 50-59.
- Barneoud, C. & Bonduelle, P. (1973) Use of fertilizers in adult stands of Picea abies and Abies alba in North Eastern France. *Rapport Annuel, Association Forêt-Cellulose 1972*, pp. 279-329.
- Baule, H. (1977). Fertilizer trials carried out during afforestation of former mountain pastures in Switzerland. *Allgemeine Forstzeitschrift*, 32, 1-7.
- Bhure, N.D. (1970). Nitrogen losses by volatilisation from urea applied to forest soils. *Bi-monthly research notes*, 26, 42-43.
- Bonneau, M. (1972). Results of fertilizer trials on Douglas fir in the west of the Massif Central. *Revue forestière française*, 25, 35-40.
- Bonnemann, A. (1970). Growing spruce on soils with impeded drainage. *Forstarchiv*, 41, 217-221.
- Busby, R.J.N. (1974). Forest site yield guide to upland Britain. *Forestry Commission Forest Record #97*.
- Chung, I.K. (1977). Experiment for comparing the effects of forest-use solid fertilizer and chemical fertilizer. *Journal of the Korean Forestry Society*, 34, 15-20.
- Dannatt, N., Davies, E.J.M., & McTavish, W.J. (1971). Kilmory 1971. An investigation into fertilizer response. *Scottish Forestry*, 25, 100-109.
- Donald, D.G.M. (1977). Silvicultural practices influencing harvesting. *South African Forestry Journal*, 101, 13-19.
- Edwards, P.N. (1974). The profitability of large-scale aerial fertilizing. *Scottish Forestry*, 28, 265-71.
- Everard, J.E. (1974). Fertilizers in the establishment of conifers in Wales and Southern England. *Forestry Commission Booklet #41*.
- Farrell, E.P. (1976). Forest fertilization in Ireland. *Forestry Chronicle*, 52, 194-196.
- Fiedler, H.J. (1975). Fertilizing Picea abies stands in water catchment areas. *Beitrag für Forstwirtschaft*, 9, 123-136.
- Gagnon, J.D., Conway, J.M. & Swan, H.S.D. (1976). An economic study of the Grand' Mère plantation 10 years after fertilizer treatment. *Forestry Chronicle*, 52, 26-29
- Guinaudeau, J. (1954). An experiment in the use of fertilizers in forest plantings. *Revue des eaux et forêts*, 83, 343-351.
- Gustavsen, H.G. & Lipas, E. (1975). Effect of nitrogen dosage on fertilizer response. *Folia forestalia*, 246, 20pp.
- Holmen, H. (1978). Forest fertilization in Sweden 1977. *Kungliga Skogs- och lantbruksakademiens tidskrift*.
- Karschon, R. (1958). Investigations on iron chlorosis in Eucalyptus gomphocephala. *La-yaaran*, 8, 30-32.

- Kirkland, A. (1977). Fertilizer use in forestry. *New Zealand Journal of Forestry*, 22, 274-282.
- Lamb, D. (1977). Relationships between growth and foliar nutrient concentrations in Eucalyptus deglupta. *Plant and soil*, 47, 495-508.
- Mayhead, G. J. (1976). Forest fertilizing in Great Britain. *Proceedings of the Fertiliser Society of London*. #158, 18pp.
- Mayhead, G. J. (in press). A comparison of different sources of rock phosphate on conifer growth. *Forestry Commission*.
- Oldenkamp, L. & Smilde K, W. (1966). Copper deficiency in Douglas fir. *Korte Mededelingen Bosbouwproefstation T.N.O., Wageningen*, 77, 203-214.
- Procter, J. (1967). A nutritional disorder of pine. *Commonwealth Forestry Review*, 46, 145-154.
- Schutz, C. J. (1976). A review of fertilizer research on some of the more important conifers and eucalyptus planted in subtropical and tropical countries, with special reference to South Africa. *Department of Forestry, Republic of South Africa, Bulletin* #53.
- Sudnitsyna, T. N. (1976). Effect of fertilizers on the growth of Scots pine plantations. *Lesovedenie i lesovodstvo*, 2, 43-50.
- Virtanen, J. (1975). Evenness of spreading of forest fertilizers. *Metsätieteellisen tutkimuslaitoksen julkaisuja*, 86. 72pp.
- Weetman, G. F., Krause, H. H. & Koller, E. (1978). Interprovincial forest fertilization program. *Canadian Forest Service Technical Report* #22.
- Will, G. M. (1966). Magnesium deficiency: the cause of spring needle tip chlorosis in young pines on humus soils. *New Zealand Journal of Forestry*, 11, 88-94.
- Will, G. M. (1971). The occurrence and treatment of boron deficiency in New Zealand pine forests. *New Zealand Forest Research Institute, Research Leaflet* #32.
- Will, G. M. (1972). Copper deficiency in radiata pine planted on sands at Mangawhai Forest. *New Zealand Journal of Forest Science*, 2. 217-221.
- Zehetmayer, J. W. L. (1954). Experiments in tree planting on peat. *Forestry Commission Bulletin* #22
- Zehetmayer, J. W. L. (1960). Afforestation of upland heaths. *Forestry Commission Bulletin* #32.



September 7, 1978

THE EFFECTS OF PLANTATIONS ON
THE PHYSICAL RESOURCE

Chairman: D.R. Johnston

Evaporation of water from
plantation forests.

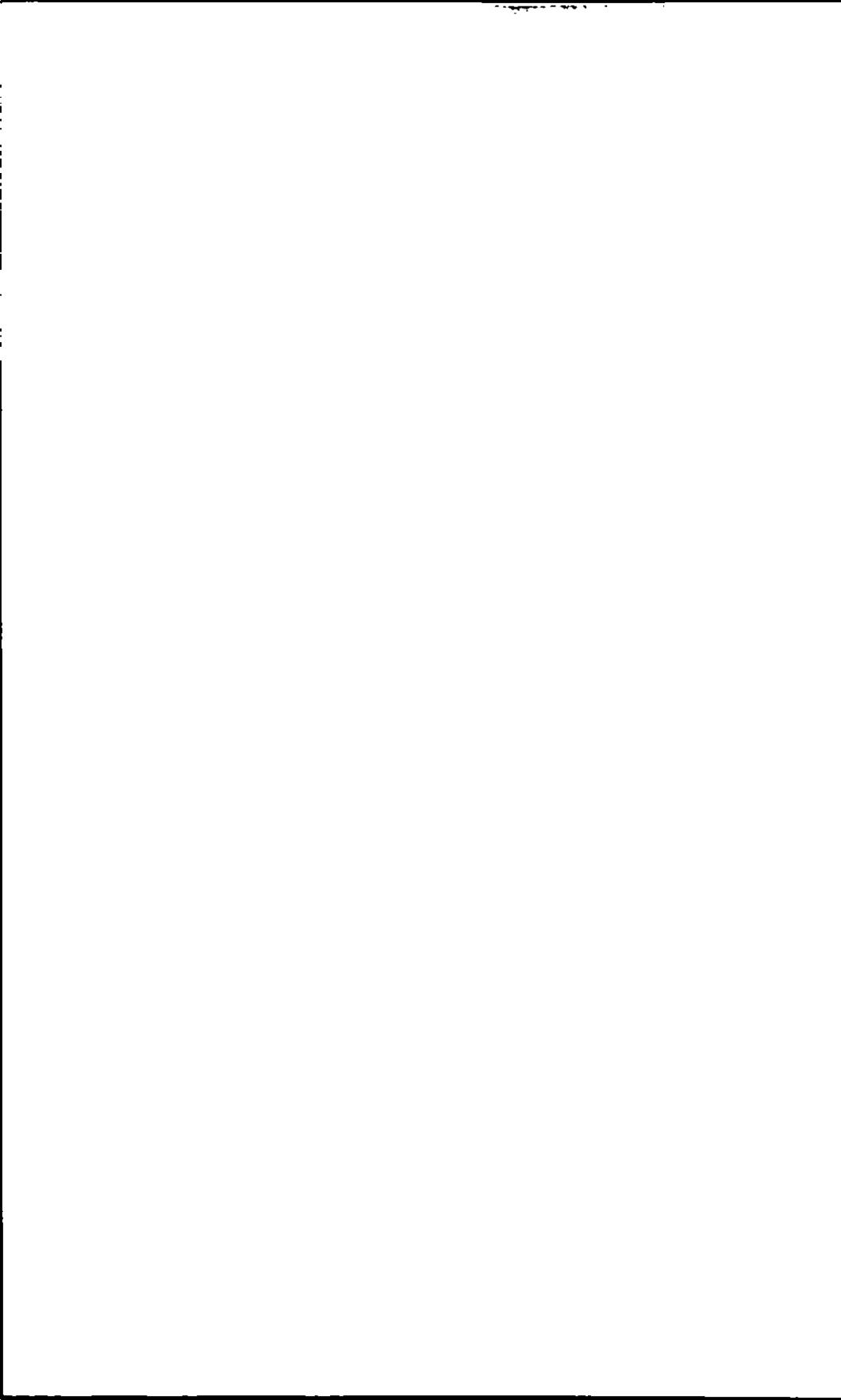
- P.G. Jarvis and
J. Stewart

Effect of forest plantations on the
quantity, quality and timing of
water supplies.

W.L. Nutter

Soil changes under
even-aged plantations.

D.G. Pyatt and
M.M. Craven



EVAPORATION OF WATER FROM PLANTATION FOREST

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SUMMARY

The transpiration and evaporation of water from plantation forest is analysed with the aid of the Penman-Monteith equation.

When the canopy is dry, the rate of transpiration is generally restricted to less than 0.3 mm/h or 3 mm/day in summer and 0.03 mm/day in winter by the combined effects of saturation and stomatal conductance. When saturation deficits are small the stomatal conductance is high, but when saturation deficits are large, stomatal conductance is low as the result of stomatal closure. Consequently transpiration uses only about 40 per cent of the available energy and Bowen ratios are large and often over 2.

When the canopy is wet, evaporation is rapid because of the very high boundary layer conductance of forest canopies. Even though the available energy and the saturation deficits are very small, rates of over 0.3 mm/h are reached. Thus, the rate of evaporation often exceeds the rate of input of available energy and the Bowen ratio is negative as a result of the addition of sensible heat to the canopy.

Despite the much lower available energy and saturation deficits on rainy days than on sunny days, evaporation rates are often 2-3 times transpiration rates because low stomatal conductance reduces transpiration on fine days and high boundary layer conductance enhances evaporation on wet days. Hence long term rates of water loss from plantation forest by transpiration and evaporation depend upon the pattern of rainfall distribution and are much

larger where frequent rainfall keeps the canopy wet for much of the time.

Because the stomatal conductance of forest is lower than that of grassland, transpiration rates from forest are lower than rates from grassland in the same meteorological conditions despite differences in the albedos. However, rates of evaporation from wet forest canopies are very much higher than from wet grasslands because the boundary layer conductance of forest is much higher than that of grassland. Thus, long-term rates of water loss from forest may be more or less than losses from grassland, depending upon the proportion of time the canopy is wet and hence the pattern of rainfall distribution.

More precise evaluation requires better information on the stomatal and boundary layer conductances of different types of forest at different stages of development, and on interception loss and duration of canopy wetness in different climatic regions.

RÉSUMÉ

La transpiration et l'évaporation de l'eau dans les plantations forestières sont analysées à l'aide de l'équation de Penman-Monteith.

Quand le couvert est sec, le taux de transpiration est en général ramené à moins de 0.3 mm/h ou 3 mm/jour l'été, et à 0.03 mm/jour l'hiver, dû à la combinaison du déficit de saturation et de conductance stomatale. Lorsque les déficits de saturation sont faibles, la conductance stomatale est élevée, tandis que lorsqu'ils sont élevés la conductance stomatale est faible à cause d'une fermeture stomatale.

Par conséquent la transpiration n'utilise que 40 per cent de l'énergie disponible et les rapports Bowen sont élevés et dépassent souvent 2.

Quand le couvert est mouillé, l'évaporation est rapide à cause de la conductance de la couche limite très élevée des couverts forestiers. Même dans le cas où l'énergie disponible et les déficits de saturation sont faibles, on arrive à des taux dépassant 0.3 mm/h. Ainsi, le taux d'évaporation excède souvent le taux d'absorption d'énergie disponible et le rapport Bowen est négatif à cause d'un léger apport de chaleur au couvert.

Malgré le fait que l'énergie disponible et les déficits de saturation sont plus faibles les jours de pluie que les jours de beau temps, le taux d'évaporation est parfois deux à trois fois plus élevé que le taux de transpiration parce qu'une faible conductance stomatale réduit la transpiration pendant les jours de beau temps et que la conductance élevée de la couche limite augmente l'évaporation les jours de pluie. Donc, il résulte que, dans les plantations forestières les taux à long terme de perte d'eau dûe à la transpiration et à l'évaporation dépendent de la distribution des chutes de pluie et sont bien plus importants dans le cas où le couvert reste mouillé la plupart du temps.

Puisque la conductance stomatale des forêts est plus faible que celle des prairies, le taux de transpiration des forêts est plus faible que celui des prairies, dans les mêmes conditions météorologiques malgré des albédos différents. Cependant, le taux d'évaporation des forêts à couverts mouillés est bien plus important que celui des prairies humides parce que la conductance de la couche limite des forêts est bien plus élevée que celle des prairies. Ainsi, le taux, à long terme, des pertes d'eau des forêts peut être, soit plus faible, soit plus élevé que celui des prairies, le tout dépendant du temps pendant lequel le couvert est mouillé et, par conséquent, de la distribution des chutes de pluie. Une meilleure évaluation nécessite plus de renseignements sur les conductances des stomates et la couche limite des différents types de forêts à des stades différents de développement, sur l'interception et le temps pendant lequel un couvert reste mouillé dans des régions de climats différents.

ZUSAMMENFASSUNG

Transpiration und Evaporation von Forstpflanzungen wurden mit Hilfe der Penman-Monteith Gleichung analysiert.

Bei trockenem Kronendach beschränkt sich die Transpiration aufgrund des Zusammenwirkens von Sättigungsdefizit und Spaltöffnungsverhalten auf weniger als 0.3 mm pro Stunde oder 3 mm pro Tag im Sommer und 0.03 mm pro Tag im Winter. Bei niedrigen Sättigungsdefiziten besteht hohe

Regulierbarkeit der Spaltöffnungen, bei hohen Sättigungsdefiziten ist sie jedoch sehr gering, da dann die Spaltenöffnungen geschlossen sind. Folglich werden nur 40 Prozent der verfügbaren Energie durch die Transpiration ausgenützt und die Bowen-Quotienten sind gross, oft über 2.

Bei nassem Kronendach ist die Evaporation intensiv aufgrund der hochliegenden Grenzschicht des Kronenraums. Auch bei knappem Energieangebot und sehr geringem Sättigungsdefizit werden Werte von über 0.3 mm pro Stunde erreicht. So übersteigt die Evaporationsrate oft den Input an verfügbarer Energie und das Bowenverhältnis wird durch die zusätzliche Wärme des Kronendaches negativ.

Obwohl die verfügbare Energie und die Sättigungsdefizite an Regentagen viel geringer sind als an sonnigen, liegen die Evaporationsraten oft zwei- bis dreimal höher als die Transpirationsraten, da die geringe Regulierbarkeit der Spaltöffnungen bei schönem Wetter die Transpiration reduziert, während die hoch liegende Grenzschicht an Regentagen die Evaporation steigert. Die Langzeitraten des Wasserverlusts durch Transpiration und Evaporation in Forstpflanzungen hängen somit von der Art der Niederschlagsverteilung ab; sie sind viel grösser, wo häufiger Niederschlag das Kronendach die meiste Zeit nass hält.

Da die Spaltöffnungsregulierung im Forst unter denselben meteorologischen Bedingungen und trotz unterschiedlicher Albedo geringer ist als bei Grasland, liegen auch die Transpirationsraten des Forsts niedriger. Andererseits sind jedoch die Evaporationswerte bei nassem Kronendach sehr viel höher als bei nassem Grasland, da die Grenzschicht im Wald viel höher liegt. So können also die Langzeitraten des Wasserverlusts im Forst grösser oder kleiner sein als bei Grasland, je nachdem wie lange das Kronendach nass ist - was natürlich von der Art der Niederschlagsverteilung abhängt.

Zu einer präziseren Darstellung wären bessere Information über die Spaltöffnungsregulierung und die Grenzschicht bei verschiedenen Forsttypen in verschiedenen Entwicklungsstadien notwendig, ausserdem über den Interceptionsverlust und die Zeit der Kronenbefeuchtung in verschiedenen Klimazonen.

GENERAL PRINCIPLES

The driving force for the movement of water from the soil through the trees to the atmosphere is provided by the evaporation of water at the liquid - air interface within the leaves. The phase change followed by the diffusion of water molecules through the stomata is here called transpiration (E_T) to distinguish it from the evaporation of intercepted water on the surfaces of the foliage, twigs, branches and other parts of the trees (E_I). E is used when either or both E_T or E_I is intended.

The transpiration of evaporation of water from the foliage depends strongly upon the available energy (A), the saturation deficit of the air (D), the wind speed (U) and, to a lesser extent, on air temperature (θ). In addition, transpiration is strongly dependent upon the stomatal conductance (g_s) of the needles and evaporation on the structural characteristics of the canopy which influence the boundary layer conductance (g_a) in addition to the windspeed.

These variables were first put together through the application of the conservation of energy to exchange processes in crop canopies by H.L. Penman in 1948 and were first related explicitly in the manner used below by J.L. Monteith in 1965. As a result the following expression for transpiration has come to be known as the Penman-Monteith equation. It was first applied to the study of water loss from trees in plantations by A.J. Rutter in 1967.

$$\lambda E_T = \frac{sA + c_p \rho D g_a}{s + \gamma(1 + g_a/g_s)} \quad (\text{W/m}^2) \quad \dots(1)$$

$$1\text{W/sq.m} = 0.0015 \text{ kg/(sq.m/h)} = 0.0015 \text{ mm/h}$$

The physical parameters c , ρ , γ and λ , respectively the specific heat of air, the density of air, the psychrometric constant and the latent heat of vaporization of water, are all weak functions of temperature (see Table A3 in Monteith 1973). The parameter s is the slope of the curve relating the saturated vapour pressure of water (e_s) to temperature (i.e. $de_s/d\theta$) at the appropriate temperature and varies appreciably with temperature. For example, it has values of 0.61, 0.83, 1.45 and 2.44 mb/ $^{\circ}\text{C}$ at 5, 10, 20, and 30 $^{\circ}\text{C}$, respectively (Monteith 1973, Table A4).

In the case of evaporation of intercepted water from a completely wet canopy, rather than the transpiration of water which has passed through the plant, g_s becomes very large indeed (Shuttleworth 1976) and equation (1) becomes

$$\lambda E_I = \frac{sA + c_p \rho D g_a}{s + \gamma} \quad \dots(2)$$

Provided that the dependence of g_a on windspeed is known, evaporation can be calculated from this equation wholly from weather station data.

The Penman-Monteith equation can be applied to single leaves or extensive canopies. When applied to canopies, an approximation is involved since the derivation assumes identical sources and sinks of water vapour and heat, whereas this is unlikely to be the case in a canopy. However, comparisons with more complex models show that this approximation does not lead to serious error (Sinclair, Murphy & Knoerr 1976; Shuttleworth 1976).

The equation can be applied successfully over periods of weeks, days, hours or minutes provided that appropriate values of the variables are available. Application over short periods of time, such as an hour, is usually limited by the availability of hourly meteorological data and hourly measurements or reliable estimates of stomatal conductance, g_s .

The equation predicts that E will increase with increases in either available energy or saturation deficit or both. The influence of available energy and saturation deficit on E appears in the numerator as additive. In the past this has led to the description of evaporation as having a radiation dependent component and a windspeed or saturation deficit dependent component. This is convenient but somewhat artificial since the maintenance of a saturation deficit depends upon the input of energy into the system. However, the relative importance of available energy and saturation deficit in deriving E can readily be defined by the ratio of the two terms in the numerator of equation (1) or (2) as

$$J = c_p \rho D g_a / sA \quad \dots(3)$$

Clearly the larger the boundary layer conductance, the larger will be the effect of saturation deficit on E . If both g_a and D are large, the deficit term may greatly exceed the radiation term. This is commonly the case for tall, rough vegetation like plantation forest when the canopy is dry. For dry canopies of coniferous plantations, J typically lies in the range 5-20.

This leads to a useful simplification of equation (1). In the first place, if J is large and transpiration is much more dependent on saturation deficit than on available energy, the radiation term can be neglected. Secondly, if the ratio g_a/g_s is also large, as will be seen later, the small terms in the denominator of equation (1) can be ignored. Thus the rate of transpiration can be approximated by

$$E_T = \frac{c_p \rho}{\lambda \delta} \cdot D \cdot g_s = K \cdot D \cdot g_s \quad \dots(4)$$

where K is the factor for converting partial pressure of water vapour into mass concentration and has a value of $740 \times 10 \text{ kg}/(\text{cu.m mb})$ at a temperature of 20°C and atmospheric pressure of 1013 mb .

Equations (1) and (2) provide a means of determining the rates of transpiration and evaporation in particular circumstances. To demonstrate how the properties of plantation forests interact with the environmental variables, it is also convenient to express evaporation in terms of the sources of energy available to drive it:

$$A = \lambda E + C \quad \dots(5)$$

where C is the convective exchange of sensible heat to or from the foliage. Two alternative parameters are commonly used to describe the partitioning of available energy: - the proportion of the available energy used in evaporation

$$\alpha = \lambda E/A \quad \dots(6)$$

- the Bowen ratio, which is defined as

$$\beta = C/\lambda E \quad \dots(7)$$

From equations (5) and (7) λE can also be written as

$$\lambda E = A/(1+\beta) \quad \dots(8)$$

TRANSPIRATION FROM DRY CANOPIES

Measured mean hourly rates of transpiration from extensive plantations of Sitka Spruce in Scotland (Forest of Mearns) and Scots pine in Norfolk (Thetford Forest) can reach 0.3 mm/h (200 W/sq.m) but are more commonly in the range 0.1 to 0.2 mm/h ($70-140 \text{ W/sq.m}$), depending on the weather and time of day. Daily rates can reach 3 mm/day in the summer but are more commonly about 2 mm/day in summer and 0.3 mm/day in winter.

These rates of transpiration account for the utilisation of only a small proportion of the available energy. On average during the daytime only 40 per cent of the available energy is used for transpiration; values of α are within the range 0.3 to 0.5 for many hours of observations at Forest of Mearns, and Thetford Forest. The daytime Bowen ratios are rarely less than 1 and frequently in the range 2-4, rising to even higher values during drought or periods of high temperature and low humidity. Such low rates of transpiration and the values of α and β are very different from what was expected ten years ago on the basis of experience with short vegetation such as agricultural crops and grasslands. The transpiration rate from such vegetation when well supplied with water may equal or

exceed the input of available energy; α for such vegetation is frequently in the range 0.8 to 0.9 and β in the range 0 to 0.5 (Penman, Angus & van Bavel 1967). That is to say, the rate of transpiration from short vegetation may commonly be two to three times larger than from plantation forest; or conversely, the rate of transpiration from plantation forest is only about 1/5 to 1/3 of the rate from crops and grassland.

To make useful generalizations about water use by plantation forests, we need, therefore, to consider the reasons for the low measured rates of transpiration, low values of α and high values of β .

As expressed in equation (1), the main variables determining the rate of transpiration are:

- the available energy, A
- the saturation deficit, D
- the boundary layer conductance, g_a
- the stomatal conductance, g_s .

In principle, the rate of transpiration could vary widely and reach very high values depending on the values of these variables. In practice, however, the range is restricted by the combinations of values of the variables which occur. These combinations depend both on the environmental variables and on the morphological and physiological properties of the foliage of the trees.

Available energy and saturation deficit

Net radiation over coniferous forest is about 75-90 per cent of the incident shortwave radiation (Jarvis, James & Landsberg 1976). For dense canopies which intercept most of the radiation, such as Sitka spruce at 4000 trees/ha, with a leaf area index of about 9, little radiation reaches the soil and in the middle of the day only about 5 per cent of the net radiation goes into storage. Thus the available energy can reach about 600 W/sq.m in summer. In more open stands such as Scots pine with a leaf area index of only 3 or 4, much more of the net radiation reaches the soil and also goes into storage in the stems and branches. Consequently the energy available to evaporate water from the canopy is rather less, reaching only about 400 W/sq.m.

The normal range of saturation deficits in temperate maritime climates is small. Over most of the British Isles, and particularly those parts in which forest plantations occur, saturation deficits only occasionally exceed 15 mb. The normal range of deficits throughout the year over the main areas of afforestation is 1-10 mb. Of course much larger deficits of up to 30 mb do occur commonly in the summer in more continental areas where plantations are grown.

Stomatal conductance

The maximum stomatal conductance of Sitka and Norway spruce forests canopies is about 0.02 m/s. The maximum conductance for Scots pine, lodgepole pine and Douglas fir is

somewhat less at about 0.01 m/s. However, measured conductances are usually less than these values, depending on the weather, the time of day and time of year. For comparison, the maximum stomatal conductances of crop canopies and grassland are somewhat larger (0.015 to 0.05 m/s).

The conductance of a canopy is the arithmetical sum of the conductances of all the individual needles. Thus it depends upon the number of needles present, i.e. on the leaf area index, and on the conductance of the individual needles. The conductance of a needle varies with the species, and depends upon the age of the needle and its position in the canopy, as well as upon the season, the time of day and the current weather. Because of the variation amongst needles in a canopy, the canopy conductance depends upon the proportion of needles of different properties which are present, i.e. on the partial leaf area indices of needles of different ages, position, branching etc.

The conductance of needles of conifers is low because of the occurrence of a meshwork of wax tubes in the stomatal antechambers (Jeffree, Johnson & Jarvis 1971). g_s is also much reduced on a daily and seasonal basis by the pronounced sensitivity of the stomata of many conifers to saturation deficit. This sensitivity is particularly marked in Sitka spruce (Grace, Malcolm & Bradbury 1975; Watts, Neilson & Jarvis 1976; Watts & Neilson 1978).

Boundary layer conductance

In comparison with diffusion through the stomata, the turbulent transfer of water molecules across the needles and shoot boundary layers and through the canopy to the air above is very effective. Consequently the boundary layer conductance is very large in relation to the stomatal conductance and hence can vary widely with little or no influence on transpiration. Values of g_a are typically 0.1 to 0.3 m/s which can be compared with the values of g_s of 0.02 m/s.

In addition, the large boundary layer conductance of plantation forest facilitates removal of sensible heat from the foliage with the consequence that leaf temperatures of conifers are seldom very different from air temperatures (Jarvis, James & Landsberg 1976). As a result of enhanced sensible heat transfer and low leaf temperatures, the transpiration rate is less than might otherwise be expected, α is smaller and β is larger. For comparison, g_a of crops and grassland is an order of magnitude lower (see under Evaporation from wet canopies), leading to lower sensible heat losses and higher leaf temperatures, both of which tend to push the transpiration rate up and β down.

In the absence of stomatal control, when the canopy is wet, the boundary layer conductance is a major factor determining the rate of evaporation and is considered later.

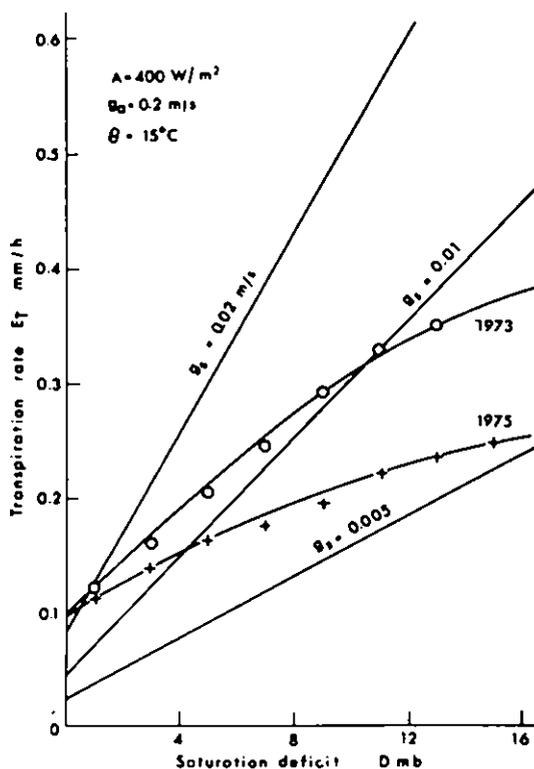


Fig. 1. The relation between transpiration rate and saturation deficit calculated from equation (1) for the conditions shown and three different values of g_s . The data points are medians of a large number of mean hourly values within saturation deficit classes for Sitka spruce at Forest of Mearns in June and July 1973 and 1975. The stand was thinned in 1974

Conclusions

From these figures and equation (1), we may estimate the rates of transpiration we would expect to find. For example, if g_s were to be maintained at 0.02 m/s on a fine summer day when $A = 600 \text{ W/sq.m}$ and $D = 15 \text{ mb}$, a transpiration rate of 0.9 mm/h, three times the maximum measured rate, would be expected, together with $\alpha > 0.9$ and a low value of β of about 0.1.

The question arises as to why the measured transpiration rates and values of α are so much lower than might be expected

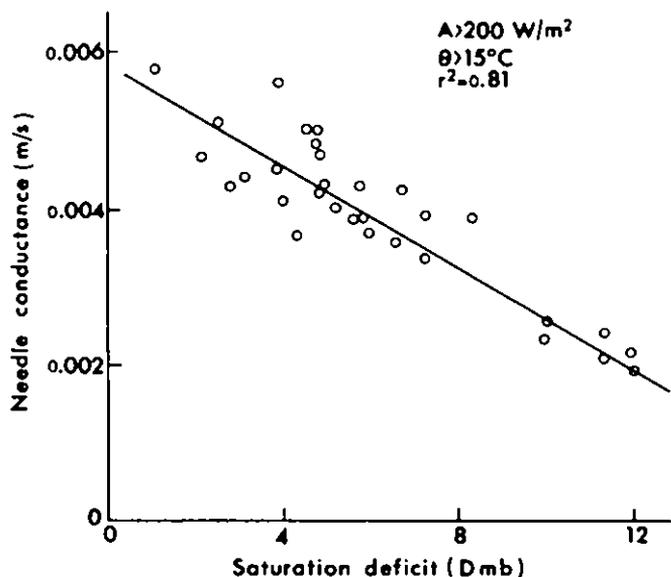


Fig.2. The relation between saturation deficit and stomatal conductance of 1-year-old needles of Sitka spruce in the upper part of the canopy, Forest of Mearns, summer 1972. Needle conductance expressed on a unit needle area basis.

and the Bowen ratios so much higher. The answer is made most clearly evident by reference to the simplification in equation (5). Essentially, E_T depends upon g_s and D . Stomatal conductance is large in humid, cool weather when deficits are small, but because of the small deficits transpiration is not large in any case. On the other hand, in warm, dry weather when the deficits are large, the stomatal conductance is small, because the stomatal conductance itself depends upon the deficit. Stomatal conductance and saturation deficit are never both large at the same time. Consequently transpiration never reaches the high rates expected.

Although the rate of transpiration does increase as D increases (Fig. 1), it does not increase to the extent that would be expected because g_s does not remain constant. During the course of a warm, summer day, g_s decreases as the saturation deficit gets larger (Fig. 2) and in extreme conditions may get so small that CO_2 uptake becomes zero or negative. Thus there is feedback in the needle which effectively prevents large rates of water loss being attained. Laboratory experiments show that this decrease in g_s results from the closing of stomata. Closure is not associated with

the development of large water stresses in soil, tree or leaf mesophyll, but is a specific response of the stomata to saturation deficit.

Influence of stage of development

Transpiration from dry canopies depends upon the stomatal conductance of the canopy. This in turn depends upon the accumulation of leaf area and development of a closed canopy, as well as upon the changing morphological and physiological characteristics of the needles and behaviour of the stomata. So far as we know, systematic studies of stomatal conductance of canopies have been made on about ten stands of five different species at varying stages of development in the U.K. No systematic studies of stage of development of g_s have been made or are in progress.

EVAPORATION FROM WET CANOPIES

The rate of evaporation of intercepted water from wet canopies can reach very high values. Rates are normally in the range 0.1 to 0.3 mm/h (70-210 W/sq.m) but can exceed 0.5 mm/h (340 W/sq.m) in the summer for short periods. The rate of evaporation often exceeds the rate of input of available energy, i.e. $\alpha > 1$, β negative. For example, the average of 245 measurements of evaporation rate over 20 min periods from a wet Scots pine canopy at Thetford was 129 W/sq.m and the corresponding average rate of available energy input was 102 W/sq.m (Stewart 1977).

At first sight this might appear surprising since canopies are wet, dew apart, either when it is raining or immediately after rain has ceased. In these circumstances it is usually cloudy so that the available energy is low. In addition, evaporation of the rain and intercepted water raises the humidity of the air and lowers its temperature, thus bringing the air closer to saturation. This combination of atmospheric conditions might be expected to result in low rates of evaporation of the intercepted water. The rates of evaporation are, of course, lower than would occur if saturation was not approached and irradiation remained high but they are nonetheless high for two reasons. In the first place, evaporation is not restricted by stomata, a large area of foliage and twig presenting a free water surface to the atmosphere at a temperature close to ambient. Secondly, because of the aerodynamic roughness of the canopy, turbulent mixing is very effective and the boundary layer conductance is very large (0.1 to 0.3 m/s), thus facilitating transfer of water vapour into atmospheres of even very high humidity.

If hourly rates of over 0.3 mm/h were sustained for twenty-four hours, very high daily rates of evaporation would result. However, the canopy rarely remains wet for long periods, because it dries out so rapidly and when it does remain wet for long periods, the humidity of the air

approaches saturation so that the rate of evaporation is depressed. Consequently daily rates of evaporation rarely exceed 6 mm/day.

Available energy and saturation deficit

In cloudy, rainy weather the available energy is small, often lying, in the range 50 to 150 W/sq.m. Nonetheless in the absence of restriction by the stomata, this can lead to an appreciable evaporation rate. Even if the air were to become completely saturated ($D=0$), equation (2) gives the proportion of available energy involved in evaporation as

$$\alpha = \lambda E/A = s/(s + \gamma) \quad \dots(9)$$

If the air were to be cooled to a dewpoint of 9°C for example, $\alpha = 0.5$ and E_T might be 0.08 mm/h. In practice, although the saturation deficit decreases as the air is cooled and humidified by evaporation, the air does not become saturated because of the influx of air which has previously passed over areas of lower vegetation where there has been a sufficient input of sensible heat to maintain a small saturation deficit. Many observations at Mearns and Thetford indicate that while the canopy remains wet, even after rainfall has ceased, the saturation deficit of the air above is less than 1 mb, compared with values of 10-25 mb in good weather when the canopy is dry. During rainfall the saturation deficit is usually also about 0.5-1 mb and evaporation goes on at similar rates.

Boundary layer conductance

The large boundary layer conductance is without doubt the most important feature of forest canopies leading to high rates of evaporation. The boundary layer conductance is large because the plantation surface is rough in an aerodynamic sense. This roughness derives in part from the spire-like structure of the canopy and from the height of the trees. The boundary layer conductance also depends on windspeed (Fig. 3) which is very rarely less than 0.5 m/s at tree top height. For these two reasons, the boundary layer conductance of coniferous forest canopies is very large both in relation to the stomatal conductance and in comparison with the boundary layer conductance of crops and grassland (Fig.4). Typically, values of g_a for plantation forests are in the range of 0.1 to 0.3 m/s. Consequently, the saturation deficit, even when less than 1 mb, contributes substantially to the evaporation rate from coniferous forest plantations.

Curves B and C (Fig. 4) calculated from equation (2), show that even at small saturation deficits, rates of evaporation would be expected to exceed the available energy if the aerodynamic conductance is large enough. If the humidity and temperature of the air were not to adjust, evaporation would proceed at very high rates indeed as

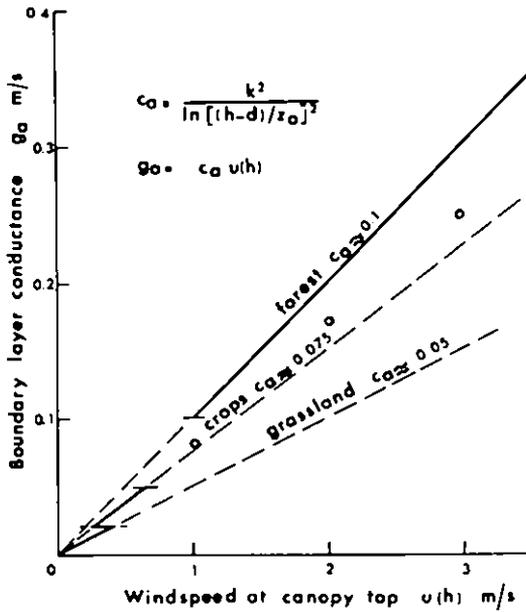


Fig. 3. The relation between boundary layer conductance and windspeed at the top of the canopy for plantation forests, cereal crops and grassland. Crop heights of 16, 1 and 0.3m were assumed. C is a non-dimensional canopy drag coefficient which is dependent upon the aerodynamic parameters z and d (Jarvis 1976). Heavy lines indicate typical ranges of values in the field. Data points are based on 66 mean hourly wind profiles measured with sensitive cup anemometers over Sitka spruce at Forest of Mearns.

indicated by curve A. However, these rates could not be supported without the abstraction of a great deal of heat from the ambient air, thus reducing D by cooling the air as well as by raising its humidity. The rate of evaporation of intercepted water will only become less than the available energy if the air approaches very close to saturation, or g_a decreases (Curve D). If the air were to become saturated (Curve E), then evaporation would proceed at a rate which was some fraction of A set by the dewpoint temperature as indicated by equation (9) above.

The 245 measurements of evaporation from the wet Scots pine canopy at Thetford mentioned previously are shown in Figure 5 in relation to the available energy (Stewart 1977). Also shown is the 1:1 line. The large number of points above the 1:1 line indicate that the evaporation rate was larger than the rate of input of available energy in the majority of

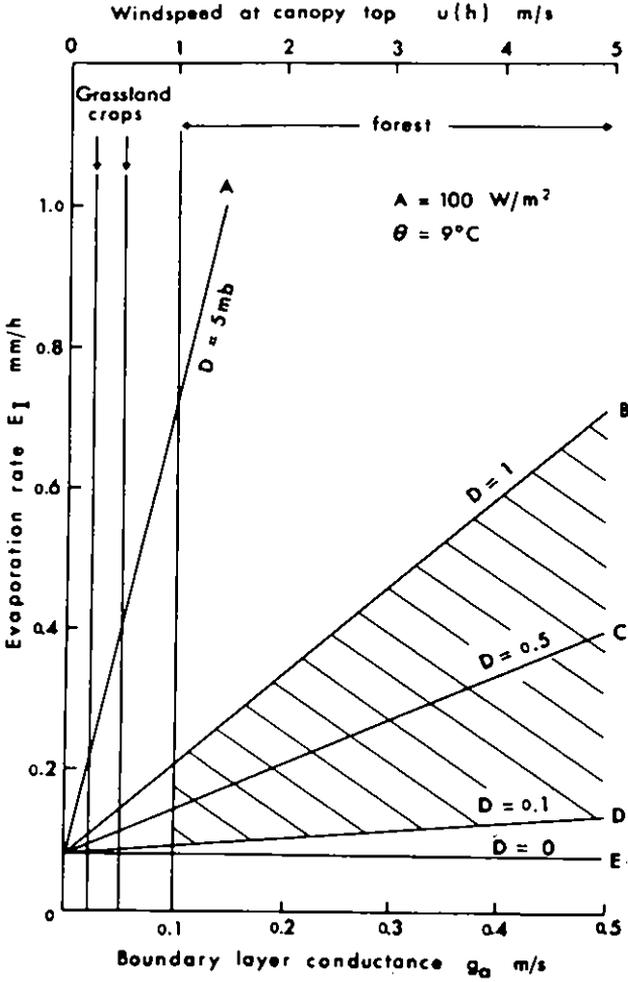


Fig. 4. The relation between evaporation rate, E_1 , and boundary layer conductance calculated from equation (2) at a range of saturation deficits, D . The letters on the curves are explained in the text. Upper limits for the boundary layer conductance of grassland and crops are indicated by arrows at the top of the figure. The shaded area indicates the range of evaporation rates from wet forest canopies

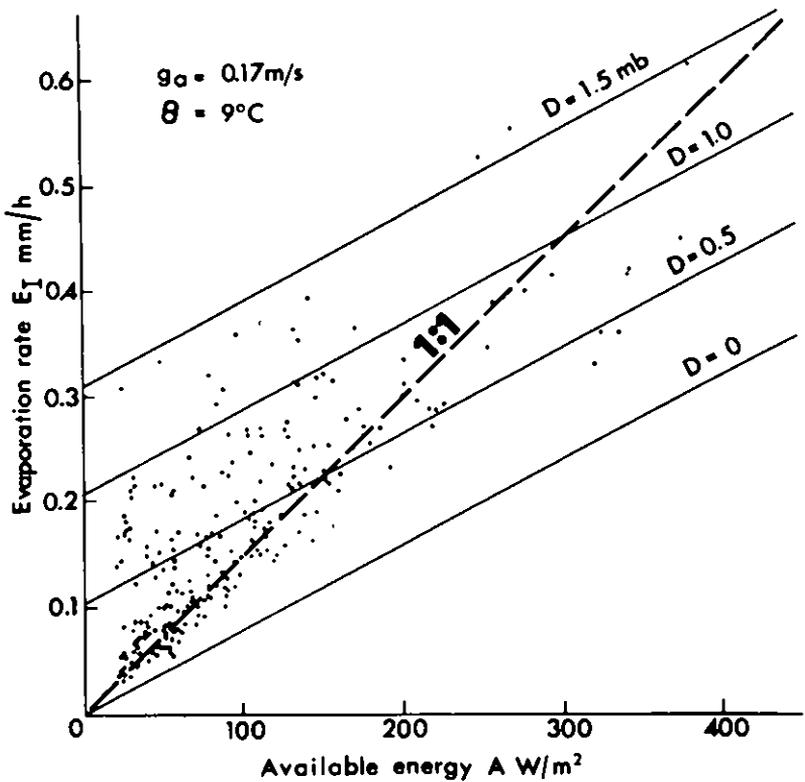


Fig. 5. The relation between evaporation rate and available energy ($A > 20 \text{ W/sq.m}$) for a wet Scots pine canopy at Thetford. The solid lines show the expected evaporation rates, calculated from equation (2) for the values of saturation deficit, D , shown by the lines. The dashed line (1:1) shows the line for evaporation rate equal to the available energy.

cases. The other four lines show the evaporation rates to be expected for the values of D given, and a temperature of 9°C . It is clear that $J (= c_p \rho D g_a / sA)$ has values of between 1 and 4 even when D is 0.5 to 1 mb and A is 50 to 150 W/sq.m . Thus even at these small saturation deficits, the high boundary layer conductance is responsible for substantially raising the evaporation rate above what would be expected from radiation alone.

Evaporation during rainfall

As a result of the high boundary layer conductance, evaporation from wet canopies goes on at high rates into

atmospheres of high humidity both when it is raining and after rainfall has ceased. It is not always appreciated that evaporation of intercepted water during rainfall accounts for a large proportion of the loss of intercepted water. This is illustrated with data provided by J.H.C. Gash (personal communication) in Table 1 which shows that about 30 per cent of the interception loss results from evaporation whilst rain is falling.

Table 1. The partitioning of the loss of intercepted water by evaporation from two plantations, one of Norway spruce in the Plynlmmon watershed and the other of Scots pine in Thetford Forest. The data were obtained from interception studies and micro-meteorological measurements and were kindly made available by J.H.C. Gash. For further details see Gash & Stewart (1977) and Gash (1979).

Evaporation occurring	Plynlmmon Norway spruce	Thetford Scots pine
From small storms (mostly during rainfall)	0.09	0.19
During wetting up the canopy	0.03	0.05
From saturated canopy during rainfall	0.26	0.34
After rainfall ceases	0.46	0.41
From trunks	0.16	0.01
TOTAL	1.00	1.00

Comparison with transpiration

Although large, the rates of evaporation are not so much larger than the rates of transpiration as might be expected simply from the absence of stomatal control, i.e. from equation (2) rather than equation (1), because, as the result of rain, the micrometeorological conditions are not the same as in fine weather. In rainy weather, cloud may reduce A to less than 100 W/sq.m, compared with values of 400 to 600 W/sq.m in fine weather, and D is reduced to less than 1 mb, compared with values of 10 to 25 mb in fine weather when the canopy is dry. A comparison between E_x and E_T , with g_a/g_s taken as 20, suggests that the rate of evaporation from a wet canopy would be over ten times that from a dry canopy in the same weather conditions. However, largely because of the small saturation deficits during and after rain, in practice the rate of evaporation from a wet canopy does not exceed two to

Table 2. Typical values of mean hourly and mean daily rates of transpiration and evaporation from coniferous forest plantations in summer and winter. The figures are based on micrometeorological measurements on Scots pine at Thetford Forest and on Sitka spruce at Forest of Mearns, and on interception studies on Norway spruce at Plynlimon (see Jarvis et al. 1976; Gash & Stewart 1977; Stewart 1977; Gash 1979).

	Transpiration E_T		Evaporation E_I	
	mm/h*	mm/day	mm/h	mm/day+
Summer	0.15	2	0.3	6
Winter	0.03	0.3	0.1	2.5

* for daylight hours only

+ in practice the canopy is rarely wet for 24 h.

three times that from a dry canopy in summer (Table 2).

Influence of stage of development

It might be expected that the surface roughness parameter of plantation canopies, and hence g_a , would vary with tree species, density of planting and stage of development of the stand. Up to 1975, fourteen published studies had been made on ten species in six countries by thirteen teams of investigators on fourteen stands of generally poorly defined structure and stage of development (Jarvis, James & Landsberg 1976). No systematic studies of the influence of stand characteristics on the aerodynamic properties of forest canopies have ever been made, despite the importance of these characteristics in the exchanges of water, CO_2 , heat and momentum; the last being also of some significance with regard to windblow!

ANNUAL WATER LOSS

As a result of the large differences in instantaneous rates of water loss from wet and dry canopies, long-term losses by evaporation and transpiration together (evapotranspiration) from plantation forest must depend upon the proportion of the time that the canopy is wet or dry, as well as upon the local climate and weather. Consequently, large differences in annual rates of evapotranspiration may be expected amongst areas with differing patterns of rainfall distribution with respect to time. If the rainfall is frequent, so that the canopy is almost continuously wet, very large amounts of water will be lost by evaporation. On the other hand, if the rainfall mostly comes in short, infrequent, heavy showers, or is very seasonal, the annual loss by evapotranspiration will be smaller because of the much lower

Table 3. The loss of water by transpiration and evaporation in 1975 from a plantation of Norway spruce in mid-Wales and Scots pine in East Anglia. The figures are based on micrometeorological and lysimetric measurements and data from automatic weather stations. Some of the data kindly provided by J.H.C. Gash. Further information is given by Calder (1977), Gash & Stewart (1977) and Gash (1979).

	Plynlimmon Norway spruce	Thetford Scots pine
Gross rainfall, mm	2002	650
Mean evaporation rate, mm/h	0.13	0.19
Mean rainfall rate*, mm/h	1.76	1.38
Proportion of time the canopy is wet	0.48	0.13
Transpiration loss, mm	340	350
Evaporation loss, mm	550	210
Total loss, mm	890	560

* for hours in which the rainfall exceeded 0.5 mm.

rates of loss by transpiration from dry canopies than by evaporation from wet ones

There is very little information available on the separate losses of water by transpiration and evaporation from forests in different climates, with which to support this hypothesis. Table 3 shows a comparison between such estimates for a Norway spruce plantation in the Plynlimmon watershed in mid-Wales and a Scots pine plantation in Thetford Forest in East Anglia, i.e. a comparison between a damp, oceanic site in the west and a dry, more continental site in the east of the country. At both sites the transpiration losses in 1975 were very similar, but over twice as much water was lost by evaporation from the Plynlimmon site than from Thetford because frequent rain kept the canopy wet there for a much larger proportion of the time.

This comparison is not only between regions of the country but is also between species, and indeed between stands of quite different age structure. This is the best we can do at present. We do not have the information to make comparisons between the same species in different regions, let alone the same species in stands at different stages of development or under different management regimes.

COMPARISON BETWEEN PLANTATION FOREST AND GRASSLAND

The main differences between plantation forest and grassland in characteristics affecting evapotranspiration lie

in

- the solar reflection coefficient (albedo);
- the stomatal conductance;
- the boundary layer conductance.

The mean daily albedo of plantation forest is generally in the range 0.10 to 0.15 (Jarvis, James & Landsberg 1976) in contrast with that of grassland and many crops which is about 0.25. This difference gives rise to about 10 per cent more net radiation over forest than over grassland and probably an equal amount more available energy.

The maximum stomatal conductance for plantation forest is about 0.02 s/m for dense canopies of spruce and about 0.01 s/m for pines and perhaps some other coniferous species. Some crops and grasslands may have somewhat higher values but a figure of 0.02 s/m is probably fairly representative for a sward well supplied with water. However, whereas the value for grassland may remain more or less constant during the day, unless drought intervenes, g_s for pine and spruce canopies may decline markedly during the day to much lower values leading to much lower transpiration rates.

The boundary layer conductance of plantation forest is typically within the range 0.1 to 0.3 s/m whereas g_a for crops is about 0.03 s/m and for grassland about 0.01 s/m. These large differences lead to substantial differences in the rate of evaporation of intercepted water from forest and grassland.

The estimated effects of these variables on water loss from wet and dry canopies are shown in Table 4.

Table 4. A comparison between the characteristics and components of evapotranspiration of dry and wet canopies of Scots pine at Thetford Forest and grassland experiencing the same meteorological conditions during twelve hours of daylight on two days in June 1973. $\theta = 15^\circ\text{C}$. Adapted from Stewart (1978).

	Canopy dry		Canopy wet	
	Scots pine	grass	Scots pine	grass
A MJ/sq.m	19.36	15.33	2.40	1.98
g_s m/s	0.01-0.003	0.02	-	-
g_a m/s	0.17	0.01	0.17	0.01
J	4.21	0.30	0.99	0.07
α	0.49	0.80	1.21	0.64
β	1.04	0.25	-0.17	0.56
Deficit term, mm	3.09	1.14	0.59	0.03
Radiation term, mm	0.73	3.75	0.60	0.49
Total, mm	3.82	4.89	1.19	0.52

Dry canopy comparison

The higher stomatal conductance of the grassland leads to

a much higher transpiration rate attributable to the radiation or available energy term than for the forest, despite the somewhat smaller amount of available energy. This is offset to a considerable degree by the much lower deficit term of the grassland than of the forest as a result of the differences in $g_a : J$ is 4.2 for the forest whereas it is only 0.3 for the grassland. However, the partitioning of energy by dry canopies is more dependent on g_s , so that the daily total of transpiration by the grassland is 28 per cent higher than by forest and 80 per cent of the available energy goes into transpiration by the grassland as compared with only 49 per cent by the forest.

Wet canopy comparison

On days on which the canopies are wet all day, there is much less energy available because of the cloudy, rainy conditions.

The evaporation from the forest is twice that from the grassland, because the deficit term contributes as much as the radiation term, whereas the deficit term contributes almost nothing to evaporation from the grassland. Consequently evaporation from the forest exceeds the input of available energy, whereas evaporation from the grassland is much less than the available energy. Thus J is negative for the forest but +0.56 for the grassland.

CONCLUSIONS

Because of the high boundary layer conductance, rates of evaporation from wet plantation forest canopies are much higher than from grassland. On the other hand, the low stomatal conductance leads to lower rates of transpiration from forest than from grassland (Table 4). The figures in the table are for daylight hours only. It may be assumed that transpiration will be much reduced at night as a result of stomatal closure, as well as from lack of energy. If the needle stomata were to remain partly open, night time transpiration might also be appreciable. Evaporation from the canopy at night is likely to be at about the same rate as that attributable to the deficit term in day time, thus further enhancing the daily loss from forest, as compared with grassland. Thus, if wet and dry days occur with equal frequency, average daily rates of evapotranspiration might be about 5 per cent higher from forest than from grassland. However, the rate of evaporation from the wet forest canopy is so rapid that the forest canopy does not remain wet for long between showers, except in the wetter, more humid, western parts of the U.K. where rainfall is frequent and often continuous for long periods. In these areas forests lose more water than grassland because of the large amount of rainfall which is intercepted by the canopy and thence evaporated. Where the pattern of rainfall is markedly discontinuous, the

total evapotranspiration from forest is unlikely to exceed evapotranspiration from good quality grassland on deep soils, well supplied with water, because of the lower stomatal conductance of the forest. However, should the grassland experience drought, because of shallow rooting, or be composed of xerophytic species with low stomatal conductance, the total evapotranspiration from the forest probably will still be higher. A more exact assessment must await better information on the comparative rates of evaporation and transpiration from forest and grassland in different climatic areas. In view of the considerable amount of information obtained on evaporation and transpiration from forest over the last fifteen years, it is perhaps desirable now that the emphasis be shifted somewhat towards accurate estimation of evaporation and transpiration from grassland and heathland in upland locations.

REFERENCES

- Calder, I.R. (1977). A model of transpiration and interception loss from a spruce forest in Plynlimon, Central Wales. *Journal of Hydrology*, 33, 247-265.
- Gash, J.H.C. (1979). An analytical model of rainfall interception by forests. *Quarterly Journal of the Royal Meteorological Society*. In press.
- Gash, J.H.C. & Stewart, J.B. (1977). The evaporation from Thetford Forest during 1975. *Journal of Hydrology*, 35, 385-396.
- Grace, J., Malcolm, D.C. & Bradbury, I. (1975). The effect of wind and humidity on leaf diffusive resistance in Sitka spruce seedlings. *Journal of Applied Ecology*, 12, 931-940.
- Jarvis, P.G., James, G.B. & Landsberg, J.J. (1976). Coniferous forest "Vegetation and the Atmosphere" Vol. 2 Case Studies (Ed. by J.L. Monteith) pp 171-240. Academic Press, London, New York, San Francisco.
- Jeffree, C.E., Johnson, R.P.C. & Jarvis, P.G. (1971). Epicuticular wax in the stomatal antechamber of Sitka spruce and its effects on the diffusion of water vapour and carbon dioxide. *Planta*, 98, 1-10.
- Monteith, J.L. (1965). Evaporation and Environment. *Symposia of the Society for Experimental Biology*, 19, 206-234.
- Monteith, J.L. (1973). *Principles of Environmental Physics*, Arnold, London. 241 pp.
- Penman, H.L. (1948). Natural evaporation from open water, bare soil and grass. *Proceedings of the Royal Society, A* 199 120-145.
- Penman, H.L., Angus, D.E. & Bavel, C.H. van (1967). Microclimatic factors affecting evaporation and transpiration. *Agronomy*, 11, 483-505.
- Rutter, A.J. (1967). The analysis of evaporation from a stand of Scots pine. *Proceedings International Symposium on Forest*

- Hydrology (Ed. by W.E. Sopper and H.W. Lull), pp 403-417. Pergamon Press, Oxford.
- Shuttleworth, W.J. (1976). A one-dimensional theoretical description of the vegetation-atmosphere interaction. *Boundary Layer Meteorology*, 10, 273-302.
- Sinclair, T.R., Murphy, C.E. & Knoerr, K.R. (1976). Development and evaluation of simplified models for simulating canopy photosynthesis and transpiration. *Journal of Applied Ecology*, 13, 813-829.
- Stewart, J.B. (1977). Evaporation from the wet canopy of a pine forest. *Water Resources Research*, 13, 915-921.
- Stewart, J.B. (1978). A micrometeorological investigation into the factors controlling the evaporation from a forest. PhD Thesis, University of Reading.
- Watts, W.R. & Neilson, R.E. (1978). Photosynthesis in Sitka spruce (*Picea sitchensis* (Bong) Carr.) VIII. Measurements of stomatal conductance and CO₂ uptake in controlled environments. *Journal of Applied Ecology*, 15, 245-255.
- Watts, W.R., Neilson, R.E. & Jarvis, P.G. (1976). Photosynthesis in Sitka spruce (*Picea sitchensis* (Bong) Carr.) VII. Measurements of stomatal conductance and CO₂ uptake in a forest canopy. *Journal of Applied Ecology*, 13, 623-638.



EFFECTS OF FOREST PLANTATIONS ON THE QUANTITY, QUALITY AND TIMING OF WATER SUPPLIES.

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SUMMARY

The role of forests and forest management in the regulation of the quantity and timing of water flow from forested catchments has been well documented in the past fifty years. In general the annual volume of flow from forested catchments is less than that expected from other types of vegetation. Annual flow from coniferous catchments can be expected to be as much as 20 per cent less than that from hardwoods, due mainly to greater annual interception loss in the coniferous catchment. For some coniferous species the annual transpiration loss also may be greater than that for hardwoods. Seasonal flows from coniferous catchments are usually less than from hardwoods; the greatest loss occurring during the dormant and early growing seasons. Flood flows, both peak and volume, are not expected to be altered by conversion of forest stands to even-aged plantations.

The degree to which natural water quality is altered by land use practices depends on the climate soil, geology, topography and vegetation type. Evidence suggests that most nutrients are retained and recycled within a coniferous forest to a greater degree than in a hardwood forest and in forests to a greater degree than in grass or successional stage vegetation. Rapid revegetation of a site after forest harvest will generally result in only a small increase in nutrient loss. Erosion is not a significant water quality factor under well-planned and executed forest management. Many of the effects of even-aged plantations on the quantity, quality and timing of water flows

are small or little different from those expected from natural forests. The major effects will result from the more intensive cultural practices common to even-aged plantation management. These effects can be minimized through careful and wise application of management practices.

RÉSUMÉ

Nous possédons depuis une cinquantaine d'années une mine de renseignements sur le rôle régulateur des forêts et de la gestion forestière en ce qui concerne la quantité et la distribution dans le temps du régime des eaux. En général le débit annuel d'eau provenant des régions forestières est moins important que celui d'autres types de végétation. Le débit annuel provenant des forêts de conifères peut être de l'ordre de 20 per cent de moins que celui des forêts de feuillus à cause d'une perte plus grande due à l'interception dans les forêts de conifères. La perte annuelle par évaporation de certains conifères peut être plus élevée que celle de certaines essences feuillues. Le débit saisonnier des forêts de conifères est inférieur à celui des forêts de feuillus: les plus grandes pertes lieu pendant la période de repos de la végétation et le début de la période végétative. On pense que ni le volume d'écoulement en général, ni les pointes de débit soient affectés par la conversion de peuplements forestiers en plantations équiennes.

Le degré d'influence de l'occupation des sols sur la qualité naturelle des eaux dépend du climat, du sol, de la géologie, de la topographie et du type de végétation. Par expérience, on sait que la plupart des éléments nutritifs sont retenus et recyclés de façon plus avantageuse dans les forêts de conifères que dans les forêts de feuillus, et aussi de façon plus avantageuse dans les forêts que dans les prairies ou d'autres stades de succession. La végétation qui apparaît dans une station après la récolte n'amène qu'une faible augmentation de la perte d'éléments nutritifs. L'érosion n'est pas un facteur significatif de qualité des eaux dans le cadre d'une gestion forestière efficace.

La plupart des effets produits par des

peuplements équiens sur la quantité, la qualité et le réglage du régime des eaux ne diffèrent que peu ou presque pas de ceux des forêts naturelles. Les effets les plus importants résultent de l'exploitation agricole intensive qui va de pair avec la gestion des forêts équiennes. On peut minimiser ces effets en se bornant à appliquer des techniques de gestion prudentes et équilibrées.

ZUSAMMENFASSUNG

In den letzten fünfzig Jahren ist sehr viel darüber geschrieben worden, welche Rolle Wälder und ihre waldbauliche Behandlung bei Menge und zeitlicher Verteilung des Wasserabflusses aus bewaldeten Einzugsgebieten spielen. Im allgemeinen liegt die jährliche Abflussrate aus bewaldeten Einzugsgebieten unter dem anderer Vegetationstypen. Aus Nadelwaldgebieten kann man Jahresmengen erwarten, die bis zu 20 Prozent unter denen aus Hartholzeinzugsgebieten liegen. Dies wird hauptsächlich auf den grösseren jährlichen Interceptionsverlust in Nadelwaldgebieten zurückgeführt. Bei einigen Nadelholzarten ist auch u.U. der jährliche Transpirationsverlust grösser als bei Harthölzern. Die jahreszeitlichen Abflüsse aus Einzugsgebieten mit Nadelwaldbestockung sind normalerweise geringer als aus denen von Harthölzern; der grösste Verlust entsteht während der Ruhezeit und den frühen Wachstumsperioden. Bezüglich des Auftretens von Hochwasser ist durch die Umwandlung von Forstbeständen in gleichaltrige Pflanzungen keine Änderung hinsichtlich Menge und Intensität zu erwarten.

Inwieweit die natürliche Wasserqualität sich durch die jeweilige Landnutzung ändert, hängt von Klima, Boden, Ausgangsgestein, Relief und dem Vegetationstyp ab. Die Erfahrung zeigt, dass die meisten Nährstoffe in einem Nadelwald in grösserer Masse zurückgehalten und wieder aufgenommen werden als in einem Hartholzwald, und dass dieser Vorgang generell in Wäldern deutlicher ausgeprägt ist als bei Grasland oder anderen höherstehenden Vegetationsformen. Wenn ein Standort nach der Holzernte schnell wieder aufgeforstet wird, so führt das zu einem nur geringen zusätzlichen Nährstoffverlust. Bei gut geplanten und gut ausgeführtem Waldbau wirkt

sich die Erosion kaum auf die Wasserqualität aus.

Gleichaltrige Bestände beeinflussen Menge, Qualität und zeitliche Verteilung der Wassermengen kaum anders als Naturwälder. Am meisten wirken sich noch die intensiveren Kulturmassnahmen aus, die normalerweise bei gleichaltrigen Beständen angewandt werden. Durch umsichtige und kluge Kulturtechnik kann dies auf ein erträgliches Minimum reduziert werden.

INTRODUCTION

"It is not enough to know whether forests influence streamflow; it is necessary to know how much, at what seasons and under what conditions of climate, soil and topography and the variations between different kinds of forest as well".

That statement was made in 1928 in the Wagon Wheel Gap study report on the effects of forest land use changes on streamflow (Bates & Henry 1928). In the fifty years since that classic experiment and the Emmenthal, Switzerland study on differences in streamflow between pasture and forest land (Engler 1919), much has been learned about the influence of forests and other vegetation types on streamflow quantity and timing. The paired catchment experimental design pioneered in the Wagon Wheel Gap experiment is the major design still used today in forest water yield research. In more recent years research emphasis has shifted to understanding and interpreting components of the hydrological cycle to predict effects on forests and changes in forest land use on the quantity and timing of streamflows. We have made progress. But if we were to turn Bates and Henry's statement into a question and ask, do we know enough, the answer is no. The biological and physical components of the forest ecosystem, vegetation type, climate, soil and topography interact in many different ways which are not precisely predictable. Predictability will improve as we learn the better to quantify the components and the interactions between components.

In recent years there has also been greater emphasis on the effects of forests and forest land use changes on the quality of streamflows as concern over long-term site productivity and environmental issues has increased. Again the biological and physical components interact in a complex way and experience is as yet too limited for us to make broad extrapolations and expect a high degree of predictability.

FORESTS AND WATER YIELD

Much of the forest hydrological research conducted over

the past sixty years has been in natural forests, a few under continuing intensive management. There have also been a limited number of studies on effects of conversion from forest to non-forest vegetation and vice versa. Examination of the impacts of plantations on the hydrological cycle is very timely as the land area in intensively managed plantations grows at an increasing rate. For instance, in the coastal plain region of south Georgia and north Florida in the United States, 25 per cent of the 4 X 10⁶ ha commercial forest is pine plantation. Since there is a paucity of research studies on the hydrological effects of even-aged forest plantations, extrapolations must be drawn from studies on natural stands under intensive management through application of our knowledge of the biological and physical processes.

Stated in its simplest form the hydrological balance for a forest catchment (Hewlett & Nutter 1969) is:

$$P_g - Q - E_t + \Delta S = 0 \quad (\text{Equation 1})$$

and

$$E_t = I_t + E_s + T \quad (\text{Equation 2})$$

where P_g is the gross precipitation, Q the catchment discharge or streamflow, E_t the evapotranspiration and ΔS the change in soil and ground water storage within the catchment. The evapotranspiration E_t is further defined as the sum of total interception loss I_t , evaporation from soil and water surface E_s and transpiration T . The time period over which this balance applies may vary, although of greatest interest for purposes of this paper are annual and seasonal periods and the shorter periods during flood flows.

Climate, physiography and vegetation are the major factors influencing the hydrological balance (Equation 1). Climate's major influence is in terms of precipitation patterns and net energy received; whether there is water available and sufficient energy to evaporate it. Physiography and geological structure determine the permeability and water storage capacity properties of the soil and rock. Vegetation type, structure, density and vigour each influence evapotranspiration. Evapotranspiration is further influenced by precipitation patterns, the availability of water in the soil to the plant and the energy to vaporize the water. The outcome of all of these factors is expressed in the rate, volume and pattern of streamflow from the catchment.

The importance of catchment physiography on the hydrological balance was demonstrated by Lull & Sopper (1967) in the northeastern United States. They found that average annual and seasonal total streamflow was significantly different between seven major physiographic provinces. On the

other hand, Woodruff & Hewlett (1970) determined that the percentage of the precipitation appearing as stormflow, referred to as hydrologic response, from moderately sized catchments in the eastern United States was not highly correlated with any single catchment physical feature. This is not too surprising considering the complexity of the physical system. There was a definite pattern; mapped physiographic provinces had unique hydrological responses. They did identify catchment storage capacity as one variable that is not readily measurable but which could probably account for a major portion of the difference in hydrological responses between physiographic provinces. Nutter (1975) showed in a large physical model that, in addition to storage capacity, length and angle of slope influence the rate at which water will be delivered to the stream channel. Increasing slope angle or decreasing soil depth each tend to increase stormflow production and decrease the duration and volume of low seasonal flows. Increasing slope length tends to have an opposite effect. Soil depth and soil physical properties are direct indicators of the storage capacity. Certainly there are exceptions to these generalizations, but the influence of physiography on catchment streamflow behaviour was demonstrated by the model study and highlighted a few problems associated with streamflow prediction from forest catchments.

In the simplest sense evapotranspiration is a function of the amount of water available and the amount of energy available to vaporize that water. How the water loss is partitioned between transpiration, interception and direct evaporation from the soil and water surfaces has been a source of disagreement among forest hydrologists.

One of the major sources of disagreement is the importance of interception. Burgy and Pomeroy (1958) studied interception and transpiration losses from grassy areas and concluded that cooling of the leaf surface by evaporation of intercepted water resulted in a similar reduction in transpiration. Leyton & Carlisle (1959) drew similar conclusions from interception studies in forests. In an excellent review of interception studies, Helvey (1971) presented sufficient evidence to conclude that concurrent interception and transpiration losses do occur and that these losses are additive. The major reason is that energy available to a leaf surface is more efficient in evaporating water from a wet leaf surface than from the internal cells of a leaf. Thus, for a given input of energy, interception loss from a wet leaf will be greater than transpiration loss.

Vegetation type, structure and density are important factors in determining interception loss. Helvey's (1971) review of numerous interception studies reveals that interception loss and leaf surface area index are correlated; they are greatest in spruce-fir hemlock forests, intermediate

in pine forests and least in hardwood forests. Age is important in determining stand structure and as a consequence, interception loss. For instance, in one study (Helvey 1967), the annual interception loss from white pine increased by 230 mm as 10-year old stands matured to 60-year-old stands. Delfs (1967) and Swank & Douglas (1974) reported differences in annual streamflow of 230 mm and 200 mm, respectively, that were attributed to the increased interception of conifers compared to hardwoods. The number, structure and timing of precipitation events also influence interception loss. The greater the number of storms with sufficient drying time between them, the greater the interception loss. Dormant season interception losses from hardwoods are less than from conifers. In summary, forest interception losses can be significant, reducing the water reaching the soil to be used in maintaining plant growth or streamflow from 8-40 per cent of the gross precipitation.

Vegetation type, structure and density are also important factors in determining transpiration losses. During the growing season, although the transpiration rates of hardwoods per unit of leaf area may be two or three times greater than conifers, the transpiration loss per tree is greater in conifers because of the greater total leaf surface area (Swank & Miner 1968). Penman (1967), through a theoretical study, indicated that summer evapotranspiration for conifers may be about 13 per cent greater than for hardwoods and during the winter may be twice as great. Although some of the differences in Penman's study are attributable to differences in interception, both between species and seasons, there is no doubt that transpiration loss is greater in conifers. Root mass and depth are correlated with transpiration; shallow-rooted grass will transpire less water than the deeper-rooted forest stands which can tap a greater volume of soil (Douglass 1967; Pyatt & Craven this volume).

To summarize, the role of evapotranspiration is one of considerable importance in determining the quantity and timing of water flows from catchments. Since vegetation type, structure and density all strongly influence both transpiration and interception losses, manipulation of forest vegetation will affect the hydrological balance, both annually and seasonally. Control of evapotranspiration through forest management offers the greatest opportunity for increasing or at least influencing water supplies from catchments.

Studies on the effects of manipulation of forest stands on the hydrological balance are numerous and this paper will only attempt to summarize the salient points. Studies on the conversion of vegetation types are not numerous but trends are identifiable. Hibbert (1967) reviewed much of the world literature describing results of forest cutting and/or conversion effects on water yield from catchments. He made the

following generalizations that summarize the studies:

1. Reduction of forest cover increases water yield.
2. Establishment of forest cover on sparsely vegetated land decreases water yield.
3. Response to treatment is highly variable and, for the most part, unpredictable."

There is little correlation between first year increase in water yield and the percentage reduction in forest cover. However, water yield increases for all studies to-date fall below a linear line between zero increase at no reduction in cover to 450 mm increase at 100 per cent cover reduction. In other words, studies the world-over have indicated that the maximum water yield increase expected following 100 per cent forest removal is 450 mm wherever precipitation exceeds evapotranspiration. The increases in water yield following forest cover reduction are primarily due to reduction in transpiration and interception losses although at the same time soil evaporation increases due to greater soil moisture levels and more energy reaching the soil surface. Regrowth of forest vegetation results in a decline in water yield (Hibbert 1967). The rate of water yield decline is directly related to the rate of regrowth.

Water yield generally decreases after forest cover is established on previously non-forested areas. The magnitude of water yield caused by establishing forest cover on non-forested areas, is about one-half the water yield increase expected if the same amount of forest cover was removed by harvest (Hibbert 1967). Several reasons are possible for these dissimilar results. One may be that the range of observations for establishing forest cover is much smaller than studies on forest cover reduction and secondly, the afforestation sites are usually occupied by vegetation that is actively evapotranspiring before the forest is established.

Converting forests to other types of vegetation often results in increased water yield. Croft & Monninger (1953) observed that replacement of an aspen forest with an herbaceous cover increased water available for streamflow by 100 mm or 8 per cent of the annual precipitation, and further removal of the herbaceous cover increased it by another 100 mm. Conversion of a hardwood forest to heavily fertilized grass resulted in no increase in water yield for the first year (Hibbert 1969). As grass productivity declined, water yield increased each successive year. At the end of the fifth year, water yield from the grass was about 1.5 times that expected from the hardwood stand. Dry matter production on the grass catchment declined at the same rate as water yield increased. Fertilization of the grass after five years resulted in reduced water yield and increased dry matter production to the original first year levels.

The manner in which water yield changes are distributed

throughout the year following manipulation of the vegetative cover appears to be a function of precipitation pattern and form, e.g. snow, rain, soil depth, topography, nature of the manipulation and type of vegetation. On an area newly planted with pine, increased interception loss in the dormant season decreased seasonal flow (Schneider & Ayer 1961). When precipitation is uniformly distributed throughout the year, initial increases in water yield may be greatest during the growing season. As the forest regrows, these increases diminish and may shift to other seasons (Hibbert 1967). The shift is particularly noticeable when a species change is involved. In a hardwood watershed planted with white pine, after fifteen years, the water yield in every month was less than that from the original hardwood forest (Swank & Douglass 1974). The greatest reductions came during the dormant and early growing season which together represented 60-70 per cent of the annual reduction in water yield. Interception losses in the dormant season were greater than they would have been under hardwood. In the early spring the pine leaves were intercepting water and actively transpiring while the hardwood leaves were still emerging.

There are only a few studies on the effects of forest manipulation on peak flows and volume of stormflow. Hewlett & Helvey (1970) observed that 100 per cent reduction of forest cover in a high precipitation mountain catchment increased peak flows by an average of 7 per cent and stormflow volumes by an average of 11 per cent. During a record storm the stormflow volume increased by 22 per cent. On the other hand, during small and intermediate storms there was little increase in peak flow and a moderate increase in total stormflow volume. Increases in stormflow volume were attributed to reduced soil water storage availability due to reduced evapotranspiration. Complete forest removal in a mountain catchment also resulted in moderate increases in peak flows and stormflow volume (Hornbeck 1973), subject to there being a considerable snow pack in winter. Peak flows and total volumes were increased (i) during the growing season due to higher soil water contents, (ii) during the snow-melt season due to more rapid melting, and (iii) were the same in the dormant season before snow-melt began because soil water contents were unchanged.

FORESTS AND WATER QUALITY

Water flowing from forested catchments is often considered to be of highest quality and suitable for most intended uses. There is, however, considerable variation possible in the natural water quality since it reflects influences of vegetation type, climate, soils, geology and topography. Forest management activities can affect water quality markedly through increased erosion, increased rate of

soil leaching and species conversion. Erosion is generally the result of non-judicious management practices and can be controlled through better planning and application of current technology. Change in forest stand characteristics by harvesting or conversion may cause biological and chemical changes in the soil, changes in soil water levels and as a result, the chemical concentration of water leached to the stream.

An often cited study dealing with forest harvest and water quality is that made at Hubbard Brook, New Hampshire (U.S.A.). Borman et al. (1968) reported that following complete harvest of a hardwood forest catchment and subsequent treatment with herbicide to control regrowth, losses of nitrogen and specific cations were drastically increased. Reasons cited were that (i) reduced evapotranspiration caused an increase in water movement through the soil, (ii) reduced root systems decreased nutrient uptake, and (iii) the rate of mineralization was increased. Although not intended to simulate a practical forest management situation, the study has been widely quoted as applicable to forest management operations.

Neary (1977) reviewed the results of eight harvesting and water quality studies, including that at Hubbard Brook. He reported that the studies support the premise that well-planned and -managed practical harvesting operations produce relatively small increases in nutrient losses to streamflow, particularly where regrowth of vegetation is swift. Swank & Douglass (1975) reported the nutrient fluxes and streamflow quality in eight mature hardwood forests and sixteen other forests that had been altered by harvesting or changes in land use. They found that the nutrient cycles of young hardwood coppice reproduction forests were as closed as those in mature hardwood forests, i.e. there was no difference in loss of nutrients. Conversion from hardwoods to white pine reduced the loss of most nutrients with the exception of nitrate-nitrogen which increased. Harvested forests returning to natural vegetation had elevated nitrate-nitrogen concentrations in the stream water for at least ten years after harvest. Partial defoliation by insects of a mature hardwood forest also caused a temporary increase in the export of nitrate-nitrogen.

Nitrate-nitrogen is one of the most mobile ions in ecosystems and species composition affects its export from catchments. Todd et al. (1975) reported that monthly averages of nitrate-nitrogen in stream water for grassed, white pine and hardwood areas in natural succession were 0.8, 0.2 and 0.003 mg/l, respectively. The populations of soil nitrifying bacteria in each ecosystem corresponded with the magnitude of export; decreasing with decreasing export. The authors postulated that as the succession approaches climax, the

nitrifying process is either inhibited, ammonia-nitrogen is better utilized by the vegetation, or both. Tamm et al. (1974) found nitrification to be greater in fertile soils and this was reflected in somewhat elevated levels of nitrate-nitrogen in ground water. They concluded that leaching from fertile sites following harvest will be somewhat offset by the more intensive regrowth of vegetation. Nitrate-nitrogen leaching would be most pronounced where regrowth is delayed by regeneration practices such as application of herbicides, burning or scarification.

Forest burning increases the solubility of some cations, notably K, Ca and Mg and the likelihood of their being leached to the streams. Total N and P are not directly increased by burning; however, soluble P and nitrate may increase due to increased soil microbial activity. Harvest and subsequent slash burning of a beech - podocarp forest increased the level of N, P, K, Ca and Mg in the stream (Neary et al. 1978). Potassium export was large and was probably caused by a hot burn of slash concentrated near the stream channel. Most studies show minimal effects of fire on water quality unless all vegetation and the forest floor is destroyed and water travels to the stream directly over the soil surface. Logging of radiata pine followed by slash burning resulted in an increase in nutrient movement within the soil profile, but nutrient levels in the ground water were not increased (Webber & Barton 1978). The volatility loss of nitrogen was considered to be more detrimental to site fertility than any leaching losses that occurred.

The effects of forest fertilization on water quality appear to be closely related to the method of application, the type of fertilizer applied and the nature of the soil and forest fertilized. Tamm et al. (1974), after a review of numerous fertilization studies, concluded that nitrate-nitrogen is the most critical problem and fertilization operations should be carried out to minimize its probability of movement to streams. Direct application of fertilizer to streams, particularly during aerial application, has often been the sole reason for fertilization affecting stream water quality (Nutter & Ike 1971; Moore 1974). The effects of direct application to the stream often last from a few days to several weeks. Except where readily leachable forms of nitrogen fertilizer are used, the application of fertilizer to forest stands has little effect on water quality when proper safeguards are employed and there is no direct movement of water over the soil surface to the stream channel. The use of pesticides and herbicides in the practice of forest management must follow similar precautions (Fredriksen, Moore & Norris 1973).

INTENSIVE PLANTATION MANAGEMENT EFFECTS ON WATER QUANTITY AND TIMING

From the foregoing discussion it is evident that manipulation of forest vegetation, whether it is a partial or a complete harvest or conversion to another forest on non-forest species, directly affects the hydrological balance of catchments. There is little evidence regarding the effects of intensive management of even-aged plantations. By applying the results of the studies discussed and the known biological and physical processes that characterize the hydrological balance, the type and relative magnitude of even-aged plantation management effects on the hydrological balance of catchments can be estimated.

Even-aged plantations under intensive management are expected to be composed of genetically superior trees with greater growth rate, vigour and density than the natural vegetation they replace. The influences on the hydrological balance, all other factors being constant, are positively correlated with the extent to which vegetation occupies the site. A dense, vigorously growing plantation will increase the interception and transpiration losses because of greater above-ground biomass.

The evidence further suggests that the increase in transpiration and interception from fully-stocked plantations will decrease soil water levels under most climatic conditions. Rogerson (1968) has shown that the amount of precipitation reaching the forest floor in a loblolly pine plantation increased by 2 per cent for every 2 sq.m reduction in stand basal area. Reduction of basal area by 50 per cent to an optimum density increased the net annual precipitation to the forest floor by 100 mm or 8 per cent of the annual precipitation. In regions of low precipitation during the growing season it is interesting to speculate whether less dense stands would have greater productivity because of higher soil water availability. Dahms (1971) reports that a precommercial thinning of lodgepole pine substantially increased productivity and soil water contents. As growth progressed the soil water contents decreased to pre-thinning levels.

The water yield from fully-stocked plantations will probably be less than from the natural vegetation, although exceptions are possible. Pereira (1973) reports that after crown closure annual water use by a pine plantation was equal to that of a natural bamboo forest in East Africa. On the other hand, a white pine plantation reduced water yield by 20 per cent, about 200 mm, from that expected from the original hardwood forest (Swank & Douglass 1974). A generalization might be that catchment water yields will be decreased if the plantation is more dense, has greater above-ground biomass and retains its leaves longer than the vegetation it is replacing.

The same factors will result in changes in monthly or seasonal water yield, with the greatest differences expected in the growing season and in the dormant season where interception loss is increased over that for a natural vegetation.

When plantations replace non-forest vegetation, the recession of growing season streamflow will be more rapid than that of the original vegetation. Wicht (1967) reports that growing season flow frequently ceases when plantations replace natural, non-forest vegetation in South Africa. Water yield increases can also be expected when plantations are heavily thinned. Experience suggests that light thinnings will not generally increase water yield because the newly available soil water resulting from initially reduced transpiration and interception loss will be used by the existing vegetation. In other words, depending on the extent to which the site is occupied by vegetation, a threshold level of vegetation removal must be reached before water yield increases occur. Harvesting at the end of a plantation rotation will lead to increased water yield. Following regeneration the water yield will steadily decline until it equals that prior to harvest (Swank & Helvey 1970).

Decreased soil water levels under plantations may result in decreased stormflow volumes and peak flow resulting from small to moderate storms. It is unlikely that there will be any difference in flood response between plantations and natural forest when large storms occur, although plantations could have a substantial beneficial effect when they replace non-forests. So little experimental evidence exists on the effect of forest harvesting and/or conversion on flood flows, that only generalizations may be drawn from the literature.

Although changes in the hydrological balance can be expected from the intensive management of even-aged plantations, the magnitude of the changes is difficult to predict. Upper bounds may be placed on the changes (Hibbert 1967) but rarely can the climatic, topographic, soil and vegetation factors of one experimental site be directly extrapolated to another. The magnitude of change in the hydrological balance may be substantial and readily detectable in small catchments. As catchment size increases and land use becomes a mosaic of plantations and other land uses, the downstream influence of the small catchment is diminished. The effects can be further reduced by scheduling management activities in a catchment so that water yield increases from some plantations compensate for water yield decreases in others. A simple way to minimize impacts is to manage a large plantation as a series of blocks, all in various stages of development and water use.

When compared with natural forests, the influence of plantations on the hydrological balance will, in most places, not be severe. If plantations replace non-forests the

magnitude of change in the hydrological balance may be substantial and reduce water supplies appreciably. On the other hand, intensive management activities often associated with plantations can result in much more drastic changes in the hydrological behaviour of the catchment. Intensive networks of roads and trails and other activities that remove the soil's protective cover result in more rapid and greater flood peaks and often in increased volumes of stormflow as well. These effects can often be more damaging to downstream water supplies than silvicultural operations in plantations.

INTENSIVE PLANTATION MANAGEMENT EFFECTS ON WATER QUALITY

The effect of intensive culture of even-aged plantations on water quality may be varied and depends on a number of site factors as well as the degree and type of management disturbance to the site. If the plantation species recycle more of the site nutrients than the original vegetation, fewer of the nutrients will be leached to the stream. In general, the establishment of plantations will not adversely affect the concentration of dissolved minerals to stream water. Wherever plantations replace non-forest vegetation, an improvement in water quality can be expected because erosion losses from non-forest vegetation are generally greater than from forests. Erosion of particles to the stream channel increases both suspended and dissolved minerals and organic matter. Shorter rotations associated with plantations may cause a greater amount of nutrients to be removed from a site, reducing the pool from which nutrients may be leached to the stream channel. This problem is magnified when whole-tree harvesting practices are employed in each rotation (Waide & Swank 1977). If a site is quickly occupied by a vigorous regrowth of vegetation following harvest, only a slight increase in the leaching of nutrients may be expected. There appears to be some correlation between lengths of growing season and the amount of initial leaching; the shorter the growing season, the greater the amount leached.

Perhaps the most disruptive of plantations effect on water quality is due to intensive management practices such as fertilization, chemical brush control, burning and regeneration practices. The judicious use of, chemicals and fertilizer will minimize impacts, particularly if the formulations used are readily utilized or are of the slow release type, excessive application rates are avoided and application is not made directly to the stream channel or its immediately adjacent area. Practices which remove vegetation or delay its regrowth such as burning and scarification, increase the possibility of increased nutrient leaching to the stream.

Intensive harvesting practices associated with plantations that require an extensive network of roads and

trails and regeneration practices that bare mineral soil, can all lead to excessive erosion. The impacts of these practices, if not well planned and executed, will likely be greater than all other effects on water quality.

REFERENCES

- Bates, C.G. & Henry, A.J. (1928). Forest and streamflow experiments at Wagon Wheel Gap, Colorado, U.S. Weather Bureau Monthly Weather Review, Supplement No. 30. 79pp.
- Borman, F.H., Likens, G.E., Fisher, D.W. & Pierce, R.S. (1968). Nutrient loss accelerated by clearcutting of a forest ecosystem. *Science*, 159, 882-884.
- Burgy, R.H. & Pomeroy, C.R. (1958). Interception losses in grassy vegetation. *Transactions of the American Geophysical Union*, 39, 1095-1100.
- Croft, A.R. & Monninger, L.V. (1953). Evapotranspiration and other water losses in some aspen forest types in relation to water available for streamflow. *Transactions of the American Geophysical Union*, 34, 563-574.
- Dahms, W.G. (1971). Growth and soil moisture in thinned lodgepole pine. U.S. Department of Agriculture Forest Service Research Paper, PNW-127, 32pp.
- Delfs, J. (1967). Interception and stemflow in stands of Norway spruce and beech in West Germany. "Forest Hydrology". *Proceedings of an International Symposium on Forest Hydrology*, pp. 179-185. Pergamon Press, New York.
- Douglass, J.E. (1967). Effects of species and arrangement of forests on evapotranspiration. "Forest Hydrology". *Proceedings of an International Symposium on Forest Hydrology*, pp. 451-461. Pergamon Press, New York.
- Eungler, A. (1919). Untersuchungen über den Einfluss des Waldes auf den Stand der Gewässer. *Mitteilungen der Schweizerischen Zentralanstalt für das forstliche Versuchswesen* # 12. 625 pp.
- Fredriksen, R.L., Moore, D.G. & Norris, L.A. (1973). The impact of timber harvest, fertilization and herbicide treatment on stream water quality in western Oregon and Washington. "Forest soils and forest and management". *Proceedings of the Fourth North American Forest Soils Conference*, pp. 283-313. Laval University, Quebec.
- Helvey, J.D. (1967). Interception by eastern white pine. *Water Resources Research*, 3, 723-729.
- Helvey, J.D. (1971). A summary of rainfall interception by certain conifers of North America. "Biological Effects in the Hydrological Cycle". *Proceedings of the 3rd International Symposium for Hydrology Professors*, pp. 103-113. Purdue University, West Lafayette, Indiana.
- Hewlett, J.D. & Helvey, J.D. (1970). Effects of forest clear-felling on the storm hydrograph. *Water Resources Research*, 6, 768-782.

- Hewlett, J.D. & Nutter, W.L. (1969). An outline of forest hydrology. University of Georgia Press, Athens, Georgia. 137pp.
- Hibbert, A.R. (1967). Forest treatment effects on water yield. "Forest Hydrology". Proceedings of an International Symposium on Forest Hydrology, pp. 527-543. Pergamon Press, New York.
- Hibbert, A.R. (1969). Water yield changes after converting a forest catchment to grass. *Water Resources Research*, 5, 634-640.
- Hornbeck, J.W. (1973). Storm flow from hardwood forested and cleared watersheds in New Hampshire. *Water Resources Research*, 9, 346-354.
- Leyton, L. & Carlisle, A. (1959). Measurement and interpretation of interception of precipitation by forest stands. *International Association of Hydrology Symposium, Publication 48*, 111-119.
- Lull, H.W. & Sopper, W.E. (1967). Prediction of average annual and seasonal streamflow of physiographic units in the Northeast. "Forest Hydrology". Proceedings of an International Symposium on Forest Hydrology, pp. 507-522. Pergamon Press, New York.
- Moore, D.G. (1974). Impact of forest fertilization on water quality in the Douglas fir region - a summary of monitoring studies. Proceedings 1974 National Convention of the Society of American Foresters, Washington D.C. pp. 209-219.
- Neary, D.G. (1977). Impact of timber harvesting on nutrient losses in streamflow. *New Zealand Journal of Forestry*, 22, 53-63.
- Neary, D.G., Pearce, A.J., O'Loughlin, C.L. & Rowe, L.K. (1978). Management impacts on nutrient fluxes in beech - podocarp - hardwood forests. *New Zealand Journal of Ecology*.
- Nutter, W.L. (1975). Moisture and energy conditions in a draining soil mass. Environmental Resources Center, Georgia Institute of Technology, Atlanta, Georgia, Report ERC 0875. 77pp.
- Nutter, W.L. & Ike, A.F. (1971). Evaluating effects of forest fertilization on water quality. *Agronomy Abstracts*, American Society of Agronomy, Madison, Wisconsin, p.161.
- Penman, H.L. (1967). Evaporation from forests: a comparison of theory and observation. "Forest Hydrology". Proceedings of an International Symposium on Forest Hydrology, pp. 373-380. Pergamon Press, New York.
- Pereira, H.C. (1973). Land use and water resources. Cambridge University Press, London. 246pp.
- Rogerson, T.L. (1968). Thinning increases throughfall in loblolly pine plantations. *Journal of Soil and Water Conservation*, 23, 141-142.
- Schneider, J. & Ayer, G.R. (1961). Effect of reforestation on

- streamflow in central New York. U.S. Geological Survey Water Supply Paper 1602. 61pp.
- Swank, W.T. & Douglass, J.E. (1974). Streamflow greatly reduced by converting deciduous hardwood stands to pine. *Science*, 185, 857-859.
- Swank, W.T. & Douglass, J.E. (1975). Nutrient flux in undisturbed and manipulated forest ecosystems in the southern Appalachian mountains. Publication # 117 de l'Association Internationale des Sciences Hydrologiques. Symposium de Tokyo. pp. 445-456.
- Swank, W.T. & Helvey, J.D. (1970). Reduction of streamflow increases following regrowth of clearcut hardwood forests. IASH-Unesco Symposium on the Results of Research on Representative and Experimental Basins, Wellington, New Zealand.
- Swank, W.T. & Miner, N.H. (1968). Conversion of hardwood-covered watersheds to white pine reduces water yield. *Water Resources Research*, 4, 947-954.
- Tamm, C.O., Holmen, H., Popovic, B. & Wiklander, G. (1974). Leaching of plant nutrients from soil as a consequence of forestry operations. *Ambio*, 3, 2211-2221.
- Todd, R.L., Swank, W.T., Douglass, J.E., Kerr, P.C., Brockway, D.L. & Monk, C.D. (1975). The relationship between nitrate concentration in the Southern Appalachian mountain streams and terrestrial nitrifiers. *Agro-ecosystems*, 2, 127-132.
- Waide, J.B. & Swank, W.T. (1977). Simulation of potential effects of forest utilization on the nitrogen cycle in different southeastern ecosystems. *Watershed Research in Eastern North America. A workshop to compare Results Vol. II*, pp. 767-789. Smithsonian Institution, Edgewater, Maryland.
- Webber, B. & Barton, P.G. (1978). Effect of logging and slash burning on the chemical properties of water passing through the soil profile. New Zealand Forest Service, Forest Research Institute, Soils and Productivity Report No. 99 (Unpublished). 14 pp + Appendices.
- Wicht, C.L. (1967). Forest hydrology research in the South African Republic, "Forest Hydrology". Proceedings of an International Symposium on Forest Hydrology; pp. 75-84. Pergamon Press, New York.
- Woodruff, J.F. & Hewlett, J.D. (1970). Predicting and mapping the average hydrologic response for the Eastern United States. *Water Resource Research*, 6, 1312-1326.



SOIL CHANGES UNDER EVEN-AGED PLANTATIONS

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SUMMARY

Most of the soils of upland Britain are seriously affected by waterlogging. Afforestation reduces the supply of rainwater to the soil because of evaporation from the canopy. Ironpan soils have a perched water table above the pan but more permeable and better aerated layers beneath. In some examples the presence of the tree crop cures the waterlogging, in others preliminary breakage of the pan by cultivation is necessary. Aeration is then likely to be satisfactory throughout the profile. Gley soils have a high water table due to low permeability of the deeper layers and drainage treatments are only partially effective. The effects of spruce crops on the soil physical properties are small and we must look to other species more tolerant of the conditions to act as soil improvers. Deep peats of the blanket peat type are highly humified and undergo progressive drying after canopy closure. Strong shrinkage produces wide cracks which dramatically alter the drainage and aeration properties of the peat.

RÉSUMÉ

La plupart des sols des hautes terres de Grande Bretagne sont mouilleux. Le boisement réduit l'apport en eau de pluie au sol à cause de l'évaporation par le couvert. Les sols d'alios ont une nappe perchée au dessus de l'alios mais des couches plus perméables et mieux aérées au dessous. Dans certains cas, la présence d'un peuplement élimine le sol mouilleux, dans d'autres, il est nécessaire de casser l'alios au préalable par un travail du sol. En conséquence, l'aération de tout le profil pédologique sera satisfaisante. Les sols à gley

ont une nappe proche de la surface à cause de la faible perméabilité des couches plus profondes et les traitements par drainage ne sont pas entièrement satisfaisants. Les effets des peuplements d'épicéas sur les propriétés physiques du sol sont moindres et l'on doit se tourner vers d'autres essences, plus tolérantes des conditions du sol, qui seraient à même d'améliorer le sol. Des tourbières profondes, présentes sur les collines, forment beaucoup d'humus et séchent progressivement après la fermeture du couvert. Un retrécissement important produit de larges crevasses qui changent, de façon dramatique, le drainage et les propriétés d'aération de la tourbière.

ZUSAMMENFASSUNG

Die meisten Böden des britischen Hochlandes sind hydromorph beeinflusst. Aufforstung reduziert den Wassergehalt des Bodens durch die Transpiration des Blätterdaches. In Böden mit Ortstein wirkt dieser wasserstauend und darunter befinden sich meist durchlässigere und besser durchlüftete Horizonte. In einigen Fällen beseitigt das Vorhandensein von Waldbeständen den Wasserstau, in anderen ist es notwendig, die undurchlässige Schicht vorher mechanisch durch Bearbeitung zu beseitigen. Dies bewirkt auch eine Verbesserung des Lufthaushalts im ganzen Profil. Gleye besitzen aufgrund der geringen Durchlässigkeit der tiefergelegenen Horizonte einen hohen Wasserstau, Entwässerungsmaßnahmen sind nur teilweise wirksam. Da Fichtenbestände die physikalischen Eigenschaften des Bodens kaum verändern können, müssen wir andere angepasstere Gattungen als Bodenverbesserer heranziehen. Die mächtigen Torflagen des Deckenmoores sind stark humifiziert und enthalten ursprünglich viel Wasser, werden aber trockener, sobald sich das Blätterdach schließt. Starke Schrumpfung lässt breite Risse entstehen, die die Entwässerungs- und Belüftungsbedingungen drastisch verändern.

INTRODUCTION

Afforestation is taking place in upland Britain on soils which carried forest in earlier post-glacial times but which have been treeless for a period ranging from a few hundred to a few thousand years. During this latter period there have

continued to be climatic fluctuations but there is little doubt that the absence of a tree cover has itself contributed greatly to widespread changes in soil conditions (Dimbleby 1962).

One of the most powerful effects of the removal of forest in our climatic conditions is to increase the supply of rainwater to the soil surface. This can have various effects including increasing the rate of weathering of rock fragments, increased leaching of soluble components, more prolonged anaerobism and the development of gley phenomena, and the faster accumulation of peat. More than three-quarters of the area of upland Britain which has been afforested carries soils which were previously seriously affected by waterlogging. These are three main groups of soils: ironpan soils, surface-water gleys and deep peats (Pyatt 1970), alternatively termed stagnopodzols, stagnogley soils and peat soils (Avery 1973).

For afforestation to be successful on these soils some kind of site improvement is usually necessary, either physical, through cultivation or drainage; chemical, through the application of fertilizers; or biological, through control of competing weeds. When the tree crop has been established and particularly after the canopy has closed, the growth of the trees introduces further changes in site conditions. This paper is mainly concerned with the effects of afforestation on the moisture regime and aeration of these three main groups of soil.

IRONPAN SOILS

Ironpan soils appear to be restricted to the most humid parts of the temperate zones of the world and to similar climatic conditions on tropical mountains (Fitzpatrick 1971; Crompton 1956). They are particularly important in Britain where they represent some 20 per cent of the uplands,

A layer of peat, commonly 100-300 mm thick, occurs at the surface. Beneath this are the two characteristic horizons of the soil, a grey-coloured, mineral horizon with eluvial and gleying features (Eg), and a thin ironpan. Beneath the ironpan, the B horizon or subsoil is brownish in colour and usually friable in consistence. Indurated material (fragipan) often occurs beneath the subsoil but may directly underlie the ironpan (horizon notation follows Hodgson (1974)). The Eg horizon often has a greenish or olive hue as a conspicuous gley feature and foresters have for many years appreciated that these soils are wet or waterlogged at the surface for much of the year. Our understanding of subsoil conditions has been much less certain, partly because penetration of the subsoil by tree roots is very variable and partly because any investigation beneath the ironpan tends to destroy the effect of the pan as a barrier to water. In areas prior to

afforestation soil pits or small boreholes often contain water even though they penetrate the ironpan. This is especially so where indurated material directly underlies the pan.

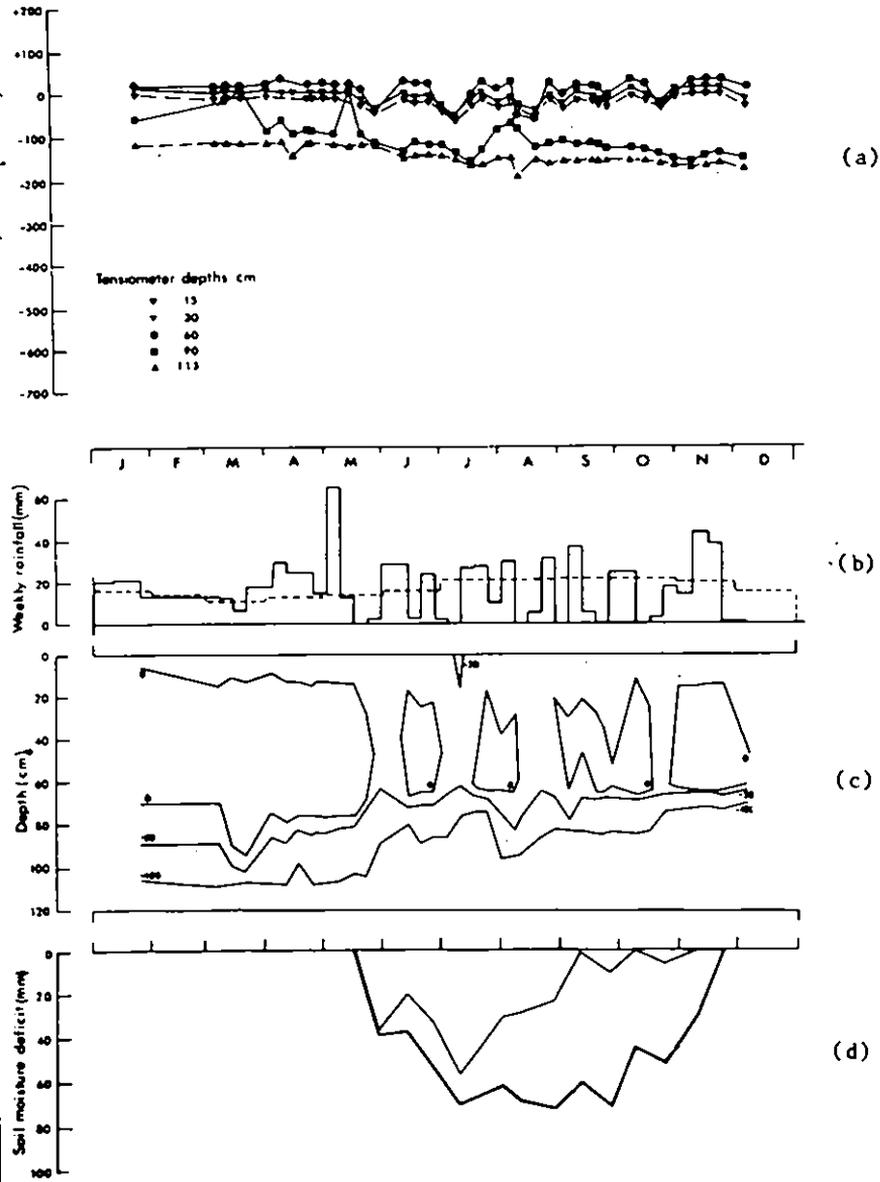
At Teindland (Speymouth Forest) in northeast Scotland research into afforestation methods has been in progress since 1926 (Zehetmayr 1960). The area is a so-called 'upland heath' with a vegetation dominated by Calluna vulgaris, with some Trichophorum caespitosum and Sphagnum species which are indicative of the surface wetness. The peat layer is thin, usually less than 150 mm, but a greenish gley colour is seen in the freshly exposed Eg horizon. A strongly indurated layer about 300 mm thick underlies the ironpan beneath which the parent material is somewhat looser. The annual rainfall of 900 mm is low for upland Britain.

The need for cultivation to break up the peat, the Eg horizon and ironpan was recognized by Muir (1934), who was of the opinion that the indurated material was more permeable than the horizons above. Early attempts at cultivation were restricted in depth by the very stony nature of the soil, but it was soon found that pines and larches could be established successfully provided that a raised planting position was provided. Improved early growth was achieved with deeper and more complete ploughing treatments and in 1952 a key experiment was laid down with large replicated plots of six intensities of cultivation, the deepest of which caused frequent breakage of the ironpan which lies at 350 mm depth. A later 'generation' of tine ploughs (Taylor & Everard 1970) has been designed to disturb these soils to depths of at least 700 mm and another experiment laid down in 1970, compares complete cultivations to depths which were sufficient to eliminate the ironpan and greatly disrupt the indurated material. Early results of the 1952 experiment confirmed previous experience that more rapid early growth of various tree species, especially Sitka spruce (Picea sitchensis (Bong.) Carr), was produced by the more intensive cultivation treatments (Henman 1964; Taylor 1970). After fifteen years, however, the growth advantage of the best treatments was sharply reduced (Thomson & Neustein 1973) and this has stimulated further research into the soil condition under the trees.

In the 1952 experiment investigations of root development in relation to the cultivation have shown that the intensity of fine rooting is greatest in the overturned peat slice, decreases in the loosened or overturned mineral soil and is

Fig. 1. Moisture regime of a heathland for 1977 (weekly data 26 Jan - 7 Dec). (a) tensiometers, (b) broken line is mean monthly rainfall on a weekly basis, (c) interpolated iso-potential lines for the soil profile, derived from (a) and borehole water levels, (d) estimated deficits thin line for grassland, thick line forest.

Teindland Ironpan soil - Heathland 1977



still less in the undisturbed Eg horizon. The undisturbed, indurated material appears to have no roots. The loosened zone is 350 mm deep, with rooting extending to 400-450 mm depth. In the 1970 experiment, the general disturbance of the soil is to 500 mm depth, although the tine is recorded as having reached 700-900 mm. At six years of age the trees have not yet fully exploited to 500 mm, so there is no indication whether cultivation has allowed penetration of the looser material beneath the former indurated layer.

Occasionally the question is asked whether the indurated material will gradually regain its hardness. The high bulk density (1.75-2.00 g/cu.cm on a dry weight basis) has been produced by glacial or periglacial processes (Fitzpatrick 1956) and the material has been further hardened by slight cementation (Pyatt 1978). Cultivation reduces the bulk density to 1.0 g/cu.cm and the disturbed material breaks up into fine fragments because it is extremely brittle. It is therefore difficult to see how cementation could recur without recompaction and that seems unlikely in material which is now much mixed with overlying horizons, including peat.

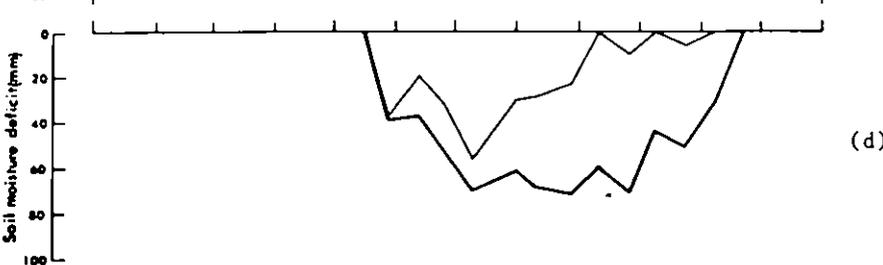
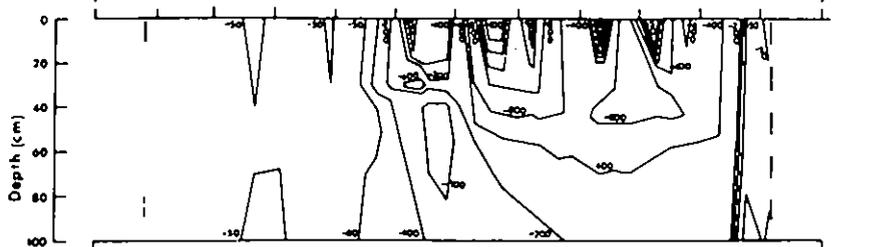
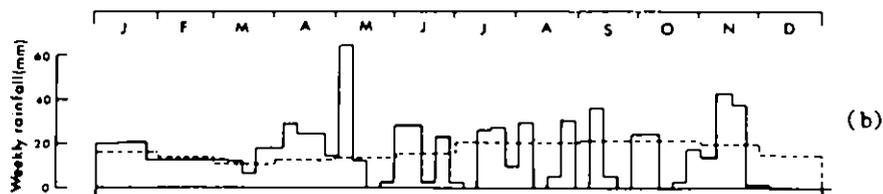
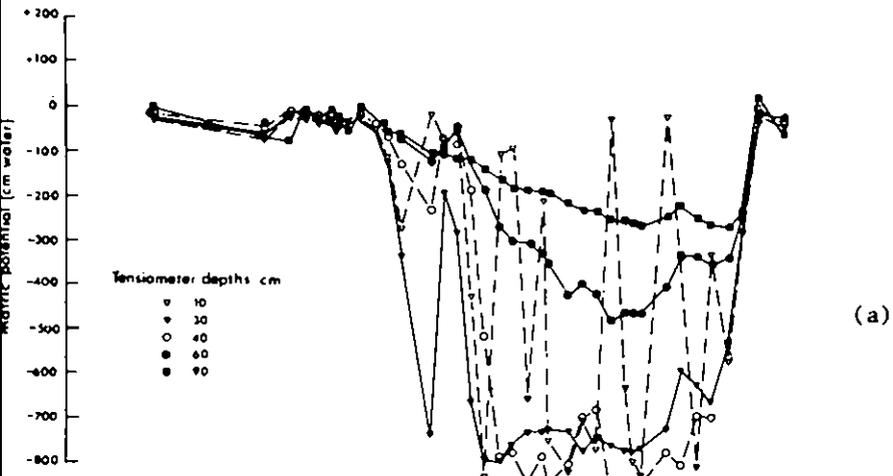
The soil water regime under the tree crop has been compared with that under the open heathland. Several cultivation treatments have been examined beneath crops of Scots pine (*Pinus sylvestris* L.), and a mixture of lodgepole pine (*P. contorta* Dougl. ex Loud.), and Japanese larch (*Larix kaempferi* (Lambert) Carr.), which are 10-13 m tall. Boreholes with perforated liners and tensiometers have been installed to various depths above and below the ironpan (Pyatt 1978).

The difference between heathland and forest water regimes is very striking, but differences between cultivation treatments are negligible. Figures 1 and 2 show results for 1977 for one set of tensiometers typical of each vegetation type. The upper part of each figure shows the matric potentials ('water pressures') recorded by each of five tensiometers assessed at weekly intervals. The second part of the figure gives the weekly rainfall recorded in the open heathland. The broken line represents the mean monthly rainfall converted to a weekly basis. In the third part of the figure the tensiometer results are used together with borehole water level data to produce a chart of iso-potentials.

Under the heathland there was a perched water table in the upper 600 mm of the soil. Since the ironpan was at 350 mm, this implies that the indurated layer was only slowly

Fig. 2. Moisture regime of Sitka spruce forest for 1977 (weekly data 26 Jan - 7 Dec). (a) tensiometers, (b) broken line is mean monthly rainfall on a weekly basis, (c) interpolated iso-potential lines for the soil profile derived from (a) and borehole water levels, (d) estimated deficits, thin line for grassland, thick line forest.

Teindland Ironpan soil - Forest (SP) 1977



permeable. The soil was not waterlogged beneath the indurated layer at any time. Shallow boreholes contained water for much of the year but those penetrating beyond 600 mm depth were generally empty. Under the forest waterlogging did not occur at any depth.

The lowest part of Figures 1 and 2 are estimated soil moisture deficits (SMD), that is the amount by which the cumulative transpiration exceeds the cumulative rainfall. This method of calculation is based on a technique developed for grasslands (Smith 1967). See Jarvis and Stewart, this volume, for a critical survey. Mean monthly potential transpiration values for the locality are obtained from tables with a correction applied for the elevation of the particular site. The mean values are then corrected to the particular year using the monthly values of sunshine duration. The calculation of the SMD proceeds on a fortnightly basis, using actual rainfall for the site and half of the monthly transpiration. During the period of deficit the actual transpiration is allowed to fall below the potential transpiration according to a simple model of moisture availability. The thin line represents the course of the SMD for an assumed short grassland. The thick line is obtained using the same transpiration values but only 70 per cent of the rainfall in each fortnight. In other words, this assumes an interception loss of 30 per cent of gross rainfall, without any adjustment to transpiration. The validity of this assumption has not yet been widely tested (Jarvis & Stewart, this volume). It is one of several possible ways of adjusting grassland transpiration values upwards to allow for the greater total evapotranspiration of a forest, and it is likely that tree species will have substantially different transpiration rates as well as different interception rates.

The SMD for forest (thicker line) fits quite well with the observed moisture regime, indicating that the assumptions used in the estimates are probably of the right order of magnitude. The very small amount of drying in the heathland soil in comparison with the grassland SMD implies that the heathland vegetation transpires only slowly.

Soil aeration is also being assessed at these sites in 1978. Air or water samples are taken by hypodermic syringe from sampling probes at two depths above the ironpan and two below. Analysis of samples is by gas chromatography (Smith 1976).

Samples have been taken at three to four weeks intervals and so far results have been similar on each occasion. Under the heathland, the oxygen concentration in the layers above the ironpan was between 1-7 per cent by volume. Beneath the pan the oxygen concentration was 15-17 per cent by volume. Under the forest the oxygen concentration was between 20-21 per cent by volume throughout the soil profile.

The elimination of the perched water table and associated anaerobism in ironpan soils after afforestation may not be so effective in regions of higher rainfall. At Newcastleton Forest in south Scotland similar studies have been made in ironpan soils with 300-400 mm of peat where spruce crops (*Picea* spp) were planted on turfs between shallow furrows which did not break the ironpan. The rainfall here is 1400 mm/yr. Under the forest the soil above the ironpan is waterlogged for periods of several weeks during the winter. Although not waterlogged in the summer, it remains wet long enough for very low oxygen concentrations to develop. This is in spite of tree roots having penetrated through to the non-indurated subsoil where good aeration persists. In general, therefore, the elimination of poor aeration in these soils requires thorough destruction of the ironpan as well as the drying effect of a tree crop.

GLEYSOILS

Fine textured soils with very low permeability in the subsoil and with pale grey or blue-grey colours, often associated with ochreous mottling, are known as surface-water gleys. Peaty gleys have a surface layer of peat 50-450 mm thick, which is a response to even wetter conditions. The water table is high for most of the year and aeration is poor except close to the surface. These soils are the most extensive in upland afforestation, accounting for some 35-40 per cent of the area. They are mainly planted with spruces which give a higher yield than other species, but neither Sitka spruce nor Norway Spruce (*Picea abies* (L.) Karst.) is capable of rooting below about 450 mm depth. The result is that premature windthrow is endemic in those forests with predominant gley soils.

Successful establishment of crops has been readily achieved using either individual turfs or plough ridges, which give the necessary improved aeration of the planting position. In an attempt to promote rooting into the subsoil many types and intensities of deep drainage have been tried. In spite of some early optimism (Fraser & Gardiner 1967), the effects on the water table have generally been insufficient to justify the cost (Neustein & Thompson 1973). The most promising results have been achieved with closely-spaced mole channels (Hinson, Pyatt & Fourt 1970) and research into this technique is continuing.

Plough furrows 300 mm deep at 1.8 m spacing do encourage somewhat deeper rooting than is achieved on individual turfs, but in terms of crop stability this is more than offset by the reduction in root spread caused by the furrows acting as barriers (Booth 1973). The current recommendation for ground preparation on these soils is therefore a compromise, double-mouldboard ploughing with furrows 450-600 mm deep at

4.5 m spacing. Deep drains intercepting the water from these furrows are sited according to the topography rather than at some predetermined frequency (Thompson in press).

Comparisons of soil moisture content and bulk density under pole-stage spruce and in adjacent unplanted rides reveals that there is a small but significant removal of water from the subsoil under the forest, and that this effect carries over from year to year. Unfortunately, however, the resulting shrinkage of the clay is not yet resulting in cracking but is being taken up by subsidence with an increase in bulk density (Pyatt 1973).

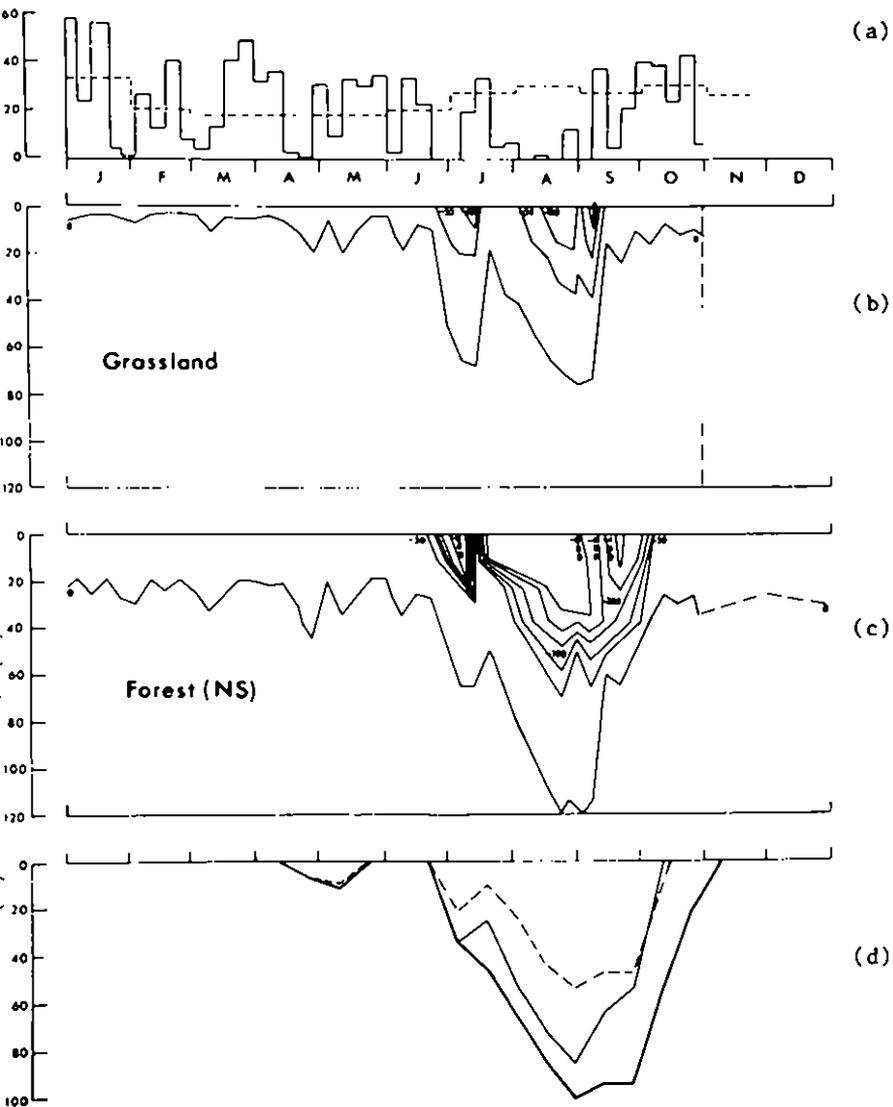
Observations of the soil moisture regime using tensiometers and boreholes show that under the trees the rooted zone dries appreciably during the summer compared with adjacent grassland sites. Figure 3 contains results for 1976 for one of four forest sites and a comparable unplanted site that were studied for three years at Newcastleton forest, Roxburghshire. Tensiometer and borehole data are combined into iso-potential charts.

The degree of drying achieved in the summer beneath the spruce was sufficient to create fissuring and the development of a better soil structure in the rooted zone, whether mineral soil or peat. The relatively small degree of drying in the subsoil was presumably due to poor capillary conductivity of the clay. 1976 was an unusually hot, dry summer, although it followed a wet spring. Drying reached a rather greater depth than in 1974 or 1975 but the general pattern was much the same.

The interception loss for a pole-stage stand of Sitka spruce during the summer months is about 40 per cent of gross rainfall (Ford & Deans, 1978). Using this figure and the same method of calculation as for Teindland— produces a SMD for forest which is too high to fit the observed soil moisture regime. It is possible therefore that the transpiration of Sitka spruce does not reach the values for grassland given by Smith (1967). Thus by setting an arbitrary limit of 1.5 mm/day for the transpiration of the spruce, about half that for grass in June, the SMD shown by the broken line is produced, a much closer fit to the soil data. The rainfall at Newcastleton is

Fig. 3. Moisture regimes for a grassland and a Norway spruce forest for 1976 (weekly data 1 Jan - 29 Oct, monthly thereafter in the forest). (a) Broken line is mean monthly rainfall on a weekly basis, (b) and (c) interpolated iso-potential lines for soil profile based on tensiometer and borehole data, (d) thin line is estimated deficit for grassland, thick line is for forest assuming same transpiration as grass, broken line is for forest with transpiration rate restricted to not more than 1.5 mm/day.

Newcastleton Surface .. water gley 1976



1400 mm/yr and the long time that the canopy is wet must substantially reduce annual transpiration.

During the years 1974, 1975 and 1976 at Newcastleton the non-forested gley soils had a water table at a depth of 0-200 mm for 7-9 months of the year. Under the forest the water table fell to 150-400 mm and the duration was reduced to 6-8 months. Without a change in the climate there is no prospect of a further reduction in the duration of high water table. Prospects for keeping the winter water table at a lower level seem to depend (a) on the extent to which mole drainage can be used, and (b) on whether alternative species to spruces can be found which are capable of deeper rooting. Those worthy of immediate attention are lodgepole pine, which is very tolerant of poorly aerated peat soils, and the alder species (Alnus). The hope would be that a species tolerant of anaerobic conditions could speed up the process of drying the subsoil producing a non-recoverable shrinkage in the form of fissures, in other words a more or less permanent improvement in soil structure, permeability and the level of the winter water table. The silvicultural possibilities include 'pioneer' or soil-improving crops of these species or a more permanent 'stability mixture' of the deep rooting species with Sitka spruce. The search has begun, but is hampered by the shortage of stands of lodgepole pine or alders suitable for study.

Meanwhile there are signs that clearfelling of the first crop of spruce allows the water tables to rise to very high levels during the first year or two when there is little or no transpiring vegetation. Unless replanting on these soils takes advantage of any raised positions, survival may be poor. Conditions during replanting appear to be more difficult for establishment than they were for afforestation.

DEEP PEATS

These are defined as organic accumulations exceeding 450 mm in depth. In the last ten years deep peats have formed an increasing proportion of the sites planted by the Forestry Commission and they now represent about 15 per cent of the total. Peats are classified for forestry primarily according to their nutrient supplying ability which is reflected in the ground vegetation (Tolcman 1973). The most important types of peat can be broadly described as the blanket peats or hill peats with a vegetation of Calluna vulgaris, Trichophorum caespitosum, Eriophorum vaginatum, E. angustifolium and various Sphagnum species. They vary in depth from 450 mm to about 3 m and beneath a fibrous layer some 300 mm thick are strongly humified (H 6-9 on the Von Post scale).

Peat is waterlogged or wet to the surface throughout the year and successful establishment of a tree crop necessitates surface draining and planting on a raised turf or plough ridge. Closely spaced plough furrows and ridges have generally

shown the best early growth; deep drains have produced little response in tree growth although a further lowering of the water table has been achieved (Taylor & Everard 1969).

Since first reported by Binns (1959) it has become increasingly evident that after afforestation, blanket peats become progressively dried and develop wide shrinkage cracks in the humified layer. This process is a non-recoverable alteration in the peat and is obviously much the same as occurs when peat fuel is left to dry in the sun. Every year there is a large surplus of rainfall over transpiration except during dry summer spells when irreversible drying can take place.

A recent survey of the older peatland plantations indicates that drying is slight until canopy closes but then speeds up, and cracks can then develop within two or three years. Drying sufficient to produce cracking takes place more rapidly under lodgepole pine than other species, but under the most suitable conditions does occur under Scots pine, Sitka spruce and Japanese larch. Conditions favourable to rapid drying and cracking are (i) relatively shallow peat, i.e. less than 2 m, (ii) a high humification value and (iii) a relatively dry climate.

Soil moisture regimes under plantations and in adjacent unplanted areas were observed for three years at Inchnacardoch Forest, Inverness-shire and for two years at Naver Forest, Sutherland. The crop at Naver has since been killed by the pine beauty moth (*Panolis flammea*), but before the defoliation was severe, the results shown in Figure 4 were obtained. The sites have relatively shallow blanket peat, 1 m, and the degree of drying shown, both in terms of the permanent crack development and the moisture potentials reached each summer, were much more striking than in peats of 2-4 m depth in the same stand. Both planted and unplanted sites are ploughed, with furrows 250 mm deep from the original surface. Moisture assessments have not been made in the ridge itself. 1976 was unusually dry in spring and summer at Naver, and this is reflected in the long duration of the soil drying season, but moisture potentials as low as those shown, were also reached in 1977 before complete defoliation occurred.

During the winter the water table rose into the cracked zone, in this site at 300-900 mm depth, though not very far because of the rapid drainage. The majority of the dried material was therefore not subjected to prolonged immersion and this may be important in preventing rewetting. There is great silvicultural interest in the possibility of widening the choice of species in the second rotation and the devastation by pine beauty moth has sharpened this interest. Following clearfelling, or perhaps a defoliation, the water tables rises into the cracked zone for longer periods and the possibility of some rewetting is increased. Certainly moisture

potentials remain high throughout the profile because of the absence of transpiring vegetation.

Aeration has not yet been directly measured in the dried peats, but air-filled pore space exceeds 10 per cent by volume even in winter so there is a likelihood that high oxygen concentrations will be maintained.

The speed with which low moisture potentials were reached in spring 1976 and the depth to which they occurred, suggest the possibility that the amount of water able to be held and made available to roots is now rather small. Preliminary calculations of water content changes do not suggest reason for concern but laboratory measurements of water retention curves are being made to check this.

The 'south coastal' provenances of lodgepole pine have shown a marked tendency to become unstable on deep peats and this certainly applies to blanket peat which has become cracked. Roots of pine, and other species, cross beneath the furrows into neighbouring planted strips but do not thicken beyond a few millimetres diameter. 'South coastal' lodgepole pine often has a leaning or bent stem and when the weight of crown is increased by a thick layer of wet snow, the roots may be torn out, in spite of the anchorage of 600-800 mm of peat. Straight-stemmed forms of lodgepole pine and other species have not shown this tendency, indeed there is reason to suppose that the stability of crops in windy conditions will generally be better on peats than on gleyed mineral soil (Booth & Mayhead 1972).

Chemical changes in peat after afforestation will be important if they affect the availability of nutrients, especially nitrogen which is expensive as fertilizer. Williams, Cooper & Pyatt (1978) have shown that drying and aeration of blanket peat enhances decomposition and produces an increase in cation exchange capacity. Exchangeable Ca^{2+} , Mg^{2+} and K^+ are replaced by Na^+ and H^+ , and pH and base saturation fall. Incubation tests of the peat under aerobic and anaerobic conditions indicate that the amount of easily decomposed nitrogen substrates has been reduced (Williams, Cooper & Pyatt, in press). No consistent changes in the total quantity of nitrogen, phosphorus and potassium have been found, partly because fertilizer applications of P and K have occurred at some sites.

Progressive drying and the development of shrinkage cracks seem hardly ever to have been reported from other countries. Carey & Barry (1975) found the process to be well advanced in the afforested cut-over raised bog in central Ireland, but the upper layer of the material consisted of replaced turf peat which had probably dried in the sun. The phenomenon may not occur in Scandinavia, and observations by the author in Finland suggest that this is mainly due to the extremely low degree of humification of the peat (H 1-2 on the

Naver Deep Peat 1976

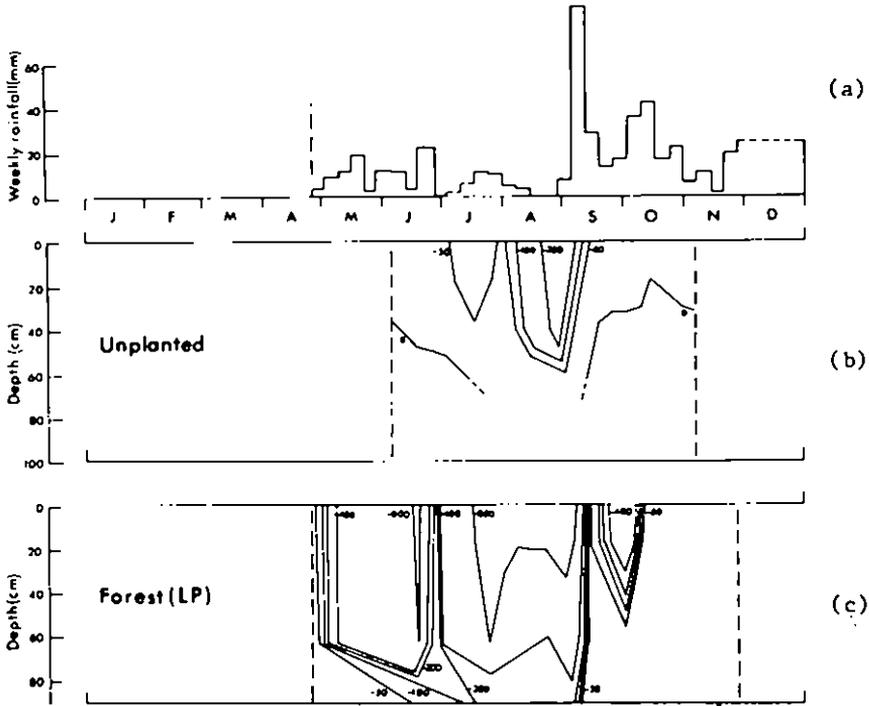


Fig. 4. Moisture regimes for unplanted and forested (lodgepole pine) peat (5 June - 6 Nov for unplanted, 26 April - 27 Nov for planted). (a) rainfall, available data, (b) and (c) interpolated iso-potential lines based on tensiometer and borehole data.

Von Post scale).

FUTURE PROSPECTS

Changes in soil moisture regime have the same causes and are in the same direction in different soils but have very varied effects. As foresters we are entitled to think of these effects as either beneficial or detrimental to long-term site productivity. Most of the effects are at least potentially beneficial because these soils are initially too wet for maximum growth of our crops. Ironpan soils offer excellent prospects for a major improvement in moisture and aeration regimes. The growth of the forest will do much to put things right but deep ploughing to eliminate the ironpan in peaty ironpan soils or to loosen indurated material beneath the pan will show a benefit in crop stability. At present we cannot foresee any such cure for gley soils. But prospects are not as gloomy as they seemed a few years ago. The forecasts of impending devastation by windthrow, based on damage that occurred in the early 1960's have been found to have been too pessimistic. Perhaps only the most susceptible stands were blowing down, perhaps we have been lucky with the winds. The realization around 1970 that the closely spaced ploughing of the period between 1940 and 1970 might lead to greater instability than we had experienced to-date, has been tempered by the greater stability achieved by unthinned crops.

The changes in some peat soils are drastic and may well be permanent. Gains in aeration and rooting depth may be offset by some loss in soil strength. Long term effects on moisture and nutrient availability are uncertain.

In general then, on the problem soils, our silviculture should have more varied possibilities in the second rotation than in the first.

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REFERENCES

- Avery, B.W.(1973). Soil classification in the soil survey of England and Wales. *Journal of Soil Science*, 24, 324-338.
- Binns, W.O.(1959). The physical and chemical properties of deep peat in relation to afforestation. Ph.D. thesis, Aberdeen University.
- Booth, T.C.(1973). Tree pulling. Report on Forest Research for 1973. pp. 72-73.
- Booth, T.C. & Mayhead, G.J.(1972). Tree pulling. Report of Forest Research for 1972. 65pp.
- Carey, M.L. & Barry, T.A.(1975). Coniferous growth and rooting

patterns on machine sod-peat bog (cutover) and trench 14, Clonsast. *Irish Forestry*, 32, 18-29.

- Crompton, E. (1956). The environmental and pedological relationships of peaty gleyed podzols. *Transactions of the 6th International Congress on Soil Science*. Paris F, pp. 155-161.
- Fitzpatrick, E. A. (1956). An indurated horizon formed by permafrost. *Journal of Soil Science*, 7, 248-254.
- Fitzpatrick, E. A. (1971). *Pedology*. Oliver & Boyd, Edinburgh.
- Ford, E. D. & Deans, J. D. (1978). The effects of canopy structure on stemflow, throughfall and interception loss in a young Sitka spruce plantation. *Journal of Applied Ecology*, 15, 807-819.
- Frascr, A. I. & Gardiner, J. B. H. (1967). Rooting and stability in Sitka spruce. *Forestry Commission Bulletin # 40*.
- Henman, D. W. (1964). Some early responses to increased intensity of heathland cultivation. *Report on Forest Research for 1964* pp. 158-165.
- Hinson, W. H., Pyatt, D. G. & Fourn, D. F. (1970). Drainage studies. *Report on Forest Research for 1970*, pp. 88-89.
- Hodgson, J. M. (1974). *Soil survey field handbook*. Soil Survey Technical Monograph No 5, Harpenden.
- Muir, A. (1934). The soils of Teindland State Forest. *Forestry*, 8, 25-55.
- Neustein, S. A. & Thompson, D. A. (1973). Drainage of soil with clay subsoil. *Report on Forest Research for 1973*. pp. 67-68.
- Pyatt, D. G. (1970). Soil groups of upland forests. *Forestry Commission Forest Record # 71*.
- Pyatt, D. G. (1973). The effects of drainage treatments and tree crops on soil physical properties. *Report on Forest Research for 1973*. pp. 62-66.
- Pyatt, D. G. (1978). Physical properties of soils with indurated material. Ph.D. thesis, Aberdeen University.
- Smith, K. A. (1976). Aeration status of upland soils. *Report on Forest Research for 1976*. pp. 56-58.
- Smith, L. P. (1967). Potential transpiration. *Ministry of Agriculture, Fisheries and Food Technical Bulletin # 16*.
- Taylor, G. G. M. (1970). Ploughing practice in the Forestry Commission. *Forestry Commission Forest Record # 73*.
- Taylor, G. G. M. & Everard, J. E. (1969). Drainage of deep peat. *Report of Forest Research for 1969*. pp. 87.
- Taylor, G. G. M. & Everard, J. E. (1970). Cultivation of ironpan soils. *Report on Forest Research for 1970*. pp. 94.
- Thompson, D. A. (in press). Forest drainage schemes. *Forestry Commission Leaflet*.
- Thomson, J. H. & Neustein, S. A. (1973). An experiment in intensive cultivation of an upland heath. *Scottish Forestry*, 27, 211-221.
- Toleman, R. D. L. (1973). A peat classification for forest use in

- Great Britain. Proceedings International Peat Society Symposium, Glasgow. Paper no. 10.
- Williams, B.L., Cooper, J.M. & Pyatt, D.G. (1978). Effects of afforestation with Pinus contorta on nutrient content, acidity and exchangeable cations in peat. *Forestry*, 51, 29-35.
- Williams, B.L., Cooper, J.M. & Pyatt, D.G. (in press). Some effects of afforestation with lodgepole pine on rates of nitrogen mineralization in peat. *Forestry*.
- Zehetmayer, J.W.L. (1960). Afforestation of upland heaths. *Forestry Commission Bulletin #32*.

September 7, 1978

THE EFFECTS OF PLANTATIONS ON WILDLIFE

Chairman: J. Morton Boyd

Plantation management and
vertebrate wildlife.

J.A. Rochelle and
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Even-aged plantations as a habitat
for birds.

D. Moss

Even-aged plantations as a habitat
for deer in central Europe.

E. König and
H. Gossow

The management of red deer in
plantations.

A.B. Cooper and
W.E.S. Mutch



PLANTATION MANAGEMENT AND VERTEBRATE WILDLIFE

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SUMMARY

A wide variety of forest types, containing numerous vertebrate species with specific habitat requirements occur in North America. In this paper we have attempted to treat species or groups of species which illustrate the major kinds of forestry - wildlife interactions that occur. Plantation management will affect populations to the extent that the combinations of resources required by a wildlife species are available in a particular phase of plantation development. Against the background of nature's forests, man's activities influence the availability of their resources mainly through:

1. modifying their distribution in space and time, and
2. increasing or decreasing their relative abundance.

Thus, plantation management may enhance forage supplied during several stages in the life of the stand, but these periods may be shortened relative to natural forest succession. Vegetative diversity is reduced in plantations since dominance of the site by crop trees is an objective. On industrial lands, rotation lengths are increasingly based on optimization of fibre yields in a context of highest financial return. Thus, rotation lengths are short with the result that forests older than 100 years will continue to diminish in area and will not be replaced. Along with this change will occur a corresponding decrease in populations of species dependent on mature forest and specialized habitats, such as snags,

i.e. large, standing dead trees.

In cases where wildlife interferes with plantation management, traditional methods of control such as population reduction or the use of repellents or physical barriers are employed, along with indirect controls through habitat manipulation. Maintenance of wildlife populations in managed forests is mainly being approached through planning to provide required resources through time and space. For species requiring large snags or old-growth timber, approaches to date center on either preservation of these kinds of habitat or extension of rotation periods on specified areas to maintain some habitats of this type. Management for snags is a reality in mixed-age forests, and snags are being preserved in some areas when clearcutting is employed. The opportunity exists to create small snags by killing plantation trees, and perhaps the feasibility of artificially providing larger snags warrants investigation.

Frameworks within which the complex interactions of forest management and wildlife can be conceptualized and displayed are only recently available (Thomas et al 1976; Bunnell & Eastman 1976). Although solutions are not readily available for all of the apparent conflicts between vertebrates and plantation management, some progress is being made. Consideration of forestry and wildlife trade-offs during the stage of development of management plans will identify further opportunities for integrated approaches.

RÉSUMÉ

Il y a en Amérique du Nord une diversité de types de forêts où vivent de nombreuses espèces de vertébrés aux habitats spécifiques. Cet exposé traite des espèces ou groupes d'espèces qui peuvent servir à illustrer les différents genres d'actions réciproques entre foresterie et faune sauvage. La gestion d'une plantation aura sur les peuplements l'influence suivante: les combinaisons entre les ressources exigées par les différentes espèces animales ne sont disponibles que pendant un stade particulier du développement de la plantation. L'activité humaine peut influencer la disponibilité des ressources des forêts de la manière suivante:

1. en en modifiant la distribution dans le temps et dans l'espace, et,
2. en augmentant ou diminuant l'abondance relative des ressources.

Ainsi la gestion des plantations peut améliorer la production en fourrage pendant plusieurs stades de la vie du peuplement, mais ces périodes peuvent être écourtées par rapport à la succession naturelle de la forêt. Dans les plantations il y a une réduction de la diversité des espèces végétales puisque la station est occupée par des essences productives. Sur les terrains industrialisés, la durée de rotation est de plus en plus basée sur une optimisation des rendements en fibres en vue d'obtenir les meilleurs revenus. Ainsi la durée des révolutions est courte et par conséquent les forêts de plus de 100 ans continuent à diminuer et ne seront pas remplacées. Allant de pair avec ce développement on constatera la diminution des populations d'espèces qui dépendent de futaies mûres et qui demandent un habitat spécialisé tels que les arbres secs.

Là où la faune sauvage entrave d'une façon ou d'une autre la gestion d'une plantation on utilise des méthodes de contrôle traditionnelles, telles que la réduction de la population ou l'usage de barrières ou de moyens répulsifs ainsi que des méthodes de contrôle indirectes en s'attaquant aux habitats. Le maintien des espèces animales dans les forêts gérées se fait principalement en s'assurant de pourvoir les ressources nécessaires dans le temps et dans l'espace. Dans le cas d'espèces qui ont besoin de grands arbres secs ou d'anciens arbres, on essaie la préservation de ce genre d'habitats ou on prolonge la durée des révolutions dans des endroits spécifiques pour maintenir ce genre d'habitats. Dans les forêts inéquennes il existe un véritable besoin de gestion quant aux arbres secs et ceux-ci sont épargnés dans les régions où l'on pratique les coupes-à-blanc. On a aussi la possibilité de créer des petits arbres secs en tuant certains arbres et on pourrait peut-être étudier la possibilité de créer artificiellement des arbres secs de plus grand taille.

On trouvera des exemples de la complexité des interactions entre gestion forestière et faune

sauvage dans des ouvrages récents (Thomas et al. 1976; Bunnell & Eastman 1976). Bien qu'il n'y ait pas de solutions toutes faites pour tous les conflits apparents entre vertébrés et gestions forestière, on ne peut nier les progrès qui ont été faits. La prise en considération des influences réciproques de la forêt et de la faune sauvage au moment de l'établissement des plans de gestion, pourra ouvrir des possibilités d'intégration pour l'avenir.

ZUSAMMENFASSUNG

In Nordamerika gibt es eine grosse Vielfalt von Waldtypen, in denen zahlreiche Wirbeltiere mit besonderen Habitatansprüchen leben. In dieser Arbeit haben wir versucht, Arten oder Artengruppen zu behandeln, die wichtige Wald-Tier Wechselbeziehungen illustrieren. Waldbauliche Massnahmen werden in dem Masse die Population beeinträchtigen, wie sie die Lebensbedingungen für eine Wildart in einer bestimmten Entwicklungsphase der Pflanzungen verändern. Im Vergleich zu Naturwäldern wird das Vorhandensein der lebensnotwendigen Bedingungen von den Tätigkeiten des Menschen vor allem beeinflusst durch:

- (1) die Änderung ihrer Verteilung in Raum und Zeit;
- (2) die Vermehrung oder Verminderung des Umfanges.

Deshalb kann eine Bewirtschaftung von Pflanzungen den Futtervorrat steigern, während mehrerer Stadien im Leben des Bestandes, aber diese Perioden können im Vergleich zu natürlichen Sukzessionen verkürzt werden. Verschiedenartigkeit der Vegetation in Pflanzungen ist zur Begünstigung der Hauptbaumart reduziert. In Industriegebieten werden die Umtriebszeiten zunehmend darauf abgestimmt, die Holzerträge im Hinblick auf die höchsten finanziellen Gewinne zu optimieren. Die Umtriebszeiten sind kurz, mit dem Ergebnis, dass Wälder, die älter als hundert Jahre sind, weiterhin an Umfang abnehmen und nicht ersetzt werden. Mit diesem Wechsel geht eine entsprechende Populationsverringerung solcher Tierarten einher, die auf alte Wälder und besondere Habitate wie stehende abgestorbene Bäume angewiesen sind.

In Fällen, wo der Wildbestand die Bewirtschaftung der Pflanzung behindert, werden sowohl traditionelle Forstschutzmethoden, wie z.B. Reduktion des Bestandes, der Gebrauch von Abschreckungsmitteln oder Zäune, zusammen mit indirekten Massnahmen durch Habitat-Management angewandt. Die Erhaltung von Tierbeständen im Wirtschaftswald wird vor allem dadurch angestrebt, dass man die notwendigen Lebensbedingungen bereitstellt. Für Tierarten, die grosse, abgestorbene Bäume oder Altbestände brauchen, konzentrieren sich die Versuche bisher entweder auf Erhaltung solcher Habitate oder auf Verlängerung der Umtriebszeit in bestimmten Gebieten.

Bewirtschaftung unter Belassung von abständigen Bäumen wird in ungleichaltrigen Beständen geübt und abgestorbene Bäume können beim Kahlschlag stehengelassen werden. Es besteht auch die Möglichkeit kleine Habitate zu schaffen, indem man gepflanzte Bäume zum Absterben bringt. Vielleicht sollten Untersuchungen ergründen, ob auch künstlich grössere 'Baumleichen' zu schaffen wären.

Erst seit kurzem verfügt man über einen Rahmen, in dem die komplexen Wechselbeziehungen von Waldbewirtschaftung und Tierleben begriffen und dargestellt werden können (Thomas et al. 1976, Bunnell & Eastman 1976). Obwohl sich nicht für alle der offensichtlichen Konflikte zwischen Wirbeltieren und Waldbewirtschaftung ohne weiteres Lösungen anbieten, gibt es doch einige Fortschritte. Die Berücksichtigung der gegenseitigen Beeinflussung von Wald und Wild wird während der Entwicklung von Kulturplänen weitere Möglichkeiten für gemeinsame Ansätze zeigen.

INTRODUCTION

Almost everywhere, forested land has the capacity to produce both wood fibre and animal tissue. Whilst we still know relatively little about the complexities of forestry-wildlife relationships in sub-tropical or tropical areas, we do know that in temperate regions the variety of resident wildlife and, thus, the complexity of the relationship can be enormous. Bunnell & Eastman (1976) noted that within British Columbia, Canada, about 70 per cent of the ninety-eight terrestrial mammal species utilized forests for part of their requirements. About 115 bird species were forest

dwelling and 32 per cent of these were cavity-nesters, exploiting a particular aspect of forest structure. They also noted that many amphibian species and a few reptiles were preferential and possibly obligate, forest-dwellers. In much of Europe the diversity of forest-dwelling vertebrates is less, in part due to a longer history of intensive human activity. Nevertheless, parallels do exist among forestry-wildlife interactions on a global scale (Bunnell 1976a). While forest-dwelling species have evolved to withstand or even exploit, dramatic changes in forest structure wrought by fire, storm or disease, the changes associated with intensive plantation management do not necessarily mimic such uncontrolled phenomena. The biological ability of forest-dwelling species to respond to intensive forest management is in many instances unknown. Equally important to management is the observation that potential conflicts between production of wood fibre and animal tissue inevitably have social as well as biological roots (Bunnell 1976a; Bunnell et al. 1978).

We do not discuss the social dimensions of management in this paper. We present an approach to wildlife research within the context of plantation management. Bunnell (1976b) noted that among 175 working parties and project groups then functioning within IUFRO, only four, or less than 3 per cent, incorporated the term 'management' in their title. This observation is consistent with the objectives of IUFRO, but may represent a syndrome hindering effective incorporation of research into management. In particular, it has potential implications for the expanding IUFRO membership among low income nations which frequently desire to transplant research results quickly (Bunnell 1976a, 1976b).

We suggest that wildlife research within the context of plantation management should address three broad themes: 1. documentation of forestry-wildlife trade-offs; 2. methods of maintaining wildlife production, and 3. methods of controlling 'damage' by wildlife.

The first theme we consider as addressing conditional or 'what-if' questions; e.g. what if the size of clearcuts is changed from 40 to 80 or 120 ha? What if the initial planting density is 1000 stems per hectare as opposed to 2500? We consider that the researcher has an obligation to document responses of wildlife to a broad range of trade-offs, rather than to document effects of a practice at a particular level of intensity. The manager then has the option of exploring the variety of 'what-if' alternatives that are congruent with a particular socio-economic background. The second theme recognizes that some plantation management practices may adversely affect particular wildlife species and encourages research on specific methods for maintaining that species e.g. artificial production of snags for cavity-nesters. The third

theme also considered specific methods, in this case to reduce numbers of those species encouraged by plantation management whose activities seriously reduce production of wood fibre e.g. Ursus americanus, Odocoileus spp or Aplodontia rufa.

Given the diversity of wildlife species and the diversity of forest types, some general model or conceptual framework is essential. We present a broad model in terms of the general requirements of wildlife and the general effects of plantation forestry on wildlife. Although a general model is essential to provide a framework for the complexity, it is important to acknowledge a common and debilitating attribute of wildlife research. Many wildlife researchers express their observations on a wildlife species as though they were facts about the species, rather than facts about that species within a particular ecosystem. It is thus impossible to position their research results along any dimension of a generalized framework. Such results can be transplanted only through faith. Bunnell et al. (1978) have discussed the problem and ways in which research can be incorporated into a more generalized framework.

GENERAL REQUIREMENTS OF WILDLIFE

Our experience with conflicts regarding wildlife and forestry resources are similar to those of Thomas et al. (1976). Our conclusions are identical. Although we may have chosen different words, they said it first;

"We concluded that lack of knowledge - though meager in some instances - was not the biggest problem. The biggest problem was the lack of conceptual framework to allow (1) consideration of all vertebrates in the planning process; (2) retention of the ability to emphasize management of a particular species and (3) identification of specific habitats requiring special attention in land alteration schemes". (Thomas et al. 1976 p. 453).

Attempts to develop a system or conceptual framework useful in guiding management have repeatedly documented that the weakest link is our inability to predict effects on wildlife populations over time (Bunnell & Eastman 1976; Thomas et al. 1976; Black, Scherzinger & Thomas 1976). Thus, our approach has been to concentrate on changes that occur during succession within forest types. The approach has the advantage that it can be related readily to forest management practices. The rationale for choosing components of the model has been expressed by Bunnell & Eastman (1976). Briefly, all wildlife species have requirements which, while particular for each species, are broadly analogous. Thus, while the Pacific mole (Scapanus orarius) feeds largely on earthworms, the Pinyon jay (Gymnorhinus cyanocephalus) on pine seeds and the black-tailed deer (Odocoileus hemionus columbianus) on browse, each is

Table 1. Resources required by wildlife (modified from Bunnell & Eastman 1976).

Resource	Resource attribute			
	Amount		Distribution	
	Ingested	Structural	Horizontal	Vertical
Energy	X		X	X
Nutrients	X		X	
Water	X		X	
Temporary shelter (from wind, snow, heat)		X		
Escape cover		X		
Habitation (dens and cavities)		X		
Space				

feeding to obtain energy, nutrients and water. Even diverse wildlife species have similar needs, but each is adapted to obtaining their needs in particular packages, be those packages earthworms or conifer seeds. We have attempted to express wildlife requirements at the simplest level that will encompass all basic needs. In their general form, we consider there to be seven basic needs (Table 1). Because animals are mobile, but show physical and behavioural limits to their mobility, we are concerned not only with the amounts and forms of packaging in the resources utilized, but also with their vertical and horizontal distribution. Forestry practices can influence not only the amount of a specific resource, but can redistribute a given amount of a resource through space and time. Because they influence the animal differently, we make a further distinction between resources that are ingested by the animals and resources whose structure is exploited, such as conifer stands which intercept snowfall or otherwise provide shelter.

GENERAL EFFECTS OF PLANTATION ON WILDLIFE

The potential packages in which individual wildlife species seek the requirements of Table 1 are enormously diverse. Fortunately, natural succession lends some predictability to the pattern in which the requirements appear over time (Bunnell & Eastman 1976). We can document how these requirements vary during natural succession following complete or partial removal of the overstory. From this knowledge, together with information on spatial patterns of application we can posit the manner in which particular management practices such as thinning or fertilizing modify the pattern of availability of particular requirements. Bunnell & Eastman

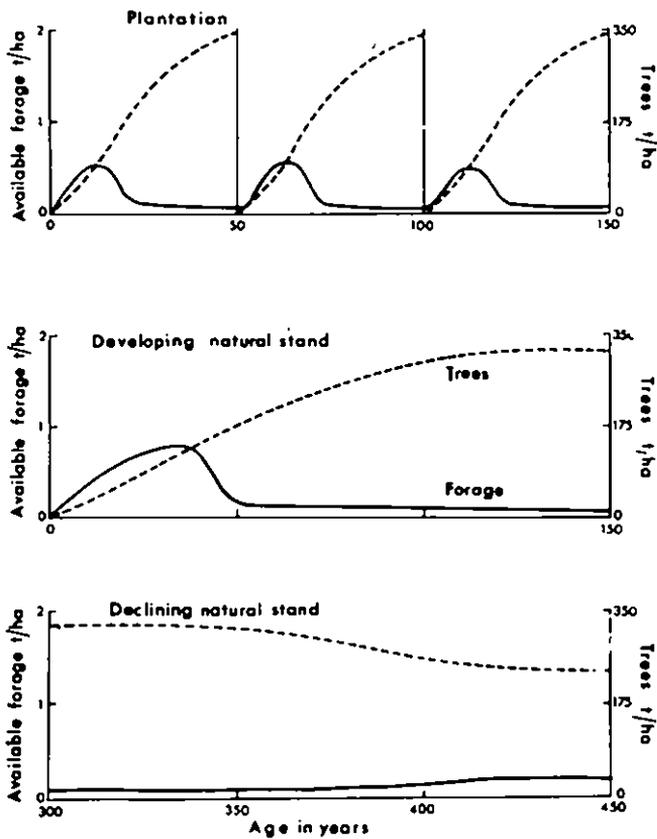


Fig. 1. Idealised responses of tree and shrub biomass in plantation management as compared to a natural stand.

(1976, their Table 1) noted the temporal patterns of the requirements following clear-cutting, but concentrated on extensive forestry practices rather than plantation management.

Fig. 1 illustrates idealized development patterns of tree and shrub biomass under extensive forestry. The patterns indicated are those which browsing ungulates would experience when fire or storms or disease followed by fire destroyed old growth forests which were replaced with new forests. Plantation management truncates the natural sere at both ends. Early seral stages are eliminated by rapid control of the site through practices such as scarification, brush control,

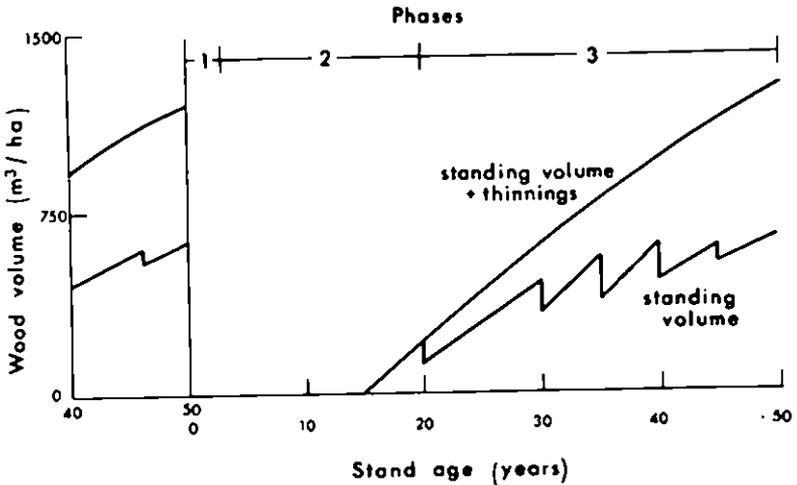


Fig. 2. Phases of the management regime in a plantation.
 Phases: (1) harvest and site preparation,
 (2) establishment to first thinning,
 (3) fertilization and commercial thinning.

prescribed burning and dense stocking rates for planted stock. Later seral stages, which have proven valuable to wintering ungulates in some areas (e.g. Jones 1974, 1975) are eliminated by the short rotation length.

Within the general framework we distinguish three phases in the management regime for any plantation. The length and specific characteristics of each phase vary between stands with rotation length and with immediate economic constraints. The phases considered are:

1. harvest and site preparation,
2. plantation establishments to first (pre-commercial) thinning, and
3. thinning and fertilization (most of rotation). These phases are illustrated in Fig. 2. Specific characteristics of each phase influence the local wildlife populations.

IMPACTS OF PLANTATION FORESTRY ON WILDLIFE

Specific examples

Acknowledging the conceptual framework presented above, we now consider specific cases to illustrate the problems and opportunities encountered during plantation management.

Practices associated with plantation forestry affect some wildlife species negatively and others positively.

Reduction of wildlife

Ungulates. Of the basic requirements we consider (Table 1), plantation forestry can seriously reduce the amounts of energy, nutrients and temporary shelter. Escape cover is commonly abundant. The ungulate's use of space may be modified temporarily by forest activities, but usually they quickly adapt to the disturbance (Beall 1973; Hershey & Leege 1976). A more important disturbance in the North American context is the increased network of roads which accompanies plantation forestry. An extended road network facilitates access, increases hunting pressure, and can lead to over-harvesting where forestry practices have altered the landscape so as to concentrate the ungulates.

Typically temporary shelter is affected adversely only in areas of high snowfall. Despite their light foot-loading, black-tailed deer are seriously impeded by snow cover deeper than 60 cm. Plantations of forty to fifty years of age are likely to have sufficient crown density to intercept snow, so reducing the snowpack on the forest floor. However, plantations of this age have little understory beneath the canopy. In contrast, old-growth forests which have opened up somewhat (Fig. 1) both intercept snow and provide browse. For these reasons, ungulates throughout North America exploit mature, typically old-growth forests when snow cover becomes deep (Prescott 1974; Telfer 1970; Edwards 1956; Kelsall & Prescott 1971).

Rodents and lagomorphs. Within mature conifer forests in coastal Washington, Oregon and northern California, mountain beaver (*Aplodontia rufa*) are present, but confined to openings within the stands. Such breaks in the canopy are associated with stream courses, springs (Hooven & Black 1976) or sites of overstory tree mortality. In response to the increased light, openings typically support a greater biomass of herb and shrub species than the understory in general. Thus, mountain beaver populations are low at the time of forest harvest and may be further reduced by slash burning which can result in direct mortality of up to 50 per cent of the population (Motobu 1976). For several years following harvest, vegetative conditions similar to those formerly associated with openings develop over the entire site, although their continued development is best in areas of greatest soil moisture. During this stage of the plantation cycle (1 and 2 of Fig. 2), mountain beaver populations expand to occupy a much greater portion of the site, though with further growth of planted trees and concomitant stand closure, the animal again becomes confined to drainage courses or slash accumulations which have caused a break in the canopy of the developing stand (Neal & Borrecco 1978). With immediate regeneration of harvested

areas, often coupled with a reduction in animal numbers through direct control, populations decline to or below the levels found in mature stands. Population levels in 25-50-year old managed plantations of Douglas fir will likely be higher than in natural stands of the same age, as commercial thinning will produce more open stands, with increased light reaching the forest floor (Lawrence 1969). The larger mountain beaver populations associated with more diverse vegetation are further reflected in the greater levels of damage to planted seedlings which occur following rehabilitation of brushfields in contrast to the period after harvest of a conifer stand.

In western Oregon, snowshoe hare (Lepus americanus) populations were reduced by timber harvest which was attributed to the removal of forest cover, i.e. escape cover of Table 1 (Hooven and Black 1976). An additional factor may have been the absence of green branches which fall during winter and are used as food. Hare populations recovered as re-vegetation took place and populations of up to 12.5 hare per hectare were documented ten years after a fire (Black 1965). These observations reflect the influence of removal and subsequent recovery of vegetation corresponding to the periods of (1) harvest and site preparation and (2) establishment of first thinning described in Fig. 2. In plantations 3-4 years old, Borrecco (1976) demonstrated the importance of vegetative cover to snowshoe hares. Removal of tall herbaceous cover including fireweed (Epilobium angustifolium) and foxglove (Digitalis purpurea) in the spring, significantly reduced both trap catches and damage to Douglas fir seedlings during the following winter. Population data are lacking for the other two phases of plantation development. Hooven & Black (1976) recorded hare densities of 0.5 to 5.0 per hectare in 125-year-old Douglas fir stands, and it is likely that similar levels will be present in younger thinned and fertilized plantations. Increased production of understory vegetation is anticipated as a result of fertilization (Lawrence 1969) but, to date, this response has not been quantified.

Birds. The specialized habitat requirements of many species of forest birds result in a variety of interactions with plantation forestry. As with mammals, different successional stages (Fig. 2) will be more or less favourable to different groups of birds. A corresponding successional pattern in the avian fauna reflects these changes in forest vegetation (Thomas et al. 1975).

Concerns for birds expressed by biologists (Thomas et al. 1975; Meslow & Wight 1975) note three major results of plantation forestry:

- (1) truncated succession
- (2) loss of old-growth habitat
- (3) removal of snags, i.e. isolated dead standing trees. All concerns revolve around the fact that the forests which

develop under a regime of intensive management will be vegetatively less diverse and will contain correspondingly fewer specialized habitats than unmanaged forests. Frequent thinning will recover trees which die and crop trees will be vigorous with rapid rates of growth.

During the initial stages of development of a plantation (Fig. 2) habitat conditions will be essentially the same as those which occurred naturally following deforestation through wildfire, windthrow or disease, or timber harvest without artificial regeneration. The use of herbicides to control vegetation competing with crop trees modifies this pattern somewhat. The major difference will be the reduced period of time certain habitat conditions persist, e.g. the grass-forb and shrub-sapling stages of Meslow & Wight (1975). These investigators listed thirty-eight and seventy-two species of birds in Western Oregon that prefer or are restricted to the grass-forb and brush-sapling stages, respectively.

While numbers of individuals will probably be reduced as a result of this contracted period of preferred vegetative conditions, it is probable that species diversity will not change. An additional consideration is that the reduction in rotation lengths from 100 to approximately fifty years means that twice the area will be in these early successional stages at any point in time. As a result total numbers of these species of birds in a forest regime will probably be comparable to those occurring prior to intensified plantation management.

The implications of intensive management to species of birds which require large dead trees, such as the pileated woodpecker (Drycopus pileatus) (Bull & Meslow 1977), or large areas of old-growth forest, such as the spotted owl (Strix occidentalis caurina) (Wight 1974) are more direct. Short rotation forestry directly eliminates the mature forests (i.e. >125 years) and the large dead trees which are components of these stands. The red-cockaded woodpecker (Dendrocopis borealis) presents a similar situation in the southeastern United States (Jackson 1971). This species, officially classified as endangered by the U.S. Fish and Wildlife Service, requires living old-growth southern pines, preferably infected with red-heart fungus (Fomes pini), in which to excavate nesting and roosting cavities. Although the species commonly occurs in even-aged stands, trees more than fifty years old are required as cavity trees. In the southeastern United States, plantation forestry employs rotation periods substantially less than fifty years in length. Thus, the options for management to accommodate the species are limited.

The degree of dependence of these species on conditions of mature forest has not been tested experimentally, but their specialized habitat requirements suggest they will probably not be able to adapt to the changed conditions resulting from

plantation forestry. Balda (1975) has demonstrated experimentally that breeding densities and species diversity of secondary cavity nesters, i.e. species utilizing cavities in snags excavated by other species, were reduced by snag removal in Pinus ponderosa stands in Arizona.

In these examples, the key resource which becomes limiting is that of habitation (Table 1). In the case of the spotted owl, mature conifer forests provide a feeding area and escape cover from predators such as the great horned owl (Bubo virginianus) The management options available to provide for these species are limited. Basically they require a departure from the standard plantation management approach, at least on selected areas.

Management schemes to provide for these species are beginning to emerge (Thomas et al. 1975; Lay & Swepston 1975; Oregon Endangered Species Task Force 1977) and are discussed later.

Enhancement of wildlife - damage

We noted earlier that plantation forestry creates conditions favourable for many vertebrate species and unfavourable for others. Further, a particular species will fare more or less well during the various stages of the plantation management regime. In the context of plantation management, considering production of wood fibre as the primary objective of management, increased population growth of certain vertebrate species has detrimental effects. Where production of wood fibre is not the major objective, 'damage' would simply be animal feeding activity.

With the exception of damage to pole-sized trees by black bear (Poelker & Hertwell 1973) and porcupine (Erithizon dorsatum) (Lawrence 1957) most wildlife damage to forest trees in North America occurs during phases 1 and 2 of the management regime (Fig. 2). These are periods of maximum increase in the population of some animal species and, at the same time are periods during which the small size of planted seedlings renders them vulnerable to injury by wildlife feeding.

Ungulates. With the exception of coastal areas of high snowfall, populations of black-tailed deer and Roosevelt elk (Cervus canadensis roosevelti) increase as a result of forest harvesting (Cowan 1945; Brown 1961; Harper 1971). This statement is made with the assumption that other resources required (Table 1) are present. Ungulates have the ability to respond quickly to increased nutrient supplies. Although Crouch (1974) did not determine population densities, he found that the peak of black-tailed deer damage to Douglas fir seedlings in western Oregon occurred within four to six years of site preparation. Effects of deer population levels were illustrated by Hines & Land (1974) who achieved approximately a 50 per cent reduction in damage to Douglas fir with a 50 per

cent reduction in deer numbers.

It is clear that forest management activities, particularly harvesting, set the stage for browsing damage by ungulates. At the same time, the advent of plantation management with its shortened rotations and reliance on high rates of seedling survival and growth, results in increased importance being assigned to ungulate damage. In the case of black-tailed deer, it is expected that the rapid restocking of logged areas and early dominance of the site by plantation trees will reduce overall damage levels. These practices should help ensure that seedlings will pass through the period of vulnerability to browsing of terminal shoots in advance of peaks in deer populations.

Rodents. Populations of rodent species which damage plantation trees expand with the improved energy and nutrient supplies associated with vegetative succession immediately after logging. Most damage is associated with early stages of plantation development. A second period of damage occurs at the time of stand closure and coincides approximately with stocking control operations. This latter damage period appears to be a function of declining food supplies and is manifested in basal girdling of saplings.

In the pine region of the western United States, pocket gophers (*Thomomys* spp) damage seedlings during the initial stages of plantation development (Barnes 1973). Removal of overstory timber and the accompanying soil disturbance (Phase 1 of Fig. 2) result in dramatic increases in herbaceous vegetation (Hedrick et al. 1968; Garrison 1961). Pocket gophers present in low densities in the forest and at high densities in forest openings rapidly occupy this newly available habitat and quickly reach high population densities (Barnes 1974). That increased forage permits this response was shown by Black & Hooven (1974) who significantly reduced gopher populations through herbicidal removal of herbaceous vegetation.

Birds. In western North America, the only instances in which significant damage by birds to plantations have been recorded are with blue grouse (*Dendrogapus obscurus*) on Vancouver Island, B.C. (Fowle 1960; P. Affleck personal communication). The response of blue grouse to development of second-growth forest on Vancouver Island was documented by Reffield, Zwickel & Bendell (1970). Population densities rapidly increase from those of mature forest upon removal of the overstory. Densities remain high for a period of five to twenty years post-harvest in a pattern which is similar to, but extended somewhat longer than that observed for rodents and deer. Subsequently, as coniferous cover becomes dense, at about twenty-five years, populations decline rapidly, to levels approximately those in old-growth forests. As with deer and rodents, damage by blue grouse is important only during

the first few years after planting.

Bears. Few data are available on the response of bear populations to the harvest of old-growth forest. Lauckhart (1955) indicated that populations increase after forest harvest, probably due in a large part to improved forage conditions. In several areas of the northwestern United States, black bear cause mortality on a number of conifer species through basal bark stripping (Levin 1954; Childs & Worthington 1955; Poelker & Hartwell 1973). Typically trees selected in natural stands by bears are in the range of 15 to 40 cm dbh and are the more rapidly growing trees which occur in wide spacings (Levin 1954). Experience with bear damage in plantations is limited, but is increasing as the area occupied by plantations of susceptible sized trees increases. Since plantation management emphasizes the production of rapid-growing trees at wide spacings, through fertilization and thinning, it is likely that damage will increase in importance in the future.

Despite several studies, the reasons why bear damage trees in some areas and not others are unclear (Radwan 1969; Poelker & Hartwell 1973). It appears that there are individual differences in tree-feeding patterns among bears even in areas where damage occurs, suggesting that behavioural factors are involved. It is likely that the pattern of variation in carrying capacity through time (Fig. 1) influences bears as it does other species discussed above. With a decline in carrying capacity, manifested primarily through a reduction in food supply, bears may turn to conifer sapwood as a food source (Lauckhart 1955).

In each of the examples discussed above, overstorey removal is the mechanism of major importance in enhancing wildlife populations which in turn damage plantation trees. The major effect of plantation development is in modifying the length of time that vegetative conditions favouring high populations of these species persist.

From the foregoing discussion, we conclude that the mechanisms through which plantation management will operate to reduce populations vary with the species involved and include:

- (1) reduction in the period of availability or the spatial arrangement of forage and cover responsible for high carrying capacity, and
- (2) elimination of preferred or required habitats.

For species whose populations are enhanced, with the result that damage to forests occurs, the mechanisms of plantation management responsible are:

- (1) increased carrying capacity through practices which promote favourable forage or cover conditions and
- (2) provisions of trees with characteristics which render them higher in feeding preference than 'wild' trees, e.g. rapid growth.

MANAGEMENT APPROACHES

The approaches taken to integrate the management of plantations and wildlife have been developed in view of the varied mechanisms described above. Selected examples follow.

Ungulates. The conceptual approach developed by Thomas et al. (1976) provides the only comprehensive framework available within which foresters can quantitatively relate timber and wildlife interactions. The framework includes timber types, successional stages within these types, arrangement of managed stands in time and space and the occurrence of wildlife as affected by these criteria. The objective of developing this framework was to provide the forest manager with the means to identify wildlife trade-offs associated with a particular forest management decision.

In the Blue Mountains of northeastern Oregon, the ratio of forage to cover and its arrangement in time and space are the primary factors determining potential levels of use of forest land by Rocky Mountain elk (*Cervus canadensis nelsoni*) (Thomas et al.) 1976. Several types of cover, having specific dimensions are required in defined amounts. The framework permits the forest manager to forecast potential increases or decreases in elk use as a result of a management activity. Plantation management alternatives, such as rotation length, can be evaluated using this system which is specific to the land types or 'ecolasses' that occur on the area. Thus, the system provides a planning tool which can be employed along with timber management planning to achieve simultaneous timber-elk production goals.

The interaction of black-tailed deer, snowfall and mature forests in coastal British Columbia was discussed earlier. The approach being employed to accommodate deer in forest management to-date involves reservation of mature forest in critical winter areas and provision of travel corridors. These areas are set aside permanently and in this regard, are not part of an active plantation management program, except that they must be incorporated into sustained yield planning.

Where plantation management enhances ungulate populations with browse damage as a result, operational management activities are basically limited to use of repellents or physical barriers to protect seedlings. Recognising that black-tailed deer use of plantation is highest in the area 45 to 60 m from the forest edge (Willms 1971) and Roosevelt elk similarly make greatest use of the area within 200 m of standing timber (Swanson 1970) then increased size of clearcuts will reduce the amount of area subject to browsing damage within a plantation.

An alternative approach that is under test in Washington and Oregon is the establishment of preferred forbs as a means of relieving deer and elk browse pressure on planted seedlings (Campbell & Evans 1975). This approach combines habitat

improvement and damage control during phase 1 of the plantation management regime (Fig. 2). A potential hazard is that in the absence of population control through adequate harvests by hunting, increases in deer numbers could offset the effect of providing preferred forbs as an alternative to conifer seedlings as forage. Campbell & Evans (1975) also pointed out the possibility of abundant herbs increasing snowshoe hare populations, creating an additional damage problem.

Rodents. Opportunities to influence rodent and hare populations in early stages of plantation development are limited. Cover and forage are the key habitat components that can be manipulated. Work referred to earlier indicates that herbicidal removal of vegetation that provides cover for snowshoe hares (Borrecco 1976) or forage for pocket gophers (Black & Hooven 1974) will reduce populations and damage caused by these species.

Bears. Opportunities to modify the plantation management regime to reduce bear damage also are limited. The characteristics of individual trees on which bear damage is concentrated are identical to those that the silvicultural practices of thinning and fertilization attempt to produce. Perhaps early dominance of the site by conifers after logging will have some influence on the carrying capacity for bears, but it appears that the current practice of direct control through sport hunting will continue to be the primary means of damage reduction.

Birds. The most serious conflicts between plantation forestry and birds concern those species requiring old-growth habitats. To overcome these conflicts and accommodate the species requires departures from the plantation management regime, at least on some portion of the land area.

For the red-cockaded woodpecker a recovery team has been appointed to develop plans for maintenance and enhancement of the species (Red-cockaded Woodpecker Team 1977). The team's primary focus is to ensure continued availability of habitat. Thus, they have recommended maintenance of forty ha of contiguous pine stands around existing colony sites to protect the colony and provide feeding areas and replacement trees. Minimum rotation length recommended is eighty years. Forest management practices that maintain the open character of stands, such as thinning and prescribed burning and that remove part of the associated hardwoods, are of some benefit. The establishment of modified plantation management regimes effective in providing for the long-term survival of the species depends on integrating these modified regimes into the overall management plan for the forest property.

Management plans have recently been developed for spotted owl (Oregon Endangered Species Task Force 1977) and are being implemented by the U.S. Forest Service and U.S. Bureau of Land

Management in Oregon. They are an additional example of a departure from a standard plantation management regime in order to maintain a species. The task force plan has the objective of maintaining 400 pairs of spotted owls. Management areas about 500 ha in size will be established for each pair. At least 120 ha of this area will be maintained in old-growth forest (i.e. >200 years) with the remainder managed to provide at least 50 per cent of the area in stands at least thirty years old. Along with this program of habitat maintenance, which clearly involves an extensive area of land, will go experimental habitat manipulations directed at assessing the species' adaptability to conditions other than old-growth forest.

The approach to integrated forest and wildlife management discussed with regard to elk (Thomas et al. 1976) considers all vertebrate species occurring in the geographic unit. Management for snag-dwelling birds and mammals requires a departure from standard plantation management regimes since young even-aged stands will not contain snags. Bull & Meslow (1977) have outlined an approach for meeting habitat needs of the pileated woodpecker. Since this species requires the largest snags and is likely to be one of the first species affected by plantation management, they reasoned that if its requirements were met, other woodpeckers would benefit as well. They recommend establishment of management units of at least 130 ha for each pair of woodpeckers. Within each sq.km containing a pileated woodpecker management unit, thirty-six snags, plus trees which will provide replacement snags (all greater than 50 cm dbh) should be retained following silvicultural treatments. This approach, like the spotted owl management plan, utilizes a modified management scheme on selected areas within an area covered by an overall management plan. Obviously, wood yields will be different than in a forest managed primarily for fibre production, with the absolute change a function of the number of special management areas deemed necessary. It is clear that socio-economic, as well as ecological considerations will influence the extent to which these management options are implemented. Calish, Ficht & Teeguarden (1978) outline an approach for assessing effects on wood yields of managing for non-timber resources, with specific regard to rotation length for Douglas fir. These kinds of assessments will be increasingly necessary in making resource management decisions.

REFERENCES

- Balda, R. (1975). The relationship of secondary cavity nesters to snag densities in western coniferous forests. United States Department of Agriculture Forest Service Southwest Region. Wildlife Habitat Technical Bulletin # 1. 37 pp. Albuquerque, New Mexico.

- Barnes, V.G. (1973). Pocket gophers and reforestation in the Pacific Northwest: a problem analysis. U.S. Department of Interior, Special Scientific Report Wildlife # 155, 18 pp.
- Barnes, V.G. (1974). Response of pocket gopher populations to silvicultural practices in Central Oregon. "Wildlife and forest management in the Pacific Northwest" (Ed by H.C. Black) pp.167-177. Oregon State University, Corvallis, U.S.A.
- Beall, R.C. (1973). Winter habitat use in the Sapphire Mountains of western Montana. Proceedings Western States Elk Workshop, Bozeman, Montana, U.S.A.
- Black, H.C. (1965). An analysis of a population of snowshoe hares (Lepus americanus washingtonii Baird) in western Oregon. Ph.D. thesis. Oregon State University, Corvallis, U.S.A. 285 pp.
- Black, H.C. & Hooven, E.F. (1974). Response of small-mammal communities to habitat change. "Wildlife and forest management in the Pacific Northwest" (Ed. by H.C. Black) pp. 177-186. Oregon State University, Corvallis, U.S.A.
- Black, H.C., Scherzinger, R.J. & Thomas, J.W. (1976). Relationships of Rocky Mountain elk and Rocky Mountain mule deer habitat to timber management in the Blue Mountains of Oregon and Washington. Transcript of the elk - logging roads symposium (Ed. by J. Peek) pp. 11-31. University of Idaho, Moscow, U.S.A. December 1975.
- Borrecco, J.E. (1976). Controlling damage by forest rodents and lagomorphs through habitat manipulation. Proceedings Seventh Vertebrate Pest Conference pp. 203-210.
- Brown, E.F. (1961). The black-tailed deer of western Washington. Washington Department of Game. Biological Bulletin #13. 124 pp.
- Bull, E.L. & Meslow, E.C. (1977). Habitat requirements of the pileated woodpecker in northeastern Oregon. Journal of Forestry, 75, 335-340.
- Bunnell, F.L. (1976a). Forestry-wildlife: whither the future. Forestry Chronicle, 52, 147-149.
- Bunnell, F.L. (1976b). The myth of the omniscient forester. Forestry Chronicle, 52, 150-152.
- Bunnell, F.L. & Eastman, D.S. (1976). Effects of forest management practices on wildlife in the forests of British Columbia. Proceedings of Division I, XVI IUFRO World Congress, Oslo, Norway. pp.631-689.
- Bunnell, F.L., Ellis, R., Stevenson, S. & Eastman, D.S. (1978). Evaluating ungulate populations and range in British Columbia. Transactions North American Wildlife and Natural Resources Conference, 43, in press.
- Calish, S., Fight, R.D. & Teeguarden, D.E. (1978). How do non-timber values affect Douglas fir rotations? Journal of Forestry, 76, 217-221.

- Campbell, D.L. & Evans, J. (1975). Improving wildlife habitat in young Douglas fir plantations. Transactions North American Wildlife and Natural Resources Conference, 40, 210-218.
- Childs, T.W. & Worthington, N.P. (1955). Bear damage to young Douglas fir. Pacific Northwest Forest and Range Experiment Station Research Note #113. U.S.D.A, Forest Service. pp. 4.
- Cowan, I.M. (1945). The ecological relationships of the food of the Columbian black-tailed deer, Odocoileus hemionus columbianus (Richardson), in the Coast Forest Region of southern Vancouver Island, British Columbia. Ecological Monographs, 15, 110-139.
- Crouch, G.L. (1974). Interaction of deer and forest succession on clearcuttings in the Coast Range of Oregon. "Wildlife and forest management in the Pacific Northwest" (Ed. by H.C. Black) pp. 133-139. Oregon State University, Corvallis, U.S.A.
- Edwards, R.F. (1965). Snow depths and ungulate abundance in the mountains of western Canada. Journal of Wildlife Management, 20, 159-168.
- Fowle, C.D. (1960). A study of the blue grouse (Dendrogeopys obscurus (Say)) on Vancouver Island, British Columbia. Canadian Journal of Zoology, 38, 701-713.
- Garrison, G.A. (1961). Recovery of ponderosa pine range in eastern Oregon and eastern Washington by seventh year after logging. Society of American Foresters Proceedings, Washington. pp. 137-139.
- Harper, J.A. (1971). Ecology of Roosevelt elk. Oregon State Game Commission, Portland, Oregon. U.S.A. 14pp.
- Hedrick, D.W., Young, J.A., McArthur, J.A.B. & Keniston, R.F. (1968). Effects of forest grazing and grazing practices on mixed coniferous forests of northeastern Oregon. U.S. Agricultural Experimental Station Technical Bulletin #103. Oregon State University, Corvallis, U.S.A. 24pp.
- Hershey, T.J. & Leege, T.A. (1976). Influences of logging on elk on summer range in north central Idaho. Transactions of the elk - logging roads symposium (Ed. by J. Peek) pp. 73-80. University of Idaho, Moscow, U.S.A.
- Hines, W.W. & Land, C.F. (1974). Black tailed deer and Douglas fir regeneration in the Coast range of Oregon. "Wildlife and forest management in the Pacific Northwest" (Ed. by H.C. Black) pp. 121-133. Oregon State University, Corvallis, U.S.A.
- Hooven, E.F. & Black H.C. (1976). Effects of some clearcutting practices on small mammal populations in western Oregon. Northwest Science, 50, 187
- Jackson, J.A. (1971). The evolution, taxonomy, distribution, past populations and current status of the red-cockaded woodpecker. Proceedings Symposium on Ecology and

- Management Red cockaded woodpecker. pp4-29. U.S. Department of Agriculture Forestry and Wildlife Service.
- Jones, G.W. (1974). Influence of forest development on black-tailed deer winter range on Vancouver Island. Proceedings Symposium on Wildlife and Forest Management in the Pacific Northwest (Ed. by H.C. Black). Oregon State University, Corvallis. 236 pp.
- Jones, G.W. (1975). Aspects of the winter ecology of black-tailed deer (Odocoileus hemionus columbianus) on northern Vancouver Island, M.Sc. thesis. University of British Columbia. 78 pp.
- Kelsall, J.P. & Prescott, W. (1971). Moose and deer behaviour in snow in Fundy National Park, New Brunswick. Department of the Environment, Canadian Wildlife Service Report #15. 25 pp.
- Lauckhart, J.B. (1955). The effect of logging old-growth timber on bear, Society of American Foresters Proceedings, pp.128-130.
- Lawrence, W.H. (1957). Porcupine control; a problem analysis. Weyerhaeuser Company Forestry Research Note. 43 pp.
- Lawrence, W.H. (1969). The impact of intensive forest amnagement on wildlife populations. "Wildlife and reforestation in the Pacific Northwest" (Ed. by H.C. Black). pp.72-74. School of Forestry, Oregon State University, Corvallis.
- Lay, D. & Swebston, D. (1975). The red-cockaded woodpecker. Texas Parks and Wildlife Department Publication. Austin, Texas 7pp.
- Levin, O.R. (1954). The South Olympic tree farm. Journal of Forestry, 52, 243-249.
- Meslow, E.C. & Wight, H.M. (1975). Avifauna and succession in Douglas fir forests in the Pacific Northwest. Proceedings Symposium on management of forest and range habitats for non-game birds. pp.266-271. U.S. Department of Agriculture Forest Service General Technical Report WO-1.
- Motobu, D.T. (1978). Effects of controlled slash burning on the mountain beaver (Aplodontia rufa rufa). Northwest Science, 52, 192-199.
- Neal, F.D. & Borrecco, J.E. (1978). Distribution and relationship of mountain beaver to openings in sapling stands. Submitted to Northwest Science.
- Oregon Endangered Species Task Force (1977). Spotted owl management plan. Oregon Department for Fish and Wildlife, Portland, Oregon. 3 pp mimeo.
- Poelker, R.J. & Hartwell, H.P. (1973). Black bear of Washington. Biological Bulletin #14 Washington State Game Department 180pp.
- Prescott, W.H. (1974). Interrelationships of moose and deer of the genus Odocoileus. Naturaliste Canadien, 101, 493-504.
- Radwan, M.A. (1969). Chemical composition of the sapwood of four tree species in relation to feeding by black bear. Forest

- Science, 15, 11-16.
- Red Cockaded Woodpecker Recovery Team.(1977). Red-cockaded woodpecker plan. 17 pp mimeo.
- Redfield J.A., Zwickel, F.C. & Bendell, J.F. (1970). Effects of fire on numbers of blue grouse. Proceedings Annual Tall Timbers Fire Ecology Conference, 10, 63-83.
- Swanson, D.O.(1970). Roosevelt elk - forest relationships in the Douglas fir region of the southern Oregon Coast Range. Ph.D. thesis. University of Michigan. 173 pp.
- Telfer, E.S.(1970). Winter habitat selection by moose and white-tailed deer. Journal of Wildlife Management, 34, 553-559.
- Thomas, J.W. Grouch, C.L., Bumstead, R.S. & Bryant, L.D.(1975) Silvicultural options and habitat values in coniferous forests. Proceedings Symposium on management of forest and range habitats for non-game birds. pp.272-287. U.S. Department of Agriculture Forest Service General Technical Report WO-1,
- Thomas, J.W., Miller, R.J., Black, H., Rodiek, J.E. & Maser, C. (1976). Guidelines for maintaining and enhancing wildlife habitat in forest management in the Blue Mountains of Washington and Oregon. Transactions of the North American Wildlife and Natural Resources Conference, 41, 452-476.
- Wight, H.M.(1974). Non-game wildlife and forest management. "Wildlife and forest management in the Pacific Northwest", (Ed. by H.C. Black), pp. 27-39. Oregon State University, Corvallis.
- Willms, W.D.(1971). The influence of forest edge, elevation, aspect, site index and roads on deer use of logged and mature forests, northern Vancouver Island. M.Sc. thesis. Faculties of Forestry and Agriculture, University of British Columbia. 184 pp.



EVEN-AGED PLANTATIONS AS A HABITAT FOR BIRDS

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SUMMARY

Large-scale afforestation of uplands in Britain has particularly affected parts of southern Scotland. Breeding song-bird populations were censused using the mapping method on selected plots at different stages of forest development, from the original use of the moorland for grazing until forty years after planting.

Song-bird densities were least on the unplanted moorland, where only skylark and meadow pipit were common. At the young and pre-thicket plantation stages, a variety of species such as chats and willow warbler colonized the plantation. Some of these prefer scrub and were displaced when the canopy closed. In thicket and thinned plantations only species typical of conifer forests, such as goldcrest, chaffinch and wren remained. Total breeding song-bird densities were about three times greater in pre-thicket plantations than on moorland, and four to six times greater in thinned plantations.

Tree species, soil fertility, the diversity of vertical structure, and breaks in the forest cover may all influence bird populations. In particular, spruce supported more song-birds than pine, and communities were diverse where foliage profiles covered a wide range. Areas within the forest replanted after wind-blow held the same species as the first rotation at the same stage. Pre-existing hardwood remnants within the plantation made little difference to the species present.

Several species use the forest as a refuge, but also require other habitats, e.g. the sparrowhawk, which nested in forests and other woodlands but often hunted outside plantations.

In southwest Scotland sparrowhawks bred more successfully in valley woods than in hill forestry plantations. In the interior of a large plantation growth rates of nestlings were lower and their mortality was considerably higher than on its lower edge and nearby valley woods. Differences were attributed to differences in the food supply, which was abundant in some woods in the valley, but sparser and more difficult to catch in plantations.

The controversy surrounding the wildlife in large forestry plantations is discussed. Against the gains in total song-bird densities when moorland is afforested, several open country species have been displaced, and the raven is declining due to afforestation and consequent loss of sheep carrion.

RÉSUMÉ

Le reboisement à grande échelle des hautes terres de Grande Bretagne a pris place en particulier dans de nombreuses régions du Sud de l'Ecosse. Des populations d'oiseaux chanteurs ont été recensés en utilisant des relevés dans des endroits choisis pendant des étapes différentes du développement de la forêt, de la lande d'origine, utilisée comme pâturage jusqu'à quarante ans après la plantation.

La population d'oiseaux chanteurs était la plus mince dans les landes avant la plantation où l'on ne trouvait que l'alouette et la farlousse. Au stade de fourré, différentes espèces, tels que le tarier et la fauvette, colonisaient la plantation. Certaines préféraient les buissons et s'en allaient au moment de la fermeture des cimes. Dans les plantations au stade de gaulis et de perchis éclairci il ne restait plus que les espèces typiques des forêts de conifères, tels que le roitelet huppé, le pinson et le troglodyte mignon. La concentration d'oiseaux chanteurs était environ trois fois plus grande dans les plantations avant l'état de fourrés, que dans les landes et quatre à six fois plus grandes dans les plantations éclaircies.

Les essences, la fertilité des sols, la diversité des structures verticales et des coupures dans le couvert peuvent aussi influencer sur les populations d'oiseaux. En particulier

les épicéas possédaient plus d'oiseaux chanteurs que les pins et la diversité des feuillages entraînait une diversité des communautés d'oiseaux. Des parties de la forêt replantées après des coups de vent possédaient les mêmes espèces que pendant la première rotation à stade identique. Des feuillus préexistants n'ont que peu d'influence sur les espèces présentes.

Plusieurs espèces utilisent la forêt comme refuge mais ont besoin aussi d'autres habitats, comme l'épervier, par exemple, qui fait son nid dans les forêts et autres régions boisées mais qui chasse en dehors de plantations.

Dans le sud-ouest de l'Ecosse, les éperviers se multiplient mieux dans les bois de vallées que dans les forêts sur les hauteurs. A l'intérieur d'une grande plantation, le taux de croissance des oisillons est plus bas et leur mortalité bien plus élevée que dans les lisières plus basses ou dans les bois proches des vallées. On a attribué cette différence aux différences de nourriture plus abondante dans les bois de vallées mais plus rare et plus difficile à attrapper dans les plantations. Il y a beaucoup de controverses au sujet de la faune sauvage dans les grandes plantations forestières. Bien que la densité totale d'oiseaux chanteurs ait été plus grande au moment du boisement de la lande, plusieurs espèces de rase campagne ont été déplacées et le nombre de corbeaux est en déclin à cause du boisement qui a eu comme conséquence une diminution des carcasses de mouton.

ZUSAMMENFASSUNG

Durch die grossräumigen Aufforstungsmassnahmen im britischen Hügelland wurden insbesondere weite Teile Südschottlands erfasst. Dabei wurde eine Kartierung brütender Singvögelbestände in ausgewählten Gebieten während verschiedener Entwicklungsphasen des Waldes von der ursprünglichen Nutzung des Moorlandes als Weide bis vierzig Jahre nach der Bepflanzung durchgeführt.

Im Moorland, wo nur Lerche und Wiesenpieper verbreitet waren, gab es die wenigsten Singvögel. In den ersten unterholzfreien Stadien der Pflanzung, siedelte sich eine

Vielfalt von Arten, wie beispielsweise Steinschmätzer und Weidenlaubsänger an. Einige von ihnen bevorzugten Buschwerk und wurden verdrängt, als sich das Blätterdach schloss. In Pflanzungen mit Dickicht und lichten Beständen bleiben nur Arten zurück, die für Nadelwälder typisch sind, wie zum Beispiel Goldhähnchen, Buchfink und Zaunkönig. Insgesamt gab es in noch unterholzfreien Pflanzungen dreimal so viel brütende Singvögel wie im Moorland und in lichten Pflanzungen vier- bis sechsmal so viel. Faktoren wie Baumart, Bodenfruchtbarkeit, Dichte und vertikaler Aufbau des Bestandes können die Vogelpopulationen beeinflussen. Zum Beispiel war die Singvogeldichte in Fichtenbeständen höher als in Kiefernbeständen. In einem vielfach gegliederten Kronendach von Laubbäumen war die Zusammensetzung der Vogelwelt artenreich. Windbruchflächen wiesen nach Auspflanzung dieselben Arten auf, wie die Erstaufforstung im gleichen Stadium. In den verbliebenen natürlichen Hartholz-Bestandesresten wurden kaum Unterschiede bei der Entwicklung der vorhandenen Arten festgestellt.

Einige Arten suchen im Wald Schutz, brauchen aber auch andere Habitate. Ein typisches Beispiel hierfür ist der Sperber, der in Wäldern und anderen Baumgebieten nistete, aber häufig ausserhalb der Pflanzung jagte.

In Südwestschottland brüteten Sperber in Auewäldern mit grösserem Erfolg als in Bergwäldern. Im inneren Teil einer grossen Pflanzung war die Wachstumsrate von Nestlingen geringer und ihre Sterblichkeit beträchtlich höher als am Waldrand und in nahen Auewäldern mit geringerer Höhe über NN. Der Unterschied wird dem Nahrungsangebot zugeschrieben, das in einigen Auewäldern reichlich, in Pflanzungen jedoch spärlicher und schwieriger zu erbeuten ist.

Die Kontroverse um das Tierleben in grossen Aufforstungsgebieten wird diskutiert. Dem Gewinn einer im ganzen grösseren Singvogelverbreitung bei Aufforstung von Moorland steht die Vertreibung verschiedener Arten gegenüber, die offenes Gelände brauchen. Zum Beispiel verschwindet der Rabe immer mehr infolge der Abnahme von Schafkadavern nach Aufforstung.

INTRODUCTION

During the past sixty years a policy of large-scale afforestation has been put into practice in Britain. The areas affected have been chiefly the uplands of Northern England, Wales and Scotland, where moorland previously used for the grazing of sheep and cattle, has been planted with conifers. Two introduced species, Sitka spruce (*Picea sitchensis*) and lodgepole pine (*Pinus contorta*) form the bulk of the plantations, which, because of their planting regimes, can be described as 'even-aged'.

Such plantations of exotic trees have often been popularly condemned as being virtually devoid of wildlife, but there have been few quantitative assessments in which changes due to afforestation have been measured. The work reported here was done under a contract from the Nature Conservancy Council.

SONG-BIRD COMMUNITIES OF PLANTATIONS

Study areas and methods

Plots were established in three forests in the Dumfries and Galloway region of southwest Scotland. These were Ae Forest, situated on the edge of the Lowther Hills; Clatteringshaws Forest, entirely on upland in the Galloway Hills; and Eskdalemuir, a large young forest also on upland. Most of the study plots were on infertile hill ground, between 150 and 350 m above sea level, except at Eskdalemuir where they were at up to 425 m.

Within Ae and Clatteringshaw Forests the range of study plots encompassed habitats categorized as unplanted sheep walk under grass and heather (*Calluna vulgaris*), and young, pre-thicket, thicket and thinned plantation. Only unplanted heather and young trees were studied at Eskdalemuir.

With the exception of one and one half plots of Norway spruce (*Picea abies*), the plots were planted with Sitka spruce, sometimes mixed with small percentages of lodgepole pine or larch (*Larix* spp.). They were chosen for uniformity within their boundaries whenever this was possible.

Territorial song-birds were censused on each plot using the mapping method, following Williamson (1964). The plot, from 10 ha in thinned plantation to 25 ha on unplanted ground, was first mapped accurately. Each census consisted of ten early morning visits to the plot between late March and mid-June on which all song-birds observed, either by sight or sound, were marked on a copy of the large scale map. At the end of the season, these maps were used for the construction of further maps, one for each species, showing its occurrence on the plot over the series of ten visits. These species maps were used to estimate the position of territories, using well-established procedural rules, such as a requirement for at least three clumped observations to constitute one

territory (International Bird Census Committee 1969). Numbers of territories on the plots were counted, and divided by the area of the plot to give densities, standardized as the number of breeding pairs/sq.km for each species occurring on each plot.

The densities of more sparsely distributed non-passerines, such as waders, grouse and raptors, were not estimated due to shortage of time and manpower, although they were present on the plots.

RESULTS

A summary of the census results is given in Table 1, where scientific names of bird species are listed.

The succession of song-bird communities can be examined by considering the densities of the commoner species in relation to tree height (Fig. 1).

The skylark, dependent on grassy habitats for food and nest sites, was the only species to be at its highest density on unplanted grassland, and was the first to disappear as tree cover developed. By comparison, meadow pipit densities increased markedly when enclosure of the land from grazing animals allowed ground vegetation to flourish, and these birds were more tolerant of the developing tree, remaining in openings and along firebreaks until the canopy closed.

Two species typical of open bushy habitats, the stonechat and whinchat, took up territories in the plantations as soon as the trees suitable perches for them, and while they could still nest in the tussocks of grass below the trees. Their period of tenure in any particular plantation area would be short, perhaps only five years.

Willow warblers which take their insect food from the needles of trees, remained in the plantations until a later stage than the ground-feeding chats. At the pre-thicket stage this was the commonest species, but their numbers dwindled as the canopy closed and their ground nesting sites were lost. They were not found in thinned plantations.

The wren was the first of the species present in mature plantations to appear on the plots of young trees planted on heather. Its requirements for food and nesting are found in cover close to the ground, and the density of wrens in thinned plantations was related to the abundance of brash and fallen trees. Other colonists of pre-thicket plantation were chaffinch and robin, which became most numerous at the thicket stage, and the canopy feeding and -nesting goldcrest, which reached high densities in the thinned plantations. The common species to occupy the plantations last was the coal tit, a hole-nesting species which frequently uses crevices at the bases of trees for its nest sites in plantations. They did not establish themselves until the trees reached the thicket stage. It is thus apparent that over a forty year period of

Table 1. Song-bird communities at different stages of forest development.

afforestation	Deplanted beather moor	Deplanted grassy sheepwalk	Young trees 'plot'	'Jubilee'	Pre-thicket	Thicket	Thinned
stage	Beather <u>Eriophorum</u> <u>vaginatum</u>	<u>Molinia</u> <u>Juncus</u> spp	Thick growth of grasses. <u>Myrica gale</u> Beather		Trees touch but do not form closed canopy. Beather. <u>Myrica gale</u> between trees.	Closed canopy. impenetrable. No ground vegetation.	Little or no ground vegetation.
Age (yrs)	0	0	2-6	7-8	12-14	23-26	34-39
ht range (m)	0	0	1-2.5	3-5	7	12-15	20
# plots	1	3	3	1	2	3	4
# censuses (10 visits)	1	4	4	2	2	5	6
2 years total densities (no km ²)	72	72-103	71-128	357-384	231-252	302-443	318-425
numbers of species	2	2-4	3-6	13-14	9	6-10	6-10

Average densities of important species

preference: open country scrub forest	
ark	20
<u>ada arvensis</u>	
ow pipit	52
<u>na pratensis</u>	
stier	
<u>antha pensilvanica</u>	
hunting	
<u>ria schoeniclus</u>	
echat	
<u>icola terquata</u>	
echat	
<u>icola rubetra</u>	
et	26
<u>ntis cannabina</u>	
ow warbler	95
<u>lincoptes trochilus</u>	33
	53
	46
<u>ilodytes troglodytes</u>	
Acrost	24
<u>ulus regulae</u>	29
	106
pell	15
<u>ntis flamma</u>	23
	15
	48
<u>thacus rubecula</u>	
ffisch	
	80
<u>gilla caelebs</u>	
tit	
	36
ster	
g thrush	
	5
<u>us philomelos</u>	
ech	
<u>ella modularis</u>	
ia	
<u>ntis spinus</u>	
ecropper	
<u>ntis familiaris</u>	

forest growth, the composition of the song-bird community changes entirely as all the species initially present lose their required habitats, and are replaced by others, some of which are themselves only present for a transitory period. The same observation can be made of the non-passerine birds, as species such as lapwing (Vanellus vanellus), curlew (Numenius arquata), redshank (Tringa totanus), snipe (Gallinago gallinago), red grouse (Lagopus l. scoticus) and merlin (Falco columbarius), are replaced in young forest by black grouse (Lyrurus tetrix), short-eared owl (Asio flammeus) and kestrel (Falco tinnunculus), and later in mature plantations by woodcock (Scolopax rusticola), woodpigeon (Columba palumbus), sparrowhawk (Accipiter nisus) and tawny owl (Strix aluco).

FEATURES OF FOREST STRUCTURE WHICH INFLUENCE BIRD POPULATIONS

Tree species

The tree species forming the forest are an important influence on song-bird communities. The greatest difference occurs between broad-leaved and coniferous woods, each of which has its characteristic species, although the majority of British woodland birds are found in both. Studies in Finland (reviewed by van Haartman 1971) showed that there were consistently more breeding birds in birch (Betula spp.) than in spruce, and in spruce than in pine. Even-aged plantations in Britain are almost entirely of conifers, particularly spruces and pines. When studying plantations at the thinned stage, it was found that total song-bird densities were approximately twice as great in spruce as in pine, when there were also fewer species (Moss 1978a). In this context Newton & Moss (1977) pointed out that pine has less foliage per unit area than spruce, and hence less habitat for insects. In Finland the differences between spruce and pine were of a lower magnitude (von Haartman 1971).

Soil fertility

Within forests of a particular tree species, soil fertility influences many aspects of productivity, including that of subsidiary vegetation and of insects. Thus it was noted earlier that in Ae Forest the 'Jubilee plot' pre-thicket plantation, where growth of trees and other vegetation was vigorous, supported a much more abundant and diverse bird population than might have been expected from the age and structure of the trees alone. Again Finnish studies showed that bird densities decreased with decreasing soil fertility, as indicated by the type of vegetation of the forest floor (Haapanen 1965).

Diversity of structure

In North American woodlands MacArthur & MacArthur (1961) found that diversity of song-bird populations was directly related to the diversity of the height structure of the vegetation, so that the more layers of trees and shrubs a wood

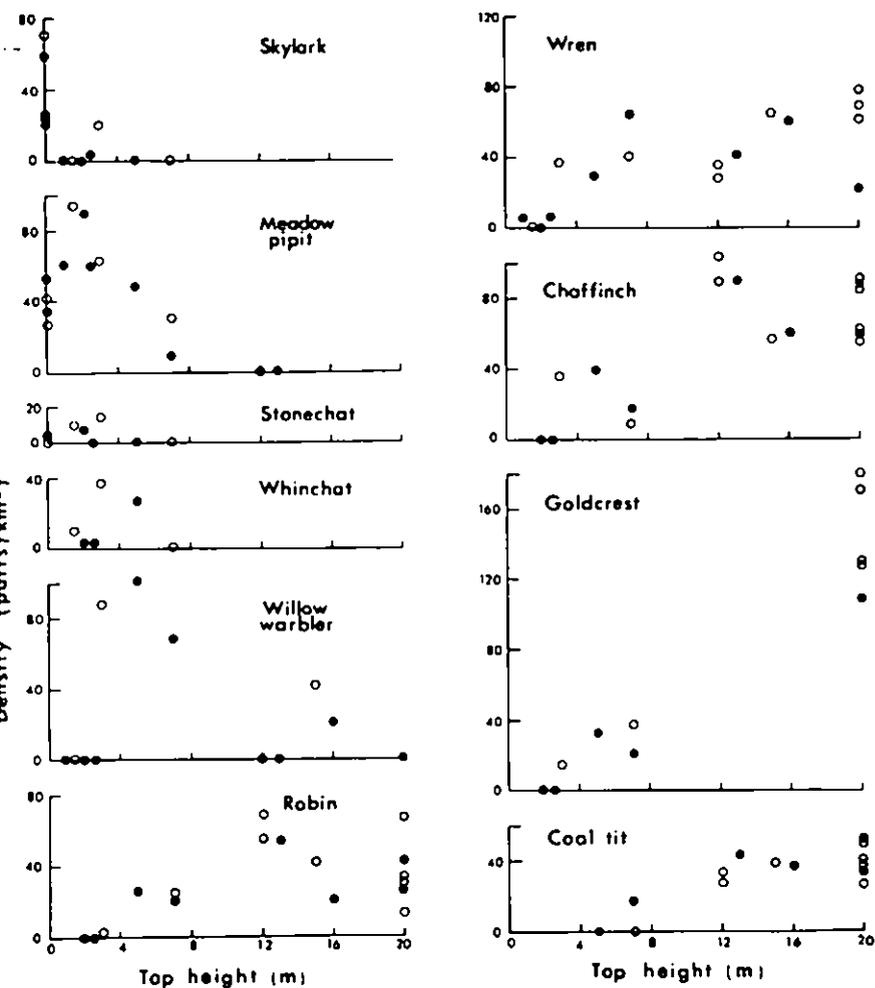


Fig. 1. The density of song birds in even-aged plantation in relation to the top height of the trees.

1976 data ○, 1977 data ●. N.B. Not all zero densities are shown.

contained, the more bird species were found there. The same relationship was found in Scotland when a sample of woods, both planted and semi-natural, coniferous and broad-leaved, was considered (Moss 1978b). This observation is easily understood, since a wood with a great diversity of vertical structure contains sufficient ecological 'niches' for a large variety of woodland bird species to find territories there. When the structure is simple, only a few species occupy all the available niches. No similar result was obtained for plantations which had not yet reached the thicket stage, probably because of the presence of a number of species adapted to scrub, rather than understory.

The implication for even-aged plantations is that because they have an artificially low diversity in their height structure, their bird populations are low in species diversity. For example, thinned spruce plantations described earlier held six to ten breeding species, while a neighbouring multi-structured mixed wood supported eighteen species (Moss 1978a).

However, a relationship between total numbers of pairs of song-birds and structural diversity was not found, since for example plantations with low diversity provided excellent habitat for a few species and so total densities there were not particularly low.

Breaks in the forest structure

The most frequent breaks occurring in the structure of an even-aged plantation are due to rides and firebreaks, to clearfelling, windblow and the practice of leaving remnants of original woodland during planting, usually in the form of hardwood fringing watercourses or on valley sides.

The large scale clearfelling of plantation blocks followed by subsequent replanting is only just beginning in Britain, and few areas exist where its effect on bird populations can be studied. However, a similar situation has occurred where large areas have been windthrown and subsequently cleared and replanted and a brief survey of some such areas was made in Ae Forest. The species present among young trees and at the pre-thicket stages of replantings were the same as on the first rotation though meadow pipits were by comparison sparsely distributed. Cleared ground before replanting appeared to be completely devoid of birds, unlike the sheepwalk before initial planting.

It has occasionally been the practice among foresters to leave existing remnants of hardwoods along stream sides or in steeply sloping gullies, and these breaks might be thought to provide a refuge for hole nesting bird species such as blue and great tits (Parus caeruleus and P. major) or redstarts (Phoenicurus phoenicurus) which favour mature broad-leaved trees. Such a gully approximately 50 m wide crossed one of the plots studied in Ae Forest, but there was no evidence that its

old oaks (Quercus spp) attracted any extra breeding birds. As an added inducement, nest boxes were provided in this gully but none was occupied in two breeding seasons. Similarly, S.J. Petty (pers. comm.) found that a belt of alder (Alnus glutinosa) approximately 50 m wide within a plantation in Galloway had no effect on the composition of the bird population there. However, a belt of rank heather, approximately 100 m wide containing rocky bluffs which had been left beside a stream in Kielder Forest, Northumberland, allowed merlins to continue nesting.

THE PLANTATION AS A REFUGE

So far, the plantation has been considered only as a habitat for those birds which are totally dependent on it for nesting, feeding and roosting, at least during the breeding season. However, for a number of species it is used as a refuge for one or more of these activities, while not usually providing all their requirements. In the majority of such species, the forest is used as a nesting habitat but the bird finds part of its food elsewhere. For example, mistle thrushes (Turdus viscivorus) nesting in the plantations often feed on adjacent pastures, and buzzards (Buteo buteo) nest in forests but hunt over surrounding open country. This type of use of the plantation can be illustrated by describing the relationship between the sparrowhawk and its habitat, a species which has been studied intensively in recent years.

The sparrowhawk is a relatively small, agile woodland predator whose prey consists almost entirely of birds. It builds its nest by preference in a coniferous tree within a forest block, but for clear access the nest is usually close to a break such as a stream or ride. It typically hunts along woodland edges, including those formed by clearings, rides or rivers, and hedgerows in more open country, and relies on a surprise attack rather than a prolonged chase in order to capture its prey. Recent research into the ecology of the sparrowhawk in southwest Scotland has investigated its relationships with the environment and with its food supply. Newton (1972) found that in continuous woodland, sparrowhawk nest sites were regularly spaced, but that the mean distance between them differed by a factor of three to four between Annandale in southwest Scotland and Speyside in the central Highlands. Data from further study areas in different parts of Britain were used (Newton et al. 1977) to show that nesting density was inversely proportional to altitude and proportional to land quality. Both these relationships were thought to arise as the result of variations in food supply with altitude and land quality.

Newton (1976) compared a number of aspects of sparrowhawks' breeding success between small valley woods, hillside forestry plantations, and the large plantations at Ae

Forest. In valley woods, compared to hill forests, mean laying dates were earlier, mean clutch and brood sizes were larger, a greater proportion of nests produced young, and more nestlings survived.

These differences were consistent in the three years studied, though not all statistically significant in every year. The net result was that sparrowhawks nesting in the valley woods were considerably more productive of young than those in the hill forests. It was thus difficult to understand why birds occupied the hill forests when there were vacant territories in the valley, unless the plantation habitat offered them some advantage balancing the reduced nesting success.

My own studies of sparrowhawks (Moss 1976, 1978c) also compared aspects of breeding performance between birds nesting in the large Ae Forest and in small woods in the adjoining Annan valley. Daily growth rates of the nestlings were measured and the causes of mortality were assessed. The results showed that the study area could be divided between nests in the valley woods and the lower edge of the plantation as one group, and those in the higher and remoter parts of the plantation in another. Nestlings gained weight at rates which were on average 20 per cent lower in the interior of the forest than in the valley and forest edge, and the birds with lower growth rates also suffered greater fluctuations in weight.

Differences in mortality were also marked, 48 per cent of nestlings in the forest interior died when aged between two and twenty-four days compared to only 5 per cent in the valley and forest edge. Only 22 per cent of forest interior broods survived without any mortality, while in the remainder of the study area 87 per cent of parents all raised their young to fledging. The major causes of mortality were starvation as a result of competition within the brood (37.5 per cent of all deaths), exposure in wet weather (25 per cent) and predation by tawny owls (17.5 per cent).

Almost all the differences observed within the study area could be attributed to the food supply. Censuses of song-bird populations in woodlands (Moss 1978a) showed that in the valley woods there were abundant sources of prey within easy reach, if not in the coniferous woods actually preferred by sparrowhawks for nesting. The species present in the valley woods, such as thrushes (Turdus spp) tended to be larger on average than those predominating in the plantations, so enhancing their attractiveness as sources of prey for hawks. Valley woods were also easily accessible to the birds breeding along the edge of Ae Forest. By contrast, birds in the interior of the forest could either hunt for the sparser prey there, for example on the edges of windblows and stream sides, or they had to fly relatively long distances to the valley

woods in search of richer sources of prey. Radio-telemetry studies showed that the birds frequently followed the latter course, and one female regularly travelled 9 km to hunt when she had large young in the nest.

The consequences for broods in the interior of the forest were that competition occurred within broods which were too large to be supported by the poor food supply, and the weaker nestlings died. The female was forced to hunt away from the nest and the nestlings died because of exposure in wet weather or were eaten by predators. Those nestlings which did survive had reduced growth rates which may well have left them less fit to survive the difficult period after fledging.

The conclusions of both Newton's and my own studies were that the large even-aged plantation offers extensive areas which are attractive to sparrowhawks as habitats in which to nest, presumably with a minimum of disturbance from other birds due to the regular spacing of nests. However, from the studies of breeding success there appears to be a selective disadvantage in nesting in the interior of the plantations, and one might expect birds to show a greater preference in choice of nest site for the valley woods than was observed. The optimum environment from the point of view of both food supply and nest site would appear to be close to a forest edge which borders the valley.

DISCUSSION

In recent years there has been frequent debate, sometimes heated and too often ill-informed, on the merits and demerits of the afforestation of Britain's uplands. As a starting point, the detractors of forestry plantations often describe the moorland which has been lost as the 'natural' vegetation of the uplands, whereas it is often the consequence of centuries of over-grazing by sheep and of burning, resulting in the removal of the natural forest cover of Scots pine (*Pinus sylvestris*), birch and oak. These circumstances should be borne in mind when comparing the effects of afforestation on bird populations in Britain with its effects elsewhere in the world where plantations have replaced natural forests; in the latter case one might expect a decline in diversity and number of birds.

Even-aged plantations as habitats for birds have both gains and losses by comparison with moorland. On one side, there is an increase in song birds, both in numbers and species. Total song-bird densities in plantations were four to six times as high after twenty-five years as they were on moorland. In the course of its development, the plantation provided suitable habitats for a range of other song-bird species typical of scrub so that the total breeding species list of a forest containing areas at each stage of growth would far exceed that of moorland alone.

In addition, plantations provide refuges for a number of other species although, as in the case of the sparrowhawk, it may be those parts of the forest which are close to outside sources of food which are of greatest value. This is an example of the classic 'edge effect' (Odum 1959), where the boundary between two ecological zones proves richer than the pure habitat of either.

Against the gain in song-bird numbers with afforestation must be balanced the loss of moorland species, which was underestimated in this study restricted to song-birds. Although they are sparse in terms of pairs/sq.km many species of waders are dependent on unplanted uplands as their breeding habitat.

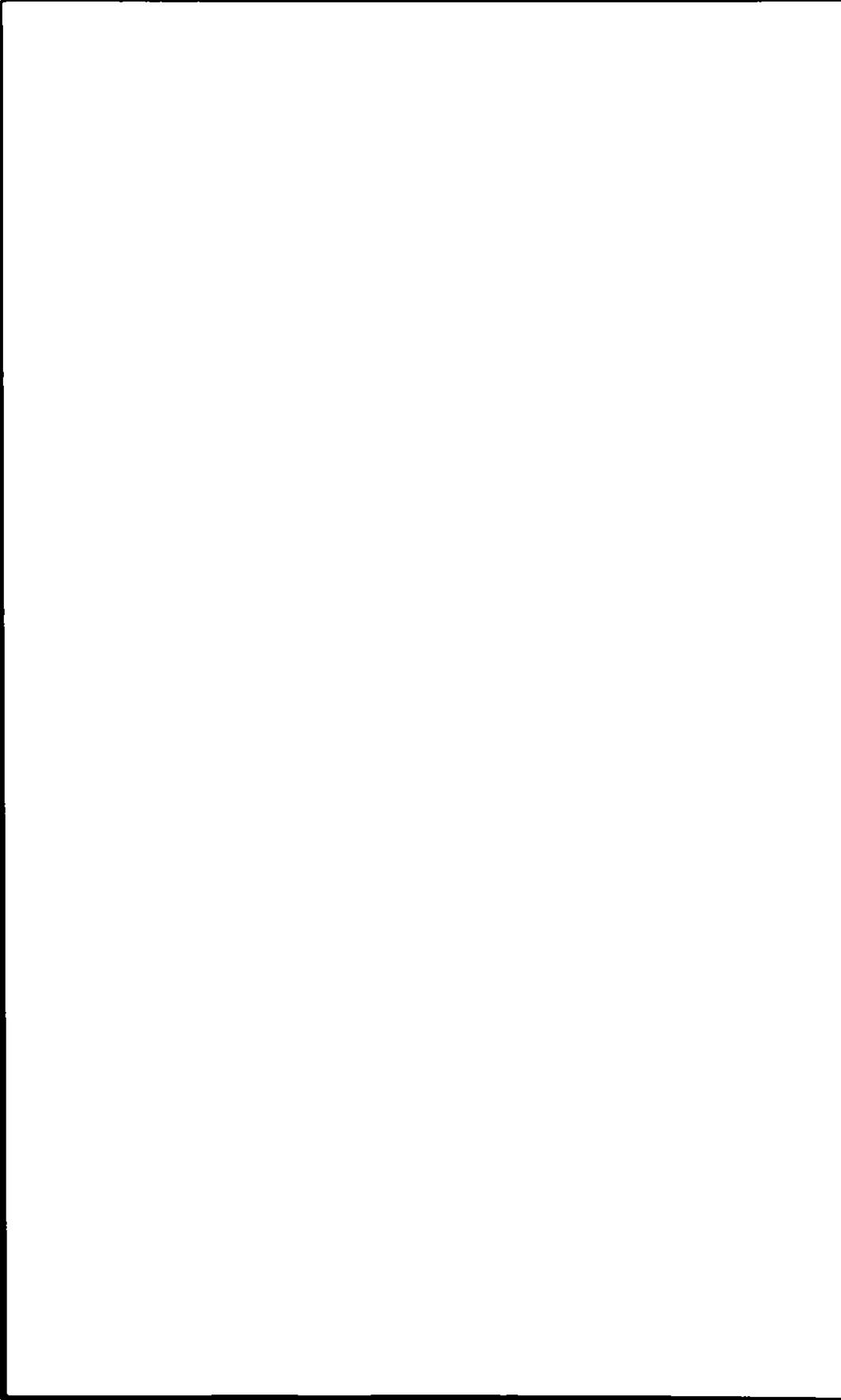
Populations of other species have also suffered from afforestation, sometimes indirectly as in the case of the raven (Corvus corax). Marquiss, Newton & Ratcliffe (1978) have attributed a 34 per cent decline in the raven population over fifteen years in southern Scotland and Northumberland to the removal of sheep, their main food source, following afforestation. Ravens often deserted traditional breeding sites concurrently with planting in the surrounding area. The merlin may also be suffering a similar reduction due to loss of its preferred moorland habitat, and deserves more detailed research.

It is often evident from arguments used by the opponents of large-scale afforestation that their aesthetic considerations favour the open moorland landscape rather than 'regimented rows of trees'. A certain amount of claustrophobia is experienced once the canopy closes, views are lost, and rides become 'tunnels through the spruce needles'. Appreciation of the birds is probably more difficult for the visitor when he is in a forest than when he is on the moor, since although they are present in the plantations at greater densities, the birds are less obvious to the observer, hidden as they often are by the tree canopy. It is much easier to see a skylark singing overhead against a blue sky than a goldcrest lost up among the spruce needles.

In conclusion, the best management of upland forestry for birds appears to be a policy favouring small, even-aged plantations forming a patchwork of blocks of differing ages within any one forest area, rather than large-scale cover by forests of uniform age. Some valleys and moorlands should be left entirely free of planting, since many species are dependent on unplanted uplands for breeding. Forest managers may plan their planting programmes to achieve such a forest containing the full range of growth stages, and unintentionally they may often be helped towards such a pattern by the occurrence of windthrows.

REFERENCES

- Haapenen, A. (1965). Bird fauna of Finnish forests in relation to forest succession. *Annales Zoologici Fennici*, 2, 153-196.
- Haartman, L. von (1971). Population dynamics. "Avian biology" (Ed. by D.S. Farner and J.R. King), pp. 391-459. Academic Press, London and New York.
- International Bird Census Committee (1969). Recommendations for an international standard for a mapping method in bird census work. *Bird study*, 16, 248-255.
- MacArthur, R.H. & MacArthur, J.W. (1961). On bird species diversity. *Ecology*, 42, 594-598.
- Marquiss, M., Newton, I. & Ratcliffe, D.A. (1978). The decline of the raven (*Corvus corax*) in relation to afforestation in southern Scotland and northern England. *Journal of Applied Ecology*, 15, 129-144.
- Moss, D. (1976). Woodland song-bird populations and growth of nestling sparrowhawks. Unpublished PhD thesis, University of Edinburgh.
- Moss, D. (1978a). Song bird populations in forestry plantations. *Quarterly Journal of Forestry*, 72, 5-14.
- Moss, D. (1978b). Diversity of woodland song-bird populations. *Journal of Animal Ecology*, 47, 521-527.
- Moss, D. (1978c). Growth of nestling sparrowhawks (*Accipiter nisus*). *Journal of Zoology* (London), in press.
- Newton, I. (1972). Birds of prey in Scotland: some conservation problems. *Scottish Birds*, 7, 5-23.
- Newton, I. (1976). Breeding of sparrowhawks (*Accipiter nisus*) in different environments. *Journal of Animal Ecology*, 45, 831-849.
- Newton, I. & Moss, D. (1977). Breeding birds of Scottish pinewoods. Symposium on Native Pinewoods of Scotland, Aviemore, 1975 pp.26-34. Institute of Terrestrial Ecology.
- Newton, I., Marquiss, M., Weir D.N. & Moss, D. (1977). Spacing of sparrowhawk nesting territories. *Journal of Animal Ecology*, 46, 425-441.
- Odum, E.P. (1959). *Fundamentals of Ecology*, Saunders.
- Williamson, K. (1964). Bird census work in woodlands. *Bird Study*, 11, 1-22.



—EVEN-AGED STANDS AS HABITAT FOR DEER IN CENTRAL EUROPE—

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SUMMARY

This paper deals with roe deer and red deer as inhabitants of Central European forests whether of mixed age or managed as even-aged plantations. It discusses to what extent they meet the deer's most important habitat requirements, namely adequate food, cover and shelter. The most critical factor, particularly for roe deer, is energy supply; cover, whether for hiding or shelter, seems to differ in importance between the various age classes of trees. Carrying capacities of forests can be improved where stands of one to ten year-old trees, for food, and eleven to twenty year-old trees, for cover, are well-mixed to increase the edge-effect. Therefore, even-aged plantations should have significantly higher carrying capacities than natural forests because they contain larger numbers of trees in the age classes favourable for deer. However, in most cases high deer densities also mean much browsing and bark stripping damage as well as poor body condition of the deer because of competition for a limited supply of food which is reflected in their growth and reproduction. It appears that especially roe deer, as a 'succession species', uses plantation forests more for cover, which encourages colonization and territorialism, than as a supply of food since the diversity and digestibility of the vegetation are reduced.

Methods, some still in a developmental stage, to assess deer condition in, as well as deer damage to plantations are discussed.

Roe deer and red deer differ in their

sociobiology, demands for food and cover, as well as in their effect on forests. Therefore, a deer habitat management, whether from the point of view of forestry or wildlife, will have to differentiate between them, in reconciling the various purposes for which the forest is grown.

RÉSUMÉ

Cette exposé traite des forêts d'Europe Centrale, qu'elles soient équiennes ou d'âge mixte, en tant qu'habitat du cerf et du chevreuil. Ces forêts procurent aux cervidés leurs besoins les plus importants: nourriture, couvert et gîte. Le facteur critique, surtout pour le chevreuil, est l'approvisionnement d'énergie; le gîte, qu'il soit abri ou cachette, diffère en importance selon l'âge des forêts. Le rôle d'abri des forêts peut être amélioré lorsqu'on juxtapose des peuplements de 1 à 10 ans, pour la nourriture, avec des peuplements de 11 à 20 ans, pour l'abri, qui augmentent l'effet de bordure. C'est pourquoi les forêts équiennes peuvent avoir des densités de cervidés plus élevées que les forêts naturelles puisqu'elles contiennent des arbres de classes d'âges favorables aux cervidés. Cependant dans bien des cas les densités élevées impliquent des dégâts (broulage et écorçage), et la condition physique des cervidés (poids) est également mauvaise à cause de la quantité limitée de nourriture à laquelle ils peuvent prétendre, reflétée par une mauvaise croissance et une mauvaise reproduction. C'est surtout le cas du chevreuil, 'espèce de succession', qui utilise les plantations comme abri, ce qui encourage la colonisation et le territorialisme, plutôt que pour sa nourriture car la variété et la digestibilité de la végétation sont réduites. Nous discutons des méthodes, dont certaines sont encore à l'état de développement, pour évaluer la condition de vie des cervidés ainsi que les dégâts qu'ils causent dans les plantations. Le cerf diffère du chevreuil de façon sociobiologique, par son besoin différent de nourriture et d'abri. Ces deux animaux ont aussi une influence différente sur la forêt. C'est pourquoi une gestion de l'habitat des

cervidés, qu'elle soit orientée vers la foresterie ou la protection de la faune sauvage, devra traiter les problèmes du cerf et du chevreuil séparément en essayant de concilier les besoins variés de la forêt.

ZUSAMMENFASSUNG

Diese Arbeit befasst sich mit den beiden in Mitteleuropa wichtigsten Wild-Wiederkäuern, Reh und Rothirsch, sowie der Frage, wie weit deren Äsungs- und Deckungsansprüche im Altersklassen-Wirtschaftswald bzw. in künstlich verjüngten, altersgleichen Reinbeständen befriedigt werden. Es wird die Bedeutung energiereicher, vor allem aber gut verdaulicher Äsung und deren Zugänglichkeit in nicht zu grosser Entfernung von den Deckung bietenden Einständen betont (Zeit - Energie - Budgets). Insofern sollten die Altersstufen 1-10, für Äsung sowie 11-20, für Deckung - insbesondere bei grenzlinien-reicher Gemengelage - auch hohe Tragfähigkeiten bzw. eher wohl hohen Besiedlungs-Anreiz bieten 'edge-effect'. Vor allem Rehwild, als 'Sukzessions-Art' findet in 'Plantagenwäldern' oft allerdings mehr Deckung und damit Anreize für Besiedlung und Territorialverhalten, als dem Äsungsmässig - insbesondere in qualitativer Hinsicht (Vergrasung bzw. Herbizideinsatz auf Kulturflächen, Nahrungsmangel in Stangenhölzern) - entspricht. Eine früher, unter Urwald(nahen)-Verhältnissen, vielleicht besser aufeinander abgestimmte Relation von Tragfähigkeit (siehe Kondition des Wildes wie auch des Waldes) und Besiedlungsanreiz (siehe Wildverteilungsdichten bzw. Waldstrukturen) klaffen im Altersklassen-Reinbestand also mehr oder minder auseinander. So besehen ist eine altersklassenweise Waldbewirtschaftung indirekt auch ein sehr wirksames Habitat Management für Schalenwild, ganz besonders für Rehe, bei denen damit zwar hohe Wilddichten provoziert, aber nur mindere Konditionen (siehe Gewicht, Zuwachs, Trophäen u.a.) erreicht werden dürften.

Möglichkeiten, die Wild-Kondition wie auch den Wald(verjüngungs)-zustand als Folge von Wildschäden zu bewerten, werden erörtert, insbesondere solche Methoden, die sich derzeit noch im Entwicklungsstadium befinden. Da sich

Reh und Rothirsch in ihrer Soziobiologie, ihren Habitatsansprüchen und hinsichtlich der von ihnen verursachbaren Waldschäden teilweise doch recht erheblich unterscheiden, sollte eine 'Schalenwildbewirtschaftung' dies entsprechend differenziert berücksichtigen. Und ebenso müsste die Forstwirtschaft sich ihrer habitat - beeinflussenden Nebenwirkungen mehr bewusst werden und diesen Umstand zum Beispiel bei der mittelfristigen Planung auch konsequenter einbeziehen.

INTRODUCTION

If animals living in the wild are to thrive they must make very specific demands on their environment. Because of the diverse and frequently major encroachment by man on the forest, ranging from exploitation and devastation to the transformation of these devastated areas into plantations of fast growing trees, prevailing ecological conditions have been transformed so drastically in certain areas that various species such as hazel grouse, capercaillie and woodpeckers have undergone a significant decline (cf. Eiberle 1976, 1977). However, other species have managed to thrive in these changed conditions. Amongst the species that do continue to thrive in many countries in Europe are the two most dominant ruminant species, roe and red deer, two species which present particular problems for the forester, who often also acts as the gamekeeper responsible. The areas in which these species can now be found in Central Europe and their numbers have multiplied in the last twenty to forty years (cf. Schröder 1976a; König 1976b; Donaubaue 1977) implying by definition productive population densities as well as increased carrying capacities.

As a rule, fundamentally wrong management decisions are thought to be responsible for these explosive increases in stock (Figs 1a + b and 2). They include the extermination of the larger predators, too low harvest quotas, especially of roe and red deer does, exaggerated winter, and on occasion even summer feeding. These policies are practised because all too often insufficient attention is paid to the changing ecological conditions of the countryside. This is particularly true of even-aged forest stands and the effects they have on the growth potential of hoofed game, especially for so-called 'succession species'.

WHAT ARE THE MAJOR DEMANDS PLACED ON THE HABITAT BY HOOFED GAME?

The primary - and therefore often also most easily limiting - ecological requirements of game are food and cover. Food has to satisfy the demand for energy as well as particular nutritional requirements; the digestibility of vegetation is a limiting factor in this respect. High demands

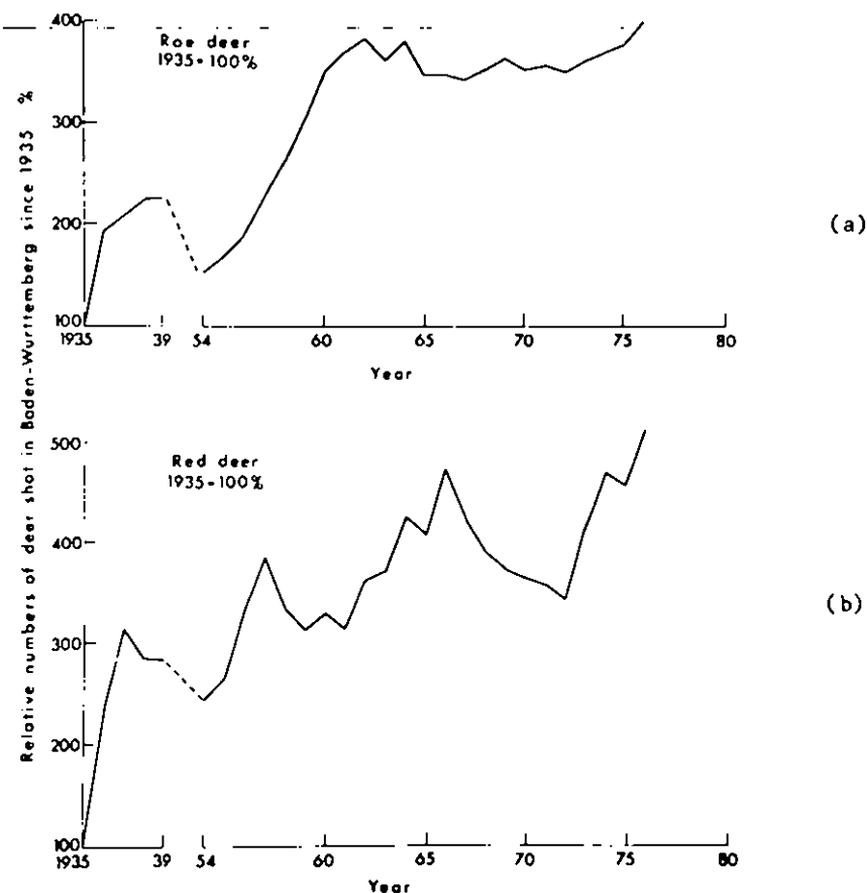


Fig. 1. Relative numbers of (a) roe and (b) red deer shot in Baden-Württemberg since 1935.

on the digestibility of food and on its energy value are made by

- females during pregnancy and, especially, during lactation;
- young animals while they are growing;
- bucks and stags defending their territory and during rutting (Eisfeld 1976; Ellenberg 1977, 1978; Geist 1974).

Availability of raw protein is highest in the late spring (Drozd & Osiecki 1973; Eisfeld 1975a, 1976) and since this coincides with the greatest period of need for roe deer,

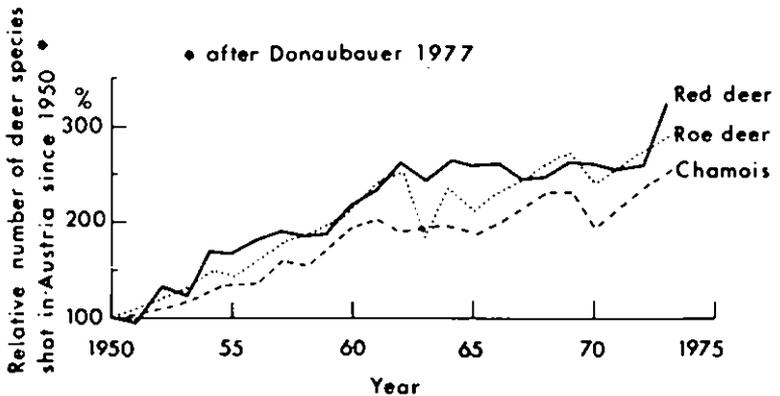


Fig. 2. Relative number of each of three deer species shot in Austria since 1950 (after Donauber 1977).

Eisfeld (1974, 1976) considers protein deficiencies to be unlikely. On the other hand, the total supply of digestible food with the necessary energy content available, threatens to become critical at this time and may be barely sufficient to maintain existing stock. At first sight the ability of ruminants to digest cellulose as well as, in quantitative terms, the slight amount of the total available vegetation they consume, makes a nutritional shortfall in terms of energy requirement seem unlikely (Bobek, Weiner & Zielinsky 1971; Bobek, Borrowsky & Dzieciolowski 1975). Nevertheless, this is a possibility, especially for the smaller ruminants and for young animals during periods of high energy demands. The limited capacity and digestive capability of the rumen are the limiting factors to an animal's ability to make use of available vegetation (Campling 1970), since it may be prevented from taking advantage of nutritious vegetation because its rumen is already filled with relatively indigestible food. Thus, depending on the level of digestibility of food, it is possible for a ruminant to starve, or at best, suffer a deterioration in physical condition. Critical digestibility thresholds change with the seasons depending on available vegetation and the calorific needs of the animal. Roe deer require light, easily digestible food if their energy requirements are to be met, more so than graminivorous ('grazer') species, such as moufflon, chamois, sheep and cattle, and much more than red deer (Hofmann & Geiger 1974; Feustel 1967; Eisfeld 1976; Ellenberg 1978;

Gossow 1976). Roe deer are very selective feeders in comparison with red deer and chamois. Of the 113 plant types which occurred in twelve test areas studied by Volz (1975), only thirty-five species (31 per cent) were used, namely six out of twenty-two available grass species (27 per cent), nine out of twelve wood species (75 per cent) and twenty out of seventy-nine herb species (25 per cent).

Differences in the composition of food in the rumen between red deer and chamois were also found by Schröder (1977b) and Drescher-Kaden (1977) and these differences were themselves found to vary according to season (Fig. 3); also compare Ahlen (1965) and Gossow (1976) for red deer versus moose.

Feeding and selection pressures of roe deer on the available plant types fluctuate considerably during the year and vary from area to area. Data on rumen contents is of little use for broad generalizations; its value lies in application to specific areas and in the demonstration of trends. This is because the available vegetation, type of hoofed game and their population density can cause varying selection pressures on the most disparate plant types (Esser 1958; Klötzli 1965; Ellenberg 1974, 1978).

Where feeding pressure is great, we are frequently confronted with untypical food preference lists and a blurring of the usual dietary differences found between species. Onderschcka & Jordan (1974) found shifts in specific food patterns during winter months in an alpine area where there had been a high grazing and browsing impact by roe deer, red deer, chamois and moufflon (Table 1).

This stemmed from an increased depth of snow and concomitantly, an impaired accessibility of grass and dwarf shrubs, but was also affected by increased feeding competition. The differences between these species in their choice of food disappeared: "Red deer manage to assert themselves in this unusually strong feeding competition by supplementing the shortfall in their preferred food at the expense of the roe deer (taking herbs and deciduous foliage). Roe deer in turn have to compensate for their food shortfall by an increased intake of reeds and conifers. Chamois, although not to the same extent as roe deer, are also victims of this increased competition and increasingly make do with reeds, shrubs and conifers."

In addition to food, the availability of cover and shelter plays an equally and sometimes even more important role. For it has been demonstrated in several cases that peaks in animal abundance do not necessarily coincide with certain times of the year or even the locations of most plentiful food. This phenomena is not confined to ruminants. Numbers of black and red grouse, for example, increase up to two years after high points in food digestibility. Moose and deer

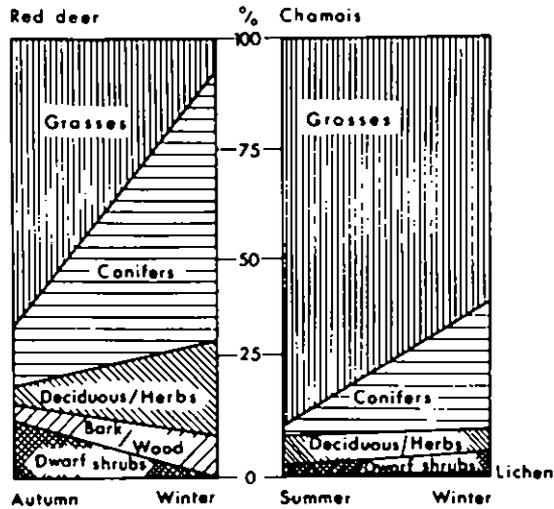


Fig. 3a. Composition of food in the rumen of red deer and chamois in different seasons (after Schröder 1977c).

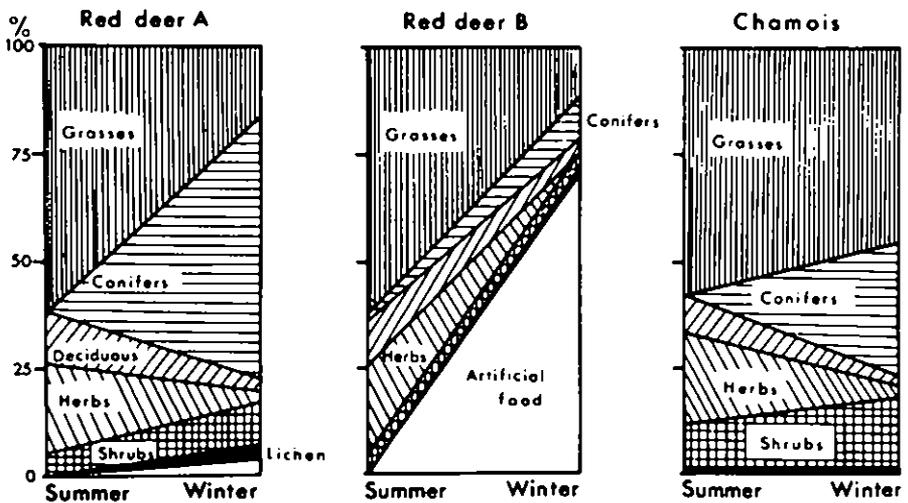


Fig. 3b. Composition of food of red deer and chamois in the months of July/August (summer) and December (winter). A - artificial food rarely accepted (deep snow), B - artificial food readily accepted in winter (after Drescher-Kaden 1975).

Table 1. Percentage of plants in the rumen of roe deer, red deer and chamois, killed in the district of Langau (Onderscheka & Jordan 1974).

	S u m m e r			W i n t e r		
	Roe deer	Red deer	Chamois	Roe deer	Red deer	Chamois
Herbs	45	18	12	11	2	2
Grasses*	5	11	26	1	1	6
Reeds**	0	15	18	6	26	25
Shrubs	9	8	9	26	1	15
Mosses	3	11	1	0	2	1
Conifers	12	14	16	24	15	45
Deciduous	22	5	4	18	1	1
Undefinable fibre	4	18	14	5	3	5
Additional feed	0	0	0	9	49	0

* *Nardus stricta*, *Lolium perenne*, *Dactylis glomerata*, *Deschampsia caespitosa*, *Festuca pratensis*, *Bromus erectus* and *Poa pratensis*.

***Juncus filiformis*, *Juncus effusus*, *Sesleria varia*, *Carex flacca*, *Carex remota*, *Scirpus silvaticus*.

numbers increase with a lag of five to eight years. The length of the lag appears to be related to the size of the game (Eygenraam 1957; Komarek 1971; Bendell 1974; Gossow 1977, 1978a).

Roe deer, living on the edge of forests, are primarily inhabitants of thickets, although Ellenberg (1978) does not consider cover to be of decisive importance in controlling numbers when there is sufficient food available. Red deer are also regarded as inhabitants of the border areas between wood and steppe biotypes (Flerov 1952; Dzieciolowski 1969). For game to feel totally at home, a definite vegetational structure seems to be necessary to ensure settlement and breeding. Ellenberg (1978) has shown that roe deer does in even-aged stands, consisting primarily of saplings and thickets, had a home range of 19.4 ha, markedly smaller than that of roe deer in stands of mature and above all pole stage forest, whose home range was, on average, 35.7 ha. Obviously, roe deer react positively to some ecological types, e.g. clearings, the edges of stands and areas of restricted visibility, and negatively to others, e.g. large open areas of pole stands and areas with limited undergrowth. In red deer, both sexes react differently to their environment (Jackes 1973; Gossow 1978b). The degree to which deer feel at home in their environment influences the extent to which they are prepared to defend it (roe deer) or to remain and concentrate there (red deer) (Gossow 1977).

Vegetation structure as cover has a number of very different functions. It acts as a retreat and hiding place from predators and as protection from competition from its own or different species. Protection afforded against climatic influences is also important, as are protected rest areas and areas for giving birth, ruminating, wallowing and suitable observation (cf. Moen 1973; Geist 1974; Bunnell & Eastman 1976; Gossow 1977).

If too large a distance has to be covered between stands affording sufficient cover and feeding areas, then the risk of confrontation with predators, competitors and other sources of disturbance and danger (e.g. hunters, tourists, traffic, agriculture and forestry) rises. At some point the energy required to reach these feeding grounds will exceed the energy gained from feeding (Moen 1973; Gossow 1976; Eisfeld 1976; Ellenberg 1977). In an alpine area of predominantly even-aged stands populated by red deer, but also with localized pasture areas for grazing by cattle, red deer population quality varied greatly from home range to home range in terms of condition, including differences in milk production, aggressive behaviour, percentage of calves born, proportion of barren animals, etc. More negative effects were experienced with high altitude pastures used as nightly feeding ground by deer, since they were either too far away, making it necessary for the deer to cover great distances and variations in height or were no longer grazed by cattle and so decreased in nutritional value for red deer (Gossow 1978b).

What conclusions can be drawn from these habitat demands for the creation of :-

optimum guidelines for a habitat management in favour of red and roe deer?

As the varying demands of large game such as food, rest, protection, procreation, wallowing etc. can seldom be fulfilled in a single biotype, it is in the interest of a optimized economic time - energy budget (Moen 1973; Gossow 1977; Bunnell & Farr 1978) to be in a position to offer the respective essential biotypes for food and cover within an operational radius appropriate to the animal species and number. In wildlife habitat management this so-called edge effect is a primary aim (Leopold 1933; Dasmann 1964; Telfer 1974; Thomas et al. 1976; Gossow 1976 and 1978a). As a result of the increase of even-aged stands and also the extent to which forests are being opened up by construction of forest paths, changes have occurred in the distribution of forest biotypes.

- i The proportion of open spaces and regeneration areas has increased (age group 1).
- ii The proportion of thickets has increased (age group 2).
- iii There has been a tendency towards smaller felling areas, i.e. between 0.5 and 2 ha.

All these changes should be favourable to the habitat demands of roe and red deer, at least in comparison to more naturally developed forests or even the primeval forests in which the breeds' unique morphological, physiological and behavioural peculiarities developed (cf. Hofmann 1977; Klein 1970; Knapp 1966; Pimlott 1967; Klein & Strandgaard 1972; Mayer 1975).

It is typical of forest ecosystems to have a pre-ponderance of long-lived primary producers, trees and shrubs, which only in part - and this during the early growth stages - have a secondary productive function for ground dwelling game species, i.e. they are eaten (cf. Dasmann 1964; Schröder 1974). When compared with the climax, primeval forest which has a relatively high proportion of mature trees, the plantation is ideal in respect of accessible feeding areas (Fig. 4). It is also superior in terms of cover, i.e. thickets and young, closely planted pole stage woods. The shorter the cutting cycle, the greater the suitability for game, as this increases the proportion of available food as well as the areas of cover (Fig. 5).

In addition to the effect of shortening the rotation length, the trend towards small felling areas now propagated in Central Europe has proved particularly beneficial in satisfying the habitat demands of red and roe deer. Although these species prefer to feed at the edges of forests or thickets, they apparently like a distance of 20 m (roe deer) or between 30 and 50 m (red deer) from the forest edge before they actually begin feeding. This is less possible where blended felling is practised, as in a selection forest, while in areas of radical deforestation we frequently have the opposite problem of large areas of potential food - at least from the point of view of deer management - and therefore waste (e.g. Rochelle & Bunnell, this volume, in respect of wapiti and black-tailed deer). In addition, the pioneering papers of Thomas et al. (1976) and Bunnell & Eastman (1976) have raised these very points in discussing guidelines for the maintenance and improvement of wildlife habitat within the framework of forest management. Unfortunately, any real practical groundwork on this for Central Europe is still lacking. But a comparison between Middle European and North American forest and game literature does show that there must be a substantial influence of forestry on the habitat of hoofed game in Europe.

Decisions about the magnitude of the cutting cycle, choice of the regeneration method, i.e. natural or by planting, size of area to be felled, method of felling, etc. can all have a dominant influence on the population dynamics of hoofed game.

Possibilities and problems in assessing carrying capacity.

Once established, forest plantations attract a range of plants, animals and insects, which compete for the favourable

conditions. The forester not only manages the forest or the plantations as a timber resource, but he also produces - though as a rule not intentionally - numerous habitats (Vité 1978). The strip cut system practised in North America in the interest of deer and grouse habitat management has exactly this aspect in mind (e.g. Telfer 1974). Many forests in Central Europe are also felled by the strip cut system. Though this is not always done in the interest of game habitat improvement, but rather for storm protection and the prevention of damage by drought, frost etc., the effect on game is favourable.

It is often the case that in these structurally and texturally more variegated even-aged stands the available food and its quality have declined. This is a combined result of increasing quantities of spruce and pine or beech, the eradication of undergrowth and other competitive vegetation, fencing, poor ground vegetation due to a dense overstory in the thickets, and feeding grounds being difficult to reach because of obstacles. Finally the increase in numbers and concentration of game leads to greater competition for available food which causes a loss of condition in game and increases damage to the forest because natural regeneration, cultivability, the survival chance of mixed tree species and general quality of the stand are all reduced. Thus we have the other side of the coin, a high population density of ruminant game and a correspondingly high level of damage to the forest. This results in poor quality of game and, particularly in even-aged stands and plantations, puts the economic viability of forestry into jeopardy.

How is it possible to establish criteria to gauge both the biotic carrying capacity for game and the economic viability of forestry by producing silviculturally sustainable forest stands.

Game

As a result of various studies (Andersen 1953; Strandgaard 1972, 1975; Ellenberg 1974, 1978; Schröder 1975, 1976b) it is clear that the numbers of roe and red deer cannot be counted accurately enough to collate concrete data (i.e. in terms of the animal numbers per 100 ha of forest) in harvest planning. But we require such figures to establish what constitutes a viable or tolerable population density, irrespective of whether this is in the interest of the condition of the game or of the condition of the forest. As indicators for the relative carrying capacity of forest biotypes it is necessary to take into account not only the condition of the game but also the condition of the vegetation, its regeneration, etc.

In hooved game deficiencies in nutrition are manifest in corresponding reproduction rates. The degree of fertility and the age at which the animals are capable of reproduction, the



Fig. 4. Effect of rotation length on the percentage of young stands (1-20 years old) in the total forest.

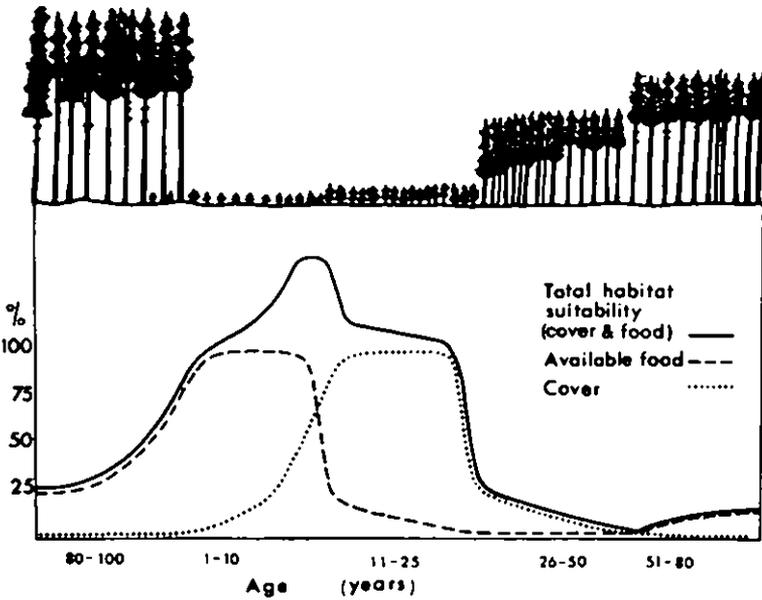


Fig. 5. Schematic representation of the suitability of the forest habitat for deer during the course of the rotation.

number of twin births, the degree of barrenness and the number of still-born fawns and calves (Mitchell & Brown 1973; Mitchell, Staines & Welch 1977; Ellenberg 1978) are all influenced by the nutritional plane of the animal as are the prerequisites for successful rearing, such as plentiful milk supply (Geist 1971; Bunnell & Farr 1978; Gossow 1978b). Gathering of evidence on reproduction requires time-consuming field work and/or examination of reproductive organs, as well as of fat reserves (e.g. kidney fat index). Animals not freshly killed but found dead supply simpler, if not quite such accurate indicators. Tests can be made on bone dimensions, e.g. measurements of the skull, lower jaw or the extremities (Eisfeld 1975b; Ellenberg 1975) which have the advantage that they do not require complicated preservation or preparation procedures. In West Germany, Eisfeld & Ellenberg (1974) recommended that the carrying capacity for roe deer should be determined by a substitute parameter of assessing body size, for which, as a result of allometrically verified correlations, the lower jaw length of adult animals, measured from the first incisor's root to its condyle, can be used (Ellenberg 1975).

A completely different starting point, although as yet hardly ready for practical application, can be made by assessing the border areas of even-aged stands that are particularly beneficial to game (Schürholz 1974). Two forest areas have been compared with reference to the influence of the edge effect on roe deer (Table 2). For roe deer the most attractive area - biotype combinations include young growth (planted in the case study) and thickets, but exclude pole stands (see above). In areas A and B, of a similar size, the number of edges and their total length were twelve and 1150 m (A) and twenty-eight and 3600 m (B), respectively. Thus area B had a much higher amount and interspersion of edge and very probably also a higher carrying capacity. However, carrying capacity was intensified by all-year round feeding just in the edge of the poorer area A. With its already sparser population density this led to a further food surplus, which of course made any direct comparison with the more densely populated area B difficult and inconclusive. This example has been mentioned in order to demonstrate the relationships of some critical forest parameters for deer carrying capacity.

Forest

The second possible way of gauging the carrying capacity of a particular environment is by assessing the conditions and changes of the available vegetation (cf. the concept of increasing vs decreasing invader plant species in range management). Critical damage to vegetation is usually apparent long before any decrease in the condition of the game. A forest can only satisfy the multiple demands made on it by society when, and if, its function as a source of protection,

Table 2. Comparison of two adjacent forest areas with regard to the biotic carrying capacity of deer (after Hilad 1977).

	Area A		Area B	
(1) Forest (%)		26.60		35.70
(2) Field, pasture (%)		73.40		64.30
(3) Area of settlement (in % of (2))		9.30		12.55
(4) Roads (m 100ha ⁻¹)		-		82
(5) Forest paths (m 100ha ⁻¹)		72		103
(6) Total forest area (ha)		148		137
of which				
- young trees (ha)		37.5		32.6
- thickets (ha)		39.5		41.4
- pole-stage (ha)		40.0		30.5
- mature forest (ha)		31.0		32.5
(7) Edge lengths* (m)	10,200		11,400	
(8) Edge factor (m ha ⁻¹)		18.35		29.69
(9) Edge areas within the forest between	Edge	Length (m)	Edge	Length (m)
young trees and thickets	4	450	9	1200
pole-stage and young trees	3	300	8	400
pole-stage and thickets	4	600	10	1000
mature wood and young trees	3	600	7	1100
mature wood and thickets	5	100	12	1300
mature wood and pole-stage	4	500	10	1100
Total edge areas	23	2550	56	6100
Reproduction observation data (as indicators of game conditions):				
-average number of fawns born in May		2.0		1.3
-number of does leading fawns May-December		1.8		1.4
Mean date of birth		7 May		24 May

* Refers only to borders between forest and fields, other cultivated areas and forest and uncultivated areas and forest.

its social function and its role as a supplier of timber remains sustainable. The aim of modern forest management must therefore be to create secure ecosystems which are capable of withstanding abiotic and biotic hazards such as storm, snow, drought and diseases and pests. The demand for such stabilization becomes more comprehensible if one considers the fact that, for example, in the state forest of Baden-Württemberg in the last twenty years approximately 25 per cent of the year's prescribed yields was unplanned and brought about by diseases and pests (König 1976b). Mixed stands of trees suited to their particular environment fulfil these demands better than large stands of a single type. The regenerative capacity of mixed stands can, however, be threatened if the density of hoofed game is too high. This happens for two reasons:

- i certain types of tree are chosen in preference to others by game, above all fir and deciduous trees;
- ii because of the better regenerative ability of certain tree types such as spruce.

Regulation of the numbers of game in accordance with the silvicultural carrying capacity of the forest is one of the most important steps in the creation of a suitable forest ecosystem (König 1976a, b). There are as yet no firm criteria with which to determine the amount of game to be shot in the interest of forest preservation. Fixing criteria will obviously not be possible on a country-wide scale because of very specific local differences in forest and game management. For this reason, Baden-Württemberg conducts an annual series of spot checks on thirty-four regeneration areas, both natural and planted, to determine the amount of browsing by game. To isolate the possibility of any influence by game, approximately 30 per cent of the sample plots in every regeneration area is fenced in. Through such checks over a number of years it is hoped to determine a damage threshold. Possibly these same figures will be of use in assessing the extent of damage in regeneration areas in edaphically similar locations and in establishing a corresponding deer density through an adequate kill quota in the interest of forestry preservation. Finally, it is possible that these test areas will enable us to check the influence of hunting on the degree of browsing or even of the influence of the structure of the forest on the efficiency of hunting (Sperber 1975). These figures could also be helpful for a large scale inventory (Speidel 1975), to make the influence of ruminant game on the forest clearer.

The level of bark damage by red deer varies greatly from area to area and only intensive investigations will produce reliable data. These data can be applied to a whole country, as in the case of Austria (Fig. 6; Plattner 1978), or to single forest districts, as in the case of Baden-Württemberg

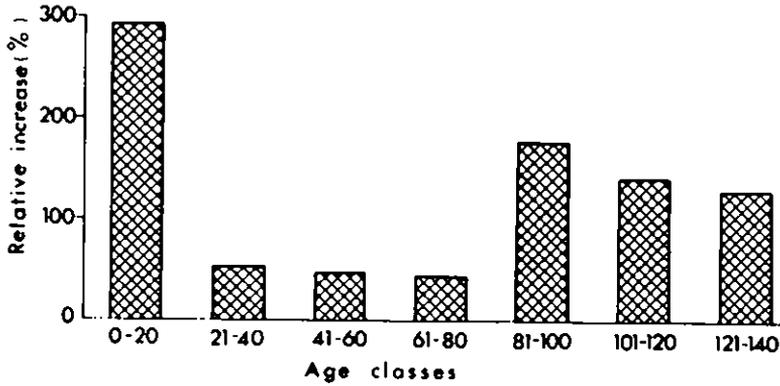


Fig. 6. Percentage increase of bark stripping damage in Austria from 1961/70 (=100%) till 1971/75 (after Plattner 1978).

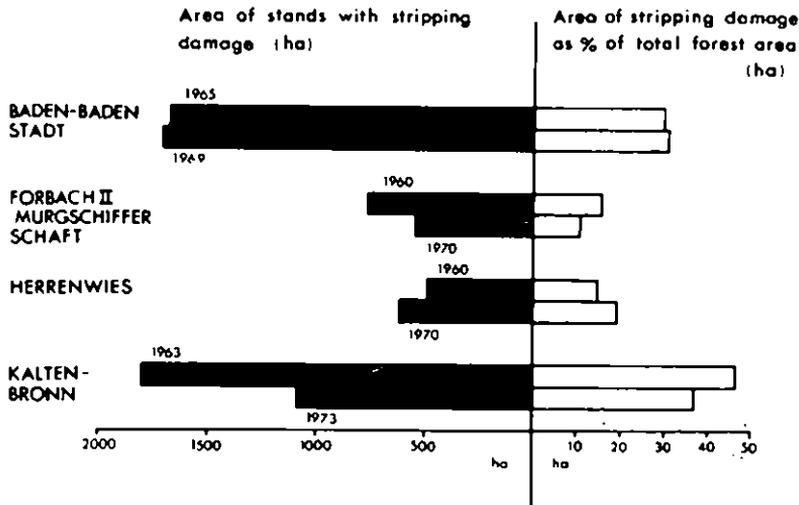


Fig. 7. Stripping damage in the Karlsruhe (Baden-Wuerttemberg) area.

(Fig. 7). Repeating the survey of such data over the space of ten years supplies us with an indication of trends in damage by bark stripping. On this basis the evaluation of the final inventory period covering the whole of Austria showed a mean increase of 66 per cent in such damage, with individual states fluctuating strongly from this figure in either direction. In the two areas populated by red deer in the Black Forest the trend is also irregular. While damage in certain areas declined over the last decade, it has increased in others. Knowledge of such developments is, however, a precondition for the implementation of the necessary measures to achieve the aims of a multiple use forest management.

For the evaluation of damage by bark stripping, fundamental investigations are required into the influence of bark stripping on the growth rate of trees (Roeder 1973) as well as the correlation between the wounds caused by stripping and the extent and intensity of woodrot (Roeder & Knigge 1972). As an aid to making decisions on the treatment of spruce stands damaged by bark stripping, e.g. to cut or fell prematurely or to reduce the cutting cycle, the reader is referred to a case study by Beisel (1973).

In future, forest management will become increasingly multi-purpose and it will not be sufficient for long-term planning or management to consider only those vegetation types directly relevant to production forestry and the game damage done to them. There are important interactions both between different vegetation types and between use made by different animals. On the basis of present knowledge (Konig 1976; Gossow 1975, 1978c; Schroder 1976a, b; 1977a) one is forced to conclude that it is unlikely that the condition of game and the condition and development of the forest can be optimized at identical densities of game stocking (cf. also Caughley 1976).

REFERENCES

- Ahlen, I. (1965). Studies on red deer in Scandinavia. III. Ecological investigations. *Viltrevy*, 3, 177-376.
- Andersen, J. (1953). Analysis of a Danish roe deer population. *Danish Review of Game Biology*, 2, 121-155.
- Beisel, R. (1973). Auswirkungen von Beschädigungen der unteren Stammabschnitte auf den Wert und die Produktionsdauer von Fichten-Betriebsklassen und von Fichten-Beständen. *Mitteilungen Forstliche Versuchs- und Forschungsanstalt Baden-Württemberg*, 48.
- Bendell, J.F. (1974). Effects of fire on birds and mammals. "Fire and Ecosystems". (Ed. by T.T. Kozlowski and C.E. Ahlgren), pp.73-138. Academic Press, New York.
- Bobek, B., Borrowski, S. & Dzieciolowski, R. (1975). Browse supply in various forest ecosystems. *Polish Ecological Studies*, 1, 17-32.

- Bobek, B., Weiner, J. & Zielinski, J. (1971). Food supply for deer in the deciduous forests of southern Poland. *Transactions International Congress on Game Biology*, 10, 271-276.
- Bunnell, F. & Eastman, D. (1976). Effects of forest management practices on wildlife in the forests of British Columbia. *Proceedings 16th I.U.F.R.O. World Congress, Oslo. Division I*. pp.631-689.
- Bunnell, F. & Farr, A.C.M. (1978). Activity budgets of Dall's sheep during lambing. II. *International Theriological Congress, Brno. (manuscript)*.
- Campling, R.C. (1970). Physical regulation of voluntary intake. "Physiology of digestion and metabolism in the ruminant." (Ed. by A.T. Phillipson), pp.226-234. *Onel Press, Newcastle*.
- Caughley, G. (1976). Wildlife management and the dynamics of ungulate populations. *Applied Biology*, 1, 183-246.
- Dasman, R.F. (1964). *Wildlife biology*. New York. 231 pp.
- Donaubauer, E. (1977). Zur Entwicklung der Rot-, Reh- und Gamswildbestände. "Wald und Wild 1977". (Ed. by H. Mayer), pp.35-45. *Wien*.
- Drescher-Kaden, U. (1975). Nahrungswahl, mikrobielle Besiedlung und biochemische Leistungen der Mikroorganismen im Ruminoreticulum der Gamsen. *Verhandlungen der Gesellschaft für Oekologie, Wien*. pp.69-75.
- Drescher-Kaden, U. (1977). Berechnungen über den Energiegewinn aus der Vergarung der Naturäsung im Pansen des Gamswildes. *Tagungsbericht 2. Internationales Gamswild-Treffen, Bled 1976*. pp.158-165.
- Drozd, A. & Osiecki, A. (1973). Intake and digestibility of natural feeds in roe deer. *Acta Theriologica*, 18, 81-91.
- Dzięciolowski, R. (1969). The quantity, quality and seasonal variation of food resources available to red deer in various environmental conditions of forest management. *Forest Research Institute Warsaw. (after Mitchell, Staines & Welch 1977)*.
- Eiberle, K. (1976). Zur Analyse eines Auerwildbiotops im Schweizerischen Mittelland. *Forstwissenschaftliches Centralblatt*, 95, pp.108-124.
- Eiberle, K. (1977). Beobachtungen an höhlenbrütenden Vogelarten. *Schweizerische Zeitschrift für Forstwesen*, 128, 750-761.
- Eisfeld, D. (1974). Der Eiweiss- und Energiebedarf des Rehes, diskutiert anhand von Laborversuchen. *Verhandlungen der Gesellschaft für Oekologie, Erlangen*, 4, 129-139.
- Eisfeld, D. (1975a). Zusammenhänge zwischen Nahrungsqualität und Stickstoffgehalt im Panseninhalt und im Kot bei Rehen. *Transactions International Congress on Game Biology*, 12 (in press).
- Eisfeld, D. (1975b). Zur Regulation der Rehdichte und Vorschlag zur Neugestaltung der Abschussplanung. *Allgemeine Forstzeitschrift*, 30, 1123-1127.

- Eisfeld, D. (1976). Ernährungsphysiologie als Basis für die ökologische Beurteilung von Rehpopulationen. *Revue Suisse de Zoologie*, 83, 914-928.
- Eisfeld, D. & Ellenberg, H. (1974). Vorschlag einer neuen Abschussregelung für Rehwild. *Die Pirsch - Der Deutsche Jäger*, 26, 858-860.
- Ellenberg, H. (1974). Beiträge zur Ökologie des Rehes. Daten aus den Stammhamer Versuchsgehägen. Dissertation Universität Kiel. 133 pp.
- Ellenberg, H. (1975). Die Körpergröße des Rehes als Bioindikator. *Verhandlungen der Gesellschaft für Ökologie*, Erlangen, 4, 141-154.
- Ellenberg, H. (1977). Das Reh in der Landschaft. *Jahrbuch Verein zum Schutze der Bergwelt*, München, 42, 1-22.
- Ellenberg, H. (1978). Zur Populationsökologie des Rehes (*Capreolus capreolus* L., Cervidae) in Mitteleuropa. *SPIXTANA*, Supplement 2. München. 211 pp.
- Esser, W. (1958). Beitrag zur Untersuchung der Äsung des Rehwildes. *Zeitschrift für Jagdwissenschaft*, 4, 1-41.
- Eygenraam, J. A. (1957). Über die Behandlung des Birkhuhnbestandes. *Zeitschrift für Jagdwissenschaft*, 3, 79-87.
- Feustel, G. (1967). Vergleichende Untersuchungen am Verdauungstrakt von Rothirsch und Reh post mortem unter besonderer Berücksichtigung der Gerbstkohlehydrate und des Ligningehaltes der Ingesta. Dissertation Veterinär-Medizinische Fakultät, Universität München. 79pp.
- Flerov, K. K. (1952). Fauna of the U.S.S.R., Mammals. Vol. 1. Muskdeer and deer. Academy of Sciences of the U.S.S.R., Moscow. English translation: Office of Technical Services, U.S. Department of Commerce, Washington. (after Mitchell, Staines & Welch 1977)
- Geist, V. (1971). Mountain sheep. A study in behaviour and evolution. University of Chicago Press. 383 pp.
- Geist, V. (1974). On the relationship of social evolution and ecology in ungulates. *American Zoologist*, 14, 205-220.
- Gossow, H. (1975). Tragfähigkeitskriterien und Schalenwildregulierung. *Forstarchiv*, 46, 254-258.
- Gossow, H. (1976). Wildökologie. Bayerischer Landwirtschaftsverlag, München. 316 pp.
- Gossow, H. (1977). Waldstrukturen und Wildstandsentwicklung. "Wald und Wild 1977". (Ed. by H. Mayer), pp. 1-27. Wien.
- Gossow, H. (1978a) Feuer im Habitat Management. VW-Symposium. "Feuerökologie". *Freiburger Waldschutz-Abhandlungen*, 1, 83-97.
- Gossow, H. (1978b). Some specific features in alpine red deer population ecology. II. International Theriological Congress, Brno. (Manuscript).
- Gossow, H. (1978c). Die Waldpflege als Grundlage der

- Wildfaunapflege, insbesondere der Wildhege. Korreferat zu M. Kotar's gleichbetitelt Vortrag. "Die Waldpflege in der Mehrzweckforstwirtschaft." I.U.F.R.O. Meeting Division I 1977. Mitteilungen der Forstlichen Bundesversuchsanstalt Wien, 124, 295-299.
- Hofmann, R.R.(1977). Wildbiologische Erkenntnisse, ein Hilfsmittel zur Minderung von Wildschaden. Allgemeine Forstzeitschrift, 32, 111-115.
- Hofmann, R.R. und Geiger, G.(1974). Zur topographischen und funktionellen Anatomie des Viscera abdominis des Rehes. Anatomia, Histologia, Embryologia: Journal der Weltvereinigung der Veterinär Anatomen, 3, 63-84.
- Jacks, A.D.(1973). The use of wintering ground by red deer in Rosshire, Scotland. M.Phil. thesis, University of Edinburgh.
- Klein, D.R.(1970). Food selection by North American deer and their response to over-utilization of preferred plant species. "Animal populations in relation to their food resources." (Ed. by A.Watson), pp.25-46. Blackwell Scientific Publications, Oxford.
- Klein, D.R. & Strandgaard, H.(1972). Factors affecting growth and body size of roe deer. Journal Wildlife Management, 36, 64-79.
- Klötzli, F.(1965). Qualität und Quantität der Rehäsung. Veröffentlichungen des Geobotanischen Instituts, Zürich, 38, 182pp.
- Knapp, R.(1966). Grundlagen und Methoden von Untersuchungen über Wild, insbesondere seine Wirkungen auf die Vegetation. Geobotanische Mitteilungen, 43.
- Komarek, E.V.(1971). Effects of fire on wildlife and range habitats. U.S.Department of Agriculture Forest Service. Proceedings Prescribed Burning Symposium, pp.46-52.
- König, F.(1976a). Wildschadenprobleme bei der Waldverjüngung. Schweizerische Zeitschrift für Forstwesen, 127, 40-57.
- König, E.(1976b). Forstschutz, Wildbiologie und Jagd. "Die Forstwirtschaft in Baden-Württemberg." Schriftenreihe der Landesforstverwaltung Baden-Württemberg (Ed.), 9, 110-122.
- Leopold, A.(1933). Game Management. New York. 481 pp.
- Mayer, H.(1975). Der Einfluss des Schalenwildes auf die Verjüngung und Erhaltung von Naturreservaten. Forstwissenschaftliches Centralblatt, 94, 209-224.
- Milad, K.(1977). Zur Wachstums- und Fortpflanzungsleistung von Rehwild (im Westerwald) bei fehlender bzw. ganzjähriger Fütterung. Diplomarbeit Forstwissenschaftliche Fakultät, Universität Freiburg. 92 pp.
- Mitchell, B. & Brown, D.(1973). The effects of age and body size on fertility in female red deer (*Cervus elaphus* L.). Transactions International Congress of Game Biologists, 11, 89-98.

- Mitchell, B., Staines, B.W. & Welch, D. (1977). Ecology of red deer. A research review relevant to their management in Scotland. Institute of Terrestrial Ecology, Cambridge. 74 pp.
- Moen, A.N. (1973). Wildlife Ecology. San Francisco. 458 pp.
- Ondersheka, K. & Jordan, H. (1974). Einfluss der Jahreszeit, des Biotops und der Äsungskonkurrenz auf die botanische Zusammensetzung des Panseninhalts beim Gams-, Reh-, Muffel- und Rotwild. Tagungsberichte 1. Internationales Gamswild-Treffen, Oberammergau. pp.53-80.
- Pimlott, D.H. (1967). Wolf predation and ungulate populations. *American Zoologist*, 7, 267-278.
- Plattner, E. (1978). Neue Ergebnisse der Forstinventur in forstpolitischer Sicht. *Allgemeine Forstzeitung*, 89, 43-46.
- Roeder, A. (1973). Zur Durchmesser- und Massenermittlung in rotwild- geschälten Fichtenbeständen. *Allgemeine Forst- und Jagdzeitung*, 143, 144-150.
- Roeder, A. & Knigge, W. (1972). Sind Rotwildschäden wirklich so schwerwiegend? *Forstarchiv*, 43, 109-114.
- Schröder, W. (1974). Über einige Fragen der Ökologie der Cerviden im Walde. *Forstwissenschaftliches Centralblatt*, 93, 121-127.
- Schröder, W. (1975). Brauchen wir den Abschussplan für Rehwild? *Allgemeine Forstzeitschrift*, 30, 1108-1112.
- Schröder, W. (1976a). Reh- und Rotwild in der Bundesrepublik Deutschland. *Internationaler Holzmarkt*, 67, 1-4.
- Schröder, W. (1976b). Zur Populationsökologie und zum Management des Rothirsches. Dargestellt an einem Simulationsmodell und der Reproduktionsleistung des Rothirschbestandes im Harz. *Habilitationsschrift Fachbereich Forstwissenschaft, Universität München*. 198 pp.
- Schröder, W. (1977a). Gamswild in Nationalparks: Möglichkeiten einer natürlichen Populationsregulation. Tagungsberichte 2. Internationales Gamswild-Treffen, Bled. pp.28-37.
- Schröder, W. (1977b). Räumliche Verteilung und Nahrungsauswahl von Gams und Rotwild im Hochgebirge. *Forstwissenschaftliches Centralblatt*, 96, 94-99.
- Schürholz, G. (1974). Quantitative evaluation of edge from aerial photographs. *Journal of Wildlife Management*, 38, 913-920.
- Speidel, G. (1975). Grundlagen und Methoden zur Bestimmung der wirtschaftlich tragbaren Wilddichte beim Schalenwild. *Forstarchiv*, 46, 221-227.
- Sperber, G. (1975). Einfluss der Altersstruktur und Mischungsform von Wäldern auf Bestand und Bejagbarkeit des Rehwildes. *Allgemeine Forstzeitschrift*, 30, 1119-1122.
- Strandgaard, H. (1972). The roe deer population at Kalø and the factors regulating its size. *Danish Review of Game*

- Biology, 7, 1-205.
- Strandgaard, H. (1975). Rehbestand und Regulation der Rehdichte auf Kalö (ost-Jütland). Allgemeine Forstzeitschrift, 30, 1129-1131.
- Telfer, E.S. (1974). Logging as a factor in wildlife ecology in the boreal forest. Forestry Chronicle, 50, 186-190.
- Thomas, J.W., Miller, R.J., Black, H., Rodiek, J.E. & Maser, C. (1976). Guidelines for maintaining and enhancing wildlife habitat in forest management in the Blue Mountains of Oregon and Washington. North American Wildlife Conference, 41, 452-476.
- Vité, J.-P. (1978). Forstschutz I (Pest Management). Unpublished manuscript. 60 pp.
- Volz, E. (1975). Der Einfluss des Rehwildverbisses bei der Begründung von Nadel- und Laubholz-Mischbeständen auf der Schwäbischen Alb. Diplomarbeit Forstwissenschaftliche Fakultät, Universität Freiburg.



THE MANAGEMENT OF RED DEER IN PLANTATIONS

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SUMMARY

It is recognised that plantation forestry in much of Scotland will not proceed in deer-free conditions. Current research is aimed at designing control schemes which will reduce deer damage to acceptable levels. The effectiveness of these schemes in controlling red deer resident in forests will be severely limited, owing to a steady inflow of deer from the reservoir of adjacent hill areas. Outside the forests, 2,500,000 ha of deer range are maintained partly or primarily for sporting purposes, with 270,000 red deer stocked at densities of up to fifteen per 100 ha.

The high cost of fencing and deer control within the forest is usually borne by forestry, but continued forest expansion with further loss of deer range will escalate the deer problem, and the sporting estates may have to accept a greater responsibility for their deer. The confrontation of deer interests and forestry will not be resolved until private estates adopt more positive management policies, and the diffuse expertise in deer, forestry and hill land use is concentrated to consider alternative allocations of hill land resources.

RÉSUMÉ

Le cerf sera toujours présent dans les plantations forestières de la majorité de l'Écosse. Des études actuelles cherchent à établir un système de contrôle du cerf qui réduirait les dégâts causés par ces animaux à des proportions acceptables. L'efficacité de ces systèmes de contrôle sera minimisée à cause de l'afflux constant de cerfs des collines

avoisnantes. En dehors des forêts, 2,500,000 hectares de terres sont des réserves de cerfs, destinées partiellement ou totalement à la chasse et où la population de cerfs est de 270,000 à raison de quinze par 100 hectare.

Le coût très élevé des clôtures et des mesures de contrôle du cerf au sein de la forêt revient aux forestiers, mais à l'avenir l'expansion de la forêt, qui empiétera sur les réserves, ne fera qu'aggraver la situation et les propriétaires de terrains de chasse devront assumer une plus grande responsabilité de leur cerfs.

Le conflit entre les intérêts de la forêt et ceux de la chasse du cerf ne pourra être résolu que lorsque les propriétaires privés adopteront une politique de gestion plus positive et que les connaissances diffuses dans la gestion et l'aménagement du gibier, de la forêt et de l'espace rural seront mises en commun pour considérer les alternatives possibles d'une redistribution de l'espace rural.

ZUSAMMENFASSUNG

In grossen Teilen Schottlands können sich Aufforstungen nicht unter 'wildfreien' Bedingungen entwickeln. Gegenwärtig zielt die Forschung darauf ab, Pläne zu entwerfen, die Wildschäden auf eine wirtschaftliche Schadensschwelle zu reduzieren. Die Effektivität, mit der diese Pläne das in Wäldern lebende Rotwild vermindert, wird durch den ständigen Zugang von Wild aus den angrenzenden Berggebieten ausserhalb des Waldes stark eingeschränkt. 2,500,000 Hektar Wildreservoir werden zum Teil oder ganz zu Jagdzwecken unterhalten, wobei der Rotwildbestand bei 270,000, also 15 pro 100 ha liegt.

Die hohen Kosten der Errichtung von Zäunen und der Wildschadensverhütung in den Wäldern trägt gewöhnlich die Forstverwaltung, aber mit der zunehmenden Ausdehnung der Wälder und der damit verbundenen Einbusse an Äsungsfläche wird auch das Wildproblem grösser werden, und die Jagdbesitzer werden wohl mehr Verantwortung für ihr Wild übernehmen müssen.

Der Interessenkonflikt 'Wild und Wald' kann erst dann gelöst werden, wenn der Privatbesitz sich zu einer positiveren Wirtschaftspolitik

bekannt und die diffuse Sachkenntnis in bezug auf Wild, Wald und Waldnutzung sich auf alternative Möglichkeiten der Verwendung des Berglandes konzentriert.

INTRODUCTION

Three quarters of the land area of Scotland are classified as rough grazing. The primary use of this land is hill farming, with extensive grazing by sheep and cattle. Because of severe ecological constraints the output per hectare is low, and so it is in this area that plantation forestry can make its strongest claim as an alternative land use.

Of the five million ha of rough grazing, over half are occupied by red deer (*Cervus elaphus* L.) at varying densities, and on approximately a million ha deer are the primary product, providing sport shooting and venison. Even on those sporting estates where deer are run at relatively high densities, the level of physical output is considerably lower than that of sheep. On one estate where the aim is to maximize venison output, up to 1.4 kg/ha/yr of meat is removed, whereas in similar conditions sheep would be expected to yield at least 3 kg/ha/yr. It is in areas reserved primarily for deer that the challenge from forestry is particularly clear and effective, given that environmental conditions make tree growth feasible.

In practice, however, the afforestation of deer range is far from simple. Forestry can entirely supplant hill farming by excluding sheep and cattle, but it is now clear that it cannot hope to exclude red deer. When the forester acquires deer range he also acquires a deer problem.

It is a measure of this problem that forest planting in Scotland is virtually never attempted within deer range without deer fencing. From the outset protection measures are necessary to establish deer free conditions, but these are short-lived. Although the forester may continue to live and work in the belief that his plantations are deer-free, deer generally become established.

A concerted programme of research in Scotland, involving the Institute of Terrestrial Ecology, Forestry Commission, Red Deer Commission and others is now under way to provide information on how this endemic deer problem can be brought under management control.

The damage which red deer can do in plantations is well known. Seedlings are destroyed, growth is checked by heavy browsing, and stems are stripped of bark. The ideal plantation would develop by rapid and even growth but this is seldom possible and an uneven age or growth structure in a forest offers red deer a desirable habitat, with shelter and cover in thickets and clearings which they will maintain for themselves

by preventing further tree establishment.

It may seem that if deer were fully recognized as a site factor before plantations were attempted, then properly planned deer control, including concessions in the lay-out of the plantations, could accommodate the deer problem. Indeed this is worthwhile and many foresters are now thinking along these lines, but it does not take account of the wider problem which exists in Scotland and is not paralleled in any country we know. We have a vast reservoir of red deer outside our forests.

To review the implications of this for Scottish plantation forestry one should consider:

1. The scale of the red deer problem.
2. The nature of afforestation in relation to the rest of the deer range.
3. Land tenure and the responsibility for deer.

THE SCALE OF THE RED DEER PROBLEM

The national red deer herd numbers between 270,000 and 300,000. These are almost entirely located on sporting estates or other privately owned land. The population has been allowed to increase by about 40 per cent in the last ten years (RDC reports), largely in response to a dramatic rise in the value of the deer products of sport shooting and venison. Currently (1978) the price charged for shooting an average stag is between £80 and £100 and a 12-pointer more than £160 (Forestry Commission, pers. comm.) and its carcase will fetch about £80. The increase in the per capita value of red deer has encouraged land owners to increase their deer stock and there are now probably more red deer than ever before in historical times.

Owing to the mountainous nature of the terrain that deer occupy and the wide dispersion of the resources they need, particularly shelter, red deer on the open hillside have to be extremely mobile. In contrast to woodland deer which can find most of their habitat requirements within easy reach, hill deer may have home ranges as large as 60 sq.km. This in conjunction with the large scale topography of the Highlands and the increased numbers of deer, cause long distance movement of large herd groups. Although the average estate extends to about 7000 ha, the deer usually move freely over the estate boundaries, so that the effective deer management unit can seldom be identified as the responsibility of one estate alone (Mutch, Lockie & Cooper 1976).

Most of the land which deer use is unsuitable for afforestation. Whereas the main mountain ridges lie at elevations between 1000 and 1300 m, the limit of economic tree planting is approximately 600 m. It is estimated that 450,000 ha lie above this contour, which is 6 per cent of the land surface of Scotland.

Red deer make good use of high ground, but they need low ground within their range, particularly in winter. The average density of red deer in the Highlands is about 10 per 100 ha, but in heavily stocked areas fifteen per 100 ha is not unusual (Mitchell, Staines & Welch 1977). Snow frequently covers all range above 300 m between November and April and deer are then concentrated for lengthy periods on low ground; in these conditions densities may exceed ten to the hectare.

It is into this widespread and intensifying matrix of deer use that plantation forestry is being inserted. Although it is unwise to consider continental management as being directly applicable in Scottish conditions, it is worth noting that foresters there generally aim to balance deer stocks against a level of damage which is regarded as acceptable (i.e. financially less than the revenue the deer bring in). In practice this means maintaining deer densities of only two or three per 100 hectares (Phillips & Mutch 1974).

AFFORESTATION IN RELATION TO DEER RANGE

Of managed woodlands and those due to be planted (by Forestry Commission and private owners), 70 per cent of the total area lies within red deer range (Fig. 1). New forests must be protected by deer fences which might present an obstacle to hundreds of deer in their attempt to make full use of their accustomed range. But once the plantation is established it is improbable that the fence will remain an obstacle for very long.

Firstly, there is a strong incentive for deer to get through the fence from a generally inhospitable, exposed and 'hungry' environment to an increasingly hospitable, sheltered and 'well-fed' environment.

Secondly, fences deteriorate. Even in apparently good fences small weaknesses such as slack wires or faulty water gates are quickly discovered by deer.

Thirdly, in exceptional but foreseeable conditions, fence lines will be bridged by snow drifts allowing hundreds of deer to walk over.

It is inevitable that deer will take up residence in plantations. While we agree that research to determine acceptable densities of resident deer is urgently needed, we believe that the presence of the large reservoir of transient hill deer is a problem which will continually thwart attempts to bring about proper management and control of deer in forests. As long as foresters underestimate the dimension of the deer problem or pin their faith on the inadequate technology of the deer fence and the rifle, the greater that problem will become.

The present forest structure is attractive to deer and vulnerable to damage. 56 per cent of all managed woodland in Scotland has been planted since 1960. Most of this, and most

of future planting, which could amount to 1.8 million ha (Locke 1976) is, or will be, in deer range. Lodgepole pine, which is particularly susceptible to bark stripping, will probably constitute the largest proportion of first rotation planting in red deer range.

Foresters are rapidly creating a habitat which a quarter of a million red deer would like to get into.

LAND TENURE AND RESPONSIBILITY FOR DEER

Because most of the national deer herd is maintained under private control, foresters have little influence on the source of their deer problem. The land use objectives of estate deer management and plantation forestry are directly opposed.

When the deer range and forest plantation are in single ownership, the issue may be resolved by the owner deciding which objective is to be sacrificed. An issue seldom mentioned is that of the 'private' plantation which takes second place to deer but which has been committed to the dedication scheme and supported by planting grant and management grants.

Usually, however, the forest and the deer range are in separate ownerships. Difficulties and bad feeling frequently arise. In contrast to the situation in, for example, Germany and Austria, there is in Scotland a very slight requirement for the proprietors of deer ranges to collaborate in management. Estate owners can pursue their own objectives regardless of the needs of their neighbours.

It is largely due to the use of the hill areas as grazing for sheep and deer that practically all of the range available to them is devoid of trees. The grazing pressure has intensified in the last 150 years but neither sheep farming nor deer management as now practised can be regarded as a truly indigenous land use. So it is ironic that forestry in trying to re-establish tree cover, should be regarded as an innovation.

As an innovator, the forester has to labour under many disadvantages. Although he might acquire a complete sheep farm, it is unlikely he would ever acquire, fence and afforest an entire deer management unit, even in a large scale state forest. It is very seldom that all the deer in an afforestation area will 'belong' to the new forestry proprietor; some will 'belong' to neighbours.

The burden of deer on forest management is six-fold:

1. The presence of deer as a site factor restricts the choice of tree species that can be planted. An increasing level of deer population progressively precludes the planting of the more vulnerable and palatable species though these may be the most productive or the most suitable in other respects. At later stages of growth such species as lodgepole pine and spruce are at risk due

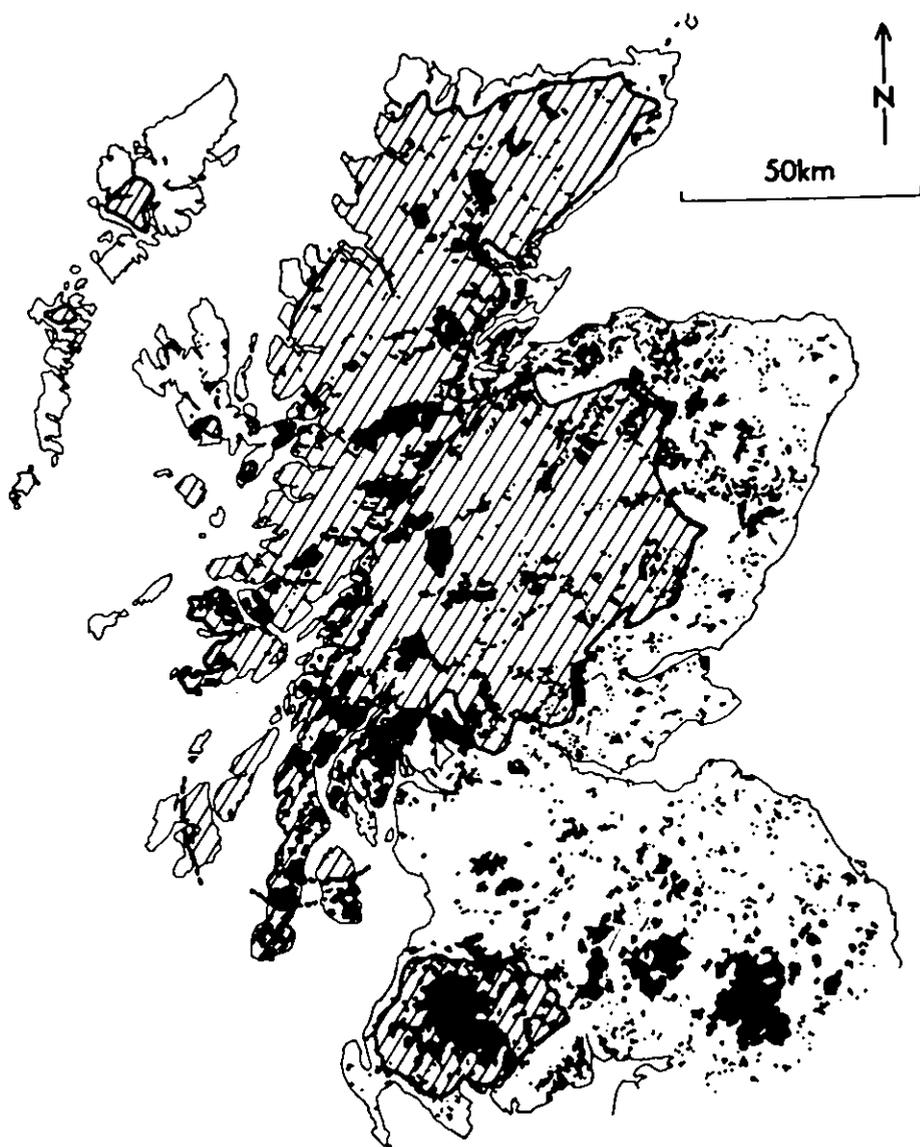


Fig. 1. The red deer range in Scotland (hatched area) and the currently planted areas of forest (solid black). 70% of the land due to be planted lies within the red deer range.

to bark stripping.

2. On the basis of experience on the European Continent deer densities of more than two or three per 100 ha may impose a browsing pressure which reduces early growth, and extends the rotation. Consequently there is a delay in the receipt of cash from intermediate and final fellings.

3. While a small population of deer in an easily accessible forest of reasonable fertility and diversity, such as Grizedale in Cumbria, can offer the possibility of quite lucrative sport shooting to continental standards, the need to control resident populations in large and remote forests requires the employment of a professional cadre of rangers. At a unit cost of about £5000/yr, even the time spent on deer control, excluding other duties, cannot be met by revenue from venison and occasional fees for sport stalking.

4. The pressure of deer at high densities imposes restrictions on forest management options by precluding the planting up or regeneration of small clearings in the forest, as might be desired in a group selection system or required by patches of windblow. The forest must then be re-established in relatively large units, and experience with roe deer in northeast England suggests that each of these may have to be fenced separately, even though the forest as a whole is ring-fenced. In this way the deer can be shot out from the regeneration area to re-create the deer-free conditions required for the first few years of the tree's life. This procedure is very expensive.

5. Fencing represents a continuing cost, a carrying charge to service the capital cost, plus maintenance.

6. A forest boundary fence is needed to keep out animals from neighbours' properties and is crucial where these are stocked at rates inimical to forest establishment. But in addition, the forester is forced into further cost and compromise. In deer range he is obliged to break up large forest blocks to provide corridors for movement of deer herds. This reduces the amount of plantable land he can put under trees, and significantly increases his fencing costs; these are now £2/m for erection. Owing to the break-in of deer from the outside reservoir forestry has to provide more labour for deer control than would be needed for the control of an endemic population.

OPTIONS

The costly constraints forestry must accept in deer range, and the compromises it must make, are a recognition that deer production is a major land use. However, this is measured more in terms of geographical scale than output or of employment. The national output of red deer meat is only in

the region of 1500-2000 tons/yr, compared with 23,500 tons derived from hill sheep (Cunningham et al. 1978). It is questionable whether forestry diminishes that output. We estimate that from managed woodlands between 0.3 and 0.6 kg/ha/yr of venison is produced. This includes roe venison, not normally a product of hill range and compares favourably with our estimate of 0.6 kg/ha/yr from a sample of deer estates covering 200,000 ha.

In terms of employment, a similar comparison shows that about 69 ha of sustained yield forest currently supports one worker (Wolfe & Caborn 1973) 4000 ha of open deer range would be needed to offer the same job opportunities (Mutch, Lockie & Cooper 1976).

We question the ability of the wood producer to practise effectively in the teeth of the present deer problem. It is becoming clear that management practices which are based on prior decisions of choice, are not always effective either in forestry or animal production. Flexibility is needed in the selection of management strategies in view of regional differences in the relative importance of wood and deer production.

Where forestry is identified as the major land user, then the problem presented by deer outside the forest should be reduced to at least the level found to be acceptable in the management of resident forest deer. This means that the reservoir of hill deer should be reduced so relieving the pressure on the forest. A two-way traffic could possibly be allowed, with the forest as part of the normal deer range, and control of numbers could be more easily effected on the open hill. Ultimately the successful application of the principle of equating deer densities in the forest and on the hill would allow the forester to work without deer fencing his plantations with a great saving of cost.

In other regions planting would be secondary to the primary use by deer, and this particularly where the timber potential is limited or where there are marketing difficulties. Here forest development would be judged by its contribution to deer as the major use, by providing shelter, etc.; new planting and regeneration would certainly require protection by deer fences and the forester would accept the cost implications of protection and of periodic damage.

With the true dimension of the deer problem now becoming apparent, however, it also appears that where production forestry is the major user, it should not be required to compromise in favour of low output deer management. In the present situation deer estates should accept some responsibility for the problem they exacerbate. If they cannot sustain or contain their deer they should participate in the cost of forest protection.

Responsibility for red deer in Scotland does not lie with

the national forest authority, as it does in most countries, but with the Red Deer Commission. This is a very small organisation in relation to the size of the red deer population and the area it occupies, and it is scarcely effective in influencing the decisions of individual private estates. There is hardly any sanction which can be applied if a proprietor acts irresponsibly. Sharp conflicts can arise when, for instance, excessive numbers of deer are maintained on land adjacent to forest or agricultural development.

Considerable research effort has been applied to red deer ecology and management but there is a wide dispersion of expertise and a division of research responsibility. Research has been undertaken, or financed, by the Natural Environment Research Council, the Institute of Terrestrial Ecology, the Red Deer Commission, Forestry Commission, Highland and Islands Development Board and several universities. There is a need for coordination to ensure that only desirable overlaps occur. There is also an urgent need for a thorough review to determine the division of administrative responsibilities and to rectify the divorce of those with responsibility for deer and those with responsibility for the major land uses of farming and forestry.

REFERENCES

- Cunningham, J.M.M., Eadie, J., Maxwell, T.J., & Sibbald, A.R. (1978). Inter-relations between agriculture and forestry; an agricultural view. *Scottish Forestry*, 32, 182-193.
- Locke, G.M.L. (1976). The place of Forestry in Scotland. Forestry Commission, Edinburgh.
- Mitchell, B., Staines, B.W. & Welch, D. (1977). Ecology of Red Deer. Institute of Terrestrial Ecology, Cambridge.
- Mutch, W.E.S., Lockie, J.D., & Cooper, A.B. (1976). Red Deer in South Ross. Department of Forestry and Natural Resources. University of Edinburgh.
- Phillips, J. & Mutch, W.E.S. (1974). Red Deer in Woodland. Published by the Authors, Edinburgh.
- R.D.C. Red Deer Commission Annual Reports 1967-77. Her Majesty's Stationery Office, Edinburgh.
- Wolfe, J.N. & Caborn, J.M. (1973). Some considerations regarding forest policy in Great Britain. Forestry Committee of Great Britain, London.

September 8, 1978

FOREST DESIGN: THE FUTURE DEVELOPMENT OF
EVEN-AGED PLANTATIONS

Chairman: C.J. Taylor

The future development
of even-aged plantations:
Management implications.

E.J.M. Davies

The future development
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Silvicultural implications.

D.C. Malcolm

Tropical forests - comparisons and
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THE FUTURE DEVELOPMENT OF EVEN-AGED PLANTATIONS:
MANAGEMENT IMPLICATIONS

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SUMMARY

This paper argues that British foresters have been slow to emulate good agricultural practice and outlines the standard regime-based silviculture that has been evolved in the Southern Scotland Conservancy.

It is suggested that with higher inputs of fertilizer, timber yields may be greatly increased to considerable economic advantage. It stresses the need for further research as being a matter of urgency.

RÉSUMÉ

Nous montrons dans cet exposé que les forestiers britanniques ont été lents à utiliser des systèmes agricoles convenables et nous décrivons la gestion et la sylviculture que nous pratiquons au sein de la Forestry Commission dans le sud de l'Ecosse.

Nous suggérons qu'une fertilisation à des doses plus élevées d'engrais améliorerait la production en bois qui deviendrait économiquement plus rentable. Nous considérons aussi que des recherches plus poussées sont non seulement urgentes mais aussi nécessaires.

ZUSAMMENFASSUNG

In dieser Arbeit wird die These aufgestellt, dass die britischen Forstleute nur sehr langsam neue Entwicklungen in der landwirtschaftlichen Praxis auf ihre forstliche Bedeutung hin überprüfen werden. In grossen Zügen werden die von der südschottischen Forstverwaltung entwickelten und standardisierten Waldpflegemassnahmen erläutert.

Es wird darauf hingewiesen, dass bei vermehrtem Einsatz von Düngemitteln die Holzerträge erheblich gesteigert und somit eine

beträchtliche Verbesserung der
 Betriebsergebnisse erzielt werden könnten.
 Ferner wird betont, wie dringend es ist, die
 Forschungsarbeit auf diesem Gebiet zu
 intensivieren.

INTRODUCTION

I felt very honoured when the organising committee asked me to contribute to this Conference, but I must emphasize from the beginning that the views which I am putting forward are personal and have been formed as a result of some twenty years experience of afforestation, firstly in the upland of Wales and then on the mountains and hills of western and southern Scotland.

One is acutely aware that although the science of forestry is still in its infancy, it is somewhat handicapped by tradition. Perhaps some of the reasons for this can be found in the academic background of university lecturers in Europe. Most of the great teachers, men like Brandis and Schlich, in Victorian times, were concerned for the management, maintenance and conservation of the great forests of the world and trained students to look after these. There was little plantation forestry taught and, in Scotland in particular, this trait persisted until recent years. Therefore, those of us who were in the afforestation business were launched into British forestry somewhat inadequately trained and unaware of the tremendous agricultural and horticultural innovations which were current and which were of great significance to us. Over 80 per cent of the sites that had been planted in Scotland in the last twenty-five years had not grown timber crops for more than 300 years, and it has taken British foresters a very long time to realise the dominion they have over their sites using techniques developed from agricultural practice. My outlook, therefore, is that of the tree farmer (Davies 1971).

Furthermore, it is clear that the future lies largely in plantation forestry and, unless foresters become more involved in improving the yield of their man-made woodlands, the rapidly increasing demand for timber from an exploding world population cannot possibly be satisfied.

Now I must admit that this particular tree farmer has been fortunate to practise his forestry in areas where the heavily yielding Sitka spruce (*Picea sitchensis*) grows fast and well, and as a manager my prime purpose is to grow spruce sawlogs for industry. Most of these will be grown on a thinning regime with a rotation of between thirty-five and fifty years, and will reach a height of between 20 and 25 m with a mean diameter at breast height of 30 cm.

THE POTENTIAL OF SITKA SPRUCE

There are huge opportunities to increase productivity way, way beyond the dreams of the early pioneers. Most of the Forestry Commission woodlands in my particular parish luckily consist of Sitka spruce and at a recent re-assessment we found that their average yield class was 12 cu.m/ha.

The recorded range of growth for Sitka spruce in the U.K. runs up to yield class 24, a very heavy yielder indeed, and I believe that it may be exceeded. I recently measured some plantations growing at yield class 30 and these were on a far from fertile, exposed site 250 m above sea level. And just before that I had the pleasure of re-editing the journals of that great botanist, David Douglas (1914). 150 years ago he wrote of Sitka spruce:

"The appearance of this species closely resembles Picea douglasii; although neither so large nor so plentiful as that species, it may nevertheless become of equal if not greater importance: it possesses one great advantage by growing to a very large size on the northern declivities of the mountain in apparently poor, thin, damp soils; and even in rocky places where there is scarcely a sufficiency of earth to cover the horizontal wide-spreading roots, their growth is so far from being retarded that they exceed one hundred feet high and eight feet in circumference. This unquestionably has great claims on our consideration as it would thrive in such places in Britain where even Pinus sylvestris finds no shelter. It would become a useful and large tree".

In the last fifty years Douglas' prescience has been vindicated, but we are still a very long way from maximizing our investment in the species.

THE REQUIREMENT FOR FERTILIZER

I have an obsession with tree nutrition. For fifty years research work in nutrition was concentrated on the infertile lands and not on the moderate or good lands which farmers had learned by long experience were far more remunerative. It was not until the 1970s that any worthwhile research effort was undertaken on the better sites, and we still do not know their true potential. Recent re-assessments have been promising in many instances and in pole-stage crops there have been some remarkable reactions to fertilizers in timber volume (Davies 1969; Miller & Cooper 1973; Dannatt, Davies & McCavish 1971; Macintosh 1978).

In the late '60s some extraordinary responses to phosphate were recorded in Argyll on surface water gleys and brown earths. Macintosh (1978) recorded an increase in leader length of 48 and 80 per cent for brown earths and surface

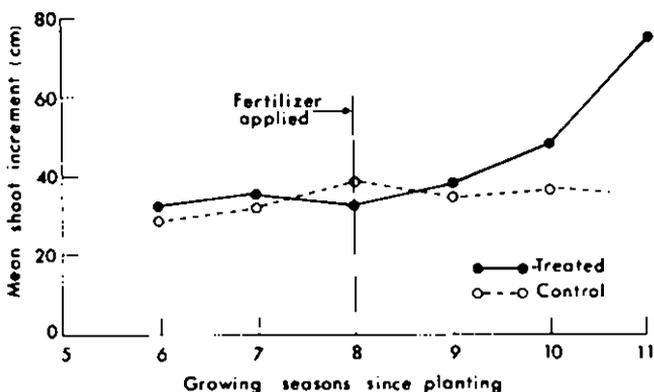


Fig.1. Tree leader increment after planting on a brown earth soil. Phosphate fertilizer was applied at year 8.

water gleys respectively over controls in Glentool Forest (Figs. 1 and 2).

An example of how British foresters have been slow to follow agricultural practice may be seen in their attitude to forest nutrition. The early research workers were men of considerable vision and they considered that the frontiers of plantability were a major challenge. Good land was to be had in abundance, but much of their excitement lay in extending the tree line further up the hill, and in developing techniques to afforest the millions of hectares of deep, infertile peat land that is such a feature of our British uplands. For nearly fifty years nutrition research was

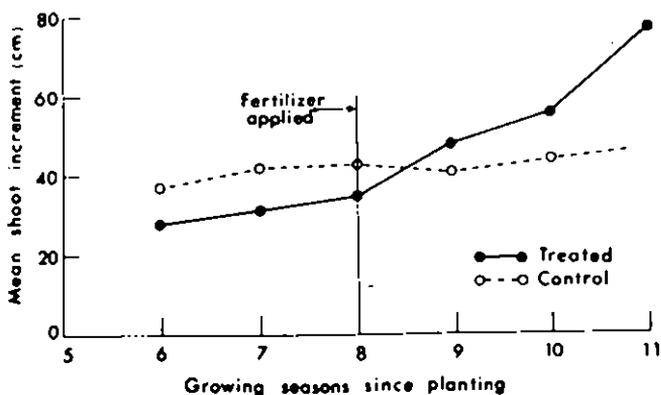


Fig. 2. Tree leader increment after planting on a surface water gley soil. Phosphate was applied at year 8.

concentrated on these infertile lands, and the nutritional needs of richer ground ignored. The commercial farmer on the other hand maximizes his yield on his good ground before he breaks in the marginal land. Thus, at the present time, although we have learned to establish plantations on very poor land, we are still unaware of what can be done to improve the richer lands.

The need to get trees to start well was quickly recognized, but once established, crops were often neglected, and because regimes had not been worked out, growth became slower and slower.

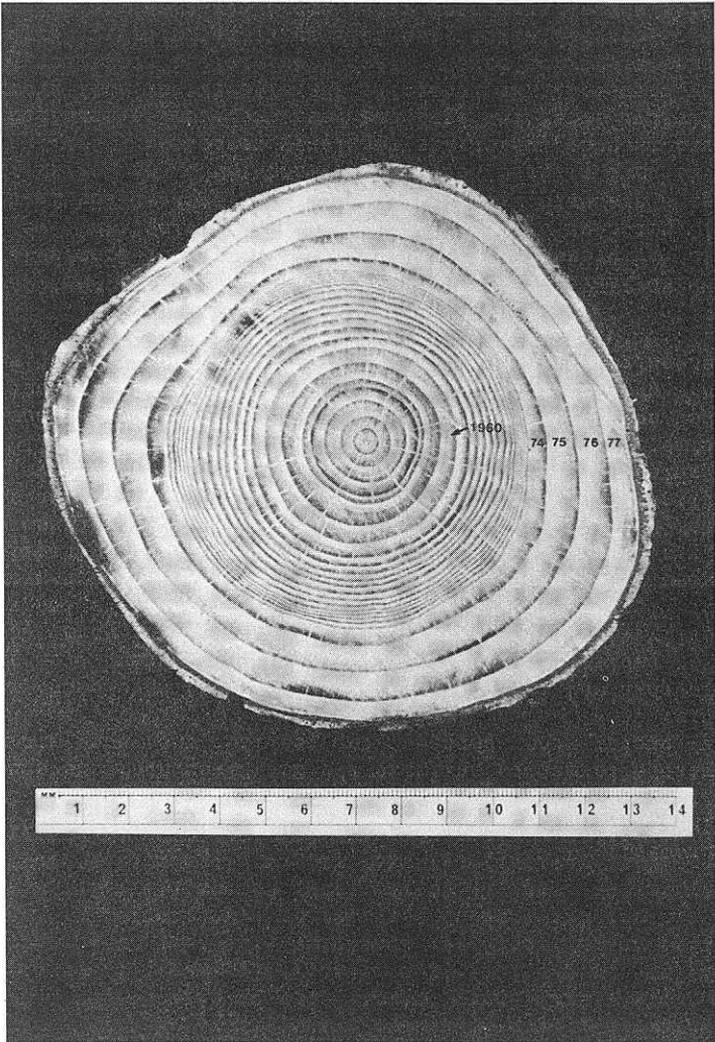


Fig. 3.

Figure 3 illustrates this. It is a disc taken from a Sitka spruce plantation grown on deep unflushed peat in Glentroot. Planted in 1952, it received a standard dose of phosphate in the first year. By 1960 growth had slowed right down because the nutrients had become exhausted. In April 1973 the crop was treated with PK and by 1977, when the specimen was taken, the basal area had increased from 60 to 140 sq.cm. At least ten years have been lost though. Would any good farmer neglect his permanent grassland in such a manner?

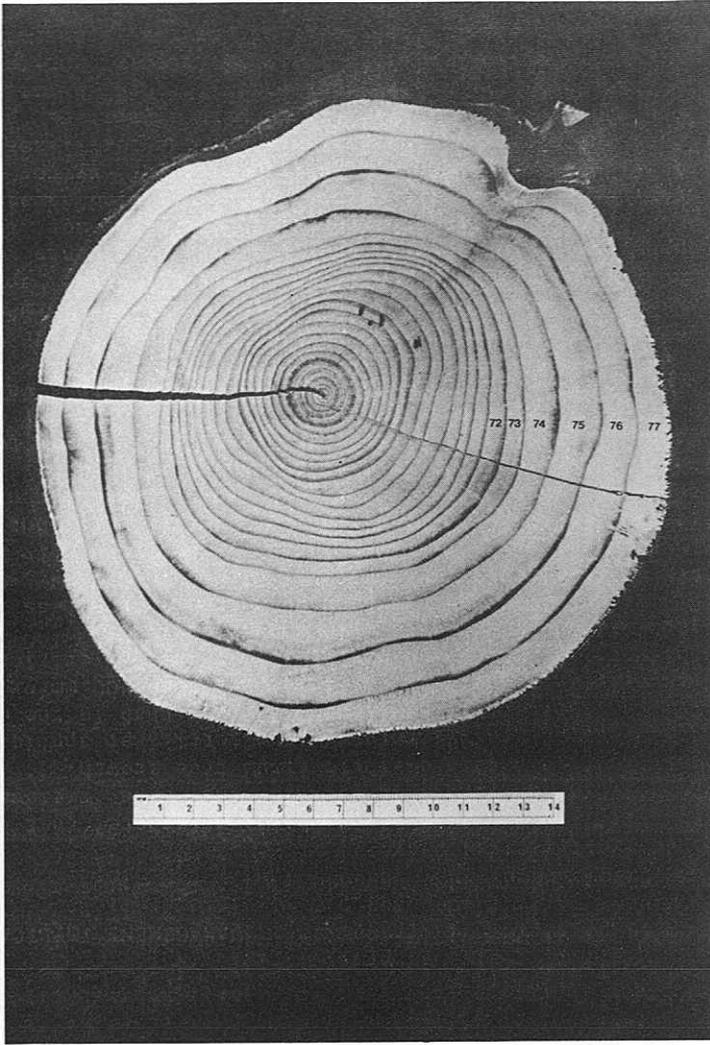


Fig. 4.

Figure 4 is also from Glentrool. It comes from a low-lying, deep flushed peat site, which is reasonably fertile. Planted with Sitka spruce in 1954, when it received a standard dose of phosphate, it grew away moderately well and kept going. In April 1973 it received PK fertilizer and there has been a remarkable response. Cut in November 1977, the basal area had increased by 280 per cent in five years. This illustrates how foresters may easily be satisfied by moderate growth on a potentially high-yielding site.

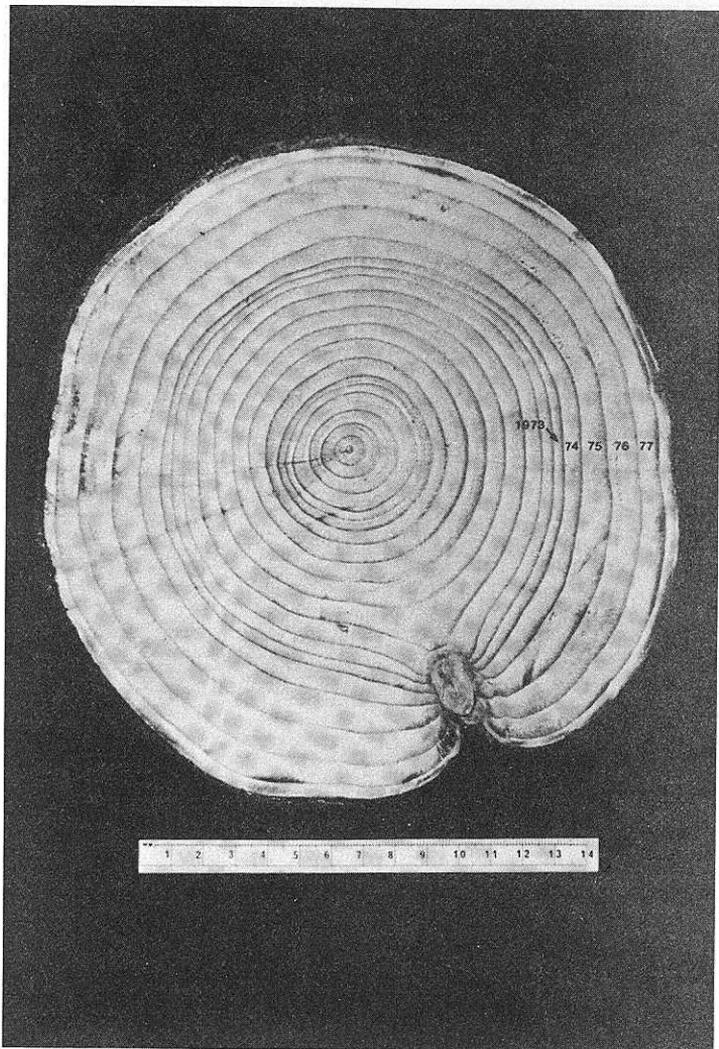


Fig. 5.

Figure 5 comes from Arecleoch Forest, Ayrshire, about ten miles to the northwest of Glentroll. Sitka spruce on a surface water gley, planted in 1958, there is no record of it receiving any fertilizer at planting. In 1973 it was growing well and had reached thicket stage. Nevertheless the foliage colour was not very good and it was decided to treat it. In October 1973 it received 575 kg/ha of P and this was followed in May 1974 with a nitrogen dressing (350 kg/ha of prilled urea). In November 1977 the plantation was thinned (yielding

50 cu.m/ha) and leaders of over 1 m long were not uncommon amongst the felled trees. This specimen was cut in June 1978. The plantation, which is now managed on a regime basis, is due for a further PK dressing next year. Examination of ring width indicates that there was a falling off in growth in the early 1970s and makes one appreciate that we could have had even better growth from the beginning if we had been using a suitable fertilizer regime from the start.

EVOLUTION OF A SILVICULTURE FOR INCREASED PRODUCTION

Since 1972 we have been managing Arecleoch Forest on a high input regime and the results are already dramatic. For example, a 1966 Sitka plantation growing at 320 m above sea level in considerable exposure is growing at yield class 20 following standard treatments of P, PK and nitrogen. With old low-input regimes the predicted yield class would be about 10 or 12.

In another compartment at 220 m above sea level, 1969 Sitka spruce has received P, PK and N and has leaders in excess of 100 cm. This crop will, if it keeps going, have to be thinned at fifteen years old. It is due for a further treatment with PK next year. With traditional methods it is unlikely that yield class 14 would have been exceeded.

We can demonstrate that this intensive silviculture is highly profitable (Edwards 1974). The Net Discounted Revenue calculations show substantial profits for the tree farmer if at the cost of four extra treatments of P, N, PK and N one can raise yield class 12 to yield class 18. In one can raise yield class 14 to yield class 24 the net gain is of the order of 500 per hectare.

During the last fifteen years I have been carrying out large programmes of aeral fertilization in western and southern Scotland. Since 1972 in South Scotland we have treated over 84,000 ha of established plantation with fertilizers (Davies, Garforth & Macintosh 1978).

	ha
P	48,759
PK	31,302
N	<u>3,971</u>
	84,032

In addition some 5,000 ha of Calluna dominated sites have been treated with weedkiller to release nitrogen during the period. The responses that we have had greatly exceeded our expectations and I have come to certain conclusions and generalizations based on our own investigations and on research work in the U.K. and abroad. As far as Sitka spruce is concerned:

1. Virtually all the soil types being afforested in south and west Scotland are phosphate deficient for optimum

- tree growth.
2. Virtually all the soil types being afforested that have a humus layer of more than 15cm in the same regions are deficient in potassium for optimum tree growth.
 3. One may expect greater returns from fertilizer applications in the wetter parts of these regions than in the drier, eastern parts where rainfall is less than 800 mm/yr. Soil moisture in spring and early summer seems critical to effective nutrient uptake in many crops.
 4. It is wasteful to add nitrogen to a tree crop unless its PK status is right.
 5. Pole-stage crops of Sitka spruce are frequently highly responsive to the addition of fertilizer, but this response should be recorded by volume measurements, as height increments at this stage can be misleading.
 6. Moreover, the older the tree, the less likely it is to show basal area response. Response is to be looked for on the trunk just below and in the live crown, with a valuable improvement in form factor.
- I believe that fertilizers applied to spruce crops before canopy closure tend to result in more uniform crops. After canopy closure I believe that the reverse applies, competition increases, and the big dominants tend to accelerate away from the rest. If one dares not thin a crop because of the probability of wind damage, one normally ends up with a high stocking of rather small trees with low sawlog content. If one fertilizes after canopy closure one should end up with a number, perhaps 200/ha, of big trees scattered through a matrix of pulpwood and small sawlogs, with a higher out-turn of valuable material, besides, of course, shortening the rotation.
8. There is no reason why trees growing fast when, say, 5 m high, cannot be kept on a high growth curve provided that there is no biological disaster, e.g. insect attack, and that nutrients and soil moisture requirements are met. This is the most important concept of all and is central to regime fertilization.

There is, of course, still a huge amount to be learned about tree nutrition and the inter-reactions of soil moisture, temperature, provenance, sunlight etc. Nevertheless, could it be that we are, as I believe, on the edge of a major breakthrough in the economics of investment in forestry? What are the implications to our silviculture? Could it be, as I believe, that in the wetter west of Britain we can already grow crops of an average yield class of 20 or better? If so, we should cut our rotation by twenty years and, provided that a site is properly rootable, the investor would only be buying a climate! I feel sure the future I.U.F.R.O. meetings will become increasingly concerned with climatic limitations on

tree growth.

If one accepts that one now has a remarkable dominion over the site, except for climate, we must seek, in the economist's terms, to maximize the Net Discounted Revenue. I rather prefer the phrase 'to realize the economic site potential'.

To this end foresters in south Scotland have been issued with a table to enable them to judge current tree growth critically. We have taken yield class 16 as the norm, and if current leader lengths fall below the appropriate length for the age of the crop, foresters should ascertain the reason. It is only a beginning but it is a step in the right direction.

We have a multiplicity of experts and researchers investigating their own subjects in depth, and not always being able to relate their work to the whole. I believe that the time has come for the general manager to weld all these together and, like the great Victorian scientists such as Darwin, who could see all creation as one, prescribe a comprehensive, if somewhat imperfect treatment, simple and clear.

A STANDARD SILVICULTURE

In my present area, which is the south of Scotland, less than 10 per cent of the soils are free draining, and we have evolved a standard silviculture. During each of the last five years we have planted between 5000 and 6000 ha using these standard methods, which are regularly reviewed.

Firstly, after the land has been acquired, a detailed soil map is prepared. We recognize six significant soil groupings and three elevation zones which, multiplied together, mean eighteen possible sites (see Toleman, this volume). With this knowledge actual treatment types are decided on and defined by markers on the ground. The area is fertilized from the air with either 375 kg/ha of coarse rock phosphate (ca. 13 per cent P) or 575 kg/ha of rock phosphate/muriate of potash mixture (PK) if the soil has a noticeable peat content. It will then be cultivated by double mouldboard ploughs, which may or may not be fitted with tines designed to penetrate into the subsoil, and cross-drained. The area will normally be planted with Sitka spruce transplants at ca. 2m spacing, and little or no weeding is needed on all but the sites with the most vigorous growth of ground vegetation. We may have to apply more fertilizers before canopy closure and certainly should late in the life of the crop. For example, on the most infertile site that we encounter, the deep unflushed peats which account for some 22 per cent of our plantable reserve, we expect to add PK at planting; nitrogen at year 4; PK at year 6; PK at year 12; nitrogen at year 16 and NP at year 20. Our object is to get the crop growing fast from the very start and keep it growing fast. Regimes have been worked out for

each of the eighteen sites.

When the crop reaches about 10 m in height, we carry out a first thinning. This is what we call mechanical - plus - worker selection: in the simplest terms we remove one row in every nine and thin some of the trees between these rows. Five years later, at perhaps age twenty-five, we carry out a second thinning and this is aimed at evening up the crop and removing any dominant, mis-shapen trees. It is done selectively and the marking is done by a forester or skilled worker. Five years later we thin the crop again. This may be the ultimate thinning or there may be even a fourth thinning. Both these latter thinnings are 'low' thinnings aimed at making the crop as even as possible and simplify the final product mix. Clearfelling would normally follow ten years after the last thinning and we tend to favour large coupes of 10 to 100 ha where landscape and conservation interests permit. Large coupes reduce edge effect losses from wind and grazing. After clearing we plant straight through the lopped branch waste left on the ground and the whole process starts again.

A SPECIFIC EXAMPLE OF THE STANDARD SILVICULTURE

Let me illustrate what I mean by reference to a bare grass/heather moorland site in a forest in southwest Scotland, 250 m above sea level, south-facing; soils mixed, but chiefly flushed and unflushed deep peat, moderately exposed. A modern regime would mean:

Year 0	Apply PK fertilizer at 575 kg/ha. Cultivate with double mouldboard plough 40 cm deep, 4 m centres; remove puddled water only by drainage. Plant say Washington provenance Sitka spruce at 2 m spacing.
Year 4	Add N as 350 kg/ha prilled urea. In autumn re-space, cutting ca. 400 trees/ha concentrating on vigorous trees showing poor genetic qualities.
Year 6	Add PK at 575 kg/ha.
Year 12	Add PK at 575 kg/ha.
Year 14	Road area for extraction
Year 15	Thin mechanically with worker selection to 1100 trees/ha. Yield 50 cu.m/ha chiefly pulp wood.
Year 16	Add N at 350 kg/ha prilled urea.
Year 20	Thin selectively to 800 trees/ha. Yield 50 cu.m. Add PK after thinning at 575 kg/ha.
Year 25	Low thinning reducing crop to 500 trees/ha. Yield 100 cu.m/ha. This will contain at least 75 per cent of sawlog material, the rest pulpwood.
Year 26	Add N at 350 kg/ha prilled urea.
Year 35	Clearfell. Height 20 m. Volume 500 cu.m/ha Mean diameter 30 cm.

Those conversant with our Forestry Commission Forest Management Tables (Hamilton & Christie 1971) will note that

the total production per hectare at thirty-five years old, under normal regimes, some 790 trees, is not reached. Under the regime advocated, total volume would be reduced, but individual trees removed in thinnings and clearfelling would be larger and obtained more quickly.

HAZARDS TO FOREST PRODUCTION

This standard silviculture is simple and straightforward but one would be idle to assume that it will not be tailored to meet special circumstances. For instance, some of our areas will not be planted with spruce, but with larch and hardwoods for amenity and wildlife purposes. Some of the areas which have been planted on unstable soils will not be thinned, but the great thing is this: to impress on managers at all levels concerned with the production of wood, the simple central concept that they are in business to produce standard spruce sawlogs for industry, and the skill of the forester can be measured in the way that he succeeds in dominating the environment and, most important, leaves easily managed forests to his successors. All of us have experienced the due consequences of over-elaborate management systems which can be so vulnerable to changes of circumstances or staff.

I know that the charge is often made against the tree farmer that life is not as simple as he would have you believe. But a senior manager must simplify and whereas a research worker may well be concerned in detecting and recognizing differences, the manager is concerned in consonance and transmitting sensible concepts and precepts to his staff.

I admit that great technical difficulties beset the British forester. Just to pick out three: and of these three I think that wind and exposure will dominate our silvicultural thoughts and actions for as long as men try to cultivate trees in these extraordinary windswept islands. Those of you who are new to the British scene are possibly unaware of the extent of this problem. The Western Isles are said to be the fifth most exposed inhabited place in the world, ranking not far below Cape Horn, the southern tip of New Zealand and Spitzbergen in average wind velocity.

In the early years of the century there was an observatory on the summit of Ben Nevis, Britain's highest mountain, a mere 1360 m above sea level. During the twenty or so years of its existence 262 gales per annum were recorded. And periodically, perhaps every twenty or thirty years, we endure a great storm which, if it is sustained for a few hours, lays trees over whole tracts of the countryside.

Since I have been practising forestry, we have had the great gale of 1952 which laid waste huge areas of forest in northeast Scotland, and in 1968 central Scotland was subjected to a sustained six hour storm during which wind speeds of well

over 160 km per hour were recorded. Wind will create irregularity whether we like it or not and my rather simplistic view indicates that large, rather than small felling coupes will become the order of the day so as to reduce the edge effect. One of the most exciting aspects of current research work has been on windthrow prediction and it was clear that the work of Dr. Calvin Booth and his exposition of it during our visit to the Forest of Ae has made a deep impression upon all of us at this meeting. You will recall that he divided our plantations into six hazard classes and predicted that thinned spruce stands will start to blow (i.e. over 3 per cent of the living trees will be thrown) at top heights as follows:

Hazard Class	Top Height m
I	25
II	22
III	19
IV	16
V	13
VI	10

In southern Scotland we have decided not to thin about 20 per cent of our plantations because of this wind hazard and new regimes involving respacing are being evolved. If only research workers could develop a height regulating hormone so that after a tree has reached say 20 m it ceased to grow in height but devoted all its energy to putting on girth, like certain human beings! In the meantime we have to devise means to get the maximum volume of sawlog on the ground before the wind-determined rotation expires.

And then there are the red deer. The red deer is a woodland animal and is native to the Highlands of Scotland. The recreation of its old habitat has enabled it to increase its numbers and range very extensively. It is difficult to control in a woodland setting and can be very dangerous to certain tree species right through their lives.

And a further example, perhaps is entirely man-made. It is obvious when one looks abroad that the pace of mechanization is accelerating, but some of the heavy, complex and expensive machines that are being developed can be very damaging to the forest and its soils. This is a huge subject and it would be idle to ignore its implications.

So much for three typical problems that will beset the manager of even-aged plantations in Britain.

RESEARCH QUESTIONS

It would be totally misleading to imagine from what I have said that the tree farmer has no need for research because he knows it all anyway. This is very far from the

truth. This particular tree farmer is in urgent need of advice on many subjects, but just take nutrition as an example. I should like to know:

1. What are the best regimes for each site type and predicted yields on these sites?
2. How sensitive are fertilizer regimes to provenance, thinning techniques and drainage intensities?
3. What are the possibilities of using fertilizers to change form factors and stand assortment?
4. What response can be expected to pole-stage fertilizing on the various sites?
5. What opportunities has one got to put extra increment on the last ten years of a crop's life?
6. How to evolve an early warning system to alert the forester that growth is falling off.
7. How to check readily on inputs likely to maximize Net Discounted Revenue.
8. How to improve foliar analysis techniques and increase their reliability.
9. How to monitor aerial application of fertilizers more effectively.
10. How seriously do wide ring width and fast growth limit timber utilization?
11. The most effective and economic rates of application of common fertilizers and the periodicity of their application.
12. The long-term effects on high input sites.

CONCLUSIONS

1. The future of the timber using industry will involve a huge expansion and intensification of plantation management.
2. We are still ignorant and inward looking and have been slow to learn from the best agricultural and horticultural practices.
3. Management must be kept simple and in forestry small is seldom beautiful.
4. There is need for a great deal of research investment into increasing wood yields.

Finally, may an inexperienced general forester be very impudent and suggest that senior research staff are in charge of the most difficult site of all: the research resource? I believe that most of the original thinking comes from the young and often from scientists from different disciplines working together. Encouraging young, lively minds and trying to prevent them going up dead limbs is not easy. Once again climate is all important!

REFERENCES

- Dannatt, N. Davies, E.J.M. & McCavish, W.J. (1971). Kilmory 1971 - An investigation into fertilizer response. Scottish

- Forestry, 25, 100-109.
- Davies, E.J.M. (1969). Further experience with aerial fertilisation in the West (Scotland) Conservancy. *Scottish Forestry*, 23, 87-99.
- Davies, E.J.M. (1971). The Argyll Tree Farming School. *Scottish Forestry*, 25, 272-274.
- Davies, E.J.M., Garforth, M.F. & Macintosh, R. (1978). New prospects in forest fertilisation. *Scottish Forestry*, 32, 37-40.
- Douglas, David (1914). *Journal kept by David Douglas, 1823-1827*. W. Wesley & Son, London.
- Edwards, P.N. (1974). The profitability of large-scale aerial fertilising. *Scottish Forestry*, 28, 265-271.
- Hamilton, G.J. & Christie, J.M. (1971). Forest management tables (metric). Forestry Commission Booklet #34 pp. 1-201
- Macintosh R. (1978). Response of Sitka spruce to remedial fertilisation in Galloway. *Scottish Forestry*, 32, 271-282.
- Miller, H.C. & Cooper, J.M. (1973). Changes in amount and distribution of stem growth in pole-stage Corsican pine following application of nitrogen fertilizer. *Forestry*, 46, 157-190.

THE FUTURE DEVELOPMENT OF EVEN-AGED PLANTATIONS:
SILVICULTURAL IMPLICATIONS

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SUMMARY

Plantations are distinguished silviculturally by uniformity of stand age, structure and specific composition. Recent developments of cultural techniques allow site amelioration to accommodate desired species while mechanisation of harvesting methods promotes clearfelling systems.

The structure and development of the unmanaged forests, from which the main species used in British plantations are drawn, demonstrate their dependence on periodic disturbance. The longevity of the main species emphasizes the importance of regeneration conditions for ultimate stand composition rather than conventional ideas on succession. Windblow and fire disturbance lead to mainly even-aged stands distributed in relation to site conditions. Ecological 'stability' of these natural forests is doubtful, but they show considerable 'resilience'.

Analogies between unmanaged, indigenous forests and intensively managed, exotic plantations can only provide possible guidelines for silvicultural treatments. The design of plantation forests should take account of the existing variability of the environment by linking forest structure to the scale of site heterogeneity, identified through terrain classification for extraction. Greater variation in plantation forests will enhance their ability to respond to changes in the physical, biological or social environments.

RÉSUMÉ

Du point de vue de la sylviculture, les

plantations se distinguent des forêts naturelles par l'uniformité de l'âge du peuplement, de la structure et des essences qu'elles comprennent. Récemment, le développement des techniques de culture a engendré une amélioration des stations permettant de cultiver des essences voulues tandis que la mécanisation des méthodes de récolte encourage les systèmes de coupes-à-blanc.

La structure et le développement des forêts non aménagées, qui sont la source des essences principales utilisés dans les plantations de Grande Bretagne, prouvent que celles-ci dépendent de perturbations périodiques. La longévité des essences principales met en relief l'importance des conditions de régénération en vue de la composition finale du peuplement, bien plus que les idées conventionnelles concernant la succession. Les vents et les incendies donnent des peuplements plus ou moins équiens, distribués selon les conditions du terrain. On peut mettre en doute la 'stabilité' écologique de ces forêts naturelles, mais elles font preuve d'une plasticité considérable.

Les analogies entre forêts autochtones non aménagées et plantations d'essences exotiques, gérées intensivement, ne peuvent fournir que les grandes lignes d'un traitement sylvicole possible.

L'établissement d'une plantation forestière doit tenir compte des conditions variables de l'environnement: la structure de la forêt doit être liée au caractère hétérogène du terrain, que l'on peut identifier par une classification du sol en vue du débardage. Des plantations très variées permettront aux forêts de mieux affronter les changements de l'environnement, qu'ils soient d'ordre physique, biologique ou social.

ZUSAMMENFASSUNG

In der Forstkultur werden Pflanzungen nach der Zusammensetzung der Altersklassen, nach Bestandesaufbau und nach der Artenzusammensetzung unterschieden. Neuere Entwicklungen in der Forsttechnik ermöglichen Standortverbesserungen, um erwünschte Baumarten einzubringen, während die

Mechanisierung der Holzernte Kahlschlagsysteme fördert.

Die Struktur und Entwicklung nicht planmässig bewirtschafteter Wälder, aus denen grösstenteils das Anzuchtmaterial für die britischen Aufforstungen stammt, zeigt deren Abhängigkeit von periodischen Störungen. Die Langlebigkeit der Hauptgattungsarten macht deutlich, dass die Bedingungen bei der Verjüngung für die Zusammensetzung des Altbestandes wichtiger sind als konventionelle Sukzessionsmodelle. Windbruch und Feuerschaden führen zu hauptsächlich gleichaltrigen Beständen, die je nach Standortbedingungen verteilt sind. Die ökologische 'Stabilität' dieser natürlichen Wälder ist zweifelhaft, aber sie zeigen beträchtliche 'Zähigkeit'.

Analogien zwischen nicht bewirtschafteten, einheimischen Wäldern und intensiv bewirtschafteten, exotischen Pflanzungen können nur grobe Leitlinien für forstwirtschaftliche Massnahmen liefern.

Die Anlage von Aufforstungen sollte die bestehende Vielfalt der Umgebung berücksichtigen, indem die Bestandeszusammensetzung der durch Geländeklassifikation erfassten Standortheterogenität Rechnung trägt. Grössere Vielfalt in Aufforstungen wird deren Pufferungsvermögen gegenüber Veränderungen in der physischen, biologischen oder sozialen Umwelt.

INTRODUCTION

Plantations of tree species may be established for a variety of purposes, chief among which is the production of industrial wood. Afforestation is also undertaken as a means of soil protection or for agricultural shelter or amenity. None of these objectives are exclusive of others and most afforestation schemes have multiple aims but in temperate countries generally, and in Britain in particular, the prime objective of afforestation is timber production.

In economic terms, afforestation involves a considerable initial investment of resources in the purchase of land, site preparation, provision of planting stock and its subsequent protection and management. Competition for scarce resources implies that investment in afforestation must be justified either in narrow financial terms or, more usually, in a broader economic view, by the provision of a range of benefits. In north temperate forests timber production alone

does not appear to be able to achieve a return of much more than 3 per cent on the capital invested in planting (Johnston 1975). In Britain this rate of interest is now used as a target against which to measure the performance of the national forestry enterprise; the difference between costs at this rate and the prevailing Government rate of interest is considered a subsidy to forestry for the provision of a range of social benefits (Forestry Commission 1978). To encourage the investment of private funds in afforestation many countries adopt fiscal inducements such as preferential tax rates, subsidies or planting grants.

Large scale afforestation schemes are most often government inspired to make good a deficiency in either present or future raw material supplies. The deficiency may arise from earlier profligate destruction of indigenous forest (e.g. New Zealand or Britain) and/or a lack of desirable native species. The aim of increasing land productivity has sometimes motivated large planting schemes. The afforestation of 900,000 ha in Les Landes, France, in the 19th century is a good example of this and a similar approach is being taken today in Spain. Sometimes, however, it has required a near critical situation to generate sufficient political will to divert funds to afforestation.

Once determined upon, afforestation programmes tend to be carried out rapidly with emphasis on the economic benefits of large scale operation, simplicity of structure and the use of relatively few species. The resource, once created, soon attracts the attention of other interests so that the forester then has to reconcile the aim of attaining the highest yield from each land unit or money unit invested, with the other justifiable demands of society for such secondary benefits as conservation, recreation and amenity.

Although these features of afforestation have been touched upon already (Holmes, this volume), it is worth reiterating them as they are the reason why it is necessary to consider the design of the forest. The term design acknowledges the man-made nature of the forest and implies an organised structure adapted to attaining defined management objectives, which include continuing high productivity. In the long term this requires a balance between the economic demands on production and the maintenance of site potential. The design of such plantation forests, so that they are also ecologically 'stable', is inevitably a speculative subject and is not susceptible to normal research methods. This paper, therefore, concentrates on the silvicultural characteristics of plantation forestry that influence long-term productivity and discusses measures that might be taken to maintain the resilience of the forest to changes in market demands, energy supply and social attitudes. Although the topic is discussed mainly in the context of the British situation, the principles

involved are applicable elsewhere.

PLANTATION FORESTS IN BRITAIN DISTRIBUTION AND RATE OF FORMATION

The historical development of afforestation in Britain has been summarized by Holmes (1975). The planting programme, which expanded dramatically after 1945, has resulted in a marked imbalance in the age class distribution on a national scale (Holmes, this volume Fig. 2). As land was acquired, without respect to any formal land use policy, plantations were distributed more or less at random in the first place. Nevertheless large concentrations of plantations have developed in several regions such as Galloway, the Borders and parts of west Scotland. In a few instances planned integration with agriculture has been attempted (Stewart 1978), with land purchase releasing capital for agricultural improvement but in general the aim has been to coalesce existing land holdings into larger units. The current rate of planting of about 29,000 ha/yr, although relatively small compared with New Zealand or Brazil which have programmes of 40,000 ha/yr and over 250,000 ha/yr (McConchie 1977; Palmer 1975), will, if continued, gradually balance the age class distribution nationally. On a more local scale this will not be possible and positive steps will be required if management desires sustention of yield and labour requirements.

Kilmichael Forest in west Scotland provides an example of the local management problems that may arise (Fig. 1). Here the fifteen planting years from 1946-60 account for about 70 per cent of the forest area and some 3400 ha, 40 per cent, was planted in a five year period. As the land available for further planting in this district is limited, adjustments to the age class distribution will have to be made by planned fellings. The estimated percentage distribution of yield classes (cu.m/ha/yr) of YC 20: 20 per cent, YC 14: 45 per cent, YC 8: 30 per cent, YC 2: 5 per cent, only indicates the range of productivity present in the forest and conceals the extent of the variation.

The stands of lowest productivity can doubtless be improved by remedial treatment but considerable site induced variation will remain a feature. Variation in lithology (Dalradian site region, Toleman 1978) and glacial geomorphology expressed in differential erosion and deposition, has resulted here, as in much of the uplands, in a complex of site types having differing aspects, slopes, soil profiles and very variable shapes and areas.

SILVICULTURAL CHARACTERISTICS OF FIRST ROTATION PLANTATIONS.

Species

The establishment of new plantations on land devoid of tree cover, demands the use of species that possess 'pioneer'

characteristics. These species are easy to handle in the nursery, tolerate transplanting and are capable of withstanding climatic stress, vegetation competition and other adverse agencies. They should also show rapid early growth, quick occupation of the site and be of high productivity. If successful in plantation culture, economic and marketing conditions then will ensure their management on short rotations so that they will be still relatively juvenile when harvested.

In British conditions all these 'pioneer' qualities are found in the main species used, Sitka spruce (*Picea sitchensis* (Bong.) Carr.) and lodgepole pine (*Pinus contorta* Dougl.). Although nationally they form 44 per cent and 11 per cent, respectively, of the growing stock (Locke 1978), their proportion in recent planting is much greater.

Monoculture

As planting has moved on to progressively poorer sites, species selection inevitably has become more restricted. On the site types available formation of stands of mixed species is possible, but does not often enhance survival or productivity, and may lead to complications in cost-effective management. The result is the development of extensive monocultures in which the stand structure is uniform, with variation existing only through differential rates of growth on different site types.

Cultural techniques

Much of the land now being afforested could not have been planted without the remarkable development of cultivation and drainage techniques over the last twenty-five years. These techniques now allow planting and successful establishment on almost any site. The capacity to alter the site through cultivation, fertilization and the use of herbicides has also had an influence on species selection. Whereas it used to be obligatory to use species that were adapted to the existing vegetation and soil conditions, it is now possible to alter the site to meet the establishment requirements of the main species.

Harvesting

The cost of harvesting timber either as intermediate or final yields, forms an important part of the overall economic performance of plantations. A balance must be struck between the costs of road construction and those of haulage from stump. The trend has been to increase the payloads of extraction machinery and reduce roading intensity. On negotiable terrain the size of machine used is still increasing and dictates less frequent interventions but with greater individual yields. For final fellings large scale mechanization entails clearfelling as the trees left in successive felling systems (e.g. shelterwood) are liable to damage on both stem and roots (Braate 1976). Risk of windthrow

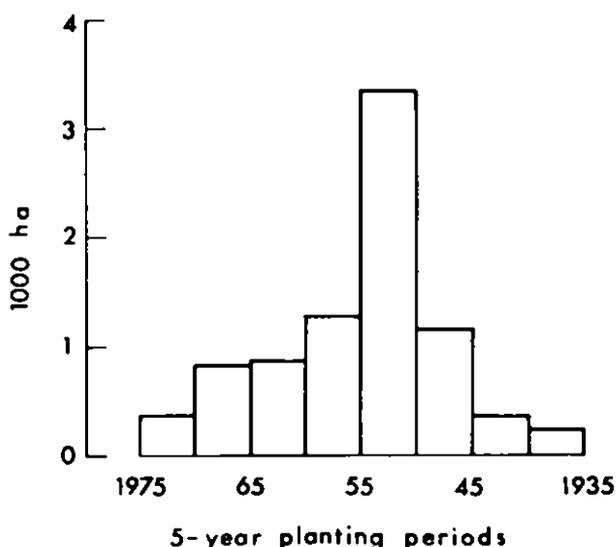


Fig. 1. Age class distribution of the forest area of Kilmichael Forest, west Scotland.

also militates against systems other than clearfelling, except in a few favoured localities. On steep or broken terrain extraction systems are based on cable cranes which are relatively expensive to set up and so become more cost-effective with increasing volumes removed. Ease of management, concentration of labour and machinery and the control of herbivores all tend to favour felling coupes of large size. This trend is tempered by the need to take account of the effects of felling on the landscape.

To summarize, upland plantation forests are developing as uniformly structured stands over relatively large areas, utilising few species of high productivity, the early site requirements of which have been met by increasingly intensive cultivation and fertilization. At economic maturity they will be clearfelled, restocked and the process started again.

From an ecological point of view the question may be asked whether these plantation forests can ever be more than aggregations of long-lived crops, managed on an agronomic basis. Can plantation forest, as described, be given a structure which is robust enough to ensure persistence in the face of environmental or biological impacts? Because of the need to limit investment of resources to the minimum consistent with an adequate return, these are questions of economic as well as silvicultural importance. Their answers are by no means clear but it is instructive to consider the development and structure of the forests from which the exotic

species in common use have been drawn.

STRUCTURE AND DEVELOPMENT OF NORTH TEMPERATE FOREST

General

There are not many detailed studies of the dynamics and development of unmanaged forest in the north temperate zone. Jones' (1945) critical review concluded that in forests of shade tolerant species a small scale group structure develops due to patches of trees being windthrown. A recent study in Italy of Abies alba/Picea abies forest found a mosaic of small even-aged patches about 0.1 ha in extent (Patrone 1975). Examples of true selection forest structure seem to be infrequent and mainly confined to mixed conifer - leaf-tree forests with a predominance of intensely shade-tolerant species (e.g. Abies alba Mill). In forests of less shade-tolerant species, the more usual structure seems to be a wide range of age classes with a continuous canopy, much like a uniform crop but often with a more or less pronounced storied structure (Jones 1945). Closer to the Arctic, simpler, more extensive, uniform stands of relatively shade-intolerant species occur which originate from catastrophic windblow or devastating fires. The importance of catastrophic disturbance of these northern ecosystems for adequate regeneration is well-known and application of fire to release accumulated nutrients in the organic soil has been a standard silvicultural treatment in Scandinavia (Nordstrom 1976 Paavanan, this volume). An extreme example of the need for this treatment is described for spruce in Finnish Lapland by Siren (1955) where without fire restarting the succession, spruce regeneration stagnates.

A form of stand in which regeneration proceeds in 'waves' with a cycle of about sixty-five years has recently been described by Sprugel (1976) for Abies balsamea (L.) Mill. forest in the northeastern United States. The 'waves' which advance into the older stand, appear to be initiated by wind damage and continue partly as a result of wind and frost accumulation on the exposed edge. The forest structure overall in this locality is reminiscent of a strip clearfelling distributed over several felling series.

In general it appears, that for forests dominated by coniferous species, conventional concepts of succession leading to a climatic climax, which remains 'stable' and self-perpetuating, are unrealistic. Dramatic disturbance on either a local scale e.g. patch windblow, or more extensive catastrophes create changing spatial patterns of forest structure. Perry (this volume) has made the interesting suggestion that soil surface litter accumulation may be an adaptation for excluding successional species. It is certainly clear that many species are adapted to periodic disruption of the forest. The interval between disruptive 'events' may be

quite short as in Sprugel's (1976) example or much longer as in the case of the 300-year-old Tsuga canadensis (L.) Carr. forest investigated by Hett & Loucks (1976) where topographic position and low deer populations had allowed small all-aged stands to develop of this shade tolerant species. In oceanic climates the return periods of catastrophic gales may be quite short, e.g. seventy-five years in Britain (Fraser 1971), while in more continental conditions, man- or lightning-induced fire has occurred in random patterns at intervals rarely exceeding 350-400 years (Heinselman 1971).

Northwest American forests

Of particular interest are the forests of coastal northwest America, where the Pacific Ocean currents result in an equable oceanic climate not dissimilar to that in western Britain, with the exception of the continual wind pressure experienced here and, away from the west coast, the prevalence of late and early frosts. North of Seattle, Washington, the soils have evolved on glacially derived materials and show many features similar to those in Britain but without extensive areas of climatically induced peats. Most of the species occurring in northwest America have populations that are well adapted to conditions in Britain. Provenance selection is most advanced with Sitka spruce and lodgepole pine, less precise with Douglas fir (Pseudotsuga menziesii (Mirb.) Franco) and grand fir (Abies grandis Lunde.) while little known of variation in western hemlock (Tsuga heterophylla (Raf.) Sarg.), Noble fir (Abies nobilis Lindl.), Pacific fir (Abies amabilis Dougl. ex Ford.) or western red cedar (Thuja plicata D. Don.).

Franklin & Dyrness (1973) have described the synecology of the coastal forest in Washington and Oregon, and Krajina (1969) in British Columbia. The former authors describe the Picea sitchensis zone forests as "typically dense, tall and among the most productive in the world" and above ground biomass accumulations of over 2000 tonnes/ha are not uncommon.

Successional trends have been identified for seral stands of either coniferous mixtures (Sitka spruce, western hemlock, western red cedar, Douglas fir) or Alnus rubra Bong. which is slowly invaded by conifers (Franklin & Dyrness 1973). The shade-tolerant western hemlock is thought to ultimately dominate the forest but only after the longer-lived and taller spruce or Douglas fir deteriorate. The time span involved may be up to 500 years so that frequently the succession is set back by disturbance before this stage is reached. Day (1957) conducted detailed ecological investigations in mixed spruce, hemlock and cedar forest in the Queen Charlotte Islands, the most common seed origin of Sitka spruce in British plantations. He describes a similar development towards an uneven-aged canopy dominated by hemlock after long periods but usually interrupted by storm or fire damage which results in

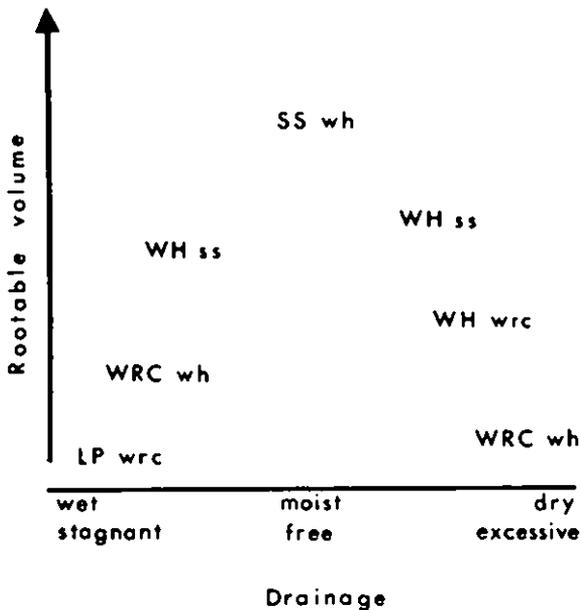


Fig. 2. Species dominance in relation to the soil conditions of rootable volume and drainage on Graham Island: SS - Sitka spruce, WH - western hemlock, WRC - western red cedar, LP - lodgepole pine, (after Day 1954).

an even-aged young stand. The species composition of this new stand appears to be determined by the physical conditions of the seed bed as much as by the availability of seed from different species. Sitka spruce in particular regenerates well on exposed mineral surfaces, whereas hemlock and red cedar seem well-adapted to organic seed beds. The proportional species composition of the upper canopy subsequently appears to depend on the site tolerances of the individual species. A simplified version of Day's (1957) findings on the competitive ability of these species, on a range of site types, is given in Figure 2. Sitka spruce is best able to maintain a dominant position, through its inherent growth potential; on moist, freely drained sites with adequate rootable volume; elsewhere it is progressively replaced by hemlock or cedar. In the area on Graham Island that Day studied, lodgepole pine only maintained a dominant position on muskegs but at Terrace on the Skeena River, in a much drier climate, this species is present also on the driest sites.

Two other features of this forest are of immediate interest. First, the ability of Sitka spruce to maintain some

representation in the upper canopy on soils with root restricting mineral horizons, either indurated till or fine textured gley, beneath a relatively thick organic (peaty) layer. Former windblown stems create 'humps' of mixed organic and mineral soil thereby providing the additional rootable volume necessary for Sitka spruce to compete effectively with hemlock, the better adapted species for this site type.

The second, related, feature is the inability of Sitka spruce to maintain a closed canopy beyond the stage when soil conditions effectively restrict further root expansion (Day 1957). There are several factors involved, such as the nutrient status of the soil, but the main effect seems to be the capacity of the soil to continue to supply water to meet the demands of increasing crown size. After canopy closure the redistribution of leaf area between dominant and suppressed stems implies a similar redistribution of soil resources but when these are fully exploited, the canopy must break up if individual healthy stems are to increase in size. Death of non-suppressed trees occurs either through their having inadequate leaf area to support net photosynthesis or through the dieback of the root system with concurrent invasion of pathogens, windthrow often expediting the process. The total stand leaf area for a number of northwest American forest types has recently been related to simple measures of seasonal evaporative demand (Fig. 3) (e.g. Grier & Running 1977) and there is no reason to suppose that Sitka spruce in Britain will perform differently when soil conditions cannot meet even the limited demands of evaporative stress experienced in high rainfall areas.

THE SILVICULTURE OF UPLAND PLANTATION FORESTS

Analogies with indigenous forest

The successful application of silvicultural techniques to the cultivation of Sitka spruce in plantations shows some similarity to the fashion in which this species performs in its native habitat. The periodic disruptions of the forest with regeneration of even-aged stands are simulated by clearfelling and restocking. Cultivation and drainage attempt to extend the area of those soil types which can meet the rooting requirements of the species, repeating on a large and more controlled scale the pattern of windblow generated soil 'humps' on shallow soils. The differences between the two ecosystems are equally obvious and reside mainly in the time scales involved. In the unmanaged forest there is a virtually closed nutrient cycle where accumulated nutrients in the organic soil horizon are released in pulses after major disruption, loss of N being made good by stimulated microbial activity. The losses in drainage are either made good by fresh rock weathering and atmospheric deposition (Miller, this volume) maintaining general levels of productivity or, on poor

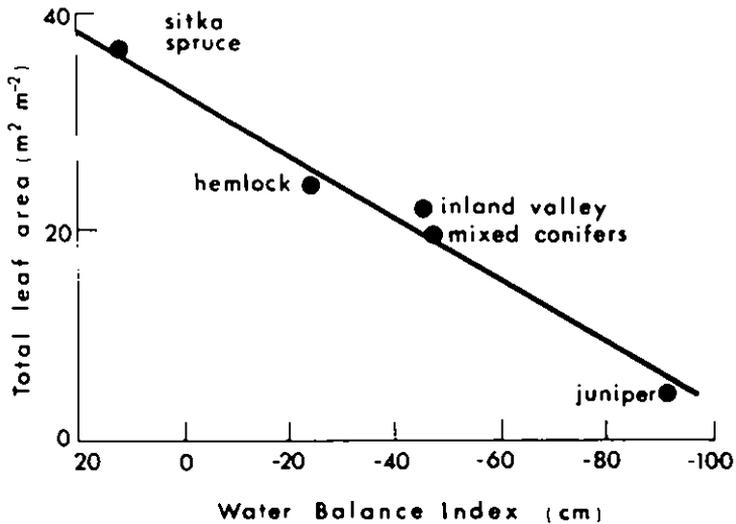


Fig. 3. Relationship between total stand leaf area and estimated water balance index for northwest American forest types (after Grier & Running 1977).

lithologies, there may be a slow decline in the productivity of successive generations and an increase in the proportion of species more tolerant of low levels of nutrition. In managed plantations the relatively frequent removal of the stand, in many cases established on already impoverished soils, demands that the losses are made good through fertilization.

In the unmanaged forest natural selection emphasizes the ability of various species to survive and reproduce in competition. The competition for regeneration niches is eliminated in the plantation and considerable effort is directed to selection for productivity, wood quality and stem form.

Clearly the analogies that can be drawn from the natural forest are limited and can provide only an indication of the likely performance of cultivated populations particularly where these have been subject to considerable artificial selection. Research effort has therefore been focussed on the autecology of the species in plantations, particularly Sitka spruce. Intensive studies of particular stands combined with work in controlled environments have elucidated many of the

physiological responses of this species to its environment.

Species performance and species selection

Although much empirical information on species performance has been obtained from the many field experiments established by the Forestry Commission, this has only recently begun to be systematised through the recognition of silvicultural site regions and an altitudinal stratification within these (Toleman 1978). The impact on practice of the more fundamental studies referred to above has to far been slight.

For most species there appears to be a slight trend for productivity to decrease from south to north in Britain but this is confused by local site variation and changes in the afforestation techniques used (Locke 1978). Attempts to relate productivity to readily available meteorological data have been disappointing and clearly local climatic variation related to topography and expressed by indirect parameters, such as elevation, is overriding (Malcolm 1976). In the few studies that have attempted to relate productivity of Sitka spruce to a range of site variables, elevation has proved the dominant factor emphasizing the importance of temperature and exposure to wind (Page 1970; Malcolm 1976). A high proportion of variability in productivity can be accounted for by elevation alone so that the altitudinal limit for economic planting of Sitka spruce can be predicted at about 550 m (Malcolm & Studholme 1972; Mayhead 1973). These studies were mainly on unfertilized and uncultivated soils and indicated the importance of soil rootable volume, as well as site phosphorus status (Malcolm 1976). No doubt early growth rates can be enhanced by soil cultivation and fertilization but the extent of the improvement apparently falls off rapidly as limiting elevations are approached (Freezallah 1974).

Comparisons between the productivity of different species are extremely difficult to make because of the obvious tendency to allocate species according to known site preferences, and the variability within sites. A further problem lies in making valid comparisons on first rotation plantings where one species acts as a 'pioneer' and the other may be more typical of later seral stages. There is no doubt that in the afforestation of exposed upland soils of generally low fertility the species in common use, Sitka spruce or lodgepole pine, have distinct advantages. On sheltered, more fertile situations the initial choice is wider. This is illustrated by the comparison (Aldhous & Low 1974), by means of paired plots, between the main species in use and four species from northwest America (grand fir, noble fir, western hemlock, western red cedar). The majority of plots were on fertile, brown earth or surface water gley sites. In terms of productivity three of these species were generally superior to Sitka spruce even though established in open non-forest

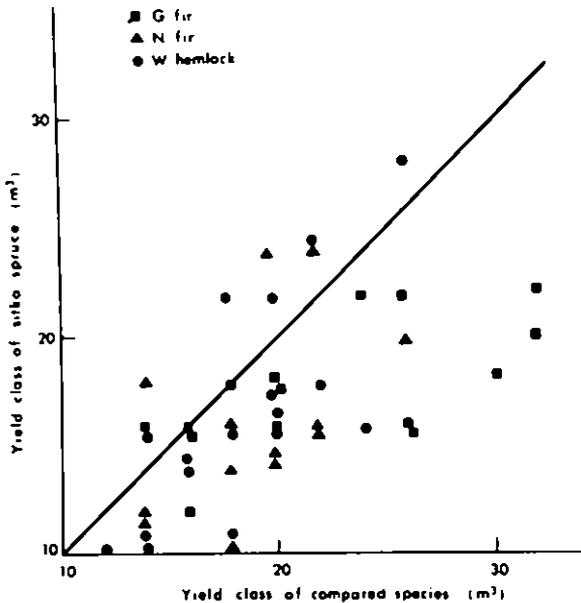


Fig. 4. The yield of Sitka spruce in relation to the yield of three other plantation species in the U.K.
 G Fir - *A. grandis*, N Fir - *A. nobilis* and
 W hemlock - *T. heterophylla*, (after Aldous & Low 1974).

conditions (Fig 4.). Western red cedar was compared in ten plots only and the growth rate was not correlated with that of Sitka spruce. Whether these comparisons can be extrapolated to more extreme sites is doubtful but there is evidence that noble fir can withstand 'exposure' at least as well as Sitka spruce. Western hemlock is most sensitive to 'exposure' in youth and appears to require shelter at this stage; unfortunately, it also appears particularly prone to fungal decay (*Fomes annosus*). Grand fir, however, is resistant to *Fomes*, is more site tolerant than its present distribution suggests and has the silvicultural advantages of shade tolerance in youth and rapid litter breakdown.

If the range of species used in upland forests is to be extended, then it is likely that, on present knowledge, alternatives to Sitka spruce are likely to be drawn from the species noted above. Other factors, such as timber quality and marketing requirements are important in assessing the suitability of alternative species but for many end uses the differences are slight.

So far, with the majority of plantations in the

establishment and small pole-stage phase, serious biological problems have not arisen with spruce, except possibly the outbreak of *Gilpinia hercyniae* in Wales (Billany & Brown 1977). Problems are more likely to arise where one species has been extended on to sites which are incapable of supporting vigorous growth for the length of the rotation or where the genetic base is allowed to become too narrow. It is not always clear what combination of circumstances gives rise to population explosions of pests, but once they are present in sufficient numbers, they can be fairly indiscriminate in food preference (e.g. *Panolis flammca*, Stoakley 1977). The need for prudence is frequently mentioned (Seal 1978; Johnston 1978; Newhook 1977) but, for the reasons mentioned before, has not yet been recognized in the proportions of species currently being planned. There is an urgent need for appraisal of the possibilities for species diversification as plantation forests begin to move into their second rotation. Particular attention should be paid to the range of variation obtainable in northwest American silver firs (*Abies grandis*, *A. nobilis*, *A. anabilis*) and western hemlock.

Cultural treatments

The development of cultivation techniques has culminated in the ability to transform mineral soils which have root restricting horizons less than 90 cm deep (Neustein 1977). These soils are consequently freely drained or, at least after canopy closure, are unlikely to require drain maintenance. Complete cultivation is now quite common and results not only in improved soil physical status but in a flush of released nutrients from the incorporated organic matter. On coarse textured material of poor lithology, however, there is some doubt whether the resultant improved growth can be maintained either through loss of nutrient exchange capacity or available water capacity (Van Goor 1954; Thomson & Neustein 1973). Nutrients may be added as long as it remains economic to do so.

In the climatically wetter areas gleys, peaty gleys or deep peats predominate. These form the major problem for site improvement. The restriction of rooting to the organic horizon due to impermeable, fine textured or compact mineral horizons beneath is critical to the maintenance of closed forest stands. This has led to the doubling of the distance between plough drains (Thompson 1977) in an attempt to widen the rooting 'platform' and, on an experimental basis, the sculpturing of the whole soil surface in an attempt to increase the rootable volume and delay windblow. Where first rotation stands have been blown down, the disturbance of the peaty layer often results in its partial disappearance through irreversible drying and oxidation. Where such stands are clearfelled the water table rises to near the surface leading to problems in establishing the next stand. Many of these

sites are technically undrainable due to the pore size distribution as well as the occurrence of stumps. Nutrient status will have to be maintained by fertilization but the factor limiting productivity in second and subsequent rotations is more likely to be water supply in periods of low rainfall, due to the small rootable volume and its low water capacity.

On the true peat soils, where root systems will never reach mineral horizons, initial drainage permits canopy closure followed by a gradual drying of the peat to at least drain depth or deeper with lodgepole pine. Irreversible drying of peat here results in shrinkage and cracking (Pyatt 1976) so that these sites probably will be very different in later rotations. Some types of peat appear to have low retention capacity for added nutrients (Malcolm, Bradbury & Freezailah 1977), are already very low in available nutrients and may thus require frequent inputs of fertilizer. Although once drained they are physically suitable for vigorous tree growth, the nutrient regimes required may not be economic for demanding species (Dickson & Savill 1974).

Fertilization of established plantation forest is becoming more frequent and, where nutrients are limiting, has achieved striking increases in growth rate. Recently more attention has been paid to volume increment and changes in tree form which might be important in utilization. The increased growth is attained by increasing leaf area and net assimilation rates in the lower canopy, and, as in other monocultures, will be limited ultimately by mutual shading in closed canopies. In brief, fertilization accelerates the development of the stand; if unthinned, the mortality rate will be enhanced; if thinned, leaf area expansion of released trees will continue, although individual crowns may become less efficient in wood production (Kramer 1966). End use of the timber is also important and too fast growth rates will result in down-grading of sawwood products. Miller (this volume) has shown that the forest soil is normally an efficient 'sink' for added nutrients and it may be that ultimately interest in phosphate levels in mineral soil will diminish relative to nitrogen, as in most temperate countries, which might make the economics of fertilization less attractive.

Stand structure

The effect of inter-plant competition in regularly spaced monocultures is the creation of a hierarchy of dominance which in terms of tree size approximates a log-normal distribution, which in the managed stand tends to become normal towards the end of the rotation. The distribution found in all-aged stands, best described by a power function of size or age (Dawkins 1971; Hett & Loucks 1976), is essentially the even-aged distribution perpetuated in the same space. In the

even-aged stand by comparison, the reduction in stem number with increasing size is a progression in time. Valid comparison of utilisable productivity between the different structures is very difficult but for uniform sites the balance of advantage would appear, on theoretical grounds, to be with the even-aged system. This is mainly due to the inefficiency of much of the leaf area in the lower parts of an irregular canopy, which is poorly illuminated despite the wide spacing of dominant trees that themselves develop inefficient crowns. Differences in transfer and interception processes, that might be more beneficial in an irregular canopy, are unlikely to counteract the main disadvantage, (Malcolm & Taylor 1979).

In reality, uniform sites do not exist and in more extreme environments there may be a case for developing an irregular structure, which must depend on shade-tolerant species and natural regeneration. The ecological 'stability' claimed for irregular forest structures is often confused with the benefits of mixed species in nutrient cycling, effects on tree form and so on. Increased physical stability in a windy climate is even more problematic, where effective rooting space is the factor limiting the size of stable trees. Catastrophic gales cannot be countered silviculturally by irregularity of structure but less damage from more normal winds might accrue in stands of a rather open structure in which the dominants were widely spaced from an early age to allow adequate root spread. Such treatment would entail loss in total production but might allow larger individual stems to develop. Day (1962) studied the root systems of Sitka spruce on sites with impenetrable mineral horizons under shallow peat and concluded that there was a choice between removal of the stand at an age before it broke up (i.e. at small pole size) or, by allowing a more open and irregular canopy to form, to take small scale variability in root penetration into account. On rather similar soil types at elevations of about 500 m in the Belgian Ardennes, plantations of spruce have been undergoing transformation to mixed stands of irregular structure (Roisin 1959) since about 1935. The aim here has been to increase resistance to possible insect attack and improve ecological conditions generally.

Stand size and distribution

Catastrophic stand destruction in unmanaged forests may be simulated by large scale clearfelling, which in cooler, humid climatic conditions may be justified on ecological grounds. In managed forests, however, there are other constraints that influence the scale of regeneration fellings. These may include visual amenity, maintenance of wildlife habitat including stream protection, and so on. The distribution of stands in relation to their demands, just as for forest age class distribution, are the province of forest management. The silvicultural interest is that their

distribution should optimize forest productivity by maintaining, and where possible, increasing site potential. At the same time stand distribution should minimize the risks of environmental or biological damage. Some of these are predictable, others are not, so that the imposition of any idealized spatial pattern of stand distribution is unlikely to persist for long.

The logical procedure is to link stand distribution with site type distribution, that is to acknowledge the variation in the physical resources. Different sites have different potentials which can be exploited more efficiently by some species than others. Different sites require different cultural treatments which, while increasing their potential, may reduce but not eliminate the variation. This variation can be used to design a forest structure that reflects the ecological realities for healthy tree growth. The scale of the stand distribution pattern will vary with that of the site types. Paterson (1975) has described how species selection, cultural treatment and harvesting might be fitted into the small scale but highly differentiated site patterns found in areas of fluvio-glacial deposits in upland Scotland. With more extensive site types like those in the southern uplands or in north England, some variation in stand size might have to be imposed by management. Stand size might need to be limited to maintain forest conditions for regeneration. This becomes of particular importance at the altitudinal limits where moderate yields of slow grown timber must be taken at long intervals.

The basis for stand differentiation already exists in the process of site mapping within silvicultural site regions but felling coupe size has also to relate to mechanised systems of harvesting. In some cases the apparently most economical extraction technique will not be appropriate to the site conditions, particularly where heavy machinery is used on poorly draining soils thereby reducing the future production potential. In general, however, extraction methods can be made to match desirable silvicultural objectives and the two related through terrain classification (Fig. 5) (Rowan 1978). There is a need for the development of machinery which can cope with rough terrain, of a size which enables economic operation and yet not so large as to cause serious site damage on wet or peaty soils (Braate 1976). The cost of imported machinery may in itself slow progress towards increasing size of extraction equipment (McGonchie 1977).

The silvicultural system adopted will be in most cases clearfelling with replanting. Apart from its ecological desirability on many sites and the requirements of most of the species in use, economic pressures in harvesting alone would lead to its retention. The introduction of superior genotypes from tree breeding programmes will require a clearfelling system, although techniques of handling and tending these

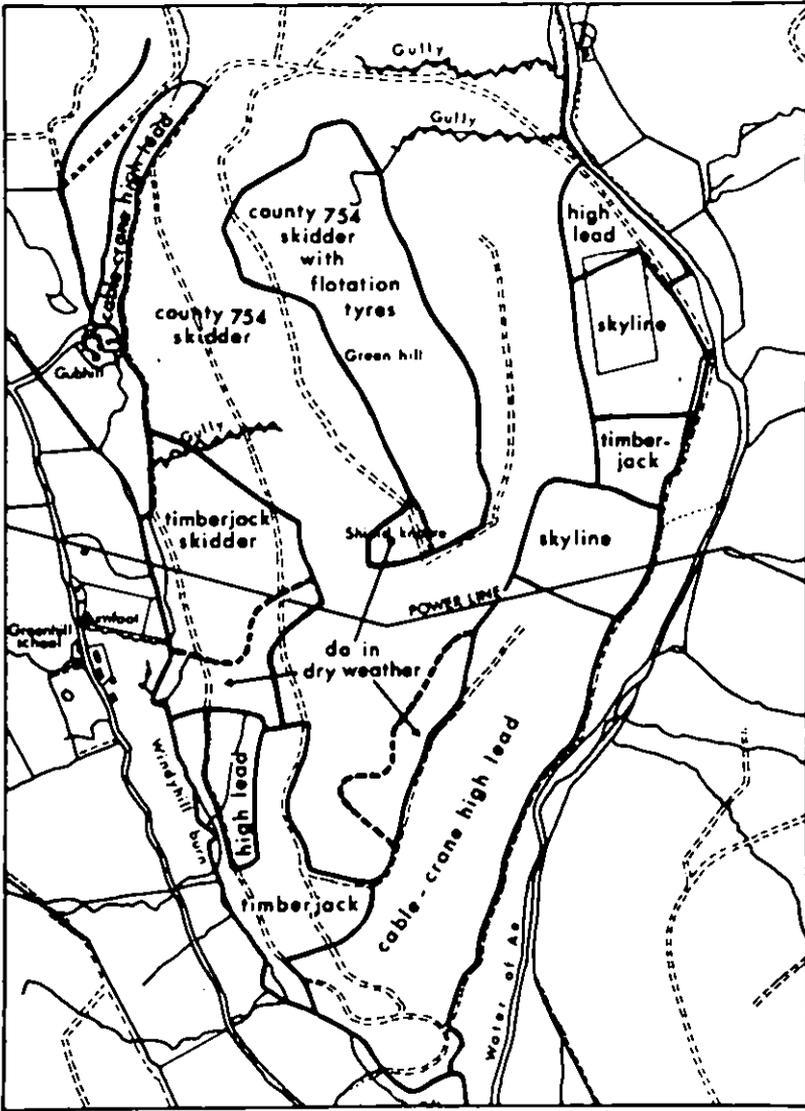


Fig. 5. A terrain classification of part of the Forest of Ae, south Scotland, indicating which of various timber extraction techniques should be used.

improved trees have not yet been developed. Other systems, such as shelterwood or irregular working, may be desirable in areas which are particularly sensitive either environmentally or for amenity and conservations reasons.

Natural regeneration may occur even where it is not desired; if it is of acceptable species and genotypes there is no real problem and suitable tending techniques are available. Almost all the species that have been used in plantations have demonstrated a capacity to regenerate naturally but, for the reasons already discussed, little effort has been made to develop silvicultural techniques to ensure its reliability.

At present, the presence of large deer populations forms a further constraint on species selection, stand size and structure. The creation of forest habitat has led to large increases in the populations of these animals which browse restocked areas and strip bark in pole-stands. More is known of the management of roe deer (Capreolus capreolus) than of red deer (Cervus elaphus) in British forests (Loudon 1978) but both are difficult to census so that culling programmes tend to be somewhat speculative. There is no doubt that control of these animals forms one of the biggest management problems as first rotation stands are felled for replanting. Policies of exclusion are too expensive and probably ineffective (Cooper & Mutch, this volume).

CONCLUSIONS

This paper has tried to assess the way the large scale plantations established in the British uplands might develop in future and in particular how they might be structured to minimize the influence of environmental and biotic hazards. The physical resource or environment for tree growth can be thought of as the combination of two gradients. The range of soil conditions in respect of rootable volume and nutritional status is one and the other is climate as an expression of heat and water balances. These gradients interact at many levels to form a complex system or framework within which the biological elements vary in space and time. The generalization of these concepts is the purpose of systems analysis (Bakuzis 1976). Systems analysis, however, depends on an appreciation of the functioning of ecological processes and it is here that detailed physiological studies find an application. A clearer understanding of the forest x site interactions will result in a greater ability to predict the consequences of silvicultural and management decisions. Added to the ecological complexities are the economic constraints on the use of the forest. Sundberg (1976) identified conflicts at two levels: one between silvicultural objectives and economic operational methods and the other between the needs of the forestry system and other 'systems' with demand on the forest. The solution he proposed to the first was a managerial structure which could

balance long and short term benefits and costs and, for the second, the application of systems analysis to avoid too narrow an approach to management problems. Whether we are yet in a position to adopt the second approach is doubtful.

At a more practical level the forester has to design the forest to meet as many of the demands on it as possible through the allocation of species to sites and the distribution of stands within the forest landscape. This he can do either by:

1. attempting to stabilize a production system based on one or two species with complementary inputs of cultivation and fertilizer to homogenize the environment as much as possible, with cosmetic adjustments of species composition and stand boundaries to provide the secondary benefits of amenity and recreation; or by
2. accepting that even with cultural treatments the environment is not homogeneous, particularly in respect of climate, that the existing heterogeneity can be used to provide variation, without necessarily reduced production, while meeting the other demands on the forest without strain.

The first option assumes stability, or at least small fluctuations, in the environment, the possibility of control of biological hazards and a continuing demand for a particular combination of physical and social benefits. The latter option assumes that future events affecting the forest are unpredictable and that change is inevitable. Variation in species composition, size and distribution of stands within the forest gives flexibility to management.

The two approaches outlined are akin to those associated with 'stable' and 'resilient' ecosystems as defined by Holling (1973). Stability is the ability of a system to return to its previous state after disturbance, while resilience is the ability of a system to persist despite disturbance.

This paper has contended that neither the unmanaged forest nor the newly created plantation in the British uplands can be expected to function as 'stable' ecological systems. It is certain that their future development will be against a background of change, in energy costs, labour supply, market demand and social attitude and use. The artificial, managed forest presents an opportunity to design a system with resilience capable of absorbing such changes.

REFERENCES

- Aldhous, J.R. & Low, A.J. (1974). The potential of Western Hemlock, Western Red Cedar, Grand Fir and Noble fir in Britain. *Bulletin of the Forestry Commission*, London, 49, 1.105.

- Bakuzis, E.V. (1976). Outline of systems analytic approach to forest growth and site evaluation. Research on site factors Section 21, XV World IUFRO Conference Gainesville 1971. pp. 156- 82. Wageningen, Netherlands.
- Billany, D.J. & Brown, R.M. (1977). The geographical distribution of *Gilpinua hercyniae* (Htg.) (Hymenoptera: Diprionidae) in the United Kingdom. *Forestry*, 50, 155-160.
- Braate, P. (1976). Silvicultural practices in modern plantation forestry. Ways and means of reconciling silvicultural and operational methods in modern forestry. Joint IUFRO/FAO Meeting XVI World Congress IUFRO, Oslo, 1976. pp. 16-26.
- Dawkins, H.C. (1971). Techniques for long-term diagnosis and prediction in forest communities. "The scientific management of animal and plant communities for conservation". Proceedings 11th Symposium of the British Ecological Society, (Ed. by E. Duffey and A.S. Watt), pp. 33-44. Blackwell Scientific Publications, Oxford.
- Day, W.R. (1957). Sitka spruce in British Columbia, *Bulletin of the Forestry Commission*, London, 28, 1-110.
- Day, W.R. (1962). The development of Sitka spruce on shallow peat. *Scottish Forestry*, 16, 219-236.
- Dickson, D.A. & Savill, P.S. (1974). Early growth of *Picea sitchensis* (Bong.) Carr. on deep oligotrophic peat in Northern Ireland. *Forestry*, 47, 57-88.
- Forestry Commission. (1978). 57th Annual Report and Accounts for the year ended 31 March 1977. pp. 102. Her Majesty's Stationary Office, London.
- Franklin, J.F. & Dyrness, C.T. (1973). Natural vegetation of Oregon and Washington. U.S. Department of Agriculture, Forest Service, General Technical Report PNW 8, 1-417.
- Fraser, A.I. (1971). Meteorology. "Windblow of Scottish forests in January 1968". *Bulletin of the Forestry Commission*, London, 45, 3-7.
- Freezaillah, B.C.Y. (1974). Climatic influences on the growth and uptake of phosphorus by Sitka spruce. Unpublished Ph.D. thesis, University of Edinburgh.
- Goor, C.P. van (1954). De invloed van de bodembewerking op een aantal eigenschappen van de droge, bruine bosgronden. *Landbouwkundig Tijdschrift*, 66, 175-181.
- Grier, C.C. & Running, S.W. (1977). Leaf area of mature Northwestern coniferous forests: relation to site water balance. *Ecology*, 58, 893-899.
- Heinselmann, M.L. (1971). The natural role of fire in northern conifer forests. Fire in the northern environment (Ed. by R.J. Slaughter, R.J. Barney and G.M. Hansen), pp. 61-72. U.S. Department of Agriculture, Forest Service, Portland, Oregon.
- Hett, Joan M. & Loucks, O.L. (1976). Age structure models of balsam fir and eastern hemlock. *Journal of Ecology*, 64, 1029-1044.

- Holling, C.S. (1973). Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics*, 4, 1-23.
- Holmes, G.D. (1975). History of forestry and forest management. Discussion of forests and forestry in Britain. *Philosophical Transactions of the Royal Society, London, B*, 271, 69-80.
- Johnston, D.R. (1978). The constraints against irregular forestry. In: Dewar, J. The case for regional silviculture. *Forestry* 51, 1-19.
- Jones, E.W. (1945). The structure and reproduction of the virgin forest of the North Temperate Zone. *New Phytologist*, 44, 130-148.
- Krajina, V.J. (1969). Ecology of forest trees in British Columbia. *Ecology of Western North America, Volume 2* (Ed. by V.J. Krajina) pp. 1-146. Department of Botany, University of British Columbia.
- Kramer, H. (1966). Crown development on conifer stands in Scotland as influenced by initial spacing and subsequent thinning treatment. *Forestry*, 39, 40-58.
- Locke, G.M.L. (1978). The growing stock of regions. In Dewar, J. The case for regional silviculture. *Forestry*, 51, 1-19.
- Loudon, A.D.I. (1978). The control of roe deer populations: a problem in forest management. *Forestry*, 51, 73-83.
- Malcolm, D.C. (1976). Site factors and the growth of Sitka spruce. Research on site factors. XV World Congress IUFRO, Gainesville, 1971, pp.269-283. Wageningen, Netherlands.
- Malcolm, D.C. & Studholme, W.P. (1972). Yield and form in high elevation stands of Sitka spruce and European larch in Scotland. *Scottish Forestry*, 26, 296-308.
- Malcolm, D.C. & Taylor, C.J. (1979). The place of irregular forestry in North Britain. In Thallow, K. Yield control and production planning. *Forestry*, 52 (in press).
- Malcolm, D.C., Bradbury, I.K. & Freezaillah, B.C.Y. (1977). The loss of nutrients from fertilized peats in an artificial system in the field. *Forest Ecology and Management*, 1, 109-118.
- Mayhead, G.J. (1973). The effect of altitude above sea-level on the yield class of Sitka spruce. *Scottish Forestry*, 27, 231-237.
- McConchie, B.D. (1977). Plantation forestry: The future - an industry viewpoint. *New Zealand Journal of Forestry*, 22, 226-228.
- Neustein, S.A. (1977). A history of plough development in British forestry. *Scottish Forestry*, 31, 2-12.
- Newhook, F.J. (1977). Plantation forestry: the reservations. *New Zealand Journal of Forestry*, 22, 246-248.
- Nordstrom, L. (1976). (Forest regeneration in the past). (Seen in abstract). *Kungliga Skogs- och lantbrukakademiens*

- tidskrift, 115, 303-314.
- Page, G. (1970). Quantitative site assessment. *Forestry*, 43, 45-56.
- Palmer, F. (1975). Wood supply and demand - the medium term prospects for Britain. A discussion on forests and forestry in Britain. *Philosophical Transactions of the Royal Society, London*, B. 271, 81-89.
- Paterson, D. B. (1975). Silvicultural practices on extensive areas of complex sites. *Scottish Forestry*, 29, 140-145.
- Patrone, G. (1975). (Studies on even-aged forest in Cadore Belluno). (Seen in abstract). *Accademia Italiana di Scienze Forestali*, 1975, 1-109.
- Pyatt, G. (1977). Site studies (north). Forestry Commission, Report on Forest Research, London. P 24.
- Roisin, P. (1959). La transformation des Pessieres. *Bulletin de Societe des Forets Belges*, 66, 153-190.
- Rowan, A. A. (1978). Terrain classification. *Forest Record of the Forestry Commission, London*, 114, 1-23.
- Seal, D. T. (1978). A summary of the case for regional silviculture. In Dewar, J. The case for regional silviculture. *Forestry*, 51, 1-19.
- Siren, G. (1955). The development of spruce forest on raw humus sites in N. Finland and its ecology. *Acta forestalia fennica*, 62, 1-405.
- Sprugel, D. G. (1976). Dynamic structure of wave regenerated *Abies balsamea* forests in N.E. United States. *Journal of Ecology*, 64, 889-911.
- Stewart, G. G. (1978). Inter-relations between agriculture and forestry in the uplands of Scotland: a forestry view. *Scottish Forestry*, 32, 153-181.
- Stoakley, J. T. (1977). A severe outbreak of the pine beauty moth on lodgepole pine in Sutherland. *Scottish Forestry*, 31, 113-125.
- Sundberg, U. (1976). Forest management affected by mechanisation and environmental concern. Ways and means of reconciling silvicultural and operational methods in modern forestry. Joint IUFRO/FAO Meeting. XVI World Congress IUFRO, Oslo, 1976. pp.27-47.
- Thompson, D. A. (1977). Cultivation. Forestry Commission Report on Forest Research, London. 19pp.
- Thomson, J. H. & Neustein, S. A. (1973). An experiment in intensive cultivation of an upland heath. *Scottish Forestry*, 27, 211-221.
- Toleman, R. D. L. (1978). The site regions of upland Britain. In Dewar J. The case for regional silviculture. *Forestry*, 51, 1-19.

TROPICAL FORESTS - COMPARISONS AND CONTRASTS

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SUMMARY

Forest plantations in the tropics include those established in the lowland rainforests, highland grasslands and arid zones. Most concern is felt over the effects of replacement of complex rainforest ecosystems by uniform, monospecific plantations. Problems of afforestation of grasslands, arid zone savannas and shrublands are mentioned but not discussed in detail.

After a brief review of the methods of regeneration and replacement of rainforest which are used to increase the yields of food and wood products, the resilience and stability of the artificial ecosystems created are considered. The importance of stand structure and succession, the effects of changes in the physical and chemical properties of the soil and nutrient cycling in a forest ecosystem suggest that more care and sensitivity in site selection for plantations than has been shown so far is essential if serious failures are to be avoided.

Recommendations for more extensive ecological research as a basis for plantation management are made and guidelines suggested in the light of existing knowledge.

RÉSUMÉ

Les régions tropicales comprennent trois zones de plantations forestières: - les forêts pluviales à basse altitude,
- les savannes des hauts plateaux,
- les zones arides.

On a exprimé beaucoup d'inquiétude sur les effets du remplacement des écosystèmes complexes des forêts pluviales par des

plantations d'essences uniformes. Les problèmes du boisement des prairies, des savanes arides et de la brousse sont mentionnés dans cet exposé mais ne sont pas traités en détail. Nous décrivons brièvement tout d'abord les méthodes de régénération et de remplacement des forêts pluviales qui ont pour but d'améliorer les rendements en nourriture et en bois. Nous passons ensuite au sujet de la résistance et de la stabilité des éco-systèmes artificiels. L'importance de la structure et de la succession des peuplements, les effets du changement des propriétés physiques et chimiques du sol et du cycle des éléments nutritifs dans l'éco-système forêt montrent que le choix du terrain doit être accompli soigneusement et raisonnablement, ce qui n'est pas toujours le cas, dans le but d'éviter des échecs sérieux.

Nous pensons que des recherches solides en écologie devraient être menées à bien, qui seraient le fondement de la gestion d'une plantation. Nous en donnons quelques grandes lignes en nous basant sur des faits existants.

ZUSAMMENFASSUNG

Forstpflanzungen unterliegen den Produktionsbedingungen so unterschiedlicher Naturräume wie z.B. tropische Regenwaldzone, montanes Grasland und Trockengebiete. Die meisten Bedenken bestehen bei der Umwandlung von komplexen Regenwald-Ökosystemen in gleichaltrige Reinbestände. Probleme der Aufforstung von Graslandgebieten, Savannen und Buschwäldern der Trockenzonen werden zwar erwähnt, aber nicht ausführlich diskutiert. Nach einem kurzen Überblick über Methoden zur Verjüngung und Umwandlung von Regenwald zur Steigerung der Nahrungs- und Holzproduktion werden die Resistenz und Stabilität der künstlich geschaffenen Ökosysteme diskutiert. Die Bedeutung von Bestandes- aufbau und -entwicklung, die Auswirkungen durch Veränderung bodenphysikalischer und -chemischer Parameter sowie deren Einfluss auf den Nährstoffumsatz in einem Wald-Ökosystem lassen vermuten, dass mehr Sorgfalt und ökologisches Bewusstsein als bisher bei der Standortwahl für Pflanzungen notwendig ist, wenn ernste Fehlschläge vermieden werden sollen.

In Anbetracht des derzeitigen Kenntnisstandes werden Empfehlungen für extensivere ökologische Forschungen vorgeschlagen, die als Grundlage und Richtlinie der Bewirtschaftung von Pflanzungen dienen sollen.

DEFINING THE CONTRASTS

The range of habitats found within 'tropical forests' is so great that any useful comparisons with temperate forests, themselves variable, require extensive qualification.

Comparisons in this paper relate to those forest formations listed in Table 1 that are currently subject to greatest interference either through planned management or indiscriminate clearing for food production by land-hungry people living under stresses caused by a rapid increase in population.

Mangroves and fresh water swamp forests which contain large timber reserves but are not under immediate threat of destruction or conversion to plantations for obvious technical reasons, do not receive consideration.

In the context of this meeting we compare the ecological and economic role of plantations both in the lowlands and highlands of the tropical zone, with the natural communities they replace, and with their analogues in temperate regions where these occur. Several forest formations grouped as tropical rainforests call for attention:

- (i) Tropical lowland rainforest and semi-evergreen rainforest, together comprise the complex - structured dry-land communities and are dominated by hygrophilous tree species characterized by the frequency of buttressing, cauliflory and leaves with driptips, abundance of climbers and epiphytes and a degree of deciduousness that increases with seasonal water stress (Richards 1952; Baur 1964; Whitmore 1975).
- (ii) Where a distinct dry season occurs, the stature, structural complexity and species diversity of the forest is reduced, though, as with the monsoon forests of teak and pine, they may still yield much of value to man. It may be noted that it was in the tropical monsoon forests in India early in the 19th century that intensive tropical silviculture was first applied and natural forest was replaced by plantations on a significant scale.
- (iii) As we move away from the optimum conditions of continuous high humidity and temperature in the rainforest zone, either to the hot, arid habitats with xerophilous woodland and grassland of higher latitudes, or to mesophilous woodland, montane forest or fire induced grasslands at higher altitudes, the problems of plantation silviculture change.

The importance of re-establishing a forest cover in the arid tropics to protect the soil and supply wood to local communities will have a long-term significance in terms of human welfare quite as great as the economically more impressive pulpwood plantation projects in the rainforest zone and on the montane grasslands.

The validity of comparisons between plantations in temperate and tropical regions must, however, be questionable even with careful definition of the ecosystems in which they are established. Economic, social and political factors frequently dominate ecological judgements unless, or until, an event occurs to reveal an instability in the plantation ecosystem, such as extensive windthrow, accelerated soil erosion or mineral deficiency. Perhaps the most useful question to ask is whether tropical plantations lead to site degradation or, put another way, whether the energy inputs to maintain the artificial ecosystem are greater than the energy yields. Have we reason to believe that there are essential differences between temperate and tropical habitats which render application of temperate silvicultural and, probably of greater significance, agricultural methods essentially unstable in the tropical dry lands? Other comparisons, e.g. of productivity, quality and diversity of products and of methodology must all be secondary. Alternative management options for existing areas of natural vegetation are not restricted to total replacement by a completely artificial system but include various degrees of enrichment and partial replacement leading to mosaic patterns of land use. The intensity of management that can be tolerated in a tropical and a temperate ecosystem cannot be assumed to be identical. There is still time in many tropical areas to plan and control development to ensure a resilient pattern of land use which maintains calculated proportions of rainforest under permanent management in association with agricultural development and plantations. Shifting agriculture at appropriate intensity is a resilient system, but under short rotations it becomes destructive. The rainforest may be a stable system but is not necessarily resilient to drastic interference on a large scale, using 'stable' and 'resilient' in the sense of Holling (1973). The spatial scale of man's interference may well be a key factor in the success or failure of land development in the tropics.

THE RISKS OF FOREST CONVERSION

Our ignorance of the ecology of tropical, compared with temperate communities confounds simple comparisons. As Janzen (1975) puts it: "We understand almost nothing of the adaptive significance of the behaviour and morphology of most tropical plants, (... nor of ...) the population structure of each species."

Table 1. Major tropical vegetation types replaced by plantations.

Tropical formation	Climate	Elevation	Regeneration system*	Some major genera planted
Lowland evergreen rainforest	Ever-wet	0-1200 m	1, 2, 3, (4)	Meliaceae Aucoumea Terminalia Chlorophora Nauclea
Semi-evergreen rainforest	Seasonally dry	0-1200 m	1, 2, 3, 4, 5	Tarrietta Tripluchiton
Monsoon forest	Seasonally dry	0-2000 m	2, 3, 4, 5	Tectona, Gmelina Cedrela, Cordia Anthocephalus Eucalyptus, Pinus
Woodland	Seasonally dry			Acacia, Prosopis
Wooded grassland	to very wet	0-2500 m	(4), 5, 7	Azadirachta
Grassland	Seasonally dry	1200-3000 m	6, 7	Pinus, Cupressus

* Regeneration systems: 1. Natural: polycyclic felling systems
 2. " uniform shelterwood systems
 3. Artificial, line and group planting systems
 4. " taungya, agri-silvicultural systems
 5. " planting following clearing and burning
 6. " direct planting
 7. Intensive cultivation with planting

The value of the Man and Biosphere (MAB) project #1 in rectifying this imbalance should not be underestimated, but there is an urgent need for many more field studies by forest researchers in the rainforest zone. Carefully designed experiments that attempt to answer the questions with which we are here concerned need not be sophisticated or costly but do require the active participation of field rather than laboratory biologists.

Among the most urgent questions this paper was invited to answer are:

1. what are the genetic, physical and biological effects of replacing complex-structured forests by even-aged plantations;
2. what are the long-term site demands of industrial wood production and can they be met;
3. is the natural forest performing an essential function by protecting soil, water and microclimate that is endangered when forest is replaced by plantations?

These questions have been frequently discussed and important reviews, to which this paper owes much, have been prepared recently. Whitmore (1975) and Ashton & Brunig (1975) discuss large and small scale variation within tropical lowland forests in relation to climate, soils, topography, altitude and regeneration patterns. They find that large scale differences in structure and floristic composition between spatially separated soil types or climatic zones are well-known and documented but knowledge of the causes of small-scale variation, on which good silvicultural treatment must depend, and by extension, the effects of substitution by plantations predicted, is inadequate. Synnott (1975) considers the physical, environmental and biological effects of logging and silvicultural operations in tropical, moist forests. He concludes that due to lack of quantitative information on floristic changes, growth processes and soil dynamics induced by forestry operations, "major mistakes will continue to be made both in forest management and in conversion of forests to other forms of land use".

The effects of interference by man with the tropical moist forest are also discussed by Brunig et al. (1975) and Brunig (1977). The former paper includes references to the few studies on litter breakdown, nutrient cycling, physical properties of the soil and erosion when forest is cleared, burnt and replanted with exotic or other species not necessarily adapted to the site. These authors, as all ecologically-minded writers discussing the management of the rainforest, again emphasize "the uncertainty of success due to the yet largely unpredictable reactions of the sensitive tropical, moist forest ecosystem to interference by man ... which makes any long-term land-use development project economically extremely risky. ... To reduce this risk ... very

much more knowledge on the ecology of the tropical moist forest is needed".

The considerable data on biomass and nutrient content of forest communities collected by Rodin & Bazilevich (1967) include relatively few results from studies in tropical rainforests and none on which direct comparisons can be made between the forest and plantation (see also Golley & Medina 1975). Golley et al. (1975), in a study prompted by the interoceanic canal project in eastern Panama, provide the most complete information available on mineral cycling in tropical, moist forests, while making comparisons with studies in other tropical areas. Poore (1976a) considers the broader implications of interference with moist forest ecosystems by reference to climatic, physical, genetic and social consequences. He concludes that the success of sustained agriculture and plantation forestry depends on careful assessment of land capability, choice of species, methods of clearing, erosion control and tending and a sustained application of skill and investment in fertilizing and pest control.

REGENERATION METHODS IN THE TROPICS

The major tropical formations which are being modified or replaced on a large scale either by agriculture, perennial crops or forest plantations are summarized in Table 2, together with an indication of the regeneration methods used for some economically important tree species. The abrupt changes between existing communities and the plantations that replace them, are often more striking than in those temperate areas where the primary forest had been modified by man millenia before modern silviculture was practised.

Rainforest replacement

Within less than a century almost all the rainforest of Nigeria has been selectively logged. The intensity of logging has increased at a rapid rate in recent years. Then, because the logged forest with 300 or more species no longer contained enough trees of commercial value, extensive areas were cleared and burnt and replaced by plantations of teak, Gmelina arborea and, on a smaller scale, indigenous 'pioneer' hardwoods e.g. Triplochiton scleroxylon, Terminalia superba and ivorensis, and Nauclea diderrichii. A rich, multi-species forest ecosystem, the result of millions of years of evolution has been suddenly destroyed and the dynamic process of regeneration and adaptation to catastrophic events or climatic change halted. Does this matter? To what extent can or should the plantations reproduce these processes? Is it possible to convert existing forest into high yielding stands without this abrupt alteration? Can artificially created forests be managed so that they not only produce a high sustained yield of products needed by society but also protect the soil and

maintain satisfactory water relations within the ecosystem? Such questions as these can only be answered on the basis of a better understanding of the ecology of the natural and artificial systems. An indication of some of the effects of rainforest modification or replacement is given in Table 2. Exploitation, conversion, replacement or destruction of tropical rainforests is going on apace. It cannot be delayed on the grounds that we do not yet understand its processes fully. We can apply certain principles provided we are sure that these 'principles' have not been based solely on studies in the mid-latitudes (Poore 1976b). Methods of enrichment and improvement of the African rainforests have been reviewed by Catinot (1965) and an account of methods of conversion to plantations by artificial methods is given by Lamb (1967).

More often than not, silvicultural treatments, aimed at modifying but not destroying the rainforest structure, are widely believed to have failed to increase yields sufficiently to justify their cost. Low cost systems with natural regeneration and little silvicultural treatment may produce an adequate return on expenditure, but low wood yields per hectare; more expensive systems with natural regeneration and much treatment frequently increase growth rates and may increase yields of certain categories of trees, but they may not be economic and their use is widely challenged for many reasons. More intensive systems that do not, however, involve the complete destruction of all the mixed forest vegetation, such as line and group planting can be highly productive and show a good return on investment, especially when the standing timber in the pre-existing forest is fully utilized. Examples of successful enrichment plantations are to be found in Ivory Coast with *Terminalia*, in the Gabon with *Aucoumea* and in Uganda with *Maesopsis* (Synnott 1977).

Where the demand for wood products is becoming acute, it is for replacement of the natural forest by intensive plantation. Lowe (quoted by Synnott & Kemp 1976) calculates that in Nigeria it will be necessary to convert the whole forest estate, of which 20,000 sq.km are in the forest zone, the balance being savanna woodland, to intensive production within fifty years. The potential yields from treated forest are not considered high enough to provide for expected demand. Conversion will be mainly to plantations, sometimes by agri-silvicultural methods and less frequently by enrichment planting. However, problems of supervising agri-silvicultural schemes mean that intensive planting under full control of the forest authority following clearfelling has greater likelihood of success in practice.

Recent studies in Nigeria present a case for second thoughts on dismissing entirely silvicultural management of natural forest for sustained yield production (Kio 1978). Leslie (1976) discusses the issues involved in increasing

Table 2. Some effects of rainforest regeneration processes.

Agency	Scale of clearing	E f f e c t o n				Productivity
		Species composition	Soil properties Physical	Soil properties Chemical	Stand structure	
<u>Natural:</u>						
Death of large trees	Small	Small random variation; negligible over large areas	None		Unchanged multi-layered	Low
Catastrophic (cyclones, hurricanes, etc.)	Large	Moderate - large	Negligible - unless associated with erosion		Variable - maybe large	Increased
<u>Artificial:</u>						
Selective cutting	Small	Small bias to less desirable economic trees	Negligible		Multi-layered uniform mosaic	Low - medium
Shelterwood silviculture	Small - large	Small to moderate; bias to desirable economic trees	Negligible		Negligible	Low - medium
Clearfelling and replanting	(Medium) - large	Extreme reduction in floristic diversity	Significant deterioration: in transition over rotation period	periods on poor soils	Single-storied	Increased - at least in short term
Clearfelling and abandonment	(Medium)	Extreme: change in species composition	May be considerable: depends on scale	especially if annual cropping is interposed between felling and abandonment	Destroyed	Nil

production by management of the natural forest rather than its replacement.

Afforestation of montane grasslands

The large scale plantations of conifers on grasslands and open woodlands in tropical and subtropical highlands appear to have many similarities with temperate afforestation projects. The origin and persistence of the disclimax grassland or moorland are explained by fire rather than impeded drainage, and the length of the growing season is limited by a dry season rather than by low temperatures, except at higher altitudes. Techniques of management are not dissimilar and productivity, despite some striking exceptions on small areas, is not very much greater, even though rotations are usually shorter.

A typical example is the Viphya Plateau in Malawi, latitude 12°S, altitude 1200-3000 m, rainfall 900-1300 mm. 40,000 ha of grassland and wooded grassland have been planted with pines for supplying the raw material for a proposed 150,000 ton/year pulpmill. Yield of pulpwood is estimated as 17.5 cu.m./ha/yr on a sixteen year rotation. The productivity of these plantations compared with that of the fire-climax vegetation they replace is greatly increased. Previous yields were confined to casual cutting of fuelwood in the woodland areas providing a maximum of 2-3 cu.m/ha/yr. The grasslands provided little more than grazing for a sparse population of wild game. The use of such areas for raising domestic cattle or sheep might provide similar increases in productivity under alternative land use. This invites comparisons relevant to the planners but outside the scope of this discussion.

Afforestation in arid zones

High temperatures and low humidity restrict the choice of species and necessitate specialized establishment methods in the arid zones. Comparisons may be made with plantations on shifting sands, such as Culbin and the Landes. The social and technical problems of large scale plantations in arid zones are perhaps greater than the ecological ones. Once again, to keep the discussion within bounds, we must be content merely to recognize the existence of a different set of questions.

PRODUCTIVITY UNDER NATURAL AND ARTIFICIAL SILVICULTURE Predictive models

Predictive productivity models, using the relation between growth and a component of water balance such as actual evapotranspiration can predict net primary production (NPP) for geographical regions (Sharpe in Lieth & Whittaker 1975). Such models are an acknowledgement of the fact that plants tend to grow faster at higher temperatures and light intensities in the presence of adequate moisture supplies and to some extent quantify observed yield differences between major tropical ecosystems. Provided growth is predicted from

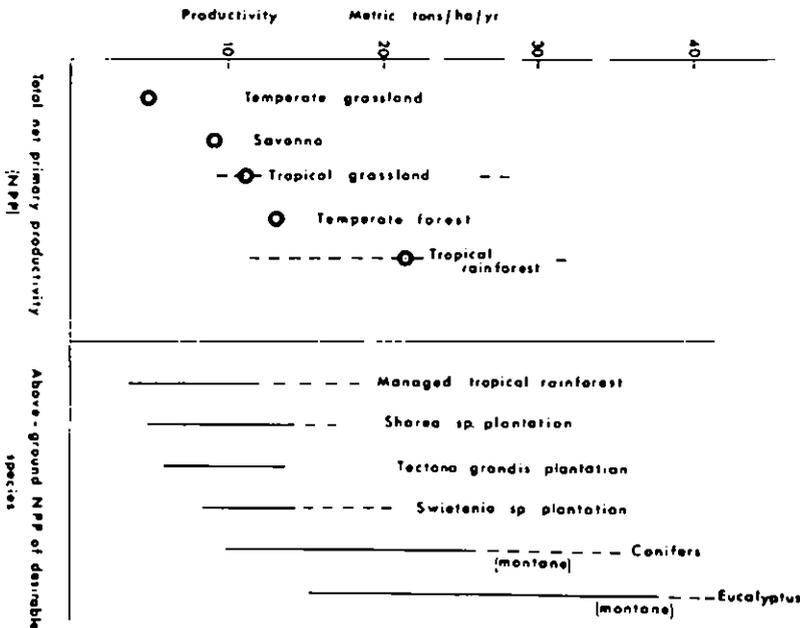


Fig. 1. Estimated productivity in some natural and artificial ecosystems (after Colley et al. 1975, Dawkins 1963, Whitmore 1975).

estimates of potential evapotranspiration, taking into account periods of water deficit, and provided such calculations are based on actual measurements on site of temperature, rainfall and moisture capacity of the soil, such predictions can be of value in making regional comparisons of potential forest yield.

Obviously, to explain growth variation within a region, we need to quantify other factors, not integrated by even such a complex parameter as actual evapotranspiration. For useful comparisons between natural forest and plantations to be made we shall briefly consider some effects of structure, succession and soil on productivity. The range of dry matter productivity illustrated in Figure 1 draws attention to the striking difference between NPP and useful wood yields and between wood yields from natural rainforest and plantations. Where the complex-structured rainforest has a mean annual NPP of over 22 tons/ha/yr (Murphy in Lieth & Whittaker 1975), the

wood yield of silviculturally treated forest on better sites has been estimated as rarely more than 8 tons/ha/yr, ranging from 3.6 to 12 (Dawkins 1963), yet plantations of even-aged exotics may produce up to 40 tons/ha/yr or more, when planted at medium altitudes on good sites. These are maximum yields estimated on small plots. Average production over large management areas tends to be much less. The yields for exotic species are usually based on data from first rotation stands with no certainty of long-term sustained yields at these levels (see Boardman, this volume).

The effect of structure and succession

It has been estimated that it would take from 200-400 years after clearing, for a lowland, evergreen, tropical rainforest to reconstruct the multi-layered and species-heterogeneous structure of the primary forest (Jones 1955; Golley et al. 1975). Brunig (1973) has shown how variation in structure is related to successional development and site differences, suggesting how structure can be interpreted by its physiological and ecological function. More research is needed on the function of structure as a factor in the stability of the rainforest ecosystem. The evolution of a complex-structured community can be seen as the result of selection of groups of genotypes developing different survival strategies. The pioneers rapidly colonize clearings, may have short life cycles and grow to the largest size in the shortest time to reproduce competitively. Shadebearers are adapted to survival and regeneration under canopy but at the expense of making sub-optimum use of incoming energy (Loucks 1970), though the evidence that there are any significant differences in carbon utilization between pioneers and shadebearers is slight (Whitmore 1975).

Neither strategy necessarily optimizes wood production. Wood merely provides the mechanical structure necessary for the support of a crown that must extend towards the light, ahead of competition, for successful reproduction and survival of individuals of some species, while other species are equipped to complete their life cycles within the lower storeys and never reach the full light. The rate of individual tree growth and physical characteristics of the wood produced are related to the ecological characteristics of the species and seral stage of the community in which it grows but the extreme cases of pioneers and shadebearers typify patterns of growth found also in plantations (Fig. 2).

Replacement of the multi-layered forest by a uniform population of light demanding individuals makes sense in terms of productivity and economics, as a similar volume of timber can be grown and harvested in a shorter period. Felling an even-aged plantation at the age when maximum mean annual increment is attained, is analogous to harvesting a natural system at the late pioneer stage of a succession when net

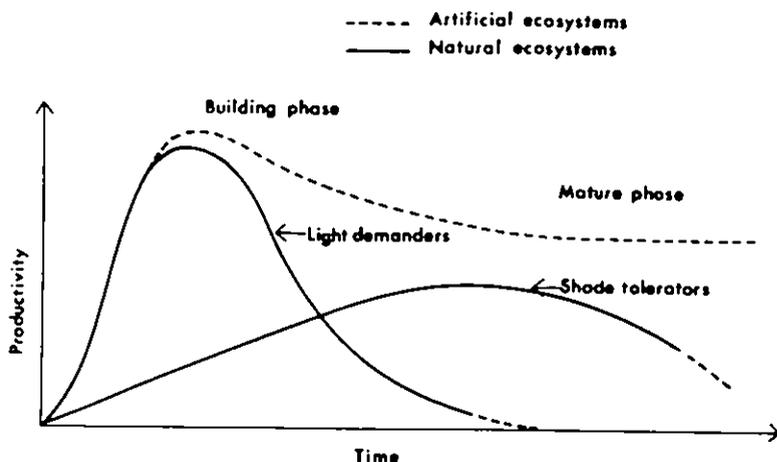


Fig. 2. Idealized diagram of the relation between productivity and successional stages in natural and artificial ecosystems.

primary production, NPP, is at a maximum (Kira & Shidei 1967). By contrast NPP in the climax forest may be entirely utilized in the maintenance of a dynamic equilibrium with a net yield of zero.

The losses incurred by replacement with a simpler artificial system are less easy to assess. The loss of 'information' in the form of genetic diversity, if the process of forest destruction continues, must be a cause of concern. Is it wise to rely on production systems that have lost the power of self-regulation and regeneration?

Soils factors

Productivity estimates based on climatic models indicate the potential growth for a region, and assume adequate supplies of available moisture and nutrients during the growing season; this applies as much to temperate as tropical areas but failure to account for these factors in productivity estimates in the tropics is likely to be more important. Soil processes, for example, differ in the tropics to the extent that higher temperatures and intensity of rainfall increase the rate and depth of leaching and weathering. Associated with rocks of older age, such developments have resulted in extensive areas of forest soils of great depth but low mineral content within the rooting zone. In the ever-wet zones,

biomass production is closely dependent on the amount of nutrients returning to the soil in litter. Stark (1972) has hypothesized that there are special mechanisms for the utilization of minerals from litter with possibly direct transfer to root systems with mycorrhizas playing an important part. Also, the role of nitrogenous plants is probably more significant in the rainforest than in many temperate forest ecosystems. Some of the more extensive areas of existing rainforest occur on poor soils, yet carry as much biomass as any vegetation type. Data from Rodin & Bazilevich (1967), summarized by Colley (1975), show tropical rainforest with 564 tons/ha as having two and a half times the vegetative biomass of temperate deciduous forest and four times that of northern coniferous forest. The importance of the closed nutrient cycle is well-known and frequently quoted in accounts of humid tropical forests, yet just as frequently ignored by land use planners, although a full awareness of the consequences of forest destruction is highly relevant when selecting soil types on which to develop plantation forestry. Hall (1977) has indicated the importance of soil types in the Nigerian rainforest, for explaining part of the floristic variation and for selecting sites for indigenous and exotic tree plantations (see also Ashton & Brunig 1975; Whitmore 1975).

The problem of the scale of interference

This problem arises in rainforest management because silvicultural treatments, including logging, which are severe enough to result in useful increases in growth rates and yields of favoured species, may be so severe that the composition and structure of the forest are drastically altered and the habitat endangered. The risk depends very much on how much of the forest is commercially valuable and hence on the flexibility of management.

There appears to be an analogy between the large scale destruction of rainforest as a result of cyclones and the destruction of extensive areas of temperate hardwood forests in North America by fire. The commercially most valuable forests in the Solomon Islands are believed to be old seral stages resulting from cyclones up to 100 years previously, composed of long-lived pioneer species now being line-planted. The Nigerian rainforest is probably a late seral stage resulting from wide-scale destruction 400 or so years ago and certain Caribbean forests owe their species composition to past cyclones (T.C. Whitmore pers. comm.). The role of fire in maintaining a proportion of a forest area in a youthful pioneer stage and the dangers to the ecosystem of fire control have been convincingly described by Loucks (1970) for Wisconsin hardwood forests. Where the destroyed areas are of such a pattern as to allow rapid colonization by pioneer species and re-establishment of soil cover, the ecosystem, far from being destroyed, may actually be rejuvenated. Where the

scale and pattern is wrong and ground cover is not re-established, or where climbers and undesirable secondary weed species prevent the germination of pioneer forest species, a particular ecosystem may be irreversibly changed and this can result in site deterioration. This may occur when the forest is cleared and burnt, especially where heavy machinery is used on fragile soils in high rainfall areas. The scale and pattern of clearing in such cases will be important. Replacement of rainforest by even-aged plantations in other circumstances may, however, not be such an unnatural process as is sometimes supposed. However, we believe there are dangers here and many foresters and ecologists have given warnings of the risks involved (Brunig 1974; Gomez-Pompa & Wiechers 1976; Poore 1976b; Richardson 1977).

Such views are a challenge to research and management; a challenge to reach an understanding of the functioning of tropical ecosystems and the ecology of tropical forest plants, but also, before many of the answers to further research are available, to apply management methods that, without prejudicing economic objectives, do not violate basic ecological principles.

One approach is to leave ecologically viable blocks of natural vegetation between areas cleared for plantations. At La Sabana in the State of Veracruz, Mexico, natural forest left in valleys during clearing for pine plantations comprise 40 per cent of the total area of nearly 8000 ha. On the Vipha Plateau in Malawi pioneer species of relict montane rainforest patches tend to regenerate in the grassland at their edges when protected from fire. Such protection is provided when small forest patches with fringing grassland are included within plantation areas. On the other hand, 'viable', i.e. self-regulating, balanced and reproduceable, areas of rainforest may have to be of considerable size, probably at least 10 sq.km and urgent research into acceptable patterns of rainforest development is needed while some options are still open. It is dangerous to plant extensive areas of single indigenous or exotic species before some understanding of their suitability for the site is obtained. Failure of early plantations of Meliaceae, including species of Cedrela and Khaya, in many countries of tropical America and Africa provide examples of misdirected silvicultural practices. More extensive were the results of shoot borer attack on Hevea brasiliensis in Surinam when grown in pure plantations although both host and insect were endemic in the natural mixed forest (Gonggry 1948).

The importance of organic matter

The important role of organic matter in tropical soils under forest is not confined to the ever-wet zones. An example may be given from the monsoon forests of southern India. Jose & Koshy (1972) correlated the soil organic matter content at

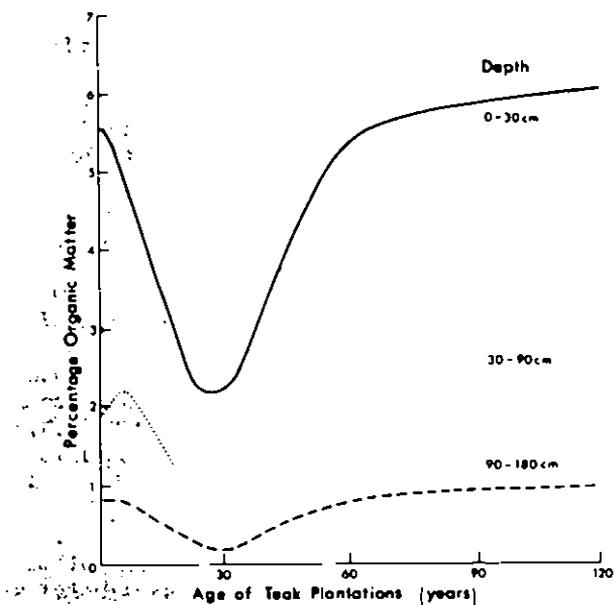


Fig. 3. Changes in organic matter content of soils under natural forest and teak plantations.

Nilambur (latitude 11°N , altitude 200 m, mean annual rainfall 2500 mm, mainly falling in June and July) under teak forest and under teak plantations of different ages (Fig. 3). A distinct surface horizon 10 cm deep, rich in organic matter with a good crumb structure as found under the natural forest, was seen only in the oldest teak plot, planted in 1846.

Bunvong, Thaiutsa et al. (1976) studied the soil of forest in Thailand, treated by three silvicultural systems: clearfelling, strip-felling and selection cutting. Organic matter showed a short-lived increase immediately following clearfelling, while dispersion ratios - a measure of structure stability obtained by wet sieving - increased from 21 to 34 per cent and porosity decreased from ca. 40 to 31 per cent. The dangers of soil erosion under pure teak plantations have long been recognized and underplanting and crop rotation suggested as remedies. The earliest teak plantations which are probably the earliest plantations of tropical trees, date from the beginning of the 19th century. At Nilambur, well over 100 years passed before the soil under plantations approached that under undisturbed forest. However, when timber was grown on the site under good management and on an 80-year rotation,

danger of site deterioration was slight. We lack data on the effect of short rotation silviculture of Gmelina arborea on soils and nutrient cycling but it is likely to be less favourable under the same conditions, owing to the almost complete suppression of an understorey and ground flora, and a succession of 10-year rotations will require careful monitoring.

Nutrient cycling

Lundgren (1978) has studied the nutrient cycling and soil physical properties under Pinus patula plantations at an altitude of 1800 m in Tanzania, with the object of determining the effect of a monoculture on site conditions. After clearing the natural forest and during the first fifteen years under plantation, organic matter in the soil declined and bulk density increased. The effect on potassium was striking: the total amount of potassium removed in logs of thinnings and at clearfelling was approximately 700 kg/ha - only slightly less than the total reserve of potassium in the top 50 cm of soil at the time of clearfelling. This was on a cool and comparatively dry site where leaching and erosion may be expected to be less than in lowland plantations. The soils were humic ferrosols of the latosolic group. The effects are very different on the more fertile andosols derived from volcanic ash, on which many coniferous plantations are established in East Africa, and which are well supplied with available mineral nutrients (Lundgren 1978).

Golley et al. (1975) found that calcium and potassium were the most abundant mineral elements in the vegetation of the natural lowland forest of East Panama but, whilst phosphorus occurred in relatively small amounts in the soil, calcium was relatively abundant. These elements are considered most likely to be in short supply following conversion to plantations. Both have a high rate of biological cycling, i.e. between soil and vegetation and are in balance in the forest ecosystem. Biological cycling is 17-21 times greater than chemical cycling, i.e. between soil and streams. After interference the amounts available to the new crop may become critical (see also Malkonen 1976), because of the inability of the geochemical cycling process to replenish the biological cycle at a fast enough rate. To rely on artificial fertilizing to replace the lost nutrients may be too simple a solution, not only because of the costs involved when natural supplies are not readily available, but also because of the high rates of leaching in tropical soils and risks to the functioning of nitrogenous bacteria and mycorrhizae that play a more important role in tropical than in temperate ecosystems.

Not all tropical soils have low fertility. Replacement of natural forest on soils with high cation exchange capacities by plantations under efficient management, need cause no significant loss of nutrients during the sensitive transition

period. Plantations on ferruginous soils in areas of moderate rainfall in Nigeria would be unlikely to cause soil degradation (Hall 1977), though those on ferralitic soils would carry greater risks. We are thus reminded of the importance of site, and especially soil studies in the preparation of planting plans and the importance of basic ecological studies before large scale conversion of forest is permitted. Studies on changes in soil properties under successive rotations of plantations, especially when related to dry matter yield, such as those of Evans (1975), are essential as a basis for the long-term planning of large-scale plantation schemes.

CONCLUSIONS

It has not been possible to answer the questions this paper was invited to discuss. This is seen to be inevitable when the state of ecological knowledge of tropical ecosystems is reviewed and one becomes aware of the limited number of completed detailed studies on the effects of changes in land use on tropical forest ecosystems. The scale of the problem becomes apparent when the range of variation in tropical habitats is appreciated as being far greater than that found in the mid-latitudes, where so much more intensive, ecological work has been done. This is the situation that the Man and Biosphere project #1 is designed to remedy, but much more than is already planned needs to be done. Subjects suitable for master's and doctor's degrees should be proposed that would challenge students from tropical countries to direct research effort to the fundamental problems of sustained yield of natural resources, without which long-term planning is an illusion.

Such research would not require sophisticated equipment but could make significant contributions to ordered development in tropical countries out of all proportion to its cost. Many thesis topics being submitted today appear to have prestige value to the student or his supervisor, but have little relevance to science and his country. Subjects for ecological research that would combine prestige and relevance for students of physical as well as biological sciences are surely not hard to define (Brunig 1974; Farnworth & Colley 1974; Janzen 1975).

Growth models of even-aged plantations based on observed growth in permanent sample plots and current growing stock inventories have been developed for use in management control systems (e.g. Alder 1977), but relations between growth and environmental factors are less well understood. Physical and biological studies on the dynamics of artificial forest ecosystems, especially over successive rotation, are needed. The establishment of permanent sample plots, not only for continuous inventory but as microsites for ecological studies,

provides the most reliable data for studying the dynamics of plantation growth. Without such data the questions before us will be answered only when evidence of site degradation has progressed so far as to be causing serious loss in yields or worse. In comparison to the cost of restoring site fertility in such cases, the cost of maintaining a network of growth monitoring plots as an insurance policy is small.

In the light of current knowledge of the effects of interference on a large scale on the rainforest, it is possible to draw up certain guidelines for increasing productivity, while minimizing the risk of site degradation.

- (1) On fragile sites maintain a mosaic of natural forest to ensure the potential for regeneration of forest conditions.
- (2) When evaluating the feasibility of a plantation scheme include the cost of replacing the nutrients removed in harvesting, leaching and burning, and the cost of protection against pests and diseases.
- (3) Convert forest to plantation with minimum habitat disturbance and soil exposure; the transition period is the period of greatest risk.
- (4) Conserve significant areas of natural forest for conservation of genetic variability of flora and fauna within each region.

Forest management, like politics, is the art of the possible. Social, political and economic pressures on land development must be balanced by ecological realism to alleviate the effects of misuse of natural resources.

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REFERENCES

- Alder, D.(1977). A growth and management model for coniferous plantations in East Africa. D.Phil. Thesis, University of Oxford.
- Ashton, P. & Brunig, E.F.(1975). The variation of tropical moist forest in relation to environmental factors and its relevance to land-use planning. "Tropical moist forest". Mitteilungen der Bundesforschungsanstalt für Forst- und Holzwirtschaft, Reinbek bei Hamburg, #109, pp.59-86.
- Baur, G.N.(1964). The ecological basis of rainforest management. Ministry for Conservation, Sydney, New South Wales.
- Brunig, E.F.(1973). Species richness and stand diversity in relation to site and succession of forests in Sarawak and Brunei. *Amazoniana*, 4, 293-320.

- Brunig, E.F. (1974). Ökosysteme in den Tropen. Umschau, 13, 405-410.
- Brunig, E.F. (1977). The tropical rain forest - a wasted asset or an essential biospheric resource. *Ambio*, 6, 187-191.
- Brunig, E.F., Buch, M. von, Heuveldop, J. & Panzer, K.F. (1975). Stratification of the tropical moist forest for land-use planning. "Tropical moist forest". Mitteilungen der Bundesforschungsanstalt für Forst- und Holzwirtschaft, Reinbek bei Hamburg #109, pp.1-58.
- Bunvong Thaitua, Wisut Suwannapinunt, Wasan Kaitpraneet & Somsak Sukurung (1976). Changes in soil properties in teak forest under different silvicultural systems. Forestry Research Bulletin #39. Kesetsart University, Thailand.
- Catinot, R. (1965). Silviculture tropicale en forêt dense Africaine. Bois et Forêts des tropiques, ##100-104.
- Dawkins, H.C. (1963). The productivity of tropical high forest trees and their reaction to controllable environment. D.Phil. Thesis, University of Oxford.
- Evans, J. (1975). Two rotations of Pinus patula in the Usutu forests, Swaziland. Commonwealth Forestry Review, 54, 69-81.
- Farnworth, G. & Golley, F.B. (Eds) (1974). Fragile ecosystems: evaluation of research and applications in the Neotropics. Springer Verlag, Berlin, Heidelberg, New York.
- Golley, F.B. & Medina, E. (Eds) (1975). Tropical ecological systems. Springer Verlag, Berlin, Heidelberg and New York.
- Golley, F.B., McGinnis, J.T., Clements, R.G., Child, G.I. & Duever, M.J. (1975). Mineral cycling in the tropical moist forest ecosystem. University of Georgia Press, Athens, Georgia.
- Gomez-Pompa, A. & Wiechers, B.L. (1976). Regeneracion de los ecosistemas tropicales y subtropicales. "Investigaciones sobre la Regeneracion de Selvas altas en Veracruz, Mexico." Comp. Editorial Continentalia, Mexico.
- Gonggry, J.W. (1948). Quelques remarques sur l'emploi d'essences exotiques et indigenes dans les silviculture tropicale. Bois et forets des tropiques, 7, 251-257.
- Hall, John B. (1977). Forest types in Nigeria: an analysis of pre-exploitation forest enumeration data. Journal of Ecology, 65, 187-199.
- Holling, C.S. (1973). Resilience and stability of ecological systems. Annual Review of Ecology and Systematics, 4, 1-25.
- Janzen, D.H. (1975). Ecology of plants in the tropics. Institute of Biology, Studies in Biology #58. Arnold, London.
- Jones, E.W. (1955). Ecological studies on the rainforest of southern Nigeria. IV. The plateau forest of the Okomu forest reserve. Journal of Ecology, 43, 564-594; 44,

83-117.

- Jose, A.I. & Koshy, M.M. (1972). A study of the morphological, physical and chemical characteristics of soils as influenced by teak vegetation. *Indian Forester*, 98, 338-348.
- Kio, P.R. (1978). Stand development in naturally regenerated forest in southwestern Nigeria. Ph.D. Thesis, Ibadan.
- Kira, T. & Shidei, T. (1967). Primary production and turnover of organic matter in different forest systems of the western Pacific. *Japanese Journal of Ecology*, 17, 70-87.
- Lamb, A.F.A. (1967). Artificial regeneration within humid lowland tropical forest. F.A.O. Commission on Forest Development in the Tropics. Report of 1st session. F.A.O., Rome. pp.73-86.
- Leslie, A.J. (1976). A note on the economics of the management of the tropical moist forests. F.A.O. Commission on Forest Development in the Tropics. Report of 4th session. F.A.O., Rome. 7 pp.
- Lieth, H. & Whittaker, R.H. (Eds) (1975). Primary productivity of the biosphere. Springer Verlag, Berlin, Heidelberg and New York.
- Loucks, O.L. (1970). Evolution of diversity, efficiency and community stability. *American Zoologist*, 10, 17-25.
- Lundgren, B. (1978). Soil conditions and nutrient cycling under natural and plantation forests in Tanzanian Highlands. Reports in Forest Ecology and Forest Soils, #31. Swedish University of Agricultural Sciences, Uppsala.
- Malkonen, E. (1976). The effect of fuller biomass harvesting on soil fertility. Symposium on Harvesting of a larger part of the forest biomass. Volume 1. F.A.O./E.C.E./I.L.O., Geneva.
- Poore, D. (1976a). Ecological guidelines for development in tropical rainforests. International Union for the Conservation of Nature, Morges, Switzerland.
- Poore, D. (1976b). The values of the tropical moist forest ecosystems and the environmental consequences of their removal. F.A.O. Commission on forest development in the tropics. Report of 4th session. F.A.O., Rome. 39 pp.
- Richards, P.W. (1952). The tropical rainforest, an ecological study. Cambridge University Press.
- Richardson, D. (1977). A Faustian dilemma. *Unasylva*, 29, 12-14.
- Rodin, L.E. & Bazilevich, N.I. (1967). Production and mineral cycling in terrestrial vegetation. Oliver and Boyd, Edinburgh.
- Stark, N. (1972). Nutrient cycling pathways and litter fungi. *Bioscience*, 22, 355-360.
- Synnott, T.J. (1975). The impact, short and long-term of silvicultural, logging and other operations on tropical moist forest. Commonwealth Forestry Institute, Oxford.
- Synnott, T.J. (1977). Final report on tropical high forest

- management project. Commonwealth Forestry Institute, Oxford.
- Synnott, T.J. & Kemp, R.H. (1976). The relative merits of natural regeneration, enrichment planting and conversion planting in tropical moist forests, including agrisilvicultural techniques. F.A.O. Commission on forest development in the tropics. Report of 4th session. F.A.O., Rome. 12 pp.
- Whitmore, T.C. (1975). Tropical rainforests of the Far East. Clarendon Press, Oxford.

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FOREST PRACTICES AND RESEARCH REQUIREMENTS -
TODAY AND IN THE FUTURE

Chairman: J.D. Matthews

The way ahead in research and
practice

- J.D. Matthews, F.T. Last
and D.T. Seal



THE WAY AHEAD IN RESEARCH AND PRACTICE.

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SUMMARY

Never doubting that timber production is, and will remain, the prime purpose of plantation forests, it was accepted that yields assessed in terms of quality and quantity must be related to, and be compatible with, the effective use and maintenance of soil and water resources, the effective capture and exploitation of solar energy, the conservation of wildlife, the prevention of environmental impairment and the provision of employment. Because of their diversity and complexity, the concurrent consideration of these different criteria necessitates a systems approach.

In seeking improvement, the meeting was concerned with design, as related to the architecture of individual trees before canopy closure, the canopy structure of tree stands subject to between-plant competition and the mosaics of large blocks of trees of different ages, the latter being important not only for harvesting but also for wildlife, notably the control of deer. With these considerations in mind, attempts were made to define ideotypes, including trees with large harvest indices, i.e. harvestable yield as a proportion of total biomass. When doing this, it was agreed that the conservation of genetic resources was of prime importance to ensure the continuing availability of material for the production of improved trees, whether propagated vegetatively or grown from seeds from controlled crosses.

The continuing appropriateness of existing methods of land classification was questioned.

Those based on past performance are likely to underestimate future yields, whereas others based on site characteristics are better indicators of the need for site preparation than of potential yields. Other methods are needed, recognizing that (i) wind is a major determinant of growth and (ii) crop improvement is an iterative process with the introduction of new variants increasingly warranting a reconsideration of silvicultural practices.

Tree nutrition is of fundamental importance. In the future, nutrient turnover should be budgeted, interrelating the application of artificial fertilizers with nutrients released during litter decomposition. The appreciable benefits of mycorrhiza were stressed in relation to events during establishment rather than in the longer term. It was foreseen that increasing amounts of nutrients might be applied in the future. But, because the production of artificial fertilizers uses appreciable amounts of energy, the need to quantify the role of nitrogen-fixing microbes and others involved in mineralization was stressed.

Plantations of different ages provide different habitats for pests, both vertebrate and invertebrate, pathogens, and also for desirable wildlife, both plants and animals. In studying the population dynamics of these plants and animals, it was stressed that their incidence should be judged against indices of damage, with the recognition of acceptable thresholds.

RÉSUMÉ

On sait que la production du bois est, et restera, la raison principale des plantations forestières; il est admis que la production définie en termes quantitatifs et qualitatifs, doit être reliée, et doit être compatible, avec une utilisation efficace des ressources du sol et des eaux, la capture et l'exploitation de l'énergie solaire, la protection de la faune sauvage et de l'environnement physique et doit constituer une source d'emplois. De par leur complexité et leur diversité ces différents critères demandent une approche systématique du sujet.

Le concept d'amélioration a été un des thèmes-clés de ce congrès, surtout en ce qui

concerne l'architecture; celle des arbres avant la fermeture du couvert, celle de la structure du couvert des peuplements sujets à une compétition entre individus, celles des mosaïques formées par de larges groupements d'arbres d'âge divers (celle-ci étant importante non seulement pour la récolte, mais aussi pour la faune sauvage et notamment le contrôle du cerf). En tenant compte de ces considérations, nous avons été tentés de définir des idéotypes, comprenant des arbres à indices de récolte importants, c'est à dire un rendement récoltable proportionnel à la biomasse totale. De cette façon il apparaît évident que la conservation des ressources génétiques est d'une importance primordiale pour assurer la disponibilité continue des matériaux producteur d'arbres meilleurs, qu'ils soient générés végétativement ou qu'on ait utilisé des semis provenant de croisements contrôlés.

Nous avons discuté les méthodes existantes et prévalantes de classifications des stations: celles qui se basent sur le rendement futur, celles basées sur la production antérieure sous-estimeront probablement les productions futures, tandis que d'autres basées sur des caractéristiques de la station conviennent d'avantage à indiquer les améliorations de la station que sa production potentielle. Il est nécessaire d'utiliser d'autres méthodes en tenant compte du fait (i) que le vent a une influence capitale sur la croissance et (ii) que l'amélioration de la plantation est un procédé itératif: plus on introduit de variantes nouvelles, plus on a besoin de remettre en question les techniques sylvicoles. La nutrition de l'arbre est d'une importance primordiale. A l'avenir, il faudra calculer exactement l'apport total d'éléments nutritifs, en essayant de relier l'introduction d'engrais artificiels avec les éléments nutritifs libérés pendant la décomposition de la litière. Les avantages appréciables des mycorrhizes ont été signalés et soulignés pendant la période de création plutôt qu'à long terme. Nous prévoyons l'utilisation de plus en plus étendue d'engrais à l'avenir. Malgré cela, à cause de l'énergie considérable utilisée par leur production, il faut essayer de quantifier le rôle des microbes

fixateurs d'azote et d'autres, présents au cours de la minéralisation.

Les plantations d'âge mûr sont la demeure d'une série de parasites, vertébrés ou invertébrés, de pathogènes et aussi d'une faune et d'une flore sauvages désirables. Nous soulignons que toute étude de la dynamique de ces populations animales et végétales devra être mesurée et pesée contre les dégâts possibles, dans des limites acceptables.

ZUSAMMENFASSUNG

Da man nie in Frage stellte, dass die Holzproduktion der Hauptzweck von Forstpflanzungen ist und bleibt, wurde akzeptiert, dass der qualitative und quantitative Ertrag von folgenden Parametern abhängt, bzw. sich mit ihnen vereinbaren lassen muss: Ausnutzung und Erhaltung der Bodenkraft und des Wasserpotentials, Ausnutzungsgrad der Sonnenenergie, Erhalt der Fauna, Verhütung von Umweltschäden und Schaffung von Arbeitsplätzen. Wegen der Unterschiedlichkeit und Komplexität der genannten Kriterien ist es nötig, sie systematisch zu untersuchen.

Auf der Suche nach Ansätzen zur Produktion besserer Genotypen beschäftigte sich die Tagung mit äusseren Baumerkmale einzelner Bäume vor Kronenschluss, mit dem Aufbau des Kronenbereiches in Abhängigkeit von der Wettbewerbssituation und mit der heterogenen Struktur grosser Komplexe verschiedenalter Bäume. Letztere sind nicht nur für die Ernte wichtig, sondern auch für das Tierleben, insbesondere für Rehwild. Aufgrund dieser Überlegungen versuchte man, ideale Bestandestypen unter Einbeziehung ertragreicher Baumarten zu definieren, wobei die verwertbaren Erträge proportional zur Gesamtbiomasse sein sollten. Dabei kam man zu der übereinstimmenden Auffassung, dass die Erhaltung genetischer Ressourcen von vorrangiger Bedeutung für die Sicherstellung der Produktion von genetisch 'besseren' Bäumen sei, die entweder vegetativ oder aus definiertem Saatgut hervorgehen können.

Es wurde gefragt, ob die bestehenden Methoden der Standortsklassifikation weiterhin angemessen seien. Diejenigen, die auf ertragsgeschichtlichen Daten basieren,

unterschätzen leicht künftige Erträge, während andere, die sich auf physische Standortseigenschaften stützen, zwar gute Indikatoren für notwendige Standortsvorbereitungen liefern, aber nur beschränkt Ertragsprognosen erlauben. Man braucht andere Methoden, da man erkannt hat, dass (i) Wind ein wichtiger Wachstumsfaktor ist, (ii) die Verbesserung der Samen ein fortlaufender Prozess ist und die Einführung neuer Varianten ein Überdenken forstwirtschaftlicher Praktiken zunehmend erforderlich macht.

Die Nährstoffversorgung der Bäume ist von grundlegender Bedeutung. In Zukunft sollte der Nährelementumsatz wirtschaftlich dahingehend überdacht werden, dass man die Anwendung von Mineraldüngern und die natürliche Nährelementfreisetzung durch Streuzersetzung sinnvoll kombiniert. Der beachtliche Nutzen von Mykorrhizen wurde mehr in bezug auf das Geschehen während der Pflanzung, und nicht so sehr unter langfristigem Aspekt betont. Man konnte davon ausgehen, dass in Zukunft zunehmende Mengen an Dünger verwendet wurden. Da jedoch deren Produktion beträchtliche Energiemengen verbraucht, gewinnt die mengenmäßige Erfassung stickstoffbindender und anderer mineralisierender Mikroben immer mehr an Bedeutung.

Alternde Pflanzungen bieten hintereinander verschiedene Habitats für Schädlinge und Krankheitserreger, aber auch für erwünschte Pflanzen und Tiere. Die Untersuchung von deren Populationsdynamik soll im Zusammenhang mit Schadensverzeichnissen erfolgen, wobei für die Praxis bestimmte Schwellenwerte erarbeitet werden müssen.

EPILOGUE

This meeting took place at a time when many pressures are forcing foresters to take stock of the circumstances in which they work. The world demand for timber and timber products is continually increasing yet the unremitting loss of natural forest is becoming recognized as unacceptable by an ever-increasing number of people. Without doubt the demand, if it is to be met, will only be satisfied by the large scale establishment of plantation forests, but this is not to minimize the contribution from natural forests managed for sustained yields.

Although the main purpose of even-aged plantations is to produce timber, their managers work and take decisions in complex circumstances. They are responsible for managing large tracts of land, the tree crops on those lands and the plants and animals dependent on the habitats so provided. They must protect water supplies, meet economic and social goals by producing timber in suitable quantities and qualities, and directly or indirectly provide employment often in remote rural areas. The concept of multiple use of forests is not new. What is new, is the increased interest in this concept taken by people living in towns and cities, and the increasing pressures that they apply, forcing foresters to re-assess their management objectives. As pressures to control the use of fossil fuels become stronger, so will the demand, already strong in some parts of the world, for plantations as renewable resources of fuel. Forest managers will also need to become accustomed to assessing costs, not only in monetary terms but also in terms of energy inputs and outputs, relating yields to energy used during silvicultural and harvesting operations.

The problems can be stated readily, but their solutions are more difficult necessitating a greater understanding of forest ecology. At some sessions, participants were concerned with applied aspects of silviculture, in others with fundamental ecology. Even-aged plantations are becoming increasingly productive with improved cultivation procedures, including soil drainage, the greater use of exotic species, the increasing availability of better cultivars with larger harvest indices; the chemical control of weeds after planting, the application of inorganic fertilizer, the improved control of damaging insects and fungi and less wasteful and more complete methods of harvesting. Moreover, the potential for further improvement appears great. However, if large yields of timber are to be sustained from even-aged plantations, silviculturists and ecologists must be able to identify and control processes that could damage their plantations and soils, and deleteriously affect non-damaging populations of wildlife, both plants and animals. Four aspects, of outstanding importance, were stressed:

- (a) the long-term effects on the ecological stability of even-aged plantations of selecting restricted numbers of productive species, provenances and cultivars, with the consequent narrowing of their genetic base;
- (b) the effects on tree growth of soil amelioration by drainage, cultivation and the application of fertilizers, the effects of even-aged plantations on the organic layers of soils and their combined influences on the prediction of tree growth by site indices;
- (c) the effects of afforestation on catchment water yields and
- (d) the need for more information about the ecology of

insects, birds and other animals, of microbes, including mycorrhizal associates, and plants, so that their effects, beneficial or damaging, can be more accurately predicted.

GENETIC BASIS OF EVEN-AGED PLANTATIONS

Throughout the world extensive even-aged plantations are formed with exotic species. The search for increased yields of timber and other forest products has progressed inexorably to the selection of those species that are easy to propagate, are suited to 'pure', even-aged plantations, can adapt to a wide range of climates and sites, are relatively free from damaging pests and pathogens, and produce above average yields of useful timber. As tree improvement programmes develop, some provenances are identified which give important improvements in quality and quantity of timber, with some selections being confined to one of a few individuals instead of populations. Species of Pinus, Picea, Larix, Betula, Eucalyptus, Cryptomeria, Tectona and many others are being subjected to selection that progressively narrows the genetic base of the stocks ultimately used for even-aged plantations. The process is well recognized, the benefits are great but experience in agriculture has amply demonstrated possible long-term hazards.

Although benefits are likely to accrue from the selection of progenies able to tolerate stresses attributable to severe cold, soil moisture deficits etc., larger yields are likely in most instances to be obtained sooner by selecting trees whose harvestable yields form increasing proportions of total biomass. Tree breeders and silviculturists must continually modify the characters of the ideal tree, or ideotype, to take account of the improved understanding of ways in which trees in plantations interrelate one to another at different stages of development; those that show promise before canopy closure may not continue to succeed afterwards. For the future, it is also desirable to know how genetically less heterogeneous stands of improved trees respond to severe competition for limited resources of water and nutrients as compared to their unimproved progenitors, remembering that sites, with improved preparation, will inevitably be less variable.

SITE CLASSIFICATION, SITE AMELIORATION AND NUTRIENT CYCLING.

Participants at the meeting recognized that site classification is an essential basis for silvicultural decisions when establishing even-aged plantations. Because of their importance, the different types of site indices, designed to predict future production of timber, were critically reviewed. Some are based on yields of previous tree crops, others focus on soil types which incidentally integrate influences of climate on soil processes. Site indices based on past yields tend to underestimate what can be achieved in the future with improved silvicultural practices, whereas those

based on soil types tell more about what needs to be done to prepare sites for planting than they do about potential yields. From our limited knowledge of forest climates - which needs to be greatly strengthened particularly for remote upland and mountain sites - assessments of exposure to wind can be made simply and effectively using standardized tatter flags. But how can the observations obtained be related to mechanisms and processes controlling stomatal behaviour and water loss? How can this information be used in early selection procedures?

Many speakers emphasized the importance of soil organic matter for the continuing success of even-aged plantations. Some suggested that large yields of timber may have been gained from the first generation of plantations at its expense, while others mentioned the development of fissures following the irreversible drying and contraction of peats in some areas after having been planted with lodgepole pine. The importance of organic matter decomposition was discussed in relation to amounts of nutrients released and relative to (i) applications of artificial fertilizers and (ii) the requirements of forest trees at different stages of their development.

A consideration of basic aspects of nutrient cycling in even-aged plantations lead to another closely related subject considered important by participants. Frequent reference was made to the knowledge and experience gained from agricultural research and practice. Farmers ameliorate their soils by drainage and ploughing; foresters have also achieved improvements in this way. Farmers amend their soils by adding organic and inorganic fertilizers and the amounts of these often are finely adjusted to the needs of individual species and cultivars; an iterative procedure with amounts of fertilizer and the nature of other agricultural practices being reconsidered and adjusted as, and when, new cultivars are introduced. For instance, the dramatically increased applications of fertilizers following the replacement in the early 60's of long- by short-strawed cultivars of wheat. This approach can also take account of local variations in climate and soil and could therefore be regarded as an example upon which to base regional silvicultural prescriptions. Silviculturists working in protection forests and with long rotations accept that their silvicultural systems must be well-buffered against hazards, but in even-aged plantations this attitude may not be so appropriate as soil scientists and engineers continue to find ways of reducing edaphic site variations by drainage, cultivation and the application of fertilizers.

In addition to discussing the use of fertilizers and the release of nutrients from decomposing litter, two other aspects of tree nutrition were debated. For some conditions it

would appear profitable to study the use of mixtures, including trees such as Alnus species, with root colonizing, nitrogen-fixing microbes and additionally there could be merit in identifying within-species variants that more efficiently exploit available nutrients. These ideas lead to a renewed interest in mycorrhizas which, at this meeting, centred on their beneficial effects on the rapid establishment of trees after planting.

EFFECTS OF AFFORESTATION ON CATCHMENT WATER YIELDS.

On many occasions during the meeting there were references, direct and indirect, linking trees and water: the need for drainage to facilitate establishment, the inter-relation between water availability and stomatal behaviour, the ability of trees to withstand stress whether attributable to drought or waterlogging and very importantly the water yields from afforested catchments. The latter are of particular significance with afforestation and the conservation of water being regarded, in some areas, as incompatible land uses. Although some catchment studies have been made there is a need for more so as to be in a position to predict the effects of trees, compared with those of other types of vegetation, in a diverse array of environments. These studies should include estimates of water quality in addition to quantity.

ECOLOGY OF THE FAUNA AND FLORA OF EVEN-AGED PLANTATIONS.

The importance to the continued success of even-aged plantations of knowledge about damaging populations of pests and pathogens is self-evident. Less obvious but equally essential in the long term, is the need to learn more about organisms that at present appear insignificant but may be potentially valuable or dangerous. If the meeting had been held in 1975 this statement would have been applicable to the pine beauty moth (Panolis flammea), whose normally quiescent populations in Scots pine growing in the U.K. have, in the interim, increased in a few plantations of lodgepole pine to damaging proportions. The large yields of even-aged plantations may justify some risks and the acceptance of limited losses, but we must seek to minimize the occurrence of large infestations and epidemics which may be uncontrollable or require the use of extensive and expensive control measures with possible side effects on wildlife and other forest assets. It is necessary to recognize that the study of associated plants and animals, including pests and pathogens, is an integral part of forest ecology. If their behaviour and population dynamics were better understood, control could be exercised with increased discretion.

RESOLUTIONS

After the main purpose of the meeting had been successfully achieved, namely the provision of a forum for discussing the ecology of even-aged plantations, participants agreed the following resolutions:

- I. Projections of world wood production and supply and of world wood demand, indicate that sooner or later, and probably by the turn of the century, there will be a world shortage of wood which will become increasingly severe.
- II. To meet this shortage it is inevitable that the use of intensive plantation forests will be extended.
- III. Economic production through plantations will only be sustained so long as foresters are fully aware of the direct and indirect effects that plantations have on the environment.
- IV. To ensure that production will be sustained at economic levels, it is essential to augment the amount and range of fundamental research upon which applied research and management can draw.
- V. In particular, the following are recognized as key research fields:
 - (a) Plantation forestry often leads to a reduction in numbers of species grown, dependence on a limited genetic base and probably, in an increasing number of instances, to the use of clones. To safeguard the future, international action is required to conserve tree species in their natural habitats, an important part of the work already being done by F.A.O. through its Panel of Experts on Forest Gene Resources; significant and fully representative areas of natural forest must be conserved with equal emphasis on trees, soil and associated fauna and flora.
 - (b) By analogy with agriculture, the use of exotic species, the narrowing of the genetic base and the intensification of management increase the risks from pests, invertebrate and vertebrate, and pathogens. Research on species, which may affect forests of the future, is needed.
 - (c) Fertilizer requirements need to be linked to nutrient budgets. In particular, the possibility of exhausting the store of soil organic matter, and hence of nitrogen, needs attention.
 - (d) Too little is known of the effects on (i) soils and (ii) yields of water catchments; the latter deficiency reflecting an imperfect appreciation of the water relations of trees in different situations, particularly when comparing evapotranspiration from forests and grasslands.
 - (e) Experience in many parts of the world has shown that damaging populations of herbivorous animals, e.g. small

rodents and deer, often develop in plantation forests. Their behaviour, reproductive ability and patterns of dispersal need to be investigated so as to define what constitutes a potentially damaging population.

CONCLUDING REMARKS.

Productive even-aged plantations are now distributed throughout the world. They include plantations of Pinus taeda in southeastern United States, Pinus radiata in New Zealand and Australia, the clonal plantations of Cryptomeria japonica in Japan, the second and third generation plantations of Tectona grandis at Nilambur in southern India, the Pinus oocarpa plantations on the Jos plateau of Nigeria and the Picea sitchensis stands of Galloway and Eskdalemuir in southern Scotland. In his opening paper, Mr G.D.Holmes emphasized the contribution that even-aged plantations must make to world supplies of timber and in his closing remarks, Professor D.Mlinsek, Coordinator of Division 1 of I.U.F.R.O. emphasized three main qualities of the forest resource, namely timber production, site protection and social benefits. Furthermore, Professor Mlinšek stressed that managers of plantation forests still had much to learn from those tending naturally regenerating forests, as in Central Europe, where there is concern for site protection, in its broadest sense, in addition to timber production.



OFFERED PAPERS

Maintenance of productivity in
successive rotations of radiata
pine in South Australia.

R. Boardman

Socioeconomic evaluation of the
recreational use of fish and
wildlife resources in Alberta,
Canada.

W.E. Phillips and
M.R. Carroll

Variation in tropical tree species

P.J. Wood



MAINTENANCE OF PRODUCTIVITY IN SUCCESSIVE ROTATIONS OF RADIATA
PINE IN SOUTH AUSTRALIA

By R. BOARDMAN

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SUMMARY

Investigation of site and silvicultural factors related to a decline in productivity in second rotations of Pinus radiata suggested no simple causal factor; rather that many factors were acting in concert. The establishment phase of developing even-aged plantation became pre-eminent for growth development, then had a profound influence on long-term productivity within the rotation. A long-term investigation has been established of two direct comparisons of first and second rotations. The whole experiment has a high level of positively-imposed site homogeneity and growth-promoting input with the aim of producing near-optimum growth rate, limited only by climatically induced factors.

RESUME

Les recherches effectuées sur les facteurs liés à la station et à la sylviculture et reliés au déclin de la productivité du Pinus radiata pendant la deuxième révolution n'ont mis en évidence aucun facteur de cause à effet mais plutôt une série de facteurs interdépendants. La phase de création pendant le développement des plantations equiennes est d'une importance prééminente pour le développement de l'arbre et influe de façon capitale sur la productivité à long terme pendant la révolution. Une étude à long terme établissant des comparaisons directes entre première et seconde révolution a été mise en route. Le sujet entier se base sur une homogénéité imposée de la station et des données capables de produire un taux de croissance presque optimum, limité seulement

par des facteurs climatiques.

ZUSAMMENFASSUNG

Eine Untersuchung des Standorts und der waldbauliche Faktoren im Hinblick auf den Produktivitätsrückgang in der zweiten Generation bei Pinus radiata ergab, dass nicht nur ein einziger Faktor die Ursache ist; es wirken vielmehr eine Reihe von Faktoren zusammen. Die Begründungsphase in der Entwicklung gleichaltriger Pflanzungen hatte hervorragende Bedeutung für die Wachstumsentwicklung der Bäume und hatte einen nachhaltigen Einfluss auf die Produktivität während der Umtriebszeit. Man führte einen Langzeitversuch durch in Form zweier direkter Vergleiche von Erst- und Zweitgeneration. Der ganze Versuch ist gekennzeichnet durch einen starken positiven Einfluss der Standortshomogenität und wachstumsfördernder Düngerezufuhr. Durch diese sollte eine nahezu optimale Wachstumsrate erreicht werden, die nur durch klimatische Faktoren eingeschränkt wird.

INTRODUCTION

South Australia has a very limited area which possesses the climatic and edaphic conditions suitable for forestry and capable of meeting the timber-based needs of the population. Negligible areas of vigorous natural forest growth survived the first decades of colonization (1830-1970) (Williams 1974) and plantation forestry, from small beginnings in 1875 has been strongly developed (Lewis 1975). These areas are dominated by a single species of pine, radiata pine, singularly well-suited to the soils and climate. At the present time the plantation estate is close to 100,000 ha (Bednall 1968; Lewis, Keeves & Leech 1976).

Most land suitable for pine afforestation has already been created as "Forest Reserves" by Act of Parliament and only minor parcels can be acquired, and these in direct competition with agriculture. Consequently yield is regulated on the 'sustained yield' principle on a median site quality area equivalent basis (Lewis, Keeves & Leech 1976).

Evidence for a decline in productivity in second rotation plantations has accumulated. This has been posed as a critical problem in forestry management as it reflects on the capacity of the forest to supply the wood-using industries, encouraged by the stability offered by sustained yield. As Bednall (1968) has stated: "... evidence ... indicates quite clearly that second rotations of Pinus radiata are overall producing less wood per acre per annum than they did in the first rotation at

similar ages and at similar stocking. A remedy for this must be found."

There are two levels of remedial condition: a relative one and an absolute one. The relative solution applies when cultural techniques applied, regardless of cost, to the second rotation raise its productivity to at least that of the historical performance of the first crop on that site. The absolute solution is more complex and requires the removal of growth-limiting factors under identical environment constraints, so far as they are known.

In this context, long-term maintenance of productivity refers to sustained development of growth rate in relation to site fertility over time, with time measured in decades rather than years. It includes the physiological changes that occur during the life of long-lived tree species in a forest-like situation and the accumulation of biomass by young trees when they replace old moribund ones. The practice of silviculture imposes more regimented systems of change upon natural systems of replacement, and these all affect the expression of site fertility in some manner.

Research into the nutritional aspects of long-term productivity, or more particularly, the maintenance of optimum rates of productivity, has been associated with the march of growth with time during the history of single stands. We have reached the point at which we can diagnose stress for, or growth limiting levels of, major nutrients and many trace elements over the life of a forest stand (Raupach 1967; Raupach, Boardman & Clarke 1969; Boardman 1973).

In comparison, the logical extension of these studies into the nutritional situation when one forest stand is replaced by another in direct succession, has been slow. The occurrence of large depressions in productivity (20-25 per cent average) in second crops of the same species on the same site, has been necessary to inspire any investigation at all. The most notable investigations which have proceeded, are the now classical case of spruce in Saxony (Wiedemann 1923), the citrus replant problem in California (Martin & Ervin 1958), similar 'soil sickness' problems associated with fruit tree orchards (Savory 1966) and, more recently, in the forest sphere, pine replant problems in South Australia (Lewis 1967; Lewis & Boardman 1969, 1973; Keeves 1966; Lewis & Harding 1963; Muir 1969).

The first significant factor which relates all these latter studies is that adequately precise knowledge of productivity in the first crop at a given time or stage of growth has been available for comparative purposes. Appreciation of the significance of any difference found is difficult nonetheless, for production with time is influenced by many factors cumulative in their effect.

A second significant factor in common is that the method

of establishing a second or successive crop of the same species, in silvicultural terms, is termed the clearfelling system and one that falls at one extreme of the possibilities encompassed by silvicultural regeneration systems (Troup 1955). H.T. Odum (1960), when describing this system ecologically in terms of energy-flow analogue circuitry, has likened it to an ecological short-circuit.

In Australia and New Zealand concern has been expressed at the demonstrated decline of Pinus radiata in successive crops of this species over a wide range of sites and soils throughout the geographical range over which it is grown. In South Australia, subsequent remeasurements on plots reported by Keeves (1966) have confirmed concurrent studies in young stands, that:

- (a) there is often a considerable growth rate depression in the early years of the second crop;
- (b) that older stands, in particular stands which have passed the so-called canopy-closure stage, regardless of rotation, show that little opportunity exists for rapid growth rate acceleration, either by 'natural recovery' or from artificial means of stimulation, such as fertilizing except in cases of readily diagnosed deficiency of a limiting nutrient.

This situation has shown strong affinity with the concepts of Maruyama (1960, 1963), which relate to self-regulating and equilibrating systems. Maruyama has recognized two aspects of these multi-variate systems with mutual causal inputs. The deviation-counteracting or equilibrating process he calls 'morphostatis'; the deviation-amplifying process he calls 'morphogenesis'.

Deviation-amplifying systems are ubiquitous and relate to all situations where an initial 'low energy' input builds up a deviation which diverges from the initial condition. Positive feedback between the elements of the situation can lead to maximization of the efficiency of development resulting from the initial 'kick' or investment.

This conceptual framework appears to offer large gains in seeking remedies to long-term maintenance of productivity. The basic 'growth development' features are presence of morphogenesis, in the so-called free growth stages, and morphostatis, during the later closed-stand stages. Silvicultural treatments offer opportunity to provide initial investments in growth producing stimuli and to reinforce the initial deviation in such a direction and with such an intensity to achieve optimization in the efficient use of them. During morphogenetic stages of growth small differences in growth-promoting and growth-retarding factors can, through combination and amplification, due to the logarithmic aspects of growth, assume major significance though minor in actual magnitude. This concept has been central to the development of

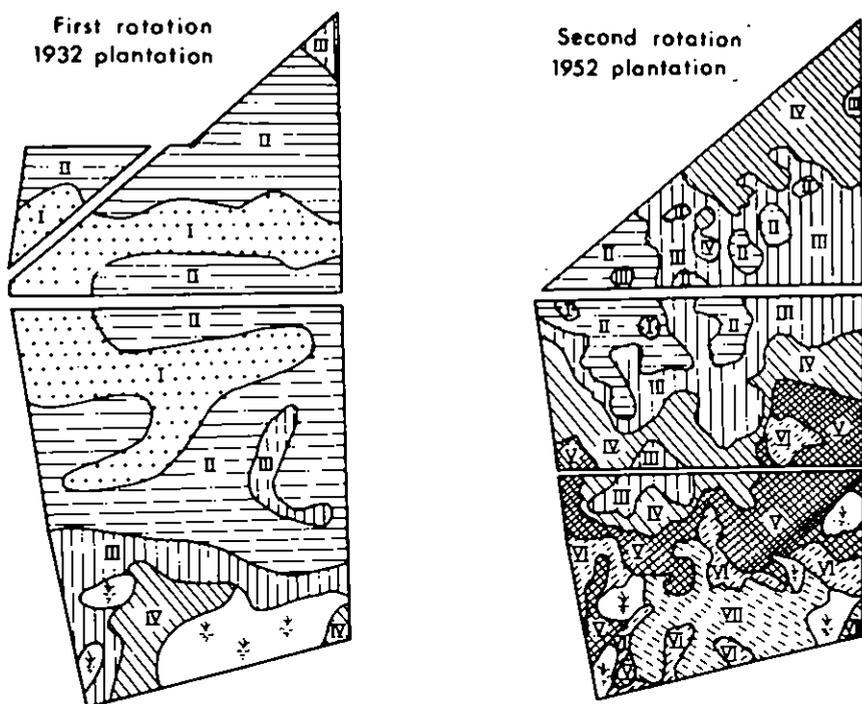


Fig. 1. Mappings of site class for an area of Penola Forest Reserve, South Australia, for the first and second rotations of radiata pine.

a comprehensive experiment allowing the examination of a wide range of site variables.

There is a considerable amount of circumstantial evidence that factors of this kind are operative in the pine replant problem. Friedel & Attiwill (1968), Friedel (1972), DeVries, Raupach & Boardman (1972) were unable to demonstrate consistently the second rotation effect in pot trials, although it was present in the field situations where the test soils were collected. In none of the cases investigated could gross nutrient deficiencies be detected, nor was any expected from the growth rates realized.

Current annual increments were measured on young, above-average sites from the second to the tenth years.

Assessment of site class in the tenth year has shown that first rotation plots class ranged from site class I to III. Figure 1 is an example. Increments in second rotation stands which demonstrated site classes I-III in the first crop have shown differences of the following magnitudes in basal area:

- 3rd year increment - 2/3 reduction
- 4th year increment - 1/2 reduction
- 5th year increment - 1/2 reduction
- 6th year increment - 1/10 reduction
- 7th year increment - 1/12 reduction.

The seventh and later years' reduction is of the same order as the difference found between the two site classes attained in the one rotation, e.g. the difference between site classes II and IV. That is, once the morphostatic stage is reached, increment is most closely associated with the site class attained at the 7-8th year and this persists.

The cumulative difference by the eighth year in the above series amounted to 12 sq.m/ha deficit, equivalent to the difference between site classes II and IV. This places the problem area mainly in the morphogenetic or formative stages of stand development.

An experiment where first and second rotations are matched has shown that opportunity to stimulate growth rates in the morphostatic (post canopy closure) stage is considerably less than in the formative stage. The best improvement in rate was with N+ P+ trace elements and amounted to an additional 0.5 sq.m/ha/yr average increase over P alone. This can be compared with the 50 per cent difference in the fourth year mentioned above which amounted to 4.5 sq.m./ha in that year alone.

The interesting feature of this fertilizer experiment was that there was no significant difference in increment between rotations for a given treatment, including P in it, although the total production with time has remained significantly different at each year's end. With the increased increment from NP+ trace element applications, it would take about twenty-five years to eliminate the difference between the second crop and the original crop (Woods and Forests Department, unpublished data).

The fertilizer treatments used here do not shed any clear light on the problem for sites not expected to show limiting phosphate. Small positive differences in response to NPK+ trace element supplements, sometimes not statistically significant, have been recorded on both first and second rotation sites of the high site classes over a range of ages. Small positive, statistically significant responses of N + P fertilizer + traces have been recorded consistently in pot trials conducted on sandy soils from matched native hardwood forest; and pine first and second rotation sites, where water has been non-limiting (DeVries, Raupach & Boardman 1972).

There is reason to believe that this may be more closely associated with soil texture than with pine species or cropping histories (R.G. Florence, personal communication).

The water or soil moisture aspects are more intriguing. DeVries, Raupach & Boardman (1972) were able to eliminate many factors involved in the failure to reproduce the second rotation depression in pots leaving factors strongly associated with the soil moisture regime as dominant among the remainder. Non-wetting behaviour of the sandy substrate has been found but it is not noticeably associated with cropping history.

The behaviour of a series of growth plots established in 1924 has been examined in relation to rainfall. Three of the seven plots were clearfelled and replanted and all three showed depressed productivity; one showed P deficiency but the other two did not. Using a basal area index it was shown, with the sole exception of the P deficient plot, that within a rotation the changes in index with age were closely correlated with the five-year running mean of rainfall. The four remaining first rotation plots, the oldest trees sixty-nine years, showed no tendency to decline in productivity with increasing age and behaved similarly to other yield plots on above site class V sites in this respect (Woods and Forests Department, unpublished records).

Yet the disturbing fact remains that attempts to correlate soil water parameters with tree growth are notoriously difficult and these have been associated with usually less than 40 per cent of the variance in dependent growth variables (Woods and Forests Department, unpublished records).

Studies of the microflora development and composition at different stages in first and second rotations have been examined from several points of view. Simpson (1967) showed that the fungal flora in young, first rotation stands was changed considerably by the fifth year and that a similar flora existed at the same age in second rotation. There were variations depending upon the site preparation, e.g. whether slash was burned or not, but differences between the expected site classes, borne out by subsequent measurements, were insignificant. At canopy closure and later mature stages differences between rotations and site classes were insignificant.

J.D. Ovington (personal communication) investigated fine root and fungal hyphae densities on matched sites and found highly significant differences between rotations at ages up to fifteen years. Second rotation soils possessed much greater dry weight of fungal matter and also of fine roots.

Theodorou & Bowen (1970) have demonstrated in forest trials the different growth rates associated with different species and strains of mycorrhizae on Pinus radiata.

Howard (1967), concurrently with Simpson (1967) investigated the microfauna regimes and found that the microfauna changed rapidly from typical pasture or eucalypt forest type to pine forest type, by nature of genera and abundances typical of populations reported for pine forests in the northern hemisphere. This change was virtually complete by the third to fifth years of the first rotation and persisted thereafter, including second rotations. The microfauna was found to be controlled to a remarkable extent by the microfloral distribution and composition, even within the F layer of the litter (J.A. Simpson, personal communication).

Florence & Lamb (1973) have investigated litter decomposition and nutrient release in first and second rotations, high and low site classes in South Australia and have found more rapid turnover of litter-held nutrients in the high site classes. The net litter development between rotations was, however, similar in size at any particular time. Differences between rotations and site classes in the morphostatic stages were minimal and lacked any consistent trends. Litter decomposition rate was correlated with nutrient element concentrations which, in turn, were closely correlated with soil types.

It seems likely that our assessment of growth-dependent factors is too crude or gross and simplistic. Whilst it may be sensitive enough to delineate the nature of nutrient problems within one rotation, there is a distinct possibility that these are gross in the biological sense of growth-limiting single- or multivariate factors.

In 1970 we began to prepare for an experiment which would allow for manipulation of site factors in such a way as to impose close to optimum positive inputs.

Differences produced by the experimental treatments are over and above those produced by a basic silvicultural package which promises to lift early growth rates considerably when compared with the very low intensity, low cost treatments which were applied to the stands which showed the second rotation decline.

The experimental treatments have been aimed to influence ecologically significant aspects of 'site' and specific methods have been selected to produce distinct effects on site. The aspects upon which information is being sought can be considered as follows:

- genotype of crop species
- rhizosphere flora
- native microflora
- humus
- soil moisture regime
- growth-limiting nutrients
- soil physical state
- soil air-temperature regime.

We have attempted to take the pine plantation ecosystem apart and examine some of the consequences. This is where we believe the results obtained in this project are so profound and potentially useful.

A number of initial difficulties had to be overcome, of which the worst was to find a satisfactory way to apply fertilizer containing ammonium sulphate to seedlings one to two months after planting.

This was solved by a colleague, R.V. Woods in 1976 in a series of studies aimed at increasing productivity on marginal soils and sites. He commenced on first rotation land and in moving on to second rotation sites with the same soil types, produced a relative solution to the second rotation which, by careful fertilizer placement, related to the buffering capacity and leaching characteristics of the sandy soils and boosted productivity by what appears to be several site quality classes.

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The magnitude of the study which we prepared has led to a major cooperative effort which, besides the Research Branch of the Woods and Forests Department (D.W.F.), includes three Divisions of C.S.I.R.O.: Forest Research at the South Australian Regional Station (D.F.R.), Soils (D.S.) and Mathematics and Statistics (D.M.S.).

Responsibility for various aspects of the studies has been distributed among the following research scientists and their technical teams:

- Conceptual aspects of the multifactor study into tree growth and nutrition: author and D.B.Boomsma (D.W.F.) in consultation with cooperators.
- Experimental design and analysis of statistical data: K.M.Cellier and R.A.Correll (D.M.S.)
- Preliminary soil and groundwater investigations: B.A.Mitchell (D.F.R.) and G.Blackburn (D.S.).
- Raising of planting stock, planting, application of field treatments, collection of tree growth data, including periodic whole-tree sampling: author, D.B.Boomsma and P.G.Zed (D.W.F.).
- Monitoring of water tables, soil moisture and climatic data including specific tree measurements associated with particular aspects: B.A.Mitchell (D.F.R.).
- Microbiological studies, including development of mycorrhizal associations and soil nitrification studies: G.D.Bowen and C.Theodorou (D.S.). Soil compaction surveys: R.Sands (D.S.) and G.Vogt (D.W.F.).
- Chemical analysis of soils: M.Raupach and the late A.R.P.Clarke; following the death of Mr. Clarke, transferred to Agricultural Chemistry Division of South Australian Department of Services and Supply (D.L.

Harvey).

The author gratefully acknowledges the considerable and active cooperation which this major project has stimulated and produced. The results will be reported elsewhere.

REFERENCES

- Bednall, B.H. (1968). The problem of lower volumes associated with second rotations in Pinus radiata plantations in South Australia. Woods and Forests Department, South Australia, Bulletin #17.
- Boardman, R. (1973). Experience with phosphatic fertilizers in the southeast of South Australia. Woods and Forests Department, South Australia, Bulletin #21. 2 volumes.
- DeVries, M.P.C., Raupach, M. & Boardman, R. (1972). Some glasshouse experiments to investigate the second rotation effect on three forest soils from South Australia. Proceedings Australian Forestry Tree Nutrition Conference (Ed. by R. Boardman), pp.301-307. Forestry and Timber Bureau, Canberra.
- Florence, R.G. & Lamb, D. (1973). Influence of stand and site on radiata pine litter in South Australia. New Zealand Journal of Forestry Science, 4, 502-510.
- Friedel, M.H. (1972). The decline in productivity of second rotation Pinus radiata (D. Don) plantations in southeastern South Australia. University of Melbourne, Ph.D. Thesis.
- Friedel, M.H. & Attiwill, P.M. (1968). Studies on respiration rates of Pinus radiata litter. Australian Forest Research, 3, 33-38.
- Howard, G.W. (1967). Arthropods inhabiting pine litter in the southeast of South Australia. M.Sc. thesis, University of Adelaide.
- Keeves, A. (1966). Some evidence of loss of productivity with successive rotations of Pinus radiata in the southeast of South Australia. Australian Forestry, 30, 51-63.
- Lewis, N.B. (1967). Regeneration of man-made forests. Paper F.A.O. World Symposium on man-made forests. Canberra, Australia. 14 pp.
- Lewis, N.B. (1975). A hundred years of state forestry in South Australia: 1875-1975. Woods and Forests Department, South Australia, Bulletin #22.
- Lewis, N.B. & Boardman, R. (1969). The maintenance of productivity under successive forest crops. Paper Symposium ANZAAS 41st Congress, Adelaide. 9 pp.
- Lewis, N.B. & Boardman, R. (1973). The second rotation problem in South Australia. Paper APPITA Congress, New Zealand. pp 5.
- Lewis, N.B. & Harding, J.H. (1963). Soil factors in relation to pine growth in South Australia. Australian Forestry, 27, 27-34.

- Lewis, N.B., Keeves, A. & Leech, J. (1976). Yield regulation in south Australian Pinus radiata plantations. Woods and Forests Department, South Australia, Bulletin #23.
- Martin, J.P. & Ervin, J.O. (1958). Greenhouse studies on influence of other crops and of organic materials on growth of orange seedlings in old citric soil. Soil Science, 85, 141-147.
- Maruyama, M. (1960). Morphogenesis and morphostasis. Methodos, 12.
- Maruyama, M. (1963). The second cybernetics: deviation-amplifying mutual causal processes. American Scientist, 51, 164-182.
- Muir, W.D. (1969). The problems of maintaining site fertility with successive croppings. Australian Journal of Science, 32, 316-324.
- Odum, H.T. (1960). Ecological potential and analogue circuits for the Ecosystem. American Scientist, 48, 1-8.
- Raupach, M. (1967). Soils and fertilizer requirements for forests of Pinus radiata. Advances in Agronomy, 19, 307-355.
- Raupach, M., Boardman, R. & Clarke, A.R.P. (1969). Growth rates of Pinus radiata (D. Don) in relation to foliar levels of nitrogen and phosphorus for plantations in the southeast of South Australia. C.S.I.R.O., Australia, Soil Publication #26.
- Savory, B.M. (1966). Specific replant diseases. Commonwealth Bureau of Horticultural Plantation Crops. Research Review #1, Commonwealth Agricultural Bureau, Farham Royal. vi + 64 pp.
- Simpson, J.A. (1967). Mycological aspects of decomposition of pine litter. M.Sc. thesis, University of Adelaide.
- Theodorou, C. & Bowen, G.D. (1970). Mycorrhizal responses of radiata pine in experiments with different fungi. Australian Forestry, 34, 183-191.
- Troup, R.S. (1955). Silvicultural systems (Ed. by E.W. Jones). 2nd Edition. Clarendon Press, Oxford. viii + 216 pp.
- Wiedemann, E. (1923). (Regress in increment and growth interruptions in spruce in middle and lower altitudes of the Saxon State Forests.) Translation by U.S. Forest Service #302. 1936.
- Williams, M. (1974). The making of the South Australian landscape. Academic Press, London.



SOCIOECONOMIC EVALUATION OF THE RECREATIONAL USE OF FISH AND WILDLIFE RESOURCES IN ALBERTA, CANADA

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SUMMARY

In managing forest resources all benefits and costs, both market and extra-market must be taken explicitly into account in order to make comprehensive socioeconomic evaluations. Recreational uses of fish and wildlife resources by resident Albertans have a value of approximately Can \$100,000,000 which is comparable to values from major commercial uses of resources. There are also other values such as those associated with conservation of the gene pool, option values to non-users who value having the option, whether or not acted upon, and heritage values.

Timber benefits are given prominence over fish and wildlife benefits in the determination of how resources are used. This is because of the occurrence of direct financial benefits in timber related industry whereas non-timber benefits are, to a large extent, non-financial. With inventories of all types of forest resources and an understanding of the trade-offs between these resources, it would be possible to carry out an economic analysis. Changes in the administrative structure away from single-resource orientated departments could then lead to land use decision making which would maximize net benefits from all resources to society.

RÉSUMÉ

Quand on considère la gestion des ressources de la forêt, il est nécessaire de tenir compte, de façon explicite, des avantages et des coûts, du marché et autres, pour pouvoir arriver à une évaluation socioéconomique complète.

L'utilisation, dans un but récréatif, des ressources animales - poissons et faune sauvage - de l'Alberta par sa population rapporte environ Can \$100,000,000, ce qui est comparable aux sommes rapportées par une utilisation commerciale de ces ressources. Aux valeurs financières il faut aussi ajouter d'autres valeurs telles que la conservation du réservoir génétique, la possibilité d'en profiter, pour ceux qui ne la prendront peut-être pas, d'en avoir la possibilité et la préservation de l'héritage historique et naturel.

Les avantages associés au bois ont priorité sur ceux qui sont associés au milieu animal quand il s'agira de déterminer la manière dont les ressources naturelles seront utilisées: les industries du bois apportant des avantages financiers directs, tandis que l'utilisation de ces ressources en dehors du cadre de l'industrie du bois n'ayant la plupart du temps aucun avantage financier. Il serait possible de faire une analyse économique des ressources de la forêt en inventariant les ressources et en exploitant les relations réciproques entre ces ressources mêmes. Des changements dans la structure administrative de la gestion forestière, à savoir le passage d'une gestion à orientation unique vers une orientation mixte, pourraient amener à des décisions au niveau de l'utilisation du terroir qui amélioreraient les avantages de toutes les ressources pour la société.

ZUSAMMENFASSUNG

Bei der Nutzung von Waldressourcen müssen sowohl Gewinne als auch markt- und marktabhängige Kosten einzeln berücksichtigt werden, um eine umfassende sozioökonomische Bilanz geben zu können. Die Nutzung des Fisch- und Wildbestandes als Freizeitbeschäftigung der Einwohner Albertas entspricht ungefähr einem Wert von 100 Millionen kanadischer Dollar. Dieser Betrag ist vergleichbar mit dem Gewinn aus dem Wald als Rohstofflieferant. Ausserdem gibt es noch andere Werte, wie zum Beispiel die Konservierung des 'Gen-Kapitals' durch den Wald, potentielle Werte, die je nach Lage und unabhängig von der sonstigen Nutzung realisiert werden können und schliesslich Traditionswerte. Bei der Rohstoffnutzung gibt man Holzerträgen

den Vorrang vor Fisch- und Wilderträgen. Der Grund dafür liegt in den direkten finanziellen Gewinnen der Holz- und Holzverarbeitenden Industrie, während die vom Holz unabhängigen Erträge grösstenteils nicht finanzieller Art sind. Mit einer vollständigen Erhebung der Waldrohstoffe und dem Verständnis der Wechselwirkungen zwischen diesen Rohstoffen auf dem Markt waren umfassende ökonomische Analysen möglich. Änderungen in der Verwaltungsstruktur, welche die auf Einzelrohstoffe ausgerichtete Bestandesgliederung beseitigt, könnten dann zu neuen Nutzungsformen führen, in der die Nettogewinne aus allen Ressourcen für die Gesellschaft optimiert sind.

INTRODUCTION

Fish and wildlife resources in North America are public goods by ownership. Historically, their value and availability has led to widespread depletion of many species. Through public legislation and enforcement continued depletion was arrested or reversed. As part of this process, fish and wildlife resources were placed in the public trust and have remained so regardless of ownership and control of land surface rights.

Two issues have emerged which are of particular importance regarding resource allocation. First, privately owned land provided habitat for publicly owned wildlife which has led to a potentially inefficient distribution of wildlife benefits and costs. Second, non-commercial use of fish and wildlife on public land has often been displaced by commercial uses. This implies that market values of commercial uses are emphasized whilst values external to the market system are ignored.

Both issues result in patterns of resource use which favour commercial rather than non-commercial uses of resources such as fossil fuels, forest land, agricultural land and hydropower. These commercial uses of resources may not be in society's best interest now or in the future. If an improvement in net social benefits is to be realized, then both non-commercial and commercial resource uses must be balanced by government. All benefits and costs, both market and extra-market, must be taken explicitly into account. Socioeconomic evaluations of the non-commercial uses of resources can assist in this endeavour. The focus of this paper is on such an evaluation of the recreational use of Alberta's fish and wildlife resources.

RECREATIONAL USE OF FISH AND WILDLIFE RESOURCES

Evaluation procedures

Socioeconomic information is essential in the assessment of recreational activities. When combined with physical and biological information, it is possible to ascertain the importance of recreational uses of fish and wildlife in relation to other uses, and in relation to other patterns of resource use which may alter fish and wildlife habitats. Two recent studies in Alberta provided such socioeconomic information (Phillips, De Pape and Ewanyk 1977; Phillips and McElhanev 1977 a,b). Their objectives were:

- i To ascertain the socioeconomic characteristics, e.g. age, income, family size, residence, occupation, etc., of participants in recreational uses of fish and wildlife.
- ii To establish detailed profiles of recreational activities, e.g., hunting fishing and informal nature study. Information was collected regarding location and duration of activities, expenditure on activities and numbers and species of fish and wildlife taken in hunting and fishing.
- iii To estimate the value of Alberta's fish and wildlife resources used for recreational purposes.

The information required to meet these objectives was obtained using mail questionnaires during 1976 and 1977 from random samples of resident and non-resident anglers and resident and non-resident hunters in Alberta.

Survey results

There are an estimated 1.39 million residents of Alberta who annually engage in observation and informal nature study of Alberta's fish and wildlife resources. Amongst these residents, 308,500 persons fish and 102,600 hunt. In addition to residents, there are annually 10,620 licensed anglers and 8,000 licensed hunters who reside in other provinces in Canada or abroad, notably the United States (Table 1). The total number of recreational users is 1.4 million persons annually.

Alberta's fish and wildlife resources provide all licensed anglers and hunters with 5,900,000 fish, 23,700 big game, 276,300 upland birds and 1,166,000 waterfowl annually.

The annual benefits on a per day basis for hunting and fishing were much higher than for observation and informal nature study. These benefits include licence fees (hunting and fishing) plus extra-market benefits, which are the sum of individuals' willingness to pay over-and-above recreation expenses actually incurred for fish and wildlife recreation activities. The benefits from hunting and fishing are equal to the benefits from observation and informal nature study, although the numbers of days spent in hunting and fishing were much lower.

Willingness-to-pay values are a type of estimate of market values. Fish and wildlife values may be more

Table 1. Selected characteristics, activity and evaluation data for recreational users of fish and wildlife resources in Alberta.

	Non-consumptive activities Resident 1976		Fishing activities Resident 1976		Fishing activities Non-resident 1977		Hunting activities Resident 1976		Hunting activities Non-resident 1977		Total	Weighted average
Annual total number of participants	1 390 890	308 500 ^a	10 620 ^b	102 600	8 000	1 406 000 ^c						
Average family size	3.2	3.4	3.1	3.5	3.1							3.25
Average family income Can\$	17 677	17 471	19 904	18 349	26 751							17 733.00
Average age - adulte	40.9	36.3	43.1	34.2	44.2							39.77
- children over 5 yrs of age	11.2											
Average formal education - adult (yrs)	12.0	12.0	12.6	12.0	13.0							12.01
Annual recreation days per participant	12.0	10.0	4.0	7.1	6.3							14.65 ^d
Annual total recreation days	16 678 600	3 089 205	42 055	731 538	50 000	20 591 398						
Annual total benefits from activities Can\$	50 035 800	23 738 860	959 092	25 673 600	2 898 880	103 296 000						

(a) Includes 164 100 angling licence holders (age 16-65 years) and an estimated 197 000 non-licence holders (under 16 years and over 65 years of age).

(b) Includes angling licence holders only.

(c) This figure is less than the sum of totals for each category since many participants engage in more than one kind of activity. In particular all resident anglers and hunters engage in non-consumptive activities as well.

(d) Consists of annual total recreation days divided by annual total number of participants (20 591 398 divided by 1 406 000).

appropriately expressed in terms of compensation values. If recreational uses of fish and wildlife are considered as 'rights to use' by residents, then compensation values should be used instead of willingness-to-pay values. For instance, to the extent that fish and wildlife resources are displaced by other resource uses, then there is an erosion of the rights of residents to fish and wildlife use for which compensation entitlement therefore exists. If one recognizes a right to be compensated then one should accept the compensation values which at present in Alberta amount to Can \$300,000,000 annually or three times the willingness-to-pay values of Can \$100,000,000 annually. An individual's willingness-to-pay is constrained by that individual's income, whereas compensation to be received in lieu of right to use does not have this constraint.

Regardless of which value figure is used, recreational uses of fish and wildlife resources by resident Albertans have values associated with them that are comparable to values from major commercial uses of resources. For example, the value of timber products from Alberta forests is Can \$85,149,000 annually and the value of coal supply is Can \$334,00,000 annually. (Alberta Forest Service, 1976; Alberta Energy Resources Conservation Board, 1977).

Concluding comment

Non-commercial uses of fish and wildlife resources are important and should be considered explicitly in social accounting. Commercial fish and wildlife harvests also provide annual benefits of course. For example commercial fur harvest by both registered and native trappers amounts to about Can \$7,100,000 annually. There are also other values such as those associated with conservation of the gene pool, option values to non-users who value having the option whether or not acted upon, and heritage values held by present generations knowing that future generations will have similar opportunities to use fish and wildlife resources.

Any activity that displaces the fish and wildlife habitat reduces the present and future use of fish and wildlife resources. The values so displaced should be accounted as a social cost against the activity which influences the habitat.

Current direct annual costs for fish and wildlife protection and management amount to about Can \$10,000,000. This amount is a small proportion of annual benefits whether expressed as willingness-to-pay (10 per cent) or as compensation values (3.3 per cent).

POLICY ISSUES

Impact of valuation on trade-offs

It has been observed above, that the total value of fish and wildlife resources may be evaluated using market values, willingness-to-pay or compensation values. The choice of type

of value which is most appropriate to use in decision making for resource allocation depends upon who is making the decision and for what purpose.

For example, one might examine the decisions made by the Alberta Provincial Government in making a disposition of timber harvesting rights over a specific area to a private corporation (a Forest Management Agreement). This would typically involve the delineation of an area of 4000 square miles which would be managed for timber input to a wood fibre pulp mill. The harvesting system would be designed in collaboration with the Alberta Forest Service so as to protect fish and wildlife, water and soil. The firm will pay royalties for the timber harvested and the government normally recognizes the additional benefits of the creation of regional incomes. The total benefits to the Province are evaluated and the Forest Management Agreement will be entered into if these benefits are considered close to the maximum likely to be available from any other competitive firm entering a similar agreement. Now, the question of evaluation of fish and wildlife resources should be dealt with in deciding how much total benefit is required from the Forest Management Agreement and what type of harvesting system should be used. The benefits from timber harvesting should be weighed against the changes in fish and wildlife values, and a timber harvesting system designed which maximizes the joint values of timber and fish and wildlife. The actual negotiated exchange point in the Forest Management Agreement would depend upon the way in which fish and wildlife were evaluated.

In fact, the process of weighing resource values against each other is carried out in an extremely rudimentary and unsophisticated way. Generally, the non-timber resource values are given very little weight in deciding whether or not to enter into a Forest Management Agreement. Then the harvesting system is determined by making marginal changes in the timber harvesting rules which apply throughout the Province and which have been determined on the basis of achieving some level of impact on fish and wildlife which is acceptable to the Alberta Fish and Wildlife Division.

In view of the high fish and wildlife values which have been discussed in preceding sections, it is clear that this fragmented, institutional approach should be replaced by an evaluation system which makes a trade-off between timber and non-timber resource values. Obviously, this trade-off will be affected by the valuation method which is used. A simple example is given in Table 2. This shows that the optimum level of joint benefits under the assumptions given will depend upon the relative values of the timber as opposed to non-timber resources. If the willingness-to-pay approach is used, the optimum level is achieved in harvesting system D and the Forest Management Agreement should be entered into, using that

harvesting system. When compensation values are used, the emphasis is much more on wildlife, the optimum harvesting system is no harvesting at all (F), and the Forest Management Agreement should not be entered into. The more general case of this trade-off would be represented by a production possibility curve for the products i.e. timber and wildlife, and the maximum revenue combination would occur where the slope of the iso-revenue curve was equal to that of the production possibility curve. This would show the combination of products yielding the maximum value for any given situation. Thus an increase in wildlife prices would shift the optimum combination towards wildlife.

Political implications of value systems

Timber benefits have been given prominence in the past and are still given prominence in current decision making. A major reason is that there has been a concentration of direct financial benefits in the forest industry whereas the non-timber valuations included a large proportion of non-financial benefits. The highly visible cash and jobs in the forest products industry carry a great deal of political influence, especially because of the way these benefits are concentrated in specific communities.

Fish and wildlife resources certainly contribute to the economy of the specific communities and the further north one goes, the more obvious this becomes, until one reaches the situation in the Northwest Territories, in which hunting and trapping incomes are the most important primary sector in certain communities. In Alberta, however, the actual incomes generated by fish and wildlife resources have to be ranked in comparison with the much higher incomes from the oil and gas industry, agriculture and forestry. This can make the management of forest land primarily for fish and wildlife resources difficult to justify in a political framework. However, despite this difficulty zoning policies have been decided upon in the eastern slopes of the Rocky Mountains, which identify large areas, the primary use for which is to be recreation-oriented activity. Predictably, this has raised a good deal of alarm and protest in the forest industry, as was brought out in the recent public hearings on the environmental effects of forestry operations in Alberta conducted by the Environmental Council of Alberta (Parching 1977).

One might summarize by observing that the fish and wildlife resources have a poor data base. Often there are mixed objectives from the resource users and there is a diffuse pattern of economic benefits as compared with a high degree of technical and economic knowledge in timber harvesting, and a single-minded and concentrated resource user group of forest industry operators.

As an example of a possible future conflict one might consider an argument put forward by the Fish and Wildlife

Table 2. Theoretical example of costs and benefits for different timber harvesting strategies.

Harvesting system	Extraction costs		Net timber revenue		(Willingness to pay) Non-timber benefits		(Compensation) Non-timber benefits	
	Can\$/ha (2)	Can\$/ha (3)	Can\$/ha (4)	Can\$/ha (5)	Can\$/ha (3)+(4)	Can\$/ha (3)+(5)		
(1)								
A. Clearfell 500 ha blocks	850	1150	200	400	1350	1550		
B. Clearfell 200 ha blocks	900	1100	300	600	1400	1700		
C. Clearfell 100 ha blocks	1000	1000	500	1000	1500	2000		
D. Clearfell 100 ha blocks plus careful road siting	1200	800	800	1600	1600*	2400		
E. Strip clearfelling 50 ha	1500	500	1000	2000	1500	2500		
F. None	0	0	1400	2800	1400	2800**		

* Harvesting system which maximizes total benefits, with non-timber benefits evaluated by willingness to pay.

** Harvesting system which maximizes total benefits with non-timber benefits evaluated by compensation.

Assumptions:

- (i) Harvesting has negative impact on non-timber resources, e.g. fish and wildlife.
- (ii) Timber extraction cost negatively correlated to non-timber benefits.
- (iii) Compensation valuation of non-timber, e.g. fish and wildlife is twice that of willingness to pay valuation.

Division of the Provincial Government and the various citizen-user-group associations, which maintains that greater net benefits could be obtained by altering timber management in favour of wildlife. For example, careful siting of logging roads to avoid disturbance in areas which provide natural grazing could well be desirable and controlled burning of open areas and deciduous cover types may provide better browse than cut-over, logged areas. However, road location decisions, non-optimum from the point of view of transport and construction costs will never be made by the forest industry unilaterally, since they have to bear the entire construction and maintenance cost of roads, but gain none of the benefits from any wildlife habitat improvement. Controlled burning involves risks to the timber resource which the forest industry and the Alberta Forest Service are unwilling to take. Obviously, if wildlife management is going to be integrated with timber management so that regulations are set out which provide the possibility of reaching an optimum trade-off between increased costs to the forest industry and increased benefits to hunting and recreation activities, then decisions must be taken by a body which transcends any single resource (see also Cooper and Mutch, this volume).

Areas have been identified in Alberta which are soon to be subjected to detailed feasibility studies for pulp mill development. The forest land will be considered first in terms of timber; an environmental impact assessment will be made of the impact of effluent of human population and fish immediately downstream of the proposed pulp mill sites, and proposed logging practices will be discussed in terms of their impact on erosion and wildlife. There will be emphasis on imposing regulations which reduce immediate physical impacts rather than devising a total management system that provides an optimum level of combined timber, fish and wildlife and indeed other forest resources. The aggregate valuations of recreation and fish and wildlife resources certainly indicate the general level of attention which should be given to the various forest and wildlife resources in Alberta and provide justification for spending Provincial funds on multi-resource planning exercises.

With full and accurate inventories of all resources, including fish and wildlife, an understanding of the relationship between different types of renewable resources and estimates of the total value of resources, the stage would be set for a comprehensive economic analysis. If all that were obtained, then changes in the administrative structure away from single resource oriented departments which determine the disposition of timber independently of fish and wildlife could eventually lead to land use decision making which would maximise net benefits from all resources to society.

REFERENCES

- Alberta Energy Resources Conservation Board(1977). Coal industry annual statistics #77-29. Calgary: Energy resources Conservation Board. Alberta Forest Service(1976). Forest statistical review 1975-76. ENR Report #15. Alberta Department of Energy and Natural Resources, Edmonton.
- Parching,D.E.(1977) Public hearings on the environmental effects of forestry operations in Alberta. Environment Conservation Authority Information Bulletin #1, Edmonton.
- Phillips,W.E. & McElhane,y,E.R.(1977) A socioeconomic evaluation of non-resident sport hunting activity in Alberta. I.M.P.A.C.T. Environomics Ltd for the Alberta Fish and Wildlife Division, Edmonton. 118 pp.
- Phillips,W.E. & McElhane,y,F.R.(1977). A socioeconomic evaluation of non-resident sport fishing activity in Alberta. I.M.P.A.C.T. Envoronomics Ltd for the Alberta Fish and Wildlife Division, Edmonton. 91 pp.
- Phillips,W.E., De Pape,D. & Ewanyk,L.(1977). Socioeconomic evaluation of the recreational use of fish and wildlife resources in Alberta with particular reference to the Athabasca oil sands area: summary and conclusions. Volume I. Department of Rural Economy, Faculty of Agriculture and Forestry, University of Alberta. 125pp.



VARIATION IN TROPICAL TREE SPECIES

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SUMMARY

Although areas of plantation in the tropics are smaller than in temperate regions, most countries have one or more planting programmes and these are generally more important than those involving the management of natural forests. The F.A.O. panel of experts on forest gene resources coordinates lists of species for research, with priorities which currently embrace tropical pines notably Pinus caribaea, P. oocarpa, P. kesiya, Agathis, Araucaria, the eucalypts and other hardwoods, including Gmelina arborea and Tectona grandis. Less is known of the biology, reproductive systems, variation patterns or even the natural occurrence of some of these species than of important temperate species, and current studies include provenance trials and investigations of genetic variation. Meanwhile, large planting schemes continue to use seeds from natural populations. The erosion of genetic variation through the disappearance of natural populations is serious in many countries and programmes for in situ and ex situ conservation of endangered populations have been started, though much remains to be done.

The response of genotype to site is at present still under study, though some information exists, notably for P. caribaea and T. grandis.

RESUME

Bien qu'ils ne possèdent que des plantations plus petites que les régions tempérées, les pays tropicaux n'en ont pas moins un ou plusieurs programmes de boisement et ceux-ci sont généralement plus importants que les programmes concernant la gestion de forêts

naturelles. Les experts de la F.A.O. responsables des ressources génétiques forestières dressent des listes d'essences destinées à des recherches concernant tout d'abord les pins tropicaux notamment le Pinus caribaea, le P. oocarpa, le P. kesiya, l'Agathis, l'Araucaria, les eucalyptus et autres feuillus, y compris le Gmelina arborea et le Tectona grandis. On n'a que peu de notions des systèmes reproductifs, de la biologie, des variations ou même de la présence dans la nature de quelques unes de ces espèces en comparaison avec les espèces des zones tempérées et des études actuelles sont en cours et traitent d'essais de provenance et de recherches sur leur variation génétique. Cependant, des programmes de plantations importants continuent à utiliser des graines provenant de populations naturelles. L'érosion des variations génétiques due à la disparition des populations naturelles est un problème sérieux dans bien des pays et des programmes pour la protection in situ et ex situ des populations en danger ont été mis en route bien qu'il reste encore beaucoup à faire de ce côté là.

La relation entre génotype et station est encore au stade de la recherche, bien que l'on ait déjà quelques renseignements sur Pinus caribaea et le Tectona grandis.

ZUSAMMENFASSUNG

Obwohl die Flächen von Forstpflanzungen in den Tropen geringer sind als in den gemässigten Zonen, haben die meisten Länder ein oder mehrere Programme für Anpflanzungen. Sie sind im allgemeinen wichtiger als die für die Bewirtschaftung natürlicher Wälder. Der FAO-Expertenausschuss für Gen-Reserven des Waldes koordiniert die Untersuchung verschiedener Arten und setzt Prioritäten. Zur Zeit gilt die Aufmerksamkeit den tropischen Kiefern vor allem Pinus caribaea, P. oocarpa, P. kesiya, Agathis, Araucaria, Eukalyptus-Arten und anderen Harthölzern einschliesslich Gmelina arborea und Tectona grandis. Über die Biologie, die Reproduktionssysteme, die Variationsmuster und sogar über das natürliche Vorkommen einiger dieser Arten ist weniger bekannt als über wichtige Arten der gemässigten Breiten. Die

derzeitigen Untersuchungen schliessen Herkunftsversuche und Analysen der genetischen Variation ein. In der Zwischenzeit werden bei grossen Pflanzungsvorhaben weiterhin Samen von natürlichen Populationen benützt. Die Abnahme genetischer Vielfalt durch das Verschwinden natürlicher Populationen ist in vielen Ländern bedenklich. Man hat Programme für die Erhaltung gefährdeter Populationen in situ und ex situ entwickelt. Es bleibt jedoch noch viel zu tun. Die Reaktion der Genotypen auf den Standort wird zur Zeit noch untersucht. Man verfügt bereits über einige Informationen, besonders für Pinus caribaea und Tectona grandis.

PLANTATION FORESTRY IN THE TROPICS

Plantation forestry in the tropics is still very much less widespread than in subtropical and temperate regions. The approximate area under plantations in 1976 was twelve million ha although several countries included in this total extend from tropical to subtropical zones e.g. Australia, Brazil. Increasing pressures on remaining areas of natural forest necessitate the extension of fast growing plantations to supply the demand for forest products, but the management of existing ecosystems, especially rainforests, still has a valuable role to play in supporting rural communities and in maintaining fragile ecosystems and sites, including soils and water supplies.

The largest areas of plantations use surprisingly few species. Four pines and a cypress account for nearly all the softwood planting: Pinus patula and Cupressus lusitanica in the highlands and P. caribaea, P. kesiya and P. oocarpa in the lowlands. Other softwoods with a great potential include Aracauria and Agathis spp. but these are not yet widely planted. Among hardwoods, the eucalypts are the most widely planted group, though the number of species involved is also small. Notable are Eucalyptus camaldulensis, E. tereticornis, E. grandis, E. urophylla and E. deglupta.

The other hardwoods in use are a more diverse group, although genera in the Verbenaceae represented by Tectona grandis and Gmelina arborea are probably the most widespread. Various Terminalia species mahoganies (Meliceae), Acacia and Albizia species make up the bulk of the other plantings, but other important species, e.g. Triplochiton scleroxylon, Pericopsis elata and Cordia alliodora under study and development in several parts of the tropics. In future one may expect more interest in what are still described as 'minor forest products' e.g. gum arabic in addition to wood-producing species.

PRIORITIES IN THE STUDY OF VARIATION IN TROPICAL TREES

The F.A.O. panel of experts on forest gene resources publishes and periodically revises, a list of species used in plantation development for priority study. The latest of these (F.A.O. 1977) includes all the species mentioned above, plus a number of others of more local interest. Table 1 gives a selection of these.

Table 2 gives a list of species included currently in international provenance trial programmes (See also Wood 1976).

From the standpoint of variation, these programmes may be expected to yield ever increasing amounts of data on the individual species on a wide variety of sites in the tropics. At the same time attempts are being made to conserve provenances either *in situ* or *ex situ* in exotic conservation plantations (see also Kemp & Burley 1974; F.A.O./U.N.E.P. 1975). It will be noted firstly that much less is known of variation and distribution of tropical species than of temperate ones, and that secondly few of the provenances, land races and individual genotypes have yet been tested exhaustively. Relatively short periods are needed to obtain the information because of the speed with which commercial and sexual maturity are attained.

Table 1. Tree species used in plantation development.

CENTRAL & SOUTH AMERICA	SOUTHEAST ASIA
Bombacopsis quinatum	Acacia nilotica
Cedrela odorata	Agathis spp.
Cordia alliodora	Albizia falcataria
Cupressus lusitanica	Anthocephalus chinensis
Nothofagus spp.	Araucaria cunninghamii
Pinus caribaea (all vars.)	A. hunsteinii
P. montezumae	Bambusa spp.
P. occidentalis	Dipterocarpus spp.
P. oocarpa	Eucalyptus deglupta
P. pseudostrobus/tenuifolia	E. urophylla
P. chiapensis	Emelina arborea
P. tropicalis	Pinus kesiya
Prosopis spp.	P. merkusii
Swietenia spp.	Tectona grandis
	Toona spp.
AFRICA	AUSTRALIA
Acacia spp.	Acacia spp.
Aucoumea klaineana	E. camaldulensis
Entandrophragma spp.	E. citriodora
Khaya spp.	E. cloeziana
Naucllea diderrichii	E. grandis
Terminalia spp.	
Triplochiton scleroxylon	

Table 2. Species included in international tropical provenance trials either in progress or in preparation.

SPECIES	AGENCY*
<i>Araucaria angustifolia</i>	F.A.O.
<i>Araucaria cunninghamii</i>	Queensland Forest Department/ Papua New Guinea.
<i>Cedrela odorata</i>	C.F.I., Oxford
<i>Cordia alliodora</i>	C.F.I., Oxford
<i>Eucalyptus camaldulensis</i>	C.T.F.T., France; C.S.I.R.O., Melbourne
<i>E. deglupta</i>	C.S.I.R.O., Australia
<i>E. urophylla</i>	C.T.F.T., France
<i>Gmelina arborea</i>	Danish/F.A.O. Seed Centre
<i>Pinus caribbaea</i>	C.F.I., Oxford and
<i>P. kesiya</i>	F.A.O./C.F.I./C.S.I.R.O./ Thai-Danish Centre
<i>P. merkusii</i>	C.F.I. and C.S.I.R.O.
<i>P. oocarpa</i>	F.A.O./C.F.I./I.N.I.F., Mexico
<i>P. patula</i>	I.N.I.F. Mexico
<i>P. tenuifolia/pseudostrobus</i>	C.F.I.
<i>Tectona grandis</i>	Danish/F.A.O. Seed Centre

- * C.F.I. Commonwealth Forestry Institute
 C.S.I.R.O. Commonwealth Scientific and Industrial
 Research Organization
 C.T.F.T. Centre Technique Forestier Tropical
 F.A.O. Food and Agriculture Organisation
 (of the United Nations)
 I.N.I.F. Instituto Nacional de Investigaciones Forestales
 U.N.E.P. United Nations Environment Programme

Features of tropical tree variation

The lack of knowledge relating to tropical species which are already known to have importance for development in tropical countries is well seen in the difficulty experienced in obtaining seed from properly characterized populations or seed sources. Floral biology and reproductive behaviour are still poorly understood, even in species which are widely planted (Styles 1972). However, several studies have been made and are in progress to determine patterns of genetic variation, in addition to provenance trials; both may often use identical material for study. Such studies involve the use of numerical and classical taxonomy (e.g. Burley & Burrows 1972; Styles, Stead & Rolph, in press), cytological study (e.g. Styles & Khosla 1976), enzyme electrophoresis (Burley 1976; Bawa 1976) and resin analysis (Burley & Green 1978, private communication).

In many of the countries where important species grow, valuable genetic material is being lost at a rapid rate

through forest destruction, often before the levels of variation present within and between populations are even partly understood, and certainly before they are adequately quantified. Genetic conservation is therefore urgent in many areas, and guidelines for action have been published (U.N.E.P./F.A.O. 1975). Although new genetic material continues to be discovered in the wild for many important species, the variation present in the established plantations and provenance trials is increasingly becoming the basis for breeding and selection for the wide variety of planting sites found in tropical countries. Massive seed purchases by commercial planting companies have been made independently of the scientific collectors of provenances, particularly of Pinus caribaea. Although they do not cover the same genetic base, the very large areas of plantation that have been raised from these seed lots will become important gene pools in their own right, both from the point of view of genetic improvement and of gene conservation.

Review of species groups for plantations

There is no space here to consider the detailed information on variation in tropical species that already exists. Reference should be made to Burley & Styles (1976); Nikles, Burley & Barnes (1978) and to other publications relating to variation in tropical species sponsored or supported by the I.U.F.R.O. working parties S2.03-01 and S2.02-08.

However, some important points covering widely planted species are outlined below.

Tropical conifers. Pinus caribaea with its three varieties

<u>P. caribaea</u> var. <u>hondurensis</u>	Central America
<u>P. caribaea</u> var. <u>caribaea</u>	Cuba and
<u>P. caribaea</u> var. <u>bahamensis</u>	Bahamas

is undoubtedly the most important single pine species at present being planted in the tropical lowlands. Seed collections and explorations carried out by the Commonwealth Forestry Institute, Oxford, since 1962 are now producing much information on patterns of variation present in the natural populations and their growth interactions with site (for details of origin see Greaves 1978). P. oocarpa is, on many tropical lowland sites, even more promising, though its taxonomy and that of the closely related P. patula is still under study (e.g. Styles 1976).

Much of the seed collected has been distributed in the form of international provenance trials. Table 3 shows the numbers of trials and countries involved in this programme, and further collections of Mexican pines have been made by the Instituto Nacional por Investigaciones Forestales, Mexico (I.N.I.F.) and are being made available through F.A.O., which has also coordinated the other trials. Other studies on pines are summarized in Table 2.

Table 3. The international provenance trials coordinated by the Commonwealth Forestry Institute.

Species	Number of provenances collected	Number of countries participating
<i>Pinus caribaea</i>	36	49
<i>Pinus oocarpa</i> (1)	45	35
<i>Pinus oocarpa</i> (2)	20*	12
<i>Pinus pseudostrobus</i> / <i>tenuifolia</i>	25	11
<i>Cedrela odorata</i>	14	20
<i>Cordia alliodora</i>	13	18

* In collaboration with I.N.I.F., Mexico.

Results for these trials show differences in survival and early growth that are difficult to relate directly to the factors of the seed collection site, and the position is further complicated by the apparent occurrence of intermediate forms, e.g. between *P. caribaea* and *P. oocarpa* and between *P. oocarpa* and *P. tenuifolia* / *P. pseudostrobus* in Central America. The latest positions are reported in Nikles, Burley & Barnes (1978). Breeding programmes with *P. caribaea* are well developed in Queensland, Fiji, Malaysia and Congo. The Asian pines have been under study longer, though trials are less widespread but the characteristics of the island and mainland sources of *Pinus merkusii* are now well understood. A 'grass-stage' in which the young trees remain very small whilst building up reserves for rapid height growth is characteristic of the mainland provenances. This is a useful adaptation to a fire-prone environment, but it makes it of doubtful economic value as a plantation tree on sites where weed growth is a problem as the phase may last for two or three years and lead to excessive weeding costs. *Pinus kesiya* has been studied in detail in Zambia and Madagascar particularly, and *P. patula* in east and central Africa.

Other conifers which are of some importance include *Araucaria* spp. (Ntima 1968) under study particularly in Queensland and Papua New Guinea, and *Agathis* (Whitmore 1977). Tropical Eucalypts. As indicated above a small number of species form the bulk of the planting in tropical countries. Of these, important provenance trials have been carried out or are in progress with *E. camaldulensis*: Eldridge 1975; Karschon 1974; Ojo & Jackson 1973; *E. deglupta*: Davidson & Fairtamb 1974; *E. grandis*: Burgess 1974; *E. tereticornis*; *E. urophylla*: Martin and Cossalter 1975/6.

Very considerable variation in all these species has been demonstrated both between and within populations. *E.*

tereticornis, with its tendency for wind pollination, appears to be a constituent of a number of hybrids found in exotic populations and is the basis of various land races adapted to local conditions, e.g. '12ABI' (Madagascar, Congo), 'C' (Zanzibar), 'Mysore hybrid' (India).

Other tropical hardwoods. An excellent summary of variation and breeding¹ work in tropical hardwoods has been compiled by Ashton, Bawa, Whitmore and others in Burley & Styles (1976). Studies of variability in plantations are few, and teak, Gmelina arborea and Triplochiton scleroxylon are the main species on which work has been done.

Teak has been the subject of provenance trials organized by the Danish/F.A.O. Forest Tree Seed Centre, sixty-five provenances being under trial in fourteen countries (Hedegart 1976; Keiding 1973). Among the most important characters determined to be under genetic influence is the age at which flowering commences, because this generally puts an end to monopodial growth. In Gmelina arborea variation may be less, although most large scale plantations (e.g. in Brazil) have used a narrow range of seed sources; information from provenance trials suggests that there is more variation in newly collected provenances.

REFERENCES

- Bawa, K.S. (1976). Breeding of tropical hardwoods; an evaluation of underlying bases, current status, future prospects. "Tropical trees: variation, breeding and conservation." (Ed. by J. Burley & B.T. Styles), pp. 43-59. Academic Press, London.
- Burgess, I.P. (1974). Eucalyptus grandis improvement programmes, Coffs Harbour. Australian Forestry Research Council Research Working Group 1. Proceedings of 4th Meeting, Melbourne.
- Burley, J. (1976). Genetic systems and genetic conservation of tropical pines. "Tropical trees: variation, breeding and conservation." (Ed. by J. Burley & B.T. Styles), pp. 85-100. Academic Press, London.
- Burley, J. & Burrows, P.M. (1972). Multivariate analysis of provenance variation in needles of Pinus kesiya. *Silvae Genetica*, 21, 69-77.
- Burley, J. & Styles, B.T. (1976). Tropical trees; variation, breeding and conservation. Academic Press, London.
- Davidson, J. & Fairlamb, J. (1974). Provenance trials of Eucalyptus deglupta in Papua New Guinea. Australian Forest Research Council Research Working Group 1. Proceedings of 4th Meeting, Melbourne.
- Eldridge, K.C. (1975). An annotated bibliography of genetic variation in Eucalyptus camaldulensis. Tropical Forestry Papers #8. Commonwealth Forestry Institute, Oxford and C.S.I.R.O. Division of Forest Research, Canberra.

- F.A.O.(1977). Report of the fourth session of the F.A.O. panel of experts on forest gene resources. F.A.O. Rome.
- F.A.O./U.N.E.P.(1975). Report of a pilot study in the methodology of conservation of forest genetic resources. Report FO:MISC 75/8. F.A.O. Rome.
- Greaves,A.(1978). Descriptions of seed sources and collections for provenances of Pinus caribaea. Tropical Forestry Papers #12, Commonwealth Forestry Institute, Oxford.
- Hedegart,T.(1976). Breeding systems, variation and genetic improvement of teak (Tectona grandis l.f.) "Tropical trees; variation, breeding and conservation" (Ed. by J.Burley & B.T.Styles), pp. 109-123. Academic Press, London.
- Karschon,R.(1974). The relation of seed origin to growth of Eucalyptus camaldulensis in Israel. Israel Journal of Agricultural Research, 23, pp. 159-173.
- Keiding,H.(1973). Status of the international provenance trials of teak, Tectona grandis L., October 1973. "Tropical provenance and progeny research and international cooperation" (Ed. by J.Burley & D.G.Nikles), pp. 300-308, Commonwealth Forestry Institute, Oxford and Queensland Department of Forestry, Brisbane.
- Kemp,R.H. & Burley,J.(1975). Depletion and conservation of forest gene resources. Symposium Man and his environment. Birmingham University. 14pp.
- Martin,B. & Cossalter,C.(1975-6). The Eucalyptuses of the Sunda Islands. Translations from Bois et Forets des tropiques nos. 163-166 by the New Zealand Forest Service.
- Nikles,D.G., Burley,J. & Barnes, R.D.(1978). Progress and problems of genetic improvement of tropical forest trees. Proceedings Joint Workshop I.U.F.R.O. Working parties 2.02.08 and 2.03.01, Brisbane. Commonwealth Forestry Institute, Oxford, in press.
- Ntima,O.O.(1968). The Araucarias. Fast growing timber trees of the lowland tropics. #3 Commonwealth Forestry Institute, Oxford.
- Ojo,G.O.A. & Jackson,J.K.(1973). Eucalyptus camaldulensis provenance trials in Nigeria at six years. "Tropical provenance and progeny research and international cooperation." (Ed. by J.Burley & D.G.Nikles), pp. 273-283. Commonwealth Forestry Institute, Oxford.
- Styles,B.T.(1972). The flower biology of the Meliaceae and its bearing on tree-breeding. Silvae Genetica, 21, 149-204.
- Styles,B.T.(1976). Studies of variation in Central American pines. I. The identity of Pinus oocarpa var. ochoterenai Martinez. Silvae Genetica, 25, 109-117.
- Styles,B.T. & Khosla,P.K.(1976). Cytology and reproductive biology of Meliaceae "Tropical trees; variation, breeding and conservation." (Ed. by J.Burley & B.T.Styles), pp.

- 61-67. Academic Press, London.
- Styles, B.T., Stead, J.W. & Rolph, K.J. (in press). Studies of variation in Central American Pines. II. Putative hybridization between Pinus caribaea var. hondurensis (Senecl.) Barr. & Golf and P. oocarpa Schiede. Silvae Genetica.
- Whitmore, T.C. (1977). A first look at Agathis. Tropical Forestry Papers #11. Commonwealth Forestry Institute, Oxford.
- Wood, P.J. (1976). The development of tropical plantations and the need for seed and genetic conservation. "Tropical trees: variation, breeding and conservation." (Ed. by J. Burley and B.T. Styles), pp. 11-18. Academic Press London.

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