Institute of Terrestrial Ecology



Natural Environment Research Council

Institute of Terrestrial Ecology

Annual Report 1982

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Printed in Great Britain by Titus Wilson & Son Ltd., 28 Highgate, Kendal, Cumbria

ISBN 0 904282 74 0 ISSN 0308-1125

Institute of Terrestrial Ecology 68 Hills Road Cambridge CB2 1LA 0223 (Cambridge) 69745

Cover illustrations
Detail from 'Kingfisher' by Simon Burr on industrial placement at
Merlewood from the Blackpool and Fylde College of Higher and Further
Education. Marram grass photograph by Richard Scott.

The Institute of Terrestrial Ecology (ITE) was established in 1973 from the former Nature Conservancy's research stations and staff, joined later by the Institute of Tree Biology and the Culture Centre of Algae and Protozoa. ITE contributes to and draws upon the collective knowledge of the fourteen sister institutes which make up the Natural Environment Research Council, spanning all the environmental sciences.

The Institute studies the factors determining the structure, composition and processes of land and freshwater systems, and of individual plant and animal species. It is developing a sounder scientific basis for predicting and modelling environmental trends arising from natural or man-made change. The results of this research are available to those responsible for the protection, management and wise use of our natural resources.

One quarter of ITE's work is research commissioned by customers, such as the Nature Conservancy Council, who require information for wildlife conservation, the Department of Energy and the Department of the Environment, and the EEC. The remainder is fundamental research supported by NERC.

ITE's expertise is widely used by international organizations in overseas projects and programmes of research.

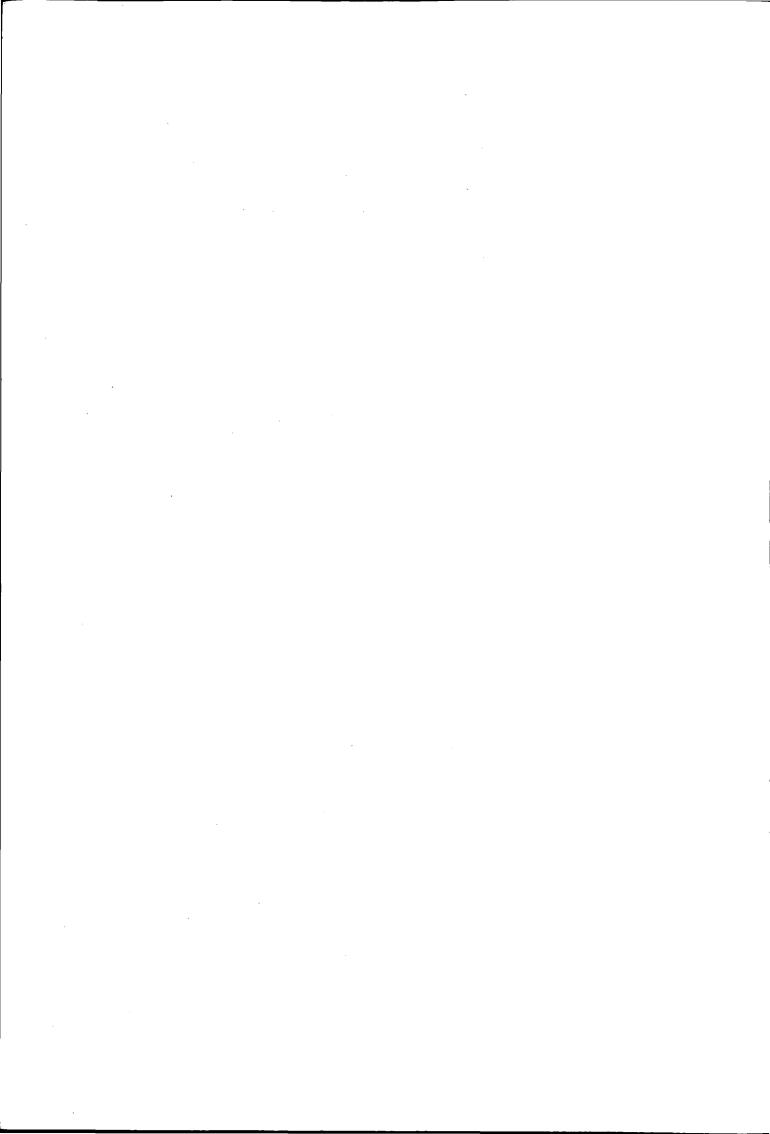
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Introduction

ITE research programmes

In the year under review in this Annual Report, a major change has been made in the organization of the Institute. The Divisions and Subdivisions which were set up at the time of the formation of ITE in 1973 have been abolished. The management and administration of the Institute is now more directly centred on individual stations, with the research of the Institute coordinated by the Assistant Directors through 15 main programmes. This change was made because it was felt that there was insufficient integration of the research projects within the Institute. By co-ordinating these projects in broad programmes, it is hoped that the research of ITE will be seen to have a more coherent structure, and will lend itself to a more comprehensive and balanced development. In all of the programmes, there is already active collaboration with relevant research in universities.

The 15 research programmes, together with the numbers of staff and the total cash expenditure on each programme in the year 1982/83, are summarized in Table 1. The Management Group and senior staff of ITE are now reviewing the research within each programme so as to identify future priorities, but the current aims of the programmes and some indication of their future development are summarized below.

1. Forest and woodland ecology

The principal aim of this programme is to develop integrated studies of the factors influencing the

Table 1. ITE research programmes and cash expenditure 1982/83

		1982/83			
		Staff	Cash		
		numbers	expenditure		
	Programme		(£K)		
1	Forest and woodland ecology	18∙5	410-5		
2	Freshwater ecology	22.0	452-4		
3	Rehabilitation of disturbed ecosystems	8.0	150∙7		
4	Management of natural and man-made habitats	11.5	246·1		
5	Survey and monitoring	19∙0	383.9		
6	Airborne pollutants, including radionuclides	26.0	510.8		
7	Plant physiology and genetics	20.0	388-0		
8	Ecophysiology and pollution in animals	19-0	346-8		
9	Plant population ecology	4.0	49.9		
10	Autecology of animals	20.0	373.7		
11	Faunistic studies	15∙0	270.6		
12	Cycling of nutrients	20.5	363-9		
13	Land classification and land use	14.0	213-6		
14	Chemical and technical sciences	11.0	170∙4		
15	Systems analysis and biometrics	11.0	190.6		

development of plants and animals in woodland ecosystems, natural and man-made. From the better understanding of forest dynamics derived from these studies, it is hoped to improve the rational management of forest and woodland resources, and to predict the consequent changes in the balance of the use of forests for wood production and wildlife conservation. programme envisages a continuation of the characterization of the forest and woodland resources within the UK which has been an essential part of ITE's work over the last 10 years, and will also sustain fundamental studies on root growth, water budgets, and stability. Investigations of the direct and indirect effects of afforestation on flora. fauna, soils and fresh waters have already been initiated and will be further developed in future. Research projects on invertebrate pests, squirrels, deer and other herbivores have also been started in order to investigate the role of these organisms in forest and woodland ecology. Future projects will concentrate on the investigation of the potential of a wide range of tree genotypes, including new species and mixtures of species. In view of the potential importance of forestry to the British economy, this whole programme of research should be expanded to at least double the present level of investment, which is about 10% of the total ITE expenditure. However, neither the science budget nor commissioned research shows any signs of expanding to meet the required investment, and this particular area of research must, therefore, remain sadly under-developed.

2. Freshwater ecology

This programme covers all of ITE's work on freshwater systems, and represents about 10% of ITE's total expenditure. The main thrust of the research is towards synoptic limnology, and the impact of terrestrial inputs on aquatic biota, eg the effects of pollutants on freshwater organisms. Existing projects have concentrated on survey and distributional studies associated with the synoptic survey of freshwater habitats, and these studies are expected to be continued at the present level. The Loch Leven Project Group, which has been studying the effects of physical and chemical factors on the interaction between phytoplankton, zooplankton and fish populations, has been maintained for some years, and this level of effort will be retained in association with universities. Pollution studies, and particularly those of heavy metals in rivers and on the impact of acidic inputs, are likely to be increased. The taxonomy and culture of freshwater algae and protozoa will be maintained at about their present level.

3. Rehabilitation of disturbed ecosystems

Revegetation of derelict land, with special reference to the creation of biologically-rich habitats on land which has previously been devoted to industry, forms the main thrust of this small group of projects. Whereas attempts are usually made to establish productive grass swards or stands of trees on rehabilitated sites of dereliction, ITE has a group of projects aiming to create biologically-rich mixtures of plants and animals. This topic is a relatively new interest for ITE, and one which has hitherto grown in a somewhat piecemeal fashion to its present level of about 3% of total expenditure. It is now hoped to develop a more concerted programme of research linked to Programme 4.

4. Management of natural and man-made habitats

The aim of this programme is to elucidate the principles necessary for the rational development of techniques for managing natural and manmade assemblages of vegetation for production, conservation, and/or amenity. The programme will continue to be concerned with assemblages of vegetation, but excluding those occurring in disturbed habitats (Programme 3) and those in forests and woodlands (Programme 1). The present level of investment is only about 5% of the total expenditure, and is expected to continue at about this level for the immediate future.

5. Survey and monitoring

ITE's interest in survey and monitoring is aimed primarily at compiling a record of national biological resources (habitats, communities, and individual species) which could form the nucleus of a national ecological data base and at describing the distribution and monitoring trends in these resources. The programme includes the maintenance of the Biological Records Centre (BRC) and the Terrestrial Environment Information System (TEIS), and is primarily supported by the science budget, representing about 8-5% of ITE's total expenditure. It is hoped, however, to attract increased support for this important function of ITE from commissioned research, and by the publication of information from the ecological data base.

6. Airborne pollutants, including radionuclides

Research on the fate and effects of pollutants that can be dispersed aerially currently occupies about 11% of ITE's total expenditure. This research is focused on pathway studies, including:

- i. the chemistry of pollutant transformations in the atmosphere;
- ii. deposition processes of gases and particles from the atmosphere to plants, soils and other surfaces;
- direct effects of pollutants on plants and animals.

Within the present financial constraints, ITE's involvement with airborne pollutants will inevitably be restricted to radionuclides, ozone, sulphur, nitrogen and fluorine pollutants. Because of the importance, actual and potential, of these pollutants, in part contributing to 'acid rain', it is highly desirable to expand the existing programme, but this expansion is unlikely unless more support is given by Government Departments and agencies.

7. Plant physiology and genetics

The understanding of physiological and genetic processes, and especially those where withinspecies variation might be exploited for plant improvements, forms a fundamental part of ITE's ecological research. Such research includes work on:

- i. photosynthesis and related processes contributing to the growth of trees;
- ii. shoot morphology and root distribution;
- iii. prediction of mature growth characteristics and identification of early selection criteria;
- iv. transition from juvenile to mature phases of tree growth, including flowering and fruiting.

The present programme of research, representing about 8.5% of ITE's total expenditure, is primarily on temperate species, with a limited degree of work on tropical species, particularly trees. However, current overseas interest in the development of plant ecophysiology and genecology, and subsequent commissions, may double the input to the programme for work on tropical species.

8. Ecophysiology and pollution in animals

In addition to studies of the basic physiological, biochemical and genetic processes in animals, this programme is concerned with the effects of pollutants. Current research on physiology concentrates on studying factors controlling the reproduction in animals basic to many of the sublethal effects of pollutants. This is essentially a long term programme, for which the fundamental research needs to be maintained at a relatively constant level (currently nearly 8% of ITE's expenditure), although the level of commissioned funding may fluctuate markedly as particular problems are identified in the agricultural, forestry and wildlife communities.

9. Plant population ecology

The study of plant demography and ecology is a relatively low key programme which is unlikely to expand markedly in the near future, and at present occupies only about 1% of ITE's research resources. The current emphasis of the programme is on the heritable variation found within natural populations of plants, and the effects of different growth strategies on plant ecology.

10. Autecology of animals

In the past, a considerable degree of research effort has been expended on the understanding of the factors determining the distribution and abundance of particular species of animals. This is again an important programme, involving about 8% of ITE's resources, and is expected to be maintained at approximately the same level, or increased if commisssioned research funding can be obtained for new work. Particular emphasis is given to examining and predicting the effects of the manipulation of animal populations by management. The programme covers basic studies of species chosen because they are easy to study, and more applied research on species which pose particular management problems, eg as pests, exploited species, and rare or endangered species.

11. Faunistic studies

Studies of associations of interacting animal populations currently represent about 6% of ITE's work. No marked changes in this level of investment are planned in the immediate future, and the present programme includes work on:

- i. species interactions and interdependencies, including predator/prey, parasite/host and herbivore/plant relationships;
- ii. effects of succession and habitat management on the diversity of fauna;
- iii. effects of habitat area and isolation on the faunas of individual sites.

12. Cycling of nutrients

The integrated programme of research which is being done in conjunction with universities and other research institutes involves the definition and examination of the major variables (including herbivores) which affect the flow of elements in contrasting natural and semi-natural ecosystems. This research involves the identification of the spatial and temporal effects of natural and manmade influences on the rates of different soil processes. The research is regarded as being of fundamental importance, and, ideally, should be greatly increased from its present 8%. Such an increase is unlikely because of the lack of recognition by Government Departments of the importance of this aspect of ecological science. ITE's current work largely represents strategic research which is funded by the science budget.

13. Land classification and land use

The improvement of the understanding of habitat characteristics and their interrelationships, and the development of improved methods of resource management represent an important applied programme which has, as yet, attracted relatively little support from the resource man-

agement agencies. ITE's research programme is centred on the rural environment, and the programme is linked to survey and monitoring to ensure a concerted approach to the monitoring of change in the rural environment. However, as problems of land use become more readily apparent, commissioned research support for this programme of research may be expected to increase from its present level of only about 5% of total expenditure.

14. Chemical and technical sciences

The provision of services of chemistry and technical sciences, together with research on the development of analytical chemistry within ecology, forms an essential base for the maintenance of efficient ecological research. Increasingly, research ecology requires a sound knowledge of the chemical inputs to ecological systems and to organisms, and developments in environmental chemistry must therefore keep pace with other research activities. Of critical importance to the maintenance of a sound research base is an adequate programme of capital investment in new equipment. This programme is not, however, merely a service programme, as a considerable amount of basic chemical research is necessary to maintain effective services in analytical chemistry. It currently occupies about 4% of ITE's total expenditure.

15. Systems analysis and biometrics

The development of appropriate techniques of Systems analysis and biometrics, and the application of these techniques to ecological research also form an important component of the ITE research capability. Indeed, increased support for this aspect of ITE's research is highly desirable but is, again, limited by the available resources, and by the limits on the availability of suitable expertise. The level of expenditure on the provision and development of these services is about 4% of the total.

The above brief description of the 15 main programmes of ITE's research is merely intended to give some indication of the range of initiatives incorporated in the whole of the ITE research programme. In this Annual Report, summaries of some of the research within each of these programmes are given, covering about one third of the whole programme of research. In reading these summaries of individual research projects, however, it is desirable to relate the immediate results to the much broader aims of the individual programmes. The philosophy underlying ITE's research was summarized in the Annual Report for 1981 and this introduction to the Annual Report for 1982 is intended to provide the expression of that philosophy in practice.

J N R Jeffers Director, ITE

Research reports

Forest and woodland ecology

BROWSING DAMAGE DONE BY RED DEER TO YOUNG STANDS OF SITKA SPRUCE

There is widespread concern about the damage being done to stands of trees by red and roe deer resident in, and increasingly colonizing, plantations. Sitka spruce, the single most commonly planted tree species in Britain, seems to be less severely affected than lodgepole pine, another economically important introduced conifer. Nevertheless, many Sitka spruce trees lose their leaders as a result of browsing, sometimes responding by the production of more than one (multiple) leader. The bark of older trees is sometimes consumed. To assess the incidence of these types of damage and record the subsequent effects on forest growth, a study of deer ecology in second-rotation Sitka spruce forest was initiated in 1978.

Randomly chosen sites, each 1.5 ha, based on subdivisions of forest compartments were monitored 4 times a year at elevations from 50 m to 500 m. To estimate deer occupance, pellet groups were counted at, and removed from, 6 'plots' at each site. At 14 sites there were young trees less than 2 m tall, and, in areas of 18×10m around each dung plot, sequential observations of damage to leading shoots and changes in numbers of leaders were made on every tree. Height was measured every March and September. With more than 2000 young trees being studied, the responses of Sitka spruce to different amounts of damage over several years will be assessed.

Incidence of damage

At any one time, substantial numbers of young Sitka spruce were lacking all or part of their leading shoots, the damage mostly being attributed to deer browsing (Table 2). Despite variation between sites, amounts of

Table 2. Incidence of deer browsing, and other damage done at Glenbranter to leading shoots of Sitka spruce up to 7 years after planting

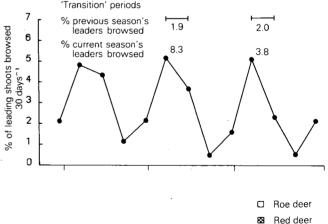
Incidence of deer browsing and other damage; percentage (%) of trees affected

	Observations made					
Year of	Sept 78/	Aug 79	Sept 79/	Aug 80	Sept 80/	Aug 81
planting	Browsing	Other	Browsing	Other	Browsing	Other
1973	30	5	26	7	23	34
1974	32	7.	22	21	10	29
1975	43	2	33	3	15	20
1978	54	7	61	7	76	12
1979	_	_	35	17	38	11

browse damage seem to reach a peak in the third year after planting. For example, browse damage done 3, 4 and 5 years after planting in 1975 affected a percentage of trees decreasing from 43% to 15%. On the other hand, 54%, 61% and 76% of trees were damaged in the first, second and third years after planting in 1975.

In the event, these percentages tend to underestimate amounts of browsing, because leaders and their replacements can both be damaged within 6 months. On average, this repeated damage occurred on 2% of trees. Usually, damage by deer greatly exceeded that from other causes, but many trees were killed in spring 1981 by an exceptionally intense series of frosts. Other losses were associated with strong winds, and with the clashing and rubbing of branches and twigs where trees were clumped. Some leading shoots were damaged by black and red grouse, hares, rabbits, field voles and stray sheep, the damage done by the latter being similar to that done by deer.

Browsing damage, which in this article is synonymous with the loss of the apical bud plus part or all of the annual increment of the leading shoot, followed a definite seasonal pattern (Figure 1). Damage increased



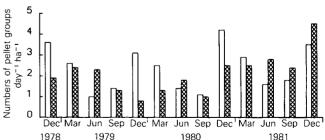
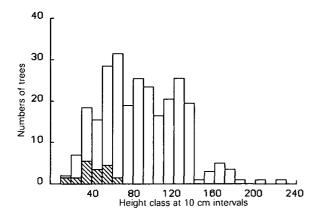


Figure 1 Seasonally varying (i) deer browsing on leading shoots of Sitka spruce and (ii) deposition of pellet groups, at Glenbranter from December 1978 to December 1981 (means of data collected from 14 plantings; intensive observations made during periods of 30 days).

after budbreak to a peak on new growth in early summer, and to another peak during winter. The latter peak in the period December-March may be attributed to a shortage of alternative foods, whereas damage done in early summer is related to the attractiveness of the young shoots — neither peak can be convincingly associated with increased numbers of pellet groups.

About 40% of all trees less than 50 cm in height lost their leading shoots, but those taller than 80 cm were rarely damaged in this way (Figure 2), as shown by the decline in browsing damage in the fourth, and later, years after planting.



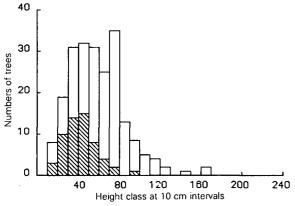


Figure 2 Total numbers (\square) of trees, and numbers of them with browsed leaders (SI) in a series of Sitka spruce at Glenbranter arranged in 10 cm height classes. Observations made on 2 stands during winters of 1978/79 and 1979/80.

Reaction of trees

Percentages of trees without leaders were usually maximal during winter, coinciding with a peak period of browsing (Figure 3). On occasions, and in some very young stands, percentages exceeded 50% in March and June. However, despite this apparently serious damage, more than 50% of the damaged trees grew new leaders during the ensuing season. Of the trees without leaders in September 1979 (11% — Figure 3), less than half had been without for more than 6 months. More than half of the trees regrew leaders within 12 months (Table 3). Only 2% of trees were without a leader for more than a year.

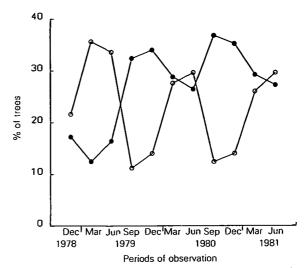


Figure 3 Seasonally and annually varying proportions of Sitka spruce, planted at 14 sites between 1973 and 1979, without leading shoots (○—○) or with multiple leaders (●—●).

Table 3. Timing of leader damage and recovery when Sitka spruce planted at Glenbranter in different years was subject to deer browsing

Year of planting	% of trees without leading shoots; Sept 79	Percentage of trees that were leaderless in Sept 79 and had lost their leaders in the previous 6 months	Percentage of trees that were leaderless in Sept 79 but developed new leaders by Sept 80
1973	16		63
1974	9	52	81
1975	5	60	100
1978	26	56	65
1979	6	96	80

New leaders in Sitka spruce regenerate from main stem lateral buds and by the 'flagging-up' of older side branches, the latter phenomenon occurring at any time of the year. Frequently young trees respond to the loss of a solitary leader by producing more than one replacement, becoming multistemmed and losing value as timber crops in the process. At present, 30% of the trees 1/8-years old at Glenbranter are multistemmed (Figure 3), but only 14% of pre-thicket and thicket stage trees (9/27-years old) have multiple stems, and fewer still have them in the pole and high forest stages. This decrease in numbers of multistemmed trees in older crops results from thinning, both natural and artificial. In the earlier stages, some subsidiary leaders 'flag-down' and revert to their positions as side branches, but the smaller number of trees with multiple stems in the older stages could also reflect a lower deer density in the past. Therefore, monitoring is continuing for several more years to assess if the response of Sitka spruce alone can account for the decline.

Browsing decreased annual height increments, the proportionate losses being greatest in the smallest trees (Figure 4). For this reason, comparisons had to be made among trees that were initially of the same height. These comparisons indicate that the annual height increments of browsed trees were not much smaller than those of their unbrowsed counterparts. This unexpectedly small effect may be explained by the small lengths of stem removed (about 4 cm) and the speedy replacement of leaders by 'flagging' or the growth of lateral buds. Additionally, it is possible that browsed trees respond by growing more rapidly, perhaps because competition from ground vegetation is decreased by grazing.

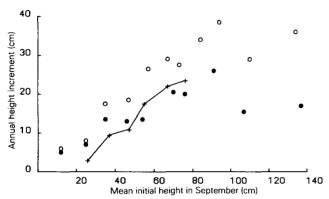


Figure 4 Annual height increments of Sitka spruce which started the growing season with their leading shoots intact (\circ) or with their apical meristems removed by browsing (\bullet). += leading shoots browsed during the growing season. Trees up to 1 m tall arranged in 10 cm height classes; trees taller than 1 m arranged in 20 cm classes—heights judged during the dormant season.

Discussion

Sitka spruce appears well able to minimize the early loss of leading shoots. However, the effects on timber quality, although probably negligible, still need to be checked. Nonetheless, it seems that the early damage done by deer to Sitka spruce is more apparent than real, although further work must be done to evaluate the economic loss attributable to multiple stems. However, bark-stripping by red deer may well prove to be a more serious form of damage. At Glenbranter, about 1% of trees, 10/40-years old, are stripped annually.

In the future, the number of pathogens infecting wounds could increase, Sitka spruce being a quite recent introduction to Britain at present lacking its full complement of pests and pathogens. Also, the habits of the deer might alter, perhaps with changes in habitat. As conifer browse constitutes only a small proportion of the food intake of both red and roe deer, a relatively minor shift in diet in either species could greatly increase the number of shoots browsed. For these reasons, deer are likely to remain a potential threat to the production of Sitka spruce in upland Britain.

D Welch, B W Staines, D Scott and D C Catt

MODELLING SUCCESSION IN A MIXED BROADLEAVED/PINE FOREST IN CHINA

(The data for this report were collected by J Miles during 1981 while a quest of the Chinese MAB National Committee)

Mixed broadleaved/*Pinus koraiensis* forest is the main natural forest type below 1100 m over much of northeast China, North Korea and south-eastern Siberia. It is scientifically interesting for its species richness and its complex development of strata. Commercially, it is valuable for its timber, particularly that of *P. koraiensis*, and for the many medicinally important herbs occurring in the field layer. However, there is doubt about the best way of managing the forest to obtain a timber harvest, while also ensuring natural regeneration. More needs to be known about the dynamics of the forest.

Records were taken during July 1981, with Chinese colleagues, of 800 canopy trees in a forest in Chang Bai Shan, north-east China. Additionally, potential regeneration was assessed by counting all saplings taller than 30 cm growing beneath these trees. The data were then used in the Markovian model of forest succession suggested by Horn (1975a & b, 1976), in which a forest is likened to a honeycomb of independent cells, each occupied by one tree in which tree-by-tree replacement occurs. The probability that species S_1 will be replaced by species S_2 is assumed to be proportional to the number of saplings of the latter, S_2 , in the understorey of the former, S_1 .

In its simple form, Horn's model assumes an even age distribution, equal longevity of all canopy species, and synchronous replacement of individuals. The predicted future equilibrium composition of the stand using this model is given in Table 4. Two features are of particular interest:

- i. the large decrease in *P. koraiensis* was quite unexpected; interestingly, it was matched by increased numbers of *Acer mono, Tilia amurensis* and *T. mandschurica*, but not of other tree species;
- ii. equilibrium is reached after 5 generations, having been nearly attained after only 2 generations, suggesting that the stand is nearly 'climax'.

Table 4. The changing composition in successive generations of a broadleaved/pine forest in north-east China, as suggested by the application of Horn's model (numbers of trees of one species expressed as % of total)

	Generation						
Tree species	0	1	2	3	4	5	6
Acer mono	18	37	29	32	31	31	31
Fraxinus							
mandschurica	14	14	17	16	16	16	16
Pinus koraiensis	34	4	3	5	5	5	5
Quercus mongolica	11	10	10	9	9	9	9
Tilia amurensis	16	20	26	25	24	24	24
T. mandschurica	1	9	6	7	7	7	7
Others	6	6	9	6	7	6	6

Forests of the type investigated typically contain 20-60% (by number) of *P. koraiensis*; it has been assumed that they are climax (Institute of Forestry & Pedology 1978; Soloduhin 1964), but clearly either this assumption is wrong or the model is not sufficiently realistic. The assumption has probably arisen because of the extensiveness of mixed broadleaved/*P. koraiensis* forest and the long life-span, 400-500 years, of dominant *P. koraiensis*, but substantive evidence is not available.

When examining the biological assumptions of Horn's model, it was found that allowances for differences in species longevity produced only small changes in the equilibrium composition. In particular, P. koraiensis never recovered beyond 10%. Changing the initial age distribution to that likely if the stand were either midsuccessional, or at or near climax, had no effect on the equilibrium composition. When testing the sensitivity of the model to some of the underlying biological assumptions, and assessing the degree of change that was needed to obtain a proportion of P. koraiensis in the simulated climax forest within the expected range, it was found that the transition probabilities were crucially important - more needs to be known about their variation in space and time, also about the validity of the indirect means adopted to estimate them. Although P. koraiensis commonly reached a frequency of 40-55% after 300-450 years before its population crashed, its proportion at equilibrium thereafter could only be increased in simulations to 30% by heavy, and probably quite unrealistic, weighting of the probability matrix. This result suggests that P. koraiensis may be a midsuccessional dominant, and the sparse available evidence tends to support this idea. If this hypothesis is correct, the existing P. koraiensis-rich broadleaved forests must reflect the historical effects of periodic disturbances, probably by fire, and more locally (as at Chang Bai) by volcanic activity.

In conclusion, the use of Horn's model to explore the successional behaviour of a stand of mixed broadleaved/*P. koraiensis* forest has:

- i. identified our imperfect understanding of the system;
- ii. indicated where more information is needed; and
- iii. resulted in the development of specific hypotheses about the successional roles of *P. koraiensis* and other tree species.

J Miles and D D French

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AN APPROACH TO THE CONSERVATION OF MOIST TROPICAL FORESTS – THE DEVELOPMENT OF A WEST AFRICAN REGIONAL PROJECT

In the absence of substantial natural regeneration, foresters are repeatedly urged to do all in their power to conserve natural moist tropical forests. Few would disagree, but ways of checking the current net loss of 50 ha min-1 are not easy to find. In recent decades, foresters have applied their usual corrective to such a set of circumstances. They have sought and planted fast-growing exotics, predominantly species of Eucalyptus, Gmelina and Pinus, to mention but a few. To an extent, this policy has been successful, for it has rapidly recreated a source of fuel wood (about threequarters of the trees felled in the tropics are used for cooking. etc) and pulp. However, it has not, and will not, ensure the continuing commercial advantage of many tropical countries. For this to be achieved, it is necessary to reestablish the resources of indigenous hardwoods, and only then will the pressures on surviving natural forests be lessened. Thus, the managed cultivation of indigenous hardwoods is a priority, particularly if 'management' could shorten the rotation length, without affecting wood quality deleteriously.

Since 1970, members of ITE have been concerned directly and indirectly with events in Nigeria where overseas sales of 'Obeche', which used to account for 65% of Nigeria's round-wood exports, have been banned. The regeneration of Triplochiton scleroxylon, the source of 'Obeche', has been hindered not only by the activities of man, but also by the dearth of viable seeds. In the absence of good seed, attention was turned to the potential of vegetative propagation, a procedure enabling the rapid capture of genetic gains. The ITE team, with members in Nigeria and UK, has devised methods of managing stock plants for the predictable production of uniform batches of rooted cuttings. Perhaps even more important has been the development, following observations of the patterns of branching, of a way to identify clones whose cuttings should produce trees of above-average form and increment. Observations of these cuttings in plantations appear promising, and suggest that managed plantations may be harvestable within 40 years, compared to the 100/150 years in natural forests.

These procedures look hopeful for the conservation of *T. scleroxylon*, but they could, and should, be applied, as a matter of principle, to the re-establishment of other important indigenous hardwoods of West Africa, including species of *Terminalia*, *Nauclea*, *Khaya*, *Entandrophragma* and *Chlorophora*. Although many of these

species produce adequate supplies of long-lived seeds, it is possible that their performance could be improved by replacing unimproved seed with blends of selected clones.

If negotiations are concluded successfully, this problem will be investigated by a Regional Project embracing Sierra Leone, Liberia, Ivory Coast, Ghana, Nigeria and Cameroon, a set of countries spanning many of the natural ranges of the species already mentioned. It is intended to have a phased programme of development in which the immediate implementation of existing knowledge about T. scleroxylon will be the focus of Phase 1, followed by a consideration of species of Lovoa, Nauclea and Terminalia in Phase 2, and species of Khaya, Entandrophragma and Chlorophora in Phase 3. However, in searching for superior clones, sometimes with tolerance to pests (eg to stem borers in Entandrophragma and Khaya), attention will not be diverted away from the development of more appropriate silvicultural practices than the oft-exploited methods of clear-felling. The conservation of trees should be linked with the conservation of water, soil, flora, and fauna, while retaining commercial advantages.

R R B Leakey and F T Last

Freshwater and marine ecology

THE PLANKTON ECOLOGY OF LOCH LEVEN

Why study plankton?

Populations of plankton are an important part of our natural environment. In energetic terms, the primary (photosynthetic) production of some lake ecosystems (Le Cren & Lowe-McConnell 1980) compares favourably with that of the most productive systems of all, tropical rain forests (see, for example, Odum 1971). Production at secondary and tertiary levels (herbivores, carnivores) is correspondingly high. Consequently, freshwater systems have considerable potential as a source of food for man, especially in Third World countries. To utilize this resource to the full, we need to understand the factors which control plankton species composition and abundance.

Man also depends on freshwater lakes for domestic water supply, power generation, irrigation, fisheries and tourism. As water quality is affected by the plankton it contains, it is, again, important that plankton be assessed and its behaviour understood.

The composition and abundance of plankton populations change rapidly. Plankton thus provides almost unlimited opportunities to study a wide range of ecological relationships over shorter periods than are possible with higher organisms with much longer life cycles.

Why study Loch Leven?

Until relatively recently, most of our limnological knowledge was based on deep stratifying lakes, and only in the last 15 years have shallow well-mixed water bodies received much attention. Nevertheless, these 2 types of lake are very different. Deeper lakes generally show a well-defined annual cycle of overturn and stratification, which tends to reduce variability within the system. In contrast, shallow exposed lakes respond rapidly to changing weather conditions, and are rather less predictable in their behaviour. Loch Leven is a good example of this type of lake.

The study of community ecology in Loch Leven has several advantages over similar studies in deeper stratifying systems. First, fewer samples need to be taken to obtain reasonable estimates of population densities. thus reducing the need for extensive, time-consuming spatial surveys and allowing sampling at more frequent intervals. Second, uniformity of the environment from which samples are collected simplifies data interpretation, particularly with respect to temperature and oxygen saturation. For example, it is almost impossible to estimate temperature-dependent rate coefficients for populations which constantly migrate through a temperature gradient. Finally, in deeper lakes, there are numerous problems in studying the population dynamics of organisms in an epilimnion which is periodically diluted by hypolimnetic water during storm conditions. These problems do not arise in shallow well-mixed lakes.

Loch Leven is also a valuable site for investigating the effects of eutrophication (nutrient enrichment). Enrichment has increased in recent years as a result of the more intensive use of agricultural fertilizers on surrounding farm land, and the increased discharge of treated sewage into the loch. Annual nutrient loadings of 2·0 g N and 0·2 g P per square metre of loch surface have been recorded. Such levels are classified as 'dangerous' for shallow lakes by Vollenweider (1968).

In Loch Leven, many biological changes have been recorded which appear to be associated with eutrophication. Walker (1970) and Johnson and Walker (1974) describe long term changes in the zooplankton, including the disappearance of the cladoceran *Daphnia hyalina* between the mid-1950's and 1970. Maitland and Hudspith (1974) comment on the decrease in species diversity of bottom-living invertebrates, especially insects, while Morgan (1974) notes the disappearance of one species of fish (the charr, *Salvelinus alpinus*), and Jupp *et al.* (1974) describe changes in the rooted vegetation. Concern over these changes and their possible effect on the world-famous brown trout fishery and wildfowl populations earned Loch Leven the status of National Nature Reserve in 1964.

In 1967, the loch was chosen for special study as a UK contribution to the International Biological Programme (Royal Society 1967). The research emphasized pro-

ductivity measurements, with the main effort in plankton studies concentrating on phytoplankton, associated physical conditions, and water chemistry. Since then, the work has continued and a virtually unbroken record of 15 years' data is now available. Crustacean zooplankton records are less continuous, with only 2 short studies before 1974 (1969-70, 1972-73). Since then, however, the records are complete. A detailed study of the Rotifera was started in 1977.

Methods

In general, 2 fixed stations (Figure 5) have been sampled at more or less weekly intervals, as weather permits. However, in some years, the sampling has been fortnightly from November to February. This short interval sampling schedule is necessary because plankton communities change rapidly, especially at higher water temperatures.

To provide sufficient data for the detailed analysis of complex interactions within the plankton, an extensive sampling programme must be maintained. The meteorological, physical, chemical and biological parameters routinely measured are summarized in Table 5 with some notes on techniques. Further details of the methods can be found in the literature cited.

Results

In the long term, our sampling programme has revealed several important trends. One of the most striking examples concerns the disappearance of *Daphnia hyalina* (see above). The return of this species to the loch was marked by the collection of a single individual in 1970. In 1971 and in subsequent years, the species was abundant, and population maxima of 75-100 individuals I⁻¹ were regularly recorded (Johnson & Walker 1974; D G George, D H Jones, unpublished data).

A general decline in phytoplankton abundance has also been recorded (Bailey-Watts 1978, 1982). Mean annual chlorophyll values of 35 mg m⁻³ from 1979-1982 contrast markedly with concentrations of 80 mg m⁻³ for the period 1968-1971 (Figure 6). In addition, certain chemical features have changed; nitrate levels have increased over the past 14 years, while phosphorus loadings have decreased significantly (Holden & Caines 1974; Holden 1976; L A Caines, R Harriman and A Kirika, unpublished data).

The changes in zooplankton, phytoplankton and chemistry described above are undoubtedly interrelated. For instance, it is likely that the long term decrease in algal biomass is due, at least in part, to reduced phosphorus

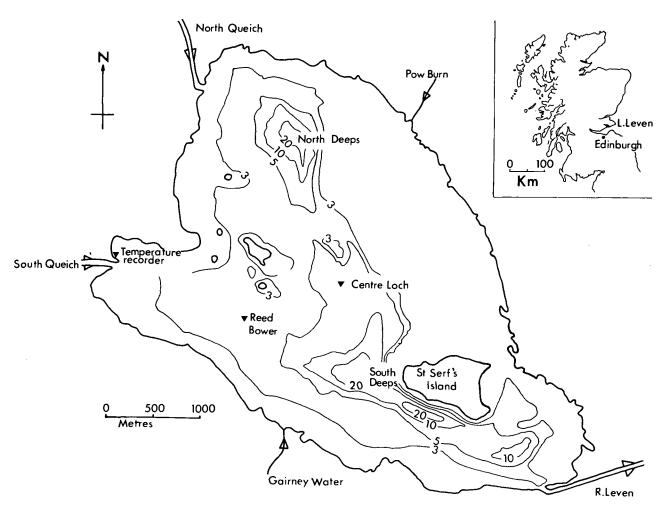


Figure 5 Map of Loch Leven showing the position of inflows, outflow, the 2 main sampling stations (▼) and major depth contours (in metres): inset shows the position of the loch in Scotland.

Table 5. Parameters measured and techniques used in the routine surveillance of Loch Leven plankton

	Parameter measured	Technique	Reference		Parameter measured	Technique	Reference
	Wind speed	(i) Continuously recording anemometer	Smith 1973		Oxygen saturation	Mackereth type oxygen probe	Mackereth 1964 Benham & George 1981
		(ii) Visual assessment according to Beaufort scale			Conductivity Nitrate	Platinum-in- glass electrode Hydrazine	Benham & George 1981 Downes 1978
ogical	Wind direction	Visual assessment				reduction to nitrate and analysis on	
	Cloud cover	Visual assessment in		lical		Technicon Autoanalyser II	
Meteorological		accordance with Meteorological Office scale		Chemical	Soluble reactive (ortho-) phosphorus (SRP)	Phospho- molybdate reaction with	Murphy & Riley 1962
2	Solar radiation	Continuously recording solarimeter			Total phosphorus	ascorbic acid As for SRP after	
	Hours of bright sunshine	Kinross weather station reports			and total soluble phosphorus	acid digestion to convert all forms of phosphorus to	
	Daily min/max air temperature	Kinross weather station reports			Soluble reactive silica	ortho-phosphate Silico-molybdate reduction with metol	Strickland & Parsons 1968
	Loch level	Loch-side staff			Phytoplankton a) Chlorophyll <i>a</i>	Absorption	Bailey-
	Inflow	gauge Continuous river level recorder			and eopigments	spectroscopy on methanol and	Watts 1973
	Outflow	Forth River Purification Board gauging records			b) Species composition and abundance	acetone extracts Tube sampling, sedimentation, identification &	Bailey- Watts 1978
	Surface water movement	Visual assessment of wave conditions	Lyle 1981		c) Size	counting Vickers image-	Bailey-Watts & Kirika 1981
hysical	Ice cover	Continual visual mapping (Nature Conservancy Warden – G Wright)		iological	d) Total weight and C, N, P and opal content	shearing module Centrifugal concentration and analysis of dried slurry	Bailey Watts & Lund 1973, Bailey- Watts 1976
۵.	Water temperature	vviight/		æ	Zooplankton a) Rotifera	Collection with weighted tube,	May 1980a
	a) Sub-surface	Mercury-in- glass thermometer				arcotization, preservation and counting of	
	b) Depth profile	Submersible thermistor	Benham & George 1981		b) Crustacea	animals and eggs Collection by tube	George & Owe
	c) Harbour mouth	Continuously recording mercury-in-steel thermograph				sampler, identification, counts by instar or size groups. Egg counts	1978

availability, and increased grazing pressure by *Daphnia*; such considerations emphasize the need for integrated studies of the whole system, if we are to understand the factors regulating species composition and abundance of plankton communities.

Although plankton in Loch Leven varies from year to year, a certain underlying seasonal regularity in its behaviour has been identified in recent years. Data from 1981 are used here to illustrate this regularity. In early

spring, when water temperatures are low (<6°C) and nutrients are abundant, algal growth is usually vigorous (Figure 7). Population doubling times of less than 3 days are not uncommon (Bailey-Watts 1974). The dominant organisms at this time are centric diatoms. These algae continue to grow rapidly until checked by a shortage of dissolved silica in mid-March. The diatoms are small (less than 20 μm in diameter), and appear to be a suitable food source for herbivorous zooplankton, but they escape heavy grazing and attain high population

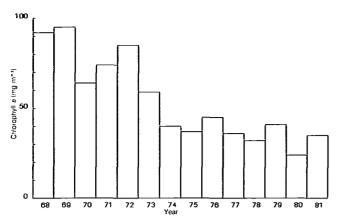


Figure 6 Bar chart showing the annual mean chlorophyll a concentrations in Loch Leven, 1968-1981.

densities because zooplankton reproduces slowly at this time of the year and its population densities remain low.

As the water temperature increases, the crustacean zooplankton becomes more abundant (Figure 8). These animals feed predominantly on phytoplankton, and it is possibly their grazing activity which prevents the accumulation of substantial algal populations from April to June.

Figure 8 shows that the crustacean population is in decline by mid-June, and total phytoplankton abundance begins to increase, followed closely by an increase in rotifer densities. It seems likely that, earlier

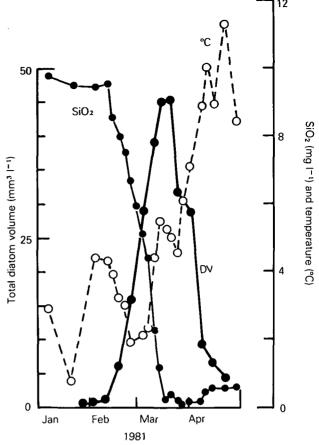


Figure 7 Fluctuations in water temperature (°C) and the concentrations of dissolved reactive silicate (SiO_2) and diatoms, expressed as total cell volume (DV) in Loch Leven during the first months of 1981.

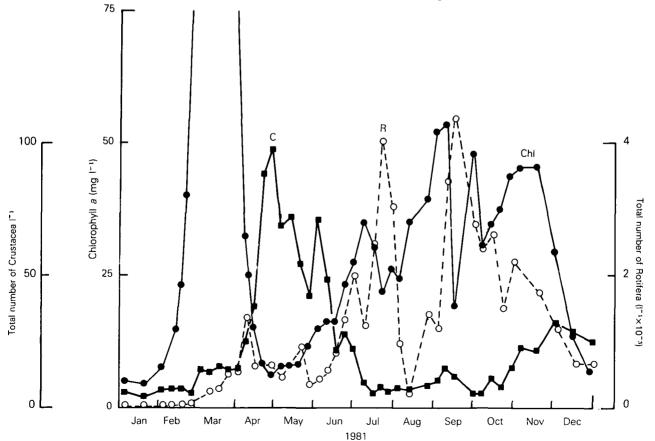


Figure 8 Seasonal changes in phytoplankton abundance (expressed as chlorophyll concentration—Chl), and the total numbers of crustacean (C) and rotifer (R) zooplankton in Loch Leven during 1981.

in the year, rotifers compete unsuccessfully with the Crustacea for food and only become abundant when crustacean densities are low. In addition, rotifers are also preyed upon by some Crustacea, particularly the cyclopoid copepod *Cyclops strenuus abyssorum* (Rutkowski 1980), which will also tend to reduce their population densities.

Rotifer numbers continue to increase until late July, when an abrupt decrease occurs, mainly as a result of the sudden reduction in abundance of the dominant species *Trichocerca pusilla*. Although chlorophyll tends to increase at this time, *Melosira granulata*, the food of this rotifer (May in press), is in decline. By the end of September, rotifer numbers are again high, and throughout the autumn their abundance tends to vary in a manner which reflects changes in algal abundance (Figure 8).

The causal relationships between variations in abundance are not easily explained by field studies alone.

For this reason, we intend to reduce our routine work to a monitoring watch, and increase laboratory studies to test hypotheses suggested by the field data. Experiments are planned to investigate the effects of physical and chemical conditions on the growth and development of plankton populations, and to evaluate biological interactions such as grazing, predation and competition.

An example of the way in which experimental data can increase our understanding of the field situation is described below. It concerns the relationship between water temperature, the rotifer *Notholca squamula*, and its food, the diatom *Asterionella formosa*. In spring

and autumn 1981, dense crops of *A. formosa* were followed by an increased abundance of *N. squamula*. A simple grazing interaction seemed the most likely explanation. However, when high densities of the diatom were recorded in mid-summer, *N. squamula* did not reappear (Figure 9). Clearly, food availability was not the only environmental factor limiting the occurrence of this rotifer. Laboratory experiments showed that *N. squamula* is unable to reproduce successfully at temperatures above 10°C in culture (May 1980b). On re-examination, the field data confirmed that the abundance of *N. squamula* in the loch was related to that of *A. formosa* only at temperatures below 10°C. Above this temperature, the rotifer was absent irrespective of food availability.

Similar species-specific investigations are planned for the future. In addition, it is hoped that manipulation of natural plankton assemblages transferred to the laboratory, or enclosed *in situ* within Butylite containers, will provide an intermediate step between laboratory and field conditions.

Concluding remarks

It is evident from the above that a large amount of data describing the plankton and physical and chemical environment of Loch Leven has been compiled since 1968. This information is now held as a computer data bank. In the past, analyses have been restricted almost entirely to the comparison of time-abundance curves generated from the field results. In the future, the data will be subjected to a more rigorous and comprehensive statistical analysis and re-examined in the light of experimental results.

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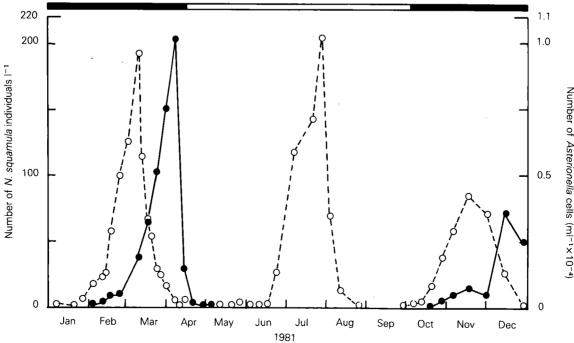


Figure 9 Seasonal variation in the abundance of Notholca squamula (N) in relation to Asterionella formosa numbers (A) and water temperature (shaded area indicates periods during which the temperature was less than 10°C) in Loch Leven during 1981.

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METALS IN FRESHWATER MUSSELS

Three species of freshwater mussel — Anodonta anatina, Unio pictorum and Unio tumidus — were collected for study from several sites along the river Great Ouse in the Cambridgeshire/Bedfordshire area. In particular, a large population of mussels from one area was sampled at about monthly intervals for 16 months. Concentrations of zinc, iron, cadmium and copper in the soft tissues of these animals were measured using atomic absorption spectrophotometry (Bull & Leach 1981).

Results indicate that copper concentrations are independent of size (or age) of mussel for *A. anatina* (Figure 10) at all times of the year sampled, and thus support the suggestion that copper may be 'regulated' in this species (Manley & George 1977). Seasonal changes of concentration do occur, however, and these are easily observed because copper concentrations are independent of size. Almost a 2-fold increase in copper concentrations occurs during the winter months (Figure 11), probably caused by weight changes in soft tissue, which also occur seasonally.

Zinc, iron and cadmium have a more complex pattern of accumulation in *A. anatina*. Concentrations of these metals show significant increases with size and age, at all times of the year. Furthermore, these increases are non-linear, even when plotted logarithmically (Figure 10). These metals do, however, follow similar accumulation patterns, and therefore show a highly significant correlation with one another (Figure 12).

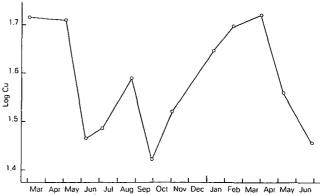


Figure 11 Mean log soft tissue copper concentrations (mg kg⁻¹ dry weight) for A. anatina—March 1979–June 1980.

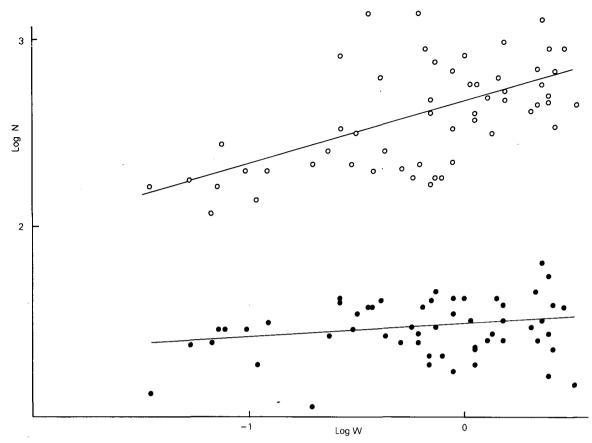


Figure 10 Log soft tissue metal concentrations (mg kg $^{-1}$ dry weight)—zinc ($^{\circ}$) and copper ($^{\bullet}$)—plotted against log soft tissue weight (g dry weight) for A. anatina collected in June.

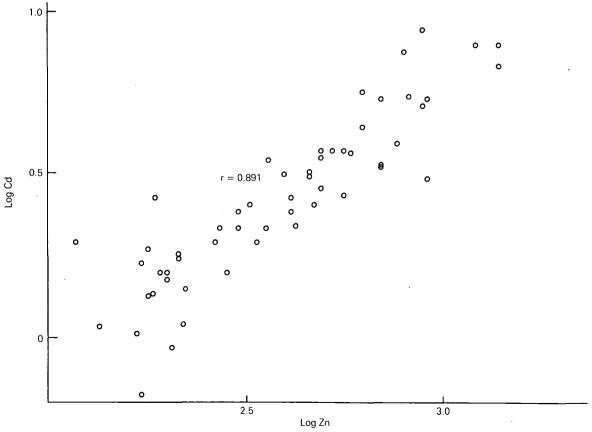


Figure 12 Log soft tissue cadmium concentration (mg kg^{-1} dry weight) against log soft tissue zinc concentration (mg kg^{-1} dry weight) for A. anatina.

Investigations on the size, age, season/metal concentration relationships should enable freshwater mussels to be used for the environmental monitoring of heavy metals.

K R Bull, Jane R Hall and D V Leach

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A SYNOPTIC STUDY OF THE FRESH WATERS OF TAYSIDE

The research on the fresh waters of the Tayside area is part of a larger project concerning the synoptic limnology of British fresh waters. This long term study of British freshwater ecosystems aims at classifying them, describing their variety, and, eventually, at understanding the structure of their communities and the habitat requirements of different organisms (Maitland 1979). The initial research defined the national resource by describing the numbers and variety of fresh waters, the range of species of animals and plants which inhabit them, and the published literature relating to freshwater sites and organisms in Great Britain. The philosophy in developing these parts of the project is to be truly synoptic, and all types of water and organisms are considered as objectively as possible. The work has extended into comprehensive multidisciplinary field studies of selected areas, notably in Shetland and Tayside.

The introductory work on Tayside involved an assessment of the freshwater resource in the area and the selection of sites for field study. Altogether, there are 925 individual standing waters and 10 317 running water segments in the Tayside Region. The bulk of these waters are small. Most of those in the upland and highland areas have base-poor catchments, whilst a majority of those in the lowland and flood plain/coastal areas have base-rich catchments. The groupings within the specified size/geological/altitude classes chosen for study tend to form continuous series, within which 74 standing and 70 running waters were selected for study and sampled during 1977 and 1978.

The physical characteristics of the waters of Tayside were examined so that information from sampled sites could be related to overall water resources. Topography and drainage data were related to natural catchments and the characteristics and numbers of standing waters, and the features of river networks were analysed. Stream flow data were analysed to estimate average flow for all running water sites. Examination of

water temperature data emphasized the influence of altitude, and the importance of slope in determining the character of running waters was demonstrated. Groups of sites of similar character were identified, as well as unusual sites. The work follows the method adopted by Smith and Lyle (1979).

Data on water chemistry were analysed by various methods, including multivariate computer techniques. The chemical information was also studied in relation to map data. The results not only describe the chemistry of the fresh waters of Tayside in a general way, but also demonstrate that it is possible to predict from map information, in broad terms, the likely water chemistry of any individual site. In addition, a multivariate classification array of sites was produced, thus enabling waters of differing chemical types to be selected for conservation, or a variety of other purposes. Most of the classifications of site data gave groups which reflected the basicity, eutrophy or salinity of the water bodies concerned.

The field sites sampled for macrophytes in Tayside were arranged in 2 series, from chemically rich to chemically poor, in terms of (i) alkalinity and (ii) a computed trophic index. The distribution of the higher macrophytes through these classifications, and between standing and running water sites, was analysed and compared to published information.

Relationships between the zooplankton and environmental parameters were investigated. As a result, species and site groupings were obtained. Running waters were found to be less rich and less diverse than standing waters, and, in the latter, 3 main groups could be recognized as biologically distinct, one mainly oligotrophic and upland, another mainly eutrophic and lowland, with a third intermediate between them.

Some 250 taxa of zoobenthos have been recorded so far. Analysis of the data has been carried out at family and species level, and both types of data have proved of value. Multivariate and simpler correlation analyses have shown that there are clear groupings of zoobenthos communities associated with marine, lotic, lentic and other types of habitat. Several sites have clearly been severely affected by man — especially where fluctuating water levels, dredging and pollution have been involved. The poorest and least diverse natural sites were mainly in the upland areas, whereas the richest and most diverse sites were large rivers in the lowlands.

An overall synthesis of the data showed that waters significantly affected by man gave many anomalies during various analyses and were probably best ignored. Another group of fresh waters had unusual characteristics and did not always fit into the main trend of relationships: these included sites which freeze for very long periods each winter and sites which regularly dry up. The main distinction among sites was between



S Standing waters

R Running waters

Figure 13 The sites studied in Tayside arranged by geology and altitude, incorporating a 5-point ranking of physical (substrate size), chemical, macrophyte, zooplankton and zoobenthos field measurements. Those ranked 1 (smallest dots) are poorest (in the case of physical-large substrate), while those ranked 5 (3 large dots) are richest.

the standing and running water groups, and these were also usually identifiable by field data, especially physical and zoological information. However, it was less easy to make this main distinction using data on chemistry or macrophytes alone. In general, there is a reasonable correlation between map data on richness and the subsequent field information. Classifications of the Tayside sites using different criteria were comparable (Figure 13), and an overall scheme for the area has been suggested. The problem of selecting freshwater

sites for conservation purposes is made very much easier if synoptic data of this type are available.

PS Maitland, IR Smith, DH Jones, KEast, KH Morris and AA Lyle

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MARINE GYMNAMOEBAE

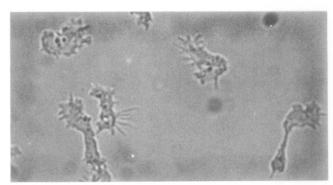
The Sarcodina, or pseudopodial protozoa, include the best-known heterotrophic Protista of the seas: the Foraminiferida and the actinopod classes (Acantharea, Polycystinea, Phaeodarea), 2 or 3 of which are still often comprehended under the term 'radiolarians'. In the past decade or so, collections from several expeditions have provided material for an increased understanding of the Xenophyophorea, giant deep-sea rhizopods consisting of a plasmodium enclosed in a branching organic tube and a massive test. (Many workers now agree that no phylogenetic relationship can be perceived amongst these groups).

It is understandable that these spectacular organisms, most of which leave intricate tests or shells, fossilized by the billions, have attracted more attention than the almost invisible, naked, lobose amoebae, which, if they die rather than divide, leave no trace.

However, such naked, lobose amoebae, the majority belonging to the sub-class Gymnamoebia, have been found in many different marine habitats: soft shores, rock pools, estuaries, bottom sediments far off-shore, even mid-oceanic surface waters. The most studied ones are from coastal and estuarine benthic habitats, and the author has never failed to isolate them from a sample from such habitats. They are, therefore, relatively common and universally distributed.

Such amoebae feed on diverse micro-organisms: bacteria (including cyanobacteria), diatoms and other algae, yeasts, flagellates, ciliates, and other amoebae. Nevertheless, only 2 reports of the possible rôle of amoebae as consumers in marine habitats appear to have been published. This neglect of the rôle of these ubiquitous organisms in the marine environment contrasts with the investigations of amoebae in the soil, where they have been shown to affect levels of bacterial populations, and even the proportions of carbon going into carbon dioxide and biomass.

Apart from lack of awareness of their presence, 2 reasons for the almost complete absence of such studies are probably the relative scarcity of published information on taxonomy and culture methods, until recent years. No serious study is possible without enrichment and isolation in culture. An ITE publication now in preparation, Marine Gymnamoebae, is intended to facilitate and encourage the inclusion of naked, lobose amoebae in such ecological investigations and to make them available as research organisms. Its central part is a key for identification, the first to employ fine structure as a source of diagnostic characters for the Gymnamoebia of any environment (Plate 1). Along with taxonomic information, the publication includes information on isolation and culture, an indication of present knowledge about distribution, suggestions for electronmicroscopical preparation and an extensive bibliography. The employment of ultrastructural characters will



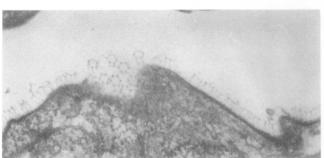


Plate 1 Vexillifera minutissima, a tiny amoeba isolated from the coast of south Wales, is easily grown on agar. The long, straight pseudopodia in the top photograph (×1000) suggest the generic identification of these amoebae, which is confirmed by the hexagonal surface structures in the electron micrograph below (×50000). In this case, species identification is soon completed by a few measurements and either light- or electron-microscopical observation of the nucleus.

(Photographs F C Page)

make the inclusion of these amoebae in marine biological studies more practical, because some of the most important genera can be quickly and accurately identified by surface fine structure.

In the course of the work upon which the forthcoming publication is based, much has been learned about the taxonomic composition of the marine fauna of Gymnamoebia. The 2 most commonly isolated genera are *Platyamoeba*, a genus first erected for organisms in fresh water, where it is much less common, and *Paramoeba*, an exclusively marine genus with a DNA-rich inclusion, the parasome, which may be a symbiont. Although several genera are exclusively marine, many isolates belong to genera with freshwater species.

Experimental results show a degree of euryhalinity in marine isolates, but no marine species has been found in fresh water, and all freshwater species isolated from salt water belong to 2 closely related cyst-forming genera. (Only one true saltwater amoeba forms cysts, and its natural habitats are largely or entirely brackish.)

The most striking overlap of species between fresh water and the seas has been demonstrated by American workers in their findings in marine sites of *Acanthamoeba*, the most common freshwater/soil genus of

amoebae, possibly the most common free-living protozöon. It is, however, far from certain that *Acanthamoeba* carries on its normal trophic and reproductive activities in sea water, because its cyst is highly resistant to chemical agents and its occurrence seems to be partly associated with the dumping of sewage and other wastes. *Acanthamoeba* and the related *Protacanthamoeba* have been found in British estuaries at sites of relatively high salinity.

Amongst the truly marine Gymnamoebia, the world-wide distribution of several genera has already been demonstrated. In addition, a fair number of species are common on both sides of the North Atlantic, and one of these is also known from the Mediterranean and the Indian Ocean. An unusual multinucleate amoeba, described from the Mediterranean more than a century ago, has been found on the Cornish coast, as has a species of the Stereomyxidae (not classified in the Gymnamoebia), also first described from the Mediterranean.

The Gymnamoebia of marine habitats are more often flattened cells and somewhat less often tubular 'limax' amoebae than in fresh water, and the adaptive significance of this difference is just one of the problems suggesting further investigation.

F C Page

THE ULTRASTRUCTURE OF THE FEEDING APPARATUS OF THE ANTARCTIC KRILL *EUPHAUSIA SUPERBA*

The antarctic krill *Euphausia superba* has for some years been recognized as an important potential food source for human beings and domestic animals. To prevent over-exploitation, an understanding of the organism and its niche in the ecological system is necessary, and to this end a study has been undertaken by the British Antarctic Survey (BAS) as part of the Offshore Biology Programme. ITE was asked by BAS to provide scanning electron-microscope facilities to examine the ultrastructure of the organism's feeding apparatus, with a view to greater understanding of the mechanics of the krill's method of feeding.

E. superba collects planktonic food by means of a filter basket formed of 12 thoracopods carried beneath the thorax. The basket is 'V' shaped, with the sides formed from forward projecting setae. It has been suggested that the rapid 'gathering' action of the limbs either forces entrapped water past the setae of the basket walls which enmesh food material, or creates a current of water across the mouth parts for food concentration and extraction.

Although the critical point drying method of specimen preparation for scanning electron-microscopy was not available for use at the time, the supportive nature of the structure enabled excellent results to be obtained by freeze-drying. To study the fine structure of the basket, thoracopods were taken from fixed krill that had been collected in antarctic waters 3–4 months earlier. Each limb was treated with wetting agent and distilled water, before being frozen in nitrogen slush at –210°C and freeze-dried. The thoracopods were examined in a JEOL 100CX Temscan electron-microscope, after coating with a 15 nm layer of sputtered gold. Detailed results obtained will be published in due course.

A typical thoracopod 12 mm long carries a row of some 150 primary setae, approximately 1.6 mm in length: each bears 2 rows of about 140 secondary setae, held at an acute angle to each other. The secondary setae are 66 µm long. In turn, a row of some 28 hook-like microsetules, each 1.2 µm long, are borne by each secondary seta. Two further rows of comb-like setae with equal spacing to the primary setae accompany these on the thoracopod, orientated towards the interior of the filter basket. Each of these comb setae, 160 µm in length, bears 2 rows of comb secondary setae, 50 µm in length, the actual number of the setae appearing to vary. The comb secondary setae carry one row of microsetules with 2 rows at the flattened distal end. The end of the comb seta itself becomes comblike, bearing a double row of large microsetule-like barbs. It has been suggested that the position and shape of the comb setae indicate a function of cleaning trapped material from the primary and secondary setae before transfer to the mouth.

The approximate intersetal spacings of the basketforming setae are: primary setae, 60 µm; secondary setae, 13 μm; microsetules, 2 μm. These distances would enable overlap of primary and secondary setae with their neighbours to produce a mesh with the ability efficiently to filter out particles down to approximately 10 μm in size. Microsetules would encourage meshing of secondary setae and also enable the somewhat less efficient filtering out of particles down to 3 µm in size (as suggested by D Morris, BAS). Recent work on the fluid dynamics of the system by S McClatchie and C M Boyd, Dalhousie University, Nova Scotia, however, suggests that the low Reynolds number obtained for the movement of setae indicates a relatively viscous environment at this level, thus preventing true setal filtering ability. If so, the basket would act more as a vane than a filter, permitting a more efficient trapping of particles of a small size (2-3 µm).

Examinations of krill stomach contents have revealed the remains of pennate and centric diatoms. Other remains, epecially those of small cells, are obviously more difficult to identify.

Whitton and Carr (1982) have pointed out that smallsized Cyanophyceae form a large part of the oceanic phytoplankton hitherto largely missed by surveys using sampling membranes of too coarse a pore diameter. If McClatchie and Boyd are correct, identification of further food cell material from krill stomachs may well reveal the utilization of this plentiful supply of small Cyanophyceae, as well as diatoms and other, larger cells.

It is hoped, after further examination of krill at various developmental stages, to extend the investigation to other antarctic filter feeders. It is also intended to attempt identification of their algal and protozoan food.

This project is being done jointly with Dr David Morris (BAS).

K J Clarke

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THE BASIS OF COLD RESISTANCE IN CHLAMYDOMONAS

The unicellular green alga *Chlamydomonas nivalis* is found in the red and green coloured snows of permanent snowfields. Winter conditions are survived by the formation of resistant zygotes, which germinate in the spring when ambient air temperatures are above 0°C to form the often short-lived vegetative phase of the life cycle. The vegetative motile green cells in the snow meltwater tolerate exposure to a diurnal freezethaw cycle. Other species of *Chlamydomonas* occurring in more temperate regions, eg *C. reinhardii*, do not show this ability to survive low temperatures.

In laboratory culture, vegetative cells of the strain of *C. nivalis* used in this study grow over a wide range of temperatures. Optimal growth occurs at approximately

20°C, but cell division still takes place at -1°C. *C. reinhardii* also shows optimal growth at 20°C, but ceases to divide at 10°C and dies below 4°C.

The morphology of the events of freezing stress in the 2 species of *Chlamydomonas* was investigated by electron-microscopy. At slow rates of cooling, water is removed from cells to form extracellular ice, thus exposing cells to freeze desiccation, which in this study was simulated by hyperosmotic stress. This simulation enabled problems encountered in the fixation of cells at low temperatures to be avoided.

The analogous response of both species to freezing and hyperosmotic stress is illustrated in the graphs. Figure 14(i) shows the viability of cells following recovery from exposure to different temperatures for 5 minutes. Figure 14(ii) illustrates the response following exposure to different concentrations of sodium chloride for 5 minutes. Seven-day old cells (early stationary phase) were grown at 20°C, and subjected to salt stress, or cooled at a rate of 0.25°C per minute to the appropriate temperature. Intracellular ice was not formed in the cells at this rate of cooling. Estimation of viability was based on the ability of cells to divide, following recovery from exposure to the conditions of stress.

Figure 14(i) shows that, under the described conditions, the median lethal temperature for *C. reinhardii* was -7.5° C. No recovery occurred following exposure to temperatures below -12.5° C. *C. nivalis*, however, showed no loss of viability following exposure to temperatures above -5° C. The median lethal temperature was -12.5° C, and approximately 15% of the cells recovered following exposure to -20° C.

When exposed to hyperosmotic stress, the median lethal concentration for *C. reinhardii* was 0.35M and for

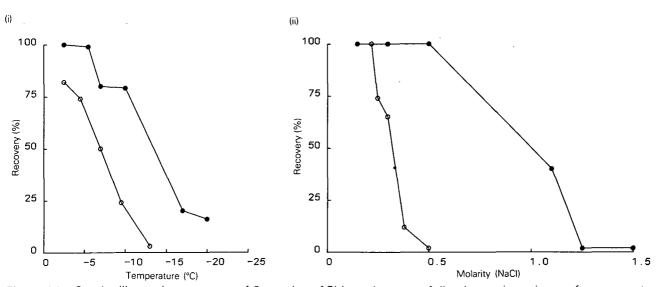
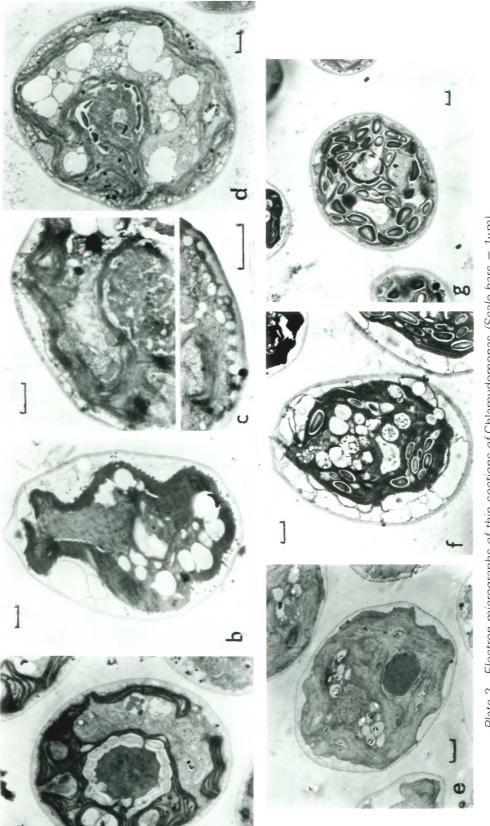


Figure 14 Graphs illustrating recovery of 2 species of Chlamydomonas following various times of exposure to (i) sub-zero temperatures and (ii) sodium chloride solutions \circ — \circ , C. reinhardii; \bullet — \bullet , C. nivalis.

C. nivalis 0.95 M sodium chloride, which represents a respective tolerance of 15 and 40 times the osmolarity of the original cell growth medium.

The micrographs (Plate 2) illustrate the sequence of events resulting from hypertonic stress in the 2 spec-

ies. Plate 2(a) shows a normal cell of C. nivalis from the 7-day old culture. Plate 2(b) shows a highly plasmolyzed cell following one minute's exposure to 0.75 M sodium chloride. In Plate 2(c), illustrating 5 minutes' exposure to 0.75 M sodium chloride, the cell is seen to be re-expanding. Vesicles have appeared in the outer



Electron micrographs of thin sections of Chlamydomonas (Scale bars = $1\mu m$) Control preparation e-g C. reinhardii e. Control pre f. Plasmolyze g. Dead cell () a-d C. nivalis Plate 2

Control preparation

Plasmolyzed cell (0.75 M NaCl, 1 min) c. b.a.

Plasmolyzed cell (0·3 M NaCl, 1 min) Dead cell (0.3 M NaCl, 5 min)

Re-expansion (0.75 M NaCl, 5 min)

Dead cell (1.25 M NaCl, 5 min)

regions of the cytoplasm, and some appear to be fusing with the plasmalemma. This event corresponds with cell viability. Plate 2(d) shows a cell which has been exposed to the lethal concentration of 1·25M sodium chloride. Breaks in the plasmalemma are visible and the whole cell has a vesiculated appearance. Plate 2(e) shows a normal cell of *C. reinhardii*. In Plate 2(f), plasmolysis has occurred after one minute's exposure to 0·3 M sodium chloride. Plate 2(g) shows a dead cell of *C. reinhardii* following 5 minutes' exposure to 0·3M sodium chloride. Expansion following plasmolysis in this species occurs on cell death, presumably due to lethal stress-induced changes in plasmalemma permeability. No vesicle can be seen in the region of the plasmalemma.

Many recent studies implicate cell membranes as the primary site of freezing injury in cells (Li & Sakai 1978). Studies with plant protoplasts (Steponkus & Wiest 1979) showed that deletion of membrane material from the plasmalemma may occur on plasmolysis, leading to cell lysis when re-expansion occurs on return to isotonic conditions. *C. nivalis* cells expand whilst under stress, probably due to cation uptake following stress-induced alterations in plasmalemma permeability. Survival in this species may be related to the production of vesicles, possibly derived from the endoplasmic reticulum, which fuse with the plasmalemma accommodating cell expansion.

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Rehabilitation of disturbed ecosystems

STUDIES ON THE COLONIZATION OF PLANTED WOODLAND BY HERBACEOUS PLANT SPECIES

Herbaceous species form an important part of the flora of natural woodland. Certain species are regarded as indicative of old woodland (Peterken 1974), and there have also been classic studies on the long term survival in woodland of some of these species (Tamm 1956). However, there has been little work done on the natural, or induced, spread of these species into, and through, recently planted woodland. The establishment of an appropriate ground flora in planted woodland would be of considerable conservation and amenity value.

Milton Keynes in Buckinghamshire is typical of our new towns. Trees have been planted in belts along all the main roads, and there will eventually be some 7 km² of these planted woodlands in a range of different aged stands. The oldest is now 10-years old, while other areas have still to be planted. There are some areas of old woodland such as Linford Wood, which could act as sources for the natural spread of herbaceous woodland species.

The establishment of a woodland ground flora is being studied in 2 ways. First, the natural rate of colonization is being assessed in relation to the distance from the sources of propagules in old woodland. Second, experiments have been set up to investigate the possibilities of artificially introducing these species by planting or sowing. For the first study, a series of 150 quadrats is now being monitored. These quadrats are 4 m × 4 m and are located at distances of up to 1500 m from the centre of Linford Wood, ie up to 1200 m from the edge of the wood. In 1982, 86 of these quadrats had already been planted. Of the remainder, 47 were down to grass, and 17 were recently disturbed bare ground. A proportion of the sites in both the latter categories is due to be planted over the next few years. The quadrats recorded showed a wide range of roadside plant communities, but there were as yet few woodland species among the 148 herbaceous species recorded, and this in an area where there is little variation in soil type. The species composition of the ground flora is being considered not only in relation to the distance from Linford Wood, but also in relation to the degree of development of the planted woodland and of any management applied.

The experimental introduction was done in 9 areas of planted woodland, ranging in age from 5 to 11 years. The development of the woodland canopy was assessed in relation to the percentage of light reaching the herb layer in summer, which ranged from 90% to as low as 9%. Six species were sown and 5 were planted in autumn 1981. The species chosen included both those with a slow natural rate of spread, such as *Primula vulgaris*, and relatively invasive species, such as *Arctium minus*.

In general, pre-treatments such as spraying or rotavating had less effect than did the nature of the plots. The development of the tree canopy clearly facilitated establishment, but it did not appear to guarantee success. The mean rate of establishment for the different species in the year following sowing varied from 0.53% (*Primula*) to 3.7% (*Endymion*), and the best pre-treatment appeared to be that of spraying with a systemic herbicide, followed by rotavating. The success of the plantings was generally high, although vandalism was a problem in some of the plots, affecting, in particular, *Carex pendula*, which was pulled up by its tufts of leaves. No less than 71% of *Primula* and 54% of *Geum urbanum* flowered in the first year after planting.

Future work will be concentrated on the determination of which factors are responsible for the differences in

success rates of sowing or planting between the plots, and also the appropriate management techniques to apply following planting or sowing.

L A Boorman

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WOODY PLANT SELECTION FOR OPENCAST COAL SPOIL REVEGETATION

(This work was largely supported by National Coal Board funds)

Current energy planning involves a continued dependence on home-produced coal as a major energy source for Britain. Maintenance of opencast production at about the current annual level of 12-15 million tons is planned (Anon 1974), and continuing efforts are being made to improve restoration and revegetation techniques, including tree planting methods. Much can be done by ameliorating site conditions during restoration to improve the establishment and growth of trees, while the choice of appropriate species has long been acknowledged to be of importance and has been studied extensively (Richardson 1975; Broad 1979).

Little attention has been given, however, to the exploitation of tolerant ecotypes of trees and shrubs, although work with herbaceous plants has shown that ecotypes able to tolerate various adverse conditions (heavy metal toxicity, infertility, waterlogging) do evolve on degraded soils (Fitter & Bradshaw 1974; Bradshaw et al. 1978). In this study, selected clones of a range of native woody species, but particularly birches (Betula pendula, B. pubescens) and willows (Salix cinerea, S. caprea), have been propagated from mother plants growing on a range of spoil materials. The establishment and medium/long term growth of these clones and of unselected commercial nursery stock (controls) are being compared in field trials on 8 restored opencast sites throughout Britain (Good 1980). Additional, smaller experiments have been set up to investigate: (i) the potential of nitrogen-fixing trees and shrubs, interplanted with selected clones of birch and willow, as a continuing source of soil nitrogen, and (ii) the effects of inoculation with selected strains of mycorrhizal fungi on survival and growth of the selected clones of birch under field conditions. Glasshouse experiments support these field trials.

Early results confirm that clones vary appreciably in their ability to survive and grow on restored opencast coal sites (Tables 6 and 7). Two of these sites have poorly drained soils of high clay content, Ty Cerrig being slightly acid and Radar North calcareous. The other 2 sites are both on nutrient-deficient shales, Whaupknowe being poorly drained and Tir-y-Gof well drained.

Table 6. Survival (%) of selected clones and unselected controls of birch and willow on 4 restored opencast sites

			Survival (%)		
Species	Ty Cerrig	Radar North	Whaupknowe	Tir-y-Gof	Mean
<u>Shecies</u>	Cerrig	NOILII	vviiaupkilovve	TII-y-GOI	
Birch					
Unselected	100	6	61	73	60
BPu 47	100	_	100	100	100
BPe 34	100	83	78	87	87
BPe 94	100	-	94	100	98
Mean	100	44	83	90	86
Willow					
Unselected	78	78	100	69	81
SCi 12	100	94	6 1	61	79
SCi 90	-	83	100	100	94
SCa 50	83	44	83	-	70
SCa 76	94	94	· –	94	94
Mean	89	79	86	81	84

- = Clone not planted at this site.

There were 18 plants of each clone, and 18 unselected controls at each site.

Table 7. Relative growth of selected clones and unselected controls of birch and willow on 4 restored opencast sites

	F	Relative	growth (cm cm ⁻¹	, 2nd year)	1
	Ту	Radar			
Species	Cerrig	North	Whaupknowe	Tir-y-Gof	Mean
Birch					
Unselected	0.05	0.38	0.42	0.22	0.27
BPu 47	0.14	_	0.17	0.31	0.21
BPe 34	0.09	0.32	-0.02	0.46	0.28
BPe 94	-0.01	-	-0.10	-0.19	-0.10
Mean	0.09	0.35	0.24	0.27	0.19
SED (5%)	0.08	0-13	0.18	0∙16	
Willow					
Unselected	0.83	0.85	0.04	1.36	0.77
SCi 12	0.26	0.17	0.24	0.83	0.38
SCi 90	_	0.95	0.11	0.88	0.65
SCa 50	0.93	1.12	0.32	_	0.79
SCa 76	0.23	0.49	-	1.82	0.85
Mean	0.56	0.72	0⋅18	1.22	0.69
SED (5%)	0.19	0.25	0∙15	0.34	

- = Clone not planted at this site.

It will be seen from Table 6 that the 3 birch clones each had a mean survival over the 4 sites in excess of that of the control, while one clone of *Betula pubescens* (BPu 47) gave 100% survival at the 3 sites where it was planted. One clone each of *Salix cinerea* (SCi 90) and *S. caprea* (SCa 76) had a higher survival rate than controls in all sites where they were planted, while a second *S. cinerea* clone (SCi 12) did markedly better on the heavier Radar North and Ty Cerrig soils than on the shaly soils at Whaupknowe and Tir-y-Gof.

Perhaps surprisingly, growth rates were not well correlated with survival rates. At Ty Cerrig, there was 100% survival of all birches, including the unselected controls, but mean relative growth rate (0.093 cm cm⁻¹

yr⁻¹) was the lowest for any of the 4 sites (Table 7). Similarly, clones with a generally high survival rate (BPu 47, BPe 94, SCi 90, SCa 76) were often those with the lowest stem growth rates. Whole plant analysis at the conclusion of the field experiments and glasshouse experiments, where root systems can more easily be recovered intact, will indicate whether survival is correlated, as seems probable, with root:shoot ratio. Surprisingly, it has been shown conclusively in the field trials that applications of mineral fertilizers at planting, or during the first or second growing seasons, have no significant effect on survival or growth rate, even on the most nutrient-deficient sites. On more fertile sites, fertilizers often suppress tree growth by enhancing competing weed growth preferentially. Effective weed control must, therefore, accompany any nutrient enhancement programme.

J E G Good and T G Williams

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SOME EFFECTS OF MOSSES ON SOIL MOISTURE

Mosses can modify the water budget of surface layers of soil in several ways that could influence the establishment and early growth of seedlings of higher plants. For instance, mosses can interfere with water input by retaining all, or part, of the rainfall. Moul and Buell (1955) found that carpets of moss could retain up to 18 mm of rain, this moisture being largely unavailable to the roots of seedlings and established vascular plants.

Mosses can also modify the patterns of water loss from soils. These effects are difficult to demonstrate in the field because of the difficulty of finding comparable areas with and without mosses. In contrast, these effects can be readily demonstrated in the laboratory using a climatological wind tunnel (Weatherley & Barrs 1959), and swards of moss grown on prepared surfaces (Bayfield 1976). In one such experiment, *Ceratodon*

purpureus was sown on shallow pots (4 cm deep) with an equal mixture of sand, peat and John Innes compost (no. 2). After 4 months, when *Ceratodon* had grown to give a complete cover, the pots were brought to field capacity and exposed to desiccation in the wind tunnel (20·5°C, 2·5 m s⁻¹, 300 μ E, 65% RH). For comparison, identical pots of unsown bare soil and pots of bare soil with a 1 cm layer of gravel (an inert mulch) were similarly subjected to desiccation.

Water loss from the bare soil initially exceeded that from the moss and gravel surfaces (Figure 15), but fell to a lower rate when the soil had lost 50% of its water and the soil surface became visibly dry. Thereafter, the moss and gravel pots continued to lose water at faster rates than bare soil. Overall, the soils covered by moss or gravel took substantially longer to reach water contents of 75%, 50%, 25% and 12½% than bare soil (Table 8). Control pots of *Betula pubescens* and *Stellaria media* seedlings reached permanent wilting points at between 12-16% soil moisture. This experiment indicates that, in some situations, a superficial layer of moss can have a similar effect to an inert mulch in reducing soil moisture loss.

Table 8. Effects of the moss Ceratodon purpureus and a gravel mulch on rates of water loss from an equal mixture of sand, peat and compost subject to drying conditions in a controlled environment wind tunnel

	Hours to reach % field capacity of					
	75	50	25	12½		
Bare soil Ceratodon purpureus Gravel	16 22 37	34 46 75	71 95 140	139 164 218		

The Ceratodon turf in this study was short (about 5 mm) and the penetration of soil by rhizoids correspondingly shallow. Deeper moss carpets, or those with internal water-conducting tissues, might have different effects on water loss. To examine this possibility, 5 species (Polytrichum piliferum, P. commune, Ceratodon purpureus, Hypnum cupressiforme and Dicranum scoparium) were sown on pots of sand, the pots being square in section and with one side of glass to facilitate observations of rhizoid growth. The glass sides were normally covered to prevent the entry of light. After 4 months, each species had produced a sparse cover of short shoots (ranging up to 21 mm in the case of P. commune) (Plate 5). When these pots were exposed in the wind tunnel, they all lost water more slowly initially than the 'control' uncolonized pots of bare sand. After 10 days, the losses ranged from 90% (D. scoparium) to 98% (P. commune) of that from the bare sand. This was a similar result to the previous study. After 9 months' growth, vigorous stands had been established, with maximum shoot heights ranging from 4 mm (H. cupressiforme) to 137 mm (P. commune), and rhizoid depths from 18 mm (D. scoparium) to 152 mm

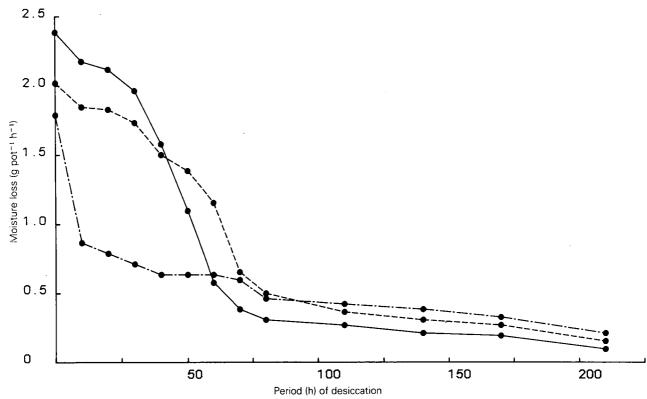


Figure 15 Effects of the moss Ceratodon purpureus (\bullet ---- \bullet) and a gravel mulch (\bullet --- \bullet) on the successive losses of water from an equal mixture of sand, peat and compost subject to drying conditions in a controlled environment wind tunnel (\bullet -- \bullet , losses from the 'uncovered' controls).

Table 9. Effects of turves of different mosses on the loss of water from pots of sand, when desiccated in a controlled environment wind tunnel

Characteristics of moss turf						
	Turgid moss cover (%)	Maximum shoot height (mm)	Rhizoid depth (mm)	*Loss of water after 24 h desiccation	*Loss of water after 10 days' desiccation	Depth of dry soil (mm) after 10 days' desiccation
Polytrichum piliferum	76	32	93	118	99	14
P. commune	97	137	152	222	122	26
Ceratodon purpureus	100	14	47	108	94	19
Hypnum cupressiforme	97	4	38	80	76	24
Dicranum scoparium	98	24	18	176	87	19
Bare sand, 'control'	-	-	_	-	-	10

^{*} Losses attributable to 'mosses' as % of those from bare sand.

(*P. commune*) (Table 9). When these pots were exposed in the tunnel, moisture loss during the first 24 hours (when most shoots were still turgid) exceeded that from bare sand in every species except the procumbent *H. cupressiforme*. These high rates of loss appeared to reflect the large surface areas of the mature moss stands. After 10 days' desiccation, however, the losses from the pots of moss, excepting *P. commune*, were less than those from sand, and the mosses were again acting like a mulch. The greater loss from *Polytrichum* pots was attributable to the great size of its shoots, its extensive rhizoid system, and internal water conduction pathway.

Although overall moisture losses during the 10-day drying period were generally reduced by the mosses,

there was an important side effect on the vertical distribution of moisture in the sand; all pots colonized by bryophytes had a greater depth of visibly dry surface sand than uncolonized pots. The depth of dry sand ranged from 14 mm (*P. piliferum*) to 26 mm (*P. commune*), compared with only 10 mm in the uncolonized controls. Thus, mosses reduce overall soil moisture losses at the expense of a more complete desiccation of the surface layers. This observation suggests that seedlings attempting to establish through well-developed moss stands could be at a serious disadvantage in a desiccating environment, compared with similar plants growing in bare soil, at least until their roots penetrate below the top few cm of soil.

N G Bayfield

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Management of natural and man-made habitats

EFFECTS OF GRAZING IN SNOWDONIA

In Snowdonia, as in much of upland Britain, sheep have a controlling influence on vegetation. Grazing is the most obvious effect, but urination, defaecation and trampling can also have large effects where sheep 'lieup' at night. However, their influence is generally less marked and less immediate, being felt mainly over the longer time-scale of nutrient cycling.

From about 1925 to 1955, effects of differing sheep densities and manuring regimes were studied on hill pastures in mid-Wales (Milton 1940; Jones 1967). Experiments showed that the composition of herbage can be changed completely by altering the density of sheep, with changes produced by experimental treatments in 1930 often being still visible 25 years later.

More recently, experimental exclosures were positioned in Snowdonia (Hughes et al. 1975). They were located at 9 sites, of which 8 are at altitudes between 350 m and 450 m (4 with brown earth soils and 4 with peaty podzols), while the ninth, a brown earth site, is at 850 m. At each site, 4 of the 12 plots (each 5 m × 6 m) were protected completely from grazing sheep, while the others were grazed throughout the summer.

Before positioning the exclosures, about 25 years ago, the sites on brown earth soils were dominated by the grasses Agrostis tenuis and Festuca ovina. After 25 years without sheep, the Agrostis-Festuca grasslands have retained their general character. The 2 original dominants have remained abundant, but sometimes decreased slightly to share their dominance with other species such as Agrostis canina, Festuca rubra and Holcus mollis (Table 10). The vegetation at the peaty podzol sites has, in contrast, responded very differently. Before exclosure, these sites were dominated by the grasses Festuca ovina and Nardus stricta. Subsequently, the tussock-grass Molinia caerulea has increased, at one site, from about 2% of the herbage (by weight) to 53%, excluding or reducing most other species (Table 10). At the other 3 sites, dwarf shrubs, notably Calluna vulgaris and Vaccinium myrtillus, have increased to become canopy dominants, often with an increase of the grass Deschampsia flexuosa.

differing sites, one feature was constant; there was almost no invasion by new species. Change consisted merely of readjustment, with the components of the original turf playing new roles. Only a few individual plants appeared to have immigrated into the plots, notably some small rowan trees (Sorbus aucuparia) introduced by birds sitting on fence posts, and a plant of golden-rod (Solidago virgaurea), which had presumably spread from nearby cliffs.

The time-scale of change varied according to species. Molinia caerulea increased for about 7 years and then remained constant. Dwarf shrubs increased for about 20 years, and then their populations mostly remained stable, except on one plot where heather was still increasing after 24 years. Generally, herbaceous plants took about 4-8 years to reach their new levels, with little change thereafter.

In a few instances, longer term changes may have been taking place. In one plot, a clump of woodrush (Luzula sylvatica) was increasing steadily, maintaining dominance once established, with a few seedlings appearing nearby. In another plot, a clump of Deschampsia flexuosa, a grass that generally benefits from the absence of sheep, seemed to be increasing, but there were no new recruits in this instance. No doubt further changes will occur, but the rate of change is now slow. Invasion of a closed turf is difficult as most plants are unable to regenerate by seed into long grass.

Grazing does not cease when sheep are removed. In the absence of sheep, most plots support abundant voles (Microtus agrestis), at least in some years. Two of the sites on better soils are also disturbed by moles (Talpa europaea). The influence of voles must be surmized from other work, because no experiments have yet been made to see what would happen in their absence in Snowdonia. Summerhayes (1941) excluded voles from upland grasslands that had recently been enclosed for forestry. He reported that there was greater diversity, and, in particular, more moss when voles were present. Their effect was chiefly to damage the dominant plants.

Damage to the dominants is doubtless also a major effect of vole activity in the study plots in Snowdonia. Certainly, there was a good growth of moss in the plots in Agrostis-Festuca grassland when, in the absence of sheep in 1981, voles were plentiful (Table 10). In the 'ungrazed' Nardus-Festuca plots dominated by Molinia caerulea, there were few voles in 1981, but an abundance in 1982. The 2 sites, separated by only 1 km, clearly do not have synchronous vole cycles.

Small exclosure experiments can give an indication of vegetation dynamics in sheep walks, but only give a very partial idea of what might happen over a larger area in the absence of sheep. Voles presumably have a stronger influence on vegetation when sheep are Although the vegetation responded differently at the absent. The exclosure plots certainly cannot be re-

Table 10. Effects of sheep exclosures on the vegetation growing on 2 soil types on Cwm Idwal, Snowdonia. Assessments of herbage (g m⁻²) made after 25 years in August 1981

		Soil t	ypes	
	Browi	n earth	Peaty	podzol
Species	'Grazed', outside exclosure	Not grazed by sheep within exclosure	'Grazed', outside exclosure	Not grazed by sheep within exclosure
1. Living herbage				
Agrostis canina	2	214	12	107
A. tenuis	54	37	2	2
Festuca ovina	78	138	79	39
Molinia caerulea	-	_	4	214
Nardus stricta	6	13	86	13
Other grasses	3	71	3	-
Herbs and shrubs Polytrichum	16	73	18	18
commune Rhytidiadelphus	355	-	3	-
squarrosus	8	58	_	1
Other mosses	79	74	41	10
TOTAL	601	678	248	404
2. Litter and moribu	nd			
tissue	754	984	500	403

garded as ungrazed. If a really large area were without sheep, cycling of the vole population would presumably be different, as a permanent population of predators could be supported. Possibly, the oscillations of vole numbers would be greater, with damage to dominant plants enabling extensive germination and the establishment of seedlings. Stability and predictability are rarely the rule in grasslands.

M O Hill

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MANAGEMENT OF ROADSIDE VEGETATION

There are approximately 126 000 ha of roadside verge in the UK – the conservationists value them as refuges for wildlife and as important habitats for many of our rarer plant species (Perring 1969), while road users benefit from a colourful display of wild flowers in spring and summer (Plate 6). Thus, the relative importance of this particular grassland habitat is far in excess of its extent in area, but the maintenance of the species-rich plant communities which have been characteristic of

British roadsides requires careful management which may conflict with more practical considerations. For instance, drivers need vegetation to be kept short, below 30 cm, to prevent obstruction of sight lines, farmers wish to keep verges free of agricultural weeds, and, most important of all, local authorities are obliged to keep management costs to a minimum. The reconciliation of these conflicting interests can only be achieved if the effects of various management options are fully understood. Sadly, much of this information is not yet available.

To correct this deficiency, a series of long term experiments testing herbicides and grass growth retardants was established (Way 1969). Two roadside sites in Cambridgeshire, one on Oxford clay and the other on chalk, were used to compare a range of management techniques, including the application of 2,4-D herbicide and maleic hydrazide growth retardant, and the use of different types of cutting machinery at different dates and frequencies (Table 11). The experiment began in 1965 and management continued until 1982. During this period, records of species frequency, vegetation height and species in flower were taken periodically. Results given here are from the site at lckleton, a relatively species-rich site on chalky soil.

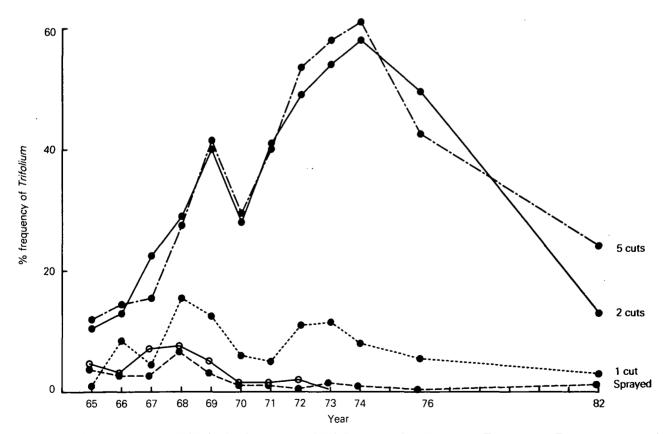
A survey in 1982, after 17 years of management, of the experimental plots at the lckleton site on chalk showed that treatments had significantly affected (P<0·001) species richness (Table 11), a useful measure of the structure of plant communities with rich swards having a correspondingly high value for wildlife.

On average, cutting, irrespective of dates, frequencies and types of machine, decreased the numbers of species from 26 in the uncut controls to 24 per plot. This is a surprising effect because the absence of cutting usually leads to the competitive exclusion of low-growing, prostrate plants, with a consequent decrease in species richness (Grime 1973). However, there was probably sufficient disturbance in the uncut roadside verges to enable prostrate species to survive, while the lack of cutting enabled shrub species such as Prunus spinosa, Crataegus monogyna and Rubus fruticosus to invade. At the start of the experiment, concern was expressed that the use of the, then, relatively new flail mowers might damage vegetation. On the credit side, they cut more closely and more evenly than the haymower, but, on the other hand, they had a tendency to create bare patches: on balance, however, the flail mowers did no more harm than the other cutting machi-

Plots sprayed with the herbicide 2,4-D had the fewest species, 13, mainly because numbers of broadleaved flowering plants were decreased; those sprayed with maleic hydrazide, a grass growth retardant, had 17 species per plot. Yemm and Willis (1962) reported that maleic hydrazide caused a decrease in coarser grasses, an increase in finer, rhizomatous grasses such as fes-

Table 11. Effects of a range of treatments, started in 1965, on plant species richness in 1982 in roadside verges on chalk at lckleton, Cambridgeshire

Treatment	Spray April	Dates of cutting						Numbers	Numbers	Total	
		May	June	July	Aug	Sept	Replicates	of grass species	of forb species	numbers of species	Proportion of grass species
Untreated control							8	7.4	18.7	26-1	0.29
Maleic hydrazide (MH)	\checkmark						4	5.5	10-0	15-5	0-35
MH + cut	√		V				4	8.3	10.0	18-3	0-46
MH + 2,4-D	\checkmark						4	5.5	5·5 .	11.0	0.50
MH + 2,4-D + cut	V		V				4	7.3	6.5	13.8	0-54
2,4-D	\checkmark						4	7.5	6.0	13.5	0-55
2,4-D + cut	V		\checkmark				4	8.7	6 ⋅5	15-2	0-60
Flail mower (×2)		V			V		4	9.3	14.0	23-3	0.40
Flail mower (×5)		\checkmark	\checkmark	V	V	\checkmark	4	9.7	14.3	24.0	0-41
Haymower (×2) cuttings raked		V			\checkmark		4 .	9.7	16.5	26-2	0.38
Haymower (×5) cuttings raked		\checkmark	\checkmark	V	\checkmark	\checkmark	4	9.3	18-0	27.3	0.35
Haymower (×2)		V			\checkmark		4	7.5	13.7	21.2	0.36
Haymower (×5)		V	\checkmark	\checkmark	\checkmark	\checkmark	4	10.3	14.7	25.0	0.42
Rotary mower (×2)		\checkmark			\checkmark		4	8.5	13.3	21.8	0.39
Rotary mower (×5)		\checkmark	\checkmark	\checkmark	\checkmark	\checkmark	4	9.5	12.0	21.5	0.45
Haymower (×1)			V				4	8.2	13.5	21.7	0.38
Haymower (×1)				\checkmark			4	9.5	13.7	23.2	0-42
MH (since 1967)	\checkmark						4	7.0	8.0	15.0	0-47
MH + cut (since 1967)	\checkmark		\checkmark				4	8.0	12.5	20.5	0-40
LSD between untreated controls	and trea	atment	s (95%	6 limit	:s)			1.62	4.28	4.85	0.092
LSD between treatments (95% limits)								1.87	4.94	5.60	0-106



cues and meadow grasses, and, in the long term, an increase in species diversity. Although fine grasses such as *Festuca rubra* and *Poa* sp. increased in abundance at lckleton, there was a decrease in species richness. Thus, contrary to general belief (Haggar 1980), observations at this site indicate that growth retardants seem unlikely to provide a means of maintaining or increasing plant species diversity.

Species richness is a relatively crude measure of community structure and may obscure changes in the abundance of different species. For instance, the application of herbicides and infrequent cutting favoured an increase in coarse grasses such as *Agropyron repens* and a decrease in low-growing plants such as clovers (*Trifolium* spp.) (Figure 16). Chemical treatments almost totally eliminated clovers which were unable to survive in uncut swards. However, one cut per year increased clover frequency to 15%; with 2 cuts, clover frequency increased to 60%, but 5 cuts had no additional effect. In this experiment, frequency of cutting was confounded with cutting date.

After a change of management, it may be many years before a new, stable plant community is established. Changes are by no means instantaneous. Between 1965 and 1974, cutting progressively increased the abundance of clover, but thereafter there has been a decline (Figure 16).

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COASTAL MANAGEMENT IN AUSTRALIA

Visits to 30 sites in Queensland, New South Wales, and Victoria during a 3-week stay in Australia from August-September 1981 provided an exceptional opportunity to learn about unfamiliar habitats and management techniques, so helping to create a fresh outlook on familiar UK problems.

The state-operated Beach Protection Authority in Queensland provides a focal point for information, and

it advises local Shire Councils on coast protection management. Experimental studies on the use of grasses, shrubs and trees in dune stabilization are in progress at its research station on South Stradbroke Island, where planting stock is raised on a large scale, eg for planting the newly-created dredge spoil sand barrier at the mouth of the Noosa estuary, a barrier which was built to protect low-lying residential properties from tidal flooding. Shrubs and trees, such as *Acacia* and *Casuarina*, are grown in the nursery in plastic tubes. *Casuarina* can grow as much as 1-5 m in a year, when planted out, in the warm, wet climate of the Queensland coast. However, the success of the tubed seedlings depends on the formation of a vigorous rooting system with appropriate mycorrhizas.

Former strandlines of ancient dune systems, up to 100 000-years old, contain valuable mineral deposits of titanium oxide (rutile) which are being mined by Associated Minerals Consolidated on North Stradbroke Island. After restoring the site, the shallow slopes are seeded with *Sorghum* sealed in by sprayed bitumen: the steeper slopes are stabilized with brushwood. Many of the cut shrubs bearing seed regenerate naturally, while the re-establishment of the more difficult species is augmented by the use of tubed seedlings. This restoration programme – the largest of its kind in the world – is achieving remarkable success.

European marram grass (Ammophila arenaria) was introduced to Victoria, Australia, in 1883. It has been planted extensively in the highly mobile dune system in Discovery Bay National Park (8400 ha). Native sand spinifex grass (Spinifex hirsutus) is also planted, but it is near the southern limit of its range in Victoria. This species can extend seawards at a rate of 14 m per year on the Queensland coast and grow up through deposits of sand deepening at a rate of 25 cm per month. Documentary evidence suggests that the Discovery Bay dunes were already mobile, prior to human settlement and stock grazing. Today, plantings are only made to protect the pastures landward from sand inundation. To control rabbits, carrots are baited with toxic substances and dropped from the air, although care is taken to avoid the territories of marsupials. Myxomatosis is also re-introduced when necessary, via its rabbit flea vector. This positive approach to the management of rabbits contrasts strongly with our own, especially in north and west Scottish coastal dune systems.

In contrast to the early settlers' policy of widespread introductions, there are now strong efforts to protect the native flora from replacement by introduced species. Introduced and invasive shrubs, such as boneseed (*Chrysanthemoides monilifera*) and myrtle-leaved milkwort (*Polygala myrtifolia*), in New South Wales, are controlled on dunes by burning, cutting, uprooting and the application of herbicides. However, there is concern that the attractive, introduced, Norfolk Island pine (*Araucaria excelsa*), widely planted in the Sydney coastal area, is dying locally as a result of the air disper-

sal of detergent pollutants. These pollutants destroy the cuticle of the leaves and render trees susceptible to salt damage, especially in the Sydney Harbour area.

D S Ranwell

Survey and monitoring

THE BUTTERFLY MONITORING SCHEME (This work was partly supported by Nature Conservancy Council funds)

In the second ITE Annual Report (Pollard 1976), the development of a method for assessing changes in the abundance of butterflies, using transect counts, was described. In 1976, a national scheme, the Butterfly Monitoring Scheme, was initiated, based on this recording method. Counts are now made annually at some 80 sites of very diverse nature, including National Nature Reserves, RSPB reserves, farmland and forestry plantations. The data are used to provide information on changes in butterfly numbers at the individual sites and, by combining site data using the method of ratio estimates (Cochran 1963), at a regional and national level.

In addition, the scheme has proved to be a valuable source of information on the phenology, migration and habitat preferences of butterflies, providing a background to more intensive research studies of the ecology of individual species. In this article, some examples of the data which have been obtained from the scheme are presented and discussed.

Individual site data

The counts are made weekly, weather conditions permitting, and the sum of the weekly counts is used as the index of abundance for each generation. One set of data is illustrated (Figure 17), that for the Adonis blue butterfly (Lysandra bellargus) at Ballard Down, near Swanage, in Dorset. The very large fluctuations in abundance shown by the Adonis blue are exceptional, but other examples of similar fluctuations have occurred. The fall in numbers in 1977 was believed to be the result of desiccation of the food-plants, horseshoe vetch (Hippocrepis comosa), during the drought in 1976. The subsequent rise occurred during a series of summers with generally poor weather conditions, which was something of a surprise for a species at the northern edge of its range in southern England. The fluctuations of the Adonis blue at this site are discussed fully by Thomas (1983).

Phenology

Data on the flight periods of butterflies are to be provided for the forthcoming *Atlas of butterflies*, to be published for ITE and NCC by Penguin. The atlas will be based largely on the distribution data of the Biological Records Centre. An example of the phenology data is given in Figure 18, and shows that for the ringlet (*Aphantopus hyperantus*) the flight period in any one season is very similar over the whole range, which in this case extends well into Scotland. One might expect that, given the lower temperatures in the north, development would be slower and the flight period later, but this does not appear to happen with the ringlet. It is certainly true that emergence of adults occurs later in cool summers than in warm ones. However, it seems that, with the ringlet and many other species,

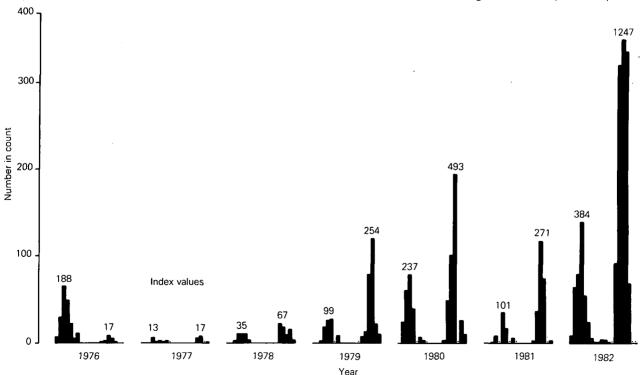


Figure 17 Weekly counts of the Adonis blue butterfly at Ballard Down, Swanage, Dorset, 1976-1982. Missing counts are indicated by a dot. Index values (sum of weekly counts for each generation) are shown.

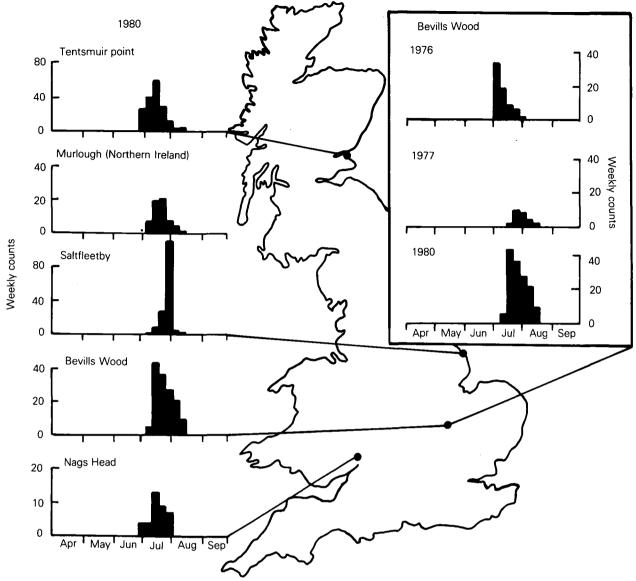


Figure 18 Weekly counts of the ringlet at 5 sites in 1980, and at Bevills Wood, Cambridgeshire, in 1976, 1977 and 1980, to show the timing of the flight period.

emergence time is the result of adaptation to local climate. Ringlets from the north, transferred to the south of England, would presumably emerge much earlier.

Migration

Some British butterflies are migrants, which overwinter in this country only occasionally, or not at all. These migratory species include the red admiral (*Vanessa atalanta*) and the painted lady (*Vanessa cardui*). Much information on the migrations of these species has in the past been anecdotal. Because data collection is regular and systematic, the monitoring scheme provides much more objective information. One example, the migration of the painted lady in 1980, discussed more fully by Pollard (1982), is shown in Figure 19. There had been a major movement of painted ladies from the west early in the season, presumably originating in the Mediterranean area and moving around an anticyclone to the west of Britain. In late July (Figure 19), there was a spectacular immigration along much

of the east coast. The winds were from the east, and it is likely that this movement originated in central or eastern Europe. This type of information should eventually prove very useful, as little is yet known of the scale, regularity or behavioural basis of the migration of many butterfly species. In addition to the major migratory movements of the painted lady, the data from the scheme have drawn attention to more local movements of the brimstone (*Gonepteryx rhamni*) between woodland sites, primarily used for overwintering, and areas such as wetlands where the food-plants, buckthorn species (*Rhamnus* and *Frangula*), are particularly abundant (Pollard & Hall 1980).

National trends

The national trends in butterfly abundance can now be shown for 7 years. This period is too short to detect trends with any confidence, or for analysis of correlations with weather conditions, but possible approaches to such analyses are being considered. It is, however, already clear that different species show strikingly dif-

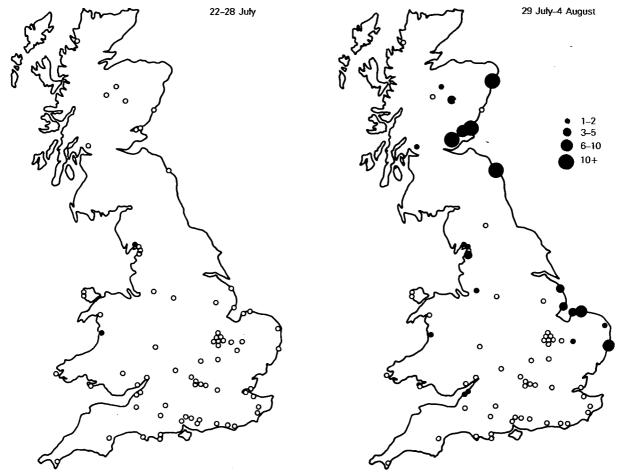


Figure 19 Counts of the painted lady in recording weeks 17 and 18, to show the arrival along the east coast in late July 1980. The open circles indicate sites at which counts were made, but no painted ladies recorded.

ferent patterns of fluctuations. Three examples are given in Figure 20. The brimstone, which overwinters as an adult and so has 2 flight periods, in autumn and spring, but only one generation each year, has remained relatively constant over the period. Numbers of the large white (Pieris brassicae), a pest of cultivated brassicas, fell sharply in the first generation in 1977, but quickly recovered. A feature of the large white butterfly data is that the index for the second brood is regularly larger than that for the first. The dark green fritillary (Argynnis aglaia) has declined fairly steadily over the recording period, but with some recovery in 1982, which was generally a good year for butterflies. This species, whose larvae feed on violets, is found most frequently in 2 very different habitat types, chalk downs and coastal grassland and dunes. The data can be separated according to region, or habitat type, and, in this case, the chalk downland data are shown in addition to the national data. There has been a relatively greater decline on downland sites during the study period.

Although no general analysis of the effects of weather is yet possible, there have been 2 striking climatic events during the recording period. In 1976, the first year, there was a summer of extreme drought, which appears to have been the cause of sharp declines of many species, mostly, it is thought, because of the

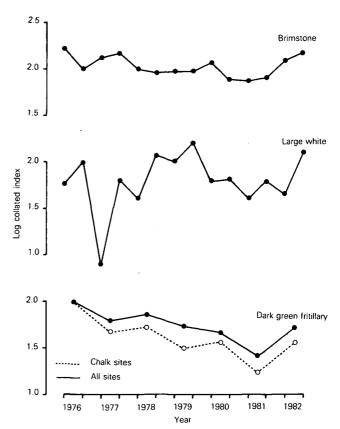
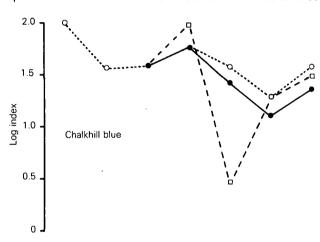


Figure 20 National trends in abundance 1976-1982 for 3 selected species.

desiccation of the larval food-plants. The declines of the Adonis blue and large white butterflies in 1977, shown in this report, are thought to have been caused by the 1976 drought. The second event was the cold winter of 1981–82, when some of the lowest temperatures recorded in this country were experienced. There seems to have been no detrimental effect on butterflies as a result of this extreme weather. The dormant hibernating stages of many invertebrates are very resistant to cold.

Effects of site management

It is hoped that a major use of the monitoring scheme will be to assess the effect of management, or other impacts, at individual sites. Such assessment is approached in 2 ways. First, the site data are compared with regional or national trends. Fluctuations in abundance of most species are similar over a region or, sometimes, even over the whole country. These widespread fluctuations are assumed to be related to wea-



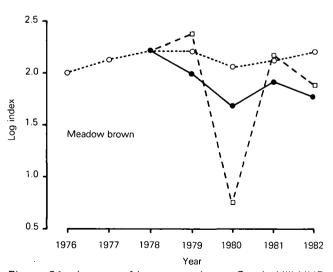


Figure 21 Impact of heavy grazing at Castle Hill NNR in 1980, showing the grazed area (¬---¬¬¬¬), the whole transect route (•——•), and the trend on all chalk sites (•——•). The grazed area showed a steep decline in numbers, followed by rapid recovery when grazing was relaxed.

ther conditions, while local departures of site data from these general trends may be associated with local habitat change. Second, the data for each site can be further divided into sections of the transect route. In this way, the data for an area affected by a particular type of management can be inspected separately. This approach has been described in a study of Monks Wood NNR (Pollard 1982), and a further example is given here (Figure 21). In 1980, part of Castle Hill, a chalk downland NNR, was grazed heavily by sheep. The initial effect was a major reduction in butterfly numbers, although the numbers have recovered subsequently. As the regional data provide a 'control', the method can be used for many types of impact assessment, provided counts are made at the site of interest before and after the 'impact' occurs.

E Pollard

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LAND SURVEY AND VEGETATION DYNAMICS: AN INTEGRATED APPROACH TO RAILWAY CONSERVATION IN BRITAIN (This work was largely supported by Nature Conservancy Council funds)

The literature of railway ecology is slight. Early work concentrated on the alien and adventive flora of railway stations and yards (eg Kreutzpointner 1876; Thellung 1905; Kent 1957, 1960), although more recently (Brandes 1979; Caspers & Gerstberger 1979) plant communities occurring in such areas have been studied in relation to their environment. Detailed accounts of the ecology of railway embankments in Finland have been prepared by Suominen (1969) and Niemi (1969), and, in Britain, local studies in Bedfordshire (Dony 1955, 1974) and Rutland (Messenger 1968) have been made. In addition, the majority of *County Floras* cite species from railway habitats, and a number of short papers on disused lines (Perring & Huxley 1965; Braithwaite 1976) has been published.

When a question was asked in Parliament (Parliamentary Debates 1961) about the introduction and use of herbicides on railway verges, it became apparent that insufficient information was available for any balanced assessment to be made.

The Nature Conservancy (now Nature Conservancy Council, NCC) had become increasingly concerned that British Rail (BR) economies in verge management (dating from 1961) would lead to radical alteration in the structure of railway vegetation. In particular, it was thought 'that much conservation interest in terms of herb-rich grassland may be affected by the development of coarser vegetation and scrub in the absence of regular management' (Way & Sheail 1977).

ITE, under contract with the NCC, was asked to provide base-line information about the vegetation and habitats occurring on BR land.

In structuring a survey, the following questions were considered:

i. What kinds of species and communities occur? Are any of these unique to railway land, or is the system more important as a *refugium* for locally characteristic forms under increasing agricultural

- or urban pressure?
- ii. How is the vegetation distributed, and over what acreage? Do areas of particular biological interest occur?
- iii. Is the system stable under the present BR ad hoc management regime, or have any deleterious changes occurred? Is intervention appropriate in any particular case or area?

Approach

The survey was based on a geographic stratification of BR land (Sargent 1983a; Sargent & Mountford 1980). Twenty-six strata (track classes) distributed along 14000 km of rural* track were recognized. The distribution of track classes occurring in Scottish Region is given, as an example, in Figure 22. Objective recording from 361 stratified random sites (3502 vegetation sam-

^{*} Safety constraints limited the survey to rural verges which occupy 30678±4542 ha (Sargent 1983b).



SCOTTISH REGION

Track classes

Pennine Coal Measures

**** Northern Sandstones

...... Pennines

Western Coal Measures

..... North Coast Carboniferous

..... Scottish Lowlands

**** North West Coastal

•••• Highland Coastal

west Highlands

Central Highlands

and Igneous Coastal



Urban area

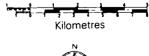




Figure 22 The distribution of track classes in Scottish Region.

ples) was coupled with visits to areas of suspected biological interest. This approach enabled quantifiable statements about the distribution of vegetation to be made, whilst ensuring that, within a limited resource, as many outstanding sites as possible were documented. A number of random sites in Southern and Western Regions were resampled after a 3-year interval, and vegetational changes were recorded and analysed.

Species

During the survey, 1021 phanerogams (including aggregates, sub-species and varieties) were recorded, of which 214 had not previously been described from BR land. Of the 271 cryptogams (pteridophytes and bryophytes only) identified, 177 were reported in this environment for the first time. Reference in *County Floras* (bibliography in Sargent 1983b) was found to a further 611 phanerogams and 52 cryptogams, giving the total number of species documented on BR land as 1955.

One UK record (*Hieracium zygophorum*; Sell and West 1980), 54 Vice County and >200 new 10 km records have been confirmed so far from information collected.

A comparison between species described during the survey and in the literature was made. In Table 12, all species occurring on >20% of survey sites, or with >20 literature records, are listed. Only one, *Chamaenerion angustifolium*, is common to both categories, whilst, of the 21 plants recorded frequently during survey, 16 are referred to fewer than 10 times. Conversely, of the 20 plants mentioned often in the literature, only

5 were found on >10% of railway sites. The low coincidence reflects a bias in earlier botanical work towards railway yards, but it may also be due to changing vegetation management practices.

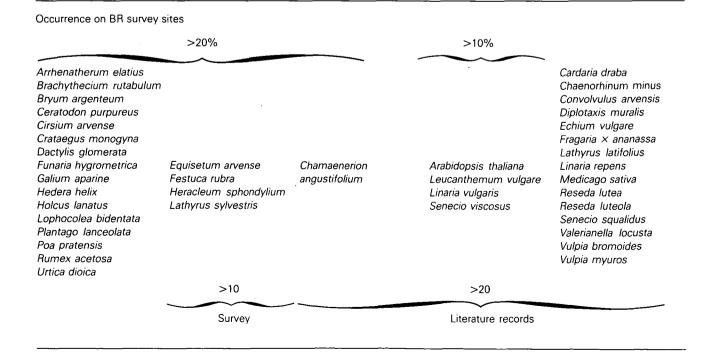
An inspection of Table 12 shows that common survey plants are native perennial grassland and scrub species and bryophytes, whilst *County Flora* records include a large proportion of annual, ruderal and alien species (>30% of total recorded; Sargent 1983b). These latter plants are characteristic of the desiccating conditions found along the railway cess (cindery track margins) and in station yards, where propagules, transported with goods and traffic, may develop and sometimes establish.

Along the Shanklin-Ryde line (Isle of Wight), Chaenorhinum minus, Senecio squalidus and Valerianella locusta are abundant. These are species occurring in the most frequent literature category, but found comparatively seldom during the survey on the mainland, where recent BR policy has been to keep the permanent way (including cess) 95% weed-free using herbicides sprayed from specially adapted trains. Such trains do not run on the Isle of Wight.

On the other hand, Senecio viscosus and Arabidopsis thaliana, in the same literature category, were recorded rather more frequently during the survey. A. thaliana is a winter annual which completes its life cycle before spraying takes place in early summer, whilst S. viscosus has a potentially long germinating season, and may not develop until after weed killing has occurred. S. viscosus is expanding its range along railway lines,

Table 12. Railway species common to survey and literature

The Table groups, by frequency class, the 40 species most common to survey and literature: the large aggregates of *Bryum bicolor, Hieracium, Rosa canina, Rubus fruticosus* and *Taraxacum officinale* which were not identified to species level are omitted.



with new Vice County (93) and 10 km records in Scottish Region.

Vegetation

Information collected during the random survey was used to construct and interpret a classification of railway vegetation. A stepwise numerical technique was developed, in which the data were divided into 6 major vegetation groups (Figure 23), prior to detailed phytosociological sorting. Use was made of software prepared by Hill (1979a, b), although final grouping was empirical.

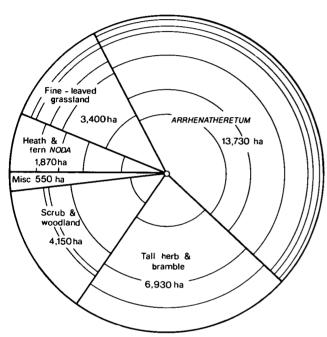


Figure 23 The distribution of vegetation noda on rural BR verges. Each major vegetation group (segment) is subdivided into several noda which are described briefly in the text. Detailed accounts and synoptic tables are given by Sargent (1983b). Each 0.5 cm² represents 100 ha.

The major vegetation groups are summarized below. Complete phytosociological tables for these groups are held at Monks Wood, and synoptic tables have been published by Sargent (1983b). Several *noda* are illustrated in Plate 7.

1. Heath and fern associations

Three heath and 2 fern associations were identified. The heaths are largely restricted to Scottish Region and are broadly comparable with *noda* defined by McVean and Ratcliffe (1962), although the railway facies consistently include more tree species (especially birch and sallow; Plate 7e) and a greater proportion of *Molinia caerulea*, probably because of comparatively light grazing along railway verges, and a history of management by burning (Muirburn Working Party 1977).

The fern associations include a widespread *Pteridietum* found preferentially on freely draining south-facing slopes and a *nodum* based on the constant occurrence

of *Dryopteris filix-mas*. On railway land, *D. filix-mas* is particularly characteristic of spent ballast tips in the north and west uplands, where it occurs with or without a deciduous canopy of ash, larch or sessile oak.*

2. Fine-leaved grasslands

Railway grasslands at extremes of pH and under heavy grazing pressure, where the Arrhenatheretum does not compete successfully, are included here. Six noda with comparatively local distributions are recognized. Species-rich chalk grassland is restricted to cuttings in Southern Region (Plate 7a), whilst Brachypodium pinnatum swards are almost exclusive to calcareous cuttings in Eastern Region, and Holcus mollis only becomes common on base-poor, freely draining verges in the London Midland Region. Of the 3 bent fescue noda recognized, a grass heath occurring on grazed, freely draining verges is the most widely distributed. One association, distinguished by (amongst others) the constant presence of Luzula campestre with abundant Rhytidiadelphus squarrosus, occurs along browse margins. These areas are grazed from adjacent pasture, but neither dunged nor trampled. The third nodum is strictly basiphilous, and found mainly in Scottish Region.

3. Arrhenatheretum

The railway Arrhenatheretum covers approximately 13730 ha of verge. Although comparable with Arrhenathereta described from other habitats (Rodwell in press), it is distinguished by the constant presence of Equisetum arvense and the relative abundance of bramble (Rubus fruticosus agg.) and Chamaenerion angustifolium. Seven noda are recognized. Those in which Poa pratensis, Centaurea nigra and Plantago lanceolata are constant occur on cutting slopes, which, having been excavated, usually support an immature mineral soil, whilst those where Urtica dioica and Cirsium arvense are characteristic grow on engineered embankment slopes, which are often disturbed by the tipping of spent ballast and the drainage of oily and nitrogenous wastes from trains (Plate 7b).

Of particular interest is a *nodum* distinguished by *Poa* angustifolia, *Potentilla reptans* and *Vicia sativa* ssp. *nigra*. This is found on warm, freely draining or cindery cutting slopes, which have usually been burnt previously. It appears, in Britain, to be unique to the particular conditions found along railway verges, where the *nodum* covers approximately 2000 ha.

4. Tall herb and bramble

These *noda* are essentially continuous with the *Arrhenatheretum*. They occur on lower embankment slopes, or footings where the soil is damp and often 'mulched' by a thin layer of spent ballast (Plate 7b). They are distinguished by abundant *Filipendula ulmaria*, *Galium*

^{*} especially on limestone in the Pennines.

aparine and *U. dioica*, and grade into stands dominated by bramble.

5. Scrub and secondary woodland

The 5 noda recognized here are identified most easily by their principal canopy species: ash, elm and oak (*Quercus robur*; Plate 7c, f) woodland, and hawthorn and calcicolous scrub. *Arrhenatherum elatius*, *Hedera helix* and bramble are constant members of the ground flora, although each *nodum* has its own characteristically associated species.

6. Miscellaneous

Ombrogenous mires, reed beds (characteristic of embankment footings), and cinder associations with *Senecio* spp. are grouped here, showing few common species amongst themselves, or with any other *noda* (average linkage with Czekanowski similarity coefficient <0.15; Sargent 1983b). Cinder associations were undersampled because of the safety constraint that limited the survey to rural verges. Four stands with *Rhododendron ponticum* thicket, and 2 of salt marsh vegetation were also recorded, but were considered too local and atypical to include in the general analysis.

Change

A preliminary look was taken at the way in which BR vegetation, under reduced management, is changing. Thirty stratified random sites in Southern and Western Regions, first surveyed in 1978, were revisited during 1981. Both datum sets (2×272 quadrats) were ascribed to the classification, and the fate of each quadrat followed. A transition matrix, showing change between the 4 major vegetation groups which occur in these Regions, is given in Table 13. Information for only 265 quadrats is shown, the other 7 belonging to vegetation groups (heaths and miscellaneous) with centres of distribution elsewhere.

Table 13. Transition matrix showing changes between 1978 and 1981 in the distribution of the 4 major vegetation types found in Southern and Western Regions

	Fine-leaved grassland	Arrhenatheretum	Tall herb and bramble	Scrub and secondary woodland	Total (1978)
Fine-leaved grassland	24	4	2	1	31
Arrhenatheretum	9	52	11	4	. 76
Tall herb and bramble	. 1	20	36	5	62
Scrub and secondary woodland	5	7 .	7	77	96
Total (1981)	39	83	56	87	265

The largest movements within the matrix are the recruitment of *Arrhenathereta* to fine-leaved grassland (9 quadrats), the reciprocal exchange of *Arrhenathereta*

with tall herb and bramble (11 and 20 quadrats), and the loss of scrub and secondary woodland to the latter 2 groups (7 quadrats each).

The balance between *Arrhenathereta* and tall herbs is tenuous, and probably influenced by disturbance (ballast tipping, accidental burning, bramble spraying), whilst the loss of scrub and secondary woodland reflects increased clearance over the past few winters (C Beagley, BRB headquarters, personal communication).

Perhaps the most interesting change, and one contrary to expectations, is the increase in area of fine-leaved grassland. Rabbit grazing pressure may be partially responsible, although the phenomenon possibly reflects recovery from a regime of annual burning, prior to 1960. The distribution of vegetation groups amongst all quadrats recorded as recently burnt (ie within the present or previous season, usually accidentally) is shown in Table 14. More quadrats belonging to the *Arrhenatheretum* were recorded than expected, implying that such treatment favours the development of a false oat sward. Conversely, fewer fine-leaved swards were recorded.

The mechanisms underlying vegetation change on rail-way land are not fully understood. The vegetation is extremely diverse, and a large number of variables are involved. However, assuming some scrub control is practised under present conditions of grazing by small mammals and comparatively little burning, there seems to be a gradual succession towards fine-leaved grassland. There is also some increase in coarse grasslands, but this is largely at the expense of scrub and tall herbs.

Table 14. The distribution of recently burnt quadrats amongst vegetation groups. This is not comparable with the overall distribution ($\kappa^2 \simeq 54.2$, P<0.1)

Vegetation groups	Number of quadrats observed	Number of quadrats expected
Heath and fern associations	9	9
ine-leaved grasslands	7	17
Arrhenatheretum	111	71
all herb and bramble Scrub and secondary	30	35
woodland	0	14
Miscellaneous	0	2
	157	157

The information contained in Table 14 may be converted into a transition probability matrix, and a Markov (population) model, predicting future distribution of vegetation groups, can be applied (Horn 1975; Usher 1979). When such a model comes into equilibrium, it predicts that the acreage of fine-leaved grassland will have increased by 96%, and that of the *Arrhenatheretum* by 18%. Tall herb and bramble, and scrub and

secondary woodland will have decreased by 16% and 35%, respectively.

Certain assumptions are implicit in this technique: in particular, the conditions remain constant, and the raw state of vegetation at each iteration has no effect on the probability matrix (which remains constant). Such conditions are almost certainly not fulfilled, and the predictions must therefore be treated with extreme caution. Long term monitoring sites have been set up, enabling a more accurate assessment of change to be made.

Biological Interest sites

Using criteria defined by Ratcliffe (1977), 185 outstanding sites were identified in the field. Detailed files for each of these sites are lodged with the NCC, whilst maps and management advice, based on the information collected, have been prepared for BR.

Selection was not supported statistically, because nonrandomly distributed data were included: 98 sites (41% of total number visited) were chosen from the subjective survey, whilst 87 sites (18%) were identified amongst the random sites. A large proportion of Biological Interest sites occurred on cuttings (42·7%) or on mixed formations including cuttings (31·4%).

Conservation and management

The BR land survey has shown that much of the grassland of conservation interest occurs on previously managed cuttings. The excavated slopes tend to have nutrient-poor mineral soil, which supports locally and regionally characteristic plants, and inhibits competition from false oat grass, even where previously burnt (Plate 9a). Topsoiled embankments and flat verges generally support a more disturbed vegetation, with many commonly occurring competitive species (Plate 9b).

A general strategy is suggested, in which priority is given to the maintenance of cuttings. This strategy coincides with the permanent way engineers' requirement that trees or scrub, likely to drop litter or branches on to the line, be controlled. Scything and occasional burning of grassland will prevent the development of scrub, whilst also encouraging diversity. Application of chemical scrub control agents is effective, but leaves standing dead material, and does little to encourage the less competitive grassland plants. The use of a flail adapted to be carried by train has been found useful for clearing bramble and low scrub in some areas.

On embankments, the spread of scrub and secondary woodland on lowland slopes may lend stability, and will provide cover and nesting habitat for birds. Casualty recordings have shown that over 70% of bird deaths occur in cuttings, where flight from oncoming trains is inhibited, suggesting that it is preferable to leave cover on embankments rather than on cutting slopes, although, where woodland on the slopes is

well developed and offers no hazard to rail traffic, it should clearly not be cut. In highland areas of Scottish Region, such woodland is often at a premium.

There is a stringent requirement that annual spraying of main lines by BR and contractor's trains should leave the ballasted width 98% free of weeds, and the cess 95% free. Probably the most serious weed along the track bed is the common horsetail (E. arvense), which is a perennating plant and could be controlled by biennial spraying of the track. The majority of plants which are killed by spraying are small annual species and bryophytes, which are adapted to survive the desiccating conditions found during high summer. Many of these plants are still found on tipped ballast and cinder, although they are no longer able to compete successfully when the vegetation closes over. It has been suggested that, on less important lines, and perhaps initially for a trial period only, tracks on either side are sprayed during alternate years. This practice will enable some annual plants to maintain their populations (Plate 7d). Further, it should substantially reduce maintenance costs without introducing hazard, as all perennating plants will be controlled.

Caroline Sargent

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BIOLOGICAL RECORDS CENTRE

(This work was partly supported by Nature Conservancy Council funds)

The Biological Records Centre (BRC) is a national data bank and archive of information on the occurrence of plants and animals in the British Isles. The data bank currently includes more than 2.5 million records of over 6000 species held on the PDP 11/34 computer at Monks Wood and the IBM computer system at the Science and Engineering Research Council's Rutherford and Appleton Laboratories. The archive consists of the originals, or microfilm copies, of over 400000 record cards, stored at Monks Wood.

The main sources of data are the National Biological Recording Schemes. A wide variety of taxonomic groups is covered by the 53 schemes now operating. Schemes are organized by scientists at universities, colleges, museums and other institutions throughout Britain, by national biological societies and, in some cases, by private individuals. The schemes obtain their data from professional and amateur specialists in the respective taxonomic groups. BRC receives data from other sources, eg survey and monitoring projects in ITE, and research at other NERC institutes and at universities and colleges.

BRC has received support from NCC since 1973 in the form of annually placed contracts, but a 3-year contract,

beginning in April 1982, has now been agreed. Through this contract, NCC provides support for the general operation of the Centre and has requested the development of methods by which records for statutory nature conservation sites may be extracted from the BRC data bank. Work on this aspect has begun by enhancing information held in the data bank, but the input of details about NCC sites and their boundaries will begin in 1983.

Work on botanical data has concentrated on the updating of the computer files for vascular plants, especially those species to be covered in the first volume of the new Flora of Great Britain and Ireland. Some pilot work on data for bryophytes has begun using a sample of 50 000 records, covering three 100 km squares in Britain. The improvement of the data on computer file for butterflies has constituted much of the work on invertebrates. Although over 113 000 records of butterflies were on file, they were of a simplified type. Over 100 000 records are now on file, containing much additional information of particular importance in providing site-related data. Work has continued on other groups, including Orthoptera, terrestrial Isopoda, Chilopoda and Diplopoda. The Orthoptera data have been used in a pilot study to develop a method of providing siterelated information. Records of vertebrates continue to be edited and processed, with some 15 000 for mammals and 1700 for freshwater fish now on computer file. Several new recording cards were designed and printed, including species list cards for Brachyura, nonmarine Isopoda and Coleoptera: Elateroidea, and 3 general cards, one of which is for use by the British Cave Research Association in recording hypogean fauna.

Output from BRC has been published in a variety of forms during 1982: volume 1 of the *Atlas of the lichens of the British Isles* (176 species), maps of 73 species of *Carex* in a handbook to the genus, provisional atlases of 100 species of Myxomycetes and 16 species of freshwater Hirudinea, preliminary atlases of 100 species of Carabidae (Coleoptera) and 54 species of butterflies. Updated distribution maps of amphibians and reptiles are in press in a major new publication on the group; also, maps of deer are to appear in a book on 'trees and deer'.

During the year, BRC staff lectured to more than 12 student and specialist groups about the work of the Centre and also represented the Centre at meetings and on committees. A meeting on recording freshwater invertebrates was organized at Monks Wood in May. It was attended by 35 people, mainly contributors to recording schemes, but including some water authority biologists and representatives of the Freshwater Biological Association and the Nature Conservancy Council. Overseas visitors to BRC included representatives of major species mapping projects in Canada and Argentina. Several specialists visited the Centre to abstract data in connection with their research on particular

species. Other visitors, seeking records from localized areas, included representatives of provincial museums, local biological records centres and the Ministry of Defence. Many enquiries were handled during the year — these came from organizations concerned with wildlife conservation; government departments, local authorities and nationalized industries; research scientists and students; and also from contributors to recording schemes and the general public.

PT Harding, Dorothy M Green, CD Preston, HR Arnold and Rosemary J Harper

Airborne pollutants

FLUORIDE IN THE MAGPIE

In a review of fluoride at different stages in a food chain, Groth (1975) noted that amounts of this substance tended to be larger in animals subjected to fluoride pollution than in plants. By analogy with the distribution of other pollutants, he inferred that animals high in a food chain are likely to be subject to more contamination than those lower down, a contention supported by Andrews et al. (1982).

For some years, the fate and effects of fluoride emitted from the aluminium reduction plant near Holyhead, on the Isle of Anglesey, have been at the centre of work on lichens and small mammals, described in previous Annual Reports by Perkins et al. (1980a) and Walton (1982). To explore another facet of the fluoride 'problem', work has started on the magpie (Pica pica) in the same locality. This new study examines the occurrence of fluoride in a predator, that is an animal close to the top of its food chain, and identifies some of the factors determining the observed patterns of accumulation. Eventually, when the life cycle of the magpie is more fully understood, and when information about concentrations of fluoride has been collected over a longer period, it should be possible to identify effects, if any.

The magpie was chosen because it is common and widespread on Anglesey and is regarded as an agricultural pest. It is also both readily accessible at most times of its life and conspicuous by virtue of its appearance and its behaviour. These are all important considerations, facilitating the collection of samples and enabling the biology of the bird to be studied in the wild. The magpie is also a member of a group of birds whose species are widely distributed, some of which have been the subject of considerable research, for different reasons, elsewhere.

The adult magpie usually feeds in open fields, mainly taking ground insects, especially beetles. It feeds insects, including caterpillars, to its young. It also takes grain and wild fruits, together with a miscellaneous selection of other foods.

Anglesey has an essentially agricultural landscape, chiefly grassland grazed by sheep and cattle, with lesser proportions of corn, potatoes and root crops. Hedgerows, dominated by hawthorn, are widespread and generally untrimmed. The common occurrence of the magpie indicates that the blend of land uses in the landscape affords it good habitat. It nests mainly in the tops of thorn hedges, with numbers of nests per square kilometre sometimes reaching 15. The birds build their nests in February-March and lay their eggs, typically 6 in a nest, between late-March and early-May. Incubation takes 18 days and the nestlings are present for a further 27 days.

Three stages in the life of the bird have been examined for fluoride: eggs, nestling birds when 24-days old (Plate 8), and adult birds — adults in 1977, and the others in 1979 and 1981 as well as 1977. Many different tissues were analysed for fluoride concentration, measured in µgFg⁻¹, so as to identify one that could provide a meaningful index of contamination.

Fluoride accumulations in different tissues

Eggs

Eggs were taken from nests in 1977 on 2 areas of Anglesey — a control site, 13 km ESE of the aluminium smelter, which was judged from Perkins' data to be relatively unpolluted, and an experimental site comprising land inside a circle of 5 km radius centred on the chimney — the principal source of fluoride emission of the Holyhead aluminium reduction plant. Each egg was divided into 'contents' (ie yolk and albumen) and 'shell' (which also included the underlying shell membranes). There were larger concentrations of fluoride in the shell than in the 'contents'. Whereas there was no difference in the mean concentrations in the 'contents', the shells of eggs taken from the polluted area had twice as much fluoride as those from the unpolluted area (Table 15).

Table 15. Accumulations of fluoride, μg F g⁻¹, in magpie eggs collected during 1977 from polluted and unpolluted areas of the Isle of Anglesey

	-	unpolluted site	Polluted site, near aluminium reduction plant 15			
Number of collections analysed		11				
	CONC	Concentrations of fluoride, μg F g ⁻¹				
				_		
	Mean	Standard deviation	Mean	Standard deviation		
'Shell' (including shell membranes)	Mean 15		Mean 29			

Table 16. Accumulations of fluoride in magpie nestlings sampled during 1979 from polluted and unpolluted areas of the Isle of Anglesey

	Control, unpolluted site		Polluted site, near aluminium reduction plant		
Number of collections analysed		15		15	
,	Concentrations of fluoride, $\mu g \ F \ g^{-1}$				
	Standard Mean deviation		Mean	Standard deviation	
Soft tissues					
Feathers	18	6	15	. 5	
Liver	9	2	. 9	2	
Heart	18	4	15	4	
Lung	13	4	15	5	
Kidney	17	10	17	6	
Muscle	14	5	13	4	
Brain	19	3	17	5	
2. Parts of skeleton					
Femur	180	74	475	160	
Vertebrae	242	114	685	334	
Cranium	116	48	249	80	

Nestlings

Nestlings 24-days old were taken in 1979 from a control, unpolluted area 25 km ESE of the smelter and from the polluted experimental area sampled for eggs.

Ten parts of the body, 7 different soft tissues and 3 parts of the skeleton were analysed, including the femur which has been used in many previous investigations by other people. Bone is generally considered to be a major site for the deposition of fluoride in vertebrates. Concentrations of fluoride in soft tissues were relatively small compared with those in bones. Like the 'contents' of eggs, the soft tissues did not accumulate much fluoride. In contrast, the bones of nestlings in polluted areas contained twice as much fluoride as those nestlings sampled from the control, 'unpolluted' area (Table 16). To conform with studies done elsewhere, the femur was chosen as the indicator for other surveys.

Adults

The results obtained did not differ materially from those obtained with nestlings.

Field survey of Anglesey

Eggs and nestling magpies were collected from roadside nests wherever they could be found.

Fluoride in eggs

Concentrations in excess of $30\,\mu g$ F g^{-1} were found in shells of collections made near coastal areas, with a slightly greater abundance on the west coast, and possibly in the south-east (Figure 24).

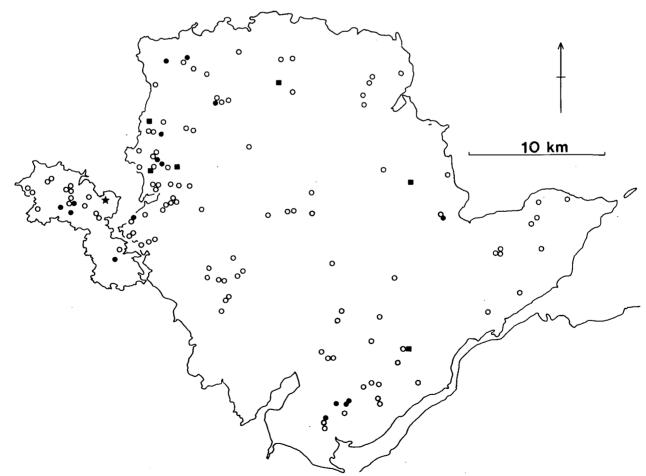


Figure 24 Fluoride concentrations in the shells of magpie eggs collected on the Isle of Anglesey during 1979 ★, location of aluminium smelter reduction plant.

Fluoride concentrations: \circ , 0-30 $\mu g g^{-1}$; \bullet , 31-60 $\mu g g^{-1}$; \bullet , >60 $\mu g g^{-1}$.

Fluoride in the femurs of nestlings

In contrast to the situation with eggs, there was a strong preponderance of enhanced fluoride concentrations in femurs from nestlings in the western part of Anglesey, notably around, and upwind, of the reduction plant (Figure 25).

Directional effects on the concentrations of fluoride Perkins et al. (1980b) indicated that the wind is a main factor determining the spatial distribution of fluorides emitted from the aluminium reduction plant, there being a preponderance of winds from the south to west quadrant. Observations of eggshells and nestling femurs indicate that their fluoride accumulations decrease progressively with increasing distance from the reduction plant, eg in an east-north-easterly direction (Figure 26). The slopes of the lines linking the logarithmic concentrations of fluoride and the distances from the reduction plant are virtually identical for shells and femurs. Interestingly, the eggshell accumulations were more variable than those in the femurs, a pattern implicit in the data presented in map form (Figures 25 and 26).

Discussion

The fluoride pathway to the shells and bones of mag-

pies is complex, starting with the emission of gases and particulate matter, their lateral dispersal by wind, dry and wet deposition to vegetation and soil, the uptake of fluoride from soil by plants, the consumption of fluoride-contaminated herbage by herbivores and, in turn, their consumption by predatory magpies. Fluoride entering adult female birds is probably first deposited in bone before being transferred, in part, to eggshell. As egg formation is probably completed within 24 hours, this short period of development may be responsible for the variable quantities of fluoride in shells. In contrast, the concentrations of fluoride found in femurs were much less variable and possibly reflect a longer period of accumulation in the nestlings which were 24-days old when analysed. However, an explanation should not ignore the possible effects of short term, and often daily, fluctuations in climate, and, in particular, wind direction.

D C Seel

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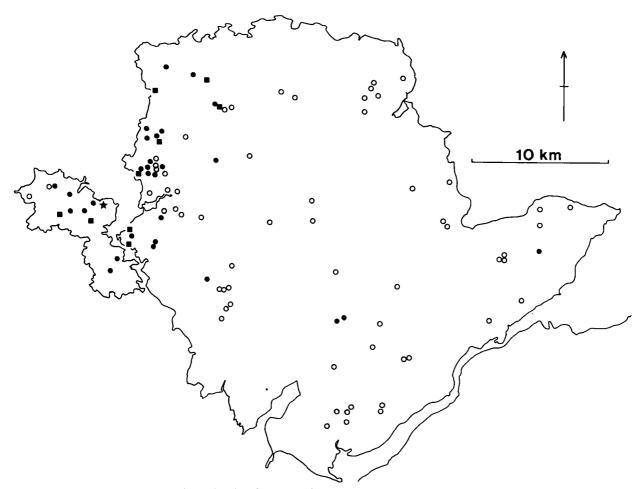


Figure 25 Fluoride concentrations in the femurs of magpie nestlings 24-days old, collected on the Isle of Anglesey in 1979

★, location of aluminium smelter reduction plant.

Fluoride concentrations: \circ , 0-250 µg g^{-1} ; \bullet , 251-500 µg g^{-1} ; \blacksquare , >500 µg g^{-1} .

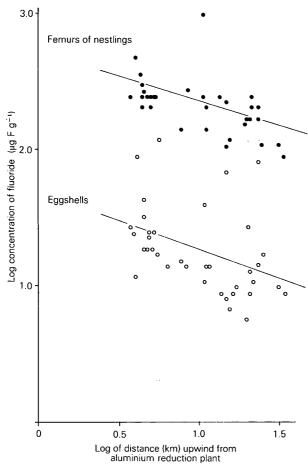


Figure 26 The changing concentrations of fluoride in eggshells (\circ) and femurs of magpie nestlings (\bullet) collected at different distances in an east-north-east-erly direction from the aluminium smelter reduction plant near Holyhead, Isle of Anglesey, during 1979.

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ACIDIFYING INFLUENCES OF AIR POLLUTANTS AND ACID RAIN

The deposition of acidic compounds from the atmosphere is a matter of considerable concern in western Europe and North America. Acidic inputs arrive by wet deposition (in rain and snow) and by continuous dry deposition of gases and particles. The contribution made by acidity in rain can be measured relatively easily in terms of the hydrogen ion concentration. Rainfall acidity is caused by the incorporation of pollutant gases such as sulphur dioxide (SO₂) and nitrogen dioxide (NO₂), and particulates (sulphates and nitrates) derived from these gases into clouds and rain. The main source of these pollutants is the combustion of fossil fuels. The contribution to acidity made by the direct input of these acidic gases and particulates through dry

deposition can only be inferred by making assumptions about the chemical reactions which may occur. Each molecule of sulphur dioxide could contribute up to 2 hydrogen ions, whereas each nitrogen dioxide molecule could yield one hydrogen ion. To offset these acidic gases, ammonia gas may also be deposited dry, neutralizing one hydrogen ion per molecule.

The effects of acidic deposition on freshwater and on forest ecosystems have been studied intensively in Scandinavia and in North America (Drabløs & Tollan 1980). Wet deposition in parts of northern Britain is at least as great as in areas of southern Scandinavia where fish populations are depleted, and there is already some evidence that fish stocks are at risk in parts of Scotland (Harriman & Morrison 1981). Reports from West Germany (Ulrich 1981) suggest that the combined effects of dry and wet deposition may be responsible for severe damage to large areas of conifers by affecting root development. Until now, similar effects have not been reported from forests in the UK. Nonetheless, it is important to examine the spatial and temporal distribution of acidic deposition in order to identify areas of the country with particularly large inputs and possibly, therefore, at risk.

Wet deposition

There is a marked concentration gradient of hydrogen ions in rain over northern Britain, ranging from 20 μg litre $^{-1}$ (pH $4\cdot7$) in the north-west to $60\,\mu g$ l $^{-1}$ (pH $4\cdot2$) in the south and east (Fowler $et\,al.$ 1982). However, when allowance is made for the larger annual rainfall in the west and at high altitudes, the largest inputs are found in mountainous areas, eg in west central Scotland where the bedrock is mostly slowly weathering, yielding base-deficient soils (Figure 27).

The extent to which soils can modify the acidity of rainfall before water passes from land to streams and lochs is dependent on soil type, annual average inputs. and, especially, the type of rainfall event. If a large input of acidity in rain occurs over a short period of time, the contact time between water and soil may be so short that even soils with large cation exchange capacities may not be able to neutralize the deposited acidity before the water enters streams. This feature is of particular concern when run-off from the land surface contributes significantly to streamflow. Studies of the distribution of wet deposited acidity at Bush (near Edinburgh) have shown that the amounts deposited daily are approximately log-normally distributed (Figure 28). Over the 5-year period 1977-1981, approximately 40% of the annual wet deposition of acidity arrived on only 2 or 3 wet days (Table 17). This observed occurrence of large volumes of rain, in conjunction with large amounts of acidity, may lead to very rapid changes in the acidity of fresh waters, because of short contact times and surface run-off, even where soils have a large buffering capacity. The episodic nature of acidic inputs in rain makes the interpretation of 'effects' studies in the field very difficult, unless the acidic in-

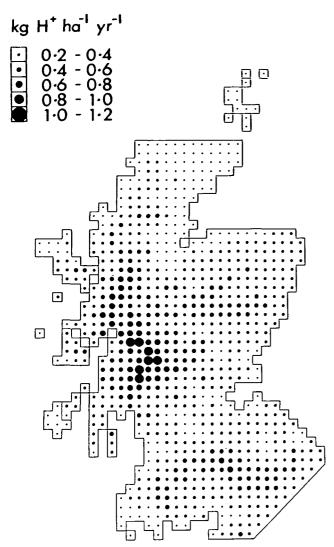


Figure 27 Estimated annual input of acidity in rainfall over northern Britain (1978-1980), expressed as the mass of hydrogen ions per hectare.

puts are monitored over short periods (eg daily). Because of the occurrence of 'extreme' events of acidity in rain (Figure 28), it would seem appropriate to mimic such episodes in experimental studies of acid rain effects.

Dry deposition

Unlike wet deposition, which is necessarily episodic, dry deposition is a continuous process depending on atmospheric and surface processes, as well as the properties of the gases. SO₂ and NO₂ are both reactive gases, and their rates of deposition on to vegetation and other natural surfaces have been shown to be one of the major factors controlling the residence times of these gases in the atmosphere (Garland 1977). The rate of deposition of SO₂, expressed as a flux (typically $0.1-1.0 \,\mu g \, SO_2 \, m^{-2}$ ground area s⁻¹), is influenced by surface and atmospheric factors, including air concentrations of SO₂. Results are frequently normalized for concentration by dividing the vertical flux by the air concentration at a reference height, the resulting quantity having dimensions of a velocity (LT⁻¹) and being known as the velocity of deposition (v_a).

Table 17. The proportion of rain days associated with annual wet deposited acidity at Bush (near Edinburgh)

1	2	3
Daily input of wet deposited acidity mg H ⁺ m ⁻²	% of total rain days on which amounts of acidity in 1 were deposited	The % of total wet deposited acidity attributable to rain events characterized in 1 and 2
0–1	95	62
1–2	2.4	13
2–3	1.6	14
3–4	0-4	5
>4	0.3	6

Fowler and Unsworth (1979) showed that the reciprocal of v_g , the total resistance to transfer (r_t) , may be treated as an analogue of Ohm's law (flux = potential difference/resistance), where the potential difference is the difference in air concentration between the reference level and the absorbing surface (Figure 29). The total resistance to transfer may be subdivided into atmospheric (r_a) and surface components (r_c) , making it possible to examine the mechanism of deposition and to identify the factors limiting the process at any time.

Measurements of the dry deposition of gases in forests, a particular interest within ITE, are limited by theoretical and practical considerations (Thom *et al.* 1975), and the choice of methods is therefore restricted. Following the development of a rapid response flame photometric sulphur analyser, SO₂ fluxes on to a Scots pine canopy have been measured using an eddy correlation technique (McBean 1972). In addition to measuring gas concentrations and the vertical component of atmospheric turbulence for the SO₂ fluxes, additional measurements of convective heat transfer and net radiation were made to obtain rates of evapotranspiration, and hence canopy resistances to water loss.

Day-time deposition rates on to a dry canopy (typically $v_g=5.0~\text{mm s}^{-1}$) are determined largely by stomatal opening, stomatal uptake representing 80% of the total flux, and the remaining 20% being the sorption by cuticles, bark and understorey vegetation. Although fluxes were generally directed towards the canopy, small upward sulphur fluxes were occasionally observed. A series of measurements for 24–25 March 1982 (Figure 30) shows the typical diurnal pattern in deposition rates for a dry canopy, and an occasional upward SO₂ flux.

The upward fluxes were generally associated with appreciable changes in SO_2 concentration, and were most probably the result of changes in SO_2 storage in the air beneath the measuring level (Thom 1976). These measurements have also shown the presence of an internal resistance to stomatal uptake of SO_2 in Scots pine. Thus, when canopy resistances for water vapour and SO_2 exchange are corrected for differences in mol-

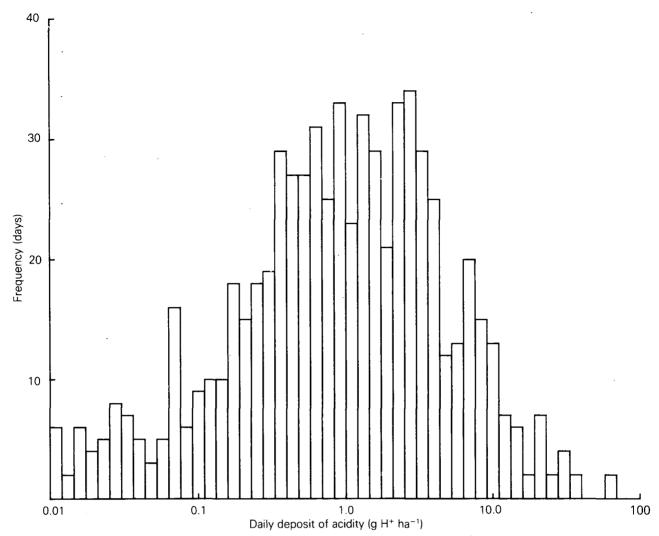


Figure 28 Distribution of the amount of acidity deposited daily in rain at Bush (near Edinburgh) from 1977-1981, expressed as the mass of hydrogen ions per hectare per day.

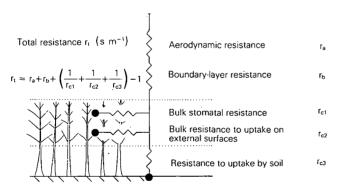


Figure 29 The resistance analogy applied to SO₂ uptake in a forest showing the main sites of uptake.

ecular diffusivities of the 2 gases, they still differ by an appreciable margin.

Garland and Branson (1977) have suggested that the rates of dry deposition on rain-wetted vegetation may be very large ($v_g = 1$ to $20~cm~s^{-1}$). However, our measurements in both light and heavy rain show small values, $v_g = 0.2$ to $0.4~cm~s^{-1}$, which suggest that there is an appreciable canopy resistance (300 s m⁻¹) even when the foliage is fully wet. In these conditions, depo-

sition is strongly influenced by chemical processes in the films of water on vegetation, and future measurements will study this aspect in greater detail.

Total deposition of acidity

Dry deposited SO₂ is oxidized to SO₄²⁻, either on the external surfaces of vegetation or within the leaves. The oxidation process releases 2 hydrogen ions for each SO₂ molecule oxidized, which enables the 'potential' dry deposited acidity to be quantified. This quantification is largely a theoretical exercise and, for vegetation, the production of acidity from this process is not directly measurable because the sites of sorption and oxidation of SO₂ are both within, and on, the surfaces of plants. Beneath canopies of vegetation, the net input of acidity to the soil is influenced strongly by processes within the vegetation and is not simply the sum of wet and 'potential' dry inputs. For central southern and eastern England, where average SO₂ concentrations generally exceed 20 µg m⁻³, the acidity 'deposited' in this way approaches 1.6 kg H⁺ ha⁻¹ year⁻¹, and may exceed wet deposited acidity by a factor of 3. In areas with large SO₂ concentrations (>50 μg SO₂ m⁻³), acidity inputs via dry deposition may exceed 80% of the total. Even in remote areas of Scotland with SO₂ con-

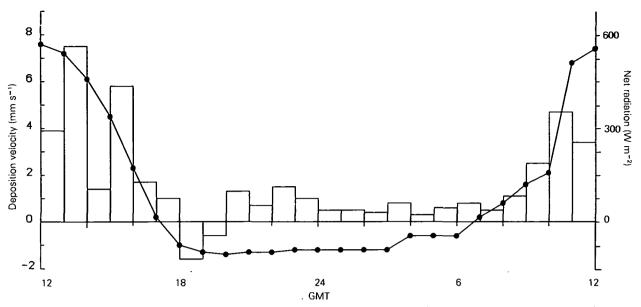


Figure 30 Diurnal changes in deposition velocity for SO_2 and net radiation above a Scots pine forest, 25-26 March 1982. For deposition velocity $(-v_g)$, positive values indicate deposition and negative values show an upward flux. For net radiation (\bullet) , positive values show a downward flux, and vice versa.

centrations of $5 \,\mu g$ m⁻³, dry deposition may still account for 40% of the total.

The concept of dry deposited acidity is simple, but the effects of dry deposited SO_2 gas in practice may be unrelated to the production of hydrogen ions. It is also important to take into account the exchange of other gases between the atmosphere and the surface. Deposition of nitrogen dioxide and nitric acid gases increases the input of acidity, whereas the deposition of ammonia gas would neutralize some acidity.

Clearly, the relative importance of the 2 mechanisms of deposition, wet and dry, varies geographically as well as in time. Furthermore, a consideration of deposited acidity cannot be complete without taking into account the net fluxes of nitrogen dioxide, nitric acid (gas) and ammonia, subjects for future research.

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BIOLOGICAL MONITORING OF THE FORTH VALLEY

A long term programme, based on the regular assessment of the performance of selected macrolichen species and assemblages, has been established to detect environmental changes in the Forth Valley, Scotland. To reduce variation and increase precision, the study is being restricted to species growing on the boles of ash trees and the tops of stone walls. A primary survey of the study area, which covers most of east central Scotland, used a sampling framework derived from a land classification based on climatological, geological and topographical features. It is hoped that this classification (or stratification) will isolate the effects of the natural environment on lichen performance from those attributable to airborne pollutants.

Having ascertained that a suitable range of macrolichen species existed in the study area, a method for repeatedly examining the same lichen assemblages has been devised, noting changes in species composition, vitality and growth rate. Marked quadrats were photographed sequentially. To obtain the necessary precision,

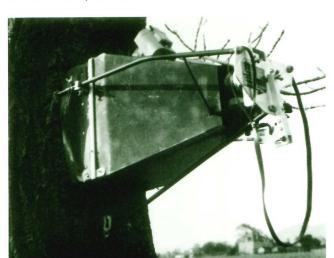


Plate 3 The photographic arrangement used when recording the growth of lichen assemblages on ash trees as part of a long term exercise monitoring environmental change in the Forth Valley, Scotland. (Photograph T D Murray)

stainless steel screws were used as permanent markers, 3 of which were inserted into the heartwood of each sample tree to provide anchorage points for a specially constructed tripod carrying an automatic reflex camera positioned to photograph the quadrat (measuring 14 cm×20 cm) between the tripod feet (Plate 3). Problems with lighting and shadow were overcome by excluding day-light and using a cameracontrolled electronic flash unit, which was positioned almost directly above the quadrat to give a 'flat' picture. Although the resulting photographs have an unnatural appearance, the limits of lichen thalli are outlined clearly. Problems associated with the curvature of the tree were minimized by using a macrolens; the use of flash enables the lens to be 'stopped down' to a small aperture, thus increasing the depth of field.

The macrolichen assemblages in quadrats on 2 trees have been photographed at 10 replicate sites of 15 different land classes to provide a base-line. A further series will be taken at intervals of 6 months. Of the sites selected in the study area, 6% were found to be already so severely affected by atmospheric pollution that macrolichens were totally missing from ash trees. Monitoring at these locations will be provided by chemical analysis of those species which have survived on walls.

Concentrations of hydrocarbons and ozone are expected to increase in the foreseeable future in the study area, as a result of the completion of a large petro-chemical complex at Mossmorran in Fife in 1985. Additional quadrats have therefore been designed in an area (11 km radius) which is likely to have enhanced concentrations of these substances, as suggested by the Forth Estuary Study (1979).

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RADIONUCLIDES IN THE TERRESTRIAL ENVIRONMENT (This work was largely supported by Department of Environment funds)

Studies of the distribution of radionuclides on salt marsh vegetation and their subsequent assimilation by sheep, which were briefly described in the 1981 Annual Report, have now been augmented by other studies, (i) defining the role of birds in the transfer of radionuclides from sea to land, and (ii) investigating the uptake of radionuclides through plant roots.

The role of birds in the transfer of radionuclides from sea to land

Minute amounts of radiochemicals are discharged into the Irish Sea near Sellafield. Some of these are taken up by, or are held on, plants and animals in the sea and littoral zone, especially in and around the Ravenglass estuary, where more than 20 species of birds feed within the tidal zone. Some of these birds are specialist herbivores (greylag geese, wigeon), insectivores (skylarks), or piscivores (mergansers, cormorants), but most of the other species enjoy a catholic diet of plants and/or animals, marine and terrestrial, and also carrion when available. Whilst overland, these birds defaecate, disgorge food remains, lay eggs, and some die or are shot for food — all ways in which birds may help increase the concentrations of radionuclides in the terrestrial environment.

With a diverse array of feeding niches being exploited by birds, the initial objective was to determine the relative importance of the radionuclide transfer attributable to each species by means of a survey. Samples of faeces from 15 species of birds were collected from all parts of their ranges within the tidal reaches of the 3 rivers which feed the Ravenglass estuary (the Irt, Mite and Esk). Regurgitated pellet material (mainly from gulls) was also collected, together with samples of eggs from black-headed gulls and crows. In addition, carcases of 8 different species of birds were sampled, but it was not permissible to obtain bodies and eggs of some of the less common species. Samples were also collected for comparative purposes from other areas (Stone Chest, Penton, near Carlisle, and the north shore of Morecambe Bay).

Before being dried or reduced to ash, the materials were examined for their general levels of γ activity, using a scaler ratemeter. A small number of the samples were then prepared for radionuclide analysis using standard geometries on the Ge(Li) γ detectors for

periods of time ranging from 7-50 hours. Analyses of the resulting spectra are not yet complete, but it is clear already that uptake is strongly influenced by the behavioural patterns of the individual flocks of birds.

Because there is a great variation in the feeding behaviour of flocks of oystercatchers, curlews, gulls and other ducks, it will not be possible to make reliable estimates of their role in radionuclide transfer until their behaviour is better understood. Many of the birds in question are migratory; some arrive in the autumn (September-October) and depart in the spring (March-April), eg overwintering flocks of ducks and waders, whereas others, eg black-headed gulls, arrive in spring and breed during the summer on the dunes in the Ravenglass Reserve; very few birds are resident throughout the year. The proportions of the different radionuclides vary with species of bird, and also with type of food. These differences may prove useful as indicators of food sources and feeding behaviour.

Plant uptake

Radionuclides taken up by plants are transferred to man, either directly as in vegetables or indirectly in meat and dairy produce. As far as direct transfer is concerned, it is desirable to distinguish between materials incorporated into plant tissues or occurring as surface contaminants. The fate of these 2 forms of transfer in grazing animals and man may be significantly different. Silt, containing radionuclides from the Ravenglass estuary, was desalinated by washing, settling and decanting — analyses of the water used for washing showed that little or no radioactivity was removed. The washed silt (1 part) was then mixed with John Innes compost (2 parts), and 3 replicate blocks each consisting of 14 2-litre pots were made up for each species. These species were Puccinellia maritima, a salt marsh grass, Lolium perenne, a pasture grass, Ranunculus repens and Rumex obtusifolium, shallowand deep-rooting weeds, and turnip, a root crop, all common in west Cumbria. To avoid contamination by splashing, the pots were watered with a drip-feed (Plate 11). After growing from May until September, the tops were harvested carefully to avoid soil contamination. The turnips were washed repeatedly before being peeled. Replicate samples were then oven-dried and ground for analyses of a and y-emitting radionuclides. Preliminary analyses indicate that concentrations of ¹³⁷Cs in oven-dried foliage ranged from 1·2-7·2 pCi g⁻¹, with significant differences between species. Similar results were obtained for ^{239/240}Pu isotopes.

In the controls grown in a substrate without contaminated silt, radionuclide levels were comparable with fall-out levels — there was a 98% drop compared with the levels found in plants growing with contaminated silt.

V P W Lowe, A D Horrill, Brenda J Howard and S E Allen

UPTAKE OF FLUORIDE BY PLANTS FROM SOILS CONTAMINATED BY AIRBORNE POLLUTANTS

(This work was partly supported by Welsh Office funds)

Soil in terrestrial ecosystems acts as a 'sink' for airborne pollutants. Emissions from aluminium smelting industries, consisting of various forms of gaseous and particulate fluorides, result in deposits on vegetation and soil. Fluoride which is not directly absorbed by plants through their leaves is washed off and subsequently accumulates in the soil. When plant leaves die, the absorbed fluoride is transferred to the soil as decaying litter. If leaves are consumed by herbivorous animals, fluoride accumulates in their tissues and bones, and, if in sufficient amounts, causes fluorosis (Allcroft et al. 1965). Fluoride then also enters the soil system in faeces and urine deposited by the grazing animals.

The fate of fluoride once in the soil is of importance because contaminated soils remain a source of fluoride which may be taken up again by plants through their roots, or which may enter water courses. All soils contain fluoride, but it is mostly chemically bound in minerals, for example in fluoroapatite (Bear 1964). It is released only in a soluble form which can be taken up by plants in small amounts as the mineral weathers naturally. Plants normally contain between 5-10ppm fluoride (F-) taken up from naturally-occurring fluoride in the soil solution. As part of longer term studies on the pathway of fluoride in ecosystems (Perkins et al. 1979), this project is investigating what happens to fluoride when soil has been contaminated by emissions from an aluminium reduction plant near Holyhead in Anglesey.

Water extractable fluoride

Some 30 soils in the vicinity of the works were examined. Whilst the parent material from which these soils are formed is similar (shallow local drift mainly derived from pre-Cambrian Mona Complex of metamorphic rocks), they differed in contents of organic matter, clay, silt and sand (Table 18). The soils could be described as acidic sandy loams and sandy clay loams, with pH varying between 4-1–7-1. Water soluble fluoride (1:5 soil/water extraction) was found in all the soils, ranging between 0-1–3-5 ppm, as determined by an ion-selective electrode. The higher values were found closest to the emissions source and were generally within 2 km in a downwind direction.

Table 18. Ranges of physical characteristics of, and amounts of water extractable fluoride in, 30 samples of soil collected in the vicinity of the aluminium reduction plant near Holyhead, Anglesey

0·1-3.5 μg ml ^{−1}
0·6–25 μg g ⁻¹
3.5–21%
2·4–22%
2·6–54%
32–93%
4-1-7-1

Resin extractable fluoride

The 1:5 soil/water extract is useful for comparing the availability of water soluble fluoride in a range of soils, but it does not give much indication of the total supplying power of the soil. Supplying power was estimated by successive 1:12.5 soil/water extractions, the fluoride being adsorbed by 5 ml (3·3g) of Zerolit FF(ip) anion exchange resin contained within a packet made of dialysis tubing and included in the mixture. Determinations of fluoride were again made by ion-selective electrode following elution from the resin with 7% potassium sulphate solution. Figure 31 illustrates the accumulative fluoride extracted from contaminated and uncontaminated soils. After 13 extractions, 223 ug F- were extracted from 1g of contaminated soil, compared with 23 µg from the otherwise similar, but uncontaminated, soil. The amounts extracted decreased with successive extractions, the small amounts in later extractions probably approaching that extractable before contamination. Calculations indicate that 26.8 g F⁻ m⁻² could be extracted from a 10 cm depth of the contaminated soil, an amount which has accumulated since emissions commenced in 1971.

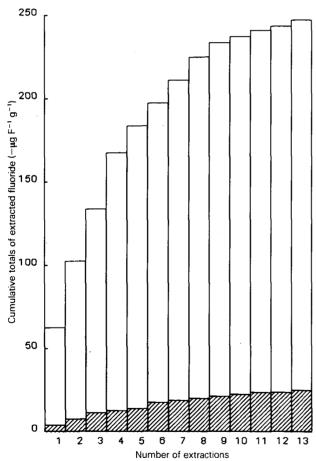


Figure 31 Accumulative quantities of fluoride removed by anion exchange resin from successive extractions of contaminated (D) and uncontaminated (D) soils mixed 1:12.5 with water.

Uptake of fluoride by plants

To investigate if fluoride can be taken up by plants growing in the contaminated soil, *Lolium perenne* (S23) was grown in potted soil in the absence of airborne

fluoride in controlled environment chambers. Seed was sown and the plants grown as a sward for 70 days at 20°C in a 16 h day-length. A harvest of clipped leaves was taken after 35 and 70 days. The results (Table 19) show that up to 132 ppm F⁻ were concentrated in the leaves, and in the total harvest of 4·3 g dry matter 422 µg F⁻ were accumulated (equivalent to 99 ppm). Plants grown in an uncontaminated soil at the same time contained <8 ppm fluoride in their leaves.

Table 19. Amounts of fluoride in the foliage of Lolium perenne (\$23) grown for different periods in soil* contaminated by fluoride emissions from an aluminium reduction plant

Days' growth	Weight of foliage (g dw pot ⁻¹)†	Concentration of F ⁻ in foliage (µg g ⁻¹)†	Total F ⁻ uptake (μg pot ⁻¹)†
28	2·4	72	168
42	1·9	132	253
70	4·3	99	422

^{*} Soil contained 174 μ g g⁻¹ water extractable F⁻; pH = 4·5, loss-onignition = 8·5%, clay = 5%, silt (Avery) = 42% and sand = 53%. † Mean of 10 pots.

These experiments have shown that, in acidic sandy soils contaminated by airborne fluorides, there are considerable quantities of water soluble fluoride. Plants subsequently grown in these soils in the absence of airborne contamination accumulated fluoride in their leaves. The concentrations of fluoride found would be considered unsuitable in herbage for animals to graze for long periods. The annual average fluoride content of herbage should not, it is generally considered, exceed 40 ppm (Suttie 1969). Whilst the dynamics of this particular plant/soil system need to be further investigated, these data indicate that water soluble fluoride derived from industrial emissions can be a source of fluoride, and contribute significantly towards the total fluoride accumulations found under field conditions.

D F Perkins, Verna Jones and Phyllis Neep

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AN OPEN-TOP CHAMBER FOR STUDYING THE EFFECTS OF AIR POLLUTION ON PLANTS

An understanding of the effects of polluted atmospheres on the growth and development of plants in the field has been slow to materialize, primarily because techniques appropriate for field experiments using realistic conditions have only recently been developed. Present activity is centred on 2 techniques:

i. field fumigation systems, in which a large area, typically 100 m² (ground area) of unenclosed field crop is fumigated with controlled concentrations of one or more gaseous pollutants. Thus, excepting the concentrations of gaseous pollutants, all other conditions are the same as those of the crop upwind of the experimental area.

ii. the use of open-top chambers enclosing 1-10 m² (ground area) of vegetation. In this instance, plants grown inside the chamber may be exposed to either clean (filtered) or polluted (unfiltered) ambient air, or to different mixtures of filtered and unfiltered air, which may be amended with controlled concentrations of individual pollutant gases. The open top enables rain to reach the experimental plants, but, inevitably, they are subjected to an altered environment the extent of which needs to be determined.

In preparing for a study of the effects of air pollution on barley, an open-top chamber has been developed which is small compared with that used by Heagle (1973) — size was largely dictated by the desire to have relatively large numbers of replicate chambers. The cylindrical chamber (Figure 32) is constructed from 'super Corolux' transparent sheeting, held rigidly at the top and bottom by rectangular section aluminium rings. The walls of the chamber transmit 80-85% of total short-wave radiation (similar % transmission for photosynthetically active radiation), although the diffuse

component of incoming short-wave radiation is increased (by up to 50%) inside the chamber by refraction and internal reflections from chamber walls. Air temperatures inside the chamber exceed those outside by <1°C for a short-wave radiation flux (S_t) of <150 W m⁻². For S_t in the range 200–700 W m⁻², the temperature difference is between 1°C and 2°C.

These differences are significant and would, if reflected in leaf temperatures, result in faster growth and development inside the chambers. However, the very turbulent air within the chamber (aerodynamic resistance 15 s m⁻¹) results in smaller air temperature differences between leaves and the air within the chamber than would be expected for the same crop outside on a sunny day with wind speeds of about 2 m s⁻¹ at 1 m above the crop surface. This method reduces the difference between crop temperatures inside and outside the chamber generally to <1°C.

Air flow is distributed within the chamber through a perforated, vertically adjustable annulus, and the filter unit on the clean air treatments removes SO₂, O₃ and NO₂ with efficiencies in the range 80–90% (Table 20). Nitric oxide (NO) is not removed by the filter and could only be eliminated from the air in the chamber by a very expensive process. The flows of air into (i) the filtered and (ii) the unfiltered units are matched by the insertion of a flow control orifice in the inlet pipe. Air

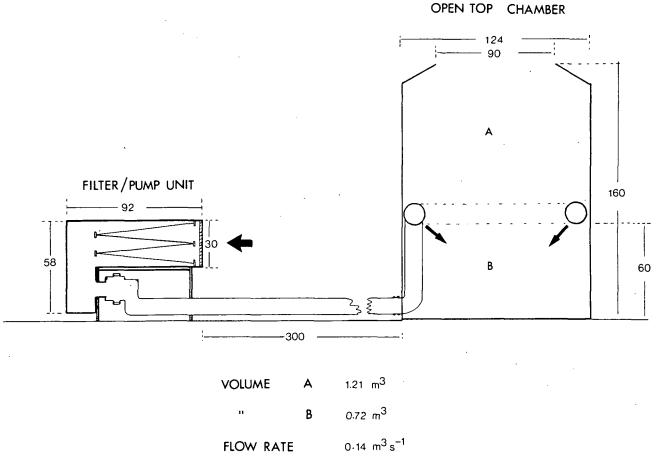


Figure 32 Dimensions (cm), flow pattern and construction of a small open-top chamber for air pollution effects studies.

concentrations of SO₂, NO₂, NO, O₃ and CO₂, and a range of meteorological variables will be monitored continuously while the chambers are in use.

G B Elphinstone, D Fowler, G H Owen and I A Nicholson

Reference

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Table 20. Efficiency of the filter unit for the pollutant gases SO_2 , NO_2 , NO and O_3

	Filter efficiency				
Gas	Range μg m ⁻³	% removal			
SO ₂	8–60	95			
NO_2	20-120	>75 (>80%			
	•	for concentrations			
		>100 µg m ⁻³)			
NO	20-140	0			
O_3	8–60	92			
Residence times 0.35s		Means of 20–100 values			

Final concentration depends upon amount of ambient air entering chamber top.

CHRONIC POLLUTION INJURY TO SOME TREE SPECIES IN RESPONSE TO SO $_2$ AND NO $_2$ MIXTURES

The growth of plants in polluted air, either in the field or in chambers ventilated with unfiltered urban air, can sometimes be decreased without the development of foliar blemishes — chronic injury. This form of injury was attributed in the past to airborne sulphur dioxide (SO₂), but recent experiments have failed to reproduce these effects when controlled fumigations were made with SO₂ concentrations similar to those occurring in urban areas. However, a close examination of the commonly occurring mixtures of atmospheric pollutants and the international literature — suggests that chronic damage may be attributable to mixtures of oxides of nitrogen (NO, NO₂) and SO₂ (Mansfield & Freer-Smith 1981). Data provided by Ashenden and Williams (1980) suggest that the damage done by mixtures of these pollutants is greater than would be predicted by examining their individual effects. To extend these observations from grasses, Lolium multiflorum and Phleum pratense, to species of woody perennials, experiments have been done with Populus nigra and Betula pubescens grown in 4 large hemispherical glasshouses, situated out of doors, in which environmental conditions were close to ambient. The glasshouses tested the 4 combinations of (i) with and without SO₂, and (ii) with and without NO2. One glasshouse, the 'control', was supplied with filtered air, which in the other 3 glasshouses was supplemented by pollutants between 0900 hours on Monday and 1700 hours on Friday.

Separate experiments were done in summer and winter, when cuttings of *Populus nigra* 'Italica' (black poplar) were exposed to weekly mean concentrations of 0.068 ppm SO₂, 0.068 ppm NO₂ and 0.068 ppm SO₂+0.068 ppm NO₂. In the 'summer' (11 June 1980-12 November 1980) experiment, when heights were measured weekly, the SO₂+NO₂ mixture decreased height increments continuously, while SO₂ increased leader extension at the beginning, but not at the end, of the exposure period. Individually, SO₂ and NO₂ decreased numbers of developing lateral shoots, an effect which was greatly magnified in the mixture treatment. Within 8 weeks of the onset of fumigation, SO₂ and NO₂ had separately decreased the dry weight gains by 4% and 17% respectively: together, they decreased the increment by 43%. During the autumn, leaf senescence and abscission were accelerated on P. nigra growing in chambers with SO₂ or SO₂+NO₂ until 12 November 1980, after 22 weeks of fumigation, when SO₂, NO₂, and SO₂+NO₂ had decreased seasonal growth (dry weight) by 33%, 30% and 66% respectively. Thus, at the beginning of the experiment, the effect of the mixture was more than additive — there was an interaction — but, by the end of the season, the effect of the mixture was no more than additive.

When dormant plants were fumigated for 10 weeks during the winter (29 January-9 April 1981), it was found that growth after budbreak in 'unpolluted' air was affected deleteriously, previous treatments with SO₂, NO₂ or SO₂+NO₂ similarly decreasing dry weight increments by 20%. Thus, fumigations made during winter on dormant plants can influence growth in the following spring.

To examine the cumulative effects of continuing exposures to 0.062 ppm SO₂ and/or 0.062 ppm NO₂, during winter and summer, the responses of 6 species of broadleaved trees were tested. One-year old plants of each species were fumigated from 22 March 1981 onwards, with destructive harvests being taken (i) at the end of the 1981 growing season (August), and (ii) in spring (May) 1982, shortly after budbreak in the second year. Whereas NO₂ alone stimulated the shoot growth of 5 of the 6 species during 1981, the effects of SO₂ alone were less predictable. As with NO₂, SO₂ increased the growth of *Tilia cordata*, but significantly decreased the growth increments of Betula pubescens and Alnus incana. These effects were usually small compared with those of SO2+NO2 mixtures, the decreases attributable to the latter being more than additive in T. cordata, B. pendula, P. nigra and B. pubescens. After overwintering, the nature of some of these responses changed, when only the growth of A. incana was significantly improved by NO2 alone. The damage done by SO₂ had usually intensified so that it was more or less equal to that attributable to the SO₂+NO₂ mixture (see Table 21).

These data show that the responses of trees to SO_2 and NO_2 mixtures are complex. Exposures to NO_2 are

Table 21. Effects of adding 0·062 ppm NO₂, SO₂, and SO₂+NO₂ to filtered air on shoot dry weights of *T. cordata, M. domestica, B. pendula, P. nigra, B. pubescens* and *A. incana* when measured after 22 and 60 weeks of exposure. The growth of fumigated trees is related to that of the control in filtered air

	Mean shoot dry weights as % of controls					
	-	August	1981	May 1982		
	afte	er 22 v	veeks of	afte	er 60 v	veeks of
	fu	migati	on with	fu	migatio	on with
	NO ₂	ŞO₂	NO ₂ +SO ₂	NO₂	SO₂	NO ₂ +SO ₂
Tir.	140	101	100	00	60	67
Tilia cordata	142	131	108	99	63	67
Malus domestica	86	92	82	95	66	64
Betula pendula	115	85	62	115	61	76
B. pubescens	108	80	48	95	48	40
Populus nigra	118	97	60	87	84	58
Alnus incana	124	48	34	165	75	58

Continuous furnigation of one-year old saplings started 22 March 1981

usually beneficial initially, while exposures to SO₂ are, in most instances, associated with small decreases in growth. The damage done by SO₂+NO₂ mixtures to B. pendula, P. nigra, B. pubescens and A. incana was greater than additive during the first season of fumigation, but differences between the effects of SO2 alone and the mixture of SO₂+NO₂ were not statistically significant shortly after the onset of the second season. A similar change was detected in the responses of the grass Poa pratensis (Whitmore & Freer-Smith 1982). Together, these results demonstrate the dangers of attempting to predict injury in the field from experiments with only one set of observations. The responses of plants to pollutants are not static and they can change in kind and extent. Sequential observations are, therefore, necessary to record the inter-relations between stage of growth, seasonal weather and changing sensitivity to pollutants.

P H Freer-Smith

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Plant physiology and genetics

MEASUREMENT AND MODELLING OF THE MOVEMENT OF WATER THROUGH SITKA SPRUCE FORESTS

Measurement of transpiration in a Sitka spruce forest

Estimate of daily total transpiration from dry canopy
The water balances of forest catchments are important

to hydrologists assessing effects of afforestation on reservoirs. Jarvis and Stewart (1979) suggested, from a theoretical study, that water losses by evaporation of newly fallen rain ('interception losses') were larger from forests than grasslands during rainy weather, whereas transpiration losses were greater from grasslands in dry weather.

Testing of the above hypothesis requires field measurements of the various water losses. By 2 independent methods, daily transpiration totals from the canopy of a 14-year old Sitka spruce (*Picea sitchensis*) plantation at Greskine, south-west Scotland, were estimated during a rainless 16-day period in summer 1976.

i. The Penman-Monteith (or 'Combination') equation for transpiration was calculated using hourly meteorological records. Canopy conductances for the equation were calculated from the relationship:

$$g_c = S_t/(7803 \cdot 14 + 41 \cdot 35 S_t)$$

where $g_c = \text{canopy conductance}$, s m^{-1}

 $S_t = hourly total solar radiation, W m^{-2}$

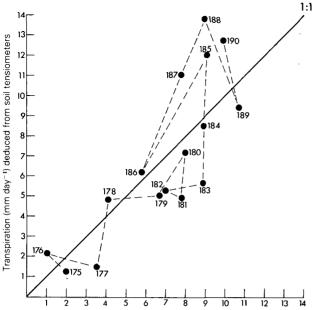
This relationship was determined from a separate experiment when hourly transpiration rates were estimated by an eddy correlation/energy balance method (Milne 1979). Hourly transpiration rates were accumulated to give daily totals in millimetres of water.

ii. Nine soil moisture tensiometers were placed in each of 5 separate soil horizons of the forest soil and read daily (Deans 1979). The volume of each horizon was estimated, and the relationship between water content and tension measured for each soil horizon type (Deans 1979). Daily values of water loss from soil were calculated, and the results compared with the estimates from the Penman-Monteith equation (Figure 33).

An unexpectedly good correlation (r=0.8) was obtained between the 2 methods of estimating transpiration rates, which ranged up to 11 mm. This rate is much greater than most published estimates and suggests that young forests may not be as conservative in the use of water as previously accepted, but many more observations are required.

Comparison of 2 methods of estimating canopy conductance

In 1978, measurements were made to enable comparisons of canopy conductances (i) inferred from eddy correlation/energy balance estimates of transpiration, and (ii) estimated from stomatal conductance measurements obtained with a porometer and the leaf area index of the canopy of the Sitka spruce forest at Greskine. While Professor Jarvis and staff of the Department of Forestry and Natural Resources, University of Edinburgh, investigated the spatial variation of stomatal conductance through the canopy, ITE staff monitored meteorological conditions and measured the sto-



Transpiration (mm day-1) estimated with the Penman-Monteith equation Figure 33 Comparison of the estimates obtained from 2 methods of determining daily transpiration from a Sitka spruce forest (14-years old) at Greskine, southwest Scotland. Measurements were made on 16 dry days in 1976 (days are identified by their Julian dates).

matal conductance of reference shoots hourly, for 2 periods of 7 days in spring and autumn. Spatial variation of leaf area through the canopy was also measured (Ford 1982).

Canopy conductance (g_c) was calculated from the stomatal conductance of approximately 50 categories of shoots, including those from 7 whorls, 3 age classes and whorl/interwhorl types (Leverenz *et al.* 1982), and from leaf areas of these categories of shoots, ie:

$$g_c = \sum_{i=1}^{N} g_{si} L_i$$

where

 g_{si} = conductance of ith shoot type L_i = leaf area of ith shoot type.

These sums could not be calculated for each hour because of the extended length of time required to measure the stomatal conductance of 50 shoot types. As a result, the variation in conductance along a particular axis of biological variation was studied relative to 10 reference shoots which were measured hourly throughout the complete study (Leverenz *et al.* 1982).

The results of these investigations showed that the total leaf area index of the canopy was 10.75, and that the mean canopy conductance was about half that of the reference shoots, ie:

 $g_c = 0.46 g_r L$

g_c = mean canopy conductance (hourly)

g_r = reference shoot conductance (hourly)

L = total leaf area index = 10.75.

On 4 dry days during the spring period of measurement, it was possible to compare the estimates of canopy conductance obtained from stomatal conductance measurements with those needed by the Penman-Monteith equation to produce transpiration rates measured by the eddy correlation/energy balance method (Figure 34). However, even after eliminating suspect porometer measurements made early in the day (probably attributable to excess moisture in the porometer gas feed tubes), the 2 methods only gave good agreement on 2 of the 4 days, there being a discrepancy of up to 80% on the worst day. The porometer method gave the larger estimates.

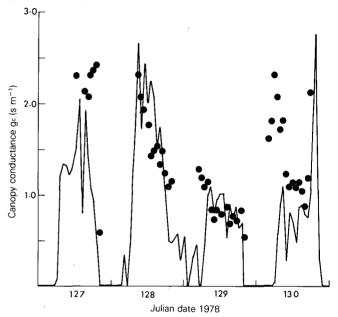


Figure 34 Hourly estimates of canopy conductance required by the Penman-Monteith equation to give transpiration rates measured by eddy correlation/energy balance (———), compared with 49 individual estimates of canopy conductance estimated from porometer measurements of stomatal conductances and leaf area distribution (•). Data obtained in 1978 from a 16-year old Sitka spruce plantation at Greskine Forest.

Taken together, the 2 sets of results suggest that, for reliable estimates of canopy transpiration, the eddy correlation method would be more useful, especially when the practical difficulties of estimating the spatial variation of stomatal conductance and leaf area are considered.

Estimates of transpiration from forest canopies will be further improved when the eddy correlation technique is applied to atmospheric moisture variations directly rather than to temperature variations, because the former does not require an energy balance for estimation of transpiration flux.

The dynamics of internal moisture in plantation Sitkä spruce trees

Hourly data for 7-day periods in July 1974 (tree height \sim 5 m) and July 1976 (tree height \sim 7 m) were used to

estimate the time lags between the diurnal changes of transpiration, shoot water potential and stem radius within Sitka spruce planted in 1962 in Greskine Forest in south-west Scotland (Milne et al. 1983). In the first period, shoot water potentials were measured at whorl 12 (whorl 1 is nearest ground), using a pressure bomb, while stem radii of 3 trees were recorded at several heights using electronic displacement transducers. In 1976, water potentials were determined at 4 positions in the canopy — (i) shoots at whorl 13, (ii) trunk at whorl 13, (iii) shoots at whorl 8, (iv) trunk at whorl 8 (Figure 35); mainstem radius changes were also recorded at whorls 13 and 8 on one tree. Weather variables were logged as in 1974, but, in addition, sensible heat flux from the forest canopy was estimated by the eddy correlation technique, which, together with net radiation and soil heat flux, was used to construct energy balances, and hence transpiration estimates, for the forest canopy.

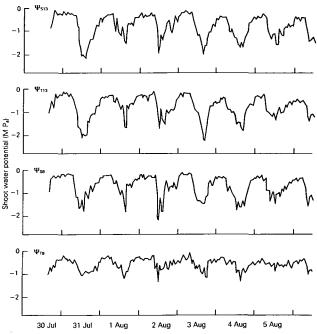


Figure 35 Hourly measurements in 1976 of water potential in shoots of Sitka spruce, 14-years old, in Greskine Forest

 $\psi_{\rm S13}$ leading shoots of branches of whorl 13 $\psi_{\rm T13}$ shoots on mainstem below whorl 13 $\psi_{\rm S8}$ leading shoots of branches of whorl 8 $\psi_{\rm T8}$ shoots on mainstem below whorl 8.

The data on stem radii contain 'trends', extending for longer than a day (Figure 36), but, as the prime interest here is in diurnal changes, a mathematical trend removal procedure was applied. This procedure involved fitting a straight line to overlapping blocks of 25 hourly measurements of radius, the middle term of the fitted line being used as an estimate of the trend at that time. The remaining diurnal variation was then determined by subtraction from the original data. Power spectral analysis showed that only 20% of the fluctuations about the trend had periods shorter than 12 hours, thus confirming the diurnal nature of the variations in stem

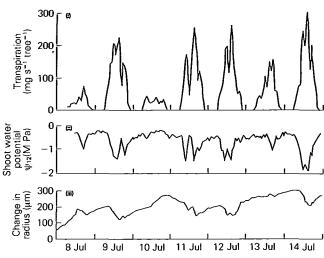


Figure 36 Hourly measurements in 1974 of:

- i. transpiration calculated by the Penman-Monteith equation
- ii. water potential in leading shoots of whorl 12 branches (ψ_{S12})
- iii. changes in the radius of mainstem below whorl 9 (tree 172) for Sitka spruce, 12-years old, in Greskine Forest.

radii (Figure 37). If these fluctuations had been sinusoidal, then the estimation of time lags would have been a relatively simple matter, but as they were not it was necessary to resort to correlation analysis. Cross correlation analysis involves the calculation of correlation coefficients between 2 series of data, x(t) and y(t), eg stem radius and shoot water potential, not only for measurements taken at the same time, t, but also at times k hours apart, ie for x(t) and y(t+k), where k is the 'lag' of y behind x. The relationship of the correlation

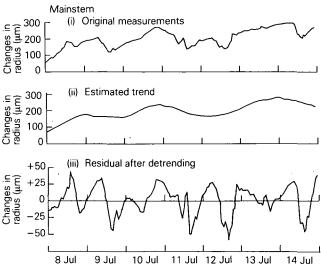


Figure 37 Detrending method applied to measurements obtained in 1974 of changes in mainstem radius below whorl 9 of Sitka spruce (tree 172), 12-years old, in Greskine Forest

- i. original measurements
- ii. estimate of trend
- iii. residuals remaining after trend is subtracted from original measurements.

coefficients and lag is called the cross correlation func- iv. changes in transpiration rate and shoot water potention, rxy(k), between series x(t) and y(t), ie:

$$r_{xy}(k) = \frac{C_{xy}(k)}{\sqrt{C_{xx}(0) \ C_{yy}(0)}}$$
 where
$$\frac{1}{n} \sum_{t = 1}^{n-k} x(t) \ y(t+k), \ k = 0,1,2$$

$$C_{xy}(k) = \sum_{t = 1}^{n+k} x(t) \ y(t-k), \ k = 0,-1,-2$$

where the series x(t) and y(t) are assumed to have zero mean. The value of k at the maximum $r_{xy}(k)$ will give a good estimate of the time lag between x(t) and y(t) for similar temporal patterns (in this case diurnal) in the 2 series (Lynn 1973). The cross correlation function of detrended radius measurements below whorl 8 of a Sitka spruce tree in 1976, with respect to water potential of whorl 13 leading shoots, suggested a lag of 3 hours (Figure 38).

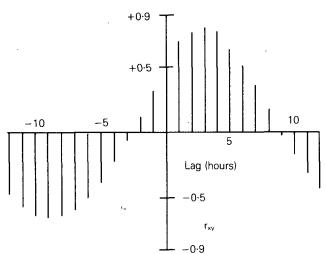


Figure 38 Cross correlation function (rxy) of detrended measurements obtained in 1976 of stem radius changes below whorl 8, with respect to water potential of leading shoots taken from whorl 13 branches (ψ_{S13}) on Sitka spruce (tree 369), 14-years old, in Greskine Forest.

Applying cross correlation analyses to the different data sets suggested that:

- i. variations in stem radius at different heights within a single tree were strongly correlated (maximum correlation 0.80-0.95); they were in phase, or, at most, lagged by 1 hour;
- ii. variations in stem radius at the same height in different trees were in phase and strongly correlated (0.76-0.95);
- iii. variations in water potential measured in shoots on the trunk and at the distal end of branches were all in phase and well correlated (0.80-0.94), irrespective of their height above ground. The variations in the water potentials of the lower trunk shoots were about half the amplitude of those elsewhere;

tials were synchronous (correlation -0.77 to -0.88), but changes in stem radii could be delayed by 3 hours (correlation 0.75-0.80).

These results are generally in agreement with evidence available in the literature.

Alternative mathematical methods of modelling the dynamics of water movement have been considered. Earlier, Ford and Milne (1980) used discrete-difference equations to model the relationship between stem radii changes and shoot water potential. However, the presence of quasi-sinusoidal diurnal variations suggests that electrical analogues might be useful. Richards (1973) has suggested a resistance capacitance (R-C) analogue for the movement of water in Sitka spruce, and the method has been applied to other crops. A general R-C network analogue for spruce can easily be proposed, but the required 10 or more elements would make it difficult to apply in practice. The phase relationship found between changes of water status in different parts of the spruce canopy, however, enables some simplification to be made.

- i. The canopy need not be partitioned vertically, as water potentials are in phase at different positions in the canopy, as are stem radius changes at different heights.
- ii. Needle water storage is probably negligible because there is no phase shift between transpiration and shoot water potential.
- iii. Impedance to water flow from storage is much greater than the resistance to flow from trunk to transpiring shoots.

With these simplifications, it is possible to suggest a network (Figure 39) which may serve as a starting point

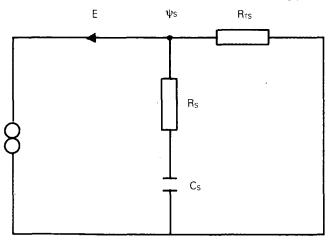


Figure 39 Simplified resistance capacitance (R-C) network for water movement in Sitka spruce

E - transpiration flow

 $\psi_{\rm S}$ – shoot water potential

R_S – resistance to water flow from trunk storage

C_S – capacitance of trunk storage

R_{TS} – resistance to flow from soil to trunk.

when analysing the water relations of Sitka spruce at the stage of development found at the study site.

Modelling the system would be based on the assumption that diurnal variations are sinusoidal, so enabling the use of alternating current network theory to calculate initial parameter values from the estimated phase shifts of the sinusoidal variations. A computer simulation of the network and a minimization routine would then be used to find parameter values which predict shoot water potentials or stem radius changes from measured transpiration.

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EARLY GENETIC EVALUATION OF LODGEPOLE PINE

The most effective way to select genetically superior trees of many species, including *Pinus contorta*, is to collect open-pollinated seeds from candidate 'plus' trees and to grow the resulting progenies at a range of sites for 6–10 years. The trees that produce the largest progenies may then be regarded as the best general combiners and be placed in seed production orchards. However, this process is time-consuming, expensive in terms of land and labour, and it delays the commercial production of genetically superior stock. Greater genetic gains per unit of time would be made if progenies could be screened at the seedling stage.

ITE studies, combined with data collected at the University of Aberdeen and by the Forestry Commission Research Branch, suggested that *P. contorta* genotypes which became tallest at ages 6–8 were those with the most prolonged periods of shoot apical meristematic activity — a characteristic which could be

measured most easily as prolonged periods of height growth on first-year seedlings. They also tended to be the genotypes which benefited most from favourable site conditions (Cannell *et al.* 1981). The evidence came from 4 sources.

- i. Differences of up to 55 days in the dates of 85% bud-set among 15 provenances of *P. contorta* accounted for 85% of the variation in 8-year heights, meaned over 5 sites (provenances which set buds latest grew tallest). Similarly, differences of 26 days in the dates of 85% height growth completion among 16 open-pollinated progenies, with different parent provenances, accounted for 79% of the variation in 8-year heights, measured over 3 sites. Differences of only 11 days in the dates of 85% height growth completion among 10 open-pollinated progenies, with similar parent provenances, accounted for 70% of the variation in 8-year heights, measured over 3 sites.
- ii. In all studies, correlations between the duration of first-year seedling growth and mean provenance or progeny heights increased with tree age. Thus, for the 15 provenances, the correlation coefficients (r) increased from 0.60 at age 1, 0.70 at age 2, 0.91 at age 5 and 0.92 at age 8. Equivalent values for the 16 progenies were 0.47, 0.51, 0.86 and 0.89, and for the 10 progenies, 0.19, 0.63, 0.74 and 0.84 (Figure 40).
- iii. It was thought that seedling growth duration was poorly correlated with seedling height, because such factors as seed weight and time of germination also played a role. However, inherent differences in the seasonal duration of shoot apical growth probably became increasingly important with age, because those genotypes with the most prolonged apical growth would produce most needle fascicles (and stem units) in their overwintered buds, grow most the next year, and so on, accumulatively. After the first year, inherent differences in shoot apical growth are revealed only by bud dissection - not by shoot elongation — because the shoots are predetermined. Consequently, buds of 8 provenances were sampled repeatedly during their seventh growing season and dissected to determine changes in apical activity, which earlier studies had shown were closely linked with changes in apical dome diameter (Cannell 1976). Provenance differences in the seasonal duration of shoot apical activity were, indeed, perfectly rank correlated with differences in 8year heights. Provenances with the most prolonged shoot apical activity were tallest.
- iv. The relative 'stability' in height of the 15 provenances at age 8 was assessed at 5 sites by calculating the regression of the individual provenance heights at each site (regressor variable) on the means of all provenances at each site (independent variable, used as a measure of site quality), following the

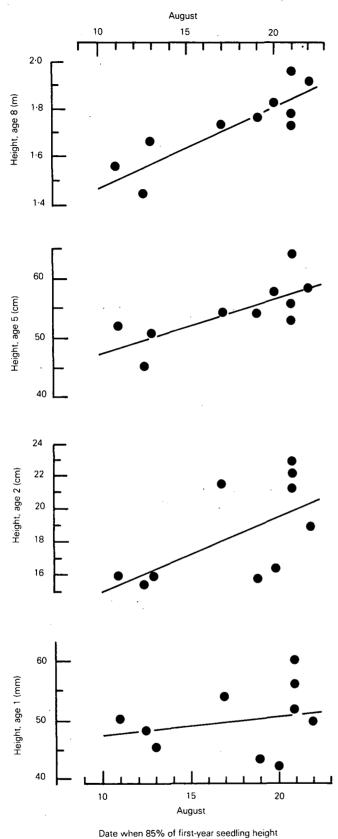


Figure 40 Relationship between the dates when first-year seedlings of 10 progenies of Pinus contorta completed 85% of their height growth, and their heights at the end of the 1st, 2nd, 3rd and 8th growing seasons after germination. Progenies with prolonged first-year seedling growth had prolonged seasonal apical meristematic activity every year, and so became progressively taller than other progenies.

growth completed

method of Finlay and Wilkinson (1963). Significant regression coefficients (r) varied from 0.6, for a provenance that grew best relative to other provenances at poor sites, to 2.0, for a provenance that grew. best relative to other provenances at favourable sites. The dates of first-year seedling bud-set of these provenances were positively and significantly correlated with their Finlay-Wilkinson regression coefficients (r = 0.72). Those provenances which set buds latest had the highest coefficients, and hence responded best to favourable site conditions. Equivalent correlations between dates of height growth cessation and Finlay-Wilkinson regression coefficients were 0.70 and 0.80 for the sets of 16 and 10 progenies, respectively. Thus, it appeared that firstyear seedling growth duration could be used not only to select genotypes with greatest height growth potential, but also to select those which were likely to contribute to genotype × site interactions.

In order to determine the date of height growth cessation in seedlings, a minimum of 25 seedlings per progeny need to be measured on 6–10 occasions. This operation has been facilitated by the development of a suitable tube-shaped seedling container, and a mobile measuring device linked to a data logger. Using this facility, seedlings of 45 *P. contorta* inter-provenance hybrids were screened in 1981 and ranked according to their predicted performance and site responses at age 8.

M G R Cannell

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COLD SHOCK IN PROTISTA AND THE DEVELOPMENT OF FREEZE-THAW INJURIES

It has long been recognized that many cell types and tissues are damaged following exposure to low temperatures. The cellular injury has been classified into 2 distinct categories.

- i. Direct chilling injury or 'cold shock', which is expressed immediately upon the reduction in temperature, is dependent on rates of cooling, with more cellular injury induced by rapid, than by slow, rates of cooling.
- ii. Indirect chilling injury, which, in contrast, occurs only following a long period, often days, at the reduced temperature and is independent of rates of cooling.

Organisms known to be susceptible to cold shock include some species of bacteria and blue-green algae (especially when exposed during their exponential phases of growth), higher plants of tropical origin, mammalian spermatozoa and embryos Additionally, many types of striated muscle are damaged following a rapid decrease in temperature, they undergo a cold-induced contraction. In the past, it has been considered that organisms which were sensitive to cold shock were atypical and that 'normal' biological material was resistant to this stress. However, recent research has demonstrated that the 'cold shock response' may be a universal cellular reaction to cooling, if the rate of cooling is too rapid and the final temperature attained is sub-zero.

With several species of Protista (Amoeba, Chlamydomonas and Tetrahymena), the extent of injury observed following exposure to low temperatures was dependent on the temperature and the time of exposure to that temperature In Amoeba, which is usually incubated at $+20^{\circ}$ C, the cellular reaction following cooling to -10° C was typical of that defined as cold shock

Maximum cellular damage at this temperature occurred within 5 minutes and was dependent on the rate of cooling. However, the loss of cellular viability, which was observed when cultures of *Amoeba* were cooled from +20°C to -10°C, took several days to appear Furthermore, the loss was independent of the rate of cooling – this cellular reaction is consistent with that of indirect chilling injury. At intermediate temperatures, there is a continuum between these 2 extreme responses. It seems that this graded response demonstrates varying degrees of damage to the same site of injury, and thus, in Protista, and possibly other cell types, a satisfactory distinction cannot be made between direct and indirect chilling injury.

Despite extensive research, the biochemistry of cold shock injury is not well understood and alterations to both membranes and cytoplasmic proteins have been implicated. It seems that cold shock injury cannot be attributed to metabolic imbalances caused by the reactions of enzymes with different temperature coefficients and/or the accumulation of by-products. Maximum damage is observed following rapid rates of cooling

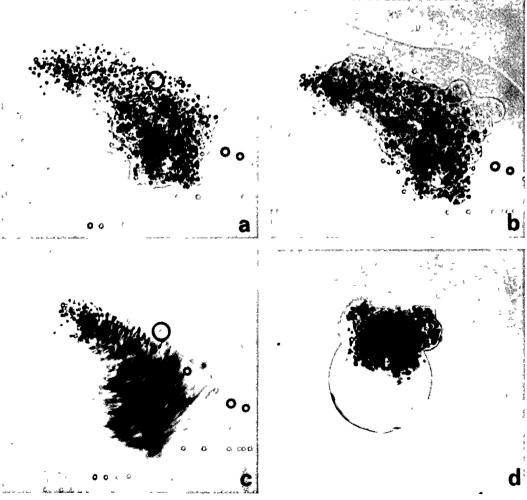


Plate 4 Morphological changes in Amoeba sp when cooled to -10° C then rewarmed a at 20° C c during rewarming at $+7.5^{\circ}$ C b at -10° C following cooling at 10° C min⁻¹ d at $+15^{\circ}$ C All magnified $\times 550$

(Photographs G J Morris)

during which the cells are exposed to low temperatures for the shortest period. Longer periods of exposure, as occur at slower rates of cooling, are protective. In Protista, as with other cell types, there is no effect on survival from the rate of warming after cold shock, indicating that the primary lesions are triggered during cooling. However, despite the association of morphological alterations with cold shock, the alterations in *Amoeba* do not become apparent until the cells are warmed (Plate 4).

Using a special microscope on which rates of cooling and warming could be controlled accurately, it has been possible to make detailed observations of the effects of changing temperatures. With amoebae, the normal cytoplasmic streaming and locomotion at 20°C (Plate 4a) are retarded as temperatures are decreased, with cytoplasmic movement ceasing at +10°C; there is no further morphological change as temperatures are dropped to −10°C (Plate 4b). Upon rewarming, the cells were moved by a force (torque) which rotated them several times (Plate 4c), before there was a violent contraction of cell contents at +15°C (Plate 4d), leading to lysis in many instances. However, cell death and granuloplasmic collapse are not necessarily related. Some cells underwent granuloplasmic collapse and subsequently recovered, while in a few cells lysis occurred after cold shock, but in the absence of cytoplasmic contraction.

Cold-induced cytoplasmic collapse was found by biochemical analyses and electron-microscope observations to be associated with a cross-linking of cellular actin whose biochemical trigger is still being investigated. However, these observations are the first direct demonstrations that low temperature stresses affect cytoplasmic proteins at an early stage, and that, in *Amoeba*, it is the potential to reverse these changes which largely determines the ability of cells to recover when rewarmed. Further work may indicate how important these stresses are in the development of freeze-thaw injuries.

G J Morris

BIRCH VARIATION AND ENVIRONMENTAL DIFFERENCES

Because it is thought that the role of *Betula* in British forestry and arboriculture has been underplayed, partly through lack of knowledge of the extent of the variation in *B. pendula* and *B. pubescens*, plans were prepared to establish a representative selection from British sources. As habitat factors are largely responsible for natural selection, the study, which is presently confined to Scotland, was focused on exploiting the system of land classification developed by ITE (Bunce *et al.* 1981a, b), in which the land mass of the UK is categorized into 32 land classes, defined by climatological, geological and topographical attributes.

Are there significant differences among individuals of the same population growing at the same site? Are specimens of *B. pendula* growing in different land classes inherently different from each other? Is the same true of *B. pubescens*? To seek answers to these questions, 211 seedlots were collected in the autumn of 1980 from replicate areas of high forest and scrub woodland occurring in 12 of the land classes found in Scotland (Bunce & Last 1981).

Seed samples were sown in the early spring of 1981. The resulting seedlings were subsequently 'potted up' and grown for the rest of the year in a randomized block design in an unheated glasshouse, before being put into a field trial. During 1981, heights and root-collar diameters were taken at 14-day intervals. Assessments were also made of numbers of branches, the lengths of the longest branches and longest leaves, the degree of shoot pubescence, and the dates of onset of dormancy. In addition, the shape and venation of the eighth leaf from the tip of the mainstem of each seedling were recorded towards the end of the growing season.

The data for *B. pubescens* indicate that the differences attributable to land classes were more significant, in a statistical sense, than those attributable to different sites within the same land class. The largest differences were related to leaf morphology, with the leaves of coastal populations of *B. pubescens* in the north and north-west being significantly smaller than those elsewhere. This distinction is akin to the difference between the sub-species *pubescens* and *tortuosa* of *B. pubescens*, the smaller-leaved form of *B. pubescens* in the north and north-west probably being sub-species *tortuosa*.

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Ecophysiology and pollution in animals

POLLUTANTS IN KINGFISHERS

(This work was largely supported by Nature Conservancy Council funds)

As part of the long term pesticide monitoring programme at Monks Wood, kingfisher (*Alcedo atthis*) livers have been analysed for residues of DDE (from the insecticide DDT) and HEOD (from the insecticides aldrin and dieldrin) since 1964, and also PCBs (indus-

trial polychlorinated biphenyls) since 1967. Although only a few carcases have been received each year, 101 have so far been examined. These carcases came from widely scattered areas of England and Wales, but mostly from south-east England. No clear geographical variations were evident in any of the residues examined; variation in HEOD is given as an example in Figure

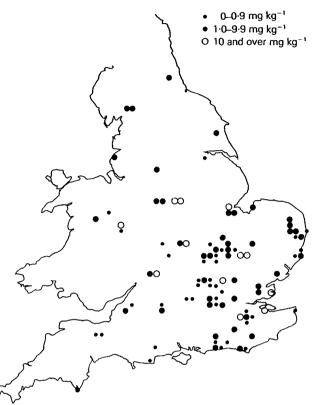


Figure 41 Geographical distribution of kingfisher carcases received from 1964-1981, showing HEOD residue levels in their livers. No kingfishers were received from Scotland.

Table 22 shows residue levels from 5 periods, chosen to coincide with successive voluntary bans on the use of DDT, aldrin/dieldrin and PCBs. The geometric mean levels of DDE residues generally declined throughout the study, and there was a significant decrease in 1981 associated with further bans on the uses of DDT. HEOD residues, on the other hand, decreased during the late 1970s, but recovered in 1981 to levels similar to those recorded in the early 1970s. The source of this HEOD is not readily apparent, but aldrin still has limited agri-

Table 22. Geometric mean residue levels in the livers of kingfishers in different years

Period	n	HEOD Mean (mg kg-1	DDE) Mean (mg kg~1)	PCBs
		- Iviean (mg kg	/ Wear (ing kg /	
1964-65	4	6.83	7.43	
1966-71	37	1.56	4.35	1.97†
1972-75	22	1.16	2.86	2.52
1976-80	25	0.17	3.62	11-41
1981	13	1.03	0.51	1.19

^{† 34} birds only for PCB

cultural uses, whilst dieldrin has various industrial uses and appears to be used illicitly on quite a wide scale as a sheep dip (Anon 1982). PCB residues increased to a peak in the late 1970s, but this increase was due mainly to very high residues in 3 specimens, one from west Kent (180 mg kg⁻¹), another from Warwickshire (120 mg kg⁻¹), and the third from south Essex (117 mg ka⁻¹). These 3 birds were found dead during early 1978. 1979 and 1977, respectively.

Seasonal variations in all 3 residues are shown in Table 23. Residues in birds from the first 6 months of the year were higher than those in birds from later in the year.

Table 23. Geometric mean residue levels in the livers of kingfishers in different months

Period	n	HEOD Mean (mg kg ⁻¹)	n	DDE Mean (mg kg ⁻¹)	n	PCBs Mean (mg kg ⁻¹)
Jan-Mar	27	1.06	27	6·47	25	9.93
Apr-Jun	19	1.17	19	5.41	16	2.29
Jul-Sep	32	0.69	32	1.52	31	1.87
Oct-Dec	23	0.62	23	1.76	22	2.36

The overall declines in DDE and HEOD levels were much as expected from the declines in agricultural usage, and the seasonal trends were similar to those found in some other bird species included in the programme (Cooke et al.1982).

Margaret B Haas and A S Cooke (NCC)

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QUEEN DISTRIBUTION. MOVEMENT AND INTERACTION IN A SEMI-NATURAL NEST OF THE ANT MYRMICA RUBRA

'Polygyny' in social insects is defined by Wilson (1971) as '... the co-existence in the same colony of 2 or more egg-laying queens'. Myrmica rubra L. is a polygynous species and has been chosen for the study of gueen control over female caste development.

It has been established that queens exercise an indirect control over caste development in the female sex, and that, as the worker population in a colony increases, queen control diminishes. There is evidence that this loss of control is due to reduced frequency of contact between the queens and their workers. Much behavioural work has been done on bumblebees and wasps in this connection (West Eberhard 1977; Free 1970), but very little is known about the relationship between queens and workers in ants. To investigate this relationship, 4 main approaches were used, one of which will be described here.

Brian (1980) found that queens tended to cluster together, leaving peripheral chambers free from queen influence, so that new queens are produced. As it was originally thought that each worker had to make direct contact with a queen (Brian 1970), the power of queens over brood rearing must become difficult when they are unable to transmit their influence throughout large colonies. Because very little is known of the extent to which queens of *M. rubra* wander about amongst workers in natural colonies, the aim was to observe queen movement in semi-natural soil nests made of glass.

Observations showed that queens were intolerant of one another and were usually widely spaced. Fighting and avoidance behaviour were common between queens. Energetic queens fought more frequently than passive ones and this suggested the existence of a dominance hierarchy. In the example shown below (Table 24), although each of the 5 named and identified queens encountered the other 4 at some stage during

Table 24. Frequency of fighting between queens

	Annabel	Beth	Deborah	Elaine	Frances	Total
Annabel		0	10	3	3	16
Beth	0		0	0	0	0
Deborah	10	0		1	3	14
Elaine	3	0	1		_ 5	9
Frances	3	0	3	5		11

the experiment, Beth was the only queen to whom the other queens never showed hostility. Annabel fought most often, and usually with Deborah. Annabel was the weakest queen, running away and being chased by her opponent at the end of a contest. Figure 42 gives an idea of the extent of nest area which individual queens covered in a short period (30 minutes). For example, Annabel (a sensitive and excitable queen) moved around the nest a considerable amount, occasionally pacing backwards and forwards in a pulsating sort of rhythm. Beth appeared to be a more quiescent and settled queen, hardly moving at all.

Each of the 5 queens varied significantly (χ^2 df 4, P<0.001) in the amount of time spent stationary or travelling, as well as in the degree of worker and gueen contact gained. Beth spent most of her time stationary (85%), and also received the highest amount of worker contact (94%) (Figure 43). However, Annabel came into contact with workers for 85% of her total time, and yet only spent half her time stationary. This result can be explained by the fact that Annabel 'bumped' into many workers while moving through the nest. The contact was only brief and of a different nature from the one or 2 workers licking and grooming a stationary queen, ie communicating. Therefore, queen mobility affected the type and amount of worker contact, which could be relevant to the control of development in the males as well as the female caste.

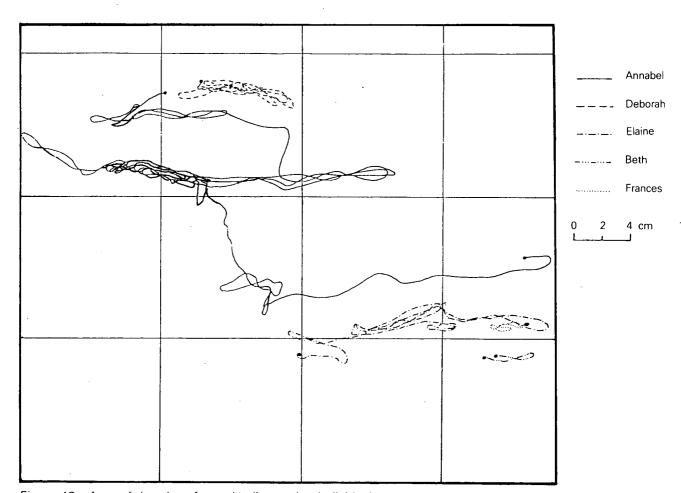


Figure 42 Area of the glass-framed soil nest that individual queens covered when observed for 30 minutes.



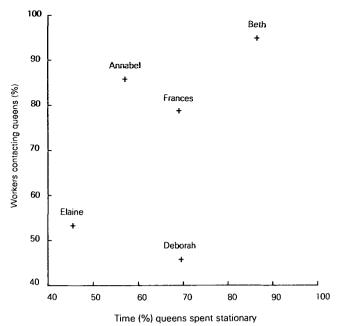


Figure 43 Time (%) that individual queens spent stationary and the worker attention (%) each queen received.

These results showed Beth to be the dominant queen. Further evidence of this dominance was provided towards the end of the experiment when Beth was unexpectedly found dead on the surface of the nest. Deborah (previously predicted to be the second most dominant gueen) had settled herself in the chamber where Beth had spent most of her time when she was alive.

It is interesting to consider what a social insect colony gains by having more than one queen, if queens compete for space, food and worker attention. Some queens obviously benefit by hanging around to inherit a nest when the foundress dies; others prefer to leave an established colony to found a nest of their own, so that all eggs laid will be sure to belong to them alone.

A detailed analysis of gueen/worker interactions made by video recordings showed that worker contact was of long duration when queens were stationary. It was also found that the queen recognition cue was only effective at a very short range. Nearby workers set off a chain reaction by hitting other workers in their excitement at perceiving a queen. This reaction may be an important means of communicating queen loss. When data were presented in graphic form (Figure 44), time of colony explosion, when queens and workers were aroused but interaction was negligible, occurred at a time which was equidistant between sunrise and sunset. This observation could be evidence for diurnal activity, but more data would be necessary to establish the fact. Lack of time has prevented further study of this promising approach. However, it has become clear that videotape is the ideal technique for observing colony life within a semi-natural nest.

Elizabeth J M Evesham

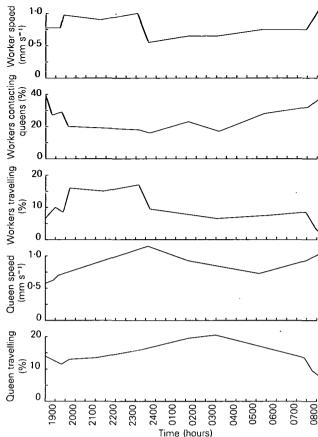


Figure 44 Queen and worker diurnal activity, calculated from a 3-way running mean.

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ECOPHYSIOLOGY OF RED ANTS

The red ants that belong to the genus *Myrmica* are very common throughout the temperate Holarctic. Historically, one species, Myrmica rubra L., has been used by ITE, and previously in the research branch of the Nature Conservancy, to investigate the social physiology of ant colonies (see M V Brian in earlier ITE Reports). Brian's work has been taken up by several schools in Europe, though most have restricted themselves to laboratory investigation of social behaviour in ants, especially in M. rubra. Yet, in Europe alone, there are at least a dozen valid species of Myrmica, each one associated with a preferred type of semi-natural habitat. Worldwide, there are more than 100 species, although most of these are poorly defined because the genus shows very little morphological variation in the worker caste.

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Despite their physical similarities, the species must differ considerably in their social biologies in order to exclude each other competitively from their preferred habitats. Furthermore, other recent work by ITE has shown that each of the species of the large blue butterfly genus Maculinea uses a different Myrmica species as its principal host during the parasitic larval stage (pp 82-83). The attempt to define and understand these differences in relation to speciation by Myrmica is the basis for the current report.

The work separates naturally into 3 parts.

- i. A study of the taxonomy of the genus to ascertain the species status of any natural populations that are examined. Mainly numerical methods have been used (Elmes 1980), and recently these have helped to determine what is either a new species, or an old, badly-described species of Myrmica that lives on a site used by a French Maculinea species.
- ii. The investigation of the structure and interactions of wild populations of the genus. Over the years, a great amount of new information on the patterns of colony density and population structure has been gathered (Elmes 1975, 1976). These field studies have recently suggested that nest temperature might be the single most important factor regulating the success of individual colonies in any habitat. As a general rule, Myrmica colonies select nest spots that are less shaded by vegetation, compared with random spots within their preferred habitat. Colonies are most successful in the least shaded spots, apart from those spots that are very exposed.
- iii. Laboratory tests consisting of comparative experimental studies of the social biology of various species. This aspect is discussed more fully below.

Four species which commonly live in the south of England were compared for their response to temperature, ie M. rubra, M. ruginodis, M. sabuleti and M. scabrinodis. All Myrmica have larvae in their nests during winter, and, when these hibernating larvae resume growth in spring, they become either workers or reproductive castes. Replicated tests were made at a set of temperatures covering the viable range of 15°C-25°C. A group of workers was given a set proportion of large, hibernated larvae to rear through to the pupal stage, when the caste is easily determined. In every test, one result remained the same: despite considerable variation between separate experiments, the average time for larval development permitted the species to be ranked always in the same order from fastest to slowest developers — M. ruginodis, M. rubra, M. scabrinodis and M. sabuleti (Figure 45). Cross replication (ie giving each species larvae of other species to rear) confirmed that this is a trait in both workers and larvae.

In the south of England, all Myrmica become active by mid-April and usually colonies have reproductive castes in the pupal stage by early June, a period of about 50 days. Using Figure 45, it can be calculated that M. rubra needs a temperature that is, on average. 1°C warmer, M. scabrinodis 2.5°C warmer, and M. sabuleti 3.5°C warmer, than is needed by M. ruginodis. A comparison with other data for the mean soil temperature at the preferred sites for the active season showed a very good negative correlation. Ignoring any possible differences between the species due to nest site location and nest structure, the differences in soil temperature more or less cancel the differences due to basal physiology, so that all the species can produce pupae at about the same time.

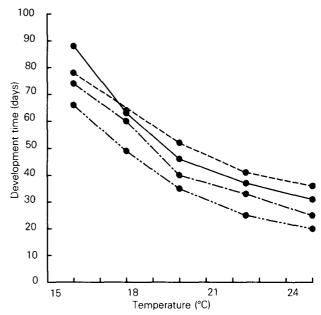


Figure 45 The mean developmental times to the white pupal stage, estimated from all the experiments at each of the 5 constant temperatures

- —---●, M. ruginodis; •—---●, M. rubra;
- -●, M. scabrinodis; ●-----●, M. sabuleti.

The lines are not the statistically fitted relationships.

The ability to produce pupae, particularly the reproductive castes, by the early summer thus seems to be an important factor in the success of a Myrmica species. Considering the genus worldwide, we know of no exceptions to this constraint. Of course, annual variations and nest site variations will affect the success of any population at the colony level, but it seems that long term adaptation might be just a simple physiological response.

As a next step, it would be interesting to see if the response to temperature varied over the range of a species, eg do M. sabuleti living in the hot regions of southern France respond to temperature in the same way as those living in Scotland? If so, how do their preferred habitats compare, particularly in respect of nest site location? Longer term questions are: (i) Do the species react in the same way as each other to different 'temperature day-lengths' encountered over the range of the genus? (ii) What are the effects of a longer or shorter growing season, eg do species living in the arctic tundra respond in the same way as those

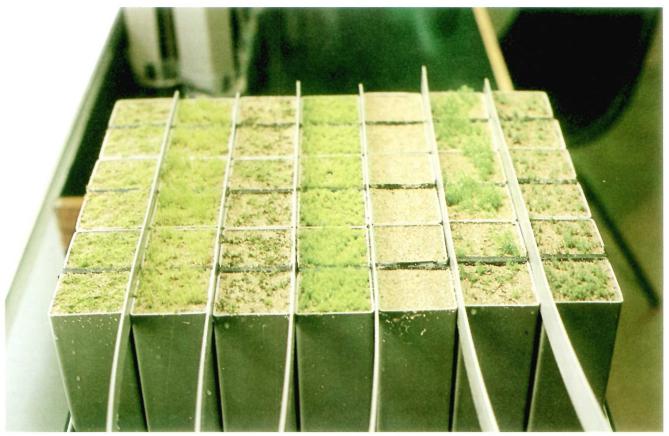


Plate 5 Mosses being grown on sand for comparative moisture loss studies. From left to right: Hypnum cupressiforme, Dicranum scoparium, Rhacomitrium lanuginosum, Ceratodon purpureus, Control (unsown), Polytrichum commune, Polytrichum piliferum. (Photograph N G Bayfield)



Plate 6 Roadside verge management experiment at lckleton, Cambridgeshire. Colourful display of wild flowers in a species-rich sward maintained by infrequent cutting and no applications of herbicides or growth retardants. (Photograph T W Parr)

living in the hot south? Our results predict that variations between and within species should be discovered if this line of research is continued.

G W Elmes and Judith C Wardlaw

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EGGSHELL THINNING AND THE BREAKAGE AND NON-HATCH OF EGGS AT GREY HERON COLONIES

Previous ITE work on the breeding of grey herons (Ardea cinerea) and the impact of pollutants has been done at Monks Wood. Intensive studies with material from 3 colonies in Lincolnshire delineated relationships between shell thickness, shell strength, and the levels of DDE residues in heron eggs (Cooke et al. 1976). Moreover, the frequency of egg breakage at these colonies was related to mean DDE levels for annual samples of eggs, with a general decrease in both during the study period 1965-1978 (Cooke et al. 1976; Conroy & Stephenson 1980). The work in Scotland, started in 1981, aimed to sample a large number of heronries in a variety of habitats and regions, using shell thickness as a bioassay of DDE. After the eggs have hatched, adult herons cast their eggshells over the side of the nest, so at least one eggshell could be collected from almost every nest with young that was visited, and its thickness measured. It was easy to distinguish hatched from broken eggs because they had the remains of blood vessels and the allantois on the inside membrane. Egg breakage took place mainly during laying, or early incubation. Causes of breakage were difficult to determine. Some thick shells showed obvious beak marks where the eggs had been pierced by a predator, but thin shells tended to curl and fragment, whatever the original cause of fracture. Some eggshells were so thin they could not have withstood the inevitable ill treatment during incubation. Some thick and thin shells were seen that looked as though they had come from eggs broken on impact after being cast or blown out of a tree-top nest.

Unhatched eggs were of 2 types: 'addled', where there was little or no development of the embryo, and 'deadin-shell', where the embryo had died near hatching. These eggs were usually found intact in nests, but also occasionally broken below the nest, presumably dislodged by well-grown nestlings. Addled eggs were always soiled outside with the faeces and regurgitations of nestlings and stained yellow inside with yolk. 'Dead-in-shell' eggs were not always fouled on the outside, but were always bloodstained on the inside, often with the putrefying remains of the large embryo still adhering.

Shell thickness

The inner membranes were stripped from pieces of eggshell where the egg was broadest, and the remaining calcified layer measured with a micrometer. Shell thickness was estimated by the mean of 3-6 measurements, depending on how much of the eggshell's waist was still present. Most shells examined came from hatched eggs, and the frequency of their thicknesses approximated a normal distribution with a mode of 260–270 µm (Figure 46). In contrast, the thicknesses of broken eggs had a frequency distribution with a mode of 280-290 µm, and possibly a second mode at 210-220 µm. Avian eggshells become thinner during incubation as the outside surface is worn and the embryo itself uses about 5% of the shell calcium (Simkiss 1967). Estimates for the total reduction in eggshell thickness with incubation vary between 7.3% for Japanese quail (Coturnix japonica) and 8.2% for blackheaded gull (Larus ridibundus) (Kreitzer 1972; Pulliainen & Marjakangas 1980), which is sufficient to explain the difference between the principal modes of broken (mainly fresh) and hatched (fully incubated) heron shells. The secondary mode for broken shells suggests that eggs are much more likely to be broken if they are less than 230 µm thick. To judge from the thinnest of hatched shells, no fresh eggs with shells of 210 µm or less survive to hatch. Broken shells measuring 170 µm were not the thinnest, but merely marked the limit at which the calcified layer survived separation from the inner membranes without crumbling. 'Softshelled' eggs with almost no calcified layer were found, crumpled, below nests at 4 colonies.

The very few 'dead-in-shell' eggs had thinner shells than most hatched eggs. Addled eggs contained no large embryos, and so should have had shells thicker than those of hatched eggs. There was, however, no significant difference, suggesting that eggs with thinner shells were more likely to become addled.

In order to compare colonies, the thicknesses of broken and unhatched eggs were ignored as they were few and their inclusion caused more sampling problems than did their exclusion. It is to be noted that their exclusion caused an overestimation of the mean thickness of eggshells from colonies where many thin-shelled eggs were broken.

Egg breakage and non-hatching

The proportion of broken eggs at colonies, expressed as the proportion of clutches containing at least one broken egg, varied from 0·09 to 0·40. For 8 colonies in Fife and Tayside, where there were sufficient data to compare years, there was little difference between 1981 and 1982, and a significant tendency for those colonies with more breakages in 1981 to suffer as much in 1982 (r=0·73, n=8, P<0·05). As was expected, egg breakage was most frequent in colonies where shells were thinnest (r=-0.73, n = 12, P<0.01). The proportion of clutches containing at least one addled egg varied from 0 to 0·20, and was also consistent

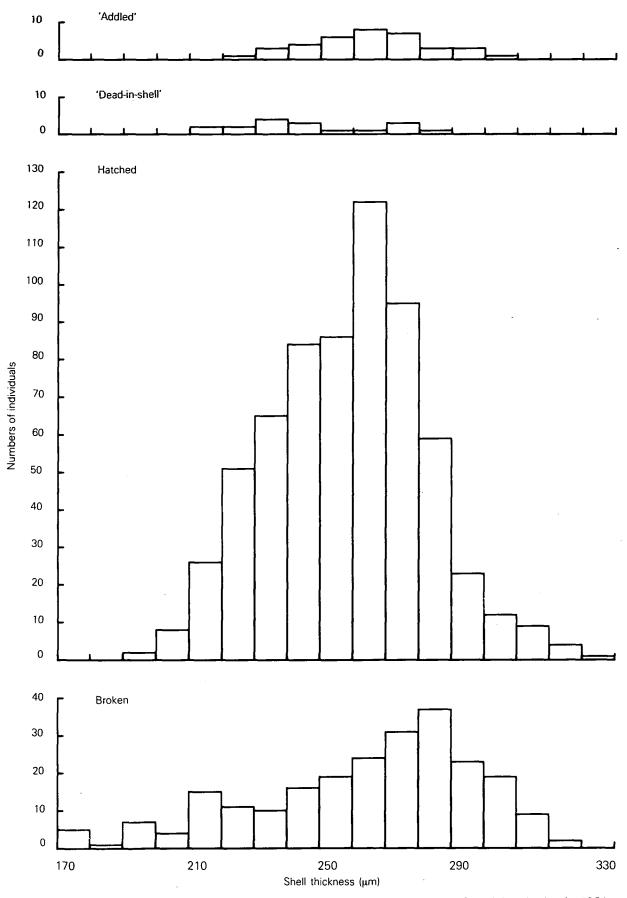


Figure 46 Frequency distributions of the thickness of heron eggshells from 32 Scottish colonies in 1981.



(a) Calcareous cutting, Southern Region



(b) Ballast-strewn embankment, Eastern Region



(c) Woodland management, Western Region



(d) Montia perfoliata, an introduced annual, on cess, Eastern Region



(e) Rock cutting through moorland, Scottish Region



(f) Water, masonry and woodland, Scottish Region

Plate 7 An example of the variety of habitats supported by the railway.

On cuttings through soil (a) the better drained and often species-rich grassland may occur, whilst on embankments (b) false-oat often colonizes spent ballast, giving way to tall herb communities along damper footings.

ments (b) false-oat often colonizes spent ballast, giving way to tall herb communities along damper footings. Such grasslands are no longer systematically managed and verges are sprayed to control the spread of scrub (c). Herbicide also keeps much of the cess weed-free, although some strategies are not successful (d). Rock (e), masonry and water (f) contribute to the diversity. (Photographs C Sargent)



Plate 8 A nestling magpie (24-days old). (Photograph D C Seel)



Plate 9 A dusky large blue butterfly (Maculinea nausithous) laying eggs on well-formed flowerhead of the great burnet (Sanguisorba officinalis). (Photograph J A Thomas)



Plate 10 A male goshawk showing antenna. (Photograph R E Kenward)

from 1981 to 1982 (r=0.81, n=8, P<0.02). The frequency of egg addling was not correlated with either egg breakage or the thickness of hatched shells in the same colony. There were insufficient 'dead-in-shell' records to demonstrate any significant trends for this character.

Variation with habitat and region

Eggshells were collected from 32 heronries in 1981, mostly in Fife and Tayside (14) and Dumfriesshire (7), but also from 11 other scattered localities in the Borders, north-east and west Scotland. The heronries in Fife and Tayside covered a wide spectrum of habitats that could be broadly categorized by altitude. Prey items recorded at nests showed herons nesting above 200 m asl fed mainly on trout and salmon parr caught in hill streams and fast-flowing rivers. Between 100–200 m, herons used a greater variety of habitats, including open drains, streams, rivers, flood water and rich lochs, all of which drain cultivated land and so could have been contaminated with DDT. At lower altitudes, most herons fed often at estuaries or in rock pools on the seashore.

In Fife and Tayside, altitude and eggshell thickness were correlated (Figure 47). Colonies in elevated areas, remote from the application of DDT, had thick shells, whereas coastal colonies, downstream from the major agricultural application, had very thin shells. There were also regional differences; hatched shells in the west and south were much thicker (means 257–278 μm) than those in north-east and central Scotland (means 230–263 μm). Exceptions to this pattern fitted well with the expected distribution of DDE residues, in that the thinnest shells on the west were in the Firth of Clyde, and the thickest on the east coast were found at a colony where the herons predominantly fed in rock pools on the seashore.

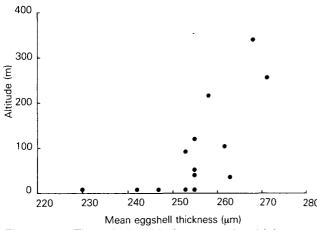


Figure 47 The relationship between the thickness of hatched eggshells and the altitude of heronries in Fife and Tayside.

There were insufficient data to examine altitudinal and regional variation in egg breakage or non-hatching. A heronry amid intensively farmed land in the north-east suffered excessive egg breakage. The highest propor-

tion of clutches with addled eggs, or 'dead-in-shell' eggs, was found at a colony beside the highly polluted Inner Forth estuary.

This report is preliminary. The work in progress will increase sample sizes in an attempt to resolve more of the variation in eggshell thinning and to investigate non-hatching. The contents of eggs are to be analysed chemically to see if the relationship between shell thickness and DDE concentration changes.

M Marguiss

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Plant population ecology

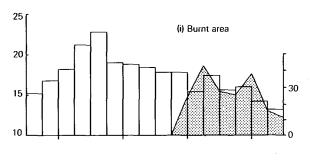
ECOLOGICAL STUDIES ON THE MARSH GENTIAN (GENTIANA PNEUMONANTHE)

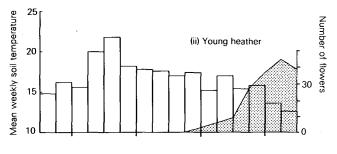
There can be many reasons for studying the ecology of an individual plant species. For abundant or widespread species, the reasons may be related to the control of 'weeds' or the encouragement of 'desirable' plants. In contrast, the reasons for studying less abundant species, and especially those with restricted distributions, are more likely to be concerned with a better understanding of the factors regulating the performance of vegetation and plant populations.

The marsh gentian (*Gentiana pneumonanthe*) is restricted by both climate and habitat. It is a plant of wet acid heathland and grassland, whose occurrence in Britain has been reduced by drainage and general loss of habitat. However, both within and outside this species' present geographical limits, there seem to be suitable habitats which are not, and in some instances never have been, occupied.

A series of casual observations suggested that the growth and flowering performance of *Gentiana pneumonanthe* during the years immediately following a heathland fire differed from that at other times. It also appeared that populations of gentians growing in areas of wet heathland that are now surrounded by forest plantations were decreasing in numbers, area and performance.

Preliminary measurements of flower production were made during the summer of 1971, when mean soil temperatures were measured weekly, by a sucrose inversion method, on 3 adjacent areas of wet heathland having similar numbers of gentians: (i) an area of old heather (15-years old), (ii) an area of young heather (4-years old), and (iii) an area burnt in the previous February. Soil temperatures were found to be consistently higher on the black, recently burnt, site than at the other locations, whereas flowering was greatly decreased on the old heather site (Figure 48).





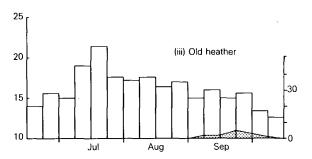


Figure 48 Association between mean weekly soil temperatures (2–5 cm deep) and flowering performance of similar sized populations of Gentiana pneumonanthe growing on (i) a recently burnt site, and sites with stands of heather 4- and 15-years old (ii and iii) respectively.

To simulate a black burnt soil surface with an altered soil temperature regime, but without adding the nutrients which are a consequence of burnt heathland, a pot experiment was started in 1977, with inert plastic granules (3 mm diameter) being applied as a surface mulch. Black granules were used to increase, and white granules to decrease, soil temperatures in pots containing *G. pneumonanthe* plants already established in a dry heathland soil. Applying the surface mulch of black granules, and removing the *Calluna* seedlings which developed from seeds naturally occurring in the heathland soil increased the numbers of flowers produced by *G. pneumonanthe*. Thus, it

seemed that the black mulch mimicked the effect of burning, but also provided insulation against cooling at night. In other experiments using soil warming cables (Chapman & Rose 1980), increasing soil temperatures above ambient increased vegetative growth and flowering (Figure 49). After the first year, the replicate pots of each treatment were arranged in 2 sets: (i) where Calluna was allowed to persist, and (ii) where Calluna was removed by cutting. The introduction of this treatment showed that the size of the effect (a decrease) of the presence or absence of Calluna on the flowering of *G. pneumonanthe* was larger than that of granular mulch.

In subsequent experiments to investigate the 'heather effect', it seems that damage done to G. pneumonanthe was more likely to be related to nutrient competition than to an allelopathic effect. An attempt has been made to identify the nature of the heather 'factor' by separating the influences of roots and aerial shoots of Calluna and Gentiana by the judicious use of barriers. The latter, separating the root systems of the 2 species, were either impermeable to both root growth and solute transfer, or permeable to the transfer of solutes but impermeable to root growth. In the event, the root barriers, but not those above ground, were associated with statistically significant effects on plant growth. Separating roots of *G. pneumonanthe* (Plate 12) from those of Calluna by a permeable barrier increased plant dry weights in addition to the proportion of flowering G. pneumonanthe. Substituting an impermeable barrier further increased the sizes of these effects (Table 25). Thus, it seems that the performance of G. pneumonanthe can be affected by root competition with Calluna but the nature of the competition remains a mystery. Do the 2 species perhaps compete for nutrients?

Table 25. Effects of competition with the roots of Calluna on the performance of Gentiana pneumonanthe (root systems were allowed to intermingle or were kept apart with either permeable or impermeable barriers)

** P<1.0%; *** P<0.1%

		Roots able to mix freely — no barrier	permeable	Roots separated by impermeable barrier
	Total (shoots, leaves and flowers) dry weight (g)	0·126	0·156	0·291**
Gentiana	Proportion of plants flowering Number of	0·17	0.48	0.77**
	flowers per flowering plant	5⋅0	2.04	2·78***

Apart from the destruction of first-year seedlings, *G. pneumonanthe* seemed remarkably tolerant to the effects of fire when the soil surface was 'burnt' for 5 minutes with a calor gas burner. A series of mowing experiments showed that removal of above-ground



Plate 11 Glasshouse experiment investigating radionuclide uptake from contaminated soil by Puccinellia maritima (foreground), Trifolium repens, Lolium perenne and turnips. (Photograph A D Horrill)

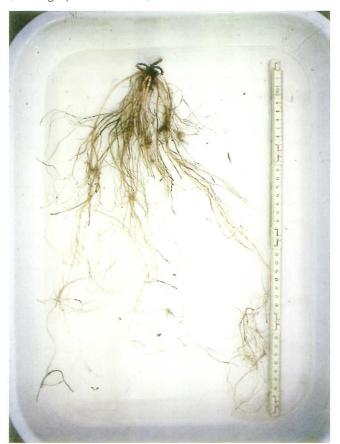
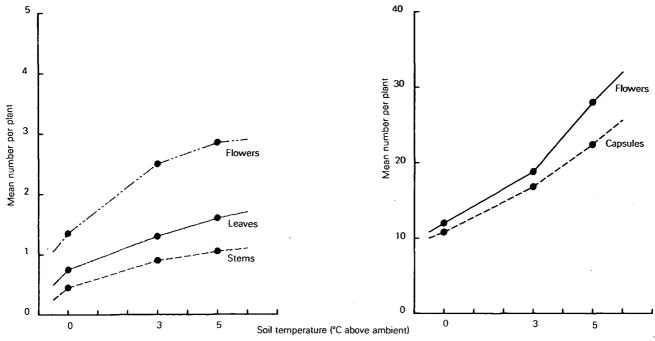


Plate 12 The root system of a Gentiana pneumonanthe plant extracted from plants grown in a glass-house experiment. (Photograph S B Chapman)



Plate 13 Beating sweet chestnut (Castanea sativa) for larval Lepidoptera at Challock, Kent. (Photograph R C Welch)





Effects of increased soil temperatures on the performance of Gentiana pneumonanthe.

growth had no effect on the current year's flower production if done before the beginning of May; some flowers were formed and seed produced if mowing continued until the beginning of June. Seed production per flower seems remarkably constant, at about 300 seeds per capsule. Seeds collected in the autumn and stored at 20°C lost their ability to germinate within 4 months, but those stored at 10°C or lower retained viability until the following spring, as might be expected of a species with a continental type of distribution, where low winter temperatures allow seed viability to be maintained until the onset of relatively high temperatures in spring and summer (Figure 50). The ability to withstand low winter temperatures may be particularly important in G. pneumonanthe, as many

100 viability 20°C 0 Jan Nov Dec May Apı

Figure 50 Effects of storage temperatures on the viability of Gentiana pneumonanthe seed.

of its seeds remain in flowerheads, where they are subjected to greater temperature fluctuations than in litter until January or February. Seeds germinate readily on a variety of substrates, but the establishment of seedlings appears to be jeopardized by the occurrence on soil of the alga Zygogonium ericetorum, whose mats of tissue may cover newly germinated seedlings. This alga may significantly retard the development of other wet heath plants, while seemingly encouraging large populations of some soil invertebrates, including mites and collembola, which congregate beneath its algal mats.

How do these observations on different facets of the growth of G. pneumonanthe relate to its performance in the field? Detailed observations of performance, mortality and establishment have been made on 4 field populations located in Dorset and Hampshire (Figure 51). Judging from 7 years' observations, it seems that the mean annual mortality is rather less than 10% and very variable relative to flower production, which depends upon the age of heathland vegetation in addition to seasonal factors. These observations agree with the results obtained from the pot experiments, and, together, the 2 kinds of observations give greater confidence to a computer model that allows simulations of Gentiana populations under different management regimes (Chapman et al. 1982). Importantly, this model substantiates the original observation that populations of G. pneumonanthe which are now protected from disturbance and/or fire are becoming less vigorous a matter of concern when considering how to sustain populations of this species.

S B Chapman and R J Rose



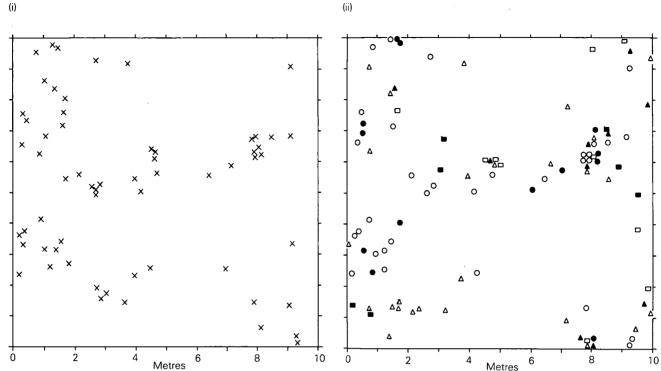


Figure 51 Changes in the structure of a New Forest population of Gentiana pneumonanthe i. location of individual plants when first surveyed in 1977—ages of individual plants unknown. ii. location of plants in 1982 when they were:

 \square , 1; \blacksquare ; 2; \blacktriangle , 3; \triangle , 4; \bullet , 5; or \bigcirc , 6 or more years old.

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THE HYBRID MARRAM xCALAMMOPHILA BALTICA IN BRITAIN

The hybrid marram grass xCalammophila baltica (= xAmmocalamagrostis baltica) is one of few intergeneric hybrids known to occur widely in nature. The parent species are marram grass (Ammophila arenaria), and bush grass (Calamagrostis epigejos) (Westergaard 1943).

Hybrid marram is found on European coasts from northwest France to the Baltic Sea. It has been reported as occurring naturally in 2 regions of the British Isles: Holy Island and Ross Links in Northumberland, and on the Norfolk Coast (Perring & Snell 1962). A small population, probably transplanted from Winterton, Norfolk, occurs at Milford-on-Sea, Hampshire, and it is possible that other such populations exist.

Hubbard (1968) and Stace (1975) suggest that the hybrids in Norfolk are morphologically different from those in Northumberland. As xC. baltica is infertile, increasing only vegetatively, hybridization may have occurred at least twice, once at each site. The extent to which the populations vary internally, which may indicate the frequency of hybridization, is unknown.

In order to investigate this problem, dry inflorescences were collected from xC. baltica and the parental species from sites in Norfolk and Northumberland in September 1979, and from Milford-on-Sea in March 1980. Twenty morphological characters (Table 26) were measured, where possible, on 10 inflorescences from each site. The resulting data were analysed using canonical discriminant analysis (Nie et al. 1975), which is well suited to the analysis of variation between putative populations.

Table 26. Flower characters recorded for collections of Ammophila arenaria, Calamagrostis epigejos and xCalammophila baltica made in Norfolk and Northumberland in September 1979

Character

	Character
1	Panicle shape, wide, lanceolate or linear
2	length (cm)
3	Longest branch on lowest node, angle to stem
4	length (cm)
5	Length of pedicel (mm)
6	Length of spikelet (mm)
7	Upper glume, roughness of keel, part or whole of length
8	length (mm)
9	number of nerves
10	Lower glume, roughness of keel
11	length (mm)
12	number of nerves
13	Hairs at base of lemma, density
14	length (mm)
15	Lemma, length (mm)
16	number of nerves
17	Awn, length (mm)
18	position on back of lemma, (mm) from apex
19	Palea, length (mm)
20	number of nerves

The entire data set was analysed, and also the sub-set of xC. baltica data. In both instances, a univariate 'F' test indicated that all characters, except the density of hairs at the base of the lemma, differed significantly between groups. Chi-squared tests (χ^2) showed that the variation along the first 2 functional axes was highly significant.

In the analysis of the entire data set where site data were combined and entered by regions, the first functional axis accounted for 77.5% of the total between-group variation, and the second axis for a further 11.5%. The parental species form 2 distinct clusters, with the hybrid intermediate between them (Figure 52). In *A. arenaria*, the plants from the 2 regions

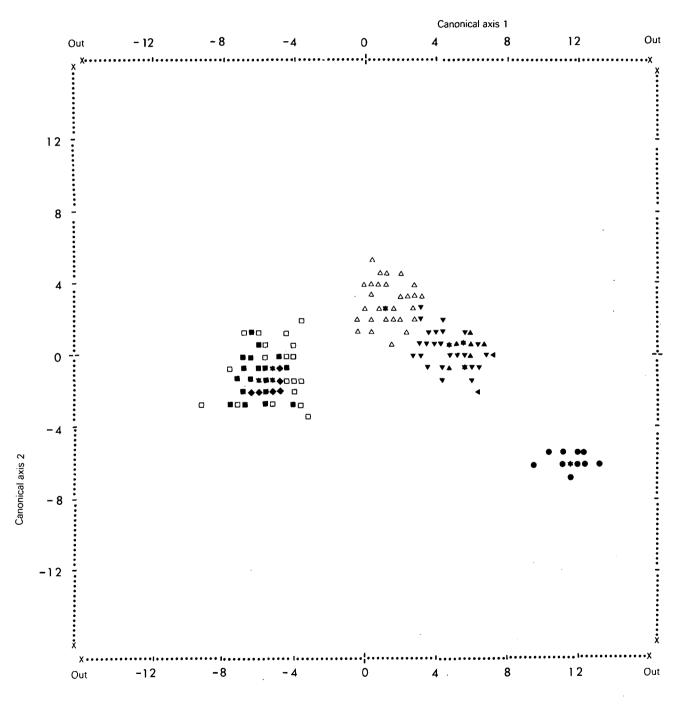


Figure 52 Scatter diagram from a canonical discriminant analysis of flower morphological data from Ammophila arenaria (\Box , \blacksquare , \spadesuit), Calamagrostis epigejos (\bullet) and their hybrid xCalammophila baltica (\triangle , \blacktriangledown , \blacktriangle , \blacktriangleleft) collected at different sites in Norfolk: \blacksquare , \blacktriangledown (Winterton), \spadesuit , \blacktriangle (Yarmouth), \bullet (Hickling); Northumberland: \Box , \triangle (Ross Links); and Hampshire: \blacktriangleleft (Milford). Group centroid \bigstar .

Table 27. Classification, as a result of canonical analysis of flower characters, of collections of *Ammophila-arenaria, Calamagrostis epigejos* and their hybrid *xCalammophila baltica*, obtained from a range of locations in Hampshire, Norfolk, and Northumberland. The Table shows the group membership derived (predicted) from the analysis for 10 replicate inflorescences of the 19 original collections (only 6, 6 and 9 inflorescences for collections 2, 11 and 17)

													ı						-	
Collections, actual groups	Membership derived or predicted	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
C. epigejos Norfolk	1	10																		
Hampshire	2		5		_															
xCalammophila .	baltica																			
Northumberla	nd 3			10	7		3										ł			
	4		ĺ																	
	5				1	6	3						ļ							
	6						10													
Norfolk	7							6		3	1									
	8	İ						4	3	2		1								
	9	Ì						1	1	8										
	10							1			9									
	11									1			<u></u>							
Ammophila aren	aria																			
Northumberla	nd 12		İ										8						1	1
	13												3	5	1				1	
	14	ŀ													9	1				
	15															10				
Norfolk	16														1		7		2	
	17													1	1			6	1	
	18												1	1	1	1	1		5	
	19												1							9

overlap completely, but the specimens of *xC. baltica* from Norfolk and Northumberland are clearly separated, a distribution which is confirmed when the analysis was restricted to the hybrid data.

The whole data set may be classified by sites in Table 27, where the rows represent the groups in which the plants were collected, and the columns show the groups in which they appear to be classified according to the nearest group centroid to each plant. This classification indicates that, although *A. arenaria* populations do not always appear closer to another group from the same region when re-classified, those of *xC. baltica* always remain within their own region. It is interesting that the evidence suggests that the hybrid plants found at Milford originated from Norfolk.

These results indicate that the populations of *xC. baltica* in Norfolk and Northumberland are the products of separate hybridization events, and strongly suggest that hybridization has occurred only once in each region.

J R Rihan and A J Gray

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Autecology of animals

NATURAL SELECTION IN CAPERCAILLIE

An animal's body size and form are often explained as adaptations to its 'ecological niche', which is usually defined as the limits of the environmental variables that allow a population to survive and reproduce. In birds, for example, beak size and shape are often said to be finely attuned to food and foraging habits. Also,

many aspects of animal form seem to be adapted to intraspecific competition: antlers, horns and bright plumages attract the opposite sex, and intimidate the same sex. Aspects of an animal's form and behaviour may also be directed towards avoiding, or dominating, other species.

It seems unlikely that all 3 selective pressures (niche requirements, intra- and interspecific competition) will act in the same direction. In the capercaillie (Tetrao urogallus), sexual selection appears to have favoured cocks so big that the cock chicks have become poorly adapted to their physical environment.

Capercaillie are polygamous: in spring, the cocks gather in small groups and display in the forest. The display lasts only a week or 10 days, fights and wounding are frequent, and beaten cocks sometimes die. Capercaillie cocks are the biggest of the grouse family, 4 kg or more when adult, and large size may be advantageous in fights. At display grounds, the hens, only 1.7 kg in weight, gather round the most dominant cock. Up to 15 have been seen round one cock, and a hen may have to wait 2 or 3 days to be mated; most prefer to wait for the favoured cock, rather than get immediate service from a less dominant bird.

Wegge (1978) first pointed out that, in years when fledged capercaillie broods were small in Norway, the percentage of cocks in the broods was also small, but the sex ratio in broods was about 50:50 in years of good breeding. Preliminary data (Moss 1980) confirmed this finding for Scottish capercaillie (Figure 53), and subsequent data strengthen the conclusion. It seems that cock chicks suffer heavier mortality than hens in years of poor chick survival.

Cock capercaillie have to grow more than hens to reach their autumn weight. The reason that more cock chicks

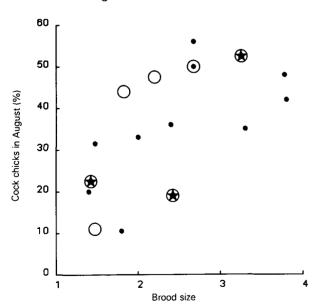


Figure 53 Percentage of cock capercaillie chicks and mean brood size in autumn: • Wegge (1978);

Moss (1980); 🗭 1980-1982.

die in years when broods are small may be because cock chicks are under more stress than hens. The nature of the presumed stress is not known, but a frequent suggestion in the literature is that survival is worse in cold, wet summers.

It has been previously argued (Moss 1980) that chilling alone was unlikely to cause differential mortality between sexes, because the relatively small hen chicks have a larger surface area in relation to total volume, and should therefore lose more heat than cocks. However, the implicit assumption that heat production per unit volume is the same in hen and cock chicks is now in doubt because of the subjective observation that capercaillie chicks are more sluggish than chicks of the other 3 British grouse species. In the same weather, they fly less readily, are easier to catch, and struggle less in the hand. Chick vigour seems to be inversely related to adult size in the 4 species, with ptarmigan (Lagopus mutus) chicks most vigorous, followed by red grouse (Lagopus lagopus scoticus), and then black grouse (Tetrao tetrix). Even within capercaillie, cock chicks are easier to catch than hens in August. Possibly, the chicks' ability to resist chilling reflects their general vigour and is inversely related to their growth rate as if more energy invested in growth means less available for muscular work, including both escape from predators and heat production by shivering. The details of this suggestion have yet to be tested, but the general idea remains that sexual selection for large size in adult cock capercaillie has resulted in a reduced resistance to environmental stress in male chicks.

R Moss

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THE GOLDEN PLOVER

A better understanding of the breeding biology and habitat selection of golden plovers (Pluvialis apricaria) is desirable because their breeding habitat is disappearing in many parts of Britain through afforestation of moorland. An experiment has now been designed in an attempt to influence golden plover densities. A preliminary study ran from 1973 to 1978, when a new landowner stopped the research, but a further change of ownership enabled a new study to be started in 1981 on the same area, at Kerloch in Kincardineshire.

In the first study (Parr 1980), adults were graded according to the amount of black on the face and belly (Figure 54). At Kerloch, males fell within grades 5-7 and females within grades 1-4, and there was evidence of assortative mating, ie darker males (grades 6 and 7) tended

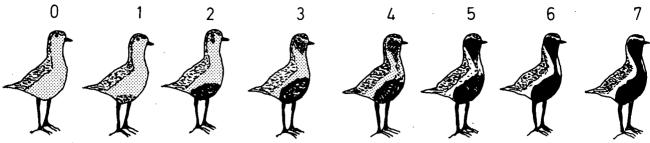


Figure 54 Grade categories of adult golden plover in breeding plumage.

to be mated with dark females (grades 3 and 4), while paler (grade 5) males were mostly seen with females of grades 1 or 2. The idea that dark pairings produce dark offspring, and *vice versa*, was considered in the previous study, but the sample size was too small to enable firm conclusions to be drawn. Observations on the colour grades of first-year birds from known parents are now being made, in order to increase the sample size and so obtain more reliable results.

Golden plovers normally lay 4 eggs, all of which, in the absence of predation, hatch. However, between 1973 and 1978, broods seen after the first week of life never had more than 2 chicks, although most pairs reared at least one chick. Broods are now being studied more closely to see when chicks die, and chicks are weighed at various ages to measure their growth rates. The suggestion of a relationship between the age of the female, egg size, and breeding success is also being examined.

Birds at Kerloch nested on areas of recently burned heather, and broods were usually found on small grassy patches (Agrosto-Festucetum) close to the nest site. As breeding pairs were not found on burned areas without grassy patches, it has been suggested that grassy patches are important in the choice of territory. To test this hypothesis, 6 new grassy patches have been created on areas of recently burned heather which have held no golden plovers since 1963. The sites were chosen at random and there are 6 controls. Each plot measures approximately 62 m², and has been rotavated and treated with lime, basic slag, fertilizer and grass seed (Festuca rubra and Agrostis tenuis). More fertilizer and grass seed will be added as necessary. It is more likely that it is the invertebrate fauna rather than the grass itself which attracts the birds, and it may take some time for this fauna to become established. Therefore, several years may elapse before the new plots are suitable as chick feeding areas. The sites will be watched closely to see if the birds populate them.

In the previous study, the majority of adults caught on the nest were cocks, mainly because they incubated during the day, when most trapping was done. In the new work, both parents are being trapped to provide better data on assortative mating and its results. At this early stage, there is nothing to add to the data already published (Parr 1980), but the extra effort involved in catching hens has uncovered an interesting aspect of the birds' behaviour. Although mate switching was known to occur between successive breeding seasons, it was not known if this followed the death of a partner, or if it had been seen within seasons. In 1982, 2 hens ringed on the nest in May were later seen on new territories with new mates. One had switched mates following a successful hatch and then relaid within 12 days, and the other paired with a new male one week after her first nest had failed. The first, deserted male reared his brood alone, whilst the other joined the flocks feeding in the fields. Perhaps these interesting cases are a form of sequential breeding (Parr 1979).

R A Parr

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THE ECOLOGICAL SEGREGATION OF 2 SPECIES OF LARGE BLUE BUTTERFLY (MACULINEA SPP)

(This work was partly supported by the World Wildlife Fund)

Research on the ecology of the large blue butterfly (*Maculinea arion*) in Britain (ITE Project 400) has been extended to include rarer Continental species of this genus. All these butterflies have similar specialized life cycles: the young larva feeds on flowers for a few weeks, but is then carried underground into a *Myrmica* ant nest where it lives for 9 months, feeding on ant brood. The short pupal stage is also spent in a *Myrmica* nest.

The dusky large blue (*Maculinea nausithous*) and the scarce large blue (*M. teleius*) breed, respectively, in a few marshlands in Europe, and more widely in the Palaearctic. Both species lay eggs on the inflorescences of great burnet (*Sanguisorba officinalis*), and actually occur together on a few sites, despite being 2 of the world's rarest butterflies. Analyses were made of 5 sites in France that supported both butterflies, with the aim of discovering their habitat requirements and whether they compete for resources.

It was soon clear that *M. nausithous* and *M. teleius* both form closed populations that may be supported

by discrete, small (0.4-1.3ha) areas of land. The flight area of both species was identical on every site examined, and the adults emerged on the same dates and flew together. However, very little interspecific competition was found between them, and, although both laid eggs on S. officinalis flowerbuds, M. nausithous invariably chose large well-formed heads (Plate 9), whereas M. teleius laid on younger inflorescences that were still in tight bud. By the end of the season, most large plants had many M. nausithous eggs on each of their (relatively few) large flowerheads, and one or 2 M. teleius eggs on most of their numerous lateral heads. An overlap occurred on the few inflorescences that had been suitable for M. teleius at the start of the adult emergence, and were well-formed enough for the last M. nausithous females that emerged. On some sites, M. teleius bred in a greater proportion of the flight area than M. nausithous, because it could also use the small terminal inflorescences of stunted plants.

The young larvae of both butterflies remained segregated within their original flowerheads until they fell to the ground to await discovery and adoption by foraging ants. Four species of *Myrmica* occurred on these sites, and all will adopt both species of *Maculinea* in captivity. However, each butterfly proved to be a successful parasite of only one species of ant: *Myrmica rubra* in the case of *M. nausithous* and *Myrmica scabrinodis* in the case of *M. teleius* (Table 28). Thus, the almost complete segregation of the 2 butterflies above ground is also maintained in ant nests.

Table 28. The emergence of Maculinea butterflies from different species of ant nests on Site 1

	Myrmica rubra	Myrmica scabrinodis	Other <i>Myrmica</i>
Estimated number of nests on site	684	892	420
Number of nests from which <i>M. nausithous</i> is known to have emerged	16	0	0
Number of nests from which <i>M. teleius</i> is known to have emerged	2	25	3

There was, however, intense intraspecific competition on some sites. No more than 2 adult *M. teleius* ever emerged from a single *Myrmica scabrinodis* nest, although the larger nests of *Myrmica rubra* each supported several individuals of the smaller butterfly, *M. nausithous*. Many more larvae than could be fed were adopted by most of the ant nests that coincided with *S. officinalis* on sites that had large *Maculinea* populations. All the ant brood was eaten in these nests, and only the largest *Maculinea* larvae survived.

The size of a colony of both species of *Maculinea* appears to be governed by the number of suitable ant nests that can be parasitized, which itself depends both

on the density of nests ('good' sites had 1-2 Myrmica nests per m²), and the distribution of flowering *S. officinalis*. The abundance of the food-plant is otherwise unimportant. Suitable conditions for *M. teleius* and *M. nausithous* occur at slightly different seral stages in marshy fields. Frequently cut meadows are unsuitable for both butterflies, but high densities of *Myrmica scabrinodis* nests and *S. officinalis* flowers occur after a few months of abandonment, after cutting or in patchily mown fields. *Myrmica rubra* proliferates in scrubby areas, and either invades later in the succession, or is confined to odd patches of scrub, hedges, the edges of woods and *Phragmites* beds. All *Myrmica* nests and *S. officinalis* disappeared rapidly in more overgrown conditions.

Maculinea nausithous and M. teleius were probably always very locally distributed, and have depended in historical times on unintensive agricultural practices. These practices are largely disappearing, and both species have declined very severely as a result. About 30 colonies of each butterfly are now known in the world, although undoubtedly many more survive. Most will probably disappear in the next 20 years, and these species may soon exist only on nature reserves. Two reserves are being established as a result of this research. It is expected that enough has already been learned about the habitat requirements of each species to be able to maintain large populations deliberately on these sites.

J A Thomas

GOSHAWK PREDATION ON PHEASANTS

Goshawk predation on pheasants during winter was first studied by radio-tracking individual goshawks in Sweden, in 1976. In that study, it was found that, whenever a goshawk killed a pheasant, the hawk normally ate the carcase or stayed near it for several hours. Thus, hawks could be checked intermittently for kills, at 1–2 hour intervals, and individual rates of kill recorded for several hawks at a time. A transmitter with a mercury tilt-switch was developed in order to avoid wasting time approaching hawks which had not killed: the mercury switch triggered a circuit to give a steady, slow signal pulse when the hawk was perched, a regular, fast pulsed signal when the hawk was flying, and an irregular pulse when the hawk was feeding (Kenward et al. 1982) (Plate 10).

Radio transmitters were also used as markers to estimate hawk numbers in the area. Every hawk seen while not radio-tracking was checked for a radio signal. In principle, if half the hawks thus sighted had radios when 6 radio-tagged hawks were present, there were 12 hawks in all. In practice, the estimation was complicated by changes in the number of radio-tagged birds throughout the study, but reasonable estimates were obtained. Then, knowing the pheasant density from

pheasant release or census data, the proportion killed by hawks (the predation rate) could be estimated as the product of hawk numbers and average individual kill rates (Kenward 1977).

Goshawk predation on pheasants was studied in this way by the author at 3 Swedish sites, in collaboration with Dr Vidar Marcström and Mats Karlbom of Uppsala University (Kenward et al. 1981), and a current joint project on goshawk population dynamics on the Baltic island of Gotland has provided data from 2 more study areas. The same techniques were also used by Ziesemer (1982) to record goshawk kills in 2 areas in northern Germany. Thus, data are now available for 7 areas with similar habitat but with a wide range of pheasant densities, from which to study the predatory responses of goshawks to variation in the abundance of this prey.

The relationship between individual kill rates and pheasant density, the functional response (Solomon 1949), is strongly convex (Figure 55). The individual kill rate tended towards a plateau of one pheasant per 2-3 days, which was above the maximum rate at which goshawks could eat pheasants (one in 3-4 days), because scavenging mammals and disturbance prevented hawks from finishing many of the carcases in the area with most pheasants. Without scavengers and disturbance, the plateau should therefore be between 0.25 and 0.33 pheasants per hawk per day. There was no tendency for the response to be concave at low pheasant densities, and thus sigmoid overall, which would indicate a 'switch' of hawk attention to pheasants as the density of this prey increased. Pheasants remained a preferred prey as their densities ranged from very high levels, in the 2 areas with released pheasants, through good to poor densities in the 5 areas with wild birds.

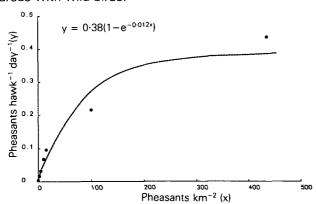


Figure 55 The average rate at which goshawks killed pheasants during winter in areas with different pheasant densities.

The change in hawk winter density as pheasant density increased (the 'numerical' predatory response, Figure 56) seemed to be sigmoid, although more data are needed for moderate pheasant densities to test this assumption. Hawk density at the site with most pheasants is shown as 90% higher than the observed value, because 11 of the 23 hawks trapped there had been removed to prevent an economically unacceptable pre-

dation rate. The value shown must be considered an upper limit, because fewer of the immigrants might have settled if the hawk density had been higher. Total predation at this site was 4% of the pheasants per month, and 5% at the other area with released pheasants. A predation rate on pheasants of nearly 6% per month was recorded in the area shown with an asterisk in Figure 56. In this area, hawks were feeding mainly on rabbits, which were not a common prey elsewhere, and the unusually small hawk range sizes signified a good food supply (Kenward 1982). It seemed that the rabbits were aggravating the goshawk predation on pheasants, by drawing in more hawks than would normally have occurred in such an area. A predation rate of 6% per month cannot be sustained by wild pheasants: a rate of 4% per month has now almost eliminated the best studied wild population.

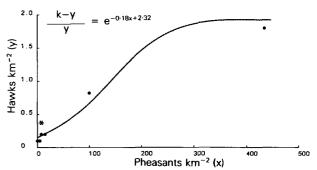


Figure 56 The density of goshawks during winter in areas with different pheasant densities.

It used to be thought that game species would be 'buffered' against predation by high availability of alternative prey (Leopold 1933). The heavy predation on pheasants in the rabbit-rich area shows that this is not always the case. We hope to do more work to discover the circumstances in which different prey 'buffer', or alternatively 'enhance', predation on each other, a subject of considerable interest to game managers.

R E Kenward

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FAECAL DEPOSITIONS AS INDICATORS OF SITE USE BY RED DEER

Ecologists have measured the faecal depositions of large herbivorous mammals in a variety of ways to derive quantitative indices of population density and range use (Neff 1968), because these mammals, unlike many others (eg carnivores and lagomorphs), distribute their faeces widely over the ground they occupy, with no obvious tendency to select special sites. We can thus estimate the population density of a particular herbivore from the rate of appearance of its faeces in sample parts of its range, if we also know its usual defaecation frequency, and this is one of the methods being tested in current ITE research on assessing the numbers of red deer in commercial forests in Scotland (Mitchell & McCowan 1980).

In theory, the method can be used for estimating population densities over large areas of deer range, or for assessing the occupation by deer (the product of density and time) of relatively small sites within an area of deer range, eg in studies of how deer distribute themselves in woodland habitats. For the latter purpose, however, it is necessary to know if the animals defaecate reasonably evenly over time, or if there are marked distortions associated with other aspects of their behaviour. Earlier casual observations had suggested that red deer tend to produce large faecal depositions after periods of rumination and rest, and smaller, more frequent depositions when feeding (Mitchell & McCowan 1980). To find whether these impressions were correct, the defaecatory behaviour of 2 exceptionally tame hinds were studied in the Nature Conservancy Council's red deer enclosure at Kinlochewe, Ross-shire, in summer 1982. This 14 ha enclosure contained about 40 red deer, most of which could not be approached closely. The 2 tame hinds were 'M' (16years old and non-pregnant) and 'S' 14-years old and pregnant), and both had been hand-reared, which presumably explained their unusual tameness. Either animal could be followed for several hours at a time, or handled, without any clear effect on her behaviour; 'S', for example, remained just as approachable after calving (27 June) as before. However, one possible consequence of the close presence of an observer is considered later. Most observations were made between mid-morning and early evening on 41 days from late April to early July. One hind was followed closely for one or more complete feeding cycles (defined below) each day, and records were made of when she defaecated, the numbers of pellets and total volumes produced at a time, and when her behaviour changed. The time from the start of one period of active feeding to the start of the next was regarded as one complete feeding cycle. The hind usually fed for a time, then ruminated, followed by rest (inactivity, rarely true sleep), and often groomed herself before moving a little way to resume feeding. 'M' was observed, by chance, on more days than 'S'; observations depended on which hind was found first.

Table 29. Some comparisons between the 2 hinds

	'M'	'S'
Observation days	26	15
Total hours	117	74
Mean size of faecal		
depositions		
i. Volume (ml)	94	135
ii. Number of pellets	48	76
Mean size when feeding		
i. Volume (ml)	79	103
ii. Number of pellets	39	59
Mean size after rumination/		
rest		
i. Volume (ml)	123	167
ii. Number of pellets	62	95
Mean pellet size (volume, ml)	2	1⋅8
Mean defaecation interval		
(minutes)	44	61
Calculated daily output of		
faeces		
i. Volume (ml)	3050	3180
ii. Total pellets	1550	1800
iii. Pellet groups	33	24
Activity budgets		
 Mean complete feeding 		
cycle (min)	72	98
ii. Mean feeding time 💢	41 (57% total)	55 (56%)
iii. Mean non-feeding time	31 (32% ,,)	43 (44%)
(a) Rumination ,,	17 (24% ,,)	22 (22%)
(b) Resting		
(inactivity) ,,	13 (18% ,,)	17 (17%)
(c) Grooming ,,	0.5 (0.7% ,,)	3 (3%)
(d) Moving ,,	0.5 (0.7% ,,)	1 (1%)

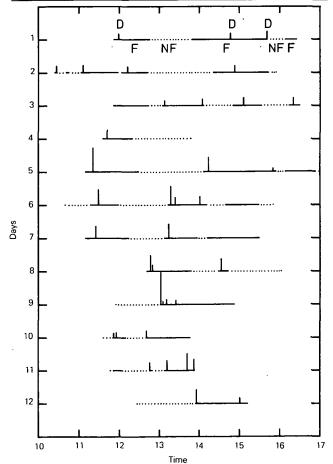


Figure 57 Activity patterns of hind 'S', showing periods of feeding (——), periods of non-feeding (-----), and when defaecations occurred (vertical bars, with height proportional to volume).

Despite their differences in reproductive status, the 2 hinds were remarkably similar in their general patterns of activity and faecal output (Table 29). Whereas 'M' defaecated rather more frequently than 'S', she produced smaller amounts at a time, so that both hinds produced much the same amount of faeces per unit time. In both volumes and numbers of defaecations per day, these results agreed well with earlier ones, derived from monthly records from sample plots, for the deer in this enclosure (Mitchell & McCowan 1980, and unpublished data on volumes).

Complete feeding cycles varied considerably in length (20-174 minutes), and differed, on average, between the 2 hinds. However, both hinds fed actively for similar proportions of their time ('M' = 57%; 'S' = 56%). Rumination, as expected, was the next major activity, accounting for 23% of their time. Very little time was spent in moving around the enclosure, except when feeding; the animals tended to move on after every few bites. There were no obvious changes in the feeding cycles of 'S' on 3 separate days soon after parturition. The short periods spent in feeding and grooming the calf were invariably after rumination and rest. At this early age, the calf spent most of its time resting in tall vegetation some distance from its mother.

It was clear that both hinds usually defaecated when they were feeding (see Figure 57 for activity records of 'S'), and that the first defaecations in feeding bouts (after rumination and rest) were generally much larger than subsequent ones (see Table 29). In all, 'M' produced 90 defaecations in 47 hours of feeding time, compared with only 2 in 35 hours of non-feeding, and 'S' 36/24 hours feeding time and 0/18·5 hours non-feeding, ie very similar behaviour in both hinds. Variation in deposition size was significantly related to the intervals between defaecations, but with a good deal of extra scatter (see results for 'M' in Figure 58). Presumably the larger defaecations made early in a feeding bout reflected the build-up of faeces in the rectum during rumination and rest. Although some of these first defaecations were made immediately at the start of feeding (see Figure 57), others were much later, the average delay being 8 minutes and the maximum 58 minutes. In this study, few defaecations occurred at the actual places where the animals ruminated and rested, most being made after a little movement away. This pattern could, however, have resulted from the close presence of an observer; in most cases, the 2 tame hinds tended to move in the general direction of the other deer, both when feeding and immediately after rumination and rest. Furthermore, examining

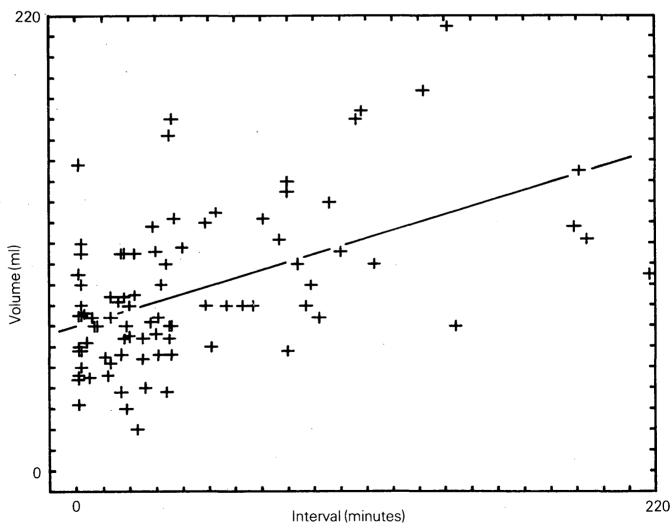


Figure 58 Relationship between the volume (ml) of a faecal deposition and the time (minutes) since the previous deposition.

other freshly used resting places elsewhere in the enclosure showed large faecal depositions within 1-3 m of most of them, so it may be that undisturbed red deer start feeding and then defaecate quite close to where they ruminated and rested. These detailed observations confirmed earlier conclusions that red deer defaecate mainly when feeding, with larger depositions after rumination and rest than later in a feeding bout. Consequently, although red deer do not defaecate evenly over time, there may be 2 useful implications in this finding. The size of faecal depositions can help to distinguish between sites used mainly for feeding and those used exclusively for resting, which could be helpful in interpreting the importance of various site features to red deer. Similarly, it may be an advantage in studies of deer impact on vegetation that the numbers of pellet groups accumulating at particular sites mainly reflect the amounts of feeding activity there; after all, feeding is usually the most important single influence of herbivores on vegetation.

We thank the NCC, North West Scotland Region, for access to the deer in the enclosure at Kinlochewe, and the Beinn Eighe Reserve Warden, Edwin Cross, for his kind help and co-operation.

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Faunistic studies

MUSSEL AND OYSTERCATCHER POPULATION DYNAMICS ON THE EXE ESTUARY

After breeding in north Britain, Norway and Holland, some 2000 adult oystercatchers (Haematopus ostralegus) arrive on the Exe estuary in south Devon, mainly during August and September, and join the several hundred non-breeding young birds that remain there throughout the summer. Most of these birds feed almost entirely on mussels (Mytilus edulis), from the time they arrive until they depart again for the breeding grounds in February and March. As each bird may eat between 50 and 100 mussels per day, the total number consumed by the population during the winter months is considerable. A principal aim of this study is to determine what effect this has on the population dynamics of the mussel population itself. This aspect is of interest partly because much theoretical work on population dynamics in recent years has focused on predatorprey interactions, although field studies are normally difficult to undertake. It is also of interest because ovstercatchers in particular, and wading birds in general, are often the subjects of controversy in applied ecology. First, oystercatchers are frequently accused of being pests of commercial shell fisheries, such as mussels and cockles (Cerastoderma edula), although their precise impact on the food populations remains obscure. Second, it is often asserted by conservationists that a serious reduction in numbers of wading birds might occur if their feeding grounds were lost from various planned developments on estuaries, such as land reclamation or water storage. It is, however, far from certain that a reduction in winter food supplies would have such an effect. Our research, therefore, has the reciprocal goals of discovering the role which the prey populations play in determining the numbers of waders, and how the predation by these birds in turn affects the numbers of the prev.

The mussel beds

There are some 31 mussel beds on the estuary, but many carry only a small proportion of the total population. Twelve beds were selected, which between them have over 80% of the total mussels on the Exe, and provide a wide variety of feeding areas for the oystercatchers (Figure 59). The mussels on each bed are sampled in September, as the adult oystercatchers return and after the main breeding season of the mussels themselves, and again in March as the oystercatchers leave and the mussels begin to breed. These bi-annual surveys give estimates of the abundance and densities of each age and size class of mussels on each bed and so provide the main information on the population dynamics of the prey. They also provide information on the food supply which the birds exploit between autumn and spring.

The oystercatcher population

The mussel beds to which the adults return in autumn vary considerably throughout the estuary. Five variables appear to be the main determinants of how many oystercatchers feed on a particular mussel bed. Oystercatchers prefer beds which (i) are in the lower reaches of the estuary, ie near to the high tide roost, presumably because they prefer to fly as short a distance as possible to feed; (ii) have a firm substrate, probably because walking in a sloppy substrate is energetically expensive; and (iii), (iv) and (v) have mussels which are large, numerous, and thin-shelled, probably because feeding is easier in such places.

Some mussel beds fulfill several of these criteria and are highly preferred, while others do not and are relatively little used. Two beds (30 and 31), near Exmouth, are especially favoured, and high densities of birds occur there at all times. Many of the several hundred non-breeding young birds that eat mussels occur there in the summer, and hardly use any of the other beds. However, as the adults arrive and the population increases 6-fold, birds spread out increasingly to the less preferred beds; whereas over 50% of the birds feed on these 2 beds in the summer, only 20% do so in winter.

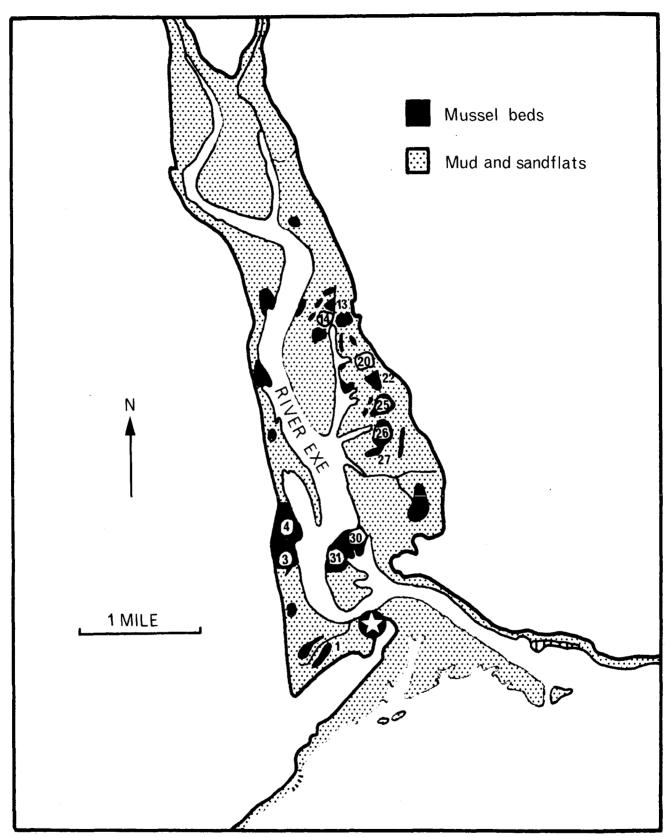


Figure 59 The mussel beds of the Exe estuary. The numbered ones are the 12 priority beds now given most attention. The star shows the location of the main roost used by the birds at high water.

As young birds are, in general, sub-dominant to the adults, they gradually leave the most preferred beds as the adults return (Figure 60). Indeed, recent studies have shown that it is the least aggressive of the immature birds that leave first. Some of these birds give up feeding on mussels and go to the mudflats to eat other foods, but most move to other, less preferred beds where the density of birds – and so the competition – is less. When the adults leave to breed in the spring, the immatures gradually return to the most preferred beds, where they spend the summer.

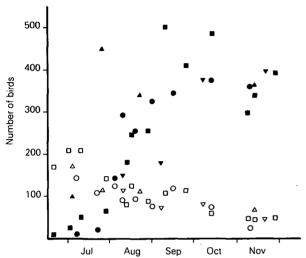


Figure 60 The numbers of immature (open symbols) and adult (closed symbols) oystercatchers on the most preferred mussel beds during the period of the year when adults return from the breeding grounds (from Goss-Custard et al. 1982b).

Competition between the birds for the mussel beds results in an ordered and predictable pattern of use by the birds at different population sizes, as shown in Figure 61, where the relative importance of the various

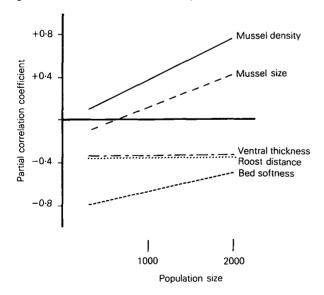


Figure 61 The influence of 5 factors on the density of oystercatchers on the mussel beds at different population sizes of oystercatchers. The lines show the average value of the partial correlation coefficients based on counts made over 5 years (from Goss-Custard et al. 1981).

factors affecting preference for mussel beds is expressed as partial correlation coefficients. When the population size is small, only substrate, proximity to roost and shell thickness influence bird density. As the population increases, the number of birds on a mussel bed becomes increasingly related to the density and size of the mussels present. Presumably the amount of suitable feeding space, ie the area containing sufficient densities of large mussels, becomes increasingly critical in determining how many birds can feed on a mussel bed, as numbers rise and competition increases.

By October, this sorting out process has been completed, and there is little change in the distribution of birds over the mussel beds until spring. In winter, most adults eat mussels, but many of the younger birds feed on other invertebrates living in the mud and sandflats of the estuary and coast. Many of these birds regularly supplement their diet at high water by feeding in adjacent fields, something which occurs much less frequently amongst adults. The proportion feeding in the fields at high tide increases through the winter, perhaps reflecting an increasing difficulty in finding sufficient food. Most birds survive, however, and only 2% of the adults die during the winter (Figure 62). A greater proportion of the young birds die, but as many do so in their first and second autumn, at a time of year when feeding conditions are thought to be good, it is not yet clear whether these deaths are related to food shortage. This key point is being studied now.

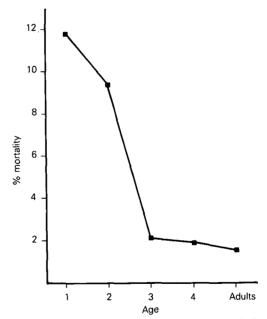


Figure 62 The mortality of oystercatchers of different ages in autumn and winter (from Goss-Custard et al. 1982c).

The mussel population

Each female mussel produces several million eggs in the summer, which are fertilized in the sea. After a few weeks in the plankton, the larva (spat) grows a shell and sinks to the bottom, where it may try several places before settling. The smallest mussels found in the biannual surveys of the Exe are only 1 or 2 mm long, and

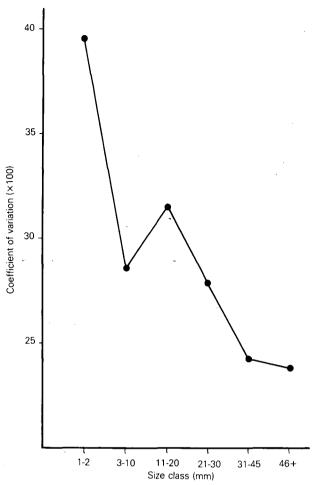


Figure 63 The coefficient of variation between mussel beds for the density of mussels of different size classes. Data from September 1981.

their density on the bed varies considerably. Indeed, variation between beds in the density of different size classes is by far the greatest in this group (Figure 63). The coefficient of variation drops rapidly in the larger size classes, and the beds become more similar.

Can this rapid change in variation between beds in the density of mussels as they grow larger be related to any environmental variables? Several factors were thought likely to be responsible, but only 2 proved to be of any real significance. The density of larvae was greatest on mussel beds with a hard substrate, which were near enough to the mouth of the estuary (Figure 64). The greater density of larvae on beds with a firm substrate occurs because of their need to attach themselves to something hard; their greater density in the lower reaches of the estuary may either be due to the high salinity (in the lower reaches of the estuary), or because many of the larvae come from adult mussels living in the English Channel. Surprisingly, the period for which the mussel bed was covered with water, and therefore the amount of time each day that spat could be in the vicinity to settle on the bed, was unimportant.

This pattern changes very quickly, however. Slightly larger mussels (3-10 mm long), which would still be less than one-year old, were actually more numerous

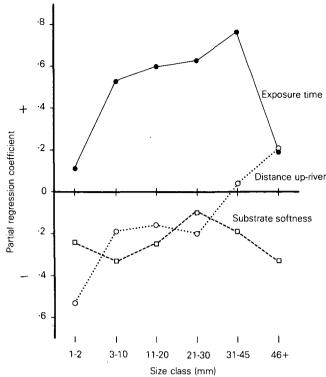


Figure 64 The change in the relative importance (expressed as partial regression coefficients) of 3 variables affecting the density of mussels on different mussel beds at various stages during the animal's life.

on beds that were covered for *less* time at high tide. This result was surprising, but it may suggest that very small mussels are eaten extensively by crabs (*Carcinus maenus*) at high tide, and are presumably most vulnerble on beds low down the beach. These beds are covered for longer periods at high water and are nearer to the low water channel whence crabs invade the mussel bed.

The sudden increase in importance of the time for which the bed is covered by water is matched by a reduction in importance of the distance of the mussel bed from the river mouth, but, thereafter, there is rather little change in the relative importance of these 3 variables until the largest size classes are reached. Although the hardness of the substrate retains its importance, the influence of distance up-river is reversed. While the smallest mussels are most numerous downriver, the largest ones are, if anything, more numerous up-river.

These results confirmed our expectation that the factors influencing the mussel population would vary between different parts of the estuary, and that it was therefore necessary to look at the dynamics of the subpopulations in each mussel bed before the dynamics of the whole population could be understood. This aspect is being studied by ageing the mussels collected in each survey and drawing up life tables from which population trends can be assessed. Figure 65 compares data from 2 mussel beds collected during the first 5 years of the study. Bed 30 is situated near the mouth of the estuary and has a very firm substrate;

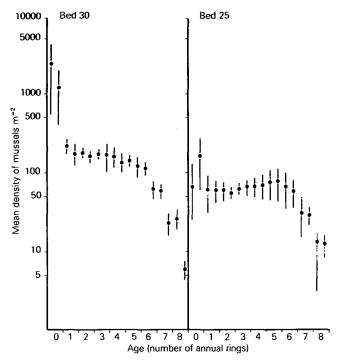


Figure 65 The numbers of mussels in each annual age class on 2 of the mussel beds, based on surveys made over 5 years.

in contrast, bed 25 is some distance from the mouth and is muddy.

Although the number of mussels settling in their first year is always much higher on bed 30 than on the muddier and more up-river bed 25, the large standard deviations show that huge annual variations in settlement occur. However, in both beds, the numbers of 2year olds is much more stable, although, again, density is higher on bed 30. In both beds, therefore, the change in numbers from the first to second year seems to be strongly density-related, particularly on bed 30 (Figure 66). The numbers then change very little, until the mussels are 5 or 6-years old. Thereafter, mussels disappear rapidly. There are, therefore, 2 main periods of disappearance. Most mussels disappear either in their first year or after they reach their sixth year, as a result either of movement or mortality. We now think that some movement of mussels does occur, because the increase in abundance of 2/4-year old mussels on bed 25 can only be due to immigration. This conclusion is surprising, because it had been previously thought that mussels were sedentary once the larvae had grown to 10-20 mm long, which they reach in their first year. Movement up-river may explain why the beds in the upper reaches contain relatively high densities of large mussels. The first-year animals may be eaten by crabs or, perhaps, squeezed out by the adults amongst which they settle and grow, and field experiments are planned to test these possibilities. The large decrease in numbers of older animals is probably caused mainly by mortality in both the summer and winter. Much of the winter mortality is caused by oystercatchers which eat only the larger and older mussels, probably taking sufficient numbers to account for most of the loss.

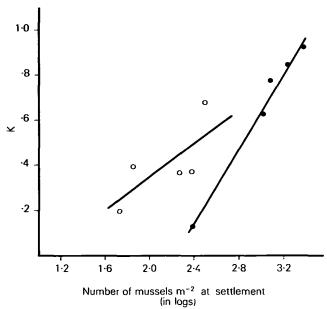


Figure 66 The disappearance of mussels on 2 beds during the first year (expressed as k-values) against their density at settlement (0, bed 25; •, bed 30).

Oystercatchers and mussels

The separate studies on oystercatchers and mussels will provide models of the behaviour and population dynamics of each species. These models can be combined to explore, by simulation, the consequences for each population of an increase or decrease in the abundance of the other.

In the case of the mussels, the relationship between mussel density and various environmental features occurs because settlement and subsequent mortality vary between beds. The intention is to establish the relationships between these variables and key parameters of the mussels' population dynamics on each bed, including, for example, rates of immigration and the slope and intercept of the density-related disappearance of one-year old animals. These relationships combined together will produce a model of the behaviour of the mussel population, describing its response to its own density and to external variables.

The model of oystercatcher predation on the older mussels is being constructed from the relationships established between (i) bird density over the mussel beds, total population size, environmental factors, mussel density and size, and (ii) the daily intake of mussels of each size by birds feeding on each mussel bed.

Because the birds spread out to less favoured beds as their numbers rise, and because only small mussels are available on such beds, the population as a whole obtains an increasing proportion of its food from small mussels as it gets larger. The birds' own mortality rate may increase, too, as more birds feed in the less preferred areas, but further studies are required to confirm this suggestion. This aspect is important because simulations with a model of the population dyna-

mics of the oystercatcher show that, if mortality of the young birds is density-dependent – and thus increases if bird numbers are increased or the mussel population is decreased, there is a surprisingly sharp reduction in the stable population size of the birds. Our findings also suggest that oystercatchers are responsible for an appreciable part of one of the 2 peaks in mussel mortality, and thus have a significant impact on the mussel population itself.

We would like to express our gratitude to the Dawlish Warren Nature Reserve Management Committee for permission to catch birds.

J D Goss-Custard, S McGrorty, C J Reading, and Sarah E A le V dit Durell

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LEPIDOPTERA ON SWEET CHESTNUT (CASTANEA SATIVA)

During 1980, as part of a study on the insect fauna of southern beech (*Nothofagus* spp.), we took some comparative samples from other members of the Fagaceae at sites in the Forest of Dean, Gloucestershire. One of the species selected was *Castanea sativa* (Welch 1981). It was immediately apparent that this species supported a fauna far greater than was expected from published records. Clearly, *Castanea* has been largely ignored by entomologists in Britain and, as a consequence, its fauna is under-recorded.

Ford (1949) listed 5 species of micro-Lepidoptera with *Castanea* as a food-plant. These were the only insect species which Southwood (1961) included when compiling his list of insects associated with British trees. Emmet (1976) increased this list to 9 species, including all Ford's species except a leaf-miner of the genus *Stigmella*.

Larval Lepidoptera were collected on 5 sampling dates, from late May until mid-September 1980, in Russell's Inclosure, where large mature *Castanea* are mixed with similar aged *Quercus petraea*. Larvae of 24 species, only one of which had been previously recorded in

Table 30. The most numerous Lepidoptera on Quercus petraea and Castanea sativa in the Forest of Dean in 1980

<i>Que</i> Larval number	rcus % of total larvae	Cast Larval number	anea % of total larvae
463 354 258 28 24 20 20	33·3 25·5 18·6 1·9 1·7 1·4 1·4 83·9	36 101 20 38 8 21 11 235	12·4 34·8 6·9 13·1 2·8 7·2 3·8 81·0
	Larval number 463 354 258 28 24 20 20	Larval total larvae 463 33·3 354 25·5 258 18·6 28 1·9 24 1·7 20 1·4 20 1·4 1167 83·9	% of Larval number % of total larvae number 463 33·3 36 354 25·5 101 258 18·6 20 28 1·9 38 24 1·7 8 20 1·4 21 20 1·4 11 1167 83·9 235

the above publications, were recorded by beating the foliage. Only 3 autumn-feeding species were not present in the May samples, which contained 82% of all larvae collected. The 7 species of Lepidoptera which accounted for over 80% of all larvae obtained from both trees are shown in Table 30. Although *Operophtera brumata* was the most abundant species on neighbouring oaks, *Agriopis aurantiaria* was by far the most common caterpillar on *Castanea* in the spring of 1980. Because of the proximity of the oaks, it is likely that some larvae, such as *Tortrix viridana*, may have dropped, or been blown, on to the *Castanea*. Larval numbers may also have been larger than expected following a peak in 1979, when there was widespread defoliation in the Forest of Dean.

During 1981, an extensive area of Castanea coppice was sampled at Challock, Kent, where, apart from some birch seedlings, it formed almost pure stands. In addition, 2 sites in Essex and 2 in the Forest of Dean were also sampled. At all sites, the Castanea had been coppiced. Of the 37 species collected by beating the foliage (Plate 13), only 18 had occurred in the 1980 samples. An additional 4 species of leaf-mining larvae were collected by hand at the 2 Essex sites in mid-September, 3 of which are in the lists of Ford and Emmet (supra cit.). Although the first samples were collected in Kent and Essex on 20/21 May, numbers of lepidopterous larvae were very low, with 56% of the species represented by a total of less than 5 larvae in all samples. The most numerous species were Alsophila aescularia and Campaea margaritata. No Tortrix viridana were found. It is possible that the peak of springfeeding species was missed at most sites sampled in 1981. Alternatively, young coppiced Castanea may support fewer larvae than mature trees, or the numbers recorded during 1981 may reflect a truer picture of the Castanea fauna for the majority of years between peaks of severe defoliation.

In 1982, one additional species was recorded on *Castanea* at Westonbirt Arboretum, Gloucestershire. Together with the records of 3 species provided by other

entomologists, this makes a total of 58 species of Lepidoptera known to occur on *Castanea sativa* in southern Britain, and includes 17 species of micro-Lepidoptera, of which 6 are leaf-miners and 3 feed in the developing chestnut fruits. *Castanea* has thus been shown to have acquired a substantial lepidopterous fauna since its introduction into Britain in Roman times. This observation must throw considerable doubt upon the state of our knowledge of the insect fauna of other introduced trees in Britain.

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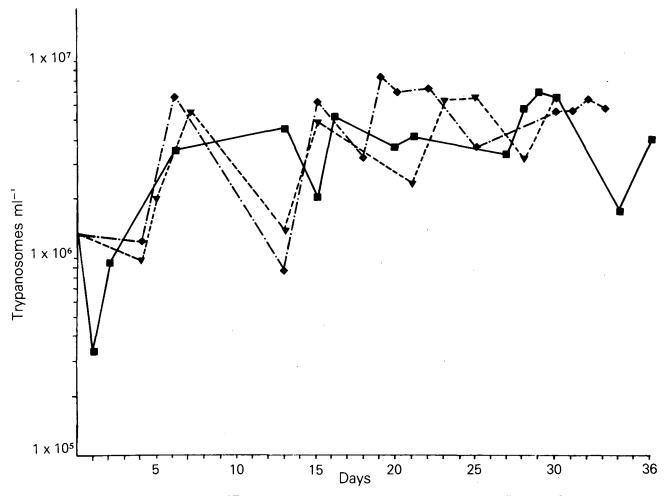
ALTERNATIVE CULTURE MEDIA FOR TRYPANOSOMES

Most species of *Trypanosoma*, apart from members of the sub-genus *Trypanozoon*, are relatively easy to

cultivate *in vitro*, often in bi-phasic media, with a liquid overlay on a blood-agar base. These media can be used only in rather small volumes, and the medium is usually contaminated with mammalian blood cells; they are also unsuitable for despatch by mail. The available monophasic media are mostly very complex, and therefore laborious and difficult to produce (Evans 1978).

The acquisition of some strains of trypanosomatids by CCAP led to the need for a simple monophasic medium which could easily be mailed and was adequate for growth of relatively large amounts of material, uncontaminated by blood cells, for use in characterization procedures (ITE Project 723). Possible alternative monophasic media were therefore investigated, using as test organism strain no CCAP 1981/13, a stock of *Trypanosoma dionisii* isolated from *Pipistrellus pipistrellus*.

Twenty-two varieties of monophasic media were tested, most of them modifications of medium L4N (Evans 1978). Adequate growth was obtained at 28°C in a version containing 2.5% of nutrient broth no 2 (Oxoid CM67), 5% foetal bovine serum, and 10% rabbit, horse or sheep erythrocyte lysate. However, the last-named ingredient is difficult to prepare and sterilize. Equally good growth was obtained in a medium consisting of 77% v/v Grace's Insect Tissue Culture



Medium with glutamine (Flow Laboratories, 27-000-49) and 23% v/v foetal bovine serum (Flow Laboratories, batch 2950078, inactivated at 56°C for 30 min) (see Figure 67). The simplicity of preparing this last medium makes it an attractive alternative. Grace's medium has been used to cultivate *Leishmania*, *T. cruzi* and other trypanosomatids (Childs *et al.* 1978; Hendricks *et al.* 1978; Sullivan 1982), and its suitability for other strains of trypanosomatids in CCAP's collection is being tested, using 30% v/v foetal bovine serum (which gives better growth than 23%).

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Cycling of nutrients

SOME FACTORS CONTROLLING GEOCHEMICAL CYCLING IN AN UPLAND GRASSLAND

To understand how an ecosystem functions, it is necessary to have knowledge of chemical inputs and outputs. Information of this kind is being sought in relation to geochemical cycling in the upland grasslands of mid-Wales, where particular attention is being paid to transfers within soils and between soils and fresh waters in order to predict the impact of modified management procedures. The study is based on several small stream catchments within the Plynlimon experimental catchment at the headwaters of the river Wye, with events in one unimproved catchment on Silurian mudstone (Table 31) being used, in due course, as a basis for judging the effects of artificial fertilizers and/or reseeding on other catchments overlying similar bedrock. So far, attention has centred on the factors influencing the inputs and outputs of elements in the control catchment, with a wide range of solutes (Reynolds 1981; Stevens 1981a, b) being analysed in weekly collections of incoming bulk precipitation, soil water and stream water.

Inputs

Chemistry of incoming bulk precipitation

Rain falling on the catchment is acid (mean pH 4-47); its conductivity is usually within the range 25-30 μ s, while concentrations of solutes are small (Table 32).

Table 31. Summary details of the catchment at Plynlimon, mid-Wales, being used as the 'control' in a study of geochemical cycling

Location	Afon Cyff (Grid Reference SN 819 841)
Altitude	435m (1427 ft)
Aspect	North-north west
Catchment area	6·486 ha (≈0·065 km²)
Distance from west coast	≈24 km
Solid geology	Silurian mudstone
Major soil type	Iron-pan stagnopodzol
Land use	Unimproved rough grazing

The chemical data are extremely variable, the variations being thought to reflect real differences in time.

Seasonal variations in chemistry

Concentrations of the elements largely derived from the sea (Na, Mg, Cl) reach peak concentrations in late autumn and early winter, and are minimal in spring. In contrast, calcium concentrations are maximal in spring, although high concentrations of calcium, sulphate, inorganic nitrogen and hydrogen ions are detected after dry periods and in samples from snowmelt. During periods of high rainfall, concentrations of nitrogen and hydrogen ions tend to be low.

Dry versus wet deposition

From a simple graphical model (Pearson & Fisher 1971; Cryer 1978), it seems that most of the calcium, sulphate, organic carbon, nitrogen and hydrogen ions entering the experimental catchment reach it by dry deposition. The model estimates that 85% of the 'airborne' nitrogen enters by dry deposition, probably explaining why the nitrogen load was independent of amounts of rain. The amounts of sulphate-S entering by dry deposition are estimated to be 7·3 kg ha⁻¹ yr⁻¹

Table 32. Mean concentrations, mg I⁻¹, of different solutes in rain (bulk precipitation), soil solutions and stream water in the experimental 'control' (unimproved grazing) catchment in Plynlimon, mid-Wales

	Soil solutions in the different Bulk horizons of the soil profile											
Solute	precipitation	0	Ea	Bs	С	water						
Na K	1·58 0·08	2·56 0·37	2·59 0·11	2·99 0·09	2·47 0·07	3·04 0·14						
Ca	0.18	0.37	0.40	0.03	0.37	1.01						
Mg Fe	0·21 <0·01	0·46 0·06	0·44 0·03	0·39 0·02	0·40 <0·01	0·70 <0·01						
Al	<0.01	0.09	0.16	0.25	0.26	<0.01						
Si No3-N†	<0.01 0.16	0·31 0·05	0·63 0·08	0·66 0·07	0·43 0·10	0·74 0·11						
SO ₄ -S	0.84	1.21	1.25	1.27	1.39	1.50						
CI HCO ₃ Total	3.01	4·86 0·0	5·08 0·0	5·52 0·0	4·95 35·09*	5·37 45·70*						
organic content	0.69	9.74	3.18	3.18	0.91	2-62						
рΗ	4.47	4.03	4.39	4.49	4.73	5.00						

[†] NO₃ = total inorganic nitrogen

^{*} quantities in microequivalents I⁻¹

or about 30% of the total sulphate-S input of 21·3 kg ha⁻¹ yr⁻¹, a proportion similar to that reported in Norway (Christophersen & Wright 1981) and eastern USA (Lindberg & Harris 1981). The dry deposition of sulphate seems to occur mainly during periods with light winds or still air. Dry deposition of chloride and associated ions (Na and Mg), however, is predominantly by impaction in windy conditions, when eddies created around the collectors reduced their efficiency in capturing salt particles (Reid *et al.* 1981). This reduced sampling efficiency leads to an underestimate of the dry inputs of sodium, chloride and magnesium by the model.

Origin of incoming ions

The influence of 'marine' and 'terrestrial' sources-on the chemistry of rain (precipitation) have been assessed by:

- i. comparing the ionic ratios of different solutes in sea water with those in precipitation;
- ii. comparing the percentage compositions of rainfall and sea water (Figure 68); and
- iii. analysing the effects of wind direction and speed on the composition of rain.

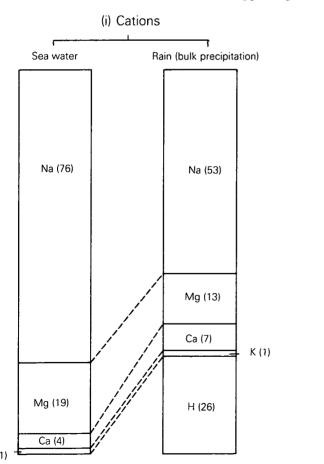
Ratios of sodium to either magnesium or chloride in rain are similar to those in sea water, suggesting a

marine origin. During south-westerly autumnal storms, the Na:Cl and Na:Mg ratios were almost identical with the theoretical ratios for sea water. In contrast, the ratios of calcium, sulphate, and, to a lesser extent, potassium in rain differ from those in sea water, probably indicating a non-marine origin.

The proportions of calcium, nitrogen and sulphate in rain were larger than in sea water — further evidence of non-marine sources. This deduction is supported by analyses of the influences of wind speed and direction. Large concentrations of nitrogen, sulphate, calcium and hydrogen ions are associated with light to moderate easterly winds from central England, whereas the larger loads of sodium, magnesium and chloride are correlated with moderate to strong westerly and southwesterly winds from the Irish Sea. In summary, the strongly terrestrial solutes seem to arrive during quiet, anticyclonic conditions, mainly in spring, whereas the maritime elements are associated with moderate to strong westerly winds, the largest loads being carried in autumn storms.

Chemistry of soil solution

Soil solutions in the 'control' catchment are weak and acidic (Table 32), and show the influence of incoming bulk precipitation and of soil processes. The predominance of sodium and chloride reflects the chemistry of rain (precipitation), the larger concentrations in soil solutions compared with those in bulk precipitation



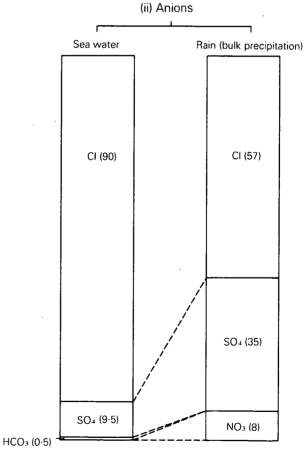


Figure 68 The proportions of different (i) cations and (ii) anions found in sea water and rain in the 'control' (unimproved grazing) catchment in Plynlimon, mid-Wales.

probably being mainly attributable to the solution of salt particles which had accumulated on vegetation by dry deposition. Concentrations of organic carbon and potassium were also larger in soil solution than in bulk precipitation, but the differences in these instances are related to their release from decomposing materials. Whereas appreciable amounts of sulphate, magnesium and calcium in solution were probably derived from both atmospheric and soil sources, those of silica, aluminium and iron seem to be derived more or less completely from soils.

Differences between soil horizons (vertical variation) Concentrations of sodium, calcium, magnesium, chloride and sulphate were fairly constant, but those of potassium and organic carbon decreased sharply beneath the uppermost O horizon. The further sharp decrease in organic carbon from the Bs to the C horizons probably reflects its adsorption in the Bs horizon. Aluminium and silica, while being virtually absent from rain, reached detectable concentrations in soil solutions beneath the organic-rich O horizon, suggesting their origins in mineral weathering. As might be expected in a podzol, the concentrations of iron, while always small, decreased in, and below, the Bs horizon.

Seasonal differences in the chemistry of soil solutions Changes are most noticeable in the surface horizons. the amplitude of the differences at greater depths being markedly smaller. Concentrations of potassium, inorganic nitrogen and dissolved organic carbon were more responsive to seasonal influences than those of other substances. Concentrations of potassium and nitrate were maximal in late autumn/winter and minimal in summer, suggesting a negative correlation with soil temperatures. On the other hand, concentrations of dissolved organic carbon were maximal in summer, suggesting a positive correlation with soil temperatures linked with changes in the rates of litter decomposition. Changes in the concentrations of other substances tended to be transitory, related to short term changes in soil moisture and/or specific events. For instance, concentrations of sodium and chloride tended to be higher during storms, reflecting maritime influences, and during dry periods, due to concentration effects. Sulphate concentrations tended to be maximal immediately after dry periods, probably as a result of either the removal of material previously accumulated on vegetation by dry deposition or a flush of material produced in the organic horizons. Calcium and magnesium concentrations were largest during and immediately after dry periods, whereas those of silica and aluminium, although variable, had no identifiable pattern of variation in time.

Overall, the ionic balances are dominated by sodium and chloride. After balancing the charge attributable to sodium, there is an excess of chloride which must be countered by other cations, most probably magnesium. The large concentration of hydrogen ion in the O horizon is probably linked to the production of organic

acids, with the apparent excess of cations in the O horizon being balanced by organic anions. The concentrations of anions and cations in the Ea and Bs horizons are more or less in balance, suggesting a limited role for organic anions in leaching from these horizons. At a greater depth, in the C horizon, bicarbonate ions are present and will be involved with the weathering and leaching of material from bedrock. Thus, the site in Plynlimon has features in common with podzols described from North America (Ugolini *et al.* 1977), where leaching was being controlled by organic anions in the upper soil and by bicarbonate ions in the C horizon. Sulphate, although important, does not seem to have assumed the dominant role it has in some 'acid rain' areas, eg north-eastern USA (Cronan 1980).

Stream water chemistry

Stream water in the control catchment has small concentrations of solutes, a mean conductivity of 34 µs, a mean ionic concentration of 0.5 meq l⁻¹ and an average pH of 5.00. Sodium and chloride, reflecting rainfall chemistry, are the most abundant ions, whereas the significant concentrations of silica and the increased amounts of calcium, potassium and dissolved organic carbon are the products of soil (and/or bedrock) water reactions (Table 32).

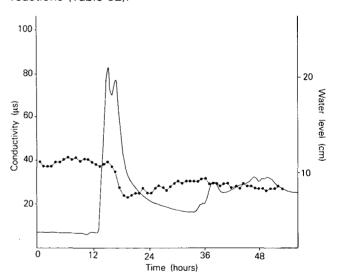


Figure 69 Variation of stream water conductivity with water level during a summer storm.

Seasonal changes

The array of ions can be separated on the basis of their seasonally changing concentrations. Thus, potassium, inorganic nitrogen, silica, bicarbonate and pH all display cyclic, seasonal patterns of variation. The changing concentrations of nitrogen and potassium in stream water parallel those found in soil solution, with minimal concentrations in summer and maximal concentrations in winter, and indications of periodic flushes associated with heavy rainfall. Silica concentrations decrease from March until June, as has been reported elsewhere, it being suggested that the decreases are indirectly related to the multiplication of diatoms (Casey *et al.* 1981; Edwards 1974). Because concentrations of silica in soil solution do not vary seasonally, it seems that

the changes in stream water silica must reflect events within the stream itself. Changes in pH and bicarbonate concentrations are closely related, both being maximal in spring and summer. To an extent, pH is probably decided by the proportion of water flowing from acid peats.

Concentrations of sodium and chloride reflect specific climatic events, with large concentrations corresponding to periods of heavy rainfall. Sulphate concentrations are also controlled by events, large concentrations in stream water parallelling large concentrations in soil solution after dry periods of weather. Calcium and magnesium have similar variations, their concentrations being inversely related to the volume of discharge. Concentrations of calcium and magnesium in streams, therefore, reflect the balance between deeply circulating soil/groundwater, on the one hand, and peat water with small Ca and Mg concentrations, on the other.

Concentration/discharge relationships

Significant correlations, accounting for a small part of the total variation, were detected between water chemistry and the volume of discharge. A 2-component mixing model (Johnson et al. 1969; Cryer 1980) has been used to explore the relationship between stream water chemistry and discharge. Water derived from a peat source and 'groundwater' were taken as the 2 components. The model gives a good prediction of base flow concentrations, but a poorer prediction of diluting water. Undoubtedly, more needs to be known about waters from other sources.

Storm effects

A few storm events have been monitored with (i) Northants automatic sampling equipment and (ii) a continuously monitoring conductivity probe. It has been found that the changes in conductivity conform to the pattern observed elsewhere, eg by Walling and Foster (1975) and Feller and Kimmins (1979), with a larger conductivity at a given discharge at the beginning of a storm event than at the end. Concentrations of sodium and chloride remained virtually unaltered through storms, while those of potassium and magnesium increased to peaks during the rising limb of the hydrograph. Concentrations of silica and sulphate were usually diluted, but the details varied greatly between storms.

Element budgets

lonic budgets indicate net gains of chloride, inorganic nitrogen, potassium and hydrogen, and net losses of other solutes. However, the losses or gains of sodium, chloride, potassium and sulphate are relatively small, 5% of the overall budget. The largest net losses from the catchment are silica, calcium and magnesium. Further experiments have shown that there is little calcium to be derived from pre-existing soils and bedrock, so it seems that the major part of the calcium 'loss' is probably derived from the solution of calcite veins within the bedrock. Silica and magnesium are released from chlorite by weathering. Aluminium and iron, relea-

sed during weathering, are mainly adsorbed in the lowest soil horizons or on the surfaces of stream sediments in response to changing pH.

The impact of land improvement

Data from soils and streams in areas where rough grazings have been given artificial fertilizers are now being analysed. However, it is already clear that the methods of land improvement and the types and amounts of artificial fertilizer are crucially important. Even when lime was the only soil amendment, concentrations of nitrogen and potassium in soil solution were increased. but only nitrogen passed into streams. Applying artificial fertilizers also increased amounts of dissolved organic carbon, presumably reflecting increased biological activity. Other changes are more difficult to explain. The increased concentrations of silica may be attributable to increased rates of mineral weathering, or they may reflect changes in acidity. Increased concentrations of sulphate may be attributable to the impurities in artificial fertilizers, to ions displaced from adsorption sites in soil, or may be produced as a result of increased biological activity. Increased concentrations of magnesium may be associated with fertilizer impurities, they may be due to increased weathering or biological activity, or they may be due to more effective leaching of soil by solutions with increased concentrations of anions. Before these exchanges can be explained and predicted, much more needs to be known about the many mechanisms controlling the pattern of geochemical cycling.

M Hornung, B Reynolds, S Hughes, P A Stevens and Aldyth A Hatton

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VARIATION IN FERTILITY OF UK SOILS

Many hundreds, if not thousands, of chemical analyses of soils are made every year. These analyses are mostly restricted to agricultural soils, with nutrient status being interpreted in terms of potential for a variety of agricultural crops. Because of the use of standardized analytical procedures, it is thus possible

to compare the status of different soil samples. To extend these assessments beyond soils suited to agricultural cropping, a study has been made of (i) fertility, using 3 test plants (*Agrostis tenuis, Trifolium repens* and *Betula pendula*), and (ii) chemical variability, of a wide range of British soils, including both lowland and upland types.

Eight soil types were investigated, ranging from acidic and basic brown earths to podzols and peats. Samples (0–20 cm) of each soil type were collected

Table 33. Mean dry weights (g) of 3 different test plants grown from August 1978-October 1979 in 13 replicate collections of each of 8 different soil types

	Test plants									
Soil types	Agrostis tenuis	Trifolium repens	Betula pendula							
Gley	23	26	1.8							
Brown earth										
(acid)	17	11	1.2							
Brown earth										
(basic)	16	19	1.3							
Brown podzol	13	3.6	0.7							
Peaty gley	9.4	2.4	1.1							
Podzol	7.0	3.1	0.9							
Peaty podzol	4.2	0.2	0.9							
Peat	4.1	0.2	0.3							

Dry weights include roots and tops.



Plate 14 Layout of pots in soil fertility study in Merlewood garden (Open Day, May 1979). (Photograph M R Smith)

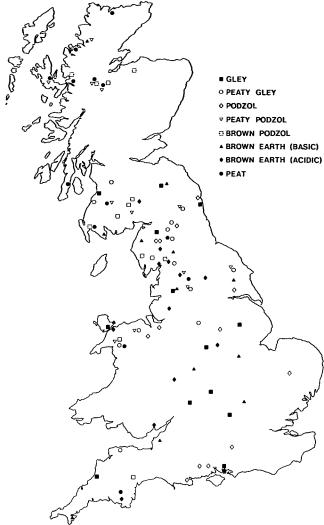


Figure 70 Sources of the 13 samples of each of 8 soil types found in the UK. The samples were used for analyses of soil fertility.

from 13 different locations spanning the length and breadth of the UK (Figure 70). After sieving the moist topsoil samples through a $\frac{3}{4}$ " mesh screen, 24 replicate pots were filled with each of the 104 (8×13) soils, and 2 pots of each soil placed per block in a 12-block layout (Plate 14). Four blocks of the 12 were each planted with *A. tenuis*, *T. repens* or *B. pendula*.

Irrespective of plant species, growth of 4 seedlings in each pot (6" diameter) was greatest in the gley soils, followed by the brown earths, with the podzols and peats being poorest (Table 33). These main effects were discernible despite the large differences in performance of the test plants in different soils of the same soil type. The degree of variation was particularly large in the upland soil types — peaty gleys, peaty podzols and peats — and least among the gleys and brown earths. These differences are being investigated in greater detail, with attempts being made to relate productivity to soil chemicals and profile data.

A F Harrison and M Hornung

INTERACTIONS BETWEEN SOILS, PLANTS AND DECOM-POSITION ACTIVITIES

Microbial characteristics of soils in relation to plant growth are being examined to improve the interpretation of biological soil tests in studies of effects of land management practices. A positive 1:1 relationship between radish (Raphanus sativus) growth and chitin (substrate) decomposition has already been reported over a range of 76 soils (Latter 1980). The relationship between plant growth and decomposition, using a similar range of substrates (chitin, hide powder, cellulose, wood veneer), is now being examined, using only 5 soils (peat, podzol, peaty gley and 2 brown earths), sometimes maintained at moisture contents, from 20% to more than 100% of field capacity, for a 6-month pre-treatment period. Estimates of plant growth and decomposition were made independently, using different replicate pots. Raphanus sativus was again used as a test plant, but Agrostis tenuis was used in the peat soil.

In general, there was a positive relationship between plant growth and rates of substrate decomposition, with growth being approximately 400% and decomposition 200% greater in the brown earths than in peat.

Rates of growth and decomposition were indirectly related to 'pre-treatment' soil moisture. Thus, growth and decomposition were fastest in the soils that had previously been kept driest. This result should perhaps be attributed to the effects of wetting after a period of drought. Pre-experimental storage at a moisture content in excess of field capacity markedly decreased plant growth and decomposition analogous to the effect of temporary flooding. These effects were greater in the brown earths than in the other soil types (Figure 71).

In a later experiment, the effects of plant growth on decomposition were tested using the brown earth and peaty gley soils. Substrate decomposition tended to be decreased by the presence of each of the 4 species of plant tested (*Trifolium repens, Taraxacum officinale, Plantago major* and *Agrostis tenuis*), the largest decrease being attributable to *A. tenuis* (Figure 72i).

This inhibition of decomposition by plants may be attributed to competition for nutrients. It has been suggested that this type of competition may be accentuated where trees are colonized by mycorrhizal fungi which receive carbon and energy from their hosts. Unexpectedly, when the effect of mycorrhizas on decomposition was tested in co-operation with Dr J Dighton, using seedlings of *Pinus contorta* and *Betula pendula* with and without inoculated mycorrhizal fungi, it was found that decomposition was usually accelerated in the presence of mycorrhizas (Figure 72ii).

Pamela M Latter

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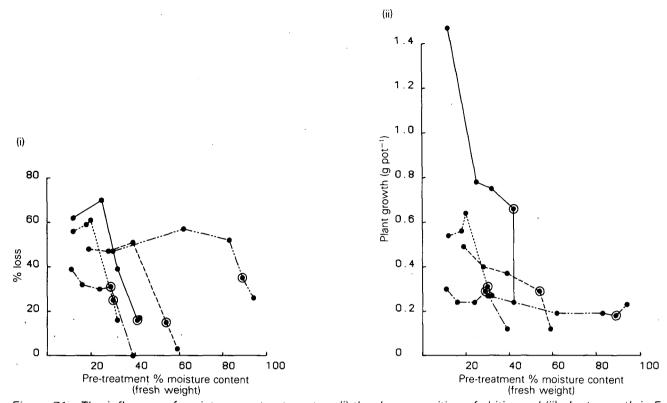


Figure 71 The influence of moisture pre-treatment on (i) the decomposition of chitin, and (ii) plant growth in 5 soils

—————, brown earths under pasture; • · · · · · · , brown earths under deciduous forest; • · · · · · · , peaty gley

under Picea sitchensis; ———, podzol under Calluna; ———, blanket peat.

(Open circles indicate the pre-treatment at field capacity).

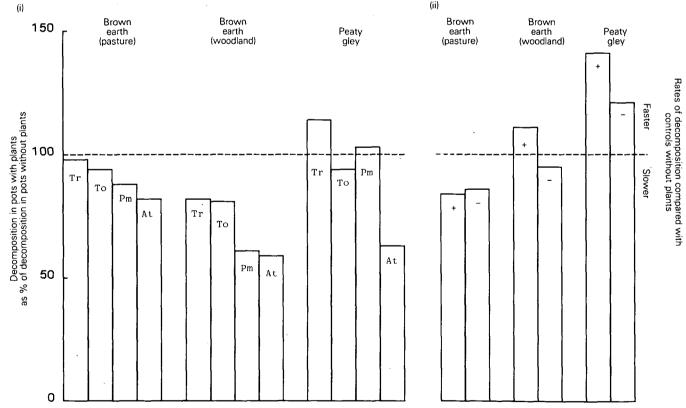


Figure 72 The influence of plants and mycorrhizas on substrate (wood veneer and chitin) decomposition in 3 soils

- i. weight loss of wood veneer after 10 months
- ii. weight loss of chitin after 40 days in the presence of seedlings of Pinus contorta with (+) and without (-) sheathing mycorrhizas
- Tp, Trifolium repens; To, Taraxacum officinale; Pm, Plantago major; At, Agrostis tenuis.

SOIL CHANGE THROUGH AFFORESTATION

The study of the effects of tree species on soils is of practical importance. It should be possible to anticipate changes likely to result from the establishment of trees on poor marginal land, and thus conserve and improve soil fertility by selecting the most suitable tree species. Past studies have generally involved measuring gross changes in chemical elements on a limited range of sites. Ovington (1953) compared soil conditions in plots, each planted with a different species, on 5 sites. In 1974, members of the Forestry Commission and ITE resampled his plots at Bedgebury, Kent (10 tree species on compact silty clay with imperfect drainage), Abbotswood, Gloucestershire (7 tree species on a fairly coarse sandy loam), and West Tofts, Norfolk (5 tree species on a sandy soil overlying chalky boulder clay). Only 2 tree species were common to all 3 sites; 5 species growing at Abbotswood also grew at Bedgebury. In analysing the data, complications have arisen because there is only one plot of each species at each site. There is thus no measure of within-site variation. Although Ovington sampled at 5 locations within each plot, there is no published indication of the within-plot variance which is needed to enable comparisons to be made of the effects of the different tree species on soil properties. It was therefore necessary to assume, somewhat unsatisfactorily, that Ovington's within-plot variances were the same as those in the 1974 sampling. There were other problems, ie the lack of a 'control' and the heterogeneity of variances between some plots. Where these problems could not be resolved by transforming the data, Fisher's randomization test was used.

With these reservations in mind, and after the application of a variety of analytical procedures, the Bedgebury pH data suggest that, in 1951, ie 20 years after planting a clear-felled site, the trees had not begun to exert their full effect. However, by 1974, effects were discernible. These were associated with:

- i. the quality and quantity of soil organic matter (LOI, pH, N, P) and changes in those properties brought about by physiological activities of soil organisms; and
- ii. elements of the soil exchange complex (extractable K, Ca, Mg, Na) which can be removed by leaching and can be replaced by weathering of soil minerals, or by minerals brought up from deeper layers by tree roots and deposited on the surface in litter fall.

Extractable Ca and Mg were lost from all the Bedgebury plots, the magnitude of the loss depending on the species; changes in the amounts of total N and P varied with species and soil depth. Bearing in mind the lack of experimental precision, it nonetheless seems possible to rank the effects of the different species during the period 1951 to 1974:

Pinus nigra > Quercus rubra, Pseudotsuga menziesii,

Nothofagus obliqua > Tsuga heterophylla, Chamaecyparis lawsoniana, Thuja plicata > Q. petraea > Larix eurolepis > Picea abies.

Because the changes occurring before 1951 may have been obscured by the effects of initial site clearance. it is natural to ask if the 1974 results suggest a stronger effect of tree species. Although Pinus nigra, unlike Q. petraea, is not a species normally associated with soils with large amounts of Ca, the P. nigra plot in 1974 had the largest Ca content between 5 and 45 cm depth. the largest Mg content between 15 and 45 cm, and the largest N content between 5 and 30 cm. However, the amounts in 1951 were even higher. At that time, the Ca content of the top 5 cm under P. nigra was more than twice that under the shelterbelt, and more than 50% greater than the next highest Ca content at that depth (under P. menziesii). These results suggest that the P. nigra plot initially had unusually large amounts of Ca and Mg, and that the changes in concentrations give a better reflection of the effects of P. nigra than absolute concentrations. The same can be said of soil properties in the neighbouring plots planted with P. nigra, P. menziesii, and N. obliqua. Clearly, spatial variation at Bedgebury is confounded with the effects, if any, of tree species.

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EARTHWORM PHOSPHATASES AND PHOSPHORUS MINERAL-IZATION IN PAPER MILL WASTE

One of the objectives of research on the use of earthworms in organic waste utilization is the production of stabilized residues as a plant growth medium. A large proportion of the phosphorus (P) present in the organic wastes used for vermiculture is present as organic complexes which are not available to plants. For example, of the P in cow manure, 50% is in organic form. The role of earthworms in P mobilization may thus be no less relevant to the disposal of organic wastes than to the management of agricultural soils.

Research on earthworms which occupy mineral soils has established that wormcasts are richer in inorganic P compounds extractable in water than an equivalent soil which has not been ingested. In part at least, this difference arises from the activity in wormcasts of the enzyme phosphatase which releases inorganic P from organically-bound P. Phosphatases have been reported from various earthworm tissues, including parts of the intestine. They are generally thought to influence the transport of macromolecules. The origin of phosphatases in wormcasts is not well understood — they may be secreted by worms or by microbes in the guts and casts of worms — but,

whatever the answer, nothing is known of the phosphatases in the species of earthworms used in vermiculture.

Cultures of 4 earthworm species were established to study these questions, 3 mainly organic matter feeders (*Eisenia fetida, Dendrobaena veneta* and *Lumbricus rubellus*) and one soil-dwelling species (*Allolobophora caliginosa*). Sterilized paper mill waste — a sludge of water, cellulose, silt and clay — was used as the culture medium, and phytin (calcium inositol hexaphosphate) — the main organic P constituent of plant litter — was added as a source of phosphorus. Eighty specimens of each type of worm were cultured in the medium at 20°C for 24 days, after which the worms were removed. The worm-worked culture

residues were then treated with disodium phenyl phosphate which, when dissociated by phosphatase activity, liberates phenol that can be measured colorimetrically.

More phosphatase was produced in cultures with worms than in the control cultures without worms (Figure 73). Fungal conidia developed on the surface of the control cultures which had a peak of phosphatase activity at pH 3·2 after 3-4 weeks. The phosphatase activity in the worm cultures had 2 peaks, one at pH 3-5 and the other at pH 9-10, the first peak showing the effect of worms in stimulating the production of microbial phosphatase, and the second peak suggesting an addition of alkaline phosphatase secreted by the worms themselves.

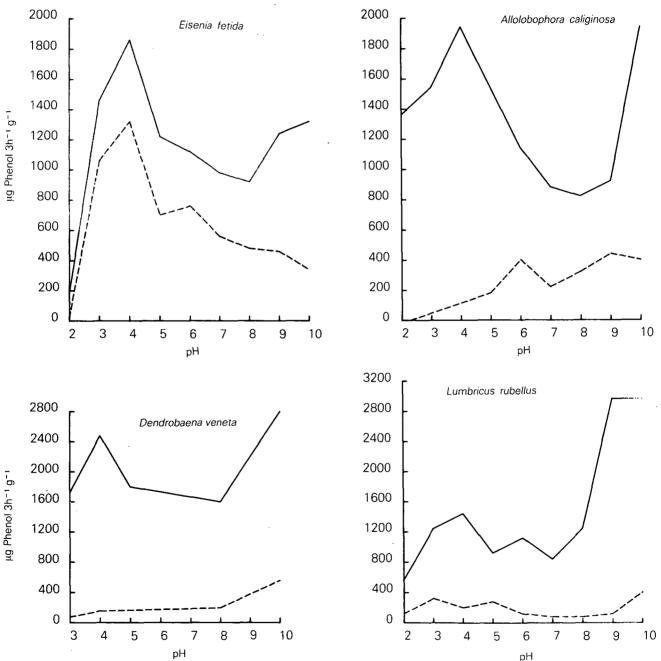


Figure 73 The release of phenol at different pH after incubating paper waste sludge (with added phytin) either with (-----) or without (------) earthworms, 4 species being tested. The amounts of phenol are directly related to phosphatase activity.

Table 34. Effects of earthworm feeding on the composition of amended sterilized paper mill waste*

Assessments	Medium	Medium i	Dendrobaena veneta		
made after	without	Eisenia			
incubation	earthworms	fetida			
Loss on ignition (%) Mineral content (%) Water-soluble P (µg g ⁻¹ dw)	53 47	45 (-15%) 55 (+17%) 19 (+71%)	42 (-21%) 58 (+23%) 23 (+110%)		

* The differences between analyses of media incubated with and without earthworms are expressed as percentages (in brackets) of the changes that occurred during incubation in the medium without earthworms.

The effect of earthworms on the mineralization of the phosphorus, in the culture medium, was studied using 2 species, *E. fetida* and *D. veneta*. Whereas the worms increased the decomposition of organic matter by 20%, amounts of water-soluble P were approximately doubled (Table 34). As this is the fraction which would be available to plant roots, the results suggest that phosphorus mineralization in organic wastes, otherwise low in phosphatase, could be increased substantially by composting with earthworms.

J E Satchell and Kyla Martin

Land classification and land use

NATIONAL LAND CHARACTERISTIC DATA BANK

The study of 'factors determining the structure, composition and processes of land and freshwater systems' and the development of a 'basis for predicting and modelling environmental trends' are among the aims of the Institute. Undoubtedly, the achievement of these objectives would be aided by the ready availability of a data set including the main land, and land use, characteristics of Britain at a broad, strategic scale, enabling analysis and interpretations to be made nationally and regionally.

Although a great deal of information was available from many primary map and statistical sources, it was decided, in the absence of a readily interrogated and analysed collection of data, to create an integrated data set, containing quantitative land and land use characteristics for each of the 2858 squares (each 10 km×10 km) of the Ordnance Survey National Grid into which the land of Great Britain is apportioned. Attributes relevant to (i) physiography (land form), (ii) climate, (iii) geology, (iv) soils, (v) topography (settlement, communication and population), (vi) land use, (vii) agricultural land classification, and (viii) conservation status were recorded, with a maximum of 128 attributes per grid square (Ball et al. 1983).

The data set, to be described in detail elsewhere, provides an information base-line that eliminates the need to make an *ad hoc* search of a wide range of sources for each study in which the broad picture of land characteristics would be helpful. The breadth of the data set ensures that a very wide range of environmental variables is explored. By its comprehensiveness, the data set obviates the restriction enforced by the limitations of an individual's own knowledge. Now that the data have been edited carefully and stored on computer files, it is possible, with the available range of standard output programs, to:

- i. provide quantitative land characteristics for each of the individual 10km×10km squares, and also totals and averages for administrative and other groupings of squares (see Table 35); and
- ii. map and list grid squares which meet particular specifications of individual or combined land and land use characteristics. This option permits the selection of areas of similar or contrasting character by means of a comprehensive search, in order to design a study programme, or to extrapolate the results of observation, experiment, or modelling studies to their most probable areas of applicability (see Figures 74 and 75).

This data set is suited for resource assessments and evaluations at a scale of 10 km×10 km or larger. It can also provide a framework with which to compare different scales of study, such as the ecological survey of Great Britain based on 1 km×1 km samples (Bunce et al. 1981), and local land type classifications such as that based on 0.5 km×0.5 km samples used to relate the land character of a series of upland areas in England and Wales to their moorland and grassland vegetation (Ball 1981; Ball et al. 1981a, b).

The measurement methods used (primarily point-count area measurements) were chosen to balance accuracy against time and effort, in relation to the quality and scale of the appropriate map and statistic sources. More flexibility in data interrogation and retrieval could be obtained by using digitized data collection to give vector data, rather than the cell-based raster data provided by the methods used. However, the cost of creating and sustaining a digitized data store for the area and number of attributes involved would be orders of magnitude greater than was involved in setting up the present cell-based data set, and the general quality of source data at this scale is hardly adequate to justify such a more sophisticated approach. The early availability of the present data set, in spite of its recognized limitations, has decided advantages over the potential availability of a more flexible and comprehensive system at some indeterminate future time.

For the future, and using different methods of classification and correlation, it is intended, for example, to provide a simpler background for the interpretation and



Figure 74 A print-out using the national land characteristic data set, showing 10 km×10 km grid squares having mean annual rainfalls of less than 800 mm per annum (1941-1970 data, Meteorological Office)

- *, squares that meet this specification
- o, squares which do not meet the specification
- -, squares for which data are not available

Statistic summaries for the distributions of Figures 74 and 75 show that

- 1 797 grid squares meet the rainfall specification These cover 67 952 km² (29% of the land in Great Britain) and include 78% of all land in this rainfall range
- 11 760 grid squares meet the crop specification These cover 69 628 km² (30% of the land in GB), of which 37% was under wheat and barley in 1970, this being 76% of the total extent of these crops then

From a similar map and summary for squares meeting both these rainfall and crop specifications, 582 grid squares are identified (23% of the land in GB) Thus,

Figure 75 A print-out using the national land characteristic data set, showing 10 km x 10 km grid squares having more than 20% of their agricultural land under wheat or barley (1972 data, Ministry of Agriculture, Fisheries and Food)

- *, squares that meet this specification
- o, squares which do not meet the specification
- -, squares for which data are not available

for these arbitrarily chosen levels of associated land and land use characteristics, 73% of the low rainfall specification squares support substantial wheat and barley crops, while, conversely, 77% of the squares with high wheat and barley crops fall in the low rainfall category as specified. These 582 squares contained 61% of the total wheat and barley crops in 1970, and 80% of that present in the main wheat and barley areas.

Such relationships can be quantitatively explored by statistical analyses but maps and summaries quickly display distributions and associations useful to research planning assessments and to the display and interpretation of resource information

Table 35. Statistics from the national land characteristic data set for groups of 10 km² in England containing National Parks (NP) and Areas of Outstanding Natural Beauty (AONB)

				Physic	ography			Clir	mate		Geo	logy	Agricultural use			
	Percentage of 10×10km Number of squares in 10×10km NP or squares AONB	each gi	ge of tot id square altitude m		Average height range (m) per 10×10km square	each gi	ge of tota rid square annual ranges mm pa		Mean daily temperature (°C) July-September	As % of area of grid s	f each	land	of agrico d in each quare gro	grid	Agricul- tural land classes 1-3 As % of total area of each	
		NP or	<122	122- 427	>427	Averaç per 10	<1000	1000- 1200	>1200	Mean July-Se	Glacial drift cover	Peat cover	than prov	lm- proved grass	Rough grazing	grid square group
Northumberland NP	10	47	13	81	6	33 1	65	29	6	12.3	52	11	8	28	64	16_
North York Moors NP	27	54	44	56	(<1)	25 1	96	4	0	13.4	33	4	38	50	12	49
Peak District NP	26	55	7	82	11	339	41	34	25	13.5	12	12	4	68	28	12
Lincolnshire Wolds AONB	13	43	92	8	0	110	100	0	0	14.8	. 49	(<1)	73	26	(<1)	94
Cotswolds AONB	30	51	54	46	0	179	100	0	0	15.0	7	0	44	53	3	80

Statistics in Table 35 are for groups of 10 km grid squares totally enclosing National Parks or AONBs, rather than for the actual administrative areas. The areas of the Northumberland and Peak District NP have similar altitude distributions and average height ranges, but the former has a greater extent of lower rainfall land, lower summer temperatures, and more glacial drift cover. There is more rough grazing and smaller amounts of improved grassland in the Northumberland than in the North Yorks NP areas. The North York Moors NP area has more lower altitude ground than the Northumberland NP area, a greater extent of the lower rainfall zone, and, partly as a consequence, a relatively substantial area of arable agriculture. Looking at the figures for the AONB areas, the Cotswolds AONB has more moderate altitude land than the Lincolnshire Wolds and a greater average height range per grid square. The Lincolnshire Wolds area has a larger glacial drift cover, and it differs from the Cotswolds in having a much larger proportion of its agricultural land devoted to arable cultivation.

presentation of the land resources in Britain, both their quantity and geographical distribution. It is also intended to interrelate the physical land characteristics held in this data set with the records of plant and animal distributions held by the Biological Records Centre at Monks Wood, also at the 10 km×10 km scale. Data will be improved as opportunity offers, and additional material can be added to the data set. Study of the relationships between map-derived data and 'classes', and remote-sensed imagery will help to improve our understanding of the relative advantages of these methods. Finally, the data will be used to provide information and assessments in response to requests from interested agencies.

D F Ball

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THE LAND POTENTIALLY AVAILABLE FOR WOOD ENERGY PRODUCTION IN GREAT BRITAIN

(This work was largely supported by Department of Energy (ETSU) funds)

To estimate the area of Great Britain which could be changed to the production of wood for energy, subject to technical, economic and institutional constraints, the Energy Technology Support Unit assembled a team with a range of disciplines, including representatives of the Forestry Commission, Aberdeen University (forestry), the Centre for Agricultural Strategy (agriculture), Dartington Amenity Research Trust (social and institutional constraints) and ITE.

To help structure the analysis, members of ITE took responsibility for the methods to be used, the supply of basic land use data for Great Britain, the co-ordination of all input data, and the construction and operation of an analytical computer model. Essentially, the study was based on land use maps and environmental data for 256 stratified 1 km×1 km squares representing the major land use types in Great Britain. There were 2 aims: (i) to define the economic value of existing and alternative land uses, and (ii) to assess the areas of land which would be 'available', given various economic, legal, conservation, hydrological and planning constraints. Four forestry systems have been considered:

- i. conventional forestry;
- ii. modified conventional forestry (where forest residues and thinnings go to an energy market);

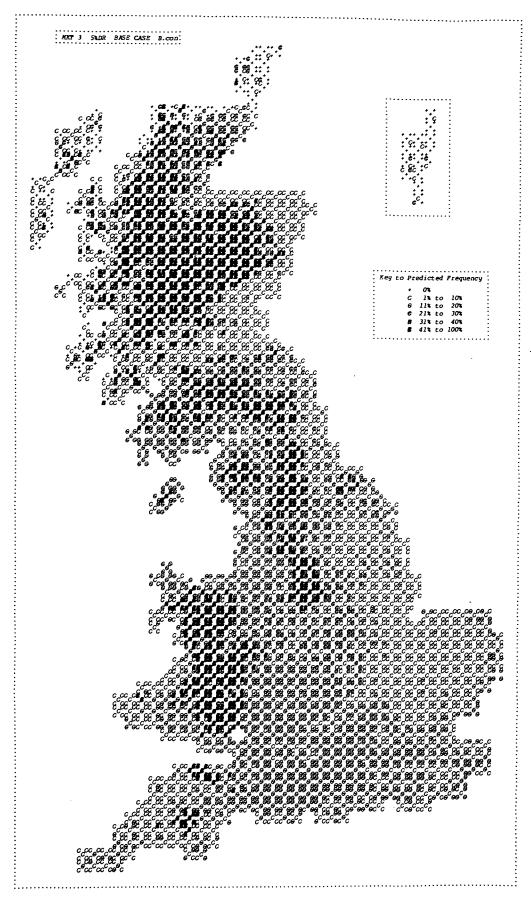


Plate 15 Map showing the predicted distribution of land which would change to forestry for wood energy production before social and institutional constraints are applied (estimates based on the exploratory scenario). The distribution picks out the uplands, but other scenarios emphasize different patterns. (Photograph P G Ainsworth)

iii. single stem energy plantations;

iv. coppice energy plantations.

Within each of the sample squares, separate areas of land (polygons) were defined by either a land use or forest boundary, and their areas were computed by the NERC Experimental Cartography Unit at Swindon. Together with agricultural, forestry and constraint data, these areas formed a data base suitable for computer analysis. Using a 'sieving technique', land not available for conversion to forestry was successively removed from the total (Bunce et al. 1981). In the first instance, 'land' which was technically unavailable — such as 'water', urban land, roads, existing woodland and environmentally unsuitable land — was removed. The economic value of the most profitable forestry option was then compared with the agricultural value for each polygon. Where the agricultural option proved to be the most profitable, the relevant areas were deleted, leaving land that was technically and economically available for a change to energy forestry. Finally, it was necessary to remove land which was subject to social or institutional constraints. The 'surviving' areas in the sample squares were then combined with the known areas of their respective land classes to provide estimates of convertible land. At the same time, it was possible to identify the types of agricultural land which would be converted, and the successful forestry enterprises, and also to estimate the weights of wood, and volumes of timber, that could be produced. Advantageously, this approach enables the effects of different underlying assumptions to be explored, while the sensitivity of the results to different (i) discount rates, (ii) types of energy market, (iii) national energy scenarios and (iv) valuations of timber and agricultural produce can also be investigated.

It has been estimated that up to 35% of Great Britain is technically and economically suitable for wood energy production, in the absence of any institutional constraints. This proportion only drops to 18% when such constraints are applied. If, however, a 5% discount rate, pipeline gas, energy market, constant timber prices and increasing energy prices — the 'exploratory case' — were imposed, the analysis suggests that 20% (4.6 M ha) of Great Britain would have a superior financial performance under forestry (Plate 15), a proportion that decreases to 8% (1.9 M ha) when all social and institutional constraints are applied (Figure 76). Forestry would not compete successfully with tilled crops, but 13% of high grade pasture, 43% of intermediate pasture, and 60% of rough grazing would have been changed to forestry prior to the application of constraints. Interestingly, 97% of all partially improved rough grazing would be converted to forestry. The 4.6 M ha of land which might change to forestry could, it is estimated, produce (i) 38M dry tonnes of wood for energy and (ii) 28 M m³ of timber for conventional purposes. After decreasing the area to 1.9 M ha by applying constraints, timber yields would drop to 10-8 M m³ (the current GB sustained yield is 14-3 M m³), with 16 M dt of wood being available for conversion to 4 M tonnes of gas (10-15% of our current consumption). Where it was lost to forestry, the better agricultural land would be converted to energy plantations, whereas the poorer land would be transferred to modified conventional forestry. Ordinary conventional forestry was never a preferred forestry option. Most of

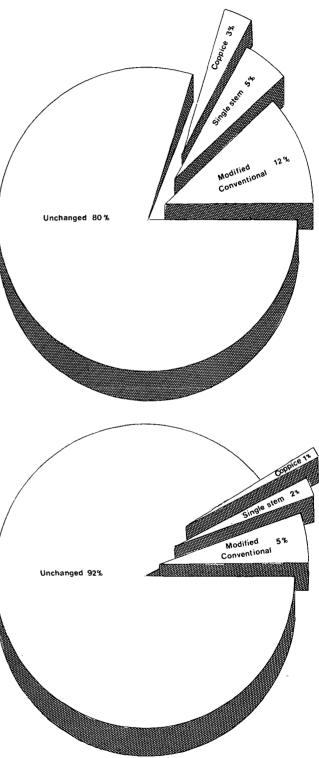


Figure 76 The percentage of Great Britain which would change to forestry for wood energy production (i) before, and (ii) after social and institutional constraints are applied (estimates based on the exploratory scenario).

the land identified in the 'exploratory case' as convertible was located in upland areas. After interpretation of the results and a sensitivity analysis, it seems that the use of thinnings and forest residues for energy from a modified form of conventional forestry is a plausible option in the agriculturally more extensive and less productive uplands, while pure energy plantations have a role to play in the lowlands (Mitchell *et al.* 1983).

C J Barr and R G H Bunce

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Chemical and technical sciences

PROGRESS REPORTS OF THE SERVICE SECTIONS

In the reorganization of research management, most of the Institute's specialist services, apart from those concerned with data processing, were included in one of the new programmes, namely Chemical and Technical Sciences. The component sections in this programme are: Analytical chemistry, Merlewood (J D Roberts) and Monks Wood (P Freestone); Radiochemistry (J A Parkinson); Engineering (G H Owen); Plant culture (R H Ottley); and Photography (P G Ainsworth). The names given in brackets are those of the section leaders.

Analytical chemistry

The demand for analytical support provided by the Merlewood and Monks Wood laboratories has remained as high as ever throughout the year, although the nature of the samples examined and chemical analyses carried out at each centre were quite different. At Merlewood, roughly equal numbers of soil, vegetation and water samples were analysed, with the emphasis on chemical nutrient elements and organic structural compounds, although some atmospheric pollutant elements were also determined. The samples came from research staff at all the stations. The Monks Wood section was mostly concerned with the analysis of animal tissue and waters for organochlorine pesticide residues and heavy metals. Most of this work originated from research being carried out at Monks Wood.

For the Merlewood laboratory, probably the biggest problems arose from having to process quickly water samples which came in weekly. Most of these came from the clear-felling study sites at Beddgelert and Kershope (ITE Project 625), with the geochemical cy-

cling study of Plynlimon (ITE Project 594) and various regular collections from other sites adding to the load. Particular care had to be taken over preservation techniques, and some analyses, notably phosphate and nitrate, had to be carried out immediately. About 4000 water samples were analysed during the year, and the phasing of these in with other laboratory work resulted in occasional difficulties. An additional problem was encountered in the spring and summer, when lysimeter solutions were found to contain organic substances which interfered with the Griess-reduction method used in automated colorimetry. This aspect is described later in the research and development section.

In addition to the waters, about 3500 soil and 4000 vegetation samples were processed in the Merlewood laboratory in 1982. Unlike the waters, which originated from only 5 projects, the soils and plant materials came from over 60 separate research projects. Most of these analyses were of a routine nature, especially those for the chemical nutrient elements, and they were processed on the automated lines (Plate 16). After extraction or digestion, all samples are transferred to the instrument feed modules. The instrumental stages are automatic and the output signals, together with those from the analytical balances, are fed through to the laboratory computer which is programmed to produce the final output sheets.



Plate 16 Transferring samples into the automated analysers in the analytical chemistry section at Merlewood.

(Photograph M R Smith)

As in previous years, the routine work at Merlewood was mixed with a variety of special analyses and investigations, eg tests on conifer shoots for starch and other carbohydrate fractions, on coal tip waste for toxic metals, on butterflies for minor elements, and on bryophytes for cellulose and lignin fractions. The work on atmospheric pollutants included tests for sulphur and fluorine in vegetation and in some animal tissue samples.

The emphasis in the Monks Wood chemical laboratory in 1982, as in the previous year, was on the analysis of

bird tissue and egg samples. Most of the birds were predatory species or sea birds, and the egg tests were carried out in support of the Nature Conservancy Council annual pollutant monitoring study (ITE Project 181). Apart from the birds, about 700 mussel samples were examined and also a few soils and plant samples. Altogether, about 5000 samples were tested for almost 16 000 chemical characteristics. In numbers, the heavy metal determinations, especially those for lead, cadmium and mercury, were the most numerous, but at least one third of the laboratory time was spent carrying out the relatively slow organochlorine determinations.

No major introductions of new instrumental sytems were possible, either in the Merlewood or Monks Wood chemical laboratories in 1982. However, at both centres, it was possible to replace thermal atomizer equipment which had become increasingly unreliable. Because of the shortage of funds for replacements, there was a need for frequent repairs to maintain equipment. The assistance of the station engineers was invaluable in this respect.

Radiochemistry

Although this section is classed as a service unit, its principal function is to provide analytical support for the research on radionuclides in the terrestrial environment (ITE Project 553).

The methods developed during 1980 and 1981 for the analysis of α -emitting plutonium and americium isotopes are now in routine use. However, some development work is still carried out in the search for improvements in recovery and precision, and for ways of shortening what are very laborious procedures. Some difficulties have been experienced in the analysis of certain soils for americium-241. Incomplete chemical separation of the americium from the rest of the sample matrix occurred. Investigations revealed that the offending element was scandium, and the problem was overcome by using smaller samples. Work is proceeding to eliminate this interference completely by modification of one of the ion-exchange steps.

Approximately 300 samples were analysed in 1982 for plutonium isotopes. These included 120 soils, 160 mammal and bird tissue and faecal samples, and about 80 vegetation samples. Over 200 of these samples were also examined for americium-241 by chemical separation and $\alpha\text{-spectrometry}.$ The rest had sufficient activity to allow americium determination by $\gamma\text{-spectrometry}.$

The extra Ge(Li) detector which was obtained early in the year meant that over 100 extra samples could be examined for y activity. In total, approximately 450 samples of soil, vegetation and animal tissue and faeces were analysed, a large proportion of which were relatively low-activity samples requiring counts of 2 days. Down-time through equipment failure was less than 5%, but almost as much time was lost through interrup-

tions in the mains power supply. Even a momentary dip in the power supply results in the loss of up to 2 days' counting time.

A rapid method for the determination of caesium-137 in soils is currently being investigated, based on the well-known ammonium molybdo-phosphate exchange reaction. After separation, the γ activity will be measured using a Nal detector, which will make it possible to take advantage of the high sensitivity of this type of detector, without spectral interference from other isotopes. The procedure looks promising, and it is hoped that it will be brought into routine use in 1983.

Engineering

Although this section is now included in the new service programme, its internal structure is little changed. The Central Engineering Unit, which exists to provide specialist support not available at individual stations, remains at Bangor. Monks Wood, Merlewood, Bush and Bangor have their own station engineers and Brathens is still able to share in the services of the technician who specializes in the radiotelemetry requirements of that station. Only Furzebrook and CCAP are not served with an on-station engineer. The engineering staff at Monks Wood, Merlewood, and especially Edinburgh, have been able to provide training for young people through the work experience programme, and in so doing have themselves gained some benefit from the extra labour.

Undoubtedly the largest of all the construction jobs handled by the section in 1982 has been the fabrication of 20 open-top plant growth chambers and filter units for the acid rain study group (ITE Project 790). This work was carried out by the station engineer at Bush, with the aid of temporary assistants. Because of the numbers required, and the large size of the chambers, the production was organized on factory lines in rented farm buildings close to the Bush estate. The design features of these chambers, which are now installed on a site in Glasgow, are described elsewhere in this report (pp 54-56). Other ventilation exposure chambers for plant pollution studies (ITE Projects 160, 669) have been developed and assembled at Bangor. Four complete units have been made and are, at the time of writing, undergoing tests and modifications. Another major support task for the Bangor station engineer has been the provision of rainwater collectors and stream level devices, needed for the geochemical cycling study (ITE Project 594).

Other large construction jobs completed during the year included a series of controlled temperature baths for frog studies (ITE Project 739) at Monks Wood; the conversion of deep freeze units for root cool boxes, to be used in experiments on plant growth at low temperatures (ITE Project 702) at Bush; and the completion of the mini-controlled environment chambers being used for the study at Merlewood on leaf photosynthesis (ITE Project 674).

Much of the time of the station engineers is spent on maintenance and repair work at their respective establishments. Some of these tasks are similar at all the stations, but others are determined by the nature of research being carried out at a particular place. For example, at Bangor much time has to be spent on servicing the growth chambers, and in future this may also be the case at Edinburgh (Bush), now that the growth chambers of that station have been brought into operation. At Merlewood and Monks Wood, there is a frequent need for repair work in the chemical laboratories, at Brathens radiotelemetry requirements are dominant, whereas at Edinburgh the station engineer has to service the boats and associated equipment used by the staff based at Craighall Road and also look after the general glasshouse maintenance requirements at Bush.

A problem that is becoming increasingly serious for all the engineers is that of equipment replacement. Most of the larger workshop machines have now had heavy use for 20 or more years, and on occasions they have not been adequate for some of the precision jobs. It has not been possible to replace any of the old machinery during the year, although a partly-used vertical milling machine in good condition was acquired for the workshop at Bush.

Plant culture

The glasshouse complex has serviced 14 projects in the past year, with those projects requiring special environments (tropical, and isolation for mycorrhizas) occupying 4 of the 8 units more or less permanently. With the reduction of space previously available at the other institutions on the Bush Estate, the use of the remaining 4 glasshouse units has had to be rigidly controlled in order to accommodate all other project needs. Even so, some propagation work had to be carried out elsewhere.



Plate 17 Repotting cuttings of Triplochiton scleroxylon. (Photograph R F Ottley)

The propagation techniques developed in the previous year were carefully scrutinized, and, in general, rooting percentages remained at an improved level (Plate 17). The technique of applying liquid feed to the mist benches once rooting had commenced has been modified. Algal growth on the foliage was a severe problem, and liquid feeding has been superseded by the introduction into the rooting medium of a short term (3-4 months) controlled release granular fertilizer. This type of fertilizer is controlled by temperature rather than moisture, which reduces losses through leaching.

The summer maintenance of the field plots proved to be much easier in 1982 than in the recent past. This improvement was due to 3 main factors:

- i. the acquisition of a larger and much newer tractor (Ford 4000) which provides a more rigid and precise control of mounted equipment and is easier for the operator to handle;
- ii. increasing the area of established grass, now totalling 80% of field plots, which can be covered much more guickly with mowers than with herbicide sprayers or cultivators;
- iii. a dry summer, which meant that the mowing could be more effective and less frequent. One particular plot was mown only 3 times during the growing season, with no detriment to tree growth.

During the severe winter of 1981/82, minimum temperatures of -8°C were regularly recorded during December 1981 and January 1982, but there were very few plant losses, mainly because much of the small and more vulnerable material was under snow cover for most of the time. However, a small plantation of 1 m tall Nothofagus obliqua was killed down to the general snow level (10 cm), although subsequent growth has been vigorous.

With the acquisition during the year of a further 1.75 ha in the field at Glencorse Mains near Bush, the field plot area now totals 7.5 ha. This last piece was acquired partly to accommodate 1500 Betula seedlings for ITE Project 717. Because of the comparatively large number of plants, coupled with constraints upon land availability on the Bush estate, plant spacing was kept to 2m×1m, with a view to thinning in a few years to 2m×2m. The whole area was sown with low-maintenance rye grass mixture, so that agricultural machinery could be used.

The only plant population changes during the year were in the Roslin experimental field, where part of an earlier amenity grass trial area was replaced by Betula progeny material (ITE Project 245). Early in the year, a Populus spacing trial was renewed.

Because of the frequent need to plant at spacings which preclude the use of agricultural machinery, a new self-propelled rotary grass cutter with a 0.5 m cut was purchased. This is a particularly efficient machine which will cut up to 2000 m² per hour.

Photography

The demand on the photographic service unit, based at Monks Wood, has remained at a fairly steady level throughout the year. One exception has been the requirement of black/white and colour slides, needed for staff lectures, which has increased sharply. The purchase of a new copy stand with lighting attached has been of considerable value for this work. There was also a slight increase in the demand for black/white, colour and caption material for ITE displays. Apart from displays mounted at stations for the benefit of visitors, there have been displays showing ITE work at conferences, exhibitions, science fairs and agricultural shows.

Much of the routine work has involved the preparation of diagrammatic and pictorial photographs for publication. Perhaps the most notable of this type of work was the provision of 'camera-ready' copy for the cover of the ITE publication *Culture Centre of Algae and Protozoa list of strains*.

A more specialized use of photography has been as an aid for counting sea bird colonies. Another research requirement has been for electron-microscope photographs of algae, both for experimental and record purposes.

S E Allen

RESEARCH AND DEVELOPMENT

Chemical interference studies

Chemical data produced for research purposes are generally examined much more exhaustively than is the case when such data are used for other purposes, eq production control, quality tests, or fertilizer applications, because a research worker usually tries to extract the maximum amount of information from his array of data, often using complex statistical techniques. There is, therefore, a constant need to be vigilant in the use of the so-called routine methods, in addition to the continuing need to vet new methods that have to be introduced to meet fresh research requirements. Two examples of the type of interference studies carried out in the Merlewood chemical laboratory are discussed below, and they illustrate that, although a method may work well for some samples, it may produce anomalous results with other materials.

1. Organic interferences with the nitrate method There are several methods available to determine nitrate in natural waters or soil extracts, but the one generally recommended utilizes a colorimetric technique based on the Griess reaction. The nitrate is first reduced to the nitrite ion, which then reacts with

a primary aromatic amine to first produce a diazonium salt, and then a coloured azo dve. Although many versions of this method are documented, most only differ in the reduction stage. The 2 most popular reduction systems are the hydrazine-copper reductants or those that are cadmium-copper based. In the Merlewood chemical laboratory, the method used in the automated colorimetric system, which is based on the reduction of nitrate in an alkaline solution with hydrazine-copper, has been found to be satisfactory for most natural waters. Recently though, there has been a need to test lysimeter waters from conifer plantations (ITE Project 625), which contain high concentrations of soluble organic compounds. These compounds are known to be troublesome in nitrate methods, but there have been few in-depth studies into ways of dealing with these interferences.

Investigation of the reaction mechanisms revealed that the copper catalyst was chelating with the polyphenols present in the samples, resulting in incomplete reduction. Optimization of the levels of copper, to give a high concentration of the catalyst, yet to avoid precipitation of copper in the automated line, was found to give good nitrate recoveries in all but the most exceptional samples. It was possible to eliminate interference in these samples by dilution. The additions of higher concentrations of copper catalyst contributed to a more stable and reliable performance. Since introducing this modification, it has been possible to achieve 100% nitrate recovery, in comparison with previously published figures of between 60% and 85%. Some interference by other soluble organic compounds in the nitrite colorimetric reaction does occur, but in this case the tolerances are much higher.

Examination of the chemical variables from these lysimeter and soil solutions has indicated that the apparent interferences in the nitrate method are very closely related to organic carbon and tannin levels. However, in specific samples, a very low concentration of the organic constitutents resulted in increased interference. Addition of tannin or fulvic acid fractions to standard nitrate solutions confirmed that very low levels of these substances resulted in severe depression of the nitrate levels. Concentrations as low as 10 mg l⁻¹ organic carbon produced a 50% reduction of a 1·0 mg l⁻¹ nitrate solution. This can be corrected, but the reaction mechanism is still being investigated.

Rainwater, canopy throughfall, stem flow, surface water, lysimeter waters and soil solutions are being examined in this study. The lysimeters were located in the litter and organic soil horizons, whilst the soil solution samples were obtained from the mineral leached horizons. Depression of nitrate values only occurred in samples collected from the litter and soil organic horizons. The extent of this interference changed in samples obtained from the same site

at different sampling times, probably due to rainfall variation.

2. Fluorine in eggshells

A similar interference problem has also occurred recently with the fluoride method which has been used in the Merlewood laboratory for several years. The method is based on the well known ion-selective electrode technique. Early studies of fluoride pollution in the Institute concentrated on grassland sites, and the original method was developed to deal with vegetation samples. As the research interests expanded, the method was adapted to analyse soil extracts and animal material. It was hoped to use the method for eggshell and bone samples, but, on test, the method was found to give erratic results.

Solution preparation is based on an alkali fusion, the neutralized fusate being buffered to pH 5·5 before obtaining a potentiometric measurement. Initial investigation, using the highly calcareous eggshell and bone materials, showed that the fluoride was liable to be precipitated out of solution. Recovery tests using standard solutions indicated that even the addition of excess potassium carbonate (used in the fusion) did not affect the fluoride yield. However, calcium carbonate did result in precipitation of calcium fluoride from solution shortly after storage at 1°C. Comparison with the eggshell samples showed a similar effect.

A reasonable recovery of fluoride was obtained from samples analysed immediately, but, on standing, calcium fluoride came out of solution. It was found that reproducible and reliable results using the standard method could be obtained, providing the sample weight did not exceed 0-3 g. Surprisingly enough, a bone sample analysed under similar conditions gave good recoveries if the sample weight did not exceed 0-7g. Presumably the more soluble calcium phosphate in the bone did not occlude fluoride to the same extent as the calcium carbonate in eggshells.

A P Rowland

An illumination device for a furnace atomizer
This modification to the atomizer furnace used in the
Monks Wood chemical laboratory was carried out primarily to aid manual injection of samples. Later it was
found to be extremely useful for aligning the injection
tip.

The first attempt consisted of building a 6 v power supply to power a 'grain of wheat' bulb. Using the flex supplied on the bulb, it was possible to hang the bulb inside the furnace when the door was open. The small size of the bulb, 3·2 mm diameter, enables the inside of tubes to be inspected when they are removed from the furnace. The bulbs, available from model shops (RS no. 587-068), are intended for 16v operation, but give considerable light even when only 6v are applied,

and the low voltage greatly extends their life. The bulbs have wire ends suitable for clamping to the terminals.

Because of the benefits possible from having a source of illumination, it was decided to build the bulb into the furnace chamber itself. Extreme accuracy was required in the positioning of the holes to mount the electrical terminations, as they were in close proximity to the sides of the furnace, and also to ensure that the bulb did not foul the door when open. It was also necessary to insulate the terminals from the furnace front cover and to obtain a gas-tight seal. To do so, Teflon bushes were used, through which ½ inch, 6 BA stainless steel screws were offered as terminals. All the materials used withstand the maximum temperature encountered within the furnace.

P Freestone and V W Snapes

Rapid recording of α -tracks

The technique of solid state nuclear track detection, discussed in last year's Annual Report, can give a great deal of information about the parent nucleus. However, this technique requires measurement of several parameters of each track using a microscope, and the careful control of all experimental conditions. In many instances, particularly in dosimetry and also in survey work, a simple count of the total number of tracks is frequently all that is required. Methods are available which give rapid results, eg spark counting and counting by thin film breakdown (Tommasino 1982). However, spark counting requires a special foil for registration and a relatively complex system to carry out the etching, whilst the thin film breakdown counter is largely untried. For our purposes, therefore, the system adopted, ie using 600 µm sheets of CR 39 etched in NaOH under standard conditions, gives a permanent record of the activity in the sample. The bottleneck occurs at the initial counting stage, even when using an image analyzer.

It was noticed that illumination at the edges of the plastic caused the etched tracks to shine so that they could be seen with the naked eye. This is an extreme form of the darkground illumination used in microscopy. A simple piece of equipment was assembled to test the idea and very good agreement was obtained between the results from this equipment and those from the image analyzer (Quantimet). The throughput rose from 8 samples a day using the Quantimet to about 60 per hour using the new device. The prototype is now being rebuilt in an attempt to increase the sensitivity and reduce the errors due to scattered light and uneven illumination.

C Quarmby

Microcomputer controller for bomb calorimetry

A Newham Electronics microbomb calorimeter has been purchased for use at Monks Wood (ITE Project 739). Ignition of the sample by a platinum fuse wire in

this instrument has been replaced by high voltage, low energy, spark ignition. To take advantage of the increased rate of sample throughput that this type of ignition allows, and to reduce user error in the operation of the calorimeter, including interpretation of the data, it was decided to semi-automate the procedure. The chart recorder normally used to record the output from the calorimeter has been replaced by a Sinclair Spectrum microcomputer, and suitable interfacing has been constructed to link it to the calorimeter.

The interface consists of a commutating auto-zero amplifier to amplify the low level output of the bomb thermocouples and a 12-bit analogue to digital converter to digitize the output for reading by the microcomputer. The firing circuit of the calorimeter is also interfaced to the microcomputer. Real time is calculated using a 20 ms internal counter that is part of the microcomputer's operating system. The temperature of the bomb prior to firing is monitored, and, when the rate of change is nearly constant, the rate of temperature change is calculated and the bomb fired automatically. The temperature of the bomb is read at 100 ms intervals and the data sorted in an array until a peak value is reached. The temperature of the bomb during the post-peak period is then monitored and, when the rate of temperature change becomes nearly constant, the post-firing cooling rate is calculated. Using the Dickinson correction formula to apply a cooling correction to the data, the microcomputer calculates the calorific value of the sample under test, using previously obtained calibration data from benzoic acid standards.

The microcomputer program was written in BASIC, although machine code was used to speed up the acquisition of data from the A to D converter. The progress of the determination is displayed on a TV monitor and a hard copy is available from a printer.

C R Rafarel

Microcomputer interfacing to photosynthesis environment chambers

A Rockwell AIM 65 single board microcomputer has been used as a data logger and system controller for 2 environmentally controlled perspex chambers. Suitable electronic interfacing has been built and the requisite software generated (Plate 18).

Initially, a total of 13 parameters are being monitored, including 2 temperature measurements plus light intensity monitoring for each chamber, ambient temperature, humidity of chamber air and readings from an infra-red gas analyser (IRGA). A signal conditioning module with a digital display is used to manually select and observe any particular parameter before it is fed to a 16-channel multiplexer under microprocessor control. The output from the multiplexer is then fed through a microprocessor-compatible 16-bit analogue to digital converter and the microcomputer programmed to look at the voltage output from a chosen sen-



Plate 18 Assembly of electronic control equipment for photosynthesis measurements. (Photograph M R Smith)

sor. The information from a number of sensors can be scanned at suitable time intervals. Scans are made in quick succession and mean values calculated. In addition, linearization, scaling, noise reduction or offset corrections can be calculated before a hard copy of the data is printed. These results can be printed as a tabular matrix with headings on a teletype or can be stored in solid state memory, on discs or cassette.

The microcomputer has been programmed as a real time clock so that time and data printouts are also available. A car battery can be connected to the microcomputer and control equipment for power back-up during mains power interruptions.

The main design features of the 2 perspex chambers in which growing leaves are contained were described in the 1981 ITE Annual Report. A fan has been incorporated within each chamber to mix the air and reduce boundary effects at the leaf surface. Temperature control of the chambers can be manually set or maintained under microcomputer control via a frequency to voltage converter and analogue comparators. The microcomputer is also used to control lighting regimes and power supply to devices such as the external printer, using logic controlled relays.

This application of a single board microcomputer demonstrates the advantages of using microcomputer technology to provide, at reasonable cost, a versatile and sophisticated measurement and control system for experimental work. However, the time required for developing software and de-bugging programs should be considered.

D G Benham

Controlled temperature incubation baths for frog studies

As part of a study of the common frog (ITE Project 739), it was necessary to incubate eggs and raise tadpoles at each of 3 constant temperatures in the range 5-30°C. Tadpoles were to be raised in plastic trays 225×170×50mm deep, each containing 1 litre of water. As no suitable constant temperature rooms were available, it was decided to suspend the trays in large shallow water baths maintained at the required temperatures, with each experimental bath containing 20 plastic trays arranged closely together to minimize the area of exposed water. Each tray was to be covered with a sheet of glass to reduce evaporation losses.

The apparatus which was constructed for this purpose consisted of a large base water tank (140 litres) fitted with a 3kw immersion heater, with an upper experimental tray 1270×686×152 mm deep, and a small centrifugal pump with associated pipework. The pump supplied water to the upper bath through a 12 mm pipe divided to give 2 separate flows, part of the pumped volume being by-passed back to the main tank, in order to limit the flow and give adequate mixing of the water in the heated tank. The return flow from the experimental tank was via a 19mm standing overflow pipe which had the effect of maintaining a constant level of water in the upper tank. The temperature of the water was controlled by a sensitive probe in the upper tank and solid state circuitry driving a heavy duty relay regulating the heater.

Four such units were constructed and located in a cold cellar so that cooling of the water would only be required at the lowest experimental temperature. In a test run carried out over a 14-day period, 3 of the tanks were operated at temperatures of approximately 24°C, 20°C and 18°C. The fourth unit was operated without heating, but with the water circulated as in the other 3 units. During this time, temperatures in the baths remained within ±0.15°C of the set temperature, and in the fourth unit the tray water temperature exceeded air temperature by about 2.5°C. No measurable differences in temperature were noted between plastic trays in any one experimental bath. The addition of a Granttype cooling unit to bath number 4 allowed the tray water temperature to be kept as much as 3°C below air temperature and made it possible to operate over most of the required temperature range, even when the cellar temperature fell to about 9°C.

V W Snapes

Field maintenance techniques for experimental trees In the course of a minor trial conducted to ascertain the incidence of birch mycorrhizas in bare soil and in grass, it was noticed that certain conditions affected the vigour of the trees. In the trial, separate plots were treated in the following ways: (i) with 2 types of herbicides; (ii) using hoeing to keep the ground clean; and (iii) by sowing with a low-maintenance rye grass sward. By

October 1982, ie 5 months after planting and grass sowing and 3 months after the ground treatments, it was found that mycorrhizas were present only in the grassed rows.

It was also observed that the trees in the hoed rows were the most vigorous.

Separate studies have shown that birches growing in a high yield agricultural rye grass sward have reduced vigour, even when herbicides have been used to eliminate grass competition. Sitka spruce clones and seedlings appear to grow better in the presence of low maintenance rye grass with competition reduced by 'Treespats' (these are biodegradable bitumen squares placed around the young tree).

It would appear from these observations that the presence of a grass cover, but with restricted growth, is beneficial for the growth of young trees. If, as suspected, herbicides depress the activity of mycorrhizas, then hoeing would seem to be preferable. Hoeing, however, can be very expensive, especially in a wet season, and can, more importantly, damage stems and surface roots. Therefore, the final choice would be to use an easily applied medium term (2 years) mulch, eg 'Treespats'.

R F Ottley and J W McCormack

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Systems analysis and biometrics

THE PROVISION OF STATISTICAL SERVICES WITHIN ITE

The task of providing statistical advice within ITE is herculean. It has to meet the many demands of the hydra-headed body of ecological research, with its wide sprawl of disciplines and its vast number of lines of enquiry. In an Institute of 250 scientists and 350 projects, 10 biometricians battle to provide a comprehensive advisory service. Each research station has its resident statistician and a small group at Cambridge provides a centralized source of statistical advice. The biologists are exhorted constantly to observe the steps in the consultative process: initial discussion of the problem and its biological background, formulation of objectives, decisions on the method of data collection and on the method of analysis, execution of the analysis, and interpretation of the results. It must be said that, in the main, ITE biologists do follow the steps of the consultation sequence.

During the last guarter century, there has been a mar-

ked change in attitudes towards the use of statistics in ecology. The increasing use of quantitative methods continues apace. Long gone are the days of purely descriptive studies. The language of mathematics is now an essential ingredient of the vocabulary of ecological literature and thinking. Though the mathematical approach can never replace inventive originality in the formulation of hypotheses and in the development of ecological concepts, these concepts are defined, refined and put to the test by the mathematical, scientific method.

From its very beginning, the research programme of ITE has adopted and made use of quantitative methods. Statistical theory was recognized as a tool of central importance, and not, as was widely expressed in those days, an irrelevancy only useful for ornamenting diagrams with asterisks of significance. The statistician has long been recognized as an indispensable member of any experimental team. The prospect revealed to the statistician confronting the ecological landscape is fascinating and challenging. Faunas of every description disport themselves in variegated vegetation. Vast regions still remain unexplored. Nature is untamed, and all is wide profusion and seemingly without pattern or design. Enshrouding the whole panorama is the thick mist of ecological variability. In negotiating this unknown territory, the statistician meets problems of great complexity and must be able to distinguish the trees from the dead wood. His fellow pioneers, the biologists, sometimes have to be gently reminded that, in these conditions, providing logistical support is a difficult enterprise.

The biometrician has to cope with an extraordinary variety of problems; in the course of a year, he may have been engaged in as many as 20 quite separate lines of enquiry. The projects that he may be involved with vary in character from the botanical, zoological, ornithological, systematical and computational to the synoptic and the global. Thus, for example, one biometrician reports that during the last year he has been involved in studies of the sparrowhawk, the Roman snail, butterflies, bats, rabbits, frogs, and insect fauna; he goes on to report studies on the effect of urbanization, acid rain, bracken control, plant succession and the mapping of vegetation from aerial photographs.

The wide diversity of problems is matched by the wide variety of statistical methodology; the statistician has an impressively large and ever-increasing choice of techniques from which to choose: experimental design, survey techniques, spatial analysis, time series, stochastic processes, etc. It is too much to expect a single statistician to be expert in all branches of the subject; some of his weaponry must necessarily suffer from rust. For this reason, whenever practicable within the limited biometrical resources of ITE, a division of labour is made and jobs are allocated to the people best equipped to deal with them.

Particularly in ecological research, one of the most important of the statistician's contributions to any research project is the elucidation of the logical issues and the objectives of the study. This contribution is, of course, made during the initial phase of the project and precedes the formal consideration of statistical design and data analysis. Regrettably, this preliminary advice is not always sought and a corresponding proportion of scientific nonsense is produced.

However, in ITE, the incidence of inadequate and of faulty initial planning is reduced to a large extent by the system of adopting the project plan as the basic unit in the research programme. The project plan, requiring as it does a clear statement of the objectives of the project and the means whereby the objectives are to be achieved, presents a golden opportunity to the statistician to identify shortcomings in the conception of the project and to assess the efficacy of the methods proposed for the collection and the analysis of the data.

The statistician engaged in ecological work is blessed with abundant opportunity to pursue research, not only jointly with his biological colleagues, but also individually following his own initiative. The wide variety of the subject matter, the complexity of ecological processes and their variability present the statistician with any number of research topics. Areas of study requiring research include spatial and temporal analysis, multivariate methods, population dynamics, environmental monitoring and systems analysis. Many of the problems met in statistical ecology are far from straightforward; more often than not, further reading has to be pursued and new methods of analysis have to be devised. Incidentally, this essential research often receives scant appreciation from the waiting biologists who cannot think why the data are not simply put on the computer and the analysis completed.

The computer plays an important part in the research programme. It has been recognized as an essential tool from the very beginning of ITE, and from before that in the days of the Nature Conservancy, long before the general acceptance of its value in ecological research. It is but 10 years ago that a distinguished academic visitor to one of ITE's research stations was overheard privately describing the station as neither more nor less than a computer laboratory. Since those distant days, the computer has everywhere prevailed, though not without some acrimony: people tend to be divided into 2 camps — they are either big computer users or they favour small computers. The abyss that separates the 2 groups, though non-transversable, does not occupy a fixed position, but is forever being updated and shifted year by year at an increasing rate. Indeed, every schoolboy now has available more computing power to play with than did the aforesaid research station 10 years ago. The biometrical staff, though eschewing ideological considerations, tended to belong to the camp of the big computer users. Their allegiance is due not simply to the greater scope for the manipulation of large data bases, but mainly because of the ready availability of the statistical languages and packages, GENSTAT, GLIM, and NAG, that so reduce the chores of programming. Not having a support service of professional programmers, the biometricians have to do their own programming of the computer. Much time could be saved for the practice of statistics if the biometrician, after merely describing the form of the data and the method of analysis, could then pass on his computing needs to a specialist programmer. On the other hand, in the same way as many of the problems of ecological research are far from straightforward, so it is only infrequently that the computer processing can be executed in one swoop. As the analysis of the problem evolves step by step, the computer program is correspondingly modified and extended. This interactive process, the somewhat halting dialogue of the statistician and the computer, would not necessarily be speeded up or rendered less incoherent if it were carried out through the intermediary of a professional programmer. Willy-nilly, the biometricians have to spend a sizeable proportion of their time sitting at a computer console.

M D Mountford

To illustrate the consultancy and research activities of the ITE statisticians, a few instances of their recent work are given below.

Predictive models of population fluctuations in red grouse

From 1963-77, red grouse numbers on Kerloch moor went through 2 population cycles. The first, lasting from 1963-69, had an approximately 2-fold amplitude in spring numbers; the second, from 1969-77, had an approximately 5-fold amplitude (Figure 77i). For each year, demographic data were available on recruitment, emigration and over-winter survival, together with observations on spring rainfall and temperature, and the incidence of egg-robbing by crows. These data have been analysed and used to develop predictive models for grouse numbers. Preliminary examination of the relationships amongst the demographic variables showed that the annual change in spring numbers was closely related to the number of young produced per spring cock. Also, over-winter survival of cocks showed a delayed density-dependent relationship with spring numbers in the previous year. More specifically, if yi denotes the logarithm of spring numbers and bi is the logarithm of (1 plus half the number of chicks reared per spring cock in year i), a predictive model:

$$y_{i+1} = 0.29 + y_i - 0.18y_{i-1} + b_i$$

was fitted to the data.

Figure 77(i) shows the close fit of this model obtained by successively using spring numbers in years i and (i-1), and observed chick production in year i to predict spring numbers in year (i+1).

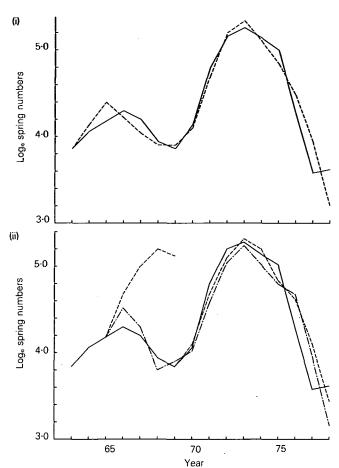


Figure 77

- i. Observed (——) log_e spring numbers of red grouse. Predicted (-----) numbers, using a model incorporating chick production and delayed density-dependent overwinter survival with lag of one year.
- ii. Observed (——) log_e spring numbers of red grouse. Predicted (-----) numbers, using model in Figure 77(i), but with chick production estimated from spring numbers 2 years previously. Predicted (— -—) numbers, using crow-robbing as an additional predictor of chick production.

Further analysis revealed that, in the second cycle, chick production measured by b_i was related to spring numbers 2 years back (r = 0.95). When this relationship was incorporated into the model (1), the fit was good in the second cycle but poor in the first (Figure 77ii), where observed breeding was low in 1965–67. A possible explanation of this result was some environmental factor affecting chick production in those years.

Previous studies have shown that chick production correlates with heather growth in the previous summer, and that this can be related to air temperature and rainfall. Also, in the first cycle, crows robbed many nests. Regression analysis failed to detect a relationship of chick production with either estimated heather production or spring temperature. However, a significant effect of nest-robbing was observed.

Model (1) was augmented to include b_i as a function of both the proportion of nests robbed and spring num-

bers 2 years back. The new model provides a good fit to the observed numbers over the 14-year period (Figure 77ii).

The models have been used to predict numbers in the early stages of an increase on another study area: in 2 years, the predicted varied from the actual numbers by 13% and 3%. The importance of numbers *per se* can, and will, be tested by controlled removal of birds in autumn.

P Rothery

Estimated bird survival from ring recoveries

Almost all we know about the age-dependent death rates in birds is based on analysing data arising from the recoveries of rings from young birds ringed and released at the beginning of each year. The analysts of ring recoveries are well aware that the survival estimates may be distorted if rings are lost, or if the recovery of dead birds is differentially affected by the age of the bird or by the calendar year. However, an additional problem arises when it is not known what proportion of dead birds is recovered. A given set of recoveries might come from a low recovery rate and a high mortality, or from a high recovery rate and a low mortality: the given set of recoveries is then consistent with an infinite number of combinations of recovery rates and survival patterns. It becomes impossible to decide which particular combination is closest to the one prevailing in nature. In practice, the problem is circumvented by imposing a constraint, eg that the mortality in a given species becomes constant after a certain age. This additional assumption appears so reasonable, biologically, that it has not been questioned.

The present work demonstrates that this apparently innocuous assumption plays such a crucial role in the process of survival estimation that, if the assumption

is violated, even in the slightest degree, then the resulting survival estimates are liable to be distorted and untrustworthy. This is true even if all the other assumptions hold, and no matter how large a number of recoveries is available for analysis.

The significance of this work is that it draws attention to the fact that, for all practical purposes, all hitherto published estimates of age-specific survival cannot be trusted if they are based solely on recoveries of dead birds. This result is important not only to ornithologists, but also to scientists in other fields where similar methods are used, eg fish and mammal studies.

K H Lakhani

Reference

Lakhani, K. H. & Newton, I. 1983. Estimating age-specific bird survival rates from ring recoveries — can it be done? *J. Anim. Ecol.*, **52**, 83–91.

Estimation of age-specific survival in hen harriers
The aim of this study, done in collaboration with N
Picozzi of Brathens, was to estimate and to compare
the survival rates of male and female hen harriers.
Colour-marked birds of known age were introduced
into the Orkney population each year from 1975–80
inclusive. The basic data are the records kept of the
resighting of marked birds during the 1976–81 breeding
seasons.

The method of estimation used in the analysis allows for age-dependent survival rates and also for age-dependent resighting rates. A suitable approach is given by Pollock (1981) who has developed a model to allow for variable rates of survival and of resighting. However, the estimates derived by Pollock are biased, and for small samples, as is the case for the hen harrier data, the bias can be infinitely large. To remedy this

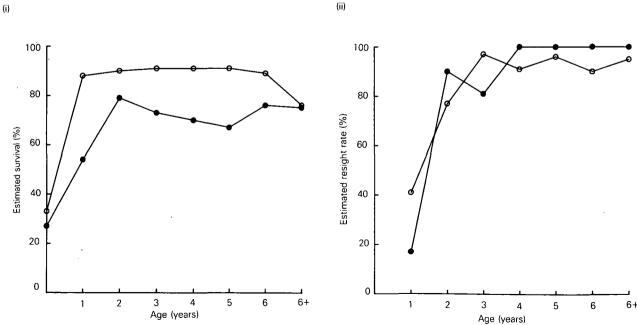


Figure 78 Estimated (i) survival and (ii) resight rates in relation to age for male $(\bullet ---- \bullet)$ and female $(\circ ----- \circ)$ hen harriers.

defect, a modification of Pollock's method, giving nearly unbiased estimates, has been developed. The estimates of survival and resighting rates of the hen harrier population are given in Figure 78. Female nestlings survive less well than yearlings; an estimated 29% of female nestlings survive to become 2-year old adults, and there is little variation in the survival rates of adult females about the average value of 90%. As in the case of females, male nestlings survive less well than adults: compared with the female nestlings, only half as many male nestlings survived to adulthood (14%), and male adults have an average annual survival rate of 72%. Figure 78 shows that marked nestlings of both sexes are much less likely to be resighted than marked adults.

P Rothery

Reference

Pollock, K. H. 1981. Capture-recapture models allowing for agedependent survival and capture rates. Biometrics, 37, 521-529.

Estimation of population fluctuations with application to the Common Bird Census

The Common Bird Census (CBC), carried out annually by the British Trust for Ornithology (BTO), monitors the changes in population size of the more common bird species. More than 250 sample plots, covering a wide range of farmland and of woodland habitats, have been included in the Census. Observers make frequent visits to the sample plots during the breeding season. On each visit, the observer records the species of the birds detected and the location of the birds within the plot. Using this information, an estimate is made of the number of territory-holding males of each species in the plot.

Until now, the BTO have analysed the Census data annually. If yi1 and yi2 are the estimated numbers of territories in sample plot i in successive years, year 1 and year 2, say, then the change in population size between the 2 years is measured by the ratio estimate:

$$r_{12} = \sum y_{i2} / \sum y_{i1}$$

the summation being carried out over those plots visited in both years.

The sequence of changes in the population over a period of several years is indirectly constructed from the products of the measures of change between successive years. Thus, for example, the change between year 1 and year 4 is estimated by:

r₁₂ r₂₃ r₃₄

No direct use is made of the data for pairs of years separated by more than one year; thus, the ratio r₁₄ does not directly figure in the estimate of change from year 1 to year 4.

If each and every site is monitored in every year, then, of course, the direct and indirect estimates of popula-

tion change between any pair of years coincide. However, a conspicuous feature of the Census is the large number of gaps in the data; they are extremely unbalanced. Over the period 1963-76, only a handful of plots were visited and counted in each and every year. With the frequent coming and going of the observers, all voluntary and unpaid, the majority of the plots were counted in less than half of the 14 years of the Census period; in the presence of this non-orthogonality, the direct and indirect estimates of change do not coincide. Consequently, the existing method of estimating population fluctuations makes far from full use of the relevant information. Accordingly, a method using both the direct and indirect measures of change has been developed, which combines the 2 types of measures to give minimum variance estimates of the relative changes in the population numbers.

When applied to the BTO skylark data, worthwhile improvements in efficiency were obtained. Figure 79 shows 2 estimates of the proportionate changes between pairs of years — the standard ratio estimate and the corresponding estimate obtained by the new method from the data of the 9-year period 1963-71; for reasons of space, only the results of the period 1963-67 are presented. The relative magnitude of the confidence intervals indicates a clear gain in precision for the new method.

The validity of the method requires mutual consistency in the relative changes of the various comparisons.

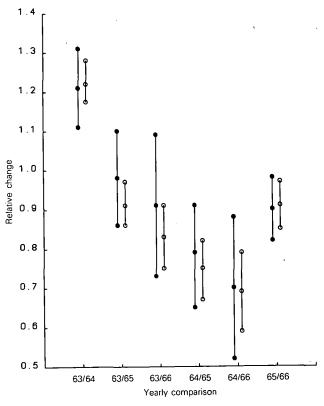


Figure 79 Estimates and 95% confidence intervals of relative annual change in skylark numbers for 1963-66 derived from ratio estimate (•) and from the 9-year analysis (0).

With the passage of time, there is an increasing possibility of change in the ecological characteristics of a Census plot and an increasing likelihood of the violation of the assumptions underlying the model. Accordingly, a test of the mutual consistency of the relative changes has been devised.

M D Mountford

Reference

Mountford, M. D. 1982. Estimation of population fluctuations with application to the Common Bird Census. *Appl. Statist.*, **31**, 135–143.

The use of environmental data in the prediction of a biological classification

The data arose from a project at the Freshwater Biological Association (FBA) River Laboratory, in which natural river communities in Great Britain were analysed. Macro-invertebrate samples were collected in each of 3 seasons at 268 sites on 41 rivers by Water Authority biologists and identified at FBA. Results from species lists combined over 3 seasons are described here. Data were also obtained on 28 environmental features for each sampling site, including time-invariant attributes such as altitude, distance from source and discharge category, and attributes measured at the time of sampling, eg channel width and depth, dominant substrate particle size, water velocity and macrophyte cover. Data on 6 chemical attributes, including pH, dissolved chloride and alkalinity, were also included.

The sites were classified from the biological data using 2-way indicator species analysis (TWINSPAN, Hill 1979). The successive levels of division resulted in 2,4,8,16,32 groups of sites. The division to 16 groups proved the most useful in terms of natural groups of sites, which ranged from top sites on upland rivers to deep water sites in south-east England.

Because collection and identification to species level of biological samples are much more demanding of time and expertise than measuring the environmental variables, the question was asked how well the biological groupings could have been predicted using environmental data alone? Multiple discriminant analysis (MDA) was used to find linear functions of the environmental variables which best discriminated between the groups. It was then possible to find the percentage of sites which were allocated to the correct TWINSPAN group using MDA (Table 36). The number of correct predictions even at the 16 or 32 group level was

Table 36. The percentage of 268 sites predicted to the correct TWIN-SPAN group, using multiple discriminant analysis on 28 environmental variables

Level of classification	1	2	3	4	5
Number of groups	2	4	8	16	32
Percentage of correct	91-4	84.3	79∙1	76-1	73-1
predictions					

thought to be highly encouraging, and work is currently in progress to find other environmental variables which would enable prediction to become even more accurate. Future work will include the development of tests of the inner consistency of the classification.

D Moss

Reference

Hill, M. O. 1979. TWINSPAN — a FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. Ithaca, N.Y.: Section of Ecology and Systematics, Cornell University.

Sub-sampling scheme for ageing size-grouped mussels

The construction of a life table of the mussel population is an essential component of the studies being carried out by ITE scientists on the interaction of the oyster-catcher and the mussel populations of the Exe estuary (pp 87–92). Counts of mussels are made twice a year. On each occasion, the lengths of a sample of mussels are measured and estimates of the relative abundances of the different size classes are calculated.

A life table cannot be constructed directly from the length data; any one size class is made up of mussels of different ages. Mussels can be aged directly by counting the number of growth rings. This direct method is extremely time-consuming; compared with measuring length, it takes 10–20 times as long to carry out. Because of this disparity of effort, the life table is constructed from the length data via the age-length relationship estimated from a smaller sub-sample of mussels.

The sub-sample consisted of the mussels found on one bed on 2 occasions. The relationship between age and length is shown in Figure 80. The relative age distribution within each size class is calculated. It is then applied to the size class data of the larger sample to give estimates of the population age distribution. The variances of the estimated age class numbers are calculated from the means, variances and covariances of the size class numbers. It is then possible to calculate the precision of any set of estimates derived from age-length data and to devise an optimal sampling strategy.

R T Clarke

Analysis of competition processes

Competition between conifers within miniature stands of Sitka spruce (*Picea sitchensis*) and lodgepole pine (*Pinus contorta*) has been studied at the Bush Estate, Penicuik. The aim was to identify aspects of tree growth affected by competition and to quantify the effects, to develop a mathematical model of the process, and to use the model to identify intrinsically high-yielding individuals. Each plot was the central array of

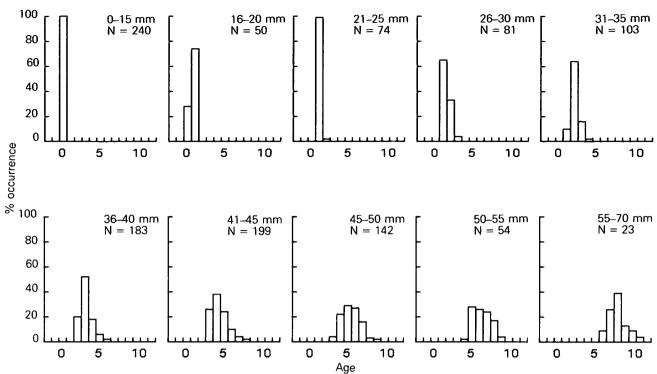


Figure 80 Percentage occurrence of mussels of different ages (years) in samples of n individuals of given size.

30×30 trees in a hexagonal lattice. Measurements of height and of height increments were taken in the 2 years before harvest, with further observations at harvest on diameter, branch structure and year of death.

The spatial pattern of dead trees was examined by comparing the number of occasions that, variously, 2 dead, 2 living, and a pair of one dead and one living trees occurred as neighbours, with the number expected when deaths occurred at random. A statistically significant departure from randomness was observed,

revealing an even, regular, distribution of mortality. A similar effect was detected using heights, with the larger trees tending to be neighbours of the smaller trees. Overall, a bi-modal distribution of heights was observed, with trees which eventually died occurring mainly in the lower mode.

A model for leader growth in the final year was developed by relating relative growth rate (RGR) of an individual to the competitive influence of its neighbours. This was measured by the tree's status (Ford & Diggle 1981), a function of the angles between the apex of a

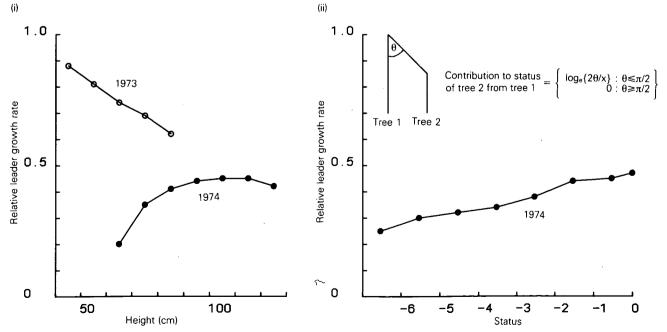


Figure 81 Relative leader growth rate of lodgepole pine in relation to:

i. height at the start of 1973 and 1974

ii. status calculated using heights of first order neighbours at the start of 1974.

tree and its competitors. Figure 81 illustrates the findings for lodgepole pine. In 1974, RGR showed an increase with tree height at the beginning of the year in contrast to the pattern in 1973. This effect can be explained by the greater competition experienced in 1974 by the smaller trees. Average RGR shows a steady increase with status calculated at the start of the period. Similar growth patterns to those of lodgepole pine were observed for Sitka spruce.

P Rothery

Reference

Ford, E. D. & Diggle, P. D. (1981). Competition for light in a plant monoculture modelled as a spatial stochastic process. *Ann. Bot.*, **48**, 481–500

Computerization of CCAP records

The Culture Centre of Algae and Protozoa's large holding of offprints and pamphlets, totalling some 11000 records, is being reproduced in computerized form so as to provide the basis of a comprehensive and efficient bibliographic service for CCAP staff and other enquirers. So far, more than 9000 records, occupying 1-8 million bytes, have been transferred to floppy disc. The software for retrieving bibliographic data according to various criteria has already been developed and proven. It is planned eventually to extend the service to include all CCAP's holding of books, as well as relevant information garnered from serial publications and abstracting journals.

A second piece of computerization is that of the data of CCAP's collection of about 2000 strains of Protista. Basic data of all the strains have been transferred to floppy disc and, after extensive editing on the Cambridge University computer to remove inconsistencies and to incorporate modern changes in taxonomy, the data were transferred to the SERC Rutherford Laboratory where they were typeset by computer. The resulting production, the fourth edition of the *Culture Centre of Algae and Protozoa list of strains*, was published in September 1982.

D F Spalding

Reference

Asher, A. & Spalding, D. F., eds. 1982. Culture Centre of Algae and Protozoa list of strains. Cambridge: Institute of Terrestrial Ecology.

Overseas activities

The involvement of ITE in ecological research on an international scale has included 2 overseas training sessions in biometrical methods.

In May 1981, P J A Howard and Doreen Howard visited Alexandria to assess the type of help which ITE could give to the SAMDENE (Systems Analysis of Mediterranean Desert Ecosystems of Northern Egypt) and RE- MDENE (Regional Environmental Management of Desert Ecosystems of Northern Egypt) projects, which aim to develop a better understanding of the structure and dynamics of the major ecosystems and to aid land use planning. As a result of that visit, 4 REMDENE trainees came to Merlewood in January 1982 for a course of statistics and BASIC programming lectures and practicals. As training of the Egyptian ecologists in data analysis is an important part of this project, the analysis of the data proceeds via fully-documented case studies of representative data sets. Methods used so far are principal component analysis, discriminant analysis, and canonical correlation analysis.

Also from Merlewood, P J Bacon and D K Lindley, armed with a BBC computer, gave a course of lectures on computing, statistics and systems analysis to the staff and students of the Institute of Environmental Studies, University of Khartoum, in March/April 1982. This course followed the visit of 12 senior members of the Institute of Environmental Studies to Merlewood in 1981 to participate in a specially-designed course on systems analysis and computing in ecology arranged by the Director.

Culture Centre of Algae and Protozoa

GENERAL REVIEW

With the adoption of a different format for this year's Annual Report, most of CCAP's research is described elsewhere. Perhaps one of the most significant events during the year has been the loss, through Voluntary Premature Retirement, of 3 of the Centre's most distinguished phycologists. Drs Erica Swale and Hilary Belcher resigned, respectively, on 31 December 1981 and 31 March 1982, and Dr D J Hibberd did likewise on 30 June: the loss of all 3 will be keenly felt. Drs Belcher and Swale have continued part-time working under contract, and so CCAP has not totally lost their expertise; they have served with NERC for 17 and 12 years respectively (initially at the Freshwater Biological Association laboratory at Windermere). Dr Hibberd's term of service (all of it at CCAP) runs a close third, amounting to 11 years. A major task for all 3, during the time available to them in the past year, has been writing up work which they had already done and which has been referred to in previous Annual Reports. This year saw the publication of Dr Belcher's and Dr Swale's third booklet in the ITE series of publications on Culturing algae — a guide for schools and colleges; also published were Parasitic protozoa in British wild animals by J R Baker and the fourth edition of CCAP's List of strains (edited by Ann Asher and D F Spalding). The list contains records of 1949 strains (177 mutants of Chlamydomonas reinhardii being omitted), and was produced by computer type-setting. This was possible because of the progress already made by Mrs Asher and D F Spalding in recording basic data relating to

all the strains on floppy discs via an Olivetti P6060 microprocessor. From this store, data were edited on the IBM 370/195 computer at the University of Cambridge, transferred to the IBM disc store of the SERC Rutherford Appleton Laboratory and type-set by the FR80 computer-output-microfilm camera there. Finally, the 100 pages of the list were printed from cameraready copy by NERC/SERC Reprographic Section at Swindon. With this project successfully accomplished, rapid progress is being made in similarly recording bibliographic data. About 10 000 of CCAP's holding of over 11000 offprints and pamphlets, and 700 books have already been recorded by Mrs Asher. Additional strain data will also be recorded, a daunting task which will, it is hoped, be facilitated by the availability of an increased memory capacity resulting from the inclusion of CCAP in the NCS network of mainframe computers, via a link with the British Antarctic Survey.

Returning to publications, CCAP has been responsible for producing 8 (including 2 editions of the List of strains) of the 50 publications currently in the ITE series, 3 of which were amongst the 'top ten' bestselling ITE publications in the first half of 1982.

Sales of cultures declined considerably during the year. presumably as a result of general economic conditions and the reduction in university finance in particular (British universities take about three-quarters of the annual output); 2584 cultures were sold between 1 November 1981 and 31 October 1982, a decrease of about 26% from the total of over 3500 despatched during the previous 12 months. Cultures were sent to 32 countries (including Britain), 4 fewer than in 1981. Sales for earlier calendar years are shown in Figure 82, which indicates a slight drop in 1968-72 and a plateau thereafter at around 4000 cultures per annum. Analysis of the sales figures shows that 73 universities in Britain took 77%, 29 British schools received 5%, and 70

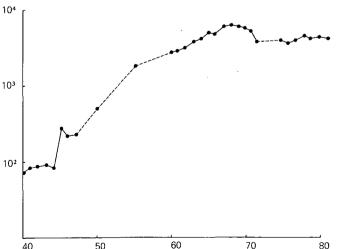


Figure 82 Culture Centre of Algae and Protozoa: annual sales of cultures 1940-1980.

overseas universities 7%. The remainder (11%) went to organizations not concerned with teaching — 8% in this country and 3% overseas. These proportions differ little from those relating to the previous year (ITE Annual Report for 1981, pp 102-103), which indicates that the reduction in numbers ordered has been fairly general. Interestingly, however, the number of cultures requested by schools (129) was identical with that in the previous year: figures for universities were down by about 25% and those for non-academic bodies were reduced by some 36%. The biggest customers (over 100 cultures each) were the Universities of London, North Wales, Edinburgh, Manchester, St Andrews and Cambridge.

On 30 September 1982, the Centre was designated an International Depository Authority under the Treaty on the International Recognition of the Deposit of Microorganisms for the Purposes of Patent Procedure, 1877 (the 'Budapest Treaty'). As yet, no deposit has been made under the terms of this Treaty.

The Centre's electron-microscopy unit, under K J Clarke, is undertaking an increasing number of collaborative projects with other ITE stations and NERC Institutes, in addition to being well used in CCAP's own research projects. During the year, the scanning mode of operation of the instrument (a Jeol JEM 100CX 'Temscan') became fully functional for the first time, and this mode is being exploited in 2 joint projects with the British Antarctic Survey — one on the feeding mechanisms of krill (Euphausia superba) (pp 24-25) and another on the morphology and taxonomy of tardigrades. A third joint project, with Monks Wood Experimental Station, involves a study of muscle of starlings (Sturnus vulgaris) at different phases of the breeding cycle.

In addition to his work on cold shock, described elsewhere in this Report (pp 62-64), Dr Morris is achieving considerable success in cryopreserving the Centre's holding of Cyanophyceae; 45 of an initial sample of 59 strains have been successfully recovered, and there seems to be no reason why a similar proportion of the remaining 30 or so strains should not survive also.

My own work, characterizing chiropteran strains of Trypanosoma and a joint project with R E Kenward (Monks Wood), is continuing but is not reported in detail this year.

During the latter part of the year, CCAP has welcomed Dr Lydia Kalinina, from the Institute of Cytology in Leningrad, on a second visit to work with Dr G J Morris and Dr F C Page.

J R Baker

The listing by Programmes also shows the numbers of other Programmes in which the project appears.

- 1 Forest and woodland ecology
- 2 Freshwater ecology
- 3 Rehabilitation of disturbed ecosystems
- 4 Management of natural and man-made habitats
- 5 Survey and monitoring
- 6 Airborne pollutants, including radionuclides
- 7 Plant physiology and genetics
- 8 Ecophysiology and pollution in animals
- 9 Plant population ecology
- 10 Autecology of animals
- 11 Faunistic studies
- 12 Cycling of nutrients
- 13 Land classification and land use
- 14 Chemical and technical sciences
- 15 Systems analysis and biometrics

Key

- @ Nature Conservancy Council contract
- + Department of Environment contract
- £ Otheroutsidecontract
- ! PhD or other student project
- § Visiting worker project
- * Project proposal, not yet approved by Management Group

Projects

listed by Programmes as at 15 February 1983

1. Forest and woodland ecology, the integrated effects (botanical and zoological) of woodland and forest management practices

Programme Leader: FT Last

Core Group: D Jenkins, E D Ford, A H F Brown

Core Gro	up: D Jenkins, E D Fora, A H F Brown		
1	Semi-natural woodland classification	R G H Bunce	1
9	Monitoring at Stonechest	J M Sykes	1
14	Tree girth changes in 5 NNRs	A D Horrill	1
17	Meathop Wood IBP study	J E Satchell	1
55	Establishment of trees at Moor House	A H F Brown	1
61	Variation in growth of birch and sycamore	A F Harrison	1
88	Surface conditions and plant establishment	J Miles	1
90	Effects of birch on soil	J Miles	1 12
137	Sparrowhawk ecology	l Newton	1 8 10
188	Woodland invertebrates	R C Welch	1 11
246	Physical environment, forest structure	E D Ford	17
359	Fibre yield of poplar coppice	M G R Cannell	1 7
386	Behaviour and dispersion of badgers	H Kruuk	1 10
389	Management effect in lowland coppices	A H F Brown	1
417	Silvicultural systems – N Ireland experiment	A H F Brown	1
442	Ecology of capercaillie	R Moss	1 10
454	Monitoring of woodlands	J M Sykes	1
463	Age class of amenity trees	J E Good	1
479	Red deer in production forests	B W Staines	1 10
514	British birch publication	A S Gardiner	1
517	Primary productivity in woodlands	J N R Jeffers	1
528	Red deer populations in woodland habitats	B Mitchell	1
549	Monitoring in native pinewoods	J M Sykes	1
574	Potential for fuel cropping in upland Wales	DIThomas	1
606	Grey squirrel damage and management	R E Kenward	1 10
609+	Biological classification of UK rivers	D Moss	1 2
619	Small rodents in a Sitka spruce plantation	A G Thomson	1 11
625£	Effects of clear-felling in upland forests	M O Hill	1 12
633	Water level and vegetation change –		
	Kirkconnell Flow	J M Sykes	1
636	Song bird density and woodland diversity	D Jenkins	1 11
692	Goshawk population dynamics	R E Kenward	1 10
711	Tree growth and climate	A Millar	1
721	Dry matter in forests: world review	M G R Cannell	1
746	Grazing in woodlands	T W Ashenden	1
758*	Effects of grazing on woodland vegn diversity	/J Dale	1
773	Silviculture of respacing Sitka spruce	E D Ford	1
793*	Ecotypic variation in oak	M W. Shaw	1
798*	Mechanisms and processes in forest		
	mixtures	A H F Brown	1
820*	Regional variation in forest dynamics	P Ineson	1 12 15

2. Freshwater ecology, with special reference to synoptic limnology and the interactions between flora and fauna

Programme Leader: J P Dempster

Core Gro	oup: I Newton, P S Maitland, I R Smith		
116	Freshwater survey of Shetland	P S Maitland	2
117	Freshwater survey of Great Britain	P S Maitland	2
123	Zoobenthos at Loch Leven	P S Maitland	2 11
124	Distribution and biology of fish in GB	P S Maitland	2
289	Residues and effects of pollutants	F Moriarty	28
447	Freshwater and marine amoebae	F C Page	2

481	Monitoring and chemistry of aquatic		
	pollutants	K R Bull	28
527	Long-term changes in zooplankton	L May	2 11
577	Predation of freshwater zooplankton	D H Jones	2 11
584	Nutrient loading, phytoplankton and		
	eutrophication	A E Bailey-Watts	2 11
585	Diatom ecology	A E Bailey-Watts	2
586	Freshwater phytoplankton periodicity	A E Bailey-Watts	2
609+	Biological classification of UK rivers	D Moss	1 2
642	Physics of freshwater systems	I R Smith	2
644	Breeding success and survival of the		
	common toad	C J Reading	2 10 11
676	Ecology of lampreys in Loch Lomond	P S Maitland	2 10
694	Zooplankton communities in freshwater		
	lakes	D H Jones	2 11
698	Zooplankton population dynamics	L May	2 11
705	Impact of barytes mine project	P S Maitland	2
739	Life history of the common frog	C P Cummins	2810
748	Temperature limits of growth for		
	Chlamydomonas	E A Leeson	2
765	Ecology of the heron	M Marquiss	2810
785	Cultivation of freshwater algae	E A Leeson	2
786	Cultivation of marine algae	N C Pennick	2
787	Cultivation of free-living protozoa	J P Cann	2
817*	Cell surface structure of marine flagellates	N C Pennick	2
J.,	The same of the same of the same same of		-

3. Rehabilitation of disturbed ecosystems, and creation of biologically-rich habitats from scratch

Programn	ne Leader: J P Dempster		
Core Gro	up: BNK Davis, TCE Wells		
102	Mountain vegetation populations	N G Bayfield	3
242@	Establishment of herb-rich swards	T C E Wells	3
265	Regeneration on lowland heaths	S B Chapman	3 4
360£	Tree planting on opencast sites	J E Good	3
408+	Arboriculture: selection	F T Last	3
500	Recolonization by spiders on Hartland Moor	P Merrett	3 4 11
567	Coastal dune management guide	D S Ranwell	3
690	Plant succession in a limestone quarry	B N K Davis	3
693	Plant species establishment in grassland	L A Boorman	3 4
707	Plant establishment in woodland	L A Boorman	3
726	Restoration of heathland vegetation	R H Marrs	3 4
796@*	Poole harbour salt marshes	A J Gray	3 4
819*	Creation of butterfly habitats on landfill sites	B N K Davis	3

4. Management of natural and man-made habitats, but excluding forests and disturbed sites, effects of management, including grazing, cutting . . . on plants, animals and soils

Programi	ne Leader: FT Last		
Core Gro	up: M G Morris, M D Hooper, C Milner		
78	Management of sand dunes in Wales	D G Hewett	4
89	Calluna-Molinia-Trichophorum management	J Miles	4
92	Effects of grazing on Nardus and Calluna		
	moorland	D Welch	4
95	Importance of dung for botany change	D Welch	4
148	Soil erosion on Farne Islands	M Hornung	4
158	Community processes (physiology)	D F Perkins	4
227	Sheep grazing on chalk grass flora	T C E Wells	4
228	Effect of cutting on chalk grassland	T C E Wells	4
230	Grassland management – invertebrates	M G Morris	4 11
243	Scrub succession at Aston Rowant NNR	L K Ward	4
265	Regeneration on lowland heaths	S B Chapman	3 4
296	Scrub management at Castor Hanglands	L K Ward	4 11

374	Sand dune ecology in East Anglia	L A Boorman	4
457	Grazing models	C Milner	4 15
467	Roadside studies	T W Parr	4
500	Recolonization by spiders on Hartland Moor	P Merrett	3 4 11
511	Landscaping at Swindon	F T Last	3
573+	Amenity grass – stage 2	M D Hooper	4
599	Bracken and scrub control on lowland heaths	R H Marrs	4
602	Modelling sports turf wear	T W Parr	4 15
634	Field plot survey – Monks Wood	R Cox	4
650	Amenity grass irrigation	M D Hooper	4
665	Coastal management	D S Ranwell	4
666	Coastal publications	D S Ranwell	4
674£	Plant species for energy in Great Britain	T V Callaghan	4
693	Plant species establishment in grassland	L A Boorman	3 4
703	Vegetation change at Dungeness and		
	Orfordness	R M Fuller	4
726	Restoration of heathland vegetation	R H Marrs	3 4
744	Effects of grazing in Snowdonia	M O Hill	4
769£	Bracken biofuel potential for energy in		
	Wigtown	T V Callaghan	4
772	Japanese knotweed control	R Scott	4
776	Long-term studies of vegetation change at		
	Moor House	R H Marrs	4
794	Rhododendrons in Snowdonia	M W Shaw	4
796@*	Poole harbour salt marshes	A J Gray	3 4
813	ITE/UCL EIA on Lake Ichkeul	M D Hooper	45915
823£*	Ecological review of North Canford Heath,		
	Dorset	N R Webb	4 13

5. Survey and monitoring of plant and animal distributions and abundance

-	me Leader: J P Dempster		
	up: P S Maitland, M O Hill, B K Wyatt	LLM O : l	_
62	National plant nutrient survey	H M Grimshaw	5
116	Freshwater survey of Shetland	P S Maitland	25
117	Freshwater survey of Great Britain	P S Maitland	2 5
124	Distribution and biology of fish in GB	P S Maitland	2 5
132	Monitoring in the Cairngorms	A Watson	5
165	N Wales bryophyte recording	M O Hill	5
181@	Birds of prey and pollution	l Newton	58
204@	Assessing butterfly abundance	E Pollard	5 10
208@	Botanical data bank	C D Preston	5
209@	Vertebrate recording schemes	H R Arnold	5
216	Register of NNRs	G L Radford	5
309	Phytophagous insects data bank	L K Ward	5 11
340	Survey of Scottish coasts	D S Ranwell	5
378	Chemical data bank	S E Allen	5 14
405	Fauna of pasture woodlands	P T Harding	5 11
406	Distribution and ecology of non-marine		
	Isopoda	P T Harding	5
424	Ecological survey of Britain	R G H Bunce	5 13
466	Ecology of railway land	C M Sargent	5
469	Scottish invertebrate survey	R C Welch	5
483	Scottish deciduous woodlands	R G H Bunce	5 13
529	Biological data bank	D M Greene	5
534	National land characterization	D F Ball	5 13
557@	Terrestrial and freshwater invertebrate		
	surveys	P T Harding	5
565	Bibliography of Shetland	N Hamilton	5
566	Islands: biogeographic analysis	N Hamilton	5
591	Terrestrial Environment Information System	B Wyatt	5 15

609+	Biological classification of UK rivers	D Moss	125
615	Heathland invertebrates	N R Webb	5 11
656@	Marine invertebrate recording schemes	H R Arnold	5
657	Biological Records Centre – general	P T Harding	5
671	Analysis of BRC data	G L Radford	5
684£	Mapping broadland vegetation with aerial		
	photographs	R M Fuller	5
732	NCR site information system	G L Radford	5
743	Railway resource monitoring	C M Sargent	5
751	National survey of fluoride in predatory birds	D C Seel	56
760£	EEC ecological mapping	B K Wyatt	5 13
761£	EEC remote sensing	B K Wyatt	5 13
771	Chemical data bank (Monks Wood)	K R Bull	5 8 14
774	Long-term trends in upland vegetation	J Dale	5
795	Standard procedures for recording data	D M Greene	5 15
799	Dutch elm disease resurvey	J Wilson	5
800@*	Poole Harbour wader survey	J D Goss-Custard	5
807	Ecobase	B K Wyatt	5
813	ITE/UCL EIA on Lake Ichkeul	M D Hooper	45915
822*	LANDSAT classification and vegetation		
	survey of Bhutan	C M Sargent	5 13

6. Airborne pollutants, including radionuclides, their pathways through and effects on terrestrial ecosystems

Programi	ne Leader: FT Last		
Core Gro	up: S E Allen, I A Nicholson, D F Perkins		
160£	Fluorine pollution studies	D F Perkins	6
380	Monitoring of atmospheric SO ₂ at Devilla		
	Forest	I A Nicholson	6
426	Preparation of sulphur review document	I A Nicholson	6 15
452	Study of precipitation	J W Kinnaird	6
453	SO ₂ dry deposition in a Scots pine forest	I A Nicholson	6
491£	Radiochemical development	J A Parkinson	6 14
524	Fluoride in predatory mammals	K C Walton	6
525	Fluoride in predatory birds	D C Seel	6
526	Biological monitoring in Forth Valley	B G Bell	6
553£+	Radionuclide pathways	S E Allen	6
556	Estimation in acid rain	K H Lakhani	6
669	Interaction of grazing and air pollution	T W Ashenden	6
704*	Atmospheric pollutants and tree growth	E Wright	6
710	Airborne pollutants and Scots pine	J N Cape	6
751	National survey of fluoride in predatory birds	D C Seel	6
753	Fluoride and magpies	D C Seel	6
756	Fluoride pathways in invertebrates	A Buse	6
790£	Effects of polluted atmospheres on crops	I A Nicholson	6
791	Effects of acid rain on Sitka spruce	D Fowler	6
792*	Studies of pollutant gases	I A Nicholson	6
797	Effects of acid rain on fresh water	K R Bull	6
809*	Fluoride toxicology	D Osborn	6

7. Plant physiology and genetics, responses of native and introduced species to environmental factors

	gramme Leader: FT Last e Group: M H Unsworth, T V Callaghan		
24	·	J Pelham	7
24	6 Physical environment, forest structure	E D Ford	17
35	9 Fibre yield of poplar coppice	M G R Cannell	17
44	9 Preservation of cultures	G J Morris	7
51	2 National collection of birch	A S Gardiner	7
70	2 Selection of frost-hardy trees	M G R Cannell	7
71	7 Birch variation and environmental differer	nces A S Gardiner	7

750	Domestication of tropical hardwoods	R R B Leakey	7
767	Formation of cones by lodgepole pine	K A Longman	7
770	Evaluation of conifer clones and progenies	M G R Cannell	7
801	Radial growth of Sitka spruce roots	J D Deans	7
805	Effects of mycorrhizas on assimilation	E J White	7
815	Control of wood density in Sitka spruce	E D Ford	7
816	IUFRO Conference 1984: trees as crop		
	plants	M G R Cannell	7

8. Ecophysiology and pollution in animals, covering broadly the same fields as the former Subdivision of Animal Ecology

	ne Leader: JP Dempster up: I Newton, R Moss		
129	Red grouse and ptarmigan populations	A Watson	8 10
137	Sparrowhawk ecology	l Newton	1810
181@	Birds of prey and pollution	l Newton	8
199	Avian reproduction and pollutants	S Dobson	8
255	Ecology of Myrmica species	G W Elmes	8 10 11
256	Protein electrophoresis	B Pearson	8
262	Digestive enzymes	A Abbott	8
289	Residues and effects of pollutants	F Moriarty	28
444	Endocrine lesions in birds	S Dobson	8
455	Heavy metals in avian species	D Osborn	8
461@	Puffins and pollutants	M P Harris	8 10
481	Monitoring and chemistry of aquatic		
	pollutants	K R Bull	28
559	Ecophysiology of the rabbit	I L Boyd	8
624	Population genetics	P J Bacon	8 10 15
630	Stress in birds	A Dawson	8 11
697	Pesticides and wildlife: historical perspective	J Sheail	8
728	Kestrels in farmland	A Village	8 10
737	Population genetics of Pardosa monticola		
	spiders	R G Snazell	8
739	Life history of the common frog	C P Cummins	2 8 10
759+	Chemicals in the terrestrial environment	S Dobson	8
763£	Data profiles on chemicals	S Dobson	8
765	Ecology of the heron	M Marquiss	2 8 10
771	Chemical data bank (Monks Wood)	K R Bull	5 8 14
810	Lead poisoning in birds	M C French	8
811	Foraging and reserve storage in red and grey		
	squirrels	R E Kenward	8 1 1
812	Grouse aviary	R Moss	8 10

9. Plant population ecology: the biology of individuals and populations, including a consideration of gene flow

Programme Leader: FT Last						
Core Group: S B Chapman, A J Gray						
82	Seed produced by montane plants	G R Miller	9			
225	Population studies on orchids	T C E Wells	9			
269	Autecology of Gentiana pneumonanthe	S B Chapman	9			
295	Survey of juniper in N England	L K Ward	9			
346	Genecology of grass species	A J Gray	9			
365	Competition between grass species	H E Jones	9			
410	Tundra plants (bryophytes)	T V Callaghan	9			
411	Taxonomy of bryophytes	B G Bell	9			
508	Botanical variation in elm	J N R Jeffers	9			
575	Regeneration and growth of bracken					
	rhizomes	R E Daniels	9			
576	Isoenzyme studies in Sphagnum	R E Daniels	9			
649	Demographic genetics of Agrostis setacea	A J Gray	9			

741!*	Distribution of morphological variation in				
	birch	S Stewart	9		
742	Population fluctuations in annual legumes	C D Preston	9		
775	Ecology of arctic alpines in Snowdonia	J Dale	9		
783	Interactions between mosses and vascular				
	plants	N G Bayfield	9 .		
813	ITE/UCL EIA on Lake Ichkeul	M D Hooper	45915		

10. Autecology of animals, with particular reference to population management for conservation and pest control

and pest control						
Programme Leader: J P Dempster						
Core Group: I Newton, E Pollard, A Watson						
54	Red deer ecology on Rhum	V P W Lowe	10			
104	Distribution and segregation of red deer	B W Staines	10			
111	Population dynamics of red deer at Glen					
	Feshie	B Mitchell	10			
129	Red grouse and ptarmigan populations	A Watson	8 10			
130	Management of grouse and moorlands	A Watson	10			
131	Golden plover populations	A Watson	10			
137	Sparrowhawk ecology	1 Newton	1810			
193	Stone curlew and lapwing	N J Westwood	10			
202	The Roman snail	E Pollard	10			
204@	Assessing butterfly abundance	E Pollard	5 10			
255	Ecology of Myrmica species	G W Elmes	8 10 11			
273	Ecology of <i>S magnus</i> and other mites	N R Webb	10 11			
291@	Population ecology of bats	R E Stebbings	10			
292@	Specialist advice on bats	R E Stebbings	10			
386	Behaviour and dispersion of badgers	H Kruuk	1 10			
393	Isolation effects in butterfly populations	J P Dempster	10 11			
400	The large blue butterfly	J A Thomas	10 11			
403	The black hairstreak butterfly	J A Thomas	10			
404	The brown hairstreak butterfly	J A Thomas	10			
441	Oystercatcher and shellfish interaction	J D Goss-Custard	10 11			
442	Ecology of capercaillie	R Moss	1 10			
461@	Puffins and pollutants	M P Harris	8 10			
479	Red deer in production forests	B W Staines	1 10			
499	Studies in mammalian taxonomy	V P W Lowe	10			
509	Wood white butterfly population ecology	E Pollard	10			
543	Population ecology of the red squirrel	V P W Lowe	10			
568	Subcortical fauna in oak	M G Yates	10 11			
606	Grey squirrel damage and management	R E Kenward	1 10			
624	Population genetics	P J Bacon	8 10 15			
644	Breeding success and survival in the	r J Dacon	8 10 13			
044		C I Pooding	2 10 11			
660	common toad	C J Reading J A Thomas				
660 676	Simultaneous butterfly population studies		10			
676	Ecology of lampreys in Loch Lomond	P S Maitland	2 10			
687	Radio location and telemetry development	T Parish	10			
692	Goshawk population dynamics	R E Kenward	1 10			
709	Techniques for rearing the large blue	1.0 \ \ \ \ \ \ \ \ \ \ \ \ \ \ \ \ \ \ \	40			
7450	butterfly	J C Wardlaw	10			
715£	Shetland otters	D Jenkins	10			
722	The habitat ecology of the spider <i>Eresus</i>	5.14				
	niger	P Merrett	10			
728	Kestrels in farmland	A Village	8 10			
734	Estimation of seabird numbers	M P Harris	10			
735	Oystercatcher population dynamics	M P Harris	10			
739	Life history of the common frog	C P Cummins	2 8 10			
764£	Habitat requirements of black grouse	N Picozzi	10			
765	Ecology of the heron	M Marquiss	2 8 10			

777	Estimation of population parameters	K H Lakhani	10 15
789	Food resource limitation in the orange-tip		
	butterfly	J P Dempster	10
*808	Effect of food on home range size in otters	H Kruuk	10
812	Grouse aviary	R Moss	8 10
818*	Increasing guillemot populations	M P Harris	10

11. Faunistic studies, including studies of the interactions between species (eg competition, predator/prey) and between fauna and their habitats (eg effects of area and isolation) Programme Leader: J P Dempster Core Group: M G Morris, J D Goss-Custard, H Kruuk, D Jenkins, J R Baker 67 Prev selection in redshank J D Goss-Custard 11 123 P S Maitland 2 11 Zoobenthos at Loch Leven R C Welch 188 Woodland invertebrates 1 11 230 Grassland management - invertebrates M G Morris 4 11 232 Butterfly studies at Porton Range M G Morris 11 252 Hartland Moor NNR survey A Abbott 11 8 10 11 255 Ecology of Myrmica species G W Elmes 270 Distributional studies on spiders P Merrett 11 273 Ecology of S magnus and other mites N R Webb 10 11 296 Scrub management at Castor Hanglands L K Ward 4 11 309 Phytophagous insect data bank L K Ward 11 370 Experimental reduction of inter-species competition in ants B Pearson 11 393 Isolation effects in butterfly populations J P Dempster 10 11 400 10 11 The large blue butterfly J A Thomas 405 P T Harding Fauna of pasture woodlands 11 407 British Staphylinidae (Coleoptera) R C Welch 11 Oystercatcher and shellfish interaction J D Goss-Custard 10 11 441 470 Upland invertebrates A Buse 11 500 P Merrett 3 4 11 Recolonization by spiders on Hartland Moor 527 2 11 Long-term changes in zooplankton L May 568 Subcortical fauna in oak M G Yates 10 11 569 Insect fauna of Helianthemum and Genista B N K Davis 11 577 Predation of freshwater zooplankton D H Jones 2 11 584 Nutrient loading, phytoplankton and eutrophication A E Bailey-Watts 2 11 Analysis of common birds census 612 M D Mountford 11 615 Heathland invertebrates N R Webb 5 11 619 Small rodents in a Sitka spruce plantation A G Thomson 1 11 11 15 621 Models of rabies epidemiology P J Bacon 630 Stress in birds A Dawson 8 11 636 Song bird density and woodland diversity D Jenkins 1 11 641 Invertebrate fauna of Nothofagus and Quercus R C Welch 11 644 Breeding success and survival in the 2 10 11 common toad C J Reading 694 Zooplankton communities in freshwater lakes D H Jones 2 11 698 Zooplankton population dynamics L May 2 11 708! Structure of spider communities on heathland P J Hopkins 11 J Sheail 718@ Impact of land drainage on wildlife 11 13 723 Characterization of Trypanosomes from bats J R Baker 11 724 Protozoan parasites of wild British animals J R Baker 11 803 Threat to Orcadian moorland by Lepidoptera R C Welch 11 811 Foraging and reserve storage in red and grey squirrels R E Kenward 8 11

T Parish

11

821*

Modern agriculture and wildlife

12. Cyc	ling of nutrients; the movement and utilization of nutrien	nts				
Programme Leader: FT Last						
	up: O W Heal, M Hornung, J Miles					
39	Phosphorus turnover in soils	A F Harrison	12			
90	Effects of birch on soil	J Miles	1 12			
153	Mineralogical methods	A Hatton	12			
266	Root dynamics of Calluna vulgaris	S B Chapman	12			
358	Earthworm production in organic waste	J E Satchell	12			
364	Early growth of trees	A F Harrison	12			
367	The Gisburn experiment	A H F Brown	12			
431	Soil change through afforestation	P J A Howard	12			
432	Effect of birch litter on earthworms	J E Satchell	12 12			
438	Ecology of Mycena galopus	J C Frankland	12			
589	Microbial characteristics in soils	P M Latter	12			
625£	Geochemical cycling	M Hornung M O Hill	1 12			
625L 645	Effects of clear-felling in upland forests Effects of soil chemistry on decomposition	D D French	12			
654	Status of mycorrhizas in the soil ecosystem	J Dighton	12			
695	Effects of mycorrhizas on tree growth	F T Last	12			
712	Organic matter quality and tree growth	O W Heal	12			
714	Role of forest vegetation in pedogenesis	P J A Howard	12			
738!	Effect of altitude on grassland at Moor	1 3 A Howard	12			
750:	House	J C Hatton	12			
820*	Regional variation in forest dynamics	P Ineson	1 12 15			
824*	Nitrogen and phosphorus cycling in forest	1 11103011	, 12 10			
024	soils	A F Harrison	12			
	50110	, , , , , , , , , , , , , , , , , , ,	,_			
13 lan	d classification and land use, habitat characteristics, the	eir interrelations and value	in site			
	ents and resource management	in interrelations and value				
Programi	me Leader: FT Last					
•	up: JNR Jeffers, OW Heal, DF Ball					
2	Meteorological factors in classification	E J White	13			
4	Soil classification methods	P J A Howard	13			
163	Ordination and classification methods	M O Hill	13			
424	Ecological survey of Britain	R G H Bunce	13			
471	Soils of Upper Teesdale	M Hornung	13			
483	Scottish deciduous woodlands	R G H Bunce	13			
534	National land characterization	D F Ball	5 13			
541	Marginal land in Cumbria	C B Benefield	13			
554	Cumbria land classes and soil types	J K Adamson	13			
561	Soil fertility	M Hornung	13			
700+	Ecological guidelines for locational strategies		13			
718@	Impact of land drainage on wildlife	J Sheail	11 13			
745£	Land availability for wood energy plantations		13			
747£	Highland region land classification	R G H Bunce	13			
760£	EEC ecological mapping	B K Wyatt	13			
761£	EEC remote sensing	B K Wyatt	5 13			
778£	Loss of agricultural land	R G H Bunce	13			
781£	Land use changes over chalk aquifers	R M Fuller	13			
806	Assessment of LANDSAT value for land use	B K Wyatt	13			
822*	LANDSAT classification and vegetation	CM Carrier	E 10			
0000*	survey of Bhutan	C M Sargent	5 13			
823£*	Ecological review of North Canford Heath,	NLD Makk	4 10			
	Dorset	N R Webb	4 13			
14 Ch	emical and technical sciences, as a service to ITE					
	me Leader: JNR Jeffers					
	up: S E Allen					
378	Chemical data bank	S E Allen	14			
484	Chemical technique developoment	J D Roberts/				
	·	P Freestone	14			

485 487 489 490 491 771	6 7 9 0 1 £	Chemical support studies Engineering development Microprocessor development studies Glasshouse and nursery maintenance Photographic development Radiochemical development Chemical data bank (Monks Wood)	S E Allen G H Owen C R Rafarel R F Ottley P G Ainsworth J A Parkinson K R Bull	14 14 14 14 14 6 14 5 8 14
788	3	Electron-microscopy of algae and protozoa	K J Clarke	14
804	1	Effect of changing environment on plant growth	E J White	14
15.	Sys	tems analysis and biometrics		
Prog	gramr	ne Leader: J N R Jeffers		
306		up: C Milner, M D Mountford, E D Ford Statistical analysis of spatial patterns	P Rothery	15
307		Index of eggshell thickness	P H Cryer	15
376		Statistical training	C Milner	15
377	7	Historical aspects of environmental		
		perception	J Sheail	15
402		Biometrics advice to NERC	M D Mountford	15
426		Preparation of sulphur review documents	I D Nicholson	6 15
434		ITE computing services	C Milner	15
457		Grazing models	C Milner	4 15
503		Development of systems analysis	J N R Jeffers	15
518		UNESCO MAB Information System	J N R Jeffers	15
591	ı	Terrestrial Environmental Information System	B Wyatt	15
602	2	Modelling sports turf wear	T W Parr	4 15
610		Computerization of CCAP records	J R Baker	15
613		Computerization of ITE/NERC costing	3 IT Daker	13
010		procedure	M D Mountford	15
621	1	Models of rabies epidemiology	P J Bacon	11 15
622		Applications of systems analysis	P J Bacon	15
624	4	Population genetics	P J Bacon	8 10 15
629	9	Systems analysis of Egyptian deserts-		
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663		Estimation of abundance of populations	M D Mountford	15
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754	4£	Development of bilateral link with IES, Khartoum	J N R Jeffers	15
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Theses and other publications by research students supervised, wholly or partly, by ITE staff 1978-82

J. M. Chard (University of Essex; ITE supervisor Dr J. C. Frankland) Chard, J. M. 1981. Development of an immunofluorescence technique for studying the ecology of Mycena galopus (pers. ex Fr.) Kummer. PhD thesis.

I. D. Edwards (University of Aberdeen; Dr D. Jenkins, Dr B. W. Staines)

Edwards, I. D. 1980. The conservation of the Glen Tanar native pinewood. PhD thesis.

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R. Henderson (University of Edinburgh; Dr E. D. Ford)

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L. May (Paisley College of Technology; Dr A. E. Bailey-Watts) May, L. 1980. Ecology of planktonic rotifers at Loch Leven, Kinrossshire. PhD thesis.

(Dr May is now a member of ITE staff; any other publications are included in the main list, Section V)

K. Newell (University of Lancaster; Dr J. C. Frankland) Newell, K. 1980. The effect of grazing by litter arthropods on the fungal colonization of leaf litter. PhD thesis.

A. M. Nicholson (University of Southampton; Dr P. Merrett) Nicholson, A. M. 1980. Ecology of the sand lizard (Lacerta agilis L.) in southern England and comparisons with the common lizard (Lacerta vivipara Jacquin). PhD thesis.

J. K. Nicholson (University of London; Dr D. Osborn)

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L. Smeeton (University of Southampton; Dr M. V. Brian)

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Smeeton, L. 1981. The source males in *Myrmica rubra* L. (Hym. Formicidae). *Insectes soc.*, **28**, 263–278.

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A. J. Truscott (University of East Anglia; Dr D. S. Ranwell) Truscott, A. J. 1978. Growth of *Enteromorpha* and salt marsh development in the Stour estuary, Essex. PhD thesis.

A. Tve (University of Cambridge; Dr R. K. Murton)

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A. Village (University of Edinburgh; Dr I. Newton)

Village, A. 1980. The ecology of the kestrel (Falco tinnunculus) in relation to vole abundance at Eskdalemuir, south Scotland. PhD thesis.

(Dr Village is now a member of ITE staff; any other publications are included in the main list, Section V).

M. S. Warren (University of Cambridge; Dr E. Pollard)

Warren, M. S. 1981. The ecology of the wood white butterfly *Leptidea sinapsis* L. (Lepidoptera, Pieridae). PhD thesis.

G. R. Wilson (University of Aberdeen; Dr A. Watson)

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Radionuclide pollutants in natural ecosystems. 3pp.

Commission of European Communities. ITE Project 553.

Fuller, R. M. 1982.

Land use identification from aerial photography. (Land use changes over chalk aquifers). 29pp.

Anglian Water Authority. ITE Project 781.

Fuller, R. M. 1982.

Vegetation mapping of Broadland using aerial photographs. 13pp.

Broads Authority. ITE Project 684.

Harris, M. P. & Osborn, D. 1982.

Birds of prey and pollution. Part IV. PCB residues in PCB-dosed puffins. 2pp.

Nature Conservancy Council. ITE Project 181.

Horrill, A. D. 1982.

Radionuclides in terrestrial ecosystems. Concentrations and spatial distribution of radioactivity in saltmarsh. 70pp.

Department of the Environment. ITE Project 553.

Jenkins, D. & Conroy, J. W. H. 1982.

Monitoring otters in Shetland. 11pp.

Shetland Oil Terminal Environmental Advisory Group. ITE Project 715.

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The fresh waters of Tayside. 300pp.

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Marrs, R. H. & Lowday, J. E. 1982.

Bracken and scrub control on lowland heaths. 79pp.

Nature Conservancy Council. ITE Project 599.

Newton, I., Bell, A. A. & Haas, M. B. 1982.

Birds of prey and pollution. Part I. Monitoring. 26pp.

Nature Conservancy Council. ITE Project 181.

Osborn, D., Bull, K. R. & Every, W. J. 1982.

Birds of prey and pollution. Part II. Mersey bird mortality. 25pp.

Nature Conservancy Council. ITE Project 181.

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Birds of prey and pollution. Part III. Incident investigations. 5pp.

Nature Conservancy Council. ITE Project 181.

Picozzi, N. 1982.

Research on black grouse in 1982. Progress report.

World Pheasant Association. ITE Project 764.

Pollard, E. 1982.

Butterfly monitoring scheme. Progress report.

Nature Conservancy Council. ITE Project 204.

Radford, G. L. 1982.

Site information system. 50pp.

Nature Conservancy Council. ITE Project 732.

Stebbings, R. E. 1981.

Population ecology and specialist advice on bats. 31pp.

Nature Conservancy Council. ITE Projects 291/292.

Sykes, J. M. & Horrill, A. D. 1982.

Regeneration in a series of enclosures at Black Wood of Rannoch. 47pp. Nature Conservancy Council. ITE Project 549.

Webb, N. R. 1982.

An ecological review of ECC Ball Clays' planning application sites in southeast Dorset. 12pp.

Land & Properties (ECC) Ltd. ITE Project 814.

Commissioned research contracts

listed by customer organizations for 1982

COMMISSIONED RESEARCH CONTRACTS UNDERTAKEN DURING 1982

Nature Conservancy Council 13 20 20 20 50 77	04 08/9/11, 557, 656 91/2 99 18 96/800	Project title Toxic chemicals and pollutants Butterfly monitoring scheme Recording of data on individual species Population ecology of bats Bracken control on heathland Effects of drainage on wildlife Poole harbour survey Impact of deer on woodlands Advice and convises
55 57 60 62	08 53 73 09 25 (pt)	Advice and services Arboriculture Radionuclides Amenity grass River communities (joint FBA) Upland management and water quality (joint FBA/IH)
	00 63	Ecological guidelines for locational strategies Biological effects of chemicals in the environment
(Department of Energy)	74	Experimental assessment of native and naturalized species
	45	Land availability for wood energy plantations
	78 90	Monitoring land use changes Effects of atmospheric pollutants on agricultural land
80	02	Environmental sampling in west Cumbria
National Coal Board 36	60	Tree planting study
72	27	Soil compaction on open-cast sites
Anglian Water Authority 78	81	Aerial map interpretation
Broads Authority 68	84	Mapping Broadland from aerial photographs
Sports Council —	_	Amenity grass drainage
Highland Regional Council 74	47	Highland region land classification
	15	Shetland otters
Welsh Office 16	61 (pt)	Fluorine pollution
62	25 (pt)	Water quality (joint IH)
	61 (pt)	Fluorine pollution
	53 (pt)	Radionuclides
	25 (pt)	Land management and water quality
67	74	Native and naturalized species for energy production
UNESCO 75	59	Toxic chemicals
	64	Black grouse studies
Expected level of income from commission		

Expected level of income from commissioned work for the financial year 1982/83

	(£1000)
Nature Conservancy Council	260
Department of the Environment	255
Other Government Departments	89
Public bodies and other UK organizations	86
Overseas customers and contracts	71
•	761

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