Natural Environment Research Council

Institute of Terrestrial Ecology

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The cover shows clockwise from the top:
juvenile meadow pipit. Photograph K. C. Walton; cinnabar moth. Photograph J. P. Dempster; flower of obeche, Nigerian timber tree. Photograph K. Longman; leaves of walnut naturally infected with cherry leaf roll virus. Photograph J. I. Cooper; military orchid. Photograph Lynne Farrell; Loch Leven, taking samples from deep water. Photograph I. R. Smith. Centre photograph is of a tigress, Similipal Reserve. Photograph A. D. Horrill.

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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.

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

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

Contents

Introduction

In this, the fourth Annual Report to be produced for the Institute of Terrestrial Ecology, we again review only part of the work of the Institute, concentrating mainly on projects which have been completed, or which have reached a stage at which summary of the conclusions is possible.

ITE has changed in many ways since its formation in 1973. It has not increased in size or in the geographical distribution of its research stations and staff, but the programme of research has been greatly modified, partly as a result of the changes introduced by the Rothschild report on Government supported research and development, and partly as a result of new fundamental research which has been developed within the Institute. The objectives of the Institute, defined as:

> *'To improve understanding of the factors determining the structure, composition and processes of terrestrial ecological systems and the abundance and performance of individual species and organisms.*
>
> *To provide a sounder scientific basis than is presently available for predicting and modelling future environmental trends, especially those resulting from man's activities, hence permitting a more critical assessment of the need for, and likely benefits of, specific measures to protect and manage the environment.'*

have helped to focus the many disciplines and to define the research opportunities in the terrestrial environment.

This Annual Report indicates many of the ways in which our research is developing. It also indicates some of the opportunities and initiatives which will need to be taken in the future, within the severe financial and resource constraints of today's world.

J.N.R. JEFFERS
Director

2 May 1978

The classification of ITE research

One of the questions which is frequently asked of a research organisation like ITE is 'How much of your research is devoted to some particular aspect or branch of science?' or, alternatively, 'Can you give me a breakdown of the research undertaken by your Institute in terms of scientific disciplines, habitats, organisms, or location?'

These questions are not easy to answer. To begin with, it is not always clear what criteria should be included in the answer. Should we, for example, include only the amount of time spent by research staff, and so express the amount of research undertaken in certain fields in terms of what is perhaps the most limiting resource, i.e. staff time and expertise? Alternatively, should we add the current expenditure devoted to particular lines of research to the staff costs, so as to give some expression of the amount of time spent in travelling, field work, subsistence and the consumption of consumable materials? Much of modern scientific research cannot be done without considerable investment in capital equipment, like computers, microscopes, growth cabinets, animal houses, chemical analysis, photogrammetry, etc. Some of this equipment can be charged to individual projects, but most, including the research facilities and buildings themselves, are a charge upon the whole Institute, and must be apportioned in some way to the individual projects. In addition there are central administrative overheads of both the Institute and, pro-rata, of the Council which must be included in the calculation of full economic charges, together with provision for persons and other benefits for the staff of the Institute. The meaningfulness of any comparisons will necessarily depend upon the choice of criteria for those comparisons, and it is not easy to decide how that choice might best be met. Strictly speaking, since much of our research is relatively long-term, we should also include a factor which enables the investment at different periods of time to be discounted at compound interest.

As if these difficulties were not sufficient, there are also problems in the design of any useful classification. No single classification of research projects can be both exhaustive and mutually exclusive, with the result that there are inevitable overlaps between different categories within any classification. Indeed, assigning particular projects to any one category of a classification may frequently be arbitrary. When these difficulties are taken with the continual changes in programmes and projects, such comparisons must frequently be qualified.

Nevertheless, this introduction presents some simple classifications of the research in ITE at the end of 1977, based on the full economic cost of the research, i.e. cost including staff time, current expenditure, capital investment, and ITE and NERC overheads. Several alternative ways of looking at the research programme are presented, together with some suggestions for correcting deficiencies in the research, and some suggested cautions in the interpretation of the figures presented.

The total cost of ITE research in the financial year 1977/78 is summarised in Table 1. Of a total cost of nearly four million pounds, 44 per cent is taken up by salaries and wages, 23 per cent in recurrent costs, and 29 per cent in overheads. The investment in capital equipment was less than 4 per cent of the total. Receipts from commissioned research and other sources, while only a little less than £1 million, represent about 24 per cent of the full economic cost of maintaining ITE.

Table 1 Total cost of ITE research in financial year 1977/78

Expenditure	Full economic cost (£K)
Salaries and wages	1760·3
Recurrent costs	924·5
Capital investment	154·0
ITE/NERC overheads	1151·4
TOTAL	3990·2
Receipts	954·0

The simplest exhaustive and mutually exclusive classification of ITE projects is obtained by allocating projects to the Subdivisions of their project leaders, and the full economic cost of the science vote and commissioned projects of the ITE Subdivisions is shown in Table 2. The total cost of commissioned projects is greater than receipts because, for some projects, ITE makes a contribution to the work commissioned by customers. The cost of projects within the Animal Ecology Division represents approximately 38 per cent of the total ITE budget, while that of the Plant Ecology Division represents 51 per cent. Within the Animal Ecology Divison, roughly 18 per cent, 13 per cent and 6 per cent of the cost of ITE's activities is distributed to the Vertebrate Ecology, Invertebrate Ecology and Animal Function Subdivisions, respectively. Within the Plant Ecology Division, the costs of the projects within the Plant Biology, Plant Community Ecology and Soil Science Subdivisions are roughly 19 per cent, 20 per cent and 12 per cent, respectively. Plant Community Ecology alone carries about 42 per cent of the total cost of the commissioned projects. The Scientific Services projects represent only 11 per cent of the total cost of ITE, with the Data and Information Subdivision representing more than half of this figure, but this per-

Table 2 Allocation of ITE costs to Divisions and Subdivisions

	Nos of scientists	Full economic cost (£K)		
		Science vote projects	Commissioned projects	Total
Vertebrate ecology	31	521	210	731
Invertebrate ecology	33	413	114	527
Animal function	14	206	43	249
Animal ecology	79	1140	367	1507
Plant biology	50	651	107	758
Plant community ecology	44	368	444	812
Soil science	22	360	99	459
Plant ecology	117	1379	650	2029
Data and information	26	215	28	242
Chemistry & instrumentation	25	98	—	98
Algal & protozoan culture	14	113	—	113
Scientific services	66	426	28	454
Total	263	2945	1045	3990

centage does not include the contributions made by members of the Subdivisions of the Scientific Services Division to other projects.

The average project cost per scientist is approximately £15K per year, but ranges from £4K a year for the scientists of the Chemistry and Instrumentation Subdivision to £24K for the scientists of the Vertebrate Ecology Subdivision. There is little difference between the average project cost per scientist for the remaining Subdivisions of the Animal and Plant Ecology Divisions, but the average project cost per scientist for the Subdivisions of the Scientific Services Division are all considerably lower, at £8K and £9K for the Algal and Protozoan Culture and Data and Information Subdivisions, respectively.

An alternative classification is given in Table 3, showing the allocations of the cost of science vote and commissioned projects by locations of the project leader. Fifty-six per cent of the total project costs are incurred at the three larger stations of ITE, namely those at Monks Wood, Merlewood, and Edinburgh. The average project cost of maintaining one member of staff (including both scientists and non-scientists) is £11.7K, but varies from £10K at Merlewood to approximately £17K at Norwich. The figure for Cambridge is artificially low because the costs of the eighteen members of the executive and clerical staff at that location are distributed in the overheads of projects at other stations.

Table 3 Allocation of ITE costs to research stations and locations

Locations	Nos of staff	Full economic cost (£K)		
		Science vote projects	Commissioned projects	Total
Monks Wood	78	513	351	863
Merlewood	64	528	95	623
Edinburgh	56	526	226	751
Banchory	36	462	116	578
Cambridge	36	157	0	157
Bangor	35	349	134	483
Furzebrook	25	342	8	350
Norwich	11	69	116	185
All locations	341	2945	1045	3990

Only 68 per cent of the full economic cost of ITE is involved in projects which are concerned with specific organisms. Twenty-one per cent of the cost is devoted to vertebrates, 12 per cent to invertebrates, and 36 per cent to plants. Some 19 per cent is devoted to research on trees and shrubs, and approximately 11 per cent is devoted to research on birds. The other groups of

Table 4 Allocation of costs where projects are species-oriented

Organisms	No of projects	Full economic cost (£K)		
		Science vote projects	Commissioned projects	Total
Deer	9	119		119
Small mammals	5	68		68
Birds	30	358	101	459
Other vertebrates	30	149	27	176
All vertebrates	74	694	128	821
Moths and butterflies	12	52	47	99
Ants	12	110		110
Other invertebrates	37	198	66	264
All invertebrates	61	360	113	473
Algae and protozoa*	9	201		201
Fungi, lichens, bryophytes & ferns	18	138	17	155
Trees and shrubs	57	571	206	777
Other flowering plants	30	192	106	298
All 'plants'	114	1102	329	1431
Totals for species – orientated projects	249	2156	570	2725

* Although animals, grouped with algae for organisational convenience.

organisms shown in Table 4 all occupy considerably smaller proportions of the total cost.

Similarly, only 53 per cent of the cost of ITE is attributable to specific habitats (Table 5). Three per cent of the cost is related to work on Antarctic, tundra, and montane habitats, with upland habitats taking a further 8 per cent. Woodland and forest habitats occupy some 7 per cent with lowland grassland and heaths a further 4 per cent. Urban and industrial habitats take up some 7 per cent, of ITE's effort, and coastal, estuarine, and island habitats some 10 per cent. Freshwater habitats occupy a surprisingly large proportion of the ITE research effort, nearly 13 per cent. An equally surprising, but low, percentage of ITE's research devoted to soil habitats, 2 per cent, is partly a reflection of the past history of ITE, and represents one of the major areas for development in the future. It is expected that the research on these habitats will be increased as rapidly as controls on expenditure will allow.

Table 5 Allocation of costs where projects are habitat-oriented

Habitats	No of projects	Full economic cost (£K)		
		Science vote projects	Commissioned projects	Total
Antarctic, tundra and montane	9	107		107
Upland	23	209	111	320
Woodland & forest	26	230	55	285
Lowland grassland and heaths	23	112	52	164
Urban/industrial	13	147	128	275
Coastal/estuaries	19	125	141	266
Islands	10	120		120
Freshwater	27	367	143	510
Soils	10	63		63
Totals for habitat-orientated projects	160	1480	630	2110

Research projects related to various human influences account for some 46 per cent of the total cost of ITE (Table 6). The largest share of these projects is still that of conservation, accounting for approximately 16 per cent of the total. Pollution is the second highest of the human influences, with 12 per cent, and land use planning follows shortly afterwards with some 10 per cent. Habitat management and the processes of reclamation, protection, and recolonization occupy only 3 per cent and 5 per cent, respectively.

Table 6 Allocation of project costs by human influences

Human influences	No of projects	Full economic cost (£K)		
		Science vote	Commissioned	Total
Land use planning	26	193	193	386
Pollution	28	306	172	478
Habitat management	20	80	53	133
Reclamation/protection/ recolonization	17	124	77	201
Conservation	45	398	221	619
Total	137	1101	716	1817

Finally, about 77 per cent of the cost of ITE can be attributed to specific orientations of particular projects. Of these orientations, survey and monitoring account for 19 per cent, and population dynamics for 17 per cent. Taxonomy and morphology, and genetics and physiology account for a further 12 per cent and 11 per cent, respectively, while autecological projects account for about 10 per cent (Table 7). Systems analysis and modelling, chemistry and instrumentation, and data processing, account for 2 per cent, 2 per cent and 4 per cent of the cost, respectively. The table indicates the present emphasis on survey and monitoring, and on population dynamics. The differentiation between population dynamics and autecology is not, however, clear-cut, since most autecology involves some element of population dynamics.

Table 7 Allocation of project costs by research orientation

Orientation	No of projects	Full economic cost (£K)		
		Science vote	Commissioned	Total
Survey & monitoring	49	255	502	757
Taxonomy/morphology	38	303	162	465
Genetics/physiology	21	394	50	444
Population dynamics	43	582	93	675
Autecology	27	340	45	385
Systems analysis/ modelling	18	98	10	108
Chemistry and instrumentation	12	96	7	103
Data processing	21	80	68	148
Total	229	2148	937	3085

While these tables are necessarily somewhat arbitrary, and are based on only one criterion of cost, they do at least indicate the general direction of current research in ITE. The full list of projects given in Section V of this

Report further emphasises the existing interests of ITE, but gives little indication of likely trends in future development. It is also apparent that there are some major imbalances in the ITE research programme at present, which will need to be corrected as soon as possible in the future, although the room for manoeuvre is relatively slight in the present economic climate. Ecological research is necessarily a long-term venture, and the projects which have already been started must be brought to completion, or, at least, to a satisfactory termination, before moving staff and equipment on to new projects. Much will also depend upon the requirements of customers, although ITE may be expected to influence the choice of research to be commissioned by emphasising those areas which are most likely to lead to development for practical purposes.

J.N.R. JEFFERS
Director

Longer research reports

Introduction

This section of the report contains descriptions of research which has been completed or has reached a stage justifying rather longer reports than those contained in Section III.

The section begins with a brief summary of a major publication marking the completion of IBP studies on the structure and function of moorland/dwarf shrub and montane grassland ecosystems. These studies have been a major commitment for ITE staff at several research stations, in collaboration with staff now in the Nature Conservancy Council and at universities.

There then follow three reports on various aspects of plant ecology, dealing, respectively, with the influence of trees on soil properties, bryophyte ecophysiology in polar regions, and the effects of the management of grassland and scrub on invertebrate fauna. All three reports emphasise the importance of a thorough understanding of the physiology and processes of ecological systems, particularly when attempts are made to manage those systems. The last of the reports also emphasises the close relationship between plants and animals within any system.

How animal populations are regulated is a central issue in ecology, and the report on the population ecology of red grouse summarises the results of twenty years' intensive research on the fluctuations in numbers of that animal, and suggests that, while changes in food caused by weather can lead to fluctuations in population, changes in the bird's behaviour may also be the proximate cause of a decline in population. The report on avian photoperiodicity also emphasises that a proportion of ITE's fundamental research is aimed at understanding the mechanisms controlling seasonal cycles in animals.

Finally, this section contains a report on discrimination between clones of *Betula pubescens* by measurements of leaf shape. The measurement of subspecific variation is an important part of ITE's research, closely linked to an increased understanding of genetic variability and the plasticity of organisms in response to management and changes in environmental conditions.

PRODUCTION ECOLOGY OF BRITISH MOORS AND MONTANE GRASSLANDS

Production Ecology of British Moors and Montane Grasslands, volume 27 in Springer Verlag's Ecological Study Series, was published in 1977. The book, which marks the completion of IBP studies done at selected sites by a team including ITE, NCC and University colleagues, gives detailed descriptions of the structure and function of moorland/dwarf shrub and montane grassland ecosystems.

Observations at Moor House National Nature Reserve, the main moorland research site, were supported by others on lowland heath in southern England and moorlands in Scotland, enabling a broader appraisal of dwarf shrub ecosystems in relation to soil fertility, climate and management. Comparative studies on grassland ecosystems were concentrated on a montane site at Llyn Llydaw, Y Wyddfa (Snowdon) National Nature Reserve.

Primary production at upland sites was low, and negatively correlated with altitude, largely reflecting the short growing season (175 days at Moor House and 200 days at Llyn Llydaw). Annual above-ground production on blanket bog at 550 m at Moor House was 250 gm^{-2}, intermediate between the 400 and 165 gm^{-2} produced by similar communities in NE Scotland at 100 and 900 m respectively. Aerial growth of montane grassland on brown earth at Llyn Llydaw (488 m) was originally estimated at 464 gm^{-2} yr^{-1} but was found to be nearer 1145 gm^{-2} yr^{-1} when corrected for losses between successive samples, an essential correction when using destructive methods of harvesting. These data for Llyn Llydaw suggest that the aerial growth of *Festuca-Agrostis* grassland at Moor House was underestimated by 190 gm^{-2} yr^{-1}.

Acid blanket bog peat produces vegetation of low nutritive value, palatability and digestibility, with less than 5% of total primary production being assimilated by herbivores, compared with 23% (90% of harvestable clipped above-ground production) on montane grasslands. Vertebrates other than sheep and grouse are rare, and numbers of species and individuals of herbivores low, primarily through the quality, rather than quantity, of available food. Sheep on the bog average 0.13 ha^{-1}, and the standing crop of vegetation is high, whereas the denser populations on grasslands (7.4 ha^{-1} at Moor House and 12.6 ha^{-1} at Llyn Llydaw) remove most of the production, cropping the grass to a short turf. Similarly, red grouse territories are larger than can be accounted for solely by availability of *Calluna* food. The birds consume less than 5% of the shoot and flower production, selecting material of higher nutritive value.

Secondary production was less on moorlands than on grasslands; production by sheep averaged 22.8 kg ha^{-1} yr^{-1} at Moor House, compared with 64 kg ha^{-1} on the Llyn Llydaw grasslands. Total herbivore and decomposer fauna production on the Moor House blanket bog amounts to only 7 gm^{-2} yr^{-1}, whereas on limestone grassland it is 40 gm^{-2} and on alluvial grassland 50 gm^{-2} yr^{-1}. Annual production of slugs at Llyn Llydaw was 2 gm^{-2}, and, although their consumption was estimated at only 16.3 gm^{-2} yr^{-1} i.e. 7% of the amounts consumed by sheep, they can have a considerable impact on the ecosystem as their period of maximal intake, like that of sheep, extended from October to April when primary production was at a standstill.

The lack of faunal diversity on the bog was attributed to (i) the absence of tall shrubs and trees as a result of exposure, and (ii) management practices such as grazing and burning. The proportion of 'top predators' to herbivores is low, and would be even lower without the variety inherent in the vegetation mosaic provided by the streamsides amd mineral soils. The severe climate is probably responsible for this lack of top predators, and also restricts parasitism.

The fertility of mineral soils is linked with large populations of earthworms and dung beetles, and root feeders may ingest much of the below-ground primary production. The smaller numbers of these groups in peat soils, and the limited vertical distribution of soil fauna result from acid and waterlogged conditions and probably reflect the non-nutritious bog vegetation. Soil animals, like grouse, seem to select nutritious food with relatively large concentrations of minerals, and, as a result, appreciable amounts of primary production remain uningested.

The restricted numbers and activity of most microbes in peat, like those of fauna, reflect poor substrate quality – particularly the lack of carbon and nitrogen – as well as acid pHs, low temperatures and the lack of oxygen. However, estimated input of nitrogen from microbial fixation ($\langle$ 5 gm^{-2} yr^{-1}) and rainfall (0.8 gm^{-2} yr^{-1}) apparently compensate for nitrogen losses by immobilisation, erosion and leaching, producing a possible nitrogen gain of about 2 gm^{-2} yr^{-1}.

The combined activities of fauna and microbes result in the decomposition of organic matter, rates being determined by environmental factors such as moisture, temperature and pH, by the numbers and activity of decomposers, and the nature of the substrate. Consequently, decomposition and nutrient release are slower in moorland than grasslands, and at depth in the peat profile compared with the surface layers. On a brown earth soil, decomposition at the surface is 2–4 times faster than in peaty podzols or blanket bog litter, and 18 times faster at 16–20 cm depth because the decline in rate with depth is less than in the bog.

The estimates of primary production and decomposition have been tested for compatibility by combining them in a mathematical model for the bog. The model emphasises the importance of litter type, and its slower rate of decay at depth. A further model of the processes involved in peat growth was used to predict peat profile characteristics which were compared with observed values. Productivity, rate of growth in length of plants, the aerobic decay rate and position of the water-table seem to be the most important parameters affecting profile development.

Analyses of nutrient distributions and rates of circulation within the montane grassland, summarised in Table 8, emphasise that the large concentrations of soil nutrients were associated with concentrations in vegetation which are larger than those in blanket bog vegetation. The increased substrate quality influenced consumption by herbivores with rapid circulation through dung, rapid decomposition of litter and greater soil fauna and microflora activity. The budgets for N, P, K, Ca and Mg, percolation experiments and growth studies indicate that P is in short supply during periods of rapid plant growth; yearly differences in production suggest that there is sufficient supply to enable climate to exert its influence, and that P may be regarded as conditionally limiting production. Rates of mineralisation of P during litter decomposition are positively

Table 8 Nutrient budget (gm^{-2} yr^{-1}) for the Agrostis-Festuca *grassland ecosystem (nd = not determined)*

Nutrient	N	P	K	Ca	Mg
Input					
rainfall (average year)	1·84	0·17	0·30	2·60	1·13
In system (to 30 cm depth, gm^{-2})					
organisms (living)	11·14	0·73	3·08	1·92	4·71
living and dead organic matter (ex soil)	17·60	1·73	4·63	3·12	8·42
soil (total)	1 046	302	1 361	277	11 340
In circulation					
in primary production	27·59	2·37	16·30	4·08	7·00
return of dead leaves and roots	10·30	1·01	2·90	1·67	
return of dung and urine	4·03	0·35	3·22	0·81	0·75
return by slugs (vegetation grazed)	0·27	0·04	0·16	0·12	0·06
recirculation and leaching from canopy	11·33	0·77	8·93	1·08	0
Output					
in sheep production	0·32	0·08	0·02	0·14	0·01
exported dung and urine	1·34	0·12	1·07	0·26	0·25
Balance: input-output	+0·18	−0·03	−0·79	+2·20	+0·87
Potential leaching (0–15 cm)	nd	0·15	0·82	4·05	2·34

correlated with temperature and moisture. Thus, conditions favouring prolific plant production may also be those in which substantial mineralisation occurs so enhancing the supply of P. It would be expected that ecosystem production would adjust to the supply to the most limiting factor within restraints imposed by climatic conditions; thus, P may be limiting production at sites when climatic conditions are optimal for growth, whereas climate, particularly temperature, may limit the start of the growing season and the annual primary production.

O.W. Heal and D.F. Perkins

THE INFLUENCE OF TREES ON SOIL PROPERTIES

Background

While ecologists are concerned with ecosystem stability, the interests of land managers are translated into a desire for sustained yields, for which the bases are climate and soil. As yet, climate cannot be controlled, but soil can be managed, and has been, with varying degrees of success, for thousands of years. Traditionally, forest yields have been determined by the natural productive capacity of soil, but, increasingly, they are subject to management practices, including ploughing and the application of fertilisers.

Substantial areas of Britain and of the rest of Europe, where soils developed largely under a cover of broad-leaved woodland, have been replanted with conifers over the last 200 years or so, the trend having greatly accelerated during the last half century. How will this change affect soil characteristics. Will these changes compare with those attributable to ploughing?

Consequences of conifer growth

It has often been claimed that coniferous monocultures are likely to impoverish and degrade soils, with consequent yield losses (Noirfalaise, 1968). Conversely, many broad-leaved species are reputed to be soil improvers. However, words like 'impoverish', 'degrade' and 'improve' need to be set against standards for comparisons. Thus, although liming an acid soil would be an improvement from the point of view of a cabbage, it would be a distinct deterioration from that of an azalea or rhododendron! In central and north-west Europe 'impoverish' and 'degradation' have regularly been used to describe the effects of podzolization.

The literature suggests that there are at least three distinct trends when conifers are grown on soils formerly under broad-leaved species; (i) greater surface accumulation of organic matter, (ii) increased acidity of surface organic and mineral horizons and (iii) an increased rate of podzolization.

(i) Surface accumulations of organic matter

Amounts of surface organic matter accumulated under conifers, 38–46 years old, may be 3 to 11 times greater than under broad-leaved species (Table 9). At Abbotswood, most organic matter accumulated under larch and least under oak. Interestingly, there was more under beech than Douglas fir, and, as a result, it seems inappropriate to write about a conifer effect in contrast to a hardwood effect.

Table 9 Dry weight ($t ha^{-1}$) of surface organic matter, and pH of the top 5 cm of mineral soil 38—46 years after planting a range of trees on a former mixed oak-beech woodland site at Abbotswood, Forest of Dean (Data from Ovington 1953, 1954)

	Dry weight	pH
European larch	35	4·1
Norway spruce	26	4·1
Corsican pine	22	4·1
Scots pine	13	4·0
Beech	11	4·7
Douglas fir	8·3	4·6
Sweet chestnut	4·1	5·2
Pedunculate oak	3·7	5·3

The usually greater surface accumulation of organic matter under conifers is, to some extent, attributable to a positional change within the profile, reflecting different processes of decomposition. Under hardwoods, litter is typically (a) comminuted very quickly by soil-living animals, including earthworms, and (b) mixed into the lower mineral horizons where it continues to be decomposed. In contrast, conifer litter usually lies on the surface for many years, microbial decomposition progressing slowly before needles are comminuted and mixed into the mineral soil; conifer litter appears to be unattractive to earthworms and other soil animals, possibly because of its acidity. Several European studies have shown that, when Norway spruce was planted in place of naturally growing beech, amounts of surface organic matter increased under spruce whereas those in the mineral soil tended to decrease, the two opposite effects having little or no influence overall on total amounts within the whole profile. However, the accumulation of surface organic matter under conifers is not constant, but varies cyclically. Page (1968, 1974) found with five conifer species in North Wales and Newfoundland that the depth of litter increased during the early phases of forest development, but decreased as the stands matured and became more open. Nevertheless, the increased amounts of surface organic matter under some conifers often reflect a real increase in the total amount of organic matter in the differing profiles. This increase has sometimes been interpreted as a 'sink' in which nutrients are immobilized, so impoverishing the soil's potentially available nutrient capital, especially of nitrogen. The validity of this argument is unknown. Part of this organically-bound nutrient pool may be utilizable by fungi forming mycorrhizas with compatible hosts? On balance however, it is probably better to regard surface organic matter as a nutrient reservoir controlling the leaching of nutrients from the profile, which might be expected in acid soils.

(ii) Increased acidity in soil profiles

Both organic and mineral horizons of topsoil are characteristically more acid under conifers than when broad-leaved species are growing (see Table 9), as suggested by reports from many parts of Europe where Norway spruce and Scots pine have been planted in place of naturally occurring beech and oak (Table 10). This acidification seems related to (a) the intrinsically more acidic nature of conifer leaves and litter, and the organic products of their decomposition, and (b) an increased amount of organic matter with concomitant increases in cation exchange capacity, which, if absolute amounts of bases present do not increase, will be filled by hydrogen ions, thus decreasing pH. It is interesting to note that, in Page's studies, topsoil acidity followed a similar but inverse cyclic trend to that already noted for surface organic matter, as would be expected from the cation exchange hypothesis. Page also stated that concentrations of calcium and magnesium tended to follow the same pattern as pH.

Table 10 Increased acidity of natural beech and oak woodland soils after planting Norway spruce and Scots pine

Country of observation	PH decrease after planting spruce or pine (increased acidity)
I Norway spruce	
South Sweden	0·4
North-west Germany	0·2–0·5
South-west Germany	0·1–0·8
South-east Germany	0·3
Czechoslovakia	0–0·9
Czechoslovakia	0·3–1·0
Czechoslovakia	0·2–0·5
West Yugoslavia	0·3–0·8
West Rumania	0·3–0·4
II Scots pine	
East Scotland	0·2–0·7
Czechoslovakia	0·5

There is good evidence that, within the natural, broad-leaved deciduous tree zone of Europe, spruces and pines also cause or accelerate podzolization. This effect however, occurs only on soils liable to podzolize, that is, on well-drained sandy soils, low in clay and bases. Thus, the depth of the eluviated horizon in podzols in North Wales planted with Sitka spruce increased as the stand aged (Page, 1968). Similar evidence for the effects of Norway spruces exists in south and central Sweden, where the incidence of brown forest soils has markedly decreased as the stands of spruce aged (Troedsson, 1972). Many profound soil changes have been attributed to different tree species. Some of these claims have been reviewed and dismissed by Holmsgaard *et al.* (1961) and Stone (1975), many soil differences being erroneously attributed to contemporary vegetation. Other claims involved paired comparisons in adjacent stands of unlike vegetation, but few comparisons were replicated, and possible sources of variation in the soil other than those attributed to vegetation were rarely examined. At one time, it was widely believed that soil changes under spruce and other conifers decreased yields of subsequent plantings, but recent studies in Czechoslovakia, Denmark and Germany have not provided supporting evidence. Differences in the type of humus formed under different species at different sites (usually mull under broad-leaved species, though beech in particular often produces mor, and usually mor under conifers, though mull can occur on particularly base-rich sites) change the physical characteristics of surface soil, but these do not appear to affect tree growth. There is no evidence to suggest that spruces decrease amounts of pore space in the deeper horizons, a change that would lead to gleying.

Effects of birch

Because birches (*Betula pendula* and *B. pubescens*), like other hardwoods, are reputed to be soil 'improvers' (implying that mull humus is formed instead of mor), and because they have sometimes been associated with depodzolization, a project was begun in late 1973 to identify the trends, rates, limits and causes of soil changes attributable to birch on poor moorland soils.

Soils under first generation birch stands of different ages were examined and compared with soils in adjacent areas not invaded by birch. Thirteen sites situated from Sutherland to north Yorkshire were selected; two of the sites were old quarry floors in heather moorland, three were felled Scots pine stands planted on former moorland, and the other seven were on heather moorland. Soil mineralogy, particle size distribution, and buried plant remains, viable seed and pollen were examined so as to gain an impression of site uniformity, edaphic and vegetational, before birch colonization, so providing baselines to judge more recent develop-

*Plate 1 Birch (*Betula *pendula) colonising heather moorland near Advie, Morayshire*

Plate 2 A podzol under the heather moorland seen in Plate 1

Plate 3 A brown podzolic soil, thought to have been derived from a podzol, under 38 year-old birch seen in Plate 1.

Photographs J Miles.

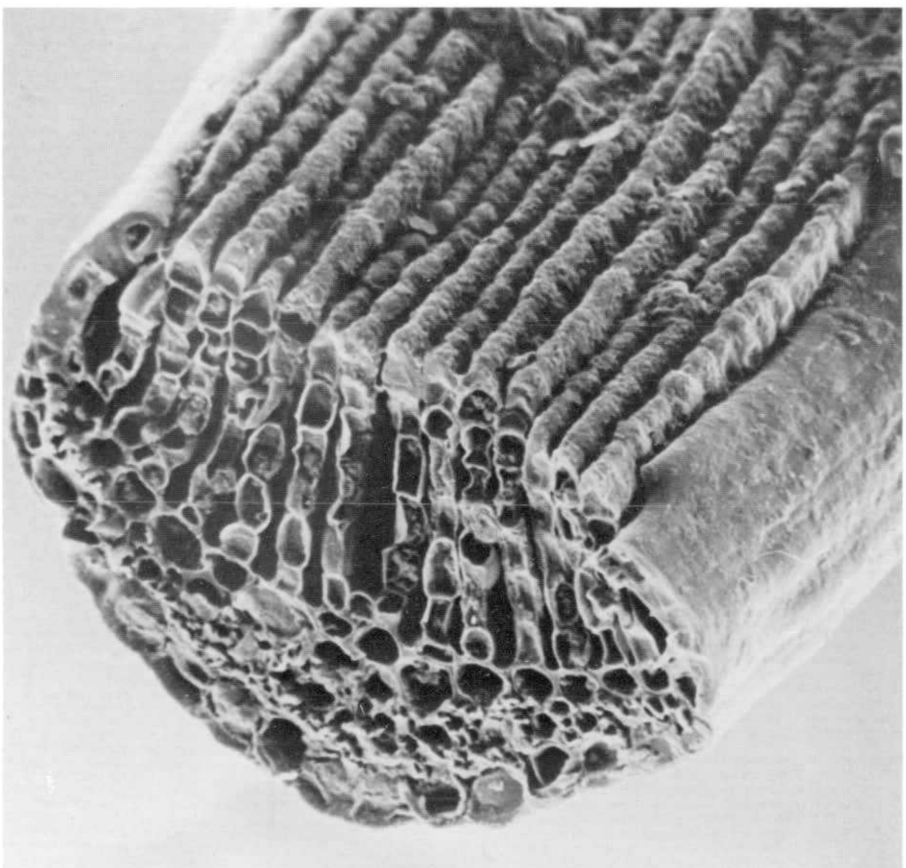

Plate 4 left Photograph of an aerial shoot of Polytrichum alpinum *with its associated underground stem; right An auto-radiograph after exposure of the current season's shoot to* $^{14}CO_2$ *showing that radioactivity is concentrated in the current season's shoot and in the apical zone of an underground branch shoot (Collins and Oechel, 1974) - ground level was immediately below the heavily 'labelled' current season's growth.*

Plate 5 Scanning electron microscope photograph of a transverse section of a leaf of Polytrichum alpinum *showing ranks of chloroplast - containing cells of the lamellae, capped by wax-coated cells. The moss cells have been impregnated with polyethylene glycol to stimulate the turgid state (Idle, 1971) Photographs by N Collins.*

ments. The following analyses were made on (i) the top 5cm of soil-bulk density, loss of weight on ignition, available water capacity and pH; (ii) the top 5cm of soil-ammonium acetate-extractable calcium, magnesium, potassium, sodium and hydrogen, 0.002 N sulphuric acid-extractable phosphorus, total carbon, nitrogen and phosphorus, rate of mineralization of nitrogen on incubation, loss of weight on ignition and bulk density. The extent of podzolization was estimated by determining 3 per cent oxalic acid-extractable iron and aluminium down the profiles, while rates of decomposition were studied at two sites using cotton strips; earthworm populations were estimated at one site. Additionally, birch root systems were described, together with the distribution of extractable and total bases in all horizons. The top 15cm of soil from the different sites were bioassayed by assessing the growth of radishes when 8 weeks old.

Insofar as changes occur, substantially the same trends are apparent at all sites, although the extent and rates of change vary considerably between sites. At a sloping site near Advie in Morayshire, studied by courtesy of the Tulchan Estate, birch colonization has been prolific (Plate1), giving closed-canopy stands after 18 to 26 years. It seems that the four differing stands of birch of different ages are all first generation, growing on former heather moorland podzolic soils; soil in the 'control' heather moorland plot is a well developed podzol (Plate 2). By comparing events in the differently aged stands, it seems that shading eliminates heather, leaving a well-developed ground layer, often with a dense mat of feather mosses, in which heather cannot regenerate, although over 10,000 seeds of the latter can usually be found per 1 m^2. Wavy hair-grass (*Deschampsia flexuosa)* and bilberry (*Vaccinium myrtillus*) predominate, in the new swards, the former especially on more mineral soils, and the latter where an organic surface horizon is better developed. Many of the species present in the original heather moorland disappeared as birch developed, and new species characteristic of grasslands and woodlands appeared (Table 11), e.g. sweet vernal-grass (*Anthoxanthum odoratum*) and slender St John's wort (*Hypericum pulchrum*), because of the changed soil conditions. It was found experimentally that plants such as self-heal (*Prunella vulgaris*), primrose (*Primula vulgaris*) and common violet (*Viola riviniana*) are unable to establish from seed on bare heather moorland soils, but survive on soils in birch stands 26 to 38 years old.

Soil pH, extractable calcium, nitrogen mineralization rate and total phosphorus were greater in soils under birch than under heather, whereas extractable hydrogen decreased (Table 12). The sharp increase in nitrogen mineralization rate and extractable phosphorus from heather to birch, 18 years old, probably reflects a change in the organic substrate from heather to birch litter; the increases in pH and extractable calcium particularly conspicuous under stands of birch, 38 years old, probably in part reflect a temporarily enhanced rate of nutrient input from lower branches shed after canopy closure between 18 and 26 years. Rates of cellulose decomposition also increased appreciably under ageing stands of birch. Changes in physicochemical properties were paralleled by biological changes. Thus radishes grew larger in soils from ageing birch than from heather moorland (Table 12). Similarly numbers of earthworms were conspicuously greater in 38 years old, than in 18 years old, birch 'soils' with an increasing proportion of *Lumbricus terrestris*. It is thought that this greatly increased and changed earthworm population is largely responsible for the elimination of the bleached Ea (or A_2) horizon (Plate 3) by the mechanical incorporation of surface organic matter and enriched minerals of the B horizon, *vide* the increase in A horizon extractable iron and aluminium between 18 and 38 years (Table 12). The tough and fibrous surface mor layer under heather contrasted with the mull humus dispersed through the surface mineral soil under 90 year old birch with intermediate ages of birch clearly showing how the old heather mor layer is gradually broken down and mixed into the mineral soil, with the loss of the Fa horizon and the sharp interface between the Ea and B horizons.

Beneath 90 year old birch, there was an apparent downward trend in extractable calcium, possibly also occurring in total phosphorus and rates of nitrogen mineralization. The early increases after 20–30 years, followed by later decreases, suggest a cyclic trend, in the opposite direction to that noted by Page under some conifers.

Table 11 Changing numbers of vascular plant species found in heather moorland and adjacent series of ageing stands of Betula pendula *(near Advie, Morayshire)*

	Age of stands of B. pendula				
	Heather	18 years	26 years	38 years	90 years
Number of species present as growing plants	12	20	19	24	30
*Total number of species present	16	24	23	28	33
*Total number of heather moorland species absent from the woodland	—	2	3	4	7
*Total number of species present in the woodland not occurring in the heather moorland	—	11	11	15	25

* Includes species present only as buried, viable seed – an important part of any flora

Table 12 Analyses of topsoil (15 cm) from heather moorland and nearby stands of Betula pendula *ranging from 18 to 90 years old*

	Age of stands of B. pendula					
	Heather	18 years	26 years	38 years	90 years	LSD at 5% level
pH (0–5 cm depth)	3·8	3·9	4·0	4·7	4·9	0·1
Extr H (mg dm^{-3})	117	108	109	101	89	25
Extr Ca (mg dm^{-3})	196	201	207	489	319	83
Extr Mg (mg dm^{-3})	114	98	84	142	98	37
Extr K (mg dm^{-3})	168	142	117	139	127	28
Extr Na (mg dm^{-3})	33	33	25	33	30	13
Extr P (mg dm^{-3})	9·6	16·1	12·8	13·5	13·9	6·4
N mineralization after 14 days incubation (mg dm^{-3} $week^{-1}$)	−1·3	25	41	45	40	10
Total N (mg dm^{-3})	2460	2340	2470	2720	2610	590
Total P (mg dm^{-3})	151	210	196	240	232	82
Mean shoot dry weight (mg) of 8 weeks old radish; shoots	8·7	18	43	59	66	18
roots	3·3	16	39	74	77	30
Mean number of earthworms per 1 m^2 (by formalin extraction)	1	5	27	127	78	26
Extr Fe* (mg 100 g^{-1})	173	125	670	590	640	530
Extr Al* (mg 100 g^{-1})	128	150	375	520	480	632

* Soil from the bottom 10 cm of the A horizon

Soil conditions before birch colonization can never be determined conclusively. Evidence obtained from a survey at any one point in time must therefore be interpreted cautiously. Although the deductions made of events at some sites may be seriously confounded with effects of slope (this could be so at Advie), circumstantial evidence does not conflict with the suggestion that birch growth results in a trend towards a brown podzolic or brown forest soil, with the formation of mull humus, increasing topsoil calcium, pH and microbial activity, and, when the soil reserve of bases are high enough, to depodzolization through increased earthworm activity. The origin of the extra calcium is at present unknown, though it seems likely that the birch, which roots more deeply than heather, is tapping a supply deeper down the profile.

To elucidate the mechanisms involved in these soil changes, also their relative importance, several long term experiments are being planned to test the effects of either planting birch on heather moorlands on podzols or felling it from woodlands on brown podzolic soils.

Implications

The evidence suggests that some conifers, in particular spruces, cause surface acidification and accelerate podzolization, whereas some hardwoods, for example birch, decrease surface acidity, and, in a class of nutrient-poor sandy soils low in clay, even cause depodzolization.

Both processes may differ in extent at different stages in the life cycles of the respective tree species, the extent, for the present, being unknown. If these deductions are correct, it seems that the large areas of Britain planted with conifers may be liable to continuing soil acidification and podzolization. In Czechoslovakia, Marzhan (1959) has estimated that up to 400,000 hectares are podzolizing under Norway spruce and Scots pine. Although these conifers are adapted to acid soils, and, as yet, there seems to be no evidence that soil changes under them have caused any decline in yield in successive generations, no-one seems to have examined critically whether these conifers would grow better if brown podzolic soil conditions were maintained–this is quite different from saying that a second generation stand on a podzol is growing no worse than the first generation which created the podzol! On 'susceptible' soils, a podzolizing crop may be undesirable, precluding subsequent rotations with agricultural crops and endangering the establishment of some hardwoods. However, it is conceivable that the trend to podzol may be halted if mixtures including hardwoods were planted. Experience in eastern Europe suggests that podzolization under Norway spruce and Scots pine may be effectively minimized by the inclusion of 10% of hardwoods, with subsequent yield increases.

'Climax' coniferous forests in northern Europe and North America commonly include some hardwoods. Instead of regenerating immediately, conifers often give way to stands of pioneer hardwoods, birch and aspen, only re-establishing numerical predominance when the pioneers die. In these circumstances, the soils will have been subject to the alternating influences of coniferous and hardwood trees, so maintaining a long term balance. It is conceivable that the maintenance and/or establishment of brown podzolic soils by the inclusion of specified hardwoods might minimize the need to apply fertilisers.

J. Miles

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BRYOPHYTE ECOPHYSIOLOGY IN POLAR REGIONS

Although the extensive polar regions of the world include some of the most extreme environments, adaptations enabling plants to grow in them are little understood. This is especially true of bryophytes (mosses), even though they frequently form a more or less continuous layer beneath canopies provided by vascular plants or exist in separate communities, in their own right, in both the Arctic and Antarctic. Mosses also contribute a large part of the biomass of other ecosystems, such as those in uplands. However, apart from notes on taxonomic variability related to habitat factors and a limited number of phytosociological studies, the role of bryophytes in these ecosystems has been little examined. To correct this deficiency, investigations were started by the British Antarctic Survey and the United States Tundra Biome Project of the International Biological Programme at Barrow, Alaska; these investigations have been continued within ITE, where field work in Scotland has been supplemented by field work at Abisko in Arctic Sweden during 1975.

Patterns of growth

Many mosses are periodic in growth, producing clear innate markers delimiting successive seasons (Figure 1). These markers not only provide reference points

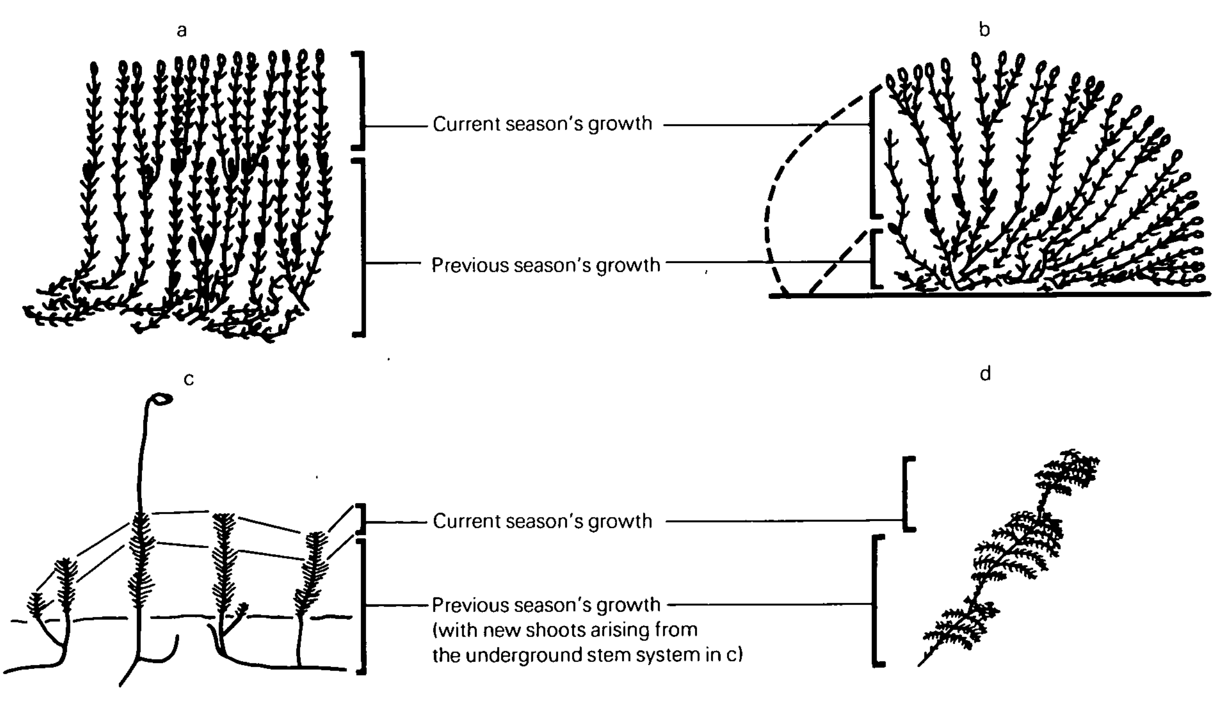

Figure 1 Growth patterns of polar mosses (a) carpets of hydric moss; (b) Hummock growth of the hydric Brachythecium austro-salebrosum; *(c) growth of shoots and underground stems of species of* Polytrichum *including* P. commune *and* P. alpinum; (d) the weft growth of Hylocomium splendens *in boreal forests (Note dead apices in (a) and (b) at interface between previous and current seasons growth)*

against which growth may be measured, but enable assessments of growth in previous seasons to be made. Using the regular bands of dead apices killed by deteriorating weather conditions at the end of each season, it was found that net annual shoot production in hydric moss carpets formed by species of *Campylium, Calliergon, Cinclidium, Drepanocladus, Philonotis* and *Pohlia* (Figure 1a) has frequently exceeded that of vascular plants, being 350 gm^{-2} in some Arctic wet sedge meadows and streamsides and even exceeding 1,000 gm^{-2} in oceanic sites in the Arctic and on islands at the fringes of the Antarctic. In many mosses e.g. *Hylocomium splendens* (Figure 1d), translocation of assimilates from photosynthetically active 'currently' produced tissues to their offspring, or to tissues produced in earlier years, is unlikely because they are functionally independent (Callaghan, Collins and Callaghan, in press). In contrast, translocation of photosynthate plays an important role in the development of new shoots of *Polytrichum alpinum* (Figure 1c), above ground shoots providing photosynthate to support the growth of branch shoots from extensive underground stem systems (Plate 4) (Collins and Oechel, 1974) as happens in many long-lived perennial higher plants. Other mosses, especially those found along the unstable margins of melt streams or on exposed rock faces, may be relatively short-lived. Thus *Brachythecium austro-salebrosum* (Figure 1b) is analogous to an annual spermatophyte in that large, 3 cm diameter hummocks may develop within a season from a collapsed mass of tissue surviving from the preceding season, these hummocks developing in different positions from year to year.

There is, therefore, a great diversity of growth strategies among mosses, notably the differing (i) persistence of photosynthetic activity and (ii) retention of physiological continuity between young and old tissues (Collins and Oechel, 1974, Callaghan, Collins and Callaghan, in press) comparable to the differences when classifying higher plants by life forms.

Like rates of growth, rates of decomposition vary greatly. In carpets of hydric mosses, as much as 25% of the material present at the end of the first year may be lost by the end of the second year. Rates of decomposition are much slower in some other mosses, especially among species of Dicranaceae and Polytrichaceae.

Metabolic activity

Over 70 years ago, Cardot (1908) noted that, 'despite the rigour of the climate, for the most part Antarctic mosses are vigorous and do not present the stunted and weakly appearance that one might expect' (transl.). Being intrigued by the vigorous growth of mosses (Collins, 1973; Collins, 1976; Collins, 1977) in seemingly adverse climates (Collins, Baker and Tilbrook, 1975), it was decided to study the metabolism of some polar mosses and the factors controlling it. Rates of net photosynthesis were assessed in experiments testing different light intensities, temperatures and water regimes. 'Field' experiments were done at Barrow, Alaska, and Signy Island, maritime Antarctic and Antarctic material was also observed in laboratory experiments done in the UK. The optimum temperature for the photosynthesis of an Arctic population of *Polytrichum alpinum* ranged from 10° to 15°C; rates were only 20% less at 5°C and 20°C, with a rate of 45% of optimal being maintained at 0°C. As dark respiration increased, rates of net photosynthesis rapidly decreased at temperatures greater than 20°C (Figure 2). At first sight, optimal temperatures of 10°C to 15°C at saturating light intensities seem higher than might be expected in an area where the mean air temperature for the warmest month is 3.7°C. In the same way, an ability to sustain relatively high rates of net photosynthesis at temperatures of 25°C may appear unnecessary. However, mosses are commonly as warm as this in the middle of the day and, for the mid-day period 10.00 to 14.00 h, temperatures were above those for optimum net photosynthesis for 45.4% of the summer at Barrow. Similar results were obtained from sub-Antarctic moss communities (Longton and Greene, 1967) and from Antarctic Moss Communities (Collins, 1977). Net photosynthesis of *P. alpinum* was maximal at radiant flux densities in excess of 0.15 cal cm^{-2} min^{-1}.

From the array of species surveyed, three generalisations can be made:

(1) there is good general correspondence between the temperatures experienced by the plants and the temperatures over which they are photosynthetically active.

(2) polar mosses, commonly growing in high light intensities, respond to a wide range of light intensities unlike mosses growing in shade conditions

(3) there is a relation, albeit variable, between water availability (in the habitat) and the amounts required to maintain rapid rates of net photosynthesis (Figure 3).

Thus, net photosynthesis of *Calliergon sarmentosum,* which occurs in areas where there is normally a permanent supply of water, is relatively unresponsive to changing water supply compared with *Polytrichum alpinum,* a species of much drier habitats. Interestingly, the leaves of the latter are complex for a moss, with the cells at the top of the photosynthetic lamellae having prominent wax coats possibly restricting water losses (Plate 5).

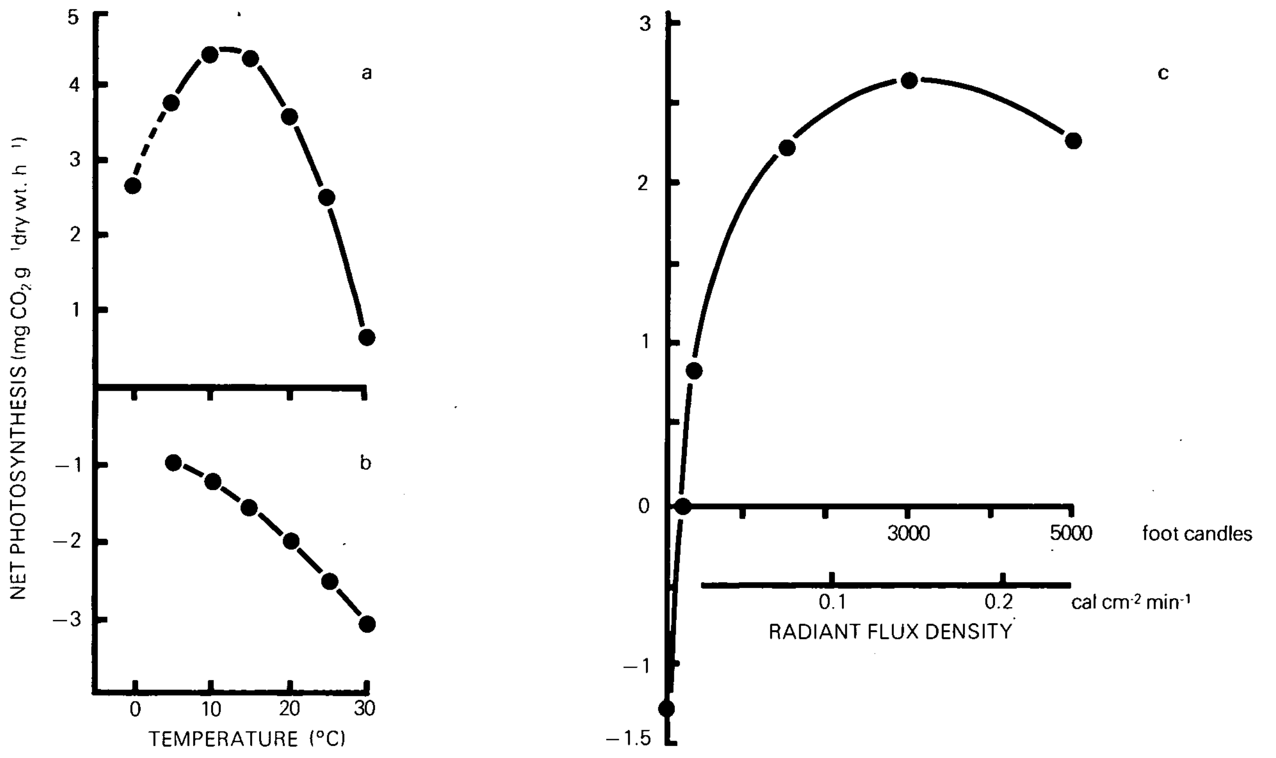

Figure 2 Effects of temperature and light intensities (radiant flux density of photosynthetically active radiation 400 — 700 nm) on rates of net photosynthesis (a) *and* (c) *and dark respiration* (b) *of* Polytrichum alpinum *(from Oechel and Collins 1976)*

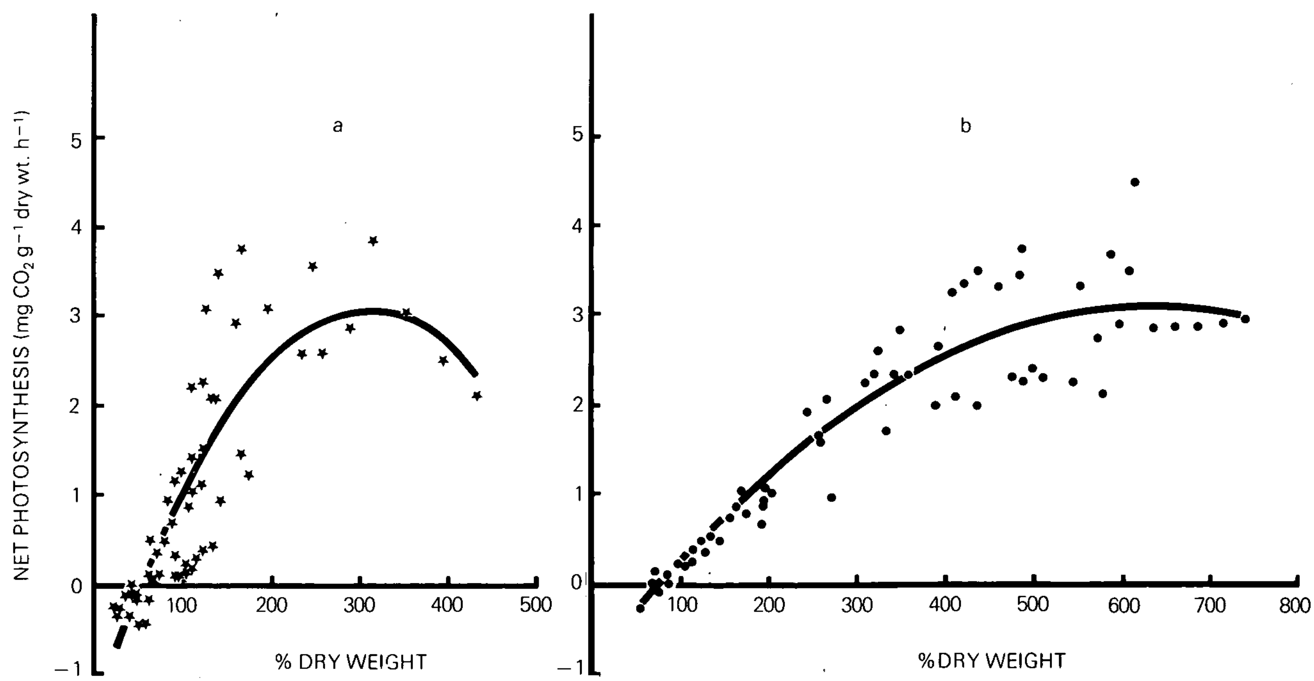

Figure 3 Effects of different tissue water contents (% oven dry weight) on rates of net photosynthesis in Polytrichum alpinum *and* Calliergon sarmentosum *(from Oechel and Collins 1976)*

Effects of previous conditions on subsequent metabolism

In addition to assessing the direct and immediate effects of weather on growth, it is desirable to note the 'residual' influences of earlier conditions. In polar regions, vegetation, particularly in autumn, and even during summer, frequently passes through freeze-thaw cycles (Longton, 1970). Subsequently, there follows the protracted period of winter freezing when plants may remain frozen for six months or more. Drought may occur in two sets of conditions (a) during summer when amounts of precipitation are small and temperatures are high and (b) during winter when snow is often blown from ridges exposing plants to desiccating winds. Three sets of composite conditions may be defined: 'hot, desiccated', 'frozen, desiccated' and 'frozen, hydrated'. The effects of these conditions (hot, 20°C; frozen –20°C) on subsequent activity were assessed by Dr McMannon when working with the British Antarctic Survey. Not unexpectedly many mosses were able to recover normal metabolic activity after periods of stress. Mosses of normally wet habitats, such as *Calliergon sarmentosum* (Figure 4a), were usually less able to withstand periods of freezing than cushion-forming species of exposed habitats, such as *Andreaea gainii* (Figure 4b). Drought and freezing combined frequently affected subsequent metabolism less than the 'frozen hydrated' combination.

These results confirm that previous conditions can greatly influence current photosynthesis. Other studies on material grown in controlled conditions have shown that mosses may become acclimatised, with optimal temperatures for net photosynthesis at high light intensities approximating to mean mid-day moss temperatures. It was found in *Polytrichum alpestre,* for example, that optimum temperatures could shift from around 5°C to between 10°C and 15°C over 15 days, after a change in temperature regimes from –5°C night and 5°C day to 0°C–5°C night and 10°C–15°C day (Collins, 1977). In lichens, acclimatization seems to occur more rapidly (Kershaw, 1977).

Patterns of photosynthetic production in polar mosses

Patterns of photosynthetic activity were monitored directly on mosses near Barrow, Alaska, in the Arctic using infra-red gas analyzers but this has not yet been done in the Antarctic. An idea of probable patterns of activity can be obtained, however, because simulations have been evolved using multiple regression equations linking weather data with those of photosynthesis and respiration in Antarctic material grown in controlled conditions.

It is possible to predict that slow growth can occur under snow at the start of a season prior to the main

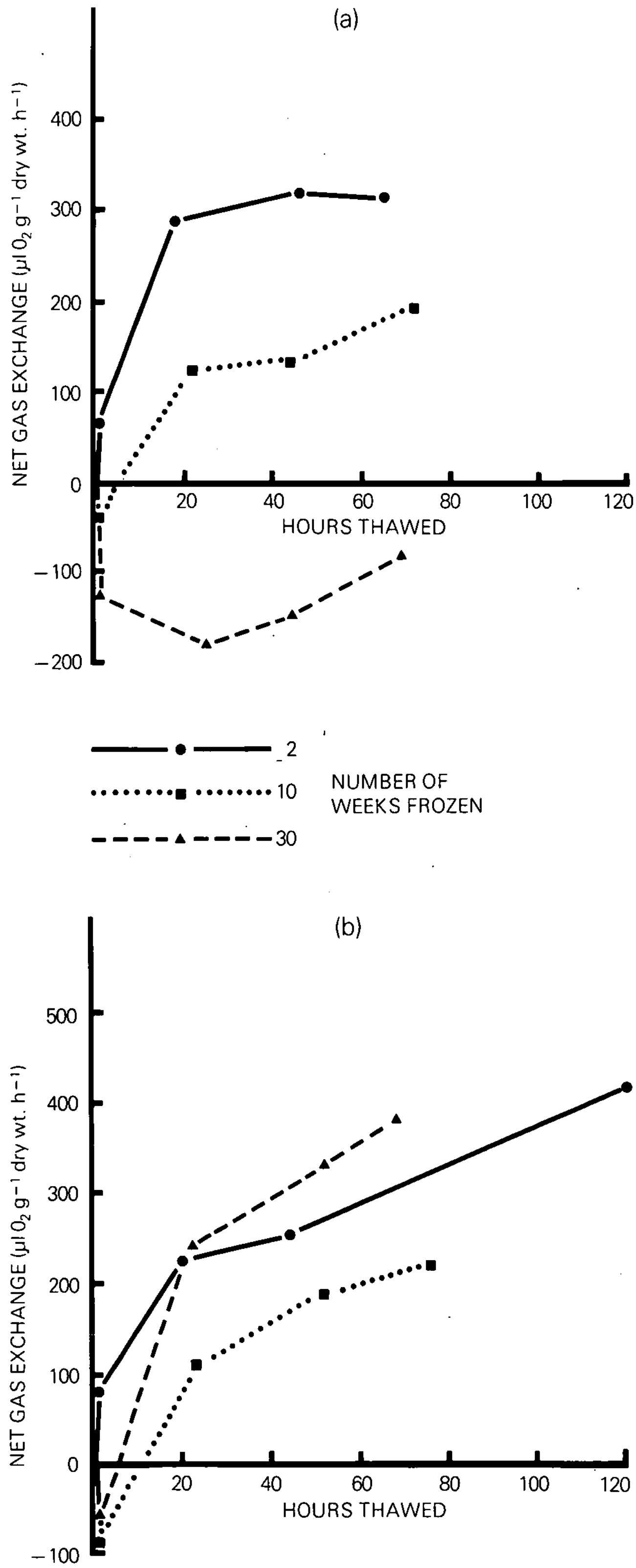

Figure 4 Net assimilation rates, on thawing of (a) Calliergon sarmentosum *and (b)* Andreaea gainii *after being 'frozen, hydrated' for two to thirty weeks*

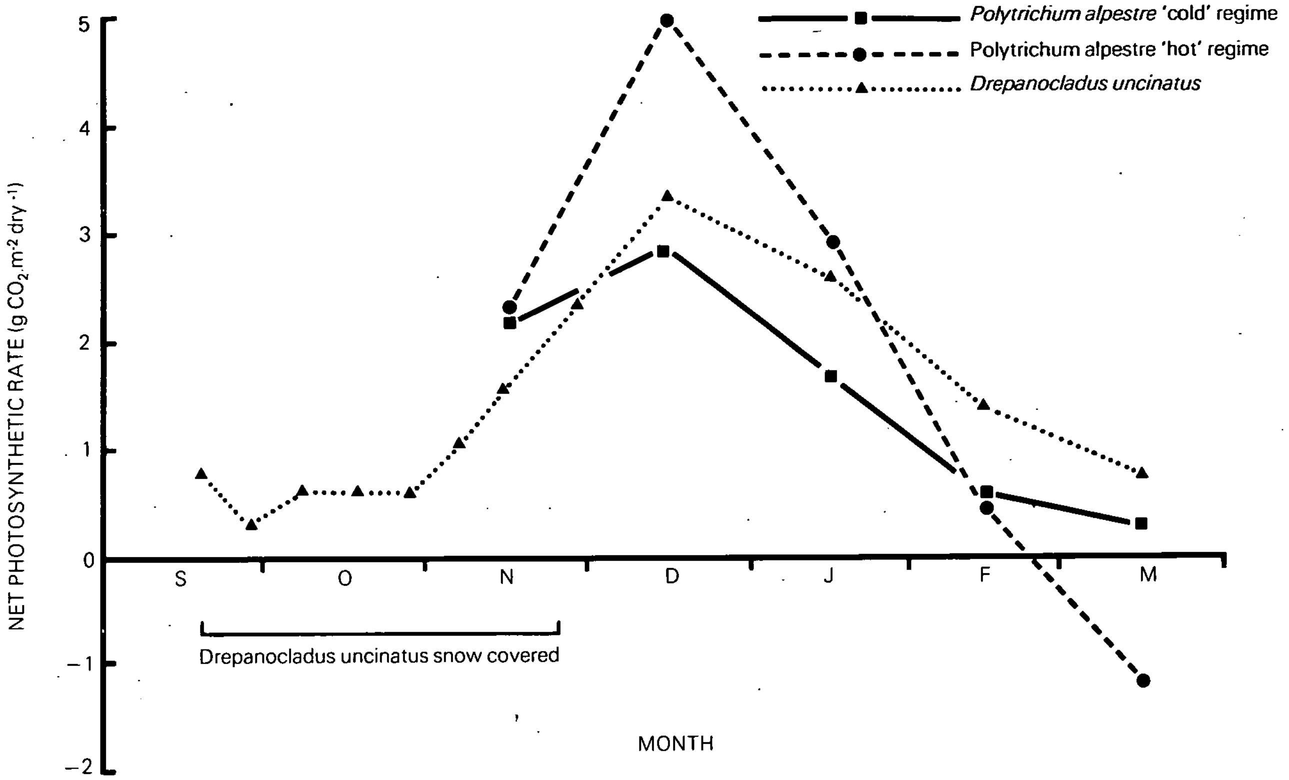

Figure 5 Annual course of mean daily rates of net photosynthesis predicted from multiple regression equations of net photosynthesis on radiation and temperature measured in controlled environmental experiments: Data for Polytrichum alpestre *and* Drepanocladus uncinatus

melt, and that, in mid-summer, high mid-day temperatures can depress rates of net photosynthesis, predictions conforming to field experiences (Collins, 1973; Oechel and Collins, 1973).

Using microclimate data as 'driving' variables, it has been possible to predict net CO_2 fixation for a complete Antarctic season (Figure 5). Slow growth under snow was predicted as occurring from the beginning of September until snow melt occurred just before the solstice in December after which rates of daily fixation progressively decreased. Previous treatments did not affect net photosynthesis in November, but *P. alpestre* previously kept in warm conditions was more active in December and January and less so in February and March than material accustomed to a 'cold' regime. It is probable that acclimatization is a continuous process. When due allowance was made, net fixation for a 120-day season amounted to 361 g CO_2 m^{-2} or 221 g C m^{-2} for *Polytrichum alpestre*. These estimates are paralleled by actual dry matter increments ranging from 340 to 600 gm^{-2}.

Summary

Ecophysiological studies in polar regions show that bryophytes are usually well adapted with habitat colonization being largely controlled by the water-relations of differing species. For maximal rates of net photosynthesis, species colonizing wet habitats must have relatively high water contents; they are seemingly ill-adapted to periods of drought and freezing which, however, they rarely experience. Mosses of exposed habitats require less water and recover rapidly from periods of drought and/or freezing. Although optimal temperatures for net photosynthesis seem to be correlated with prevailing conditions, they can be influenced by preceding weather–acclimatization has been recorded in some species.

Because acclimatization may be more important than previously considered, it is being studied in a population of *Polytrichum alpestre* at a field site in the southern uplands of Scotland. This project forms part of a wider study of the genecology of *P. alpestre* which occurs in the northern and southern hemispheres.

N.J. Collins and T.V. Callaghan

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THE EFFECTS OF MANAGEMENT ON THE FAUNA OF GRASSLAND AND SCRUB

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Grasslands and scrublands (scrub) are classically contrasted as good examples of plagioclimaxes and seral stages respectively. Although these terms embody an important principle of the ecological theory of succession, the differences between plagioclimax and seral stages are not always clear and are often a matter of degree. Under some environmental conditions, grassland and scrub appear to be maintained, or at least to change very slowly; examples are the communities developed under maritime influences where exposure can be too severe for woodland to develop. Grasslands usually develop under temperate climates where vegetational succession is continually opposed and matched by some other process. Such processes include management. It is often supposed that scrub communities lack stability and cannot be managed. However, Niering and Goodwin (1974) have shown that some kinds of scrub can be stable under management, whilst consideration of scrub in Britain suggests that management is not attempted because no end-product useful to Man would be produced. Where scrub is of use, for example as hedges, management can produce a dynamic equilibrium and the scrub then maintains a characteristic flora and fauna. Dr E. Pollard has studied the fauna of hawthorn hedges and is currently investigating the effects of management by cutting at various intervals of time (ITE 205). Previous work on management by removal of the bottom flora from hawthorn hedges (to simulate herbicide drift) has shown that this results in a reduction of the fauna of the foliage (Pollard, 1968a) and ground-living Carabidae (Coleoptera) (Pollard, 1968b).

Management of grassland and scrub normally has some specified objective. Usually this will be the provision of some product or attribute useful or interesting to Man. Until the twentieth century, objectives of management were almost always agricultural, but the complexity of modern Man's needs and interests means that wildlife conservation, amenity, recreation, road, rail and air safety, and other objectives are now included. In addition, the accidental changes brought about by 'public pressure', mainly by trampling and burning, can be included under the broad heading of 'management'. A conceptually useful distinction may be made between management which essentially maintains a *status quo* (maintenance management), e.g. continual grazing of downland, and management aimed at producing change, e.g. scrub clearance, or the application of fertilisers. Scrub clearance, aimed at restoration of grassland after a period of management cessation or neglect, is an example of reclamation management. Maintenance and changing (including reclamation) management may employ the same methods, but the objectives are different. Management of grassland and scrub is characterised by a lowering of the mean vegetation height, reduction of the biomass of the standing crop, partial or complete destruction of the litter layer, and changes in both microclimate and structure of the vegetation associated with these processes. Cessation of management reverses these changes, and the rate of change is both variable and important. Different methods of management also have special effects as well as these general ones. Grazing includes effects of treading and fertilising as well as defoliation, and introduces animals associated with animal artefacts—carrion, dung and wool, etc., whilst burning, when severe, can destroy humus and lead to soil erosion and impoverishment. Management aimed at producing change will usually also induce floristic changes by differentially affecting the competitive ability of plant species, for example by favouring grasses against broad-leaved plants. A general account of the effects of management on vegetation and plants is given by Duffey *et al* (1974).

Suitable habitat management is the key to the maintenance of populations of nationally important invertebrates, particularly butterflies. (ITE 400—Dr J.A. Thomas, *ITE Annual Report, 1976,* p. 25). The large blue butterfly is a particularly interesting and important case because it is the lack of grazing and burning on suitable grassland sites which has reduced populations of the ants *Myrmica sabuleti* and *M. scabrinodis,* with the effect that the continued existence of the butterfly, whose larvae feed on the brood of these two ant species, is extremely precarious in Britain. A long-term and extensive programme of assessment of butterfly populations of most species by regular observations along standard transects is being mounted by Dr E. Pollard (ITE 204, *ITE Annual Report, 1975,* p. 13) and will monitor the effects of management *inter alia,* particularly of woodland, but also of grassland and scrub. ITE 232 (Dr M.G. Morris) is a study of butterflies at the extensive experimental ranges of the Chemical Defence Establishment at Porton, Wiltshire. The remarkable abundance of many species of butterfly on the chalk grassland here appears to be largely due to lack of management.

Maintenance management produces few, if any, floristic changes and its effects on invertebrate, and also on vertebrate, animals are brought about by changes in the structure of both the vegetation and individual plant species populations. The latter type of effect was discussed by Morris (1967, 1971b). Many phytophagous insects feed only in or on particular plant structures, such as fruits, flowers, stems, aerial leaves and buds, both reproductive and vegetative. Management, particularly when it is intensive or timed to coincide with, for example, flower production, can have very severe effects in reducing populations of these stenophagous herbivores and their specific parasites. The phytophagous insects data bank (ITE 309), currently being developed by Dr L.K. Ward and Mr D.F. Spalding, will be useful in predicting the effects of management on phytophagous insects. The importance of structure to populations of leafhoppers (Auchenorrhyncha) has been emphasised by Andrzejewska (1965), Morris (1971a), Waloff and Solomon (1973) and Denno (1977) among others, and is relevant to many other groups of animals. Spiders utilise field-layer vegetation in several different ways (Duffey, 1962). The importance of structure more generally, in relation to the faunal differences between trees and herbaceous plants, and in the response by insects to the changing morphology of plants, such as bracken (*Pteridium aquilinum*), with time has recently been underlined by Lawton (in press).

The interaction of structural changes brought about by management with temporal considerations has been emphasised by several authors. Timing of even gradual and more or less continuous management, such as grazing, may have considerable effects (Morris, 1973), whilst the importance of the timing of more catastrophic management, such as burning or mowing, is obvious. Animals with different life cycles may be affected very differently by management. Management may also change the biochemical quality of vegetation by 'rejuvenating' physiologically old plants. As many phytophagous invertebrates respond to available nitrogen in plants this may have important indirect effects, although these have not yet been studied in any detail.

Arthropods respond markedly to changes in stocking density when management of grassland is by grazing animals. King *et al* (1976) showed that populations and numbers of species of Collembola in sown grassland were reduced under high stocking rates of sheep, although species-diversity showed no consistent change.

Current work on the effects of management on grassland faunas is focussed on mowing and its timing (ITE 230, 233—Dr M.G. Morris), on burning (ITE 234—Dr M.G. Morris) and on re-establishment of grassland on agricultural land (ITE 236—Dr E. Duffey, *ITE Annual Report 1976,* p. 57). ITE 231 (Dr M.G. Morris) is a continuation of earlier work on the effects of grazing and its cessation. Comparison of the coleopterous (beetle) faunas of 'recently grazed' and 'long (*c.* 8 yrs.) ungrazed' chalk grassland shows that the latter includes many fungivorous and decomposer species not found in the former, which, however, contains a much larger number of phytophagous species (*ITE Annual Report, 1974,* p. 18–19).

The main differences between the hemipterous faunas of calcareous grassland cut in May, July, both May and July, and not cut at all (control treatment) were described in *ITE Annual Report, 1975,* p. 53–54. A more detailed analysis is in preparation. First conclusions from a study of burnt and unburnt grassland in Monks Wood fields (ITE 234) suggest that, although the effects of a single burn on Hemiptera were severe, the effects were not so long-lasting as supposed from preliminary observations on carboniferous limestone grassland in Derbyshire.

Much of the past work on the effects of management on grassland animals in ITE has been directed towards management for wildlife conservation.

The principles of rotational management to conserve both vegetation and all characteristic animal species continuously in time (though not in space) have been widely promulgated. Management to conserve a particular species and associated ones (parasites, predators and competitors, for example) may need to be more specific, particularly in regard to timing. Such management is best defined by detailed study of the populations of the species concerned. It is perhaps necessary to place this work on conservation of grassland wildlife in a more general context. The series of papers presented at a symposium on grassland fauna held in Dublin in March 1977, to be published shortly by the Royal Dublin Society, will help to achieve this.

Because scrub can be considered as a seral stage, it is not usually maintained by management. On the other hand, scrub is very often established by a change in management, usually by its cessation. Juniper scrub is important to conservationists and has a characteristic fauna (Ward, 1977), although the scrub is not normally 'managed' in the usual sense of the term. Box (*Buxus sempervirens*) also has a characteristic, though small, fauna, which is being studied by Dr Ward (ITE 241); again, management of the scrub is not usual, although at Chequers, Bucks, bushes have been selectively felled for their valuable wood. By analogy with juniper (Ward and Lakhani, 1977), this felling could reduce the number of associated invertebrate species by an 'island effect'. Other kinds of scrub, especially hawthorn, are also established by cessation of management. Dr L.K. Ward is currently investigating the establishment and succession of scrub at Aston Rowant NNR, Oxon. (ITE 243).

An attempt to manage scrub by rotation, such as can be done with grassland, is being made by Dr Ward (ITE 296). The problems are much greater with scrub than with grassland. The clearing of mature bushes is difficult, the time needed for adequate rotation of treatments much greater, much larger experimental plots are needed, and replication is correspondingly more difficult. The effects of the treatments on the scrub faunas are being investigated.

Research on management of grassland and scrub has been an intensive activity of the Nature Conservancy's Research Branch and, latterly, ITE for more than a decade. Experience has shown that managers of nature reserves value the work that has been done and welcome its continuation. Perhaps interpretation is the weakest link in the chain between research and its implementation in practical management of reserves.

M.G. Morris

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POPULATION ECOLOGY OF RED GROUSE

Introduction

The problem of how animal populations are regulated is a central issue in ecology. Some populations change little in numbers from year to year, others fluctuate irregularly due to obvious external factors, such as catastrophes in climate or food supply, and others show fairly regular cycles in numbers. Ecologists now have a fair understanding about how stable populations are regulated and which aspects of the life history and environment of these species are involved. Some causes of irregular fluctuations due to external changes in climate, food supplies or habitats are also reasonably well understood; these days, we see many man-induced examples as a result of pollution, overfishing, and human alteration of animal habitats. Cycles, however, are less well understood, despite a voluminous literature on the subject; what causes fairly regular changes in the numbers of lemmings, voles or grouse is still a matter of much controversy and speculation.

Fluctuations in numbers of red grouse

(a) *Introduction.* Red grouse (*Lagopus lagopus scoticus*) are common and valuable birds on the moors of Britain and Ireland, where they feed mainly on heather (*Calluna vulgaris*). Research on their population ecology is done at Banchory by W. Glennie, R. Moss, R. Parr, A. Watson, D. Watt and PhD student G. Wilson. The team is interested in the mechanisms by which animals limit their populations, and has found the red grouse a useful example. During the last twenty years, intensive population research on red grouse has covered two fluctuations in numbers. This means that we have only two observations of the phenomenon we are studying, thus illustrating the need for more long-term studies of animal populations if ecologists are to understand them properly.

The first fluctuation which we observed showed that changes in food supply can cause changes in grouse numbers on a moor. This led to other research showing that differences in grouse numbers on different areas can be explained by the fertility of these areas and by certain aspects of management which also operate through the birds' food. In 1972, we felt that differences in food supplies could explain both fluctuations within areas and differences between areas (Watson and Moss, 1972). The decline during the recent second fluctuation did not, however, follow a change in food supply. Thus, although food offers a sufficient explanation for some changes in numbers, a deterioration in food supplies is not a necessary condition for decline in numbers (see section c).

(b) *Irregular fluctuations.* One of the most important questions about populations is 'Why are there more animals on a given area in some years than in others?' The largest number of red grouse each year occurs in late summer after the breeding season. Chick survival, which can vary greatly from year to year, has been shown by experiment to depend largely on egg quality. In turn, egg quality is affected by material nutrition. Grouse rear bigger broods in years when much green heather is left in late winter and when there are more days of new fresh growth during the period of egg formation, in other words when the mothers' nutrition has been good. This obvious importance of food seems to conflict with the fact that red grouse eat only a minute percentage of the green heather available. However, the apparent paradox of food limitation amidst excess can be explained by the discovery that feeding grouse are very selective.

After the breeding season from May to July, the social behaviour of grouse changes greatly. Each autumn, both young and old cocks defend areas of ground against other cocks. A redistribution of land holdings follows, some old cocks being evicted and some young cocks being successful. Many cocks fail to get territories, however, and many hens fail to pair with territorial cocks. Nearly all these non-territorial birds die before the next summer, mostly from predation, whereas territorial birds usually survive well. Experiments show that some of these non-territorial birds will take territories and breed if territory owners are removed. Much of this mortality is therefore socially-induced, and territorial behaviour sets an upper limit to the breeding population in spring.

Within areas and years, cocks with large territories are more aggressive, have more hens and survive better than cocks with small territories. Cocks with the smallest territories tend to be unmated. Implants of male sex hormone make territorial cocks more aggressive and take bigger territories, and enable non-territorial cocks to take territories and survive. Aggressive behaviour therefore appears to govern an individual's chances of survival, recruitment into the breeding population, and probability of producing young. These observations have led us to more detailed current studies of aggression and dominance in controlled conditions in captivity (Moss *et al.,* 1974).

The first fluctuation in red grouse numbers that we observed involved a decline following a deterioration in food, and then a subsequent increase during a period of good food. Severe winter browning of the green shoots during cold dry weather greatly reduced the food supply in two successive springs. Some territorial birds of both sexes died in poor condition in April-June, and the chicks survived poorly. The young cocks that got territories in autumn took larger territories and survived better than older territorial cocks. Numbers therefore declined. During the subsequent increase, the young territorial cocks showed the reverse by taking smaller territories than old ones, and they also were less aggressive.

The next step was to test this observation about food by doing experiments. The easiest method was to spread fertilisers on study areas, as fertilising was known to increase the heather's nutritive value. These experiments showed that red grouse on fertilised areas took smaller territories and reared larger broods. The most obvious explanation of the population fluctuations was therefore that the birds adjust their numbers by their own social behaviour, in relation to changes in the heather's feeding value. This was the basis of our published model of the grouse populations (Watson and Moss, 1972).

(c) *Cyclic fluctuations.* Several unexpected events in the last few years have made us change this explanation. On our main study area, near Banchory, red grouse increased to very high densities in 1972-73. This increase coincided with a run of mild winters and springs when there was much green heather in late winter and also much new growth of heather in spring, and consequently large broods of grouse. The average territory size dropped to about one territory per hectare. Subsequently, numbers declined without a deterioration in food supplies. The birds have continued to rear fairly large broods, and have maintained good condition, and yet numbers on a fertilised area have decreased as much as on unfertilised ground. The decline was due to: (a) many cocks taking territories, but not pairing with hens; (b) many parents emigrating with their chicks and returning in autumn without them; and (c) many territorial birds losing their territories during the winter. Our current view is that changes in food supplies are sufficient to cause declines in numbers, but are not necessary for these declines. The recent decline is, however, associated with differences in the social behaviour of birds produced during periods of high density, decline and increase.

These findings are of general relevance to cycles in other species of northern birds and mammals. Possibly the ability to undergo declines in numbers without a prior decrease in food supplies is characteristic of the 'Cyclic' species. Nevertheless, the tendency to a fairly regular pattern may be hidden sometimes, when irregular fluctuations caused by changes in food, or other external factors, become superimposed upon the basic pattern.

Management

Research on the effect of food on grouse numbers has led to a better understanding of moorland in general. This understanding has been useful for advising many individuals and organisations concerned with conservation, land use and grouse management on moorlands. In eastern Scotland and England, the dry climate favours heather growth and red grouse occur abundantly. Grouse shooting on these heather moors, which cover 1½ million hectares of Britain, is the most profitable land use and brings in an appreciable sum in foreign exchange. This ground also supports hill sheep (and red deer in some places), the only alternative use being afforestation and that only at low altitudes. During 1973, capital values on good heather moor stood at £500 per ha for grouse and £50–125 for sheep, higher figures than afforestation could reach except on the lower moors (Phillips, 1974).

Grouse populations fluctuate on all areas, and some places support more birds than others. Average grouse stocks are larger on dry, eastern, heather-dominated moors than on the wetter and grassier moors in western parts of Scotland, England and Ireland. Within a region of similar climate, moors over base-rich rocks, such as limestone and epidiorite, support heather of higher nutritive value than over poor, acid rocks such as granite, and grouse there rear bigger broods on average and have larger breeding stocks. On ground over the same rock and with the same climate, stocks are higher where the heather occurs in many small patches of different age as a result of burning or grazing. This variation in age provides the young heather that grouse prefer as food, close beside the taller heather that they need for shelter and cover. The aim of moor management for grouse should be to increase diversity in the sward's structure and composition by the wise use of fire, combined with the correct level of rotational grazing by sheep and cattle. Too wide an area burned at a time, too great a reduction in the heather's height due to continuous hard grazing, or too large a change from heather to grass due to heavy grazing, trampling and dunging, can exterminate grouse locally, as has happened on many hill farms. It is therefore particularly interesting that there is now evidence that 'grouse-type' burning benefits the performance of sheep as well as grouse (Lance and Triggs, 1974).

Recently, Butterfield and Coulson (1975) found that grouse on wet moors ate many craneflies in summer, and suggested that these organisms might be important for grouse management. However, there is no evidence that the eating of craneflies contributes to higher grouse stocks, and, moreover, the wet moors that support many craneflies carry fewer grouse. Heather management is the key to grouse management in most places.

One exception is that, in certain parts of Scotland, such as Morayshire, the sheep tick (*Ixodes ricinus)* is an important reason for the scarcity of red grouse on some moors. The ITE team is helping to study this effect with John Phillips, James Duncan, and Dr Hugh Reid of the Moredun Institute (Duncan *et al.* in press). Grouse on tick-infested moors are scarcer than on nearby tick-free moors, and rear smaller broods. Both chicks and adults have been found very susceptible to mortality from louping ill, a tick-borne virus disease. This susceptibility contrasts with *Trichostrongylus tenuis* in the grouse caeca, a nematode worm being studied by PhD student G. Wilson. Although some birds can die in the presence of a high worm burden, others compensate and survive even higher burdens. Apparently, red grouse have become fairly well used to the nematode, but, possibly, louping ill in grouse is too recent for a similar adjustment to have evolved.

Conclusion

We now have some understanding of how changes in food and habitat can alter grouse numbers; this understanding has proved useful for making management recommendations. Changes in food caused by weather can lead to fluctuations in populations. However, we have recently observed a decrease in numbers without any prior deterioration in food supplies. Changes in the birds' behaviour were the proximate cause of the decline in population. We feel that these results have the potential for helping to explain cyclic changes of numbers in general.

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AVIAN PHOTOPERIODISM

Wild animals undergo marked, adaptive, diurnal and seasonal cycles in body function so that fat accumulation, preparation for migration, onset of reproductive capability and a host of other physiological changes occur at set seasons. Much of the work being done on pollution and vertebrates in the Subdivision of Animal Function has this seasonal periodicity as its theme and the relevance of this periodicity in defining the mode of uptake and mechanism of action of organochlorine compounds and heavy metals has been illustrated in last year's report (*ITE Annual Report* 1976, 22–25) and on page 55 of this report. Defining the nature of these physiological rhythms is also necessary for a full appreciation of how animal species and populations perform ecologically. For these reasons, a proportion of our fundamental research effort is aimed at understanding the mechanisms controlling seasonal cycles in animals. Most physiological rhythms are controlled by photoperiodic stimuli, that is, animals and plants use the 24 h periodicity resulting from the alternation of day and night to entrain endogenous rhythms of body function, which themselves are not exactly 24 h in duration; animals have 'biological clocks' which are corrected and held at the correct running-rate by the environment.

For practical purposes, our research effort is aimed at discovering how birds measure daylength and translate this information into the appropriate hormone secretions, which in turn regulate seasonal gonad development, fat deposition, moult and other functions. The programme is concerned with evolutionary aspects of photoperiodism and the way different species have adapted their responses to suit their individual ecological needs. To this end, we are making detailed studies of the starling *Sturnus vulgaris* and feral pigeon *Columbia livia* var. and, in collaboration with Dr Janet Kear of the Wildfowl Trust, Martin Mere, Lancs, are using a range of waterfowl (Anatidae) species for comparative and evolutionary studies.

Biological clocks cannot be examined directly, although their location can be inferred from lesion experiments, where discrete areas of the brain are destroyed, and their manifestations can be quantified–which is a bit like trying to deduce how a wrist-watch works by watching the hands go round. Students of biological rhythms have long used the activity rhythms of mammals and birds as a convenient measure of the properties of the clock. The 'clock' controlling motor activity is located in the pre-optic region of the anterior hypothalamus. A first question is whether the same 'clock', or another one like it, is involved in the photoperiodic regulation of endocrine secretions from the pituitary. For various reasons, the 'clock', presumably comprising a group of nerve cells, is thought to comprise a coupled oscillator system. Motor activity is thought to occur when the oscillators are above some biochemical threshold. Figure 6 shows the actual daily activity rhythm of a captive starling, obtained by fixing on-off microswitches to the perches in its cage. The bird was kept outdoors on a natural daylength cycle and that part of the activity record obtained from September through December is depicted. There is a clearly defined period of intense activity in the morning and another in the afternoon, which current theory would attribute to the manifestations of the two coupled oscillators. Figure 6 is a diagrammatic representation of this coupled oscillator with a solid curve representing the so-called 'morning' oscillator and the dotted line the 'evening' oscillator. The whole activity rhythm is in phase with the daily cycle of day and night, that is, the oscillators controlling activity are entrained by the oscillation produced by the daily photo-stimulus. When the proportion of light in a 24 h cycle is increased, the relationship between the two components of the coupled oscillator system changes and allows them to move apart, that is,

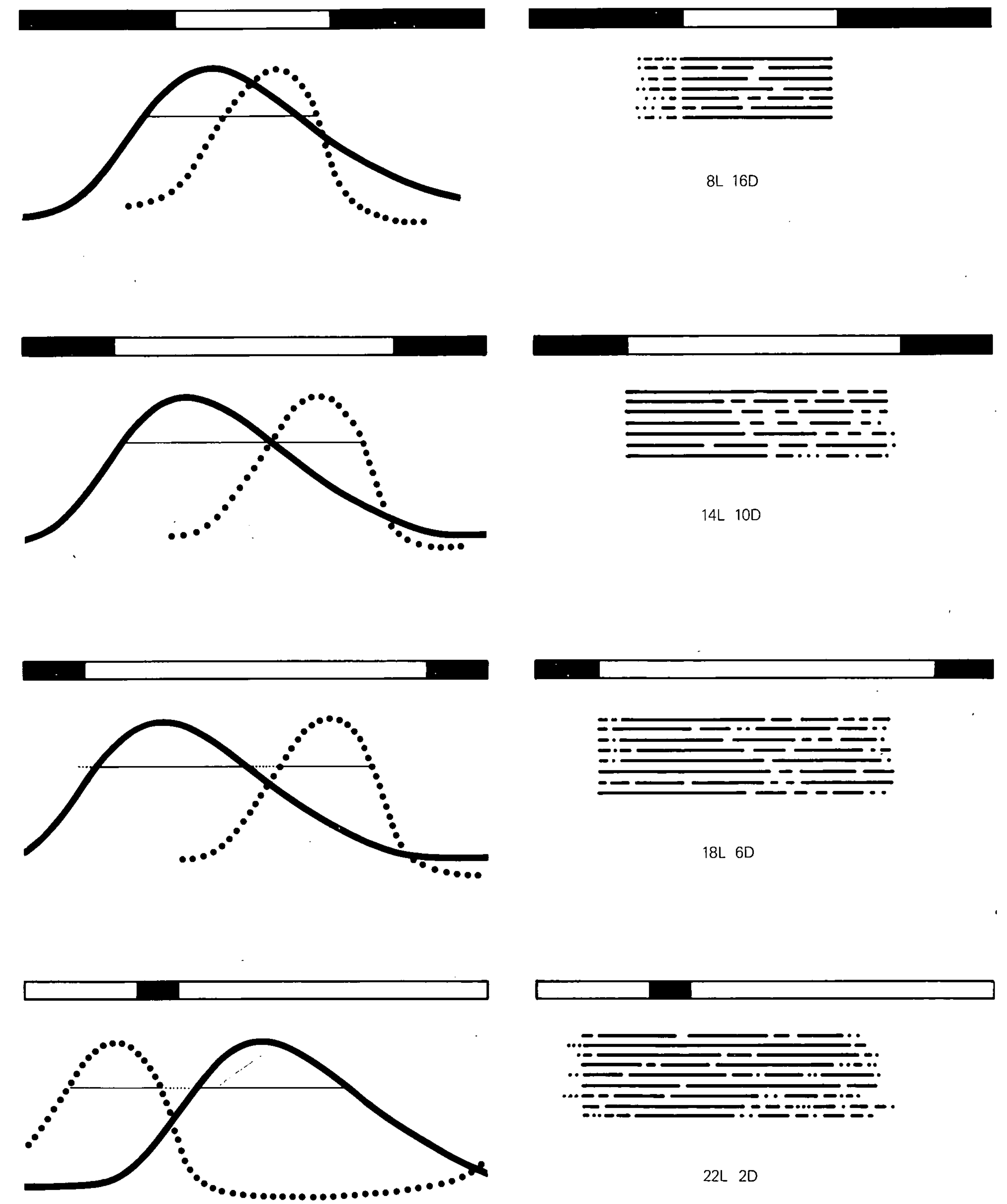


Figure 6 *Schematic diagram to illustrate how two coupled oscillators might control activity rhythms. In the model, based on Pittendrigh and Dann, 1976, one oscillator is entrainable by light and the other is closely entrained by the first, but with an opposite frequency change in relation to a change in light intensity. Increase in the daily photoperiod causes the coupling to weaken and the oscillators become phased apart. Activity, shown in the right-hand panels, occurs when the oscillators are above some 'biochemical' threshold, depicted as a horizontal line in the left-hand panels. (from Murton and Dobson, in press)*

they become re-phased. At the same time, the phasing of the whole system is altered in relation to the entraining light cycle (see Figure 6).

We are concerned to discover whether the 'distance' between the two oscillators, or more correctly their phasing, allows the release of neuro-hormones in the median eminence of the hypothalamus and in turn the secretion of pituitary hormones, like luteinizing hormone. While there are several lines of evidence to indicate that the photoperiodic induction of gonadotrophin secretion is a phasing phenomenon, involving a coupled oscillator system, we do not know how such a system could work in biochemical terms. If the photoperiodic clock is the same as the clock controlling activity, or very similar, we may wonder whether the morning oscillator acts like a 'switch on' and the evening oscillator as a 'switch off' or whether there are no qualitative differences between the two components of the system. Experimentally, we can examine these possibilities by breaking the coupling holding the two oscillators.

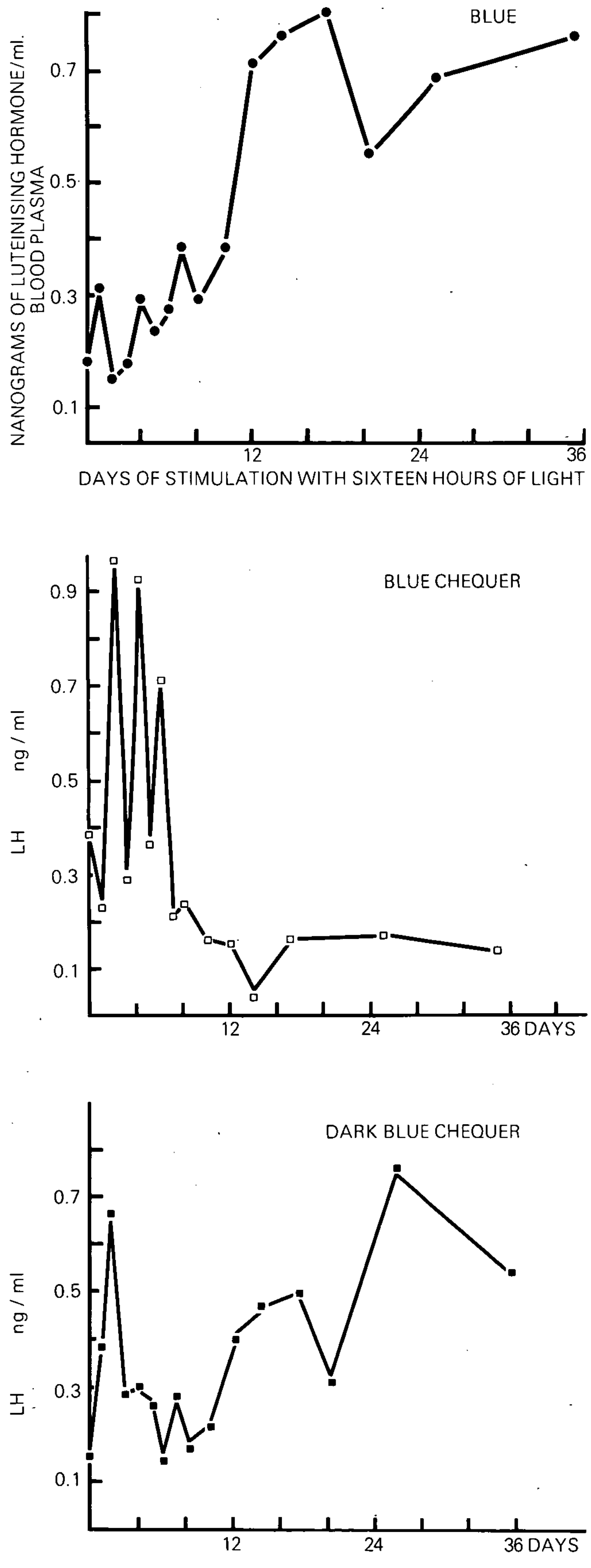
On certain light schedules, the bird's endogenous oscillators have two stable phases of entrainment and which ones occur depends partly on the past history of the subject, for example whether it has previously been kept on long or short days, and partly on random chance. Figure 6 (bottom panel) shows how under a critical long day schedule the evening oscillator (E) of day 1 has broken away from the morning oscillator (M) of day 1 and has instead become the leading oscillator of day 2. In other words, during a period of, say, four days, the oscillator sequence normally runs ME, ME, ME, ME. With increase in the daily photoperiod the sequence stays the same but the phase difference between the morning and evening oscillators increases to give M–E, M–E, M–E, M–E. Under critical conditions this coupling is so weakened that stable entrainment is possible only if E phase jumps to the next day to give (E)→ M,→ EM, EM, EM, E→(M). Plate 7 depicts the activity rhythm of a starling which spontaneously underwent a phase jump of this kind while held on a photoperiod of 14-h light and 10-h dark. We have been manipulating the light cycle to induce changes of this kind and then measuring associated hormonal changes.

A second major area of research follows from the initial observation that different colour morphs of the feral pigeon have slightly different breeding seasons, as judged by seasonal changes in gonad size (Lofts, Murton and Westwood, 1966). Wild-type morphs of the feral pigeon resemble the ancestral wild rock dove in being coloured grey-blue and in having two small black marks on each wing; such individuals are homozygous for the black bar condition and are designated (++). A dominant autosomal allele (C) exists which causes the melanin normally confined to the wing bar to be deposited as flecks over the remaining body and wing feathers and such blue checkers, as they are called, can be homozygous or heterozygous (CC or C+). A third allele (C^T), dominant to both the others, causes an even more pronounced black flecking over the body and such phenotypes are known as dark blue checkers or T-pattern and genotypically can be a homozygote or one of two heterozygotes (C^TC^T, C^TC or C^T+). The genes causing melanism are associated with a lowered photosensitivity so that breeding occurs over a longer segment of the year; such individuals also appear to be more fertile, except that the homozygous T-pattern condition is associated with a lethal factor. Thus, within a single species, we can examine one of the mechanisms whereby the photosensitivity threshold is altered to allow the potential breeding season to be lengthened or shortened. Similar manifestations are observed between closely related species and this appears to be the simplest level at which evolutionary change is possible (see below).

In some free-living feral pigeon populations, a complicated mating system has evolved, with the females showing a differential preference for males which are unlike themselves. This mating system leads to a balanced polymorphism which favours melanic heterzygotes. Most of these facts were ascertained for free-living populations in the Manchester Docks some while ago (Murton, Westwood and Thearle, 1973), and more recent work has focussed on detailed laboratory studies of the mating preferences. A genetical model, first used to define mating preferences in the Arctic skua *Stercorarius parasiticus,* has been fitted to the pigeon data and the same parameters shown to hold (Davis and O'Donald, 1976).These show that, if the female mating preferences cause the negative assortative mating, they are the results of preferences for the melanic phenotypes. No females prefer the wild-type, while the proportion preferring blue checks is 0.508 and 0.376 prefer T-pattern males; the preferences are only expressed when the male is a different phenotype from the female.

Differences in breeding periodicity would be expected to be reflected in the underlying endocrine secretions. When three different morphs were transferred from short (8-h light) to long (16-h light) photoperiods, there were marked differences in the pattern of LH secretion (Figure 7). There is insufficient space here to discuss the endocrine implications of these differences, but the identification of a series of alleles which affect both a plumage character and cause a physiological change is exciting, because the prospect is offered of studying the mechanism of gene action.

Our third approach to the study of avian photoperiodism



is a comparative one, the aim being to define the evolutionary processes and constraints that have led to the presently expressed diversity of ecological adaptation. Swans, geese and ducks of the family Anatidae provide excellent research tools for this purpose, because so much is known about their taxonomy and life history, and because a splendid captive collection is maintained by the Wildfowl Trust.

When an ancestral species radiates to new latitudes, it becomes exposed to an altered photo-regime. After the spring equinox, the intensity of the entraining light cycle is increased as a bird moves towards the poles. The natural frequency of the bird's own oscillators are increased as a consequence, so that the phase angle during entrainment becomes more positive–we are essentially discussing the kind of system depicted in Figure 6. This process would result in the subject producing gonadotrophins and assuming breeding condition earlier in the season. Obviously, birds nesting north of the Arctic Circle need to begin breeding later, and not earlier, than their relatives living further south. Selection must favour some kind of re-adjustment of the photoperiodic clock so that gonadotrophin secretion is not stimulated too early in the year. The mechanisms whereby this is achieved appear to operate in a systematic manner, for, when a relatively newly emerged line of closely related species is held under the same entraining cycle, differences in response which evolved at different latitudes become expressed as endogenous differences in response to the same light cycle. This effect was shown by Murton and Kear (1973) who compared the onset of egg laying in a range of closely related waterfowl species held captive at Slimbridge. Figure 8 shows the daylength at which different species and races of *Branta* geese lay eggs at Slimbridge depending on their latitude of origin. The Hawaiian goose or Ne Ne (*Branta sandvicensis)* from 20°N begins egg laying in late January, but the Brent goose (*B. bernicla*) which nests around lat 71°N does not lay eggs at Slimbridge until late May. Obviously, we have used egg-laying as a measure of endocrine state, in this case the initial stimulation of gonadotrophin release leading to androgen/oestrogen secretion. We are now checking this reponse in collaboration with Dr Janet Kear by measuring annual hormone secretion patterns in a range of carefully selected species. Space does not permit more detailed

Figure 7 Average changes in plasma concentrations of luteinizing hormone in three different morphs of the feral pigeon when subjects were transferred from short to long days.

Plate 6 *Daily record of perch hopping activity of a caged starling from September until December. Note the tendency for two separated periods of intense activity*

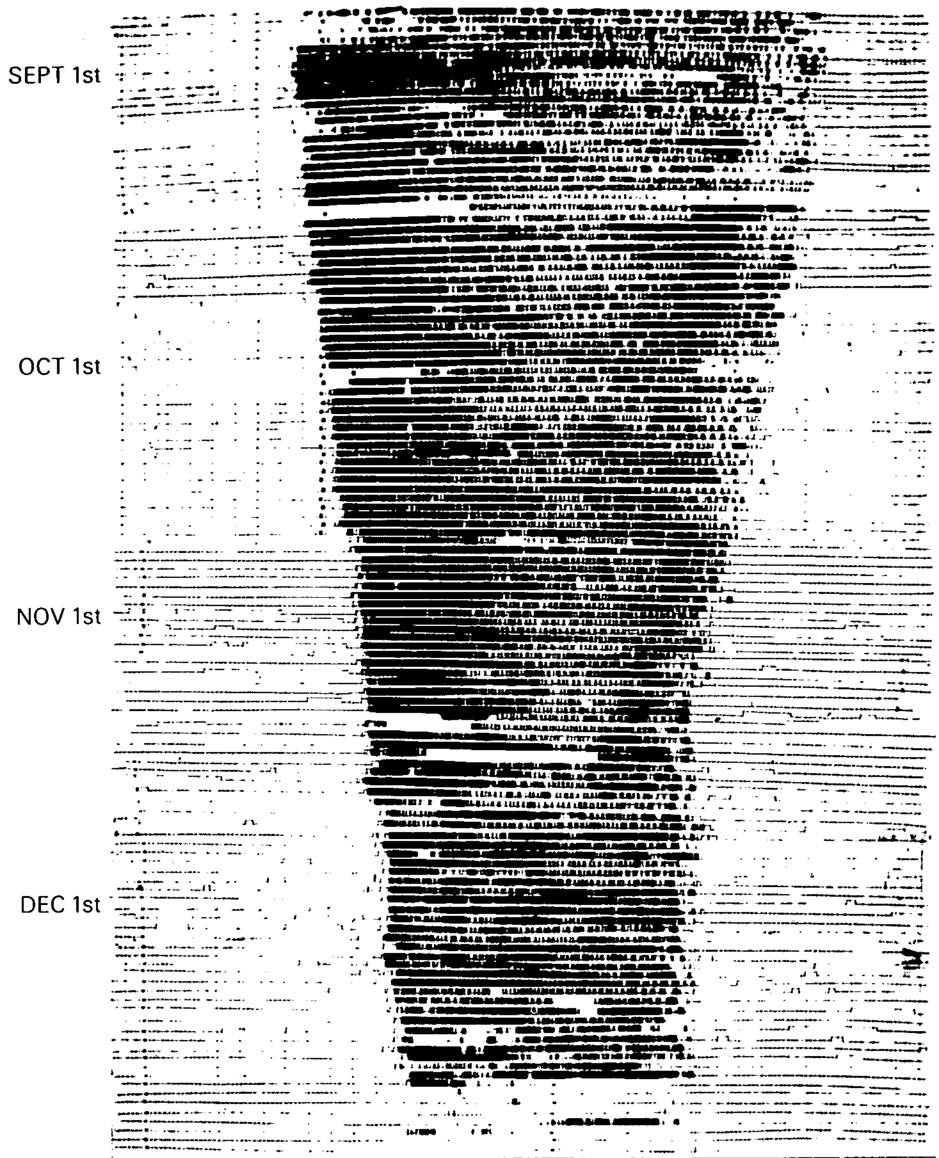


Plate 7 Perch-hopping activity of a caged starling held on a light-dark regime of 14:10 which spontaneously showed a phase jump.

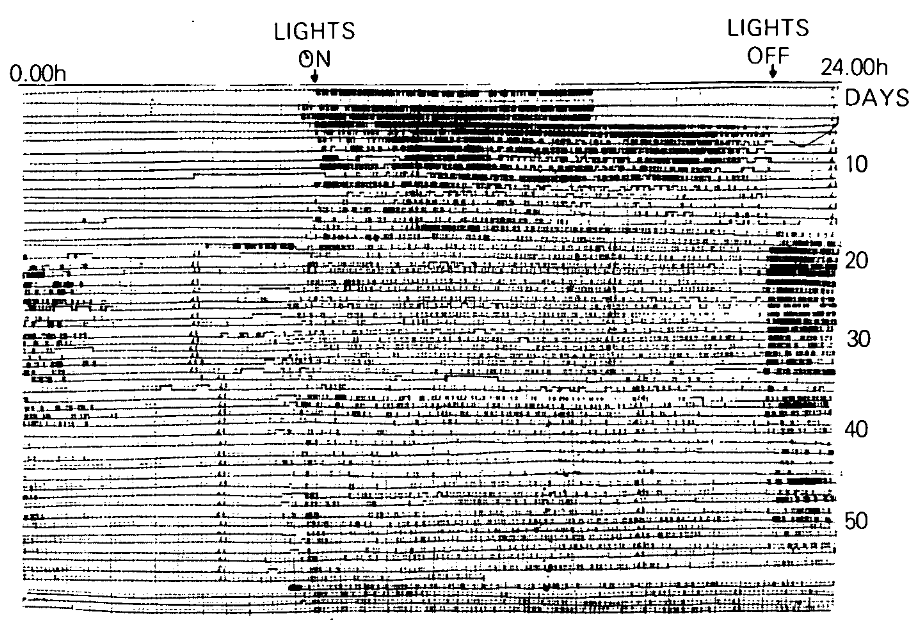


Plate 8 A semi-mature tree of T. scleroxylon *(Obeche) standing in farm land. Photograph by R Leakey*

Plate 9 Naturally occurring specimens of birch, willow and Scots pine growing on deep-mined colliery waste, Midlothian. Cutting material was taken from them, and rooted to enable test plantings of a range of opencast and heaps of other reclaimed spoils. Photograph by J E G Good

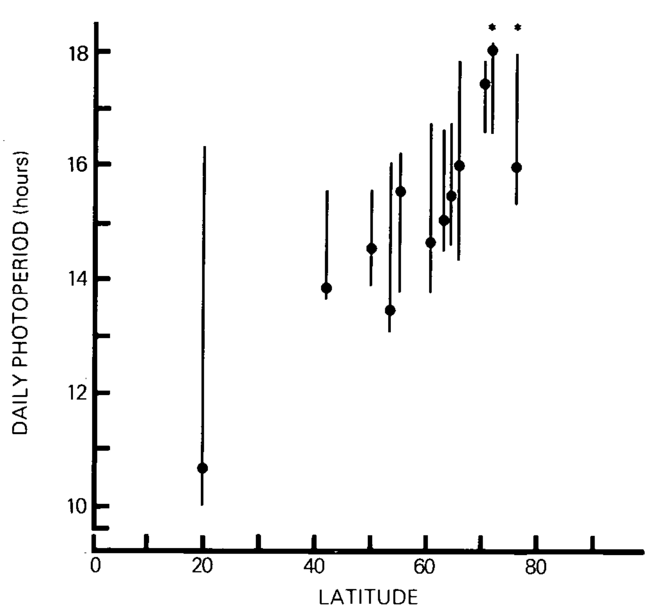


Figure 8 Relationship between the egg-laying season of different species and races of Branta *geese in the Wildfowl Trust collection at Slimbridge and the mid-latitudes of their natural breeding range. Vertical bars depict the egg-laying season in terms of the shortest and longest daily photoperiod under which eggs have been laid, while solid dots give the median photoperiod for first eggs, based on records collected over a series of years.*
(from Murton and Dobson, in press).

Asterisks denote that in these two species egg-laying continued beyond the summer solstice

discussion, but it should be emphasised that the secretion of gonadotrophins is only part of the story. Steroid feed-back mechanisms are also involved in regulating breeding periodicity, photo-refractoriness is an important topic, and other endocrine systems become implicated when moult and other functions are considered; these topics are not being neglected.

B. Dobson, S. Dobson, R.K. Murton and N.J. Westwood

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CLONAL DIFFERENCES IN THE LEAF-SHAPE OF *BETULA PUBESCENS* EHRH.

Introduction

Since 1970, several studies have been undertaken to examine the range of variation in leaf-shape within populations of British birch (*Betula pendula* Roth and *B. pubescens* Ehrh.). The methods used have been based on the work of Professor Janina Jentys-Szaferowa (1937) in Poland, who first discovered that the shape of leaves growing on vegetative short shoots was relatively stable. She subsequently developed a simple method for identifying unknown leaves and for exploring intra- and inter-specific variation between six European birch taxa using thirteen leaf measurements and drawing graphical comparisons between sample means and a number of species standards, (Jentys-Szaferowa, 1949–51).

A principal component analysis (Gardiner and Jeffers, 1962) showed that the number of variables could be reduced and that the relationships between the six taxa could be summarised and illustrated by projections along the significant axes of the principal component analysis. Further modifications have been made, and a method developed (Gardiner, 1973; Gardiner and Pearce, in press) by which leaf images are projected on to a standard grid by means of an episcope (see Figure 9) from which eleven variables are recorded. In 1976, an opportunity arose for examining the ability of this method to discriminate between clones of *B. pubescens.*

Materials and Methods

A small collection of three clones of *B. pubescens* and one of *B. pendula* has been planted at the ITE Research Station at Bush, Penicuik. The *B. pubescens* clones originated from seedlings from a single parent tree at Crathie, whilst the *B. pendula* clone originated from Sluie Wood, both sources being located in the Dee Valley in east Scotland. The plants were three years old and had already developed a system of short shoots. Clone A *(B. pendula)* contained six ramets, Clone B & D *(B. pubescens)* four ramets and Clone C *(B. pubescens)* five ramets.

Sets of ten leaves were collected at random, from each ramet in turn, photocopied on to separate sheets of paper and, using the method described earlier, eleven variables were measured. The nineteen sets of data were submitted to a principal component analysis, based on the mean values for each set, and the results are shown in Table 13.

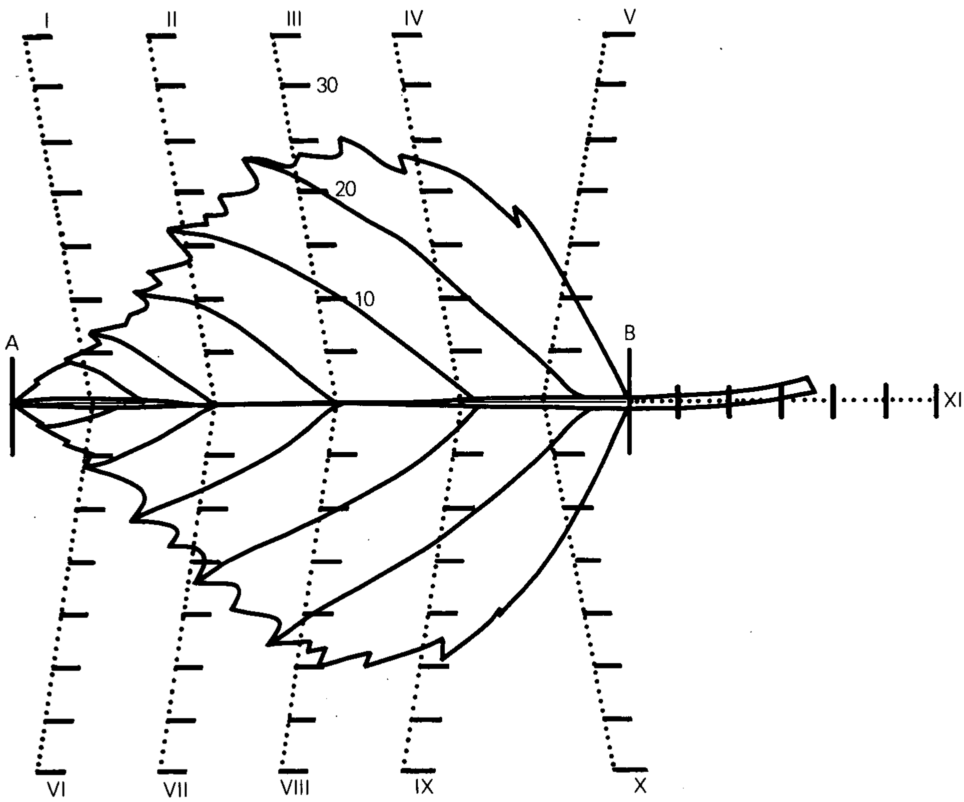

Figure 9 Standard grid with leaf image superimposed

Table 13 The first two principal components

	1	2
Eigenvalue	8·0	1·8
Eigenvector elements		
I	0·35	0·09
II	0·35	0·07
III	0·35	0·03
IV	0·34	−0·01
V	0·08	−0·69
VI	0·35	0·07
VII	0·35	0·07
VIII	0·35	0·04
IX	0·35	0·00
X	0·14	−0·67
XI	−0·09	−0·21
% of total variation	72	16

Results

The first three components accounted for 97% of the variation within the eleven basic variables, and a projection of the values of the nineteen ramets for the first two components is illustrated in Figure 10. This analysis clearly separates the two species and by enclosing the appropriate ramets of *B. pubescens* with continuous lines their clonal relationship is demonstrated. In addition, the distinction between B and D can be improved by removing the influences of clones A (*B. pendula*) and C and repeating the analytical procedures (see Figure 11). Clonal separation was not seriously improved by increasing the number of original variables to fifteen.

Discussion

In the first analysis, the weights given to the original variables by the first components are almost equal in the first four variables on either side of the lamina, namely I to IV and VI to IX (see Table 13) and have the effect of separating the two species. The second component, which is weighted in favour of the variables at the base of the leaf, namely V and X, detaches C from the two other *B. pubescens* clones. The biological reason is possibly the smaller frequency of cordate leaves within this clone, which is higher in B and D.

In the second analysis, involving the clones B and D only, the structure of the components is more complex (see Table 14), particularly that of the second component. In this case, several contrasts are confounded e.g. between the upper and lower parts of one side of the lamina (II and IV) and between both sides of the

Distribution of the nineteen ramets according to their values for the first (vertical) and second (horizontal) components.

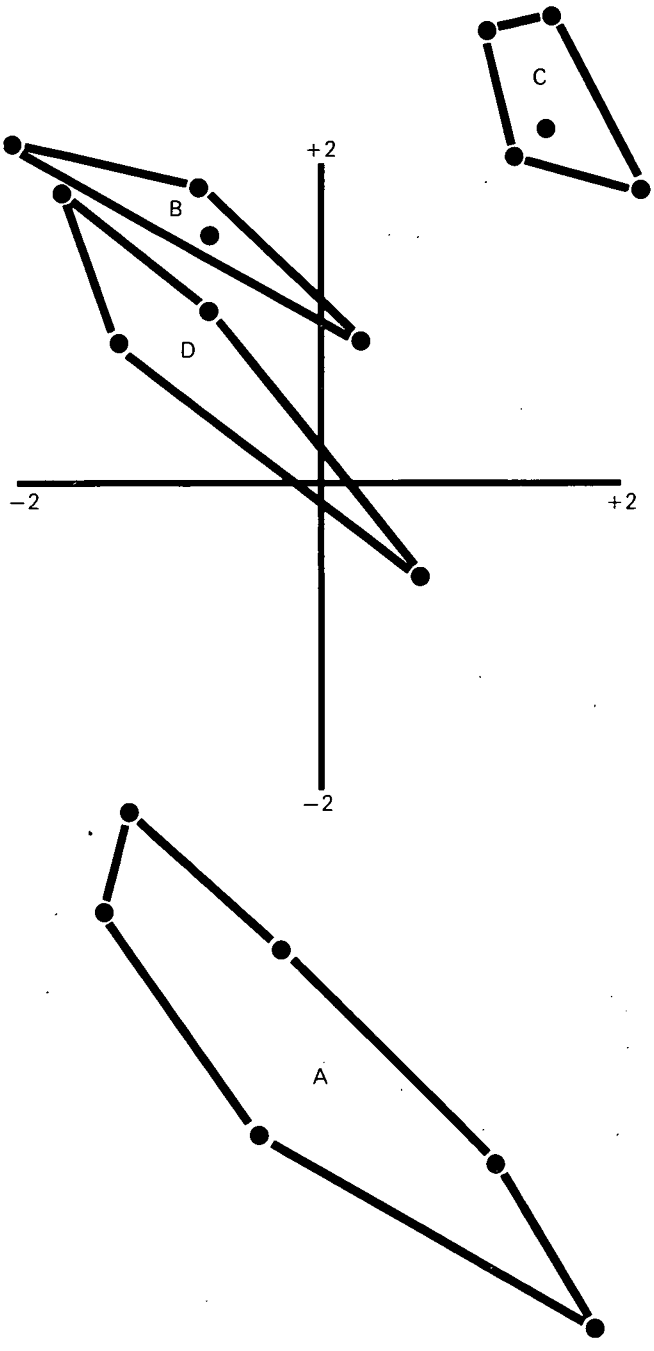

Figure 10 *Clone A* (B. pendula)

Distribution of Clones B and D according to their values for the first (vertical) and second (Horizontal) components.

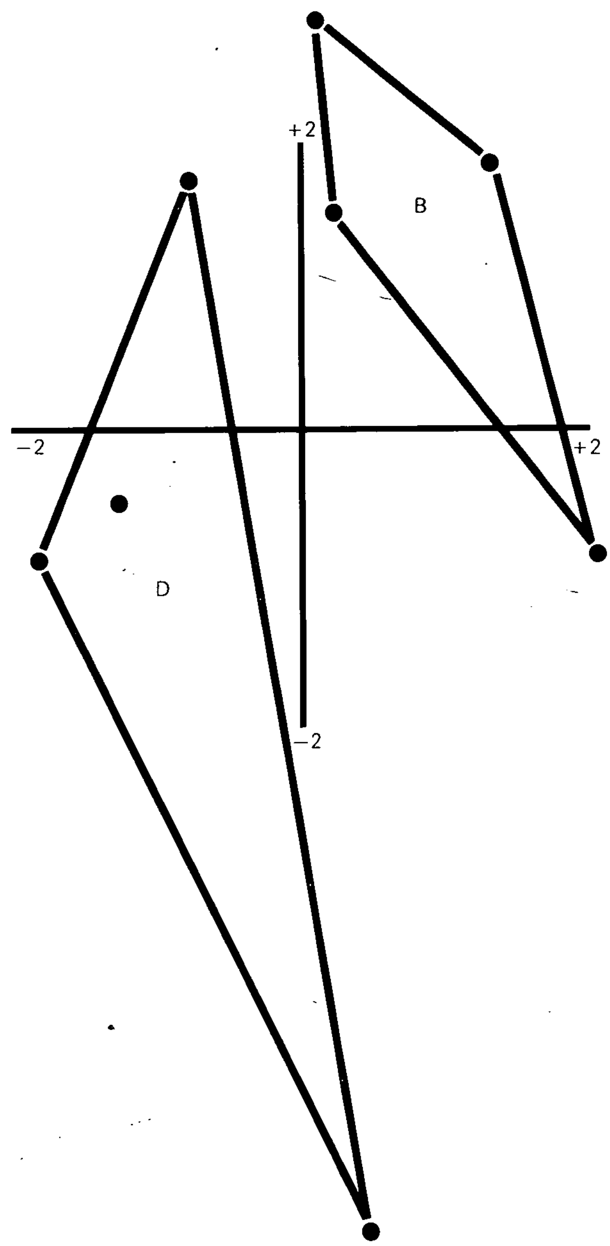

Figure 11 *Clone B* (B. pubescens)

blade at the tip (I and VI) and the weighting given to the relative petiole length is twice as great as that in the first analysis (cf. Tables 13 and 14). It is these complex contrasts which have the most effect in separating the two clones, whilst the distribution along the first axis, which accounts for 64% of the total variation, indicates that, of the two, D is the more variable.

Table 14 The first two principal components: clones B and D only

	1	2
Eigenvalue	7·1	1·7
Eigenvector elements		
I	0·33	0·26
II	0·31	0·34
III	0·36	0·15
IV	0·21	−0·56
V	0·29	−0·14
VI	0·33	−0·14
VII	0·34	0·10
VIII	0·33	0·23
IX	0·31	−0·37
X	0·32	−0·22
XI	−0·09	−0·45
% of total variation	64	16

Since they share the same maternal parent, all three clones of *B. pubescens* are half-siblings and it is tempting to suggest that B and D may be full siblings because of their close relationship.

The study demonstrates the value of the exploratory work of Jentys-Szaferowa (1937), although there have been criticisms of her later papers in that some degree of subjectivity was employed in setting species standards. Although we assumed that we were dealing with one clone of *B. pendula* and three of *B. pubescens*, the nineteen ramets were allowed to contribute individually to the wide spectrum of variation. In summarizing the total variation through the use of a principal component analysis, the specific differences and clonal affinities have been demonstrated, distinctions which could be further enhanced through the medium of discriminant analysis.

Because of the high degree of correlation between the eleven variables, it is possible to reduce considerably the number of variables which need to be used. In an earlier investigation of three Scottish birch populations in the Dee valley (Gardiner and Pearce, in press), similar results were achieved from sets of the eleven variables used here, and a reduced set of six variables, obtained by taking the means of corresponding variables on either side of the lamina e.g. I and VI, II and VII. In the present study, this form of reduction was not undertaken, but a pilot trial of a method described by Jolliffe (1972, 1973) for reducing variables prior to a principal component analysis produced effective results.

A.S. Gardiner

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Research of the Institute in 1977

Introduction

This, the main section of the report, gives relatively short accounts of research projects in ITE during 1977. The main emphasis of these accounts is on projects which have been completed or in which significant progress has been made during the year. A full list of the ITE research projects will be found in Section IV of the report.

No single classification of ITE research projects can be both exhaustive and mutually exclusive. The accounts of this Section have therefore been grouped so as to illustrate some main concentrations of the ITE research. They begin with a group of projects concerned with the survey of ecological systems, or the monitoring of changes taking place in those systems. An increasing emphasis on survey and monitoring is becoming evident in the research undertaken by the Institute, mainly as a response to the requirements of commissioning agencies, and the design and interpretation of ecological survey are as intellectually stimulating and demanding as any other aspect of scientific research. Indeed, the ability to undertake surveys which are as economical as possible of the scarce resources available and, at the same time, capable of providing the information required with a designed precision, represents a considerable scientific advance.

Trees and woodlands form an important component of the semi-natural vegetation of Britain, as well as of the planted broadleaved and coniferous forest. A considerable proportion of ITE's research is therefore concerned with woodland habitats and with woody plants. The reports in this group emphasise the considerable variety of the research currently being undertaken, and the importance of that research. There then follows a group of reports on various aspects of land management, and dealing with other habitats, including heathlands, grasslands, and estuarine muds and sands.

The next two groups of reports deal with research on vertebrate and invertebrate organisms, respectively. These organisms are found in several habitats, and the emphasis of the research is on the population dynamics and distribution of the organisms, rather than on their relationships with any particular habitat. Similarly, the reports on bryophyte taxonomy and biological records are relevant to more than one habitat.

Finally, the work of special Subdivisions and Centres is summarised. The contribution of these service subdivisions is particularly important to ITE, and enables many of the research contracts and the fundamental research to be undertaken effectively and economically. Without these services, it is doubtful if any useful progress could be made.

Survey and monitoring

PREDICTION OF CLIMATE IN DIFFERENT PARTS OF THE UK FROM SITE VARIABLES

Ecologists often wish to have estimates of the climate at sites where climatological instruments are not available. For this purpose, an attempt has been made to predict weather from site features read from Ordnance Survey maps.

From principal component analyses of daily observations, usually taken at 09.00h, at 68 climatological stations scattered over Great Britain, it was found that dry bulb screen temperatures, rainfall visibility, wind direction and snow depth accounted for most of the climatological variation. Subsequently, the calculation of stepwise multiple regressions enabled the values of (i) the main variables and (ii) the principal components to be linked with, and assessed from, 14 Ordnance Survey 'site' variables including latitude, longitude, altitude, distance from sea, aspect. Of these, those describing geographical position were overridingly important–it was also necessary to derive separate equations for the four quarters of the year.

With the equations so produced, which differed for the differing quarters of the year, it was predicted that the 09.00h dry bulb temperatures at Kinlochewe would be 3.8, 10.6, 13.0 and 6.0°C in the first, second, third and fourth quarters of the year compared with means of actual data collected from 1960–69 inclusive, of 3.8, 10.7, 13.3 and 5.9°C. Not surprisingly, the extent of agreement differed at different sites and according to the factor being assessed. Thus actual mean snow depths at East Malling, Kent, were 0.97, 0.00, 0.00 and 0.16cm in successive quarters compared with 'predictions' of 0.69, 0.00, 0.00 and 0.06cm.

E.J. White

ECOLOGY OF VEGETATION CHANGE IN UPLAND LANDSCAPES

(This research is supported by the Department of the Environment)

Following the desk study, *Upland Land Use (Annual Report 1976,* pp. 10–15), a report on which is currently being prepared jointly by the Countryside Commission and ITE, DOE have commissioned an investigation of twelve upland parishes in England and Wales. In this investigation, the course and rates of actual and potential changes in upland vegetation types will be assessed in relation to land characteristics and to past, present and predicted land uses and systems of management. Particular attention will be paid to small-scale and gradual (often unanticipated) changes which can have a significant effect on the landscape in the long term, rather than on 'instant' conspicuous intentional large-scale changes such as the conversion of moorland to forestry or agriculture.

Of the twelve study areas, also being used by a team of consultants for landscape studies, six, totalling some 300 km², were surveyed by ITE during 1977: Shap and Shap Rural, Cumbria (Lake District); Bransdale, North Yorkshire (North York Moors); Heptonstall, West Yorkshire (South Pennines); Glascwm, Powys (Radnor-Clun Forests); Ystradgynlais Higher and Glyntawe, Powys (Brecon Mountains); and Buckland-in-the-Moor and Widecombe-in-the-Moor, Devon (Dartmoor).

A three-part approach was adopted. The core of the work is botanical, recording the occurrence and % cover of plant species on a standard list at some 70 randomly selected 'main plot' sites including the full range of agricultural, agricultural marginal, and unenclosed 'unimproved' land within each parish. The agriculturally marginal sectors, where gradual or small-scale vegetation changes are most likely to have an impact on upland landscape, are being sampled more intensively than others; main plot data are supplemented by other data from woodlands, field boundaries and road verges. The data will be analysed for parishes individually and as a group, hoping to establish vegetation classes and their probability of occurrence, also their potential for change.

Because they will have affected the distribution and development of vegetation assemblages, details of historical settlement patterns, recent and current management practices and physical land characteristics are being sought. Concentrating on developments since the seventeenth/eighteenth centuries, attempts are being made to (a) determine when the present parish landscapes were created and (b) identify specific locations where vegetation types may be related to contrasting past histories. Land characteristics are being taken mainly from Ordnance Survey maps by quantitatively recording altitudes, slopes, aspects, settlement data and other attributes using the 0.5 × 0.5 km grid square as the recording unit. To facilitate retrieval and analyses, data are stored on computer files.

By relating historical events and land characteristics to present day vegetation, a basis should be established for predicting future rates and directions of vegetation changes when implementing different systems of management.

D.F. Ball

ECOLOGICAL SURVEY OF CUMBRIA

(This work was done in conjunction with Cumbria County Council)

Ordnance Survey maps contain a wealth of information that can be used to identify ecological characteristics of the landscape. However, the information is complex, and, although some areas may be readily identifiable and easily categorised, others, without outstanding features, are difficult to classify.

One hundred and eighty six attributes were assessed within 1km² throughout Cumbria and arranged to give 16 land classes using Indicator Species Analysis (Hill, Bunce and Shaw, 1975). Subsequently the vegetation in a sample series of squares was surveyed and it was found that vegetation and map characteristics were sufficiently well correlated to enable the development of predictions. The accuracy of these predictions has since been tested, and, although varying between land classes, was shown to reflect the principal features of the vegetation to an acceptable level of detail.

The descriptions of the 16 land classes have been augmented by a consideration of landscape features, the occurrence of trees and hedgerows, and descriptions of soils.

The results of the survey are currently being applied to a range of planning problems, thus helping to identify specific uses. They are of value in strategic planning and, with field visits, they can be used to compare potential reservoir sites and to examine the affinities of upland valleys in Cumbria. The ability to make these comparisons by using map criteria and to establish data banks based on previously defined land classes is important. In conjunction with ITE, parallel ecological surveys are being made by the Yorkshire Dales National Park authority and Lancashire County Council.

R.G.H. Bunce

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MONITORING CHANGES IN PLANTS AND ANIMALS AT STONE CHEST, CUMBRIA

Hill and Evans (1976) described a wide-scale survey to assess effect of afforestation on semi-natural vegetation. In contrast, the changes in a relatively small area at Stone Chest, Cumbria, which was poor rough grazing before being planted in 1971–72, have been assessed by an intensive series of samples. To ensure the game-carrying capacity of the property, the main species Sitka spruce (*Picea sitchensis*) was supplemented by lesser planting of larch (*Larix leptolepis* and *L. eurolepis*) and western hemlock (*Tsuga heterophylla*) plus the addition of a number of indigenous and exotic shrubs. The latter were concentrated alongside extra-wide rides; the habitat diversity of the locality was further increased by the construction of three ponds.

Following the removal of sheep, deep ploughing of the site prior to planting, and subsequent tree growth, surveys made in 1972 and 1975 on a permanently-marked sampling grid with intersections at 100 m have detected vegetation changes. In the first three years after planting, the herbaceous and rushy vegetation of a poorly-drained pasture has become dominated by coarse grasses and colonizers of bare-ground such as willow herb (*Epilobium* spp. and *Chamaenerion angustifolium*), foxglove (*Digitalis purpurea*) and thistle (*Cirsium vulgare*) (Plate 11). Species of meadows (*Ranunculus acris*) and heaths and moors (bilberry) (*Vaccinium myrtillus*) and deer grass (*Trichophorum caespitosum*) have decreased.

The distribution of vertebrates to some extent reflects habitat changes–a study of these inter-relations being an integral part of the project. Of five species of wading birds which bred on the area in 1972, only one pair of curlews (*Numenius arquata*) remained in 1977. In contrast, passerines, such as the whinchat (*Saxicola rubetra*), have become more numerous, with a pair of breeding goldcrests (*Regulus regulus*) being recorded in 1977. The woodmouse (*Apodemus sylvaticus*) was recorded in 1972 and 1977, but not in the intervening years, whereas the common shrew (*Sorex araneus*), which was uncommon in 1972, had become the most abundant small mammal species by 1976. Numbers of field voles (*Microtus agrestis*) reached a peak in 1974–75 and then decreased, with those remaining in 1977 being widely distributed in small colonies.

J.M. Sykes and V.P.W. Lowe

Reference

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SCOTTISH DECIDUOUS WOODLANDS

(This work was commissioned by the Nature Conservancy Council as part of its programme of research into nature conservation)

Before a resource can be rationally managed it is desirable to have a detailed understanding of its amount and distribution. Because observations suggested that the decreases, noted by Forestry Commission censuses made in 1947 and 1965, may be continuing, ITE was asked to make a total enumeration of Scottish deciduous woodlands (Plate 12). Accordingly a map search of Scotland was made using the 7th series Ordnance Survey maps. This identified 3500 woods marked with broadleaf symbols and individually larger than 5ha. All sites excepting the most remote have now been visited; in the instance, it was first necessary to establish the presence of woodland before making visual estimates of canopy composition including the abundance of birch, oak, beech, sycamore, elm, ash and others. Woods with over 50% of non-native species were omitted but 'policy' woods were included. A data bank is now being established with details of canopy composition being allied to the name, location, grid reference, area and altitude of each wood. It will provide a framework for assessing the significance of individual sites and the need for more intensive sampling in the future. Additionally, by comparing with the FC survey done in 1965, it should be possible to assess if the loss of deciduous woodlands is continuing or has been arrested–there was a 21% loss between 1947 and 1965.

R.G.H. Bunce and R.C. Munro

LICHEN MONITORING OF AIRBORNE FLUORIDE POLLUTION

Lichens, not having roots, absorb nutrients directly from the air and from solutions bathing their thalli. Whereas those growing on the bark of trees (corticolous species) absorb substances from stemflow, which is often enriched with tree leachates, those growing on relatively dry rock surfaces (saxicolous lichens) are, to some extent, dependent upon minerals released from those rocks, the weathering process often being influenced by the lichens themselves. Many lichens, particularly epiphytes on hedgerow twigs, depend almost entirely for their nutrition on substances (ions) captured from aerosols and suspended rainwater droplets.

Because they continue to absorb ions even if non-essential or required only in very small quantities, it has been possible to use lichens when monitoring the occurrence and dispersion of airborne pollutants. In North Wales and elsewhere, corticolous lichens have been shown to accumulate airborne pollutant fluoride more efficiently than saxicolous species. On accumulating 50 to 80 $\mu g\ F^{-}g^{-1}$ thallus dry weight, lichens begin to be adversely affected and death may ensue. In continued studies of a series of permanent quadrats, using assessments made on annual photographs, it has been found that the growth of saxicolous lichens was retarded, without obvious blemishes, by sub-lethal concentrations of fluoride, a relation extending the range of concentrations of fluoride that can be detected in the 'field'.

Not all lichen species are affected equally by pollutants, sensitivity appearing to be related to habitat and life-form. Observations for 6 years since the release of airborne fluoride indicate that corticolous species are affected before fructicose (erect) saxicolous species, e.g. *Ramalina* sp, which are good absorbers of airborne substances. The foliose (leaf-like) saxicolous forms, e.g. *Xanthoria parientina* and *Anaptychia fusca*, are usually less sensitive than the types already mentioned, but more sensitive than the slow growing and resistant crustose forms.

Although saxicolous lichens are less sensitive to air pollutants than corticolous species, they are more useful for long-term monitoring because they grow on more permanent substrates. 80% of the quadrats of saxicolous species less than 2 km from a source of fluoride pollutants were damaged. In control quadrats 'remote' from the source of fluoride pollutants, some quadrats were damaged by animals, others by chemical sprays and fertilizers, but, in these instances, the accidentally damaged lichens recovered.

During the year, the ability to monitor concentrations of fluorine and sulphur pollutants in air and rain was developed. Airborne gaseous and particulate pollutants were sampled by differential absorption and filtration through impregnated filters. Because large volumes of air were sampled, it was possible to lower the minimal ambient concentrations that could be detected when using solution scrubbing techniques.

D.F. Perkins, R.O. Millar and P. Neep

STANFORD PRACTICAL TRAINING AREA

(This work was commissioned by the Nature Conservancy Council as part of its programme of research into nature conservation)

Stanford PTA is a Ministry of Defence training area some 25 square miles (17,500 acres) in extent. Some of its peripheral areas are let for arable farming and there are blocks of woodland, mainly coniferous, managed by the Forestry Commission, but most of the area (12,000 acres) is grassland grazed by sheep–there are a number of lakes, meres, ponds and streams. Although the PTA has never been devastated by tanks and heavy artillery, numbers of soldiers being trained have increased from 20,000 men per annum in the late '60s to 75,000 in 1976. The major part of this increased military pressure is, however, concentrated on limited 'Impact Areas' and specific firing ranges. As reports suggested that the conservation values of some parts of the PTA were much greater than others, the NCC commissioned ITE to do a comprehensive survey.

The land use history of the area have been investigated and the grasslands have been classified according to the dates when the land they occupy was last cultivated (see Figure 12). Heath and grassland types have been identified and mapped (see Figure 13), and current survey work is improving their delimitation. Both figures show that the vegetation types so far recognised corre-

Figure 12 Grassland ages on Stanford Practical Training Area

late well with grassland ages, with bracken-gorse-heather occupying much of the land not cultivated since the 1880s, whereas *Festuca/Agrostis* or *Poa/Dactylis/Arrhenathrum* are found where cultivations ceased some time during the last 30 years, and Figure 14 shows that the distribution of invertebrate species follows the same pattern.

None of the recognised Breckland plant rarities have been discovered, but many species, typical of the Breck, have been recorded. Many invertebrate species not previously recorded have been found, including some which are rare, not only within the Breck, but also within Britain. As yet, the ecology of the 'Impact Areas' has not been affected significantly by increased military activities.

M.D. Hooper, J. Sheail, E.J. Mackintosh, G.J. Moller and M.A. Palmer

A BIOASSAY FOR DETERMINING PLANT AVAILABILITY OF PHOSPHORUS IN SOILS

Phosphorus deficiency is a major factor limiting the productivity of many forests, and upland grasslands. Because existing analytical procedures do not take adequate account of the complex and dynamic physico-chemical and biological nature of the soil phosphorus/plant relationship, it is difficult to obtain reliable estimates of plant-available phosphorus in soils by using routine laboratory techniques. To overcome this problem, attempts were made to evolve an appropriate plant bioassay.

The suitability of Bowen's (1971) bioassay for early detection of phosphorus deficiency based on differential uptake of p^{32} labelled phosphorus over a period of 15 minutes from 5×10^{-6}M phosphate 'test' solution was investigated. It was applied to seedlings of birch *(Betula pendula* Ehrh.) and sycamore *(Acer psuedoplatanus* L.) previously grown 'pretreated': (i) for six weeks in sand culture with Hewitt's (1952) nutrient solution containing different amounts (1–100ppm) of phosphorus supplied as NaH_2PO_4; (ii) one season in uncultivated phosphorus-deficient soils, with and without added phosphate or; (iii) two seasons in a range of uncultivated soils of different fertilities.

The uptake of p^{32} phosphorus by birch seedlings from the 'test' solution was negatively and exponentially related to concentrations of phosphorus in the pretreatment sand cultures (Figure 15). Similarly, the uptake of p^{32} was decreased by adding phosphate to deficient soils during the pretreatment phase: it was also inversely related ($R^2 = 0.80$, $p < 0.01$) to amounts of PO_4 already within seedlings after growing in different soils for two seasons. In this instance, the uptake

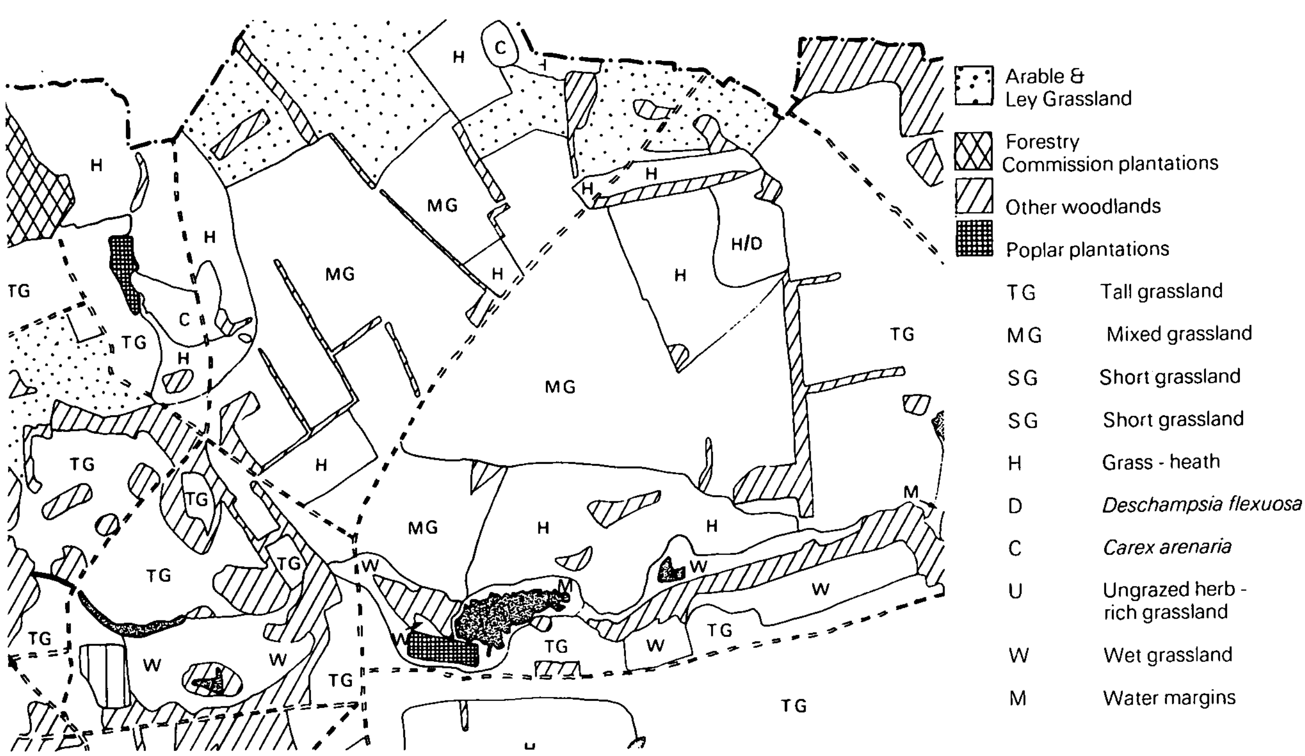

Figure 13 Vegetation types on Stanford Practical Training Area

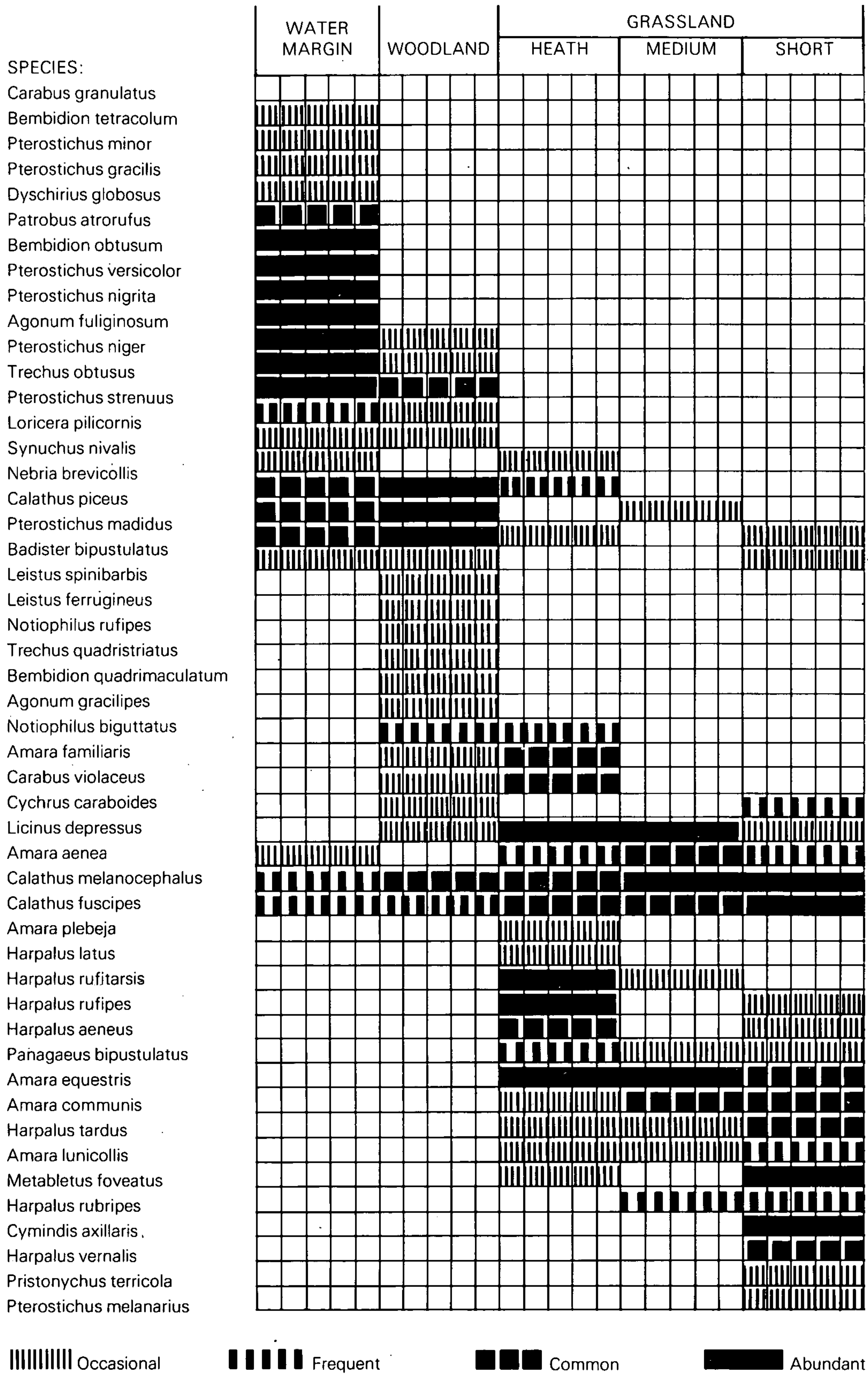

Figure 14 Distribution of Carabidae (Ground beetles) in different habitats found in the Stanford Practical Training Area

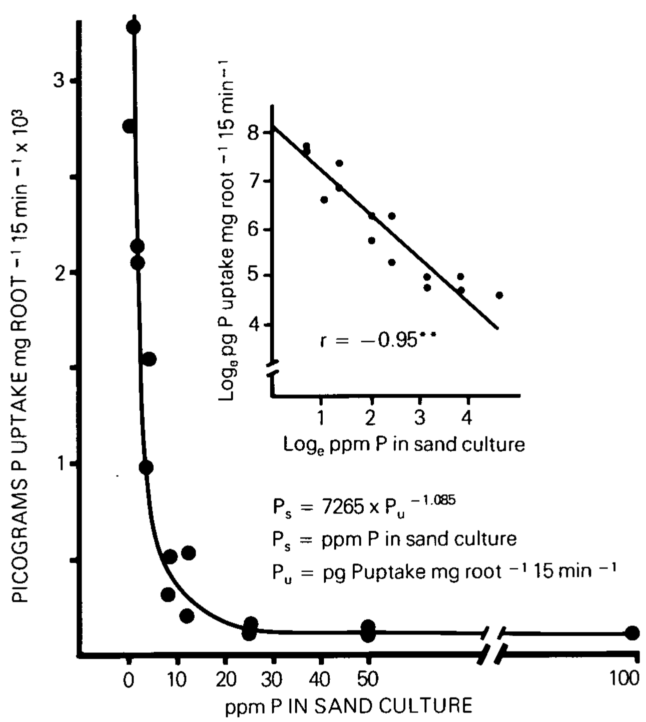

Figure 15 The uptake of p^{32}-labelled phosphorus from 5 x 10^{-6}M phosphate after transferring birch seedlings previously grown for six weeks in sand cultures with different PO_4 concentrations

of p^{32} was also negatively related to amounts of isotopically exchangeable, and acetic acid extractable, phosphorus and phosphatase activity in the pretreatment soils.

Although they were more variable, the responses of sycamore seedlings were similar to those of birch. The greater variability of sycamore may be attributed to different amounts of nutrient contained in their relatively large seeds or to the erratic root development of endotrophic mycorrhiza (see Frankland et al, p 40).

It seems that Bowen's method offers a means of indirectly obtaining an integrated assessment of the availability of soil phosphorus for plant growth.

A.F. Harrison and D.R. Helliwell, with J.C. Frankland

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MONITORING VEGETATION AND VERTEBRATES IN INDIAN TIGER RESERVES

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

Population of the Indian tiger (*Panthera tigris tigris* L.) decreased alarmingly from 40,000 at the end of the nineteenth century to approximately 1850 in 1972. In an effort to (a) reverse this decline, attributable to hunting and poisoning where cattle were endangered, and the destruction or disturbance of forest habitats, and (b) ensure the maintenance of sustaining populations, the Government of India has designated nine Tiger Reserves. These Reserves, known to be frequented by tigers, are thought to include a representative range of the different types of tiger habitats found in India: some were Nature Reserves or Game Sanctuaries, whereas others were commercial production forests before Project Tiger was launched in 1973. By controlling the activities of man, it is to be expected that vegetation changes will occur, with consequent effects on animals which either compete with, or are the prey of, tigers.

To aid the Indian Government programme, the World Wildlife Fund commissioned ITE to recommend how populations of plants and animals within the Reserves should be repeatedly recorded, there being a need for a straightforward standardized method that could cope with a diverse array of habitat features and a range of population densities.

It is recommended that vegetation should be sampled in a series of permanent plots located in strata based on existing information, detailing the species contributing to forest canopies and dealing with physiognomy and ground features. Where areas can be identified as being of special significance to wildlife or are otherwise of particular interest, separate sampling schemes have been suggested. Observations of a limited number of animals, including indication of their presence, will be related to vegetation in the permanent sample plots: records obtained from other localities in the Reserves will be complemented by parallel assessments of habitat characteristics. It is recommended that attempts to obtain total counts of some animal species should cease and should instead be replaced by observations which can be treated as indices of relative abundance. For illustrations see cover photograph and Plate 13.

J.M. Sykes, V.P.W. Lowe and A.D. Horrill

Trees and woodlands

WATER AND THE GROWTH OF CONIFEROUS PLANTATIONS

Britain's plantation forests have been established mainly on upland moors, in wet regions, where soils are frequently waterlogged and where precipitation exceeds evaporation for most of the year. In these conditions, the growth of saplings is restricted and successful establishment has required extensive drainage.

Surprisingly, however, the distribution of fine roots in an upland plantation of Sitka spruce (*Picea sitchensis*), 11 years old, was found to be similar to that in dry regions of the world with largest concentrations of roots occurring in the top 2–3 cm of soil and more roots developing close to the boles than in the spaces between trees. Because it was thought that this pattern of development may reflect the distribution of soil moisture, the inter-relationship between roots and soil moisture was studied at the Institute's field site at Rivox in Greskine Forest near Moffat, Dumfriesshire.

Partitioning of incident precipitation

Weekly measurements were made of stemflow in a plantation during its fourteenth year. Additionally, an array of rain gauges was systematically distributed to collect throughfall, i.e. the fraction of incident precipitation reaching soil directly or dripping from branches. The forest canopy was dense, with areas of needles and branches exceeding that of the supporting ground by factors of ×12 and ×3 respectively. During the period of root growth from May–August, 393 m of rain were received by the forest, i.e. some 1203 litres/tree. Of this moisture, 23% was recorded as stemflow, 37% as throughfall and the balance ('interception loss'), 40%, was estimated to have been lost by evaporation to the atmosphere. This large 'interception loss', which is typical of forest canopies with large amounts of well ventilated foliage, decreased to 15% during winter months.

Thirty-nine per cent of the water reaching the forest floor during the period of root growth was attributable to stemflow, the amount per tree being positively related to the horizontal spread of its crown. The balance, 61%, reached the forest floor as throughfall and was distinctively patterned (Figure 16). Throughfall, as a % of total moisture falling on the forest floor, was greatest close to the boles and between trees in the same row, where the greatest concentrations of roots occurred. As with stemflow, the pattern of throughfall was influenced by the structure of the forest canopy, being least where the crowns of many trees overlapped.

Seasonal patterns of root growth

An intensive study made of roots 20 cm below ground and near to the base of a bole showed that populations of fine roots increased from 3 May until 2 June, a period of (i) high rainfall input, (ii) increasing soil temperatures and (iii) high soil moisture potential, i.e. wet soil (Figure 17). When rainfall decreased between 2 and 27 June, and although a high soil moisture potential was maintained, the population of roots decreased slightly, possibly because of the redistribution of reserves with the

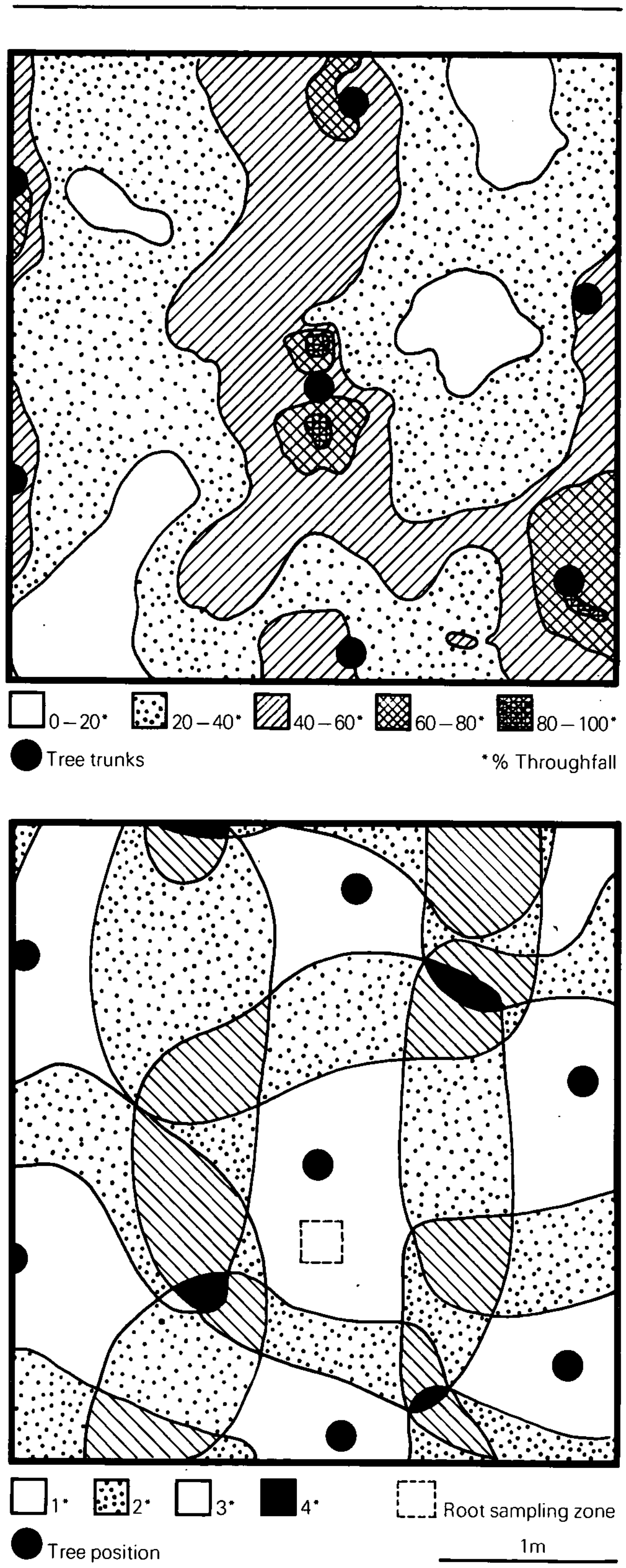

Figure 16 (above) The pattern of throughfall reaching the forest floor in a 14 year plantation of Picea sitchenis *for one week of 26.4 mm rain. (below) The pattern of overlapping tree crowns over the area shown above*

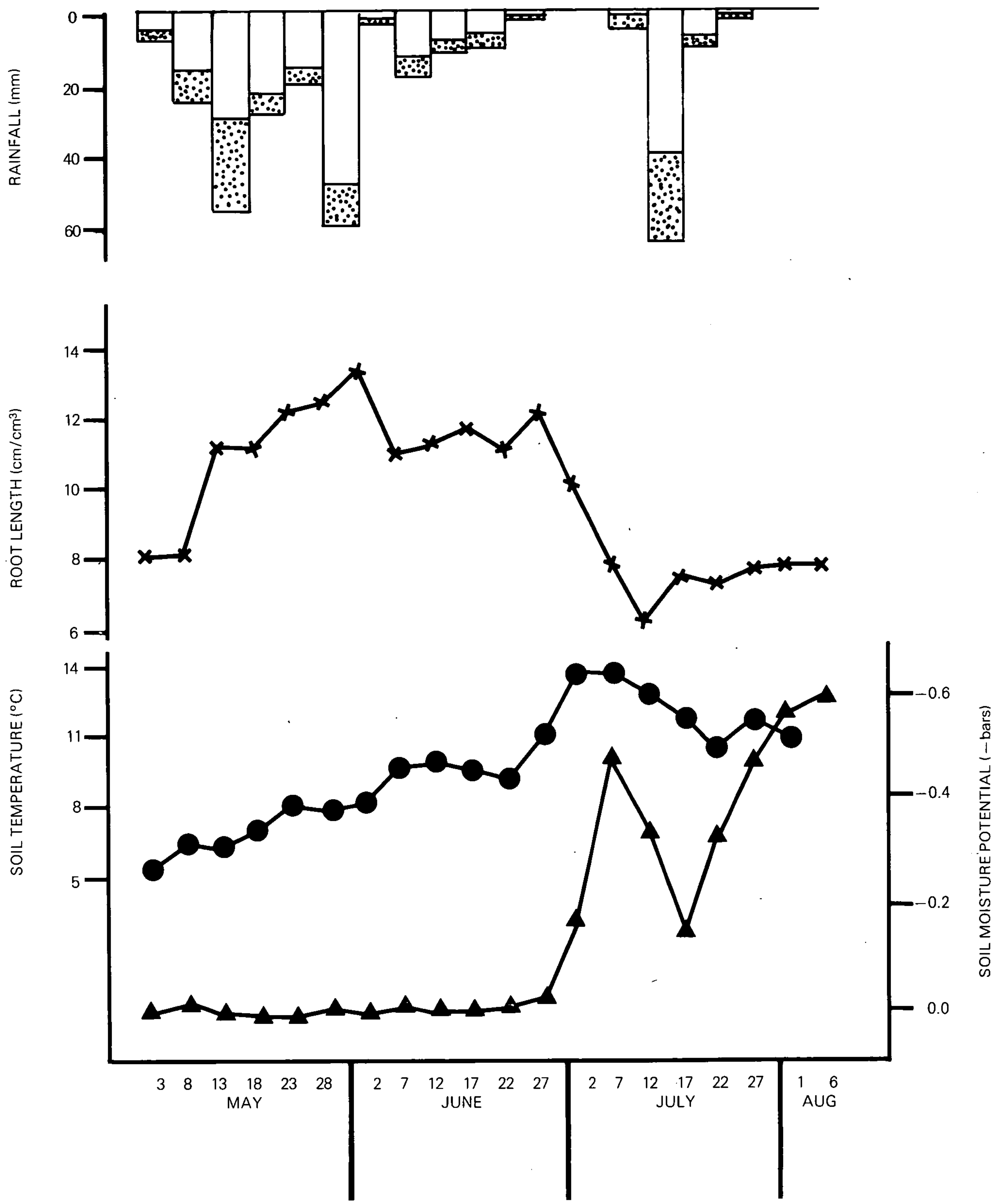

Figure 17 Tree root growth in relation to environmental factors in an organic soil horizon of the forest soil. The stippled proportions of rainfall indicate 'interception loss' from the forest canopy.

start of the major period of shoot extension. Later, in a dry period (27 June until 7 July) when soil water potential decreased, root mortality increased appreciably with the loss of 46% of fine roots in 15 days. Heavy rain in the period 12 to 17 July partially rewetted the soil. Some root growth was recorded, but it stopped when soil water potentials decreased as a result of water uptake by the trees.

Loss of water by transpiration

Water loss by evaporation can occur either by evaporation of surface water from the wet canopy (interception loss), or by transpiration, with water drawn from the soil through the conducting tissues of the tree. Interception losses are high at Rivox where there is a shortage of soil moisture. Transpiration was measured with equipment loaned by the Institute of Hydrology. Hourly estimates were obtained of sensible, i.e. 'dry', heat loss from the canopy (H). As there must be neither a net gain nor a net loss of heat by the forest surface because its temperature remains approximately constant (during periods of an hour), then, knowing the net input of radiation energy from the sun (R), the amount of energy lost in the evaporation of water (E) can be estimated

$$R = H + E$$

By deduction, it was found that transpiration losses were typically 3 mm of precipitation per day during part of August. This amount is equivalent to 6 litres/tree/day, which is comparable to the amounts of rain reaching the forest floor in the period May–August as stemflow and throughfall. Although these estimates have several sources of error, it seems that transpiration can account for the rain reaching the forest floor and be responsible for decreased soil moisture contents which limit root growth. In forests, transpiration rates are largely controlled by amounts of atmospheric humidity and by the surface resistance of the canopy, i.e. the resistance to water loss which depends on both the species of tree and its canopy structure. Comparative measurements with other forests have shown that transpiration rates were higher at Rivox in Dumfriesshire than at a Sitka spruce forest near the coast of Aberdeenshire, the difference being attributable to the drier atmosphere at Rivox and not to differing surface resistances.

E.D. Ford, R. Milne and J.D. Deans

GENE CONSERVATION AND THE IMPROVEMENT OF TROPICAL TREES

(This work was supported by the Ministry of Overseas Development)

During the last decade, the contribution made by *Triplochiton scleroxylon (Plate 8),* the source of the timber (Obeche), to the export of timber from Nigeria has decreased from 60% to virtually zero following the severe exploitation of natural forests and their destruction by shifting agriculture, the construction of new roads, etc. The conservation of *T. scleroxylon* is therefore of immediate importance, the problems encountered – poor seed production and low seed viability – being typical of those of many trees. To some extent, these problems can be circumvented by vegetative propagation which can provide a supply of planting stock, and, at the same time, enables gene banks to be established.

These gene banks, in due course, may provide material for tree improvement and breeding if flowering can be controlled.

Work on *T. scleroxylon* is being done at ITE, Edinburgh (Bush), and in Ibadan, Nigeria, both groups being funded by the Ministry of Overseas Development. Colleagues in Nigeria collected seed of *T. scleroxylon* from much of its natural range, extending from Sierra-Leone to Cameroun. Subsequently, seedlings were multiplied vegetatively and used in an experimental 40 hectare planting.

Vegetative propagation

Environmental and hormonal factors affecting rooting are now sufficiently well understood to enable cuttings to be taken and grown in controlled conditions. Essentially, cuttings should be taken from young seedlings, 'juvenile' clonal material or coppice shoots; they should have a leaf or part of a leaf, and be maintained in humid conditions at about 30°C. Auxins (Napthalene acetic acid (NAA) and Indolylbutyric acid (IBA)), applied to cuttings, enhance rooting in most clones. Some clones which, in the absence of auxins, rooted indifferently responded greatly to concentrations ranging from 8 to 200μg/cutting, whereas others which rooted more prolifically were less responsive. A few clones responded most to 8μg/cutting, being severely inhibited by 200μg/cutting.

Current studies have been concentrating on those factors which affect rooting within a clone, phase change and apical dominance. Traditionally, cuttings from the base of a tree are considered to be juvenile and easy to root, whereas mature crown cuttings are hard to root: the decreased rootability of 'apical' cuttings is detectable even in small specimens of *T. scleroxylon,* recent experiments suggesting that the inability to root may be attributable to competition for root-derived factors, nutrients and/or possibly 'hormones'. According to the position and type of shoot used, rooted cuttings may grow erectly with a radial leaf arrangement or plagiotropically with distichous leaves, the latter being worthless in forestry. To minimise the occurrence of plagiotropic growth, it is essential to manage stock plants correctly.

Clonal selection

While maintaining bush-like stockplants for producing cuttings, it became clear that the branching characteristics of clones differed appreciably. Attempts are being made to develop a predictive test for 'branchiness', the first step being the removal of the apical bud. In due course, however, it will be necessary to consider the relation between form in young and old trees.

Flower induction

In West Africa, the flowering of *T. scleroxylon* is seasonally erratic, rarely occurring before trees are 40 years old, and 100 or more feet tall. At Bush, plants 2–3 years old have, in some instances, flowered so providing excellent material for programmes of flower induction, a requirement for active programmes of tree improvement.

R.R.B. Leakey and K.A. Longman

INTENSIVE CULTURE OF POPLARS FOR WOOD FIBRE

It has been suggested that much of the wood currently used in Great Britain for making paper, chipboard and fibreboard could be obtained from short-rotation coppices of fast-growing broadleaved trees. For this reason, experimental plantings of a fast-growing clone of *Populus trichocarpa* were established in March 1974 on four agricultural sites in Midlothian, Argyllshire, Worcestershire and Suffolk. At each site, 15 cm cuttings were planted at spacings systematically ranging from 32 to 141 cm, where plants per hectare decreased from 100,000 to 5,000. After three years the trees, except at the closest spacings, were 4–5 m tall. The diameters of individuals at the closest spacing were 2–3 cm each with < 500 g dry matter, whereas at the widest spacings stems weighing > 1,000 g were 5–6 cm in diameter. On balance, however, dry weights of wood per hectare were greatest at the closest spacings (Figure 18).

The yields of stems plus branches (with bark) in excess of 5 tonnes per hectare per annum, and averaged over 3 years with more than 20,000 trees/ha, are unlikely to be achieved for 20 years by conifers on traditional forest sites (Figure 19), suggesting that the commercial prospects of short-rotation fibre production warrant further examination, as is happening at several centres in the USA (Steinbeck et al, 1972; Anon, 1975, 1976).

M.G.R. Cannell

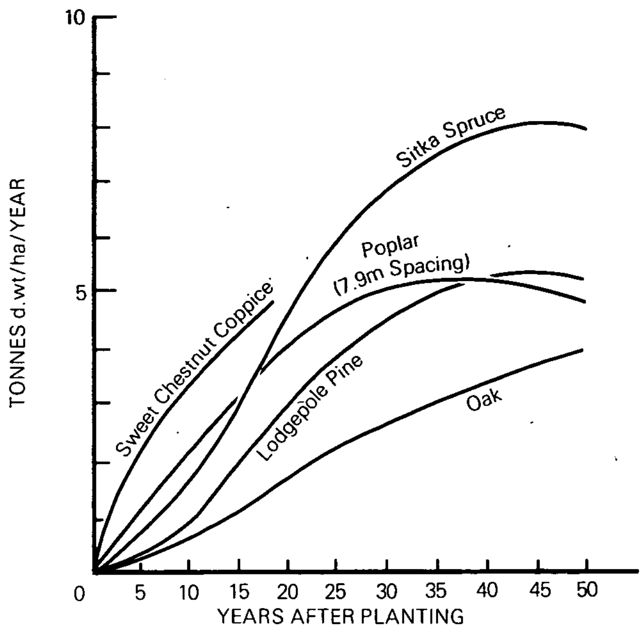

Figure 18 Effects of spacings on mean annual dry weight increments (stems plus branches (with bark)) of Populus trichocarpa *grown for three years at 'agricultural' sites in Argyll, Midlothian, Suffolk and Worcestershire.*

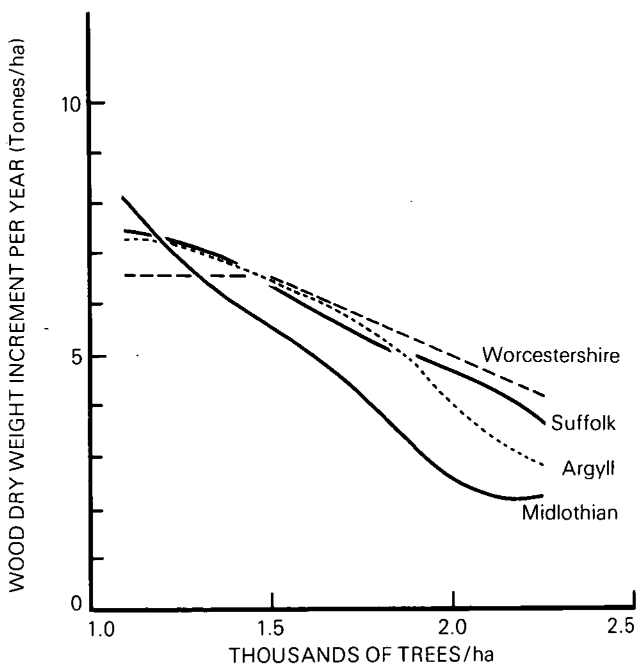

Figure 19 Annual dry weight increments of different trees grown with their conventional management on traditional sites in Britain. (Sweet chestnut data taken from Ford and Newbould (1970); others from Bradley et al (1971) where stem over-bark volumes of the largest yield classes (most productive stands) were converted to dry weights using factors from Anon 1941).

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TREES FOR PLANTING INDUSTRIAL SPOIL

(This work was supported by the National Coal Board)

Attempts have been made for many years to plant industrial spoil and restored opencast land, whether or not graded, with trees for amenity and, in some instances, timber. From time to time, problems have been encountered, some attributable to poor water regimes (either flood or drought), others to damaging concentrations of toxic substances, nutrient deficiencies, cementation and compaction, unfavourable acidity/alkalinity.

Although plantings fail, natural vegetation often establishes itself on difficult sites (Plate 9). Because some populations of naturally occurring grasses and herbs have subsequently been shown to be tolerant, it was decided to consider the exploitation of naturally occurring and possibly tolerant woody perennials, including trees. In this project, begun in 1974 and to be funded by the National Coal Board for three years from 1977, the first objective was to identify spoil heaps with naturally occurring woody perennials. Two types of collections were then made (i) young saplings and/or (ii) cuttings from larger trees. The latter were then rooted and, with the supply of saplings, formed an array of stockplants concentrating on pioneers such as willow (*Salix* spp.), birch (*Betula* spp.) and elder (*Sambucus nigra* L.). These stockplants are being multiplied vegetatively prior to exhaustive tests of field performance and possible commercial exploitation.

J.E.G. Good

VARIATION IN BIRCH

Clones of *Betula pendula* and *B. pubescens* have been maintained in a juvenile condition for as long as 5 years when cultured aseptically on nutrient agar in continuous light. Originally they were grown individually in flat-bottomed tubes with 'slopes' of nutrient agar (Pelham and Mason, 1978). Though still used for the maintenance of clones, the tubes have been replaced, for experiments, by a container, formed by sealing a clear plastic beaker into the lid of a plastic petri dish where plants grow faster, larger, and more uniformly (Plate 14). Additionally, it is possible to obtain a permanent record of root form by a photocopying process.

With the new system, it has been possible to compare the responses of different clones to different amounts of phosphate and/or calcium. Experiments are also being done with clones derived from seedlings from plants found growing on mine wastes rich in lead and zinc. Because lead salts precipitate phosphorus in the standard medium, the latter has been simplified, at the same time changing from a solid to a liquid substrate. Clones that have proved of interest in these experiments have subsequently been cultured in glasshouses, the transfer from aseptic to non-sterile conditions being at least 90% successful.

In addition to assessing varying responses to nutrients and heavy metals, variations in growth form have been recorded. These have included the effects of latitude of origin on dates of leaf emergence and leaf fall when a wide range of seedlots was grown at the same site. When three clones were derived from a single seedlot of *B. pubescens,* one consistently produced a strong basal shoot, another produced side branches in a single vertical plane, whereas the third was repeatedly branched because its leading shoots did not survive winter conditions. Leaf shape is being studied biometrically in collaboration with A. S. Gardiner (Merlewood), some clones being readily distinguishable by simple leaf measurements.

Provenances from different latitudes have been successfully cross-pollinated. Clones from the hybrid seedlings are being propagated in (i) aseptic and (ii) glasshouse conditions before assessing their patterns of growth, their ability to form mycorrhizas with different fungi and their responses to different nutrient combinations.

J. Pelham and P.A. Mason

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OCCURRENCE OF MYCORRHIZAS ON ROOTS OF BIRCH AND SYCAMORE

For many years, mycorrhizal research, often done in the laboratory, has been concentrated on those mycorrhizas developing in plantation forests and agricultural crops; much less is known of mycorrhizas on natural vegetation, and virtually nothing about their occurrence on naturally regenerating trees. The development of mycorrhizas, the intimate and usually beneficial associations between plant roots and symbiotic fungi, was investigated when studying the growth of seedlings

Uplands Survey Map of Cumbria 1:750,000 showing land classes 1-16.
(see list for description of types)

Magenta	*1-4*	*open circle = 1*	*single bar = 2*	*closed circle = 3*	*double bar = 4*
Blue	*5-8*	*open circle = 5*	*single bar = 6*	*closed circle = 7*	*double bar = 8*
Green	*9-12*	*open circle = 9*	*single bar = 10*	*closed circle = 11*	*double bar = 12*
Black	*13-16*	*open circle = 13*	*single bar = 14*	*closed circle = 15*	*double bar = 16*

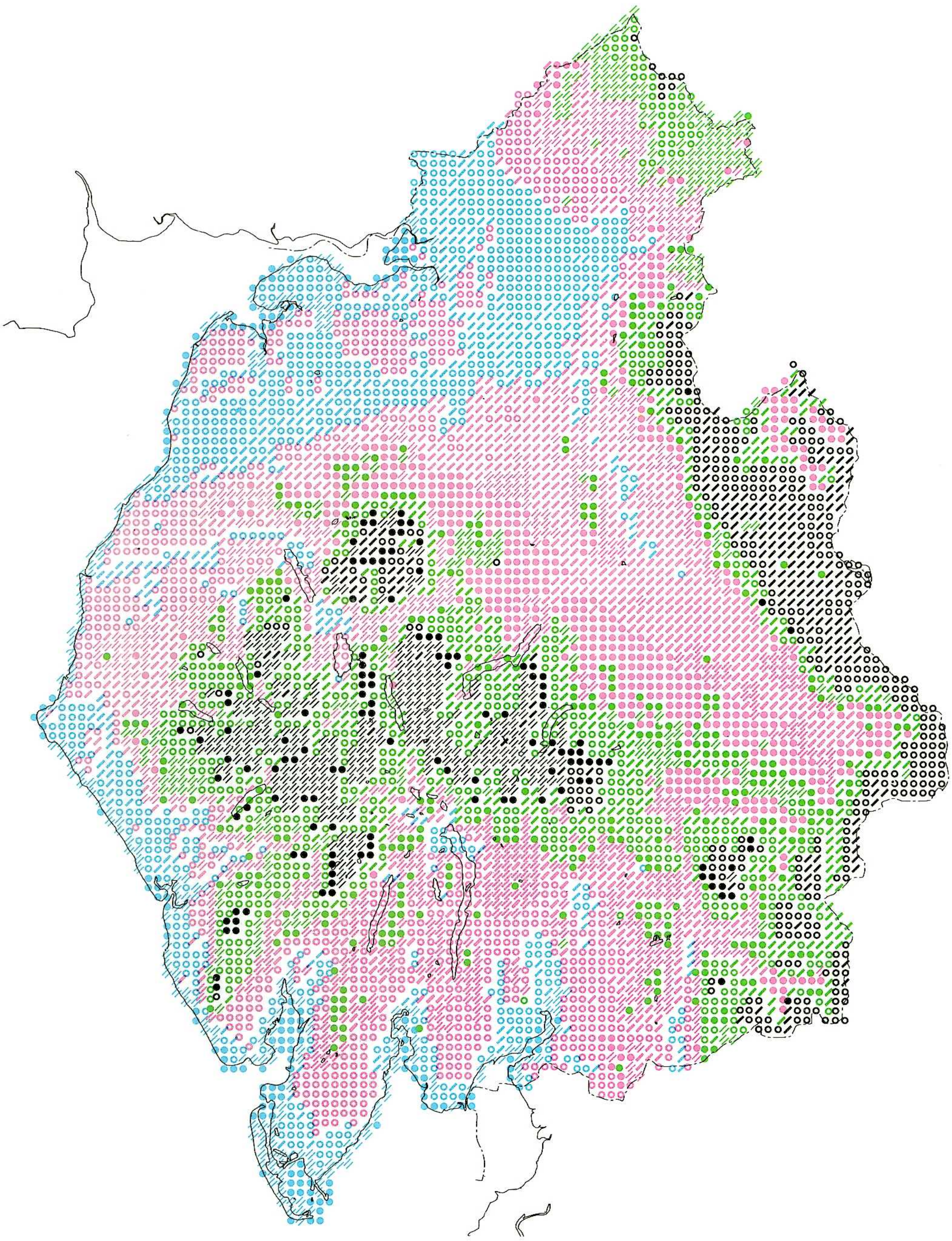


Plate 10 Distribution on a 1 km square grid of 16 land classes in Cumbria derived by analysis of map data. The close correlation in a series of sample plots between map characteristics and the occurrence of vegetation, hedgerows, woodlands and other landscape characteristics enables predictions of the latter to be made when only map attributes are known. The map was produced by the Experimental Cartography Unit.

Plate 11 Stone Chest, Cumbria. An example of change in vegetation between 1972 (above) and 1975 (below) on part of an area where the effects of afforestation on plants and animals are being studied. Photographs by J Sykes.

Birch, Loch Sunart, Lochaber District, Highland region.

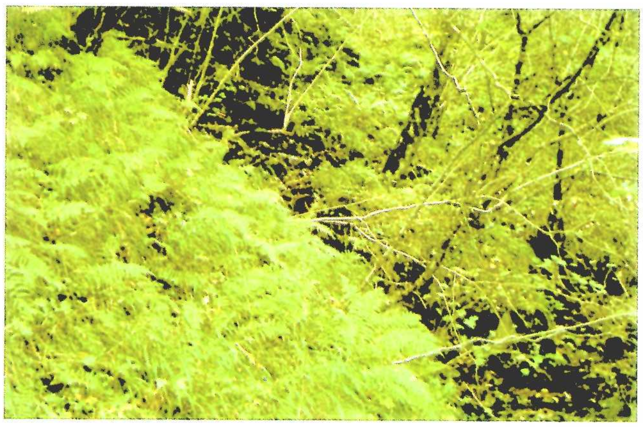
Birch and oak, Glen Creran, Argyll and Bute District, Strathclyde region.

Birch and oak, Letterewe, Ross and Cromarty District, Highland region.

Birch and oak, Port Appin, Argyll and Bute District, Strathclyde region.

The first phase of the project is to make visual estimates of the canopy composition of the woodlands. The species of birch and oak cannot therefore be separated and care is required to ensure consistency between observers.

Birch, Lettoch, Moray District, Grampian region.



Ash and birch, Glasdrum NNR, Argyll and Bute District, Strathclyde region.

The second phase of the project will be to sample within woods to check the accuracy of the visual estimate and to examine the distribution of both sites and species throughout Scotland.

Plate 12 These photographs were taken during an enumeration of Scottish deciduous woodlands to aid understanding of their amount and distribution. Photographs R G H Bunce

Bandipur Reserve

Lantana camara, *an abundant climber on many reserves*

Group of Chital (Axis axis) *at Bandipur Reserve (tiger prey species)*

Common Langur (Presbytus entellus) *Bandipur Reserve (prey species)*

Indian elephant Kahna Reserve

Tigress, Similipal Reserve

Plate 13 These photographs were taken during a visit made to advise on the monitoring of vegetation and vertebrate mammals in the Indian tiger reserve. Photographs by J M Sykes and A D Horrill from different seedlots of birch and sycamore in 25 Lake District soils (Harrison and Helliwell, *ITE Annual Report, 1974,* p.53). When examining mycorrhizal development at the end of the second growing season, either by scanning intact roots or by examining root squashes after clearing and staining, it was found that mycorrhizal frequency differed greatly in different soils. Mycorrhiza are of two types ecto-and endo-trophic, the former being associated with stubby roots. Whereas 12–100% of birch roots were ectomycorrhizal (Plate 15), 47–100% of sycamore roots were endomycorrhizal. As yet, the analyses are incomplete but the origin of the different sycamore seedlots did not affect mycorrhizal frequency. The interplay between mycorrhiza and tree growth is being explored.

J.C. Frankland, A.D. Bailey, and P.L. Costeloe

SYNTHESIS OF MYCORRHIZAS AND THE NATURAL OCCURRENCE OF MYCORRHIZAL 'TOADSTOOLS'

During the year, our knowledge of mycorrhizas was enhanced by examining the interplay between *Betula pendula* and *B. pubescens* from a more diverse array of sites, and isolates of *Amanita muscaria* from an extended geographical range, including India. It was found that the responses of clones were similar to those obtained with seedlings and that they were comparable whether cultured on agar media or on a vermiculite-peat mixture. When Melin Norkran's medium was added to the latter, numbers of mycorrhizas produced by one strain of *A. muscaria* were appreciably decreased as compared to numbers developed when Ingestad's solution was used. On the other hand, the few mycorrhiza produced were much more branched. The successful experimental production of mycorrhizas on inoculated vermiculite-peat has stimulated interest in the mass inoculation of seedlings for commercial use. In preliminary trials, mycorrhiza developed on seedlings growing in the tubes now widely used in forest nursery practice. These trials, done in aseptic conditions, will be tested for their wider applicability to conditions where contaminating microbes are not rigorously excluded.

Since planting replicated and randomly arranged seedlings of *B. pendula* and *B. pubescens* in 1971, annual flushes of fruitbodies (toadstools) have emerged in the late summer/autumn. Nearly all of the fruitbodies have belonged to fungi known to form mycorrhiza with species of birch. In 1977, the co-ordinates of more than 19,000 fruitbodies belonging to 20 species of fungi were recorded in close proximity to a total of 60 trees, the number of fruitbodies doubling since 1976. Whereas numbers of the previously recorded species increased, fruitbodies of *Leccinum versipelle, L. varicolor, Inocybe asterospora,* two species of *Cortinarius* and the truffle-like *Hymenogaster tener* appeared for the first time. Mean numbers of sporophores per tree differed greatly between different seedlots. Thus, there were 700 fruitbodies associated with *B. pendula* from a latitude of 50°40″ N but only 2 with the same birch species from 66°30″ N. The commonly occurring *Lactarius pubescens* was particularly associated with *Betula pendula* and *Hebeloma sacchariolens* with *B. pubescens*.

P.A. Mason and J. Pelham

THE GISBURN EXPERIMENT: EFFECTS OF DIFFERENT TREE SPECIES ON THE ACTIVITY OF SOIL MICROBES

When tested at Gisburn, 20 years after planting, evidence was obtained for the hypothesis that different tree species appreciably affect the activities of soil microbes. Using changes in the tensile strength of cotton strips buried in different soil horizons beneath oak, alder, Norway spruce or Scots pine it was found that:

(i) microbial activity decreased with increasing depth in oak, alder and Scots pine soil profiles, but there was no effect of depth under Norway spruce.

(ii) microbial activity was usually greatest in soils planted with alder and least under Norway spruce, with oak and Scots pine soils being intermediate and reacting similarly (Figure 20).

Further evidence of differing microbial activity beneath the different stands of trees was obtained when autumnal agaric fruitbodies were assessed by Dr T.F. Hering. There were 60, 325, 3500 and 30,000 fruit bodies beneath alder, oak, Scots pine and Norway spruce respectively (Table 15). All of those associated with alder were thought to be of mycorrhizal species whereas those under Norway spruce were predominantly of litter-decomposing species, including *Marasmius androsaceus*.

A.H.F. Brown

Table 15 Estimates of two groups of agaric sporophores counted in 0·2 ha plots of different trees, 20 years after planting at Gisburn

Groups of agaric sporophores	Types of tree			
	Alder	Oak	Scots pine	Norway spruce
(1) those of mycorrhizal associates	60	300	400	30
(2) those of litter decomposers	0	25	3100	30,000

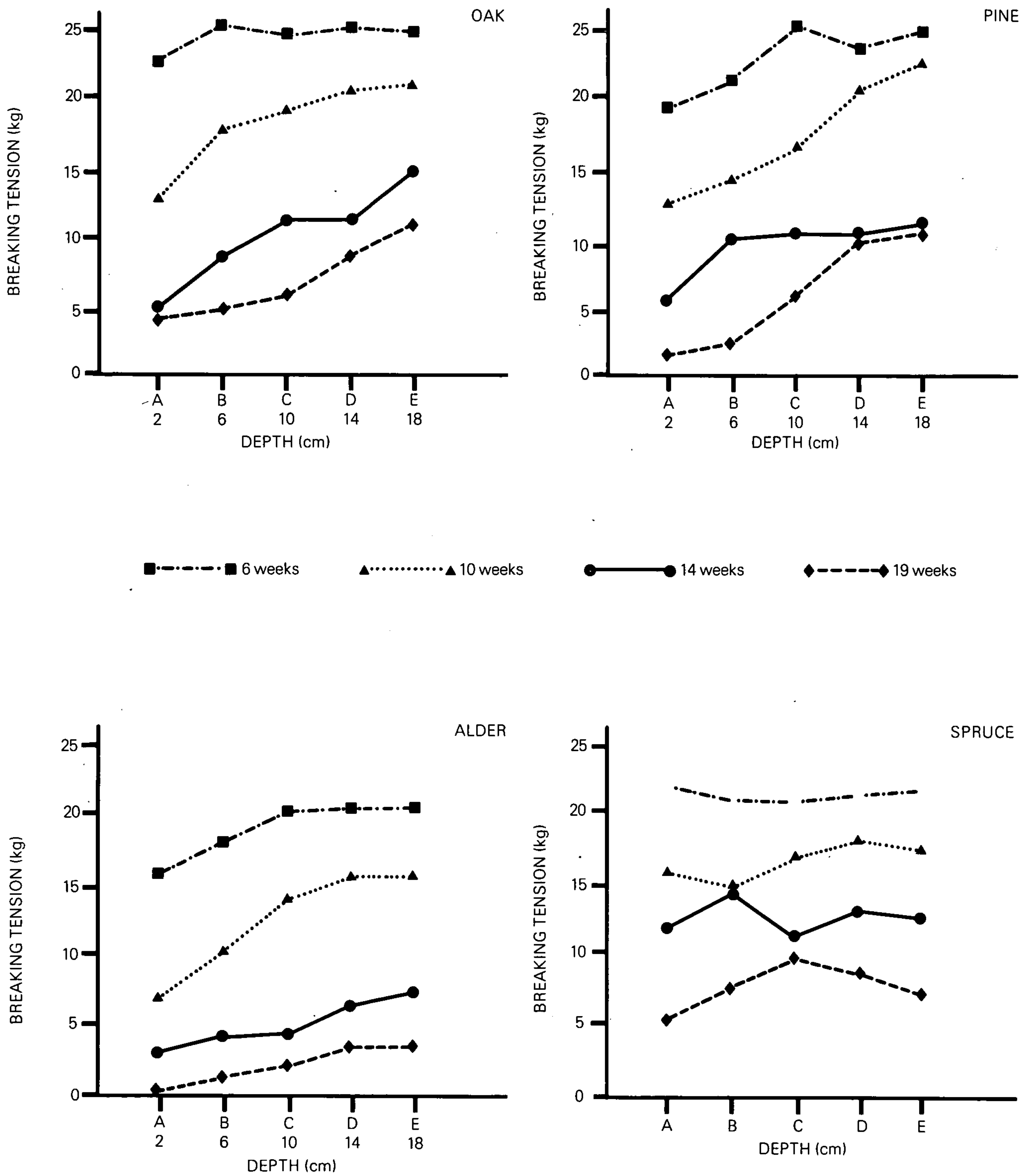


Figure 20 Effects of different tree species, 20 years after planting, on the decomposition by soil microbes of cotton strips buried at different depths. (Microbial activity indirectly proportional to tensile strength which was 25 kg initially; assessments made 6, 10, 14 and 19 weeks after burying).

VIRUSES OF TREES

Cherry leaf roll virus (CLRV)

In addition to damaging birch CLRV was, for the first time in Great Britain, associated with symptoms in walnut *(Juglans regia)* where yellow-brown rings were found in fewer than 25% of the leaflets of a tree 25 years old, the tree having been grown from seed imported from Italy. The isolate of CLRV from walnut was distinguishable serologically from birch isolates, so lending support to the realisation that isolates of CLRV from different natural host genera are different, a degree of specialisation possibly linked with its transmission through pollen/seed. However, even if pollen grains are highly specific vectors of viruses it is possible that other species exposed to massive amounts of wind-borne pollen might, in rare instances, become infected. To test this suggestion, infected birch pollen was applied to the stigmatic surfaces of glasshouse grown clones of sweet cherry (*Prunus* sp) flowering for the first time. For 6 months after pollination, CLRV has not been detected in the cherry foliage. To test if CLRV affects viability and pollen tube, *in vitro* methods of pollen germination are being explored. There is already evidence to suggest that the germ tubes of pollen from CLRV-infected trees grow less than those from trees without this virus.

Efforts to locate virus-like particles in birch pollen have so far failed, primarily because of inadequate fixation and embedding, and possibly because of interference from large amounts of oil.

Poplar mosaic virus (PMV)

Continuing observations on the spread of PMV were made at three study sites in southern England, but no new infections were detected during the past year. Until now, the detection of PMV has depended upon biological assays using a series of indicator herbaceous hosts inoculated with sap from test foliage. However, in common with other virus infections of trees, PMV is not distributed evenly and therefore detection is influenced by sampling procedures and additionally by unknown dilution factors. To minimize the impact of these factors, the sensitivity of two serological techniques is being assessed: (i) the use of antibody-sensitised latex (Berks, 1967) enables PMV in leaves of poplar and solanaceous hosts to be detected within minutes, but the method is somewhat less sensitive than bioassay; and (ii) the enzyme-linked immune sorbent assay (ELISA) test (Voller *et al*, 1976) is in some aspects more promising because it is more sensitive than sensitised latex. Unlike bioassay, these serological methods can be used to detect PMV in frozen leaves, a great advantage when it is not possible to cope with freshly-collected foliage.

Other viruses

Arabis mosaic virus (AMV) was detected at least as frequently in 'unaffected' ash (*Fraxinus excelsior*) as in specimens with symptoms of die-back. Typically, the virus was associated with foliar chlorotic chevron patterns, but the leaflets of one infected tree were grossly distorted.

AMV was detected in weeping ash, *(F. pendula)*, where it was associated with chlorotic mottling and foliar malformations in addition to ring and line patterns.

When experimentally inoculated, alfalfa mosaic virus was found to infect *Viburnum lantana* systematically with the reddening of foliage; in contrast, another isolate of this virus failed to induce symptoms in *V. tinus* within a seven month period of inoculation.

J.I. Cooper, M-L. Edwards and D. McCall

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Land management

RESPIRATION AND ORGANIC MATTER ACCUMULATION IN A LOWLAND HEATHLAND SOIL

Measurements of soil respiration have been used as indicators of soil metabolic activity or, where the ecosystem in question could be considered to be in a steady state, as estimates of net production plus root respiration. Published estimates of root respiration have ranged from < 10% to 70% of total soil repiration, the upper limit agreeing with results from studies of lowland heathlands. In these studies, root production was of the order of 400 $gm^{-2}\ y^{-1}$, and, when combined with previously obtained estimates of above ground production (Chapman *et al*, 1975), gave a total net production by the *Calluna* heathland of 700 $gm^{-2}\ yr^{-1}$, a figure comparable to the lower levels of production in woodland communities on similar soils.

Results obtained have been used to examine rates of heathland soil formation and were found to support the idea that the surface horizons of the soil may reach steady state conditions after about 800–1000 years (Figure 21), but that considerable changes still occur within the soil profile even after such a period of time.

S. B. Chapman

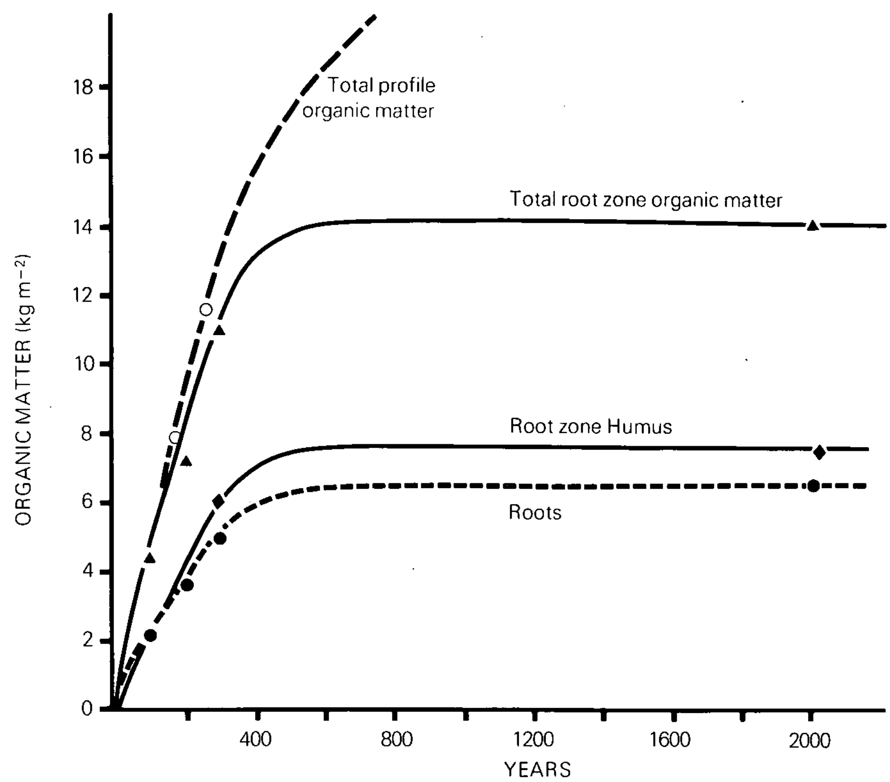

Figure 21 Simulated accumulation curves of organic matter compared with observed values from heathland and dune heath sites in Dorset.

Reference

Chapman, S.B., Hibble, J. and Rafarel, C.R. (1975). Net aerial production by *Calluna vulgaris* on lowland heath in Britain. *J. Ecol.*, **63**, 233–258

SHOOT PRODUCTION BY *CALLUNA VULGARIS* IN EAST SCOTLAND

Heather *(Calluna vulgaris)* is a 'key' species in the ecology and economy of the Scottish uplands being, (i) a major component of the vegetation of some 3 million hectares of moorland, and (ii) a major food for the associated wild and domestic herbivores. Because herbivores prefer to graze the current year's shoots of young, rather than old, *Calluna* bushes, moors are burned periodically to ensure a continuing supply of young plants. To enable the development of a rational system of management, optimizing the production of nutritious shoots, observations were made of the immediate and longer term effects of burning on the aerial growth of heather simultaneously recording seasonal fluctuations.

Calluna stands differ greatly in their rates of recovery after burning. In part, this recovery is a function of the physical environment and of the heat generated during burning; it is also a function of the densities of the original stands, because regeneration starts from buds at stem bases. When comparing two stands, both 10 years old, but one with 1,455 and the other only 641 stems m^{-2}, it was found that almost complete ground cover had been regained within 4 years of burnings in the stand with the greater original stem density; cover in the other stand reached 75% after 7 years. The production of shoots parallelled increases in cover, the annual rate of shoot production being maintained in the more rapidly regenerating stand at 250 gm^{-2} after the third year.

In other stands, the 'constant' rate of annual production was sometimes not reached until the tenth year after burning; it was thereafter maintained with seasonal variations until ground cover decreased. Production in good and bad years differed by 50%, the differences being related to weather during the May–August growing season, when warm and dry conditions appeared to favour growth. Growth was directly proportional to mean air temperatures, presumably regulating photosynthesis, and indirectly to rainfall, these two variables explaining about 94% of the variation from year-to-year (Figure 22). Because the growth of *Calluna* depends on

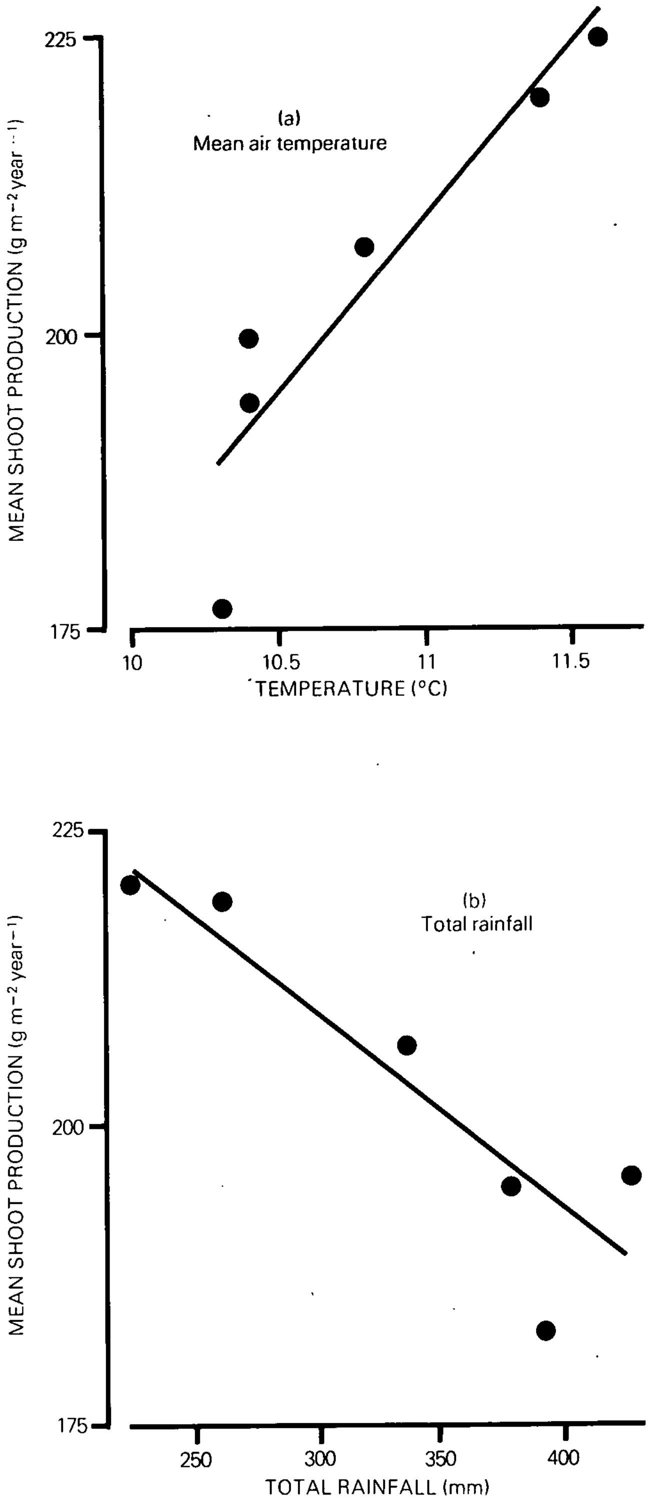

Figure 22 Shoot production by Calluna vulgaris *in East Scotland. Relation of weather in May—August with aerial growth of heather: (a) mean air temperature and (b) total rainfall.*

the availability of soil nitrates, which in turn reflects the mineralization of organic residues, it is possible that the inverse relation with rainfall may reflect the increased mineralization in dry, but not rainless, summers (Schreven, 1968).

Chemical analyses of 50 stands showed that concentrations of nutrients, particularly nitrogen and phosphorus, decreased rapidly during the first few years after burning (Figure 23). Thus, in years immediately following burning, *Calluna* productivity progressively increases, whereas concentrations of nutrients start high and then decrease. Burning therefore only temporarily improves the nutrient content of a heather stand. To burn every 4 years, before most stands have fully recovered, would be unwise because there would be a serious risk of causing soil erosion and/or the replacement of *Calluna* by less palatable species. For this reason, burning should usually be delayed for 8, and sometimes up to 20 or more, years.

G.R. Miller

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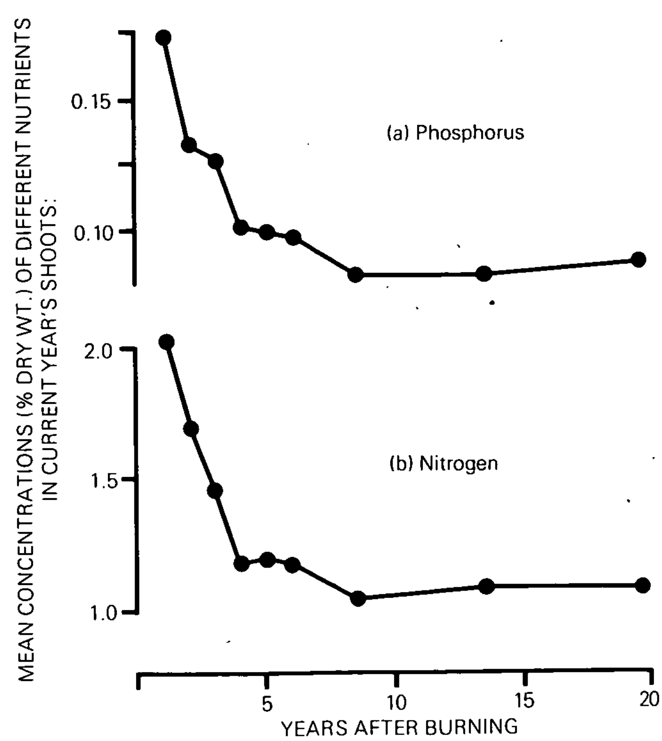


Figure 23 Shoot production by Calluna vulgaris *in East Scotland. Mean concentrations of (a) phosphorus and (b) nitrogen in the current year's shoots of stands of heather sampled at different intervals after burning.*

RE-ESTABLISHMENT OF HERB-RICH GRASSLANDS

(This work was commissioned by the Nature Conservancy Council as part of its programme of research into nature conservation)

Hay-meadows, chalk grassland and other permanent grasslands which once contained colourful and attractive plants are fast disappearing from the landscape of lowland England. At the same time, new grasslands are being developed on roadsides, on motorways, in Country Parks and in new towns, but they are not being sown with mixtures which produce herb-rich swards. In part, this change is attributable to the unavailability of seeds of many wild species, to a lack of information about the differing mixtures to sow on different soil types, and the present high cost of those seeds that are available.

To find the most suitable species to use for establishing herb-rich swards, the collection, storage and germination of seed of more than 120 chalk and meadow grassland species have been studied since 1973. A replicated experiment comparing the establishment and subsequent growth of a range of grass-herb mixtures was started in 1973 on a previously arable site on chalk soil at Royston, Hertfordshire. Ox-eye daisy (*Chrysanthemum leucanthemum*) soon dominated, it being one of the 27 or more of 36 herb species that established themselves; all 7 grass species became established. During the next 3 years, successional changes have occurred leading to a grassland consisting of an intimate mixture of herbs and grasses which is both attractive and provides food for insects (Plate 17).

T.C.E. Wells and S.A. Bell

THE COLONISATION OF SOWN GRASSLAND BY INVERTEBRATES

New grasslands are often created on areas of land where the objectives of management include conservation of wildlife. Commercial grass seed mixtures are commonly used, or the land may be allowed to develop a flora from the seed source of nearby vegetation. Botanical studies are being made on recreating species-rich swards, but the re-establishment of animal communities in such grasslands has not yet been studied. It is not known how successfully, or how rapidly, species which are characteristic of older grasslands can colonise new swards.

The site selected for study is on chalky boulder clay adjacent to Royston Heath in Hertfordshire. Before the experiment, the land had been cultivated mainly for cereal production. Following the harvest of 1972, the land was ploughed, cultivated and rolled, and prepared for sowing (April 1973). Two agricultural grass seed mixtures were used; the first consisted of 4 species of tall, rather coarse grasses, while the second mixture (5 species) consisted mainly of *Festuca* and *Agrostis* species. The objective was to establish 2 types of vegetation which contrasted in structure, but which were of the same age and growing on a newly cultivated soil from which most of the previous fauna had been eliminated. The seed was sown in mid-April 1973 and the first trapping programme began on 1 May. Because the soil was loose and exposed at this stage, only pitfall traps and hand-collecting could be used. When the vegetation became established, turf samples for heat extraction and vacuum samples were also taken. Germination began in early May, and, within 3 months, a fine-leaved turf (mean height c. 17 cm) and a taller, broader-leaved vegetation (mean height c. 30 cm) had developed. This height difference was maintained in subsequent years although the density of the vegetation and of the proportion of bare ground changed with time.

The catch of beetles and spiders (the 2 groups studied) in the first 2 weeks' trapping period was poor, but increased soon afterwards. This suggested that more animals were living in the surface soil of the bare cultivated ground, before trapping began, than was at first thought. To test this suggestion, an additional area adjacent to the experimental plots was ploughed and cultivated in the autumn of 1974. Immediately after this preparation (1 Oct.), 4 cages, each measuring $2\frac{1}{2} \times 2\frac{1}{2}$ m, were erected over the ground, alternating with 4 control plots of the same size. The cages, of fine nylon mesh over a metal frame, penetrated 15 cm into the ground to prevent immigration. Three pitfall traps were placed in each cage and control plot and the contents emptied every 2 weeks.

Although immigration into the caged plots was prevented, the pitfalls continued to trap many spiders and beetles for $4\frac{1}{2}$ months throughout the winter 1974/75. The most abundant spiders were the same in cages and controls and apparently represent those species best able to survive in the surface soil from year to year in spite of ploughing and cultivation. This experiment was repeated in the winter of 1975/6 with similar results. The numbers of spiders in the cage traps were 21%–45% of the totals from the control plots. Similar results were obtained by G.R. Potts and G.P. Vickerman (unpublished) in a spring barley field.

Not all the material from the Royston exclusion experiment is identified, but the available results indicate that many 'grassland animals' survive winter cultivation and are able to exploit the new habitat when growth begins in the spring. Although growth forms of the 2 contrasting swards were very different to the eye, the quantification of habitat structure, and the assessment of its influence on the fauna, is difficult. Measurements were made of increase in vegetation cover, height and biomass of vegetation, proportion of dead material in winter and summer, and leaf-width (Figure 24). The proportion of bare ground declined more rapidly in the

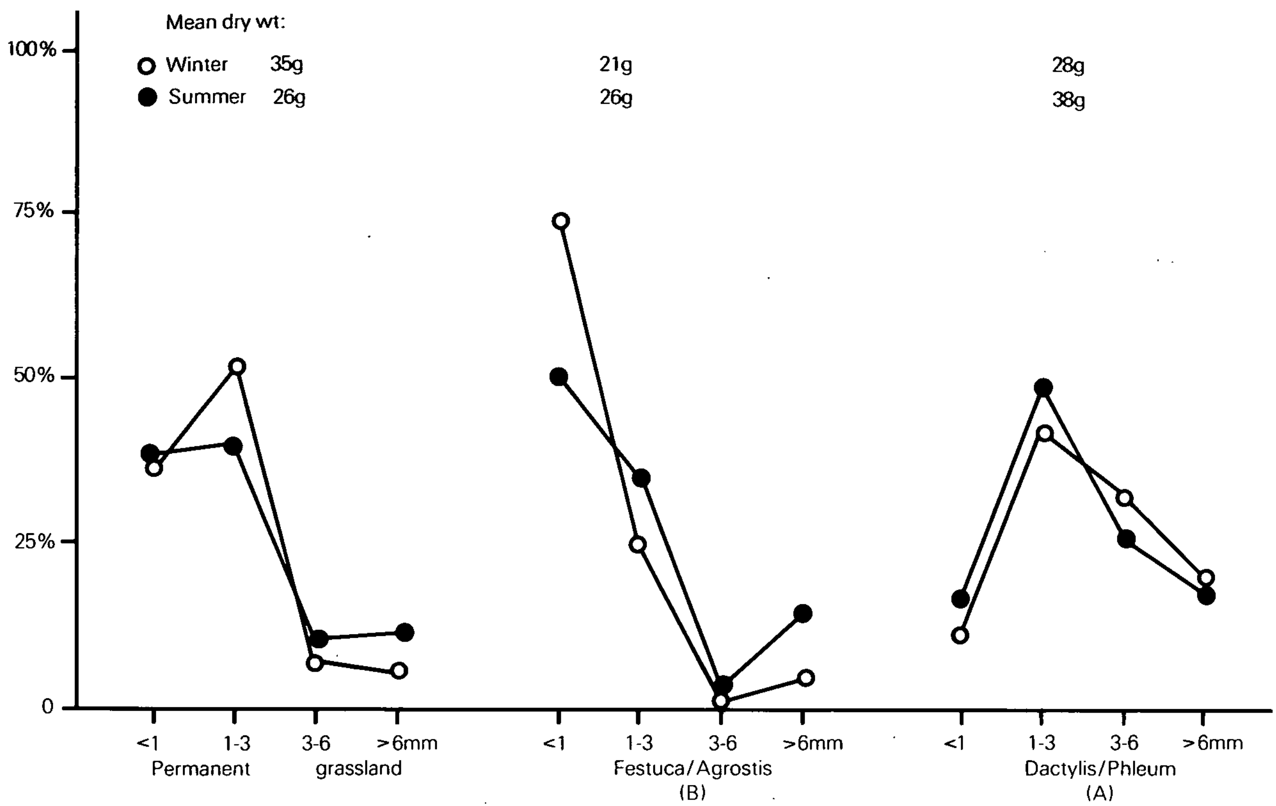


Figure 24 Leaf width profiles for three types of grassland.

fine-leaved turf because mosses and *Trifolium repens* were able to colonise and grow faster than in the taller grass areas. The proportion of dead material in the total plant biomass (dry weight) continued to increase with time until February 1976, but then fell in comparison with the nearby permanent grassland on Royston Heath. This decline was perhaps due to the long dry summer of 1976.

Samples of leaves from the 2 experimental swards and nearby permanent grassland had distinct width-profiles (Figure 24). The tall grassland was coarsely structured, with most material in the 1–6 mm size range. The fine-leaved turf had most stems and leaves < 1 mm, while the permanent grassland was intermediate. The permanent grassland, which was not cut or grazed, also produced a greater biomass of plant material in winter than in summer, but the reverse was true in the experimental grasslands. They were cut for hay in late June each year and probably much of the potential litter was removed. Although much material from pitfall and vacuum sampling has not yet been determined, some indication of fauna change in the 2 grass swards during 1974/5 is given by the quadrat samples which were taken throughout 1975 in the experimental plots and permanent grassland nearby. The 2 experimental grasslands were similar in species and numbers of spiders but contrasted strongly with the permanent grassland. For example, 17 species were found only in the permanent grassland while each of the experimental swards only had 2 species which were not taken elsewhere.

Fieldwork at Royston ended in spring 1976. Determination of the material continues prior to a detailed analysis of all the data.

E. Duffey

COLONISATION OF CHALK GRASSLAND BY SHRUBS AND TREES AT ASTON ROWANT NATIONAL NATURE RESERVE

(This work was commissioned by the Nature Conservancy Council as part of its programme of research into nature conservation.)

A management trial was set up in the winter of 1968–9 to study the effects of continuous grazing, no treatment, one burn, and one rotivation on the succession of chalk grassland to scrub. The invasion of woody plants into grassland is a dynamic process, and data on individual plants have been collected annually since 1969 in order to study the population dynamics. Herbaceous species have been recorded in permanent quadrats in the plots and by less detailed recording in the whole plots.

All the woody plants which will eventually predominate in the scrub communities are already present in the grassland, and detailed study of the grazed plots shows that, although the total numbers of plants may appear relatively stable, this stability is achieved by a balance of mortality and recruitment. When grazing ceases, as in the untreated plots, the plants already in the grassland grow on and their mortality is less, while, at the same time, recruitment of new plants is strongly enhanced. Later, the increasing growth of the other vegetation prevents or reduces recruitment. The more open conditions of the burnt and rotivated plots in early years favour slower-growing species such as *Taxus baccata* and *Rhamnus catharticus*. The replicate positions are important in determining the abundance of particular woody species, and a study of the local seed parents and the seed input in bird droppings has given some explanation of this abundance. There is closer correlation of seed input and number of plants in the plots within plant species rather than between species.

Lena K. Ward

GRASS TRIALS IN THE WASH

(This work was supported by the Central Water Planning Unit (CWPU) of the Department of the Environment).

Trials were made on two sediment-filled embankments built in the intertidal area of the Wash. The embankments, with an inner bank just below the lower limit of the salt marsh at Terrington and an outer bank about 3 km from the sea wall near the River Nene outfall, were constructed, by the consulting engineers to the Wash Feasibilty Study, to test physical and hydraulic properties of materials which might be used if a full-scale Wash reservoir bank were to be constructed.

Although our main objective was to provide a rapid stabilising grass cover for the banks, the opportunity was taken to assess experimentally the performance of a number of species sown singly or in mixtures. Varieties with a known high level of salt tolerance were sown and their growth assessed taking note of the structure (i.e. compactness) and cover provided by the resultant swards. In some plots, grasses such as *Puccinellia* spp., which occur naturally in saline habitats, were sown, whereas, in others, varieties of *Festuca rubra* and *Lolium perenne* being bred and developed by Dr M.O. Humphries (University of Liverpool) were grown.

Although complete results and recommendations will not be available for another year, it seems that the highly saline conditions on the inner bank have proved less of a barrier to grass establishment than was anticipated. On the outer bank, where soil washings from a sugar beet factory were used as topsoil, the input of salt from spray has so far been low and, not surprisingly, a mixture of common forage grasses has grown well. More recently, and presumably because of leaching, salt concentrations in the inner bank have decreased to the stage where agricultural grasses prosper.

For the future, even with ryegrass-free mixtures of red fescue, *Festuca rubra,* and creeping bent, *Agrostis stolonifera,* which have produced tall swards, it seems that maintenance will be the major problem. Techniques to encourage low growth, dense tillering and low litter accumulation are needed.

A.J. Gray and R. Scott

Vertebrate organisms

THE NUTRITION OF WILD ANIMALS

While studying the nutrition of wild red grouse *(Lagopus lagopus scoticus)* and ptarmigan *(Lagopus mutus),* we have greatly benefitted from the established techniques and concepts of nutritional science. However, this discipline has been concerned almost entirely with man and his domestic animals. Ecologists are gradually becoming aware that wild animals are by no means identical to captive ones. For example, the caeca of wild willow grouse *(Lagopus lagopus)* contain numerous amoebae and spirochaetes, but captives contain none and have a microbial fauna more like that of a chicken (Hanssen, 1975). Also, captive willow grouse and red grouse have much shorter guts than wild birds (Moss, 1972; Hanssen, 1975). It is therefore not surprising that captive red grouse eating heather digest only 27% of the dry matter ingested, whereas wild ones digest 46% (Moss, in press).

This fact suggests caution before applying the results of studies of captive animals to the wild. Uncritical acceptance of the concepts developed for agricultural research might be unwise, but examining and testing them for ecological purposes may teach us much.

Efficiency

Cows in a field eat almost all the grass there, whereas grouse on a heather moor eat only 2–3% of the green shoots available (Savory, 1974).

Why are grouse so 'inefficient'? The wild animal does not need to be 'efficient' in the agricultural sense, but does need to survive, and produce as many offspring as possible. If the prodigal use of resources enables an animal to maximize its contribution to the species' gene pool, then natural selection will establish prodigality as a characteristic of that species.

Food selection

Although grouse and ptarmigan (Moss, 1968) eat only a small fraction of the food available to them, variations in their food supplies are followed by variations in breeding and numbers (Moss, Watson & Parr, 1975) and

Plate 14 *Aseptically sealed container for growing* Betula spp. *clones. Photograph J Pelham*

Plate 15 *Mycorrhiza on birch roots colonised by* Cenococcum. *Photograph A D Bailey*

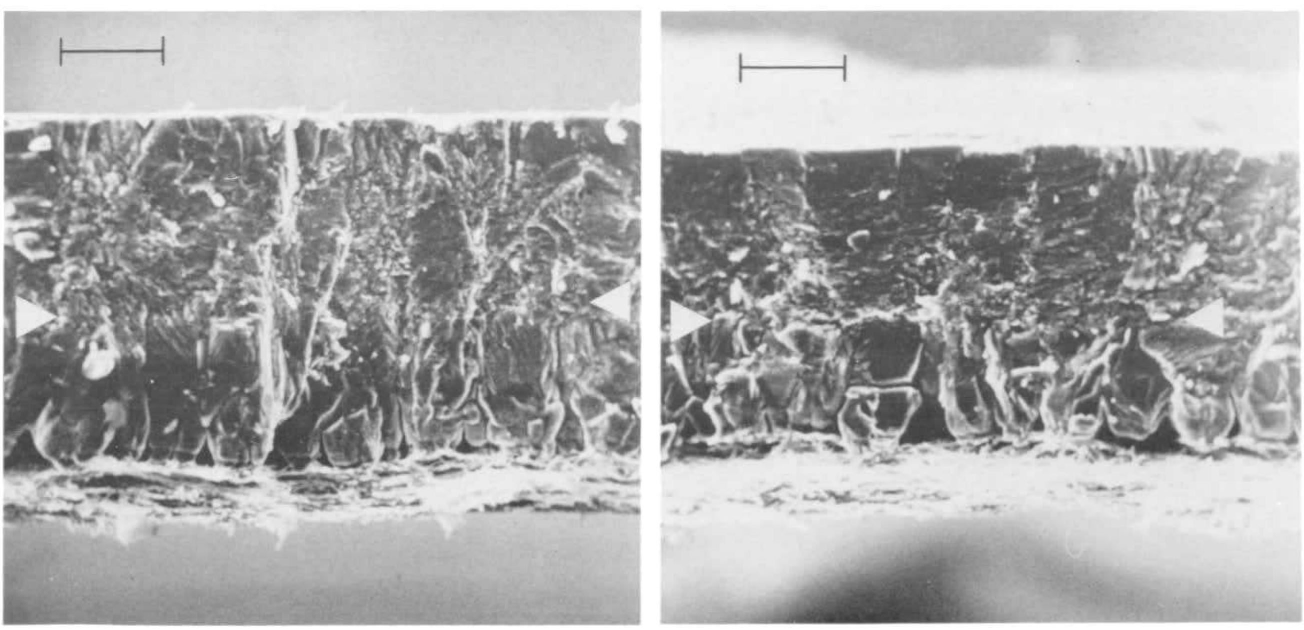
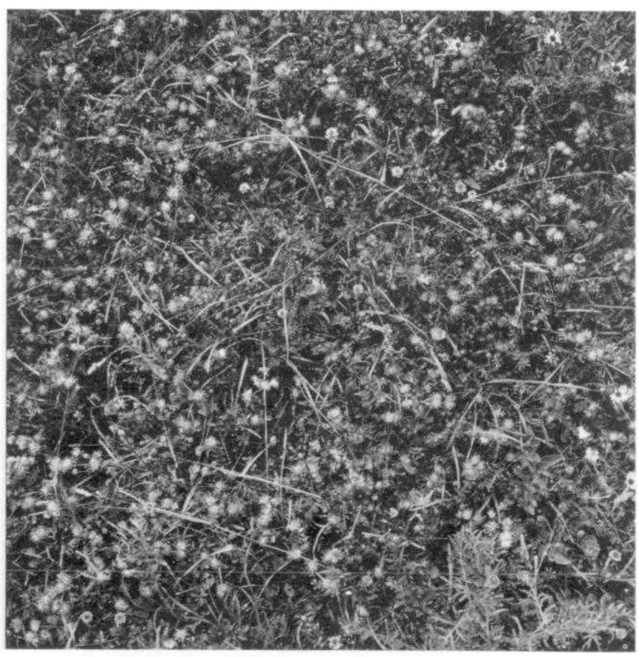


Plate 16 *(left) Scanning electron micrograph of a fractured radial face of an egg shell laid by a hen on a normal diet. The arrows denote the approximate position of the boundary between the inner mammillary layer (below) and the outer palisade layer. The fibrous shell membranes can be seen beneath the calcified shell. Scale bar = 100 μm. (right) Micrograph of a thin shell produced by a hen maintained on lower rations than normal. There are similar reductions in total thickness, mammillary layer thickness, palisade layer thickness and in the height of the mammillae, the projections at the base of the mammillary layer. Scale bar = 100 μm. Photographs by Mrs L C Lamont.*

Yellow oat-grass (Trisetum flavescens) *and upright brome-grass* (Zerna erecta) *prominent in mixture containing 7 species of grass.*

Commercial mixture with perennial rye-grass (Lolium perenne), *red clover* (Trifolium pratense) *and white clover* (T. repens), *with some invasion by unsown species.*

A 50:50 mixture of grasses and herbs. Note the abundance of kidney vetch (Anthyllis vulneraria) *rough hawkbit* (Leontodon hispidus) *and greater knapweed* (Centaurea scabiosa)



A mixture which contains 26 species of chalk grass-land herbs, including horseshoe vetch (Hippocrepis comosa), *kidney vetch* (Anthyllis vulneraria), *rough hawkbit* (L. hispidus) *and salad burnet* (Poterium sanguisorba).

Plate 17 The general appearance in July 1977 of 4 plots sown in April 1973 with different mixtures of herbs and grasses. Photographs T C E Wells there is evidence of competition for food between grouse and hares (Moss & Miller, 1975). This seeming paradox is rationalized by pointing out that wild herbivores are selective feeders, and by suggesting that the more food present, the easier they find it to select material of high quality.

However, what is 'poor' food in one place may be 'good' in another. If *Calluna* is the only food available, then successful individuals will eat it. If, however, a better food (e.g. *Salix*) is available in a different area, then successful individuals will eat *Salix* and ignore *Calluna*. Although *Calluna* might be adequate nutritionally, *Salix* will give the animal eating it a competitive advantage. Hence, *Calluna* will be ignored and a seemingly 'inefficient' situation results (Gardarsson and Moss, 1970). Food selection is more important to the wild animal than to the domestic one. Relatively little work has been done on this problem by agricultural nutritionists, and some workers have even questioned the ability of animals to select good quality food (Gordon, 1963).

Plane of nutrition

Herbivores tend to select foods which enable them to perform as well as possible. In agricultural terms, 'performance' simply means growing flesh, secreting milk or laying eggs, but wild animals have much more to do. In particular, a wild species competes with other species. It may increase its chances of survival by behavioural, physical and physiological specializations, becoming highly adapted to a certain niche, that is, more expert at gathering a restricted range of foods and more efficient at digesting them than if it attempted to take a more catholic diet. Tetraonids adapt to different foods by having guts of different size (Moss, 1974). Long guts and large gizzards allow an animal to digest fibrous foods, but they exact a penalty in terms of extra weight and maintenance requirements.

Situations such as this have made it necessary to refine the concept of 'plane of nutrition', when studying wild animals (Moss, 1975). Consider two foods, food A providing a higher plane of nutrition than food B, that is, more nutrients and energy per unit weight. When only one species of animal is present, it will be advantageous for it to eat food A. It will spend less time feeding and will develop a smaller digestive system than if it ate food B. The smaller digestive system will require less food to maintain it, and less effort for the animal to carry it. If two species of animal are present, each will find it advantageous to avoid competition, and one of them may adapt to food B. Once it has made the necessary adaptions, it is no longer adapted to food A. Hence, it is likely to perform better on, and to prefer, food B. The optimum plane of nutrition for a wild animal is not necessarily the most concentrated diet, but the diet to which it is best adapted.

Nutritive value

The chemical composition of a food is a useful indication of its nutritive value. Much practical experience has led agricultural nutritionists to conclude that the protein content of a food is usually positively related, and fibre content negatively related, to its digestibility. This conclusion has been reached on the limited range of foods used as agricultural feedstuffs, but is confirmed by a study on a wide variety of ptarmigan foods (Moss, Gardarsson, Olafsson & Brown, 1974).

Measurement of the chemical composition of foods eaten by herbivores has helped considerably in explaining variations in animal numbers between areas. Ecologists have reached a similar conclusion to agricultural nutritionists in this respect–that fertile soils produce more and better food which supports higher animal densities. Beyond this conclusion, the viewpoints of the two disciplines tend to diverge. In agriculture, high densities of animals eat much of what is present and this feeding is associated with gross deficiencies of specific nutrients such as cobalt or phosphorus. Similar deficiencies may occur in wild populations, but have not been documented. The occurrence is probably less frequent in natural situations, where animals use a smaller proportion of the plant material available and where numbers are limited by a complex of factors, of which nutrition is only one.

Conclusion

In the last 15 years ecologists have become more interested in the nutrition of wild animals than formerly, and have looked to the established scientific discipline of nutritional science for guidance. This discipline has been valuable; but ecological nutrition is a growing science and is in the process of formulating its own distinctive ideas and concepts.

R. Moss

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RED DEER REVIEW

In 1975, a review was requested by the Nature Conservancy Council of our present knowledge on red deer and their interactions with the environment. A major series of long-term studies by NC and ITE, largely on population dynamics and performance, was nearing completion, and it was timely to highlight the gaps for future research. Also, it was felt desirable to take a world-wide perspective on red deer ecology and bring together the results of many relevant studies in a form convenient for those concerned with deer management and research.

The review (Mitchell, Staines, and Welch, 1977) has three main sections, on (1) dispersion (feeding, social and other behaviour affecting distribution), (2) impact on the habitat, and (3) population dynamics and performance. Also included are an account of the importance of red deer to man, an appraisal of research priorities, a critique of some current management practices in Scotland, and an appendix summarising the history of Nature Conservancy and ITE involvement in red deer research. Over 600 references are quoted, mostly foreign.

Synopsis

Red deer in Scotland are at a higher density than elsewhere in their world range, at present approximately 270,000 living on 2½ million ha of exposed hill land. Scottish red deer are smaller than those in other parts of the world, being, for example, less than half the size of deer in Hungary and Yugoslavia. A good relationship has been found between fertility in each age class and body size. Maximum body size is reached at about 8 years of age, natural mortality is highest in calves, and becomes increasingly heavy beyond 8 years, with few individuals living beyond 15 years. Single births are normal, and often puberty is late (2-3 years) and conception biennial, population turnover thus being reduced in the poor-quality Scottish environments. Red deer cannot react quickly to favourable habitat changes, at best increasing by about one third in number each year, whereas some other wild ruminants can double their numbers annually. The low performance of Scottish red deer may be due solely to the poor environment, or to their high densities, or to both. A significant relationship was found between density and performance, but habitat quality was not assessed in the areas studied, shich also differed in altitude, vegetation type and management.

In Scotland, red deer are at the northern edge of their range, and are perhaps not such hardy animals as commonly thought, having relatively thin coats and little superficial body fat. Compared to domesticated sheep, they have higher maintenance requirements, partly because of their poorer insulation, but also because of their greater activity. Indeed, their ability to travel long distances to obtain favourable conditions and food is a major adaptation enabling them to overcome the difficulties of their environment.

Red deer are less selective of food than sheep, and do not utilise grasslands so intensively. They are also apparently less capable of digesting some forages. These facts, coupled with their higher maintenance requirements, mean that red deer need about one third more food per unit of body weight than sheep. They have, therefore, a different feeding strategy, higher intake offsetting greater selectivity. Stocking an area with red deer alone is likely to lead to a greater predominance of heather than when cattle and sheep are present, since these domesticated herbivores maintain grasslands on the better soils.

Red deer have most impact on vegetation in preventing scrub and woodland regeneration or succession to woodland, but tree establishment in the presence of deer in former times, and in some areas now, gives grounds for the expectation that woodlands could regenerate if browsing pressure were reduced, or sapling density increased. A tentative suggestion is that, with an overall density of 1 deer per 10 ha, and sapling numbers averaging 1 per m² in 20% of the area occupied, tree establishment would occur if the deer spent less than 50% of their time on this ground.

It is concluded that more information is required on many aspects of red deer ecology before precise predictions can be made of the effects of managerial decisions. The most important fields concern the interrelationships of deer and vegetation, i.e. (a) the influence of deer on vegetation dynamics, (b) the influence of vegetation patterns on dispersion, and (c) the effects of habitat quality and animal density on population turnover and performance. Studies in woodland environments should have high priority, because existing knowledge is scant, and deer are likely to cause serious losses in the commercial plantations now being established in upland areas.

B.W. Staines, D. Welch and B. Mitchell

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SOME PROPERTIES OF A HIGH-DENSITY POPULATION OF RED DEER *(CERVUS ELAPHUS* L.)

There is good evidence that habitat quality and population density are the two main environmental influences on the performance of red deer, although their effects cannot yet be quantified adequately. In the Scottish Highlands, red deer are almost at the northern limit of their natural range, and they occur mainly on poor-quality, exposed hill-land, at relatively high densities of population. Not surprisingly, the deer in this environment grow and reproduce less well than those living more typically in woodland-edge habitats, at lower altitudes, and at lower population densities. Moreover, it has been shown that red deer of Scottish origin are genetically capable of higher performance; they can grow faster, become heavier as adults, become sexually mature earlier, and produce more calves, when reared under more favourable conditions.

The average population density of red deer on Scottish hill-land is about 100 deer/1000 ha in late winter and spring, with some regions having two to three times the average density, and others much less. These values relate to large blocks of deer range; the deer occur at much higher concentrations locally on the best grazings, or in low-lying wintering areas. Inverse relationships between aspects of performance and population density, admittedly with a good deal of variability, were suggested by the results of earlier research in several parts of Scotland (Mitchell, Staines & Welch, 1977).

Opportunities to assess the structure and performance of an exceptionally high-density population arose through a partial shoot-out of red deer on Scarba, an island of 1500 ha (maximum altitude 449 m) about 5 km off the mainland of S.W. Argyll and 1 km north of Jura. The control operation to allow agricultural developments on the island was undertaken by the Red Deer Commission (p.10, *R.D.C. Annual Report for 1974, 1975,* HMSO), and the shooting was non-selective.

The deer population on Scarba had been increasing over the previous decade because of under-cropping. Previously, deer numbers were kept low by a combination of heavier shooting and high stocking with sheep. Compared with other areas of deer range in Scotland, Scarba was perhaps above average in quality, but not amongst the best. The eastern third of the island had the best grazings and shelter–mineral soils (overlying black schist) bearing grassland (some being improved by fertilisation and reseeding) and mixed woodland (covering 20% of the block)–and, here, some 200 Luing-breed cattle were confined by a stock fence. The greater part of the island had a more rugged terrain, mainly of quartzite, with peaty soils and more typical moorland vegetation dominated by *Molinia* and *Calluna*. Herb-rich flushed grasslands and coastal greens were only a very small proportion of the total area. The red deer had access to the whole island. Apart from red deer and cattle, the only other large herbivores were fallow deer; about 40 of these occurred in the woodland area.

A count in the spring of 1974 gave a total of 527 red deer (165 stags, 260 hinds and 102 calves), a density of 356/1000 ha. This density was about 3·5 times the average on Scottish hill-land, and over twice that found on Rhum (Lowe, 1969, 1971) and at Glen Feshie (Mitchell, Parish & Crisp, in preparation), which were both considered as high-density study areas. By the autumn of 1974, the population on Scarba would have increased to about 645 red deer (216 stags, 311 hinds and 118 calves) with the new generation of calves born in late May and June.

About half the population was shot in late November 1974, and just over half the remainder in autumn 1975, with searches for extra carcases (mainly natural deaths) between the two periods of shooting. We assessed sex, age, carcase weight, skeletal size, condition, and reproductive status, in all the shot deer (491 deer: 186 stags, 241 hinds and 74 calves), and sex and age in those found dead (37 deer: 13 stags, 17 hinds and 7 calves). In all, therefore, we were able to account for 81% (521 deer: 191 stags, 239 hinds and 91 calves) of the population present in autumn 1974 before the shooting began.

In view of the exceptionally high population density on Scarba, it was reasonable to expect very low performance in the deer. But, in general terms, the deer were remarkably similar in performance and population structure (Figures 25 and 26) to those studied previously in other high density areas of Scottish hill-land, especially Rhum and Glen Feshie. In no aspect of performance were the Scarba deer inferior to those in the latter areas; indeed, both stags and hinds were slightly larger in terms of skeletal size (jaw length) and body

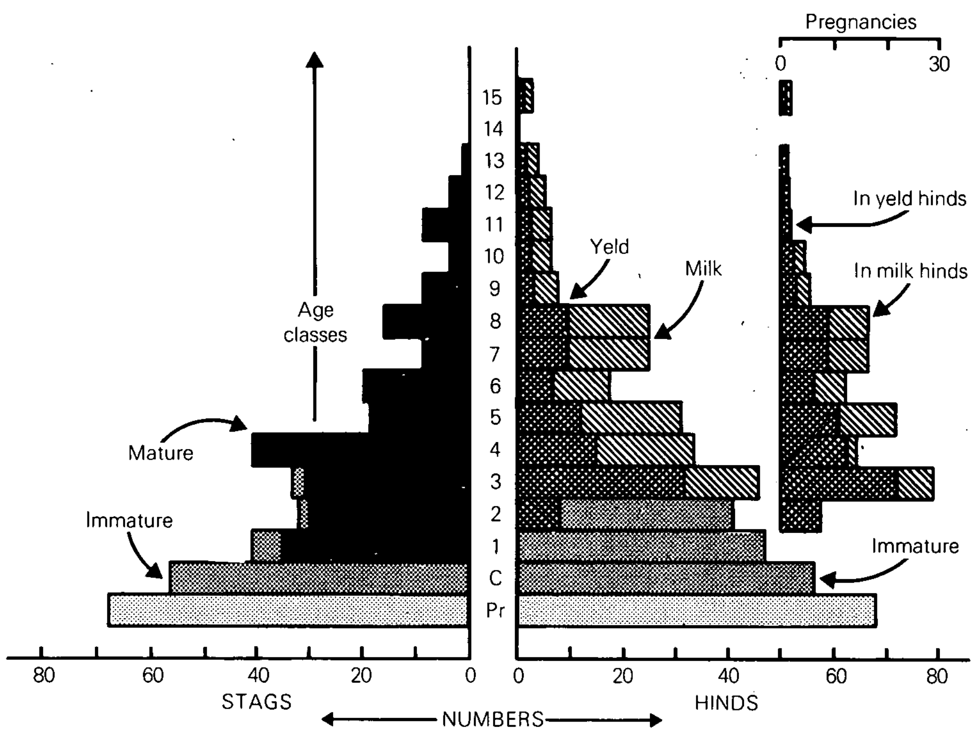

Figure 25 Composition and demographic features of the red deer population on Scarba in autumn 1974; population by sex, age and breeding status. Pregnancies in hinds shown first as contributions from the yeld and milk hinds in each age class, and second as potential births into the population.

weight (dressed carcase with skin), and slightly lower in condition (kidney-fat-index), although the differences were not statistically significant. Reproductive features were also much the same as on Rhum and at Glen Feshie. Most stags became sexually mature in their second autumn of life, i.e. as yearlings. Hinds first became sexually mature as 2-year-olds and 3-year-olds, calving for the first time at 3 and 4 years respectively. Amongst the sexually mature hinds, 36% failed to ovulate and conceive, and these gave rise to the yeld (non-lactating) adult hinds in the population. Within each age class of mature hinds, those supporting calves (milk hinds) were lower in body weight condition and pregnancy rate than those (yeld hinds) not supporting calves; the pregnancy rates in milk and yeld hinds aged 5–10 years were 59% and 96% respectively. Whilst the population contained 38 calves/100 hinds in autumn 1974, the total number of pregnancies (Pr on Figure 25) indicated a potential birth rate of 46 calves/100 hinds. Both the birth rate, and the apparent loss of 17% in calves from parturition to mid autumn agreed well with the results of other research on Scottish hill-land. Further losses in calves, mainly over the winter, were suggested by the relative proportions of calves and yearlings in the population. In total, it appeared that 35% of the calves died in their first year or so, giving an intake of about 30 yearlings (both sexes)/100 hinds. In consequence, this population could have sustained a cropping rate of about 15% of the adult deer annually, a rate which is very close to the 'one-sixth cull' recommended by the Red Deer Commission for use on Scottish hill-land.

In conclusion, the deer on Scarba showed no features associated with their exceptionally high population density, and it is difficult to account for this lack of effect on performance. It may be that there is little further reduction in performance above a certain level of density, say 150 deer/1000 ha, and that most change occurs below this level. Heavier animals in the younger age classes, and pregnancies in yearling hinds, were found mainly in those populations well below the average density (Mitchell 1973).

B. Mitchell

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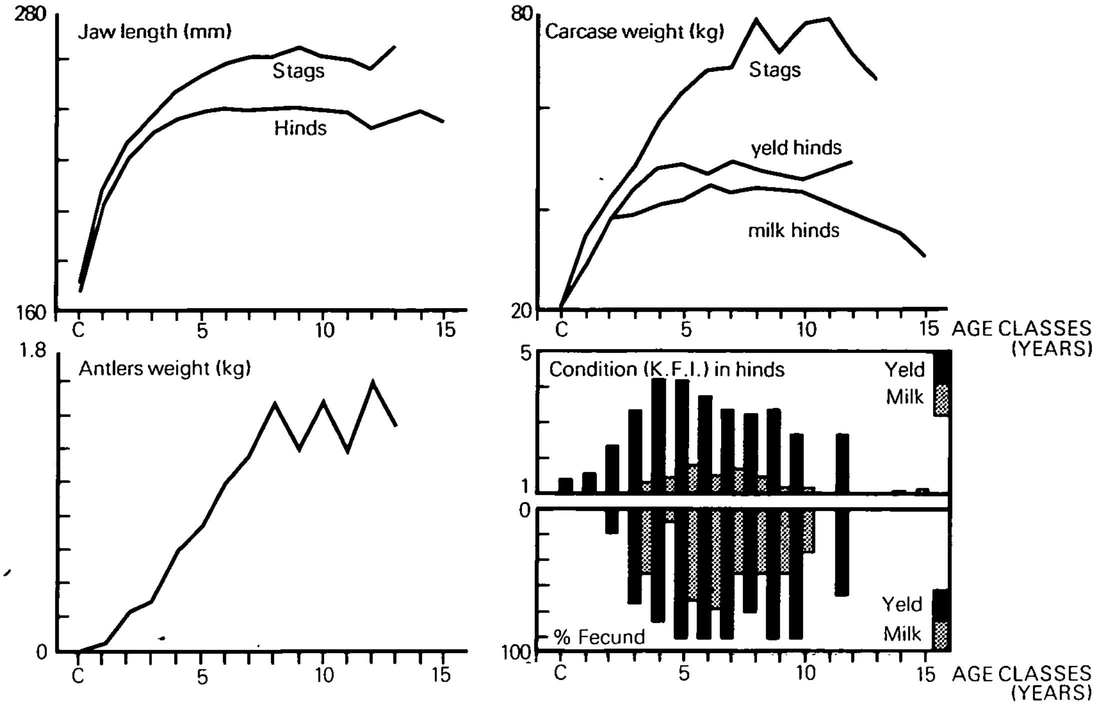

Figure 26 Some aspects of deer performance. Upper left: jawbone length (an index of skeletal size) in stags and hinds. Lower left: antlers weight in stags. Upper right: carcase weight (dressed carcase with skin ie about 52% of live weight) in stags and hinds. Lower right: condition (kidney-fat-index) and fecundity (pregnancy rates) in yeld and milk hinds.

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A POPULATION STUDY OF THE MEADOW PIPIT IN SNOWDONIA

In the British Isles, the meadow pipit is one of the most widespread breeding species on grassland and similar habitats, but its density varies considerably from one habitat to another, presumably as a reflection of differences between habitats. These results suggest that the meadow pipit might be used as an indicator of the state of the habitat, say, in relation to land-use. The main objective of the present study, carried out in 1972–75 in Nant-y-Benglog, a glaciated valley in Snowdonia, North Wales, was to measure the actual numbers of meadow pipits on a 15 ha site.

The meadow pipits mostly migrate to Spain and south-west France for the winter, only a few remaining in lowland or coastal Britain at this time. Migrants return to Britain in March. Breeding occurs between late April and early August. Two broods are reared, and only the female incubates the eggs, although both sexes feed the nestlings. While it is probable that most males are mated and monogamous, the population includes unmated males and possibly also polygynous males. The adults depart again in August, but juvenile birds remain another month or so after the adults have left.

On the breeding area, both sexes spend very nearly the whole of their time on the ground or perching on rocks, fence posts or wires, and very little time in the air. Combined with the drabness of the plumage, this behaviour renders the birds comparatively inconspicuous. The only conspicuous and clearly identifiable activity relating to the holding of a particular piece of ground was the aerial song-display of the male. The consequence of this behaviour was that the male colour-ringed pipits on the study area were seen on only 36% of the days between the dates of their first and last sightings or 30% of the days during the period when the breeding population as a whole was believed to be present. Females were seen even less frequently and were consequently unsuitable for a population census. Males were recorded giving song-displays on only 8% of the days the population was present, that is, on 28% of the days when they were actually found. To say whether a bird was 'resident' on the study area or not, it had to be seen on at least two separate days. The number of days of observation which passed before all ringed males were seen at least twice was twelve, a situation which suggests that the number of days a site must be visited in order to count meadow pipits would seem to be larger than other workers have considered necessary for censuses in general. In addition, the composition of the meadow pipit population on mountain grassland can be understood only when most birds are individually marked.

The home range of each male comprised a core area where it spent most of its time, and a peripheral area which both adults also visited to collect food for their nestlings. The size of the male population declined from 11 birds in 1972 to 5 in 1975, figures which correspond to 74 and 33 pairs per km². The annual average was 48 pairs per km². At the highest density, the core ranges over lapped to some extent, indicating that each piece of ground is not always for exclusive use and occupation. While providing living spaces for the adults, the range system also disperses the nests, which have a high failure rate. The peripheral areas used for food collecting overlapped considerably with adjacent ranges.

Those birds seen in succeeding years were on, or very near to, the same area of ground occupied in previous years. A bird returning to the same location occupied in a previous year is probably more likely to find a vacant space for itself than if it goes elsewhere. Despite the change in population size, the mean size of the core range remained relatively constant from year to year— the mean size was 21800 m². There was an increase in the amount of the study area unoccupied, and a decrease in the extent to which the individual core ranges overlapped with adjoining ranges during the population decline. Coulson (1956) estimated that adult pipits collecting food for themselves and their nestlings at Moor House in the north of England ate only 1% of the adult tipulids, the principal food. This being so, it would seem that the available food may be in excess of the requirements of the birds. Consequently, when the population density is low, there may be no need to increase range size, even though the absence of other birds would allow it.

Making comparisons with the findings of other authors on population size is difficult, owing to the variety of methods employed to count birds, but it seems likely that previous studies of unmarked birds probably gave measures of population size which were too small.

D.C. Seel

FAT AND PROTEIN RESERVES OF STARLINGS

Seasonal changes in the body condition of wild starlings collected in Cambridgeshire are being followed by routine carcass analysis. Some 900 individuals, mostly from communal roosts or nest boxes, were processed during 1977.

The lipid content of each individual, obtained by Soxhlet extraction, provides a measure of its energy reserves, while the lean (fat-extracted) dry weight of its pectoral muscles indicates the level of its protein reserves (Figures 27, 28). The reserve of protein, thought to be located mainly in the sarcoplasm of muscle cells, has previously been found to vary seasonally in tropical species, and it has been suggested that variations in its quantity, alone or along with other body condition parameters, may serve as an internal regulator of major events such as reproduction and moult (see Ward, 1969; Jones and Ward, 1976). This hypothesis is now being examined in the light of data from the starling.

Seasonal changes in lipid content were unexceptional for a temperate zone species. In January and February, the birds generally carried large reserves of fat–sufficient at least for metabolism during the long cold nights. The level was greatly reduced at the end of winter, and remained low throughout the summer and autumn.

Protein reserves rose markedly in late winter, faster in males than in females (Figure 28). Intense breeding activity by the males began in late February and early March, though the females did not begin laying until mid-April. The protein reserves fell during the breeding period, especially when the young were being reared, and remained low throughout the subsequent moult period. At the end of the moult, the protein condition again improved, and at the same time (from mid-August) 'autumn sexual activity' began. Autumn sexual activity, including prospecting for nest-sites and pair-formation, continued into November, but was then largely curtailed with the onset of cold conditions.

Changes in the protein condition of the starling are due in part to seasonal variation in the availability of protein-rich food items. For example, the food in mid-winter consists largely of grain and 'scraps', but, in late winter, leather-jackets become the main food (as they are through the breeding season). Protein condition may also depend on the protein requirements of the individual, which may vary seasonally. It is greater (in both sexes) during moult, and (in females) also during egg-formation.

Rapid testis growth in males in spring was not synchronous in time, but was consistent in that it occurred only in individuals that had reached a high protein level and had dropped their fat to the summer level. In

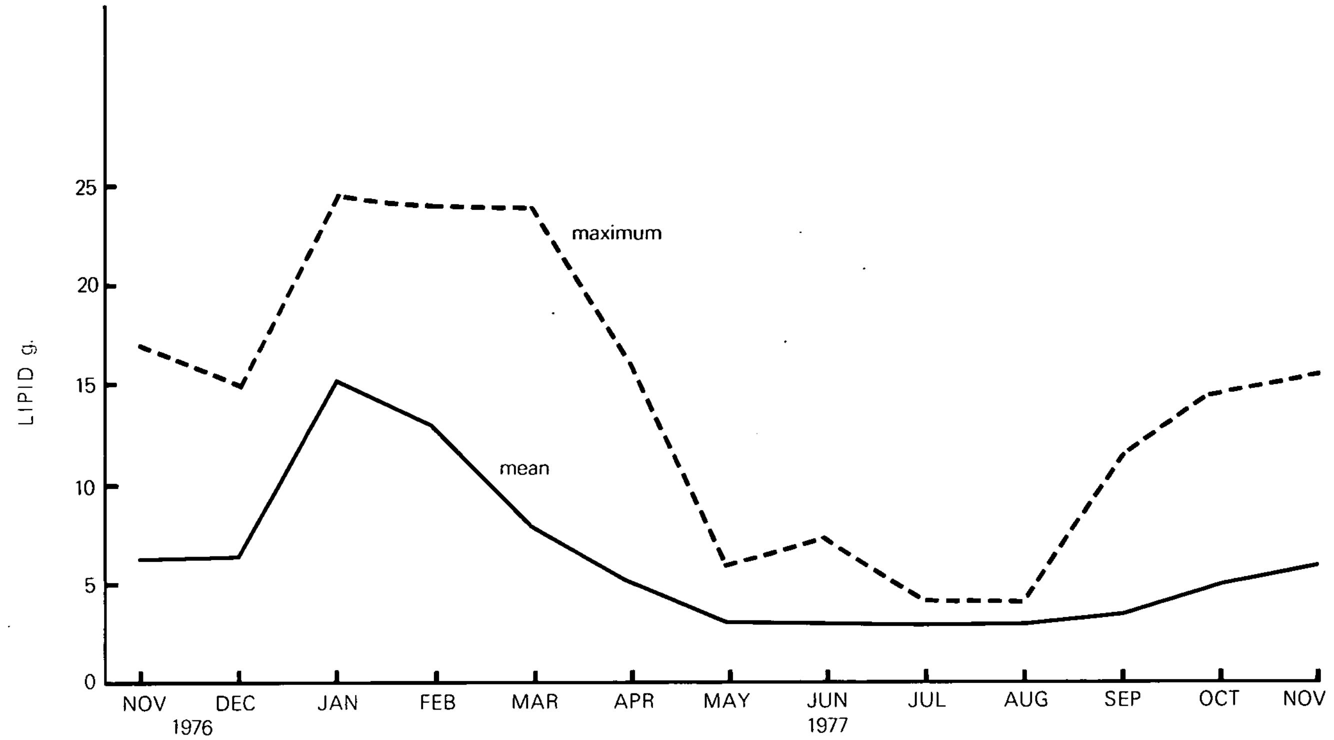

Figure 27. Seasonal changes in the mean and maximum monthly values for the fat content of adult wild starlings, (both sexes) in Cambridgeshire.

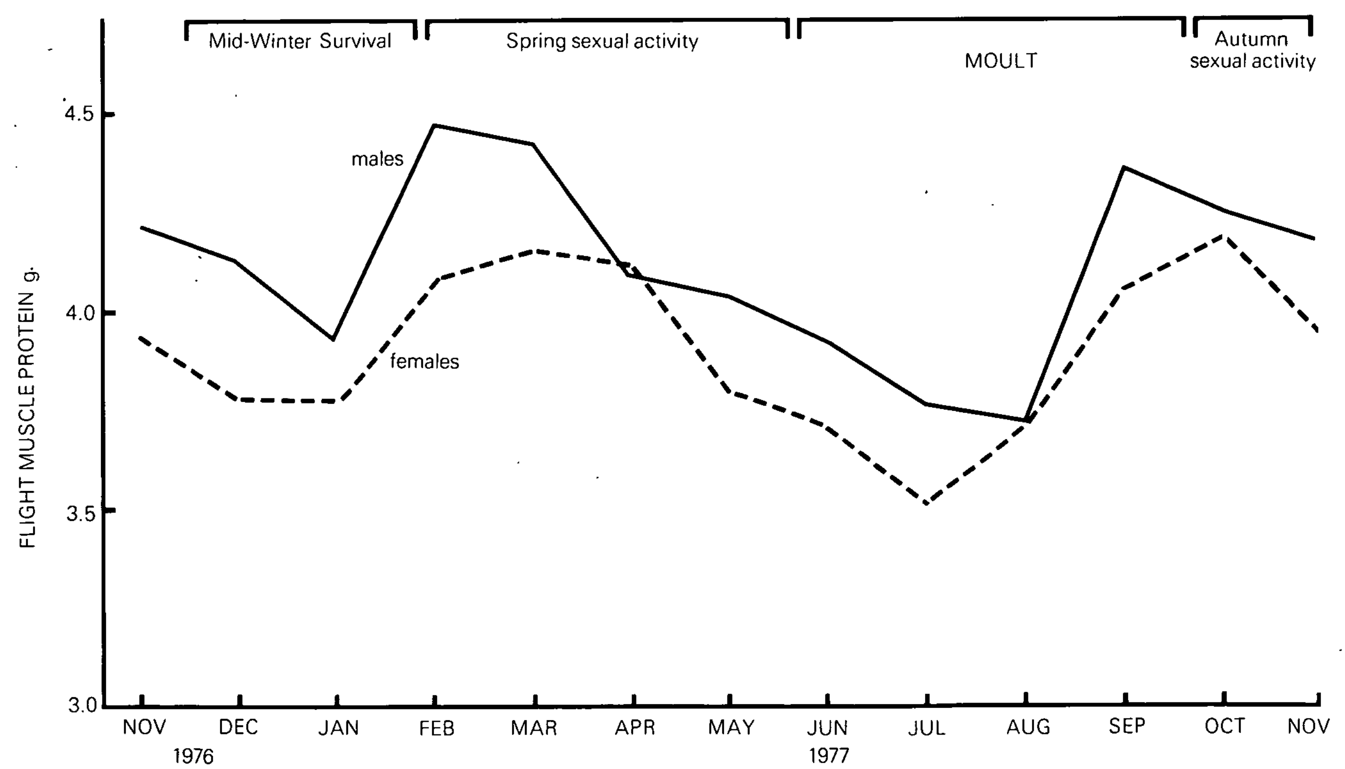

Figure 28 Seasonal changes in the mean protein content of the flight muscles of adult wild starlings in Cambridgeshire.

autumn, only a small amount of gonadal recrudescence had occurred before the protein condition began to fall in November. Nevertheless, autumn sexual activity is regarded as the first stage of a breeding season that is normally prevented from proceeding by the onset of winter conditions. In exceptionally mild winters some starling pairs are known to lay at the end of November, and to raise young in December (Snow, 1955).

P. Ward

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MERCURY RESIDUES IN CARCASES OF KESTRELS, SPARROWHAWKS AND BARN OWLS

In the last *ITE Annual Report* (pp. 22–25), we described how, in response to appeals advertised via the ornithological and conservation journals, dead bodies of various predatory birds are sent to Monks Wood as part of a scheme to monitor pesticide residues; monitoring in this context has been aimed at checking whether various Government measures, such as banning the use of dieldrin in December 1975, have led to noticeable reductions of residues in those wildlife species which are of conservation interest. After autopsy, portions of various organs have been stored in deep freeze to provide a tissue bank, so that, if new pollutants emerge, or new chemical techniques for measuring old ones are developed, samples of the material can be analysed.

Much research has been done by Swedish workers on the toxicological, biochemical and general physiological effects on wildlife of organomercury compounds, particularly when in the methyl form, and this work has generated pressure within the European Economic Community to limit the use of these agents in agriculture. In Sweden, the use of alkyl mercury compounds as fungicides in the wood-pulp industry and in agriculture resulted in serious environmental pollution and harmful effects on wildlife species. In Britain, seed dressings containing a mercurial fungicide have been used extensively, with over 90% of cereal seed being so treated. However, as has been emphasised by Stanley and Elliott (1976), mostly aryl compounds have been used and wildlife incidents of the kind which were once prevalent in Sweden do not seem to have occurred in this country.

Mercurial fungicides are relatively cheap and efficient and their use has resulted in considerable savings in crop damage. It is by no means clear how effective any alternative may be if EEC legislation becomes operative in Britain. In this context, it is important to define the extent to which British wildlife species are contaminated by mercury. Stanley and Elliott assessed the situation by examining residues in the tawny owl *Strix aluco* and barn owl *Tyto alba* and they concluded that these species had not been significantly contaminated by mercurial seed-dressings.

We have examined the situation in 172 kestrels *Falco tinnunculus,* 77 sparrowhawks *Accipiter nisus* and 133 barn owls sent to Monks Wood during the period 1970 to 1976 (except for one kestrel in 1968 and one in 1969). Residues in wildlife samples are not normally distributed and so presenting means ± standard errors can be misleading. In Figure 29, monthly average mercury residues in the liver are presented as geometric means without error terms (that is, the original residue readings were converted to logarithms before averaging and the anti-logarithm is graphed). The broad seasonal trends are statistically significant.

Both the kestrel and barn owl exhibit a peak in liver mercury residues in December, the source of this mercury presumably being the autumn cereal dressings accumulated via the small rodent prey which both these species eat. In the kestrel, mercury residues decline during the spring months to reach their lowest level in May, in spite of the fact that most spring barley is planted in March and early April and is dressed with mercury compounds. A proportion of birds then show high liver residues in June. In contrast, in the barn owl mercury residues start to rise during the spring, so that peak residues are found in May, a trend consistent with contamination from the spring sowings. It is extremely difficult to account for these species differences on ecological grounds and it is likely that they reflect physiological differences. We are concerned to understand the physiological mechanisms which could account for such species variability, and are focussing particular attention on the role of metallo-proteins (see report by D. Osborn in *ITE Report 1976*, pp. 59–60).

It is not the purpose of this report to argue whether the mercury loads found in kestrels and barn owls constitute a hazard. Before this can be decided, it will be necessary to define what proportion of the total mercury load was present in the organic form and this work is in progress. A more important general point is that it *might* have been a reasonable conclusion that two predatory species, which regularly prey on rodents on farmland, mostly do not carry excessively high mercury loads. A high proportion of the sample came from the arable regions of the eastern Midlands, East Anglia,

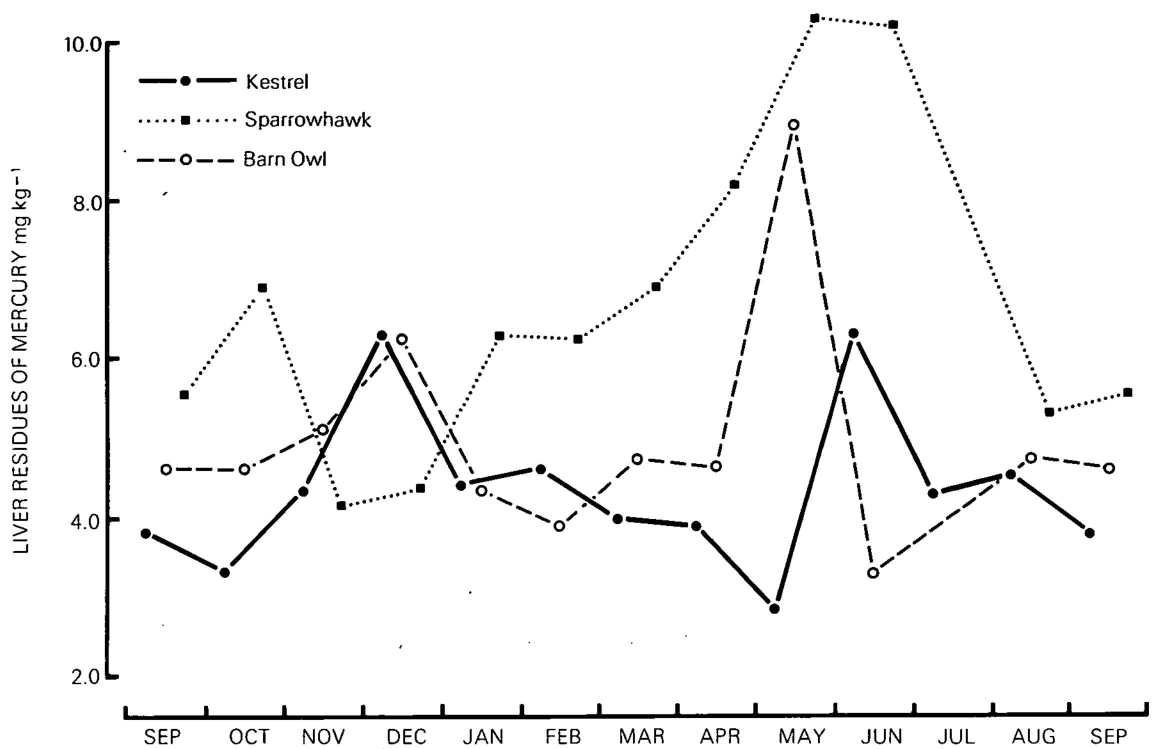

Figure 29 Monthly residues, presented as geometric means, of mercury (mg kg^{-1}) in the livers of kestrels, sparrowhawks and barn owls which were found dead.

Hampshire and Wiltshire, that is the cereal-growing areas. In contrast, the sparrowhawk has been virtually exterminated from this region (see distribution map in Sharrock, 1976). Most sparrowhawk carcases originated from the periphery of the arable region of England, coming from areas of mixed farming where extensive woodlands still occur. Thus, many carcases came from Kent, Surrey, Wiltshire, Gloucestershire, Dorset, the west Midlands and north-east Lancashire. Nevertheless, Figure 29 shows that liver mercury loads were generally higher in this species than in the kestrel or barn owl. It is not yet clear whether it is the ecology or physiology of the sparrowhawk which renders it more prone to accumulating mercury than the other two species.

From a biological monitoring viewpoint it is obviously important to consider a wide range of species in assessing the environmental hazards of a chemical. From a conservation viewpoint, it is the odd, sensitive species which gives cause for concern. Twenty-one % of all sparrowhawks examined had liver residues exceeding 10 mg kg^{-1} and 8% were higher than 17 mg kg^{-1}. It is possible, therefore, that a significant proportion of sparrowhawks could be suffering from mercury poisoning, but, at this stage, we have no knowledge about the toxicological significance of residues of this magnitude. Further investigation is demanded.

A.A. Bell, M.B. Haas and R.K. Murton

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EFFECTS OF REDUCED FOOD INTAKE ON EGG SHELL THICKNESS AND STRUCTURE

Papers are frequently published reporting the production of thin shells following the experimental treatment of birds. Unfortunately, many of these papers, particularly those involving the addition of pesticides to the diet, carry no mention of the effects of treatment on food intake. During the administration of compounds such as insecticides, food intake can be reduced because of loss of appetite or because of reduced dietary palatability, and this reduction in food intake may, itself, lead to a reduction in shell thickness. The effects of reducing food intake on shell thickness and structure have been investigated for the domestic fowl *Gallus* *domesticus* in order to help to resolve whether treatments that can affect food consumption do indeed have direct effects on shell formation mechanisms. Recently, at Monks Wood, attempts have been made to derive information on the mechanisms involved in shell thinning by studying the structural differences between thin shells and normal shells. As part of this study, the structure of thin shells induced by decreased food intake has been examined to aid the recognition of thin shells caused by starvation in both laboratory and field situations.

For the hens, the reduction in diet needed to be at least 15% in order to achieve significant egg shell thinning. A dietary reduction of 20% led to 7% fewer eggs and shell thickness was also decreased by an average of 7%. Reducing the diet still further to 35% below normal lowered egg production by 24% and shell thickness by 9%. So, as the conditioning became more severe, egg production was affected rather than shell thickness. When hens were returned to full rations, shell thickness recovered within a few days. On the basis of this information, reduced food intake appears to contribute to shell thinning when hens are exposed to polychlorinated biphenyls in the diet or maintained at high ambient temperatures, since such treatments can result in a reduction in food intake of 30% or more.

Light microscope and scanning electron microscope studies revealed that as the shells became thinner during partial starvation, so all the main component layers of the shell were reduced in thickness to about the same extent (Plate 16). Such changes are also seen in thin shells laid by hens on treatments that lower the availability of calcium or carbonate ions in the shell gland lumen. These structural changes seem to be indicative of a decreased rate of deposition. Similar structural modifications have been noted in thin shells being laid in the field in Britain by several species (e.g. the peregrine, *Falco peregrinus*) known to be exposed to organochlorine pollutants; here shell thinning is most likely to be due to enzyme inhibition in the shell gland.

A.S. Cooke

BATS OF CONIFER FORESTS

(This work was commissioned by the Nature Conservancy Council as part of its programme of research into nature conservation)

A five-year programme was begun in the autumn of 1975 to ascertain the size and species composition of bat populations in large Forestry Commission plantations. Most temperate-zone, insectivorous bats can be described as forest inhabitants. Under natural conditions, species differentiation would probably have depended largely on their feeding niche, rather than their specialist roosting requirements. With the felling of forests, the construction of buildings and changes in climate, bat populations have changed in species composition and relative densities. Some species now successfully exploit a formerly rare habitat, while others have declined. Britain's most common species, *Pipistrellus pipistrellus,* is probably more common now than a few centuries ago, because of its adoption of roosts in buildings.

At present, we know little about the habitat requirements or preferences of the 15 British bat species, but it is probable that some of our now rare species depend on forests. One such species is *Myotis bechsteini,* of which one or two small colonies, each with about 30 individuals, have been found in southern Britain during the past 100 years. It was formerly commoner and many bone remains attributable to this species have been identified from archaeological excavations in Norfolk, where it is now absent. Another species, *Nyctalus leisleri,* appears to be very rare in Britain (although common in Eire) and may depend on large tracts of mature forest.

In eastern Europe, *M. bechsteini* was thought to be very rare until the early 1950s when roost boxes were installed in conifer forest plantations. These boxes were essentially similar to the common bird box, but usually have a slit at the base rather than a hole in the side. Within a few years, colonies of *M. bechsteini* became established within the boxes. It was not clear whether those bats already existed adjacent to the plantations and moved into the boxes and were discovered, or whether the boxes aided the increase of a generally sparse population. Since commercial conifer plantations are usually more or less devoid of natural holes suitable for bat roosts, both factors were probably significant. Other tree-roosting bats also moved into the boxes. However, it was not known whether overall bat density was increased by the provision of boxes, because no comparable 'before' and 'after' observations were made.

In the present study, forests in 6 areas of Britain were selected with the help and co-operation of the Forestry Commission. Large forests were selected, so that any bats found living in the forests were likely to be totally forest-dependent, rather than moving in for roosts or feeding, and spending part of their lives outside the area. Wareham Forest, Dorset; Bramshill Forest, Hampshire; Cannock, Staffordshire; and Thetford Forest, Norfolk/Suffolk were essentially similar areas of mostly Corsican/Scots pine mixtures planted in the 1920s. A site in Kielder Forest, English/Scottish borders, is a Norway spruce/larch compartment, and the site in Ardross Forest, Ross-shire, contains a mixture dominated by Norway spruce and Scots pine.

Three thousand boxes were purchased by public sponsorship (BBC Nationwide Appeal) and 2,880 constitute the main experiment. In each forest, 480 boxes were placed, arranged along 4 sides of a forest compartment (north, south, east and west) and placed at 3 metres and 5 metres height on each tree. Four boxes were placed at each height facing each aspect. Therefore, the 480 boxes occupied a total of 60 trees per compartment. The boxes face different ways in order to examine the effects of different degrees of exposure. Trees with boxes were alternated between the outer and the second row of trees, so that preferences for height, aspect on the tree, as well as aspect on compartment site and degree of exposure, might be tested simultaneously.

Observations at the boxes in Thetford on nights immediately following installation and using light intensification equipment revealed that bats found the boxes and began investigating them shortly after sunset. This observation was particularly interesting, because no natural food holes had been found within several hundred metres of the compartment, and the bats must have flown directly from their roost to their feeding grounds.

Relative bat densities are being estimated each year using night viewing equipment and a bat detector which, through a microphone, picks up the ultra-sounds that the bats make and makes them audible to us. The boxes are being inspected several times each year, and occupancy can be inferred by the presence or absence of bat droppings, and, on occasions, by the presence of bats. Any bats found are caught and marked using magnesium alloy numbered rings, and, in this way, total numbers, movements, family group associations and population dynamics can be studied.

To date, 100 bats have been marked in the 6 forests, over half in Thetford. Four species have been found, *Plecotus auritus, Pipistrellus pipistrellus, Nyctalus leisleri* and *Myotis nattereri*. By far the most common is the *Plecotus auritus* (88% of captures), but two *N. leisleri* have been found which are the sixth and seventh records from Britain in the last 10 years.

Generally, upper boxes have been used twice as frequently as lower boxes, with no difference in aspect on each tree. However, boxes on the east side of compartments are occupied only half as frequently as the others. One-sixth of all the boxes have been occupied regularly by bats, and about 235 have been used by birds, and in some cases have had nests. During June/July, bats have been breeding in the boxes, and a maximum of 29 have been found in one box. Following capture, marking and release back in the box, bats tend to fly off immediately, particularly on warm days, and it is obvious that they are aware of the exact position of each box, because they usually fly directly into another box without hesitation. Now that bats are being recovered regularly, the presence of family groups has been established, and it may be possible to discover that different sex or age classes have different preferences.

The experiment is due to run for another 3 years, during which time it is hoped that the population dynamics of the forest bat fauna will be studied and that recommendations might be drawn up as to how bat populations might be managed in forest plantations.

R.E. Stebbings

Invertebrate Organisms

A SIMPLE POPULATION MODEL FOR THE CINNABAR MOTH AND ITS FOOD PLANT

Using population data for the cinnabar moth *(Tyria jacobaeae)* and ragwort *(Senecio jacobaea)* from Weeting Heath, Norfolk, a mathematical model has been constructed to describe the main fluctuations in abundance which have been observed since 1966. During this time, the moth has fluctuated dramatically in numbers and has completely defoliated its food plant over large areas in 1967, 1968, 1971, 1973 and 1976.

The performance of ragwort depends heavily upon the pattern of rainfall, and this, together with the impact of the moth, determines the biomass of food available to the moth's caterpillars in any one year. The plant is normally biennial, but, if prevented from flowering, it acts as a perennial by repeated regeneration from root buds. A large part of the variation from one year to another in the biomass of ragwort present can be accounted for by rainfall and cinnabar numbers (Figure 30).

The numbers of the cinnabar are in turn determined largely by availability of food. In years following those when the food supply is short, the surviving moths are small and lay few eggs. Fecundity (number of eggs per female) is dependent upon adult size (i.e. larval density in the previous year) and adult density, since more adults emigrate when their numbers are high. Mortality during the caterpillar stage is exceedingly high in those years when food is in short supply. The effect of this mortality is so great that it swamps all other mortality factors, such as parasites and predators, and larval mortality is dependent upon larval density per unit of ragwort biomass. Thus, the numbers of the moth can be predicted from the interaction between its population and that of its food plant, acting through both fecundity and mortality.

Using this model, the main trends in the moth's numbers are simulated, but the extent of the fluctuations is less adequately described (Figure 31). We are now looking into ways of improving this model.

J.P. Dempster and K.H. Lakhani

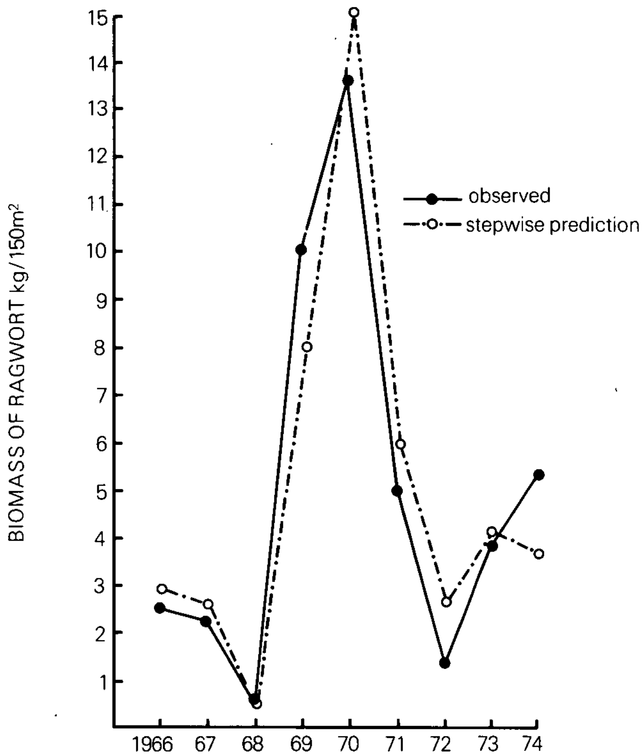


Figure 30 Changes in the actual and predicted biomass of ragwort present

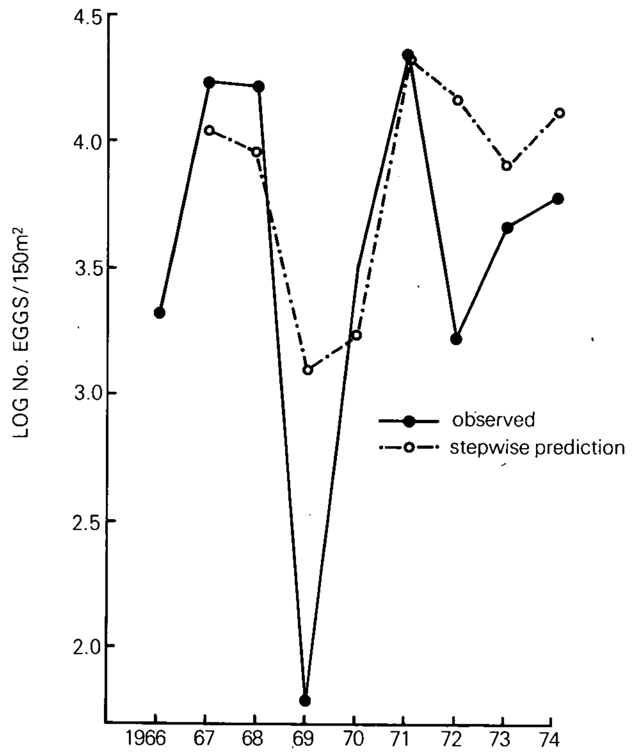


Figure 31 Changes in the actual and predicted number of cinnabar eggs in each year.

LARVAL ECOLOGY OF TACHYPORINAE (COLEOPTERA: STAPHYLINIDAE)

In Britain, the subfamily Tachyporinae is represented by some 63 species belonging to nine genera of distinctive appearance. The adults are generally active, broad-bodied species with a small head and strongly tapered abdomen. Some of the species, especially in the genera *Tachyporus* and *Tachinus,* may be extremely abundant and widely distributed, whilst others may have more restricted range and habitat requirements. Little is known of their general biology.

In order to obtain a better understanding of the general ecology of the Tachyporinae, initial studies have concentrated on collecting adults of as many species as possible and attempting to establish them in culture in the laboratory. It should then be possible to determine the food requirements of the adults and to breed larvae from them, at the same time obtaining information on larval feeding. Nearly all tachyporine larvae which have been reared previously have been collected in the field. As a result, most of the limited larval material in museum collections is of mature third instar larvae taken with similar larvae which have been reared to adults. Such results require close scrutiny since adults of two or three closely related species often occur together. First instar larvae frequently differ significantly from mature larvae, not only in general appearance and colouring, but also in their chaetotaxy. Thus, if adequate keys to species identification are to be constructed, material of all immature stages, including pupae, will be required.

It has been found possible to collect larval exuviae after each moult and to make microscopic preparations revealing details of structure and chaetotaxy. Thus, the identity of a single field-collected larva can be confirmed and the structure of one or more larval instars also established. Preparation of exuviae is difficult and segments of antennae, mouth parts, etc., may easily become detached during moulting. However, material obtained in this way is valuable since mortality appears to be unusually high at the prepupal stage in laboratory-bred larvae.

Although it has proved relatively easy to keep adult beetles alive for several months, and even over winter, many species failed to produce larvae. In such species, no eggs were seen to be laid but there is a possibility that other adults in the culture could have eaten them. However, it is more probable that eggs were not laid owing to some dietary deficiency or to unsuitable environmental conditions. To date, adults of all four British species of *Lordithon,* and five *Mycetoporus* spp. have been maintained in culture with no breeding success, despite collecting adults at a time when dissection revealed mature eggs to be present in the oviducts. All adults and larvae in culture are provided with the contents of *Musca* puparia and yeast pellets. Where a litter substrate is provided, various species of Collembola and other micro-arthropods are retained as a possible source of food. Only the larger predatory species are removed.

The larvae of seven *Sepedophilus* species have been bred and reared through all stages in laboratory cultures. Although all the material has not yet been critically examined, it appears likely that there are sufficient constant characters to be able to separate larvae (Plate 18a). Adult *Sepedophilus* fed on banana in culture, but did not attack aphids or Collembola. They were also seen to eat the flesh and browse the spores from the gills of mushroom. Adults and larvae also ate yeast mycelia and some *S. marshami* (Steph.) larvae were reared to adult with this as their only food. Third instar larvae also showed a tendency to be cannibalistic on younger larvae. In the field, there can be little doubt that the one group of four species feeds predominantly upon fungal mycelia either beneath bark or in rotting wood or leaf litter beneath logs, etc. Three smaller species occur in a much greater range of habitats but are found more commonly in sedge refuse, grass and leaf litter.

The predatory habits of several species of *Tachyporus* have been confirmed. Adults and larvae of four common species will devour numbers of nettle aphids. In culture, adults will eat the larvae of their own species and larvae will eat eggs and attack other larvae, although these are possibly more accessible in the cultures than they would be in nature. Normally, the female *Tachyporus* will cover the surface of an egg with soil particles and will carry it at the tip of the abdomen until a suitable crevice is found into which to place it. Since predation appears to be visual and not olfactory, it is very doubtful whether *Tachyporus* eggs are eaten by their own or other species of the genus. Three other species have been maintained in culture for long periods without breeding freely. These species may require a different, more varied, diet.

Adult *Cilea silphoides* (L.) were collected from fairly fresh pony dung and both they and the larvae which were subsequently bred were found to actually ingest the dung.

The phylogenetic position of two very distinctive species, *Trichophya pilicornis* (Gyll.) and *Habrocerus capillaricornis* (Gr.), has been much discussed. Kasule (1968) regarded the complex male genitalia and unusual hind coxae of *Habrocerus* as specialised structures, but considered differences in the larvae insufficient to warrant subfamily separation. The structure of the eggs indicates the unique nature of this species. All tachyporine eggs so far examined are thin-walled, ovoid, and with no noticeable surface sculpturation. *Habrocerus* eggs are thick-walled, strongly ridged and larval eclosion is by means of a circular 'trap door' at one end (Plate 18c). The larvae of *Trichophya,* whilst superficially resembling those of the Tachyporinae, differ significantly, not least by bearing only two ocelli on each side of the head, compared with five in *Habrocerus* and six in the larval Tachyporinae so far known.

In the Staphylinidae, a study of the immature stages not only provides clues towards a better understanding of the phylogeny of this taxonomically complex family, but also enables an understanding to be gained of the true habitat requirements of species in which the adults are highly mobile and may be caught in a wide variety of situations.

R. C. Welch

Reference

Kasule, F.K. (1968). The larval characters of some subfamilies of British Staphylinidae (Coleoptera) with keys to the known genera. *Trans. R. ent. Soc. Lond.,* **120**, 115–138.

FIVE YEARS LIGHT-TRAPPING OF MOTHS AT FURZEBROOK

A light trap has now been operated at Furzebrook Research Station since 1970 (ITE 227). During 1970 and 1971, the trap was not operated regularly and these years were used to enable us to become familiar with the fauna and to settle problems of identification. In 1972, it was decided to operate the trap every night and to record not only the species which occurred, but also their numbers. The nightly trapping programme is now in its sixth year and includes the exceptional year of 1976. It is fortunate that detailed records exist for the years before and after 1976 so that the year can be seen in context.

Throughout, trapping has been with a Robinson-type trap fitted with a 125 watt mercury vapour bulb. The trap has remained in the same position on the main lawn in front of Furzebrook House. To the east of this lawn is a dampish mixed woodland consisting mainly of oak, ash and sycamore, together with some beech and horsechestnut and with scattered Scots pine. Bordering the west side of the lawn are more pines and a number of *Cupressus macrocarpa,* together with other ornamental shrubs and trees. The area to the south is mainly of regenerated willow. The woodland edge is mostly between 20 and 50 yards from the trap. Beyond the grounds of the house are further mixed damp woodlands, as well as heathland and old fields.

For the purposes of analysis, the five years from 1972 to 1976 have been examined. During this period, the trap was operated on 1,757 nights out of a possible 1,827 nights (96·2% of the time). The 70 missing nights occurred mainly during the winters of 1972/73 and 1973/74, when there were restrictions in the public power supplies, but only four nights has been missed through equipment failure during the five years.

Each night, the numbers of individuals of each species have been recorded, but only for those species described by South in his *Moths of the British Isles.* However, the genus *Eupithecia* and its allies have been omitted from the analyses.

During the five years, 202,750 moths were caught, representing 391 species. During the exceptional year of 1976, when 370 species were caught, catches of individuals were about three times that of the average of the previous years. In an average year, 27,700 individuals, representing 315 species, were caught.

The ten commonest species and their yearly catches are set out in Table 16. Next in the succession are *Ochropleura plecta* (L.), *Apamea monoglypha* (Hufn.), *Poecilocampa populi* (L.), *Agrochola macilenta* (Hubn.), *Autographa gamma* (L.), and *Mythimna pallens* (L.). It is evident from the table that the catches of four of these species in 1976 were exceptional and the inclusion of *Agrotis puta* and *Conistra vaccinni* in the top ten rests largely with the 1976 results. These ten species contribute 88,390 individuals, or 43·6%, to the total catch. Besides these ten species, a further 35 species have occurred in numbers exceeding one thousand. Less than ten individuals have been caught of 95 species, and of these, 24 have been caught only on a single occasion in the five years.

Most of the record catches occurred during 1976, and, in June 1976 alone, almost as many moths were caught as the total catches in previous years. Despite the large numbers caught during 1976, the proportion of the year's catch caught each month was similar. Normally, about 50% of the annual catch is taken during July and August (Table 17). In 1976, the proportion was slightly higher and commenced in June. The largest catch of individuals ever made was on the night of 28 June 1976, when 3,466 moths representing 109 species, were caught. The largest number of species recorded in one night's catch was 113 on 2 July 1976. The previous largest catch was on 19 July 1972, when 1,221 indi-

Table 16 The yearly catches of the ten commonest species of larger moth caught at Furzebrook between 1972 and 1976

Species	1972	1973	1974	1975	1976
Agrotis exclamationis (L)	940	530	870	430	18790
Noctua pronuba (L)	750	5470	1370	2700	9630
Luperina testacea (Denis & Schiff.)	290	710	430	500	3950
Agrotis puta (Hübn.)	50	60	100	520	3480
Lycophotia porphyrea (Denis & Schiff.)	4970	2150	1760	1040	2260
Mesapamea secalis (L)	440	1590	1220	1560	2300
Orthosia gothica (L)	670	890	1210	1110	1490
Conistra vaccinii (L)	70	180	1000	1140	1780
Noctua janthina (Denis & Schiff.)	380	830	920	1070	870
Orthosia stabilis (Denis & Schiff.)	320	390	900	950	1390

Table 17 The percentage of the annual number of species caught each month

Month	% of annual no of species
January	1
February	1
March	3
April	5
May	3
June	17
July	25
August	24
September	8
October	6
November	4
December	3

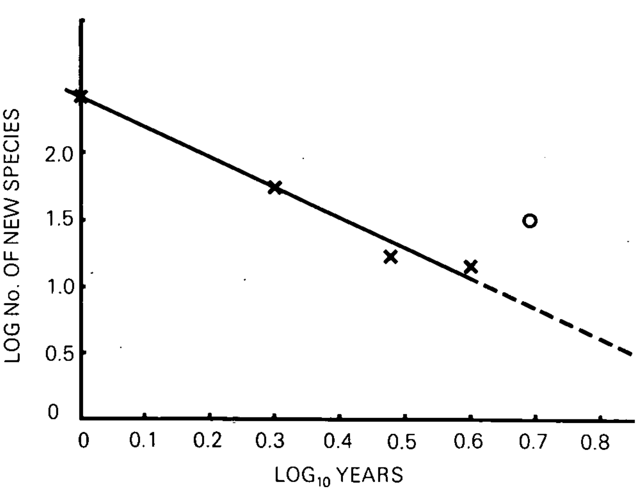


Figure 32 The rate at which new species of moth were caught between 1972 and 1976.

viduals were caught; on this occasion, the catch was mainly of *Lycophotia porphyrea,* a common heathland species. The previous largest number of species caught in one night was 89 on 3 August 1975.

In 1972, 270 species were recorded, and a further 57 new species were caught in 1973, 17 in 1974 and 14 in 1975. This trend shows a logarithmic decrease (Figure 32) when plotted against the logarithm of the number of years of trapping and the expectation was that in 1976 few new species (about 7) would be added. However, because of the exceptional trapping conditions, 33 new species were recorded.

This account has only touched on the highlights of the five years of trapping, and more detailed analyses of the data are being undertaken, but, although these analyses include examination of the pattern of changes of both numbers of species and of individuals, they are mainly concerned with the detailed phenology of the commoner and more regularly occurring species. For this reason, it is hoped to continue the nightly trapping programme for a few more years.

N.R. Webb and D.C. Malt

SPIDERS ON DORSET HEATHLANDS

The results of a survey of spiders on a wide range of southern heathlands in 1968/69 showed that some interesting differences exist between the spiders present in heathland areas in the New Forest and those occurring on Dorset heathlands south and west of Poole Harbour (which will be referred to here as Purbeck heaths). It was thought, therefore, that it would be of interest to investigate the spider fauna of some intermediate heathland areas, north of Bournemouth and west of the Avon valley, which are about 8–12 km from the western fringes of the New Forest and about 20–30 km from the Purbeck heaths. Four of these heaths have been surveyed since 1973–Cranborne Common in the north, Parley Common in the south, and Holt Heath and Horton Common in between. They were studied mainly by pitfall-trapping, supported by collections with a D-Vac suction net and by some hand-collections.

As might be expected from their geographical position, the Avon valley heaths show closer affinities to the New Forest in their spider fauna, but also show some affinity to the Purbeck heaths and a few interesting peculiarities of their own. *Zelotes pusillus, Evarcha arcuata, Pirata uliginosus* and *Walckenaera melanocephala* are four species which are widespread and common in the New Forest and on the Avon valley heaths, but, on the Purbeck heaths, *Z. pusillus* and *W. melanocephala* are rare and the other two species are completely absent. Among rarer species, *Haplodrassus umbratilis* is restricted in Britain to the western parts of the New Forest and to Holt, Horton and Cranborne heaths; it is interesting that it apparently does not occur at Parley, although the habitats available are similar. On the other hand, *Meioneta beata* is common in the New Forest and at Parley, but has not been found on any other Dorset heaths; similarly, the rare *Xysticus robustus* is known on heathland only in the New Forest and at Parley. An interesting species is *Ero aphana,* which was first found in Britain at Parley in 1974, and again at Horton in 1976, but was not found at Holt which lies between these sites; similarly, the rare *Tegenaria agrestis* is common at Parley and Horton and occurs in the New Forest, but not in Purbeck. Of species which are widespread on Purbeck heaths but rare or absent in the New Forest, *Gnaphosa lugubris* and *Aelurillus v-insignitus* were found only at Parley among the Avon valley heaths, *Scotina palliardi* only at Cranborne, and *Araeoncus crassiceps* only at Holt. An odd distribution is shown by *Micrargus laudatus* which is common in Purbeck and the New Forest, but which has not been found on any of the Avon valley heaths. At present the reasons for these differences in distribution are obscure.

In August 1976, about 90% of the study area at Horton Common was accidentally burnt, but trapping has been continued at the same points as a small-scale comparison with the results of a much larger project which was started at about the same time, after an extensive fire at Hartland Moor NNR in Purbeck (ITE 500). This fire covered an area of 483 acres, compared with 346 acres at Horton. Eight plots have been laid out at Hartland in order to study the recolonisation of the area by spiders, the plots being arranged so that two are close to adjacent farmland, two close to unburnt heathland, two in the centre of the burnt area, and two in wet heath which was burnt less severely than the dry heath. At each plot, nine pitfall traps are being used to collect ground-active spiders and six water traps supported several inches above ground level to catch aerial immigrants. Later, this investigation will be supported by quadrat sampling and collecting with the D-Vac suction net, but, at present, the population densities are too low to make these methods worthwhile. The vegetation near each trap will also be recorded annually. So far, the efficiency of the traps has been considerably reduced by extensive erosion, causing them to fill with sand and burnt litter. This problem arose as a result of the extreme severity of the fire, which, in some areas, burnt off the humus layer and exposed bare sand which was then shifted by the high rainfall and winds during the winter of 1976–77. The erosion appears now to be lessening, however, as the early stages of recovery of the vegetation help to stabilise the soil surface.

Some interesting results have been obtained from the trapping even in this difficult first year. Perhaps the most striking are the differences between the spiders caught in the pitfall traps and those caught in the aerial traps. The latter have caught several species which are never normally found on heathland, and a large number of species which, although occurring on heathland, would never normally be found in the type of habitat present where the traps are situated. As examples may be quoted *Anelosimus aulicus,* which spins webs only on large gorse bushes, taken in aerial traps in the middle of the burnt area, and *Pirata piraticus,* a typical bog or marsh species, taken in traps on dry burnt heath at the top of a hill. These species have clearly been trapped during random aerial dispersal, and they would not have stayed in the habitat where they alighted. The spiders caught in the pitfall traps, however, have nearly all been typical heathland species. Some of these almost certainly survived the fire in very small numbers under stones or in a few small areas which escaped the full severity of the fire. During the first year, there has been little sign of the immigration of species usually typical of recently-burnt areas. Earlier work on recolonisation of burnt heathland by spiders was done in a much smaller area after a less severe fire, and by pitfall-trapping alone.

P. Merrett

EARTHWORM PRODUCTION FROM ORGANIC WASTES

A large quantity of organic waste is produced in agriculture, industry and from domestic sources, representing a potential energy and protein resource which is only partially utilized and which, in some instances, presents disposal problems.

Current work on recycling these materials is on an industrial scale, using sophisticated technology with high energy inputs and expensive plant costs. An alternative strategy of low cost, intermediate technology conversion through a microbe-invertebrate-domestic omnivore food chain is envisaged for small and medium scale outputs of organic wastes, for example from antibiotic fermentation plant.

The most promising invertebrates for this purpose are earthworms of species normally associated with high concentrations of rotting organic matter. The commonest of these is the brandling worm, *Eisenia foetida,* found in compost and manure heaps, but little is known about its production potential.

Preliminary studies have been made of its survival in the basic culture medium, farmyard manure, which was dried, milled and rewetted to (a) avoid introucing unwanted earthworms and (b) produce a more homogeneous substrate. Earthworms placed in containers of prepared manure died within 24 hours, the ammonia concentrations being *c.* 10 times greater than those of untreated dung and dung macerated without drying. Concentrations of ammonia decreased after 10 days and worms introduced after that time survived.

Worm growth rates were significantly increased by adding a 1:1 glucose/peptone supplement to dung at rates up to 6% d.w. *E. foetida* prefers higher temperatures than soil-dwelling species of worms and can tolerate temperatures *c.* 25–28°C which kill other temperate species. In an experiment to determine the optimum growth temperature, newly hatched worms were cultured for 100 days at temperatures between 12 and 30°C. During the first 50 days, the weights of worms increased with increasing temperatures. Further increases in weight during the next 50 days only occurred at temperatures below 24°C (Table 18). It is possible that worms lose weight after reaching their maximum size, the maximum being attained earlier at higher temperatures or, alternatively, the faster growing worms may have exhausted the nutritive resource of the culture medium so depriving themselves of food in the later stages of the experiment. These possibilities are being explored so that productivity of the brandling worm, and therefore its potential as a protein producer, can be assessed in ideal conditions.

J.E. Satchell and M.R. Smith

Table 18 Median weights of worms reared at different temperatures

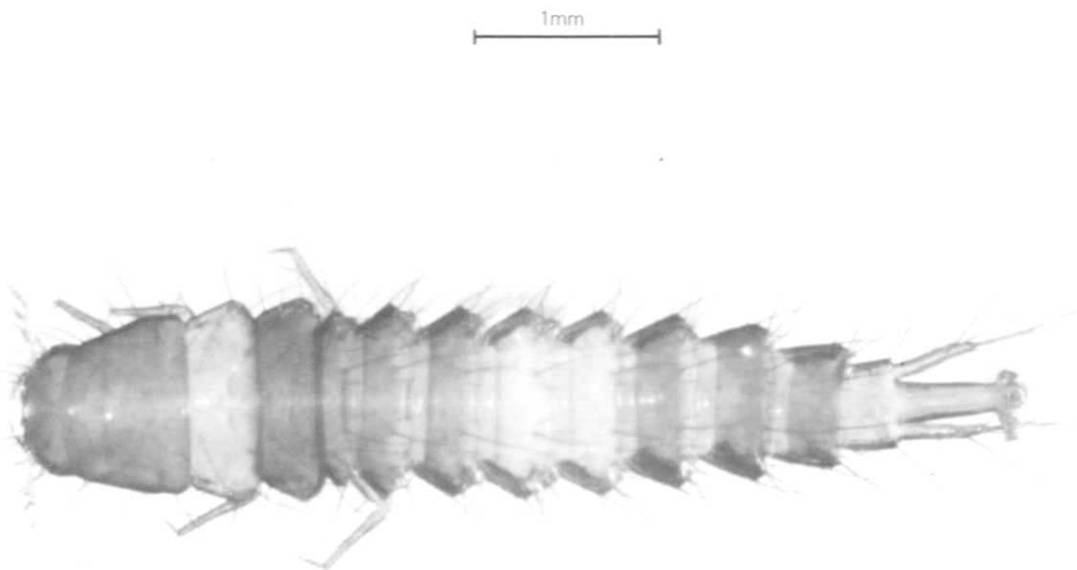
Temp (°C)	Median weight mg		
	Start	50 days	100 days
12	10	19	32
15	8	14	28
18	8	26	39
21	8	26	36
24	9	34	34
27	7	39	35
30	9	51	30

Taxonomy and distribution of organisms

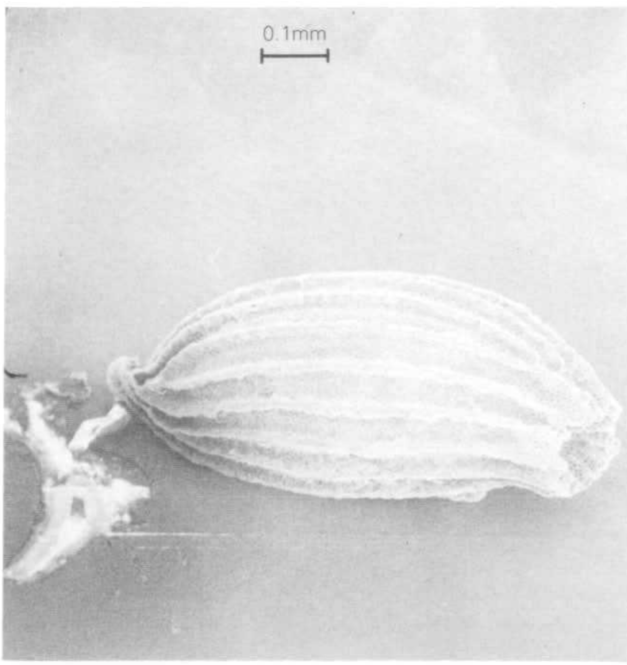
BRYOPHYTE TAXONOMY AND DOCUMENTATION

Taxonomic revision of the moss genus *Grimmia* from South Georgia reached the stage of relating anatomically and morphologically defined groups, recognized earlier, to (i) taxa described in the literature, and (ii) their type specimens. Six species have so far been satisfactorily delimited.

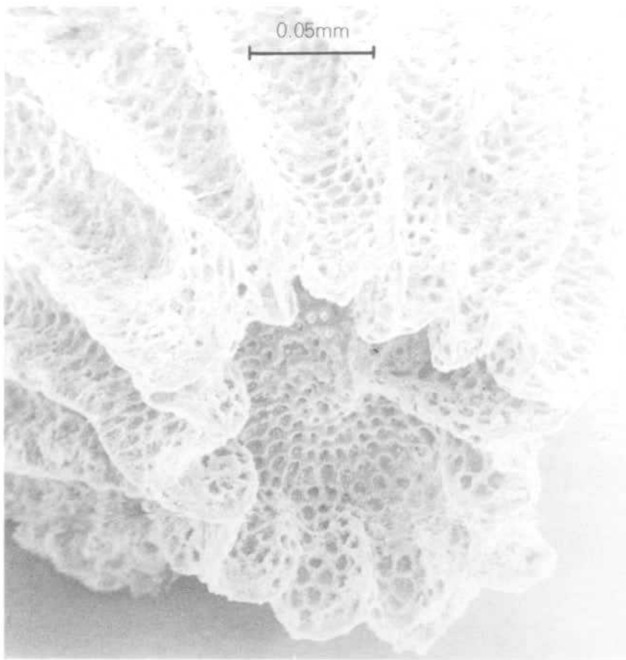
Many new collections of bryophtes from southerly latitudes in the Southern Hemisphere have been received for identification and incorporation into the herbarium, including specimens from Isla Hoste in



Sepedophilus testuceus *(F.) (Coleoptera; Staphylinidae) 3rd instar larva, dorsal view showing distinctive colour banding of thoracic and abdominal tergites. Photograph J N Greatorex-Davies*



Habrocerus capillarcornis *(Gr.) (Coleoptera; Staphylinidae). Egg side view. Photograph Mrs L C Lamont*



Habrocerus capillarcornis *(Gr) (Coleoptera; Staphylinidae). Egg showing operculum which splits round convoluted ridge at larval eclosion. Photograph Mrs L C Lamont*

Plate 18

Plate 19 Taking samples from deep water in Loch Leven (Kinross). Photograph I Smith

southern Chile, gathered by a Cambridge expedition, and others from many of the smaller islands in the South Shetland Island group provided by the Second Joint Services Expedition to Elephant Island. More collections have been received from British Antarctic Survey (BAS) personnel to whom identifications have been supplied.

A new growth facility for cold climate bryophytes, based on an enclosed air-conditioned bench, is now fully operational. Living material from the Antarctic and sub-Antarctic was collected in 1977/8 by BAS personnel to form the basis of a representative stock collection which is now flourishing after eight months in the new facility.

Two major documentary projects are underway. The first is a literature review of all moss species reported from Chile, Argentina, Uruguay, the islands of the Scotia Ridge and Antarctica, the South American area being regarded as the main species reservoir for the present day bryophyte flora of deep Southern Polar regions. The document, which is nearing completion, lists some 6,000 epithets and is supported by a bibliography of over 750 references. It will provide a framework against which current taxonomic revisions, as well as local and regional ecological and distributed studies, can be evaluated. The second project, the *Conspectus of bryological taxonomic literature,* which is still in its infancy, has wider objectives aiming to provide an annotated guide to world bryological taxonomic literature arranged on a geographical basis. It is being organised under the aegis of the International Association of Bryologists and is being developed in collaboration with bryologists in the British Museum (Nat. Hist.). For each country, relevant floras, identification manuals, check lists, mapping schemes and/or bibliographies are being listed while other sections will deal with world monographs and regional revisions as well as other important literature. Currently, the data base of some 10,000 references, many of which have been provided by bryologists the world over, is being assessed in terms of a primary coding into geographical areas and content.

S.W. Greene, D.M. Greene and B.G. Bell

BIOLOGICAL RECORDS

1977 has seen the publication of the *Red Data Book* for British vascular plants, the result of surveys done during the last 10 years characterizing the distribution of 321 rare species. These species have been recorded in no more than 15 squares (10 km) since 1930.

Additionally, the *Red Data Book* contains a threat number for each species, the number taking note of the rate of decline of particular species, their attractiveness, the accessibility and vulnerability of their differing sites. Of a possible score of 15, nine species have threat numbers of 13, with Lady's Slipper *Cypripedium calceolus* almost certainly the rarest plant species in the British Isles. Of 46 endangered wetland species, 6 are considered extinct and a further 23 threatened; 21 of 23 endangered arable species are threatened.

The *Red Data Book,* by providing an analysis of threat for the first time, should help the Nature Conservancy Council when considering Schedule 2 of the Conservation of Wild Creatures and Wild Plants Act, 1975, which should be revised in 1980. More immediately, it should stimulate interest and ensure that other species are not eliminated and it may encourage autecological studies. During the year, work on the *Atlas of Ferns* was completed, so bringing to an end the first complete revision of any group included in the *Atlas of the British Flora.* It contains new maps, especially of subspecies and hybrids, each map having accompanying taxonomic and biogeographical notes.

Several entomological atlases were completed, including those for *Odonata* (Dragonflies) edited by J. Heath, *Orthoptera* (Grasshoppers) edited by M.J. Skelton, *Hymenoptera Formicidae* (ants) edited by K.G. Barrett and the *Trichoptera Hydoptilidae* edited by Jane E. Marshall. They will be published early in 1978 as *Provisional Atlases* but some of the data have been quoted in *The Dragonflies of Great Britain and Ireland* by C.O. Hammond and in *Ants* by M.V. Brian.

H.R. Arnold has completed the second edition of the *Provisional Atlas of Mammals;* incorporating 58 maps of 56 species which should aid the preparation of a *Red Data Book* for vertebrates scheduled for 1978.

Continued contributions have been made to European Atlases. Data for 20 species of Lepidoptera and Hymenoptera from the British Isles were provided for the first European maps to be published by the European Invertebrate Survey, of which J. Heath is Secretary-General, whereas vascular plant data have been prepared for some 50 maps for part 4 of *Atlas Florae Europaeae* covering the *Polygonaceae* which will be published in 1978.

The increase in map production, resulting from the many distribution schemes started 10 or more years ago and which are now coming to the end of their recording phases, has put a severe strain on existing automated map-making facilities. Since 1972, distribution maps have been produced on a modified IBM electric typewriter from data on punched cards. This process was slow and labour-intensive, and the equipment became increasingly unreliable. In 1976, the Experimental Cartography Unit of NERC was asked to develop a replacement mapping system based on a

Laser-Scan HRD1 high-resolution plotter. Using this method, data for over 100 species of British bryophytes have been processed to form the basis of the first atlas to be produced by this system.

Following the close-down of the ATLAS computer at the Computer Aided Design Centre, Cambridge, biological records have been incorporated into the G-EXEC data management system developed by the Institute of Geological Sciences on the dual IBM 360/195 configuration at the Science Research Council's Rutherford Laboratory. Additionally, means are being sought to increase the usefulness of the data to include sophisticated analyses linking species occurrence with aspects of habitat.

F.H. Perring, H.R. Arnold, L. Farrell, J. Heath and D.W. Scott

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Work of special subdivisions and centres

CULTURE CENTRE OF ALGAE AND PROTOZOA

The Collection

The usual annual list of additions and amendments to the last list of strains (1976) was distributed, recording about a hundred new strains in culture and sixteen strains lost or discarded, while eight strains formerly with bacteria were made pure. Fifteen new strains were type material of newly described species. Among the acquisitions were ten *Neochloris spp* from soil or freshwater habitats in USA and fourteen *Chlorella* strains from acid sulphurous springs in Italy. Professor Olive deposited four strains of protostelids, slime moulds of terrestrial origin intermediate between strictly cellular and acellular forms. Our collection of Sarcodina now comprises 109 strains in 80 different species, and, though there are important omissions, it is almost certainly the most comprehensive in the world.

Several strains of planktonic blue green algae have been added, mostly axenic and including some mutants isolated by Booker and Walsby. Five *Dunaliella* strains from saline waters in Israel and six algae from Antarctica were also added.

The importance of well established service collections such as CCAP was emphasised when Dr Provasoli of Yale announced his retirement and the breakup of his algal culture collection. Several hundred strains were involved and many were unique. Doubtless many will be lost, but we have taken about fifty, some to add to the collection, others for research interest.

The demand for cultures continues satisfactorily, showing a 10% increase over last year (Tables 19, 20).

Table 19 CCAP culture output

	1977	1976
Number of orders	1,090	962
Cultures to UK:		
Academic	3,214	2,925
Hospitals	16	27
Government	57	111
Commercial	113	77
Cultures to EEC countries	197	200
Cultures to other countries	476	323
Total	4,073	3,663

Table 20 Countries ordering cultures during 1977

Australia	India	Portugal
Austria	Iran	Rhodesia
Belgium	Ireland	Saudi Arabia
Canada	Israel	South Africa
Czechoslovakia	Italy	Spain
Denmark	Japan	Sweden
Finland	Kuwait	Switzerland
France	Malta	Tahiti
East Germany	New Zealand	Turkey
West Germany	Nigeria	USA
Holland	Norway	USSR

Though customers do not always specify the purpose for which cultures are required, there has been a detectable increase in the requests for research purposes accompanied by requests for information and advice on choice of strains and relating to the selected strains. At present, data storage is entirely based on card indexes, but preliminary steps have been taken towards establishing a computer based system.

It can be misleading to draw too many conclusions from one year's figures, but the overseas demand continues to be strong, well above the 10% which was the proportion for many years.

Preservation of cultures

Progress continues in developing the liquid nitrogen freezing technique. Using the two-step cooling method devised for *Chlorella,* 40 strains of Ulotrichales have been successfully cryopreserved with recovery rates of at least 60%. Work with Chaetophorales, Xanthophyceae and Eustigmatophyceae is in progress and initial results are promising. Volvocales and Euglenophyceae are presenting problems, with initial survival less than one cell in a million. However, as might be expected, Chlamydomonas strains from snow are more amenable, and further research together with freeze-fracture microscopy of the cell membranes should lead to further progress. An unexpected success occurred with freezing *Euglena* using methanol as a protective agent in place of the more usual dimethyl sulphoxide.

Results from experiments designed to improve preservation techniques may have a wider significance in the general tolerance of cells to freezing. Following a shift from autotrophic to heterotrophic nutrition, *Chlorella* cells became more sensitive to the stresses of freezing and thawing, and it was shown that, unlike the suggested mechanism with other cells, hypertonic solution in the cell was not damaging.

Taxonomic research

This continues to be mainly of a fundamental nature because of the nature of the problems that arise so often when conscientious identifications are attempted. Similar problems with higher plants and animals of Europe or North America were usually solved perhaps a century or more ago. The importance of such work becomes clear when one considers that, in many situations, the biomass, and more especially the activity of microorganisms, equals or exceeds that of the larger forms.

Following the publication of the *Illustrated Key to Freshwater and Soil Amoebae,* F.C. Page is preparing a similar work for amoebae of brackish and marine waters. A major step towards this was the publication of a paper on *Thecamoeba,* a genus of particular interest as its species are widely distributed in freshwater, occur in salt water and are among the largest protozoa in soil. Nine species were investigated in culture and nine other probably or possibly valid species were reviewed from the literature. They can now be identified with reasonable ease, and, as they feed on a variety of protozoa and algae as well as bacteria, they recommend themselves to ecologists as well as cell biologists for further research.

D.J. Hibberd is continuing research into the vast assemblage of organisms that botanists used to put in or near the Chrysophyta. *Chrysonebula* which forms mucilaginous masses on rocks in mountain streams is of particular interest in that its zoospores resemble those of *Hydrurus foetidus* which forms tough leathery plants up to a foot long in similar habitats. The finding of a golden-brown flagellate *Diacronema vlkianum* on the site of an old manure heap near Cambridge stimulated a joint paper with Dr J.C. Green of MBA as the same species is also in culture from sea water. It proves to belong to the Prymnesiophyceae, a group of mainly marine organisms including the coccolithophorids which played a large part in the formation of Cretaceous chalk deposits. The material examined by electron microscopy enabled a very detailed reconstruction of the flagellar apparatus to be produced.

Symbiosis is a lively topic in biology, not only as an interesting relationship between different organisms, but also as a likely evolutionary origin of essential organelles such as chloroplasts in plants. *Mesodinium rubrum* from The Fleet behind Chesil Bank in Dorset was examined as it is a ciliate with a cryptomonad endosymbiont, the latter showing considerable structural modification and the symbiosis appearing to be obligatory for both partners. The success of the partnership is proved by it often being associated with marine 'red water' phenomena which may extend over 100 square miles.

Investigations by H. Belcher and E. Swale, following their successful *Guide to Freshwater Algae,* and leading to a work on river plankton algae, have shown that small centric diatoms of the genera *Cyclotella, Stephanodiscus* and *Thalassiosira* are of common occurrence in both large and small rivers especially in the spring.

N.C. Pennick and K.J. Clarke have continued examining the external features of the marine flagellates *Pyramimonas spp.* Each species seems to have a distinct set of 5 or 6 different kinds of ornamental scale (Figure 33) arranged in layers over the body and along the flagella. They have also recorded comparable scales from the dinoflagellate *Heterocaps atriquetra,* though in this case, there is only one scale type. The increasing ability to identify solitary scales found in natural material will be valuable in ecological work and in micropalaeontology, though in some cases scales do not persist.

E.A. George

SUBDIVISION OF CHEMISTRY AND INSTRUMENTATION

Introduction

The Subdivision continues to provide the specialised technical support required by both the Institute's scientists and the Nature Conservancy Council, the latter under contract. Assistance is also provided for some NERC workers and outside organisations concerned with environmental problems, if this is compatible with current ITE research commitments.

Direct service work of this type accounts for approximately 60% of the Subdivision's work commitment. A further 20% of the Subdivision's time is devoted to the

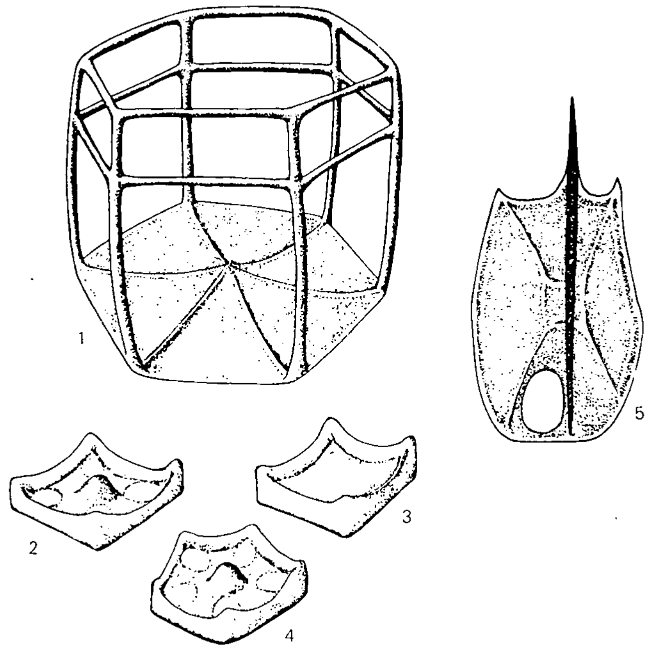

Figure 33 Scales of Pyramimonas virginica *Pennick. 1 & 3 body scales 2, 4 & 5, flagellar scales. Scale: 1 is about 230 μm across. Drawn by N. Pennick.*

development studies that are necessary to maintain service efficiency. Work in this category includes such subjects as the development of chemical techniques, the improvement and development of instrument designs and studies of new photographic processes. The remaining time of Subdivision staff is allocated to research projects, some of which are done jointly with other Subdivisions.

Apart from its practical duties the Subdivision has an important administrative and advisory role. Much of this work is handled by the Subdivision Head, for example, the vetting of ITE's capital equipment requirements, the co-ordinating of radiochemical experiments, and the provision of technical advice to management.

The Service Sections

Chemistry

1. *Merlewood Laboratory.* The routine analysis of soils and vegetation samples for the nutrient and structural constituents, in support of the Institute's research projects, continues to be the principal single task of this laboratory. However, a considerable variety of other sample materials and analyses were also processed and collectively occupied almost as much time as the routine work. In particular, there was a marked increase in the number of water analyses and pollution tests carried out during the year.

Around 5000 soils were analysed for the main nutrients and in many cases the trace nutrient elements were also determined. The larger proportion of these samples arose out of research into the effects of afforestation and woodland management on the soil. These included studies on New Forest soils, birch-soil relationships in moorland situations, Scots pine distribution and the effect of management on coppiced woodlands. Investigations into soil-forming processes and structure generated a need for information about the total, as opposed to the extractable, element content of the soils. Most of this work was done using X-ray fluorescence techniques.

Compared with 1976, there has been a sharp decrease in the numbers of vegetation samples processed by the Merlewood laboratory, although a considerable number of chemical characteristics have had to be examined. The largest single block of service work (involving almost 1000 samples) was carried out for the NERC Unit of Comparative Plant Ecology, and these samples required the determination of eleven separate elements (K, Na, Ca, Mg, Fe, Al, Mn, Cu, Zn, M and P) on each sample. At some time during the year, most elements of biological importance and of known toxic effect have been determined on vegetation and to some extent on animal tissue samples. Vegetation analyses also included a few samples for proximate organic tests in connection with litter decomposition and animal and bird nutrition studies.

The requests for water analyses, which, as already mentioned, have increased during the year, mostly arose from the regular monitoring studies of lakes and streams. A survey of the Tay catchment and, towards the end of the year, a similar survey on the larger Scottish lochs accounted for much of the work. In addition, analyses were carried out in connection with the Continuous Flow Project (482) and on a number of estuarine surveys. As many as sixteen different parameters, including the principal nutrient elements and anions, were examined for most of these samples and usually the changes in the concentration of nitrogen and phosphorus ions were also investigated.

Soil and vegetation samples have been tested on a number of occasions for the presence of pollutants arising from the seepage of sewage and excess fertilizer applications. Much of this work has been carried out for the Nature Conservancy Council. Other pollution studies have included the regular analysis of atmospheric precipitation samples as a part of air pollution studies (Projects 244 and 452) and the analysis of fluorine in almost 2,000 samples of soil, litter, vegetation and animal materials from sites close to an aluminium smelter (Project 160).

2. *Monks Wood Laboratory* Throughout the year, there has been an increasing demand for analytical support, particularly from the Animal Function team based at Monks Wood. There has also been more diversity in the chemical tests carried out. In particular, the analysis of some stored samples, from the Monks Wood Tissue Bank, has resulted in over 5000 analyses for heavy metals being carried out on 1700 tissue samples. A considerable amount of metal analysis has also arisen from Project 456 concerned with monitoring the metal-protein relationship in birds.

During the past few years, there has been a growing interest in the use of chemical analysis in taxonomic studies. Following the analysis of monoterpenes in resin from Scots pine and Lodgepole pine, this category of work has extended to include Sitka spruce (*Picea sitchensis*). The monoterpene composition in a resin sample provides a 'finger-print' which can be related to the genetic origin of the tree. Because of the volatile nature of monoterpenes' resin, the samples are analysed by gas chromatography with flame ionisation detection and using 5% carbowax 20M for column packing. Identification and calibration is carried out by reference to known standards.

The most important extension to the instrumental facilities in 1977 was the purchase of a nitrogen phosphorus selective detector for use with the gas chromatographs. This incorporates a rubidium bead which gives a high degree of sensitivity and selectivity and enables a wide range of organophosphorus compounds and carbonates to be determined.

The expansion in laboratory accommodation referred to in the last Annual Report has resulted in marked improvements in the working conditions. Conditions were further improved by the installation of an air conditioning plant in the metals laboratory. This measure became imperative because of the need for a clean environment when analysing biological samples for low levels of metal residue.

3. *Colney Laboratory* The work of this laboratory is concerned with the use of electrophoresis techniques to examine variation in natural populations of plant species. The main work in 1977 has been the conclusion of the studies on the genecology of *Puccinellia maritima* referred to in the 1976 report. Recently work has commenced into the screening of populations of *Poa pratensis* and *Festuca rubra* for isoenzyme variation in connection with the project (464) on interspecific competition and invasion. Encouraging trials have also begun using *Agrostis setacea* and it is expected that electrophoresis will be used for screening *Spartina* variants and possibly some animal tissue material in the immediate future.

The technique remains essentially the same as that described in the 1976 report. The only modification has been the addition of artificial cooling of the gel during electrophoresis. This cooling improves band separation and prevents false RF values which are caused by temperature differences within the gel. A gel scanning device is being developed to facilitate the location of the band position.

J.A. Parkinson, M.C. French and R.J. Parsell

Engineering

During the year, the demand for engineering services and expertise has continued. The Central Engineering Unit at Bangor, together with on-station engineers at Merlewood, Monks Wood and Bush, have provided major engineering support for several research projects as well as general engineering advice and support.

Major or specialised engineering work is allocated by the Senior Engineer. Work that requires specialised electronic engineering is carried out at Bangor or by the station engineer at Merlewood. All the Institute's workshops have mechanical engineering facilities and, where staffed by a member of the engineering section, can give on-station support as well as assisting the Central Unit.

The workshop at Bush has been re-sited and improved to accommodate the new engineering equipment obtained and installed during the year. The increased facilities, together with their full-time station engineer, will enable some of the work required by the research stations in Scotland to be handled on a more local basis.

Work by the Central Engineering Unit and the station engineer at Monks Wood on the continuous flow project has continued during the year with the installation and testing of the water re-mineralisation plant. Additional control equipment has also been added.

A new development of the year has been the purchase of microprocessor evaluation equipment for the Bangor and Merlewood engineering laboratories. This equipment will be used initially for familiarising engineering staff with microprocessor operation so that they will be able to design and repair microprocessor circuitry used in control and data systems.

G.H. Owen

Nursery Unit

Most of the facilities and all the permanent staff of this Unit are based at Bush, although work is carried out for staff elsewhere and the Senior Officer of the Unit has advisory responsibilities on glasshouse and nursery matters throughout the Institute. Although there are only three permanent staff in the Nursery Unit, they have had valuable assistance from staff working for the Job Creation Scheme and from other Subdivision staff based at Bush, who are now making greater use of the glasshouse facilities.

The proposed purchase of a temperate glasshouse for Bush and a cool glasshouse for Merlewood has resulted in extensive planning and site preparation work. Preliminary surveys have also been carried out into the feasibility of providing new cool glasshouses at Bangor and Banchory and additional temperate facilities at Bush. Present glasshouse space is still mainly committed to long term projects, although a few additional jobs have been accepted. These include the production of seeds from calicole species for the re-establishment of chalk grassland (project 242) and a small experiment has been set up to assist the Merlewood Chemical laboratory in their studies on reserve nutrients. During the year, a standby generator was installed so that the glasshouses at Bush are now protected from power cuts.

General field plot maintenance and construction work has been assisted by the purchase of a tractor-mounted rotary cultivator and the completion of storage space to house field equipment. Recent construction work at the field plots includes the preparation of irrigation beds for Sitka spruce and Lodgepole pine seedlings, the construction of beds of industrial spoil for trials on tolerant clones of selected hardwoods, and the establishment of hillide capillary beds for high altitude (300m) studies. The last of the field plots currently available have been sown with grass ready for the *Betuletum* studies, but the Unit has an option on a further four hectares of land adjacent to the Bush estate.

R.F. Ottley

Photography

The limited service of developing and printing initiated at Colney Research Station, Norwich, last year has now been extended to include colour printing; both negative-positive and direct reversal processes can be handled. Manual processing is in use at the moment although exposure and filtration are controlled by a four-channel programmed colour analyser. During October, the capacity of the unit was severely tested by the demand from Monks Wood for over 1,200 photographs of various kinds for use in their Open Week. This demand included 250 colour photographs, mainly in Cibachrome.

Colour reversal film is currently being issued at the rate of 10,000 frames a year, which indicates that photography is playing an important role in recording the activities of the Institute. Some of this material finds its way into the newly established photographic collection. It is hoped that this collection can be expanded in the forthcoming year, as it has already proved its value as a source of illustrations for lectures and publications.

C. Quarmby and P.G. Ainsworth

Research and Development

Plant Nutrient Survey

This nationwide survey was designed to provide information about the nutrient status of common native plants sampled only at sites where they were a prominent feature of the plant community. Constraints introduced into both the sampling programme and statistical processing techniques enabled the results to provide an assessment of the widespread (but sometimes criticised) use of foliar nutrient data for indicating plant nutrient status. The sampling procedure minimised, though it did not eliminate, the frequently reported effects of space-time variation on plant nutrient values.

The nutrient inter-relationships were examined following the computation of correlation matrices, but their interpretation has always been uncertain because of the instability of the coefficients themselves, particularly with small sample numbers. This was allowed for by pinpointing the number of degrees of freedom required to achieve a specified certainty about the significance of the coefficients shown by the published tables. Fifteen tree, herb and grass-like species were judged to have been sampled at a sufficient number of sites for this purpose and attention was concentrated upon them. It was also necessary to be aware of the influence of relatively extreme sites on the coefficients for any given pair of nutrients, although this problem was largely confined to the soil data.

Ten elements including five macro and five minor nutrients were estimated in the main photosynthetic component of the plant and the means and standard deviations computed. These elements accounted for between 2·5% (*Calluna vulgaris*) and 11% (*Mercurialis perennis*) of the dry matter content. Unusual means levels were rare but *Betula* was outstanding for zinc (235 μg g^{-1}) and *Juncus effusus* for sodium (0·29%). In spite of the nationwide coverage of sites, the coefficients of variation were less than 100%, except for sodium.

The correlation matrices revealed that some plants, notably *Deschampsia caespitosa* and *Pteridium aquilinum,* displayed a greater number of significant coefficients than others, but there was no consistent pattern in terms of species type or habitat. Six elements (N, P, K, Fe, Cu, Zn) accounted for most of the coefficients whose significance (at $p<0·05$) was not in doubt due to instability, and implied that, for these elements at least, a 'balance' was required for healthy growth of native species in their habitats. Significant negative correlations were rare. The existence of significant nutrient inter-relationships within the plant strengthens the view held by several workers that plant nutrient values are to be regarded as integrating the influence of a number of chemical and other parameters.

A principle component analysis showed how far the variability of the data could be attributed to particular elements. The first component accounted for about a quarter of the variability for most species, although it could not always be labelled in terms of just one or two elements. However, nitrogen was prominent for many species. Graphical projection of the component scores for individual elements within a species sometimes revealed a group whose contributions to the ecological status of the plant could be interpreted as fairly similar. The groupings revealed by *Pteridium aquilinum* in Figure 34 illustrate this point, but their elemental composition varied between species.

H.M. Grimshaw

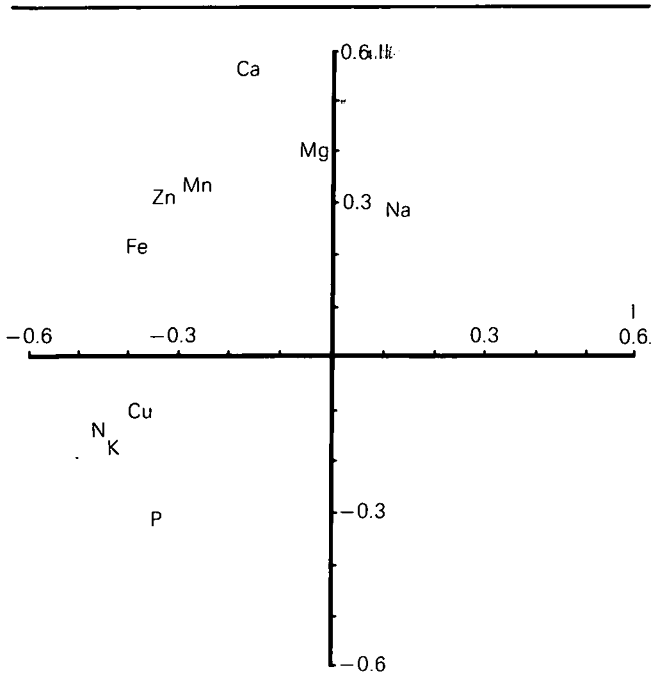

Figure 34 Pteridium aquilinum *(ultimate pinnules): projection of scores for components I and II revealing tentative groups of elements contributing similarly to the 'ecological' status of this species.*

Long-term nutrient status of soils

In assessing the nutrient status of soils, ecologists have generally followed the practice of agricultural chemists in using chemical extractants such as ammonium acetate or acetic acid which extract the exchangeable or soluble nutrients. Although these methods provide useful information about the readily available nutrient content of the soil, they are of less value in assessing the ultimately available or 'reserve' nutrient status. In this respect, soil totals are also of limited value since they include the structural components. Clearly, in the study of many ecological processes where long-term availability is of importance, there is a need for a method to measure the long-term nutrient availability.

Mineralogical and biological assay procedures were considered, but it was decided to concentrate on chemical extraction procedures because they are less time consuming and are also simpler to use. Tests already carried out demonstrate how difficult it is to obtain a single procedure which is suitable for all elements of interest, but the use of strong acid mixtures appears to be hopeful. Already one method has been used to examine soil samples in connection with the project on birch growth in upland situations (Project 90) and these reserves in the lower soil horizons appear to make a significant contribution to plant growth.

Parallel experiments are also being carried out on exhaustive cropping of selected soil samples. The soils from these experiments are being examined at regular intervals to compare the efficiencies of the chemical extractants with nutrient uptake and plant response.

A.P. Rowland and S.E. Allen

Analytical evaluation

(1) *Water preservation*

When compared with other ecological materials, water samples are relatively homogeneous, although, once removed from their environment, they become extremely labile. Therefore, preservation techniques are required to prevent deterioration of the sample.

Methods of preservation vary according to the analyses required, the levels of the constituents present and the time lapse between sampling and analysis. Over a period of years, evaluation of the problems of water preservation have been continually assessed, taking into account types of sample containers, suitability of chemical preservatives, storage at reduced temperatures and the ultimate effect of subsequent preservation techniques on analytical procedures.

The comparison of the common methods of preservation in relation to the present analytical techniques used in the two chemical laboratories has been investigated. These preservation methods are summarised in four general categories:

(a) storage at reduced temperature e.g. 0°C, −20°C

(b) addition of ametabolic poison to inhibit biodegradation e.g. mercuric chloride
(c) organic preservatives e.g. formalin
(d) acidification to prevent precipitation and absorption e.g. sulphuric acid.

Reduction of sample temperature to just above 0°C was generally the most acceptable method for the short term storage of the common nutrients, although freezing is satisfactory in the long term provided silicon and some heavy metals are not required.

Clearly, no single preservation technique is satisfactory for all components of interest, and for certain components, early, or even immediate, analysis is desirable. Constituents of particular concern include phosphorus and nitrogen fractions which are subject to change through microbial activity. Currently an improved code of practice to meet current requirements is being prepared for nutrients and pollutants in natural waters.

(2) *Recovery of iron and aluminium from acid digest solutions*

The difficulty of obtaining quantitative recovery of iron when using mixed and digestion procedures for bringing plant material into solution has already been demonstrated. It has now been observed that similar low recoveries of iron and also aluminium are obtained when using the sulphuric acid-hydrogen peroxide digestion mixture. In view of the advantages in using this digestion procedure to obtain a single solution, suitable for all nutrient estimations, ways were sought to avoid this problem. Tests were carried out covering different digestion conditions, and it was found that the introduction of an aqueous boiling stage immediately after the digestion proper was sufficient to give full recovery of these elements. The modified procedure can be used for samples containing up to 0·5% of iron and up to 0·3% aluminium.

(3) *Methyl mercury*

Following requests from members of the Animal Function team, there was a need in the Monks Wood Chemical Laboratory for a routine analytical technique for the determination of methyl mercury in vertebrate tissue. The method adopted was based on the Westöö technique perfected at Chelsea College by Dr K.R. Bull, one of the team members.

The tissues are homogenised in water, treated with hydrobromic acid and extracted into toluene. The extract is 'cleaned up' by partitioning with 1% cysteine acetate which selectively removes the methyl mercury. The pH of the cysteine phase is then adjusted to allow the methyl mercury to be transferred to fresh toluene. The final organic extract is analysed using gas liquid chromatography equipped with an electron capture detector at 200°C, and using a 1 M 5% Carbowax column at an operating temperature of 140°C. Trial tests carried out on this technique have given 100% recovery at the 1, 5 and 10 ppm level.

(4) *Toxic metals*

In conjunction with projects centred upon the Continuous Flow System at Monks Wood, a powerful atomic absorption spectrophotometer with background correction facilities and flameless atomiser has been purchased. This equipment enables the analysis of toxic metals such as lead and cadmium to be carried out at the ng g^{-1} level or lower. Such sensitivity is essential for measuring metal concentrations in minute biological specimens and samples of naturally occurring waters. In order to push the sensitivity to its maximum, tests have been performed to work out the optimum drying, ashing temperature and atomisation conditions. Procedures for the initial treatment of the samples have received special attention, partly because of the small available weights of aquatic invertebrates and mollusc shells. In the latter case, the high concentrations of calcium in solution have posed severe interference problems. It has been found that the use of citric acid to dissolve these samples reduces calcium interferences, avoids the depression effects of inorganic acids, and also increases absolute sensitivity.

(5) *Sulphur*

The monitoring of sites for atmospheric particulate sulphur (Project 453) has involved the trapping of the aerosol on filter paper discs. In view of the large number of discs produced, it was desirable to have a rapid analytical method available for processing these samples. For this reason the feasibility of using X-ray fluorescence spectrometry rather than the more laborious wet chemical techniques was first explored.

In fact, the X-ray spectrometer proved to be particularly suitable for accepting filter paper discs. It was also found that the sulphur K α lines were sufficiently intense, and could easily be resolved. Correlations were obtained between the X-ray intensities and the sulphur contents (obtained by separate wet analyses) of calibration samples for:

(1) the front of the disc alone
(2) the ratio between front and back of the disc
(3) the sum of the front and back of the disc.

The best correlation was obtained in the third case and a suitable procedure was developed on this basis. However, it proved to be necessary to obtain frequent blank results due to the variation between filter paper batches. The procedure enables as many as 200 discs to be processed each day.

(6) *Fluorine*

As mentioned in the report on the Merlewood Chemical Laboratory, there has been a marked increase in the number of samples being analysed for fluorine. This work is being done mainly in support of the studies into the effect of fluorine fall-out around an aluminium smelter (Projects 160, 524, 525). In addition, a small number of fluorine analyses have been carried out in samples collected in the vicinity of brickworks.

Material examined has ranged from mosses and lichens to soils, shell fish, animal bones and tissue, bird feathers and eggs. Such a wide range of sample material has resulted in development work into the suitability of standard techniques. The fusion technique followed by fluorine determination using a specific ion electrode was evaluated in detail, and resulted in analytical modifications. It was shown that it is necessary to use fresh or freeze-dried material rather than air or oven-dried sample material to obtain maximum recovery in all cases. Some of the most serious difficulties were encountered in the treatment of the animal materials but these have been largely overcome. Particular attention was also paid to the need for a rapid technique to process large numbers of samples and the technique was modified to make this possible.

S.E. Allen, K.R. Bull, M.C. French, J.A. Parkinson, J.D. Roberts and A.P. Rowland

Engineering construction

(1) *Physiological stimulation apparatus*

A method of electrically stimulating the hormone release centres of birds and the marking of the area stimulated was required for a project on the physiological effect of pollutants. The engineering section designed and built a stimulation unit for this purpose. The unit, which can be pre-set, generates a constant current bipolar pulse train at a frequency of 100 Hz. A timing system and means of monitoring electrode current is included in the unit, together with a separate constant current source for producing marking lesions in the stimulated area. Positioning of the stimulation electrode is recorded using an X-ray technique. Some of the hardware required for this technique was also assembled by the section.

(2) *Underwater monitoring equipment*

Project 381 is concerned with the dynamics of plankton populations in Loch Leven which involves the regular monitoring of the phytoplankton and zooplankton for spatial distribution. Plankton growth is largely related to nutrients, temperature, oxygen and sunlight. These characteristics need to be measured at the same time. Commercially available instruments which can measure individual parameters are available but no system is available for combined recording. This makes the logging of data difficult, and causes handling problems on board a small boat. It is necessary to take measurements to a depth of 25 metres which present difficulties when using several lengths of non-standard cable. An integrated measuring system was therefore desirable and this was developed and constructed in 1977. The electronics, which control the multi-purpose probe, are contained in a watertight box with a transparent plastic lid that protects the visible panel meter, but allows the operator to take readings. A single rechargeable power pack powers all equipment. At present, temperature, conductivity, light ratio, oxygen and water depth can be sequentially displayed on the panel meter. All parameters can be monitored simultaneously on a portable multiple recorder.

The underwater probe incorporates the temperature, conductivity and light ratio transducers but separate oxygen and depth transducers are used. This is because inexpensive commercial units with compatible cables are available commercially. It was found that the standard oxygen sensing probe needed an impellor attachment to draw water over the oxygen membrane. This improves response and accuracy. Through the use of integrated circuits and miniature components it has been possible to keep the equipment compact. It has now received heavy use in the field and has proved to be rugged and reliable.

D.G. Benham, G.H. Owen, C.R. Rafarel and V.W. Snapes

SUBDIVISION OF DATA AND INFORMATION

Introduction

The work of the Institute continues to develop in quantitative and mathematical ways and this has put considerable pressure on the biometric and computing service of the Subdivision. In order to reduce this pressure as much as possible, the policy of the Subdivision has been to extend the expertise in biometrics and modelling into Subdivisions, by personal contact and training and more formally by training courses at various stations and two central courses held at the Monks Wood Experimental Station. An initial course on BASIC programming attracted a wide range of applicants and an Experimental Design course proved extremely useful. It is hoped to extend these courses in the near future, since there is unlikely to be sufficient increase in staff in the forseeable future to satisfy the many demands made on the quantitative scientists in this Subdivision.

Biometrics

The mathematical and statistical problems now being encountered in ITE research have involved the biometrics staff in providing advice on a wide variety of topics. These include the design and analysis of planned experiments, the design of sample surveys of plant and animal populations, the use of a wide range of multivariate techniques, the analysis of animal behavioural data, examination of spatial pattern, estimation problems in studies of the chemical analysis of precipitation and other analyses of pollutant experiments. This advice has been given in Britain, but the Subdivision has also had responsibility for providing biometrical advice to the UNEP/MAB Integrated Project in arid lands in Kenya including the counting of animals by air survey and the experimental design of camel and goat grazing trials. Advice to contracts of this sort are an important feature of the year's work and the Subdivision has been responsible for biometric and computing advice to other major contracts, including the British Trust for Ornithology, Common Bird Census and the Wildfowl Trust. Some important biometric research has been necessary in order to estimate the annual fluctuations in bird populations from the Common Bird Census.

M.D. Mountford

Computing

A visiting group on NERC computing facilities was established in 1977 and ITE presented its policy statement to this group in September. A further development during the year was the advancement of the case for a replacement computer system for the eight year old PDP 8/I at Merlewood. A review of the computer market was undertaken and recommendations made to the Management Group for a new system.

Considerable exploration work took place at Monks Wood over the use of the IGS data base system, G-EXEC, which runs on the Rutherford laboratory IBM 360/195. It is planned to use this system for manipulating the Biological Records Centre's data banks. Increased demand on the PDP 11/10 at Bangor has led to the introduction of multi-user BASIC, additional terminals and memory and to more intensive use of the DEC 10 computer of the University College of North Wales, Bangor.

Support on computing by the Subdivision has not been confined to scientific work, and members of the biometric staff in Cambridge have given support to the ITE Finance Section by providing a fully computerised costing system, saving considerable staff effort.

D. K. Lindley

Mathematical modelling

There have been many developments in mathematical modelling in the year under discussion. This modelling has not been confined to biological topics and considerable work has been put into the development of a computer model of the Natural Environment Research Council written in BASIC and running on the DEC 10 computer at the University College of North Wales, Bangor. The model manipulates an NERC employee population comprising all personnel on incremental salary scales and is segregated into nine groups, e.g. science, administration etc. The model anticipates wastage, recruitment, promotion and deaths and as presently programmed is designed to estimate the annual salary bill drift due to the existence of incremental pay scales. Model behaviour, as one might expect, is dominated by the science group, which comprises about 1,500 employees. The model, which was designed for NERC's administration, can allow predictions of the salary drift over a five-year period and to simulate this period consumes about ten minutes of core time on the DEC 10 computer.

The major input of effort has been in modelling animal and plant populations and ecosystems. Examples of the models developed are

(i) the relationship of a cinnabar moth to its food plant;

(ii) the structure of an ant colony;

(iii) the movement of camels and sheep in the Hedad area of northern Kenya; and

(iv) various models of the grazing process.

There have been major developments in the use of Markov chain models for describing the movement of sheep in free range grazing systems. A further advance in the Markov modelling area has been to examine change in upland vegetation in relation to project 398.

C. Milner

Data banks

Biological Records Centre data processing

Since 1972, the BRC distribution maps have been produced using punched cards, either generated by computer, or punched manually, to drive a modified IBM electric typewriter. This process was slow and labour-intensive, and the equipment was becoming increasingly unreliable. In 1976, the Experimental Cartography Unit was asked to develop a replacement mapping system, using their Laser-scan HRD2 high-resolution plotter. Data for over 100 species of bryophytes have been prepared, and will form the first atlas to be produced by this system.

Following the close-down of the ATLAS computer at the CAD Centre, Cambridge, a new host computer was sought for the BRC data bank. The data are now being incorporated in the G-EXEC data management system (developed by IGS) on the dual IBM 360/195 configuration at the SRC's Rutherford Laboratory. Use of this system will permit much greater flexibility in the types of output available from the data bank, and in the long term should enable us to make more use of the accumulated data for research than has hitherto been possible.

In addition, staff have been recruited to begin to develop the general environmental data service, which is, of course, closely linked to the BRC. The general use of data banks in the Institute continues to expand and many specialist programmes are available for handling this type of operation. The major developments in data banking have been at Bangor, Merlewood and Monks Wood.

Miss D. W. Scott

Library

Library facilities and services are provided at all locations of the Institute, while senior library staff, with remits to organise services which require central control, are based at Merlewood, Monks Wood and Bush. During the year since the contract for library services with the Nature Conservancy Council was terminated, maximum effort has been devoted to establishing efficient procedures in the acquisition and organisation of journals (co-ordinated at Monks Wood) and books (co-ordinated at Bush).

A 'Current contents of journals received' is distributed weekly to all locations, and a 'List of periodicals held in the libraries of the Institute of Terrestrial Ecology' has been published. A union catalogue of books is maintained at Bush, and accessions bulletins are produced monthly. Compilation of a thesaurus of terms used in library catalogues is nearing completion. Data have been gathered during the latter part of the year which may prove helpful in determining an optimum retention and storage policy for journals, given the present high cost of binding and the limits on available shelf space. Lists of publications by members of ITE staff are produced bi-annually, from records which are stored in machine-readable form, and are distributed to libraries of organisations with similar research interests.

J. Beckett

Publications and public relations

The Institute has a duty, as a component body of NERC, to provide ecological data and advice. This is done mostly through scientific papers in established journals, and in contract reports to customers for our research. To complement this work a range of publications for a wider readership has been developed over the last three years (see Section VI, Publications). Some are highly technical reports with a limited but professional circulation. Others are ecological reviews such as those on red deer and the native pinewoods of Scotland, or survey reports as that done for the Maplin Sands and coasts of Suffolk, Essex and north Kent. The Biological Records Centre continues to produce distribution atlases which serve as a model for the rest of Europe and even further afield. While all these publications have an educational content, one was produced specifically for schools and colleges. This was *A beginner's guide to freshwater algae.* Thousands of copies have been sold, with the result that the third impression will be on sale within a year of its publication. The Institute will continue to increase the range and number of its publications in the coming year, as these are the key to good public relations.

M.J. Woodman

Special reports

(1) The analysis of maps of point patterns using distance methods

The spatial distribution of individuals in a population can sometimes be conventiently studied using distance techniques. These methods involve the measurement of distances within the population. Existing preliminary tests of randomness of the distribution of the individuals assume samples from large populations. This assumption avoids problems arising because of boundary effects and lack of statistical independence of the distances. However, the assumption is unrealistic when a complete map of individuals is available and some test procedures have been shown to be inapplicable.

An alternative approach based on computer simulation has been devised to overcome these problems. The method was developed for detecting local regularity in the spacing of nests of various species of duck. Two test statistics–the squared coefficient of variation of nearest neighbour distance squared, and the ratio of the geometric mean to the arithmetic mean of the squared distances–are particularly appropriate to testing for local regularity. Further work has shown that the statistics are effective at detecting this type of departure from randomness, and that, unlike some others, the effectiveness is not reduced by the global features of the pattern.

Approximations to the test, not requiring computer simulation, which would give satisfactory results in some situations have also been developed. Details of a computer program to carry out the test are available.

P. Rothery

(2) The effect of wind on lakes

The ultimate fate of dissolved and solid matter introduced into rivers and the internal chemical balances of lakes, particularly shallow ones, may depend on the transfer rates to and from lake sediments and the overlying water. The hydraulic conditions in a lake resulting from the interaction of wind and lake geometry determine whether the sediment is a sink or merely a temporary store for material.

The hydraulic conditions in other than the layer affected by wave action can be defined by the current speed and direction at any depth. These can be measured by tracking the path of large drogues using a photographic technique. Such drogues are illustrated in Plate 19 and consist of a large aluminium vane, a surface float and a target above the water line, the length of line between vane and float being variable. To allow for the effect of wind and surface current on the float target, a technique has been developed for converting the velocity indicated by the drogue to true velocity.

In order to use the drogues efficiently, each drogue run should be a test of some hypothesis about the pattern of water circulation generated by the wind. The main feature of such a circulation is the requirement of the continuity law–unless the quantities of water entering and leaving any portion of the lake balance, the lake would move to a new position. A mathematical model has been developed which indicates the way water velocity changes with wind speed and depth as the continuity requirement is met in different ways. As well as providing a logic for the planning and interpretation of on-lake observations, the model can be used to classify the hydraulic regime of lakes in terms of wind speed and lake geometry.

I.R. Smith and A.A. Lyle

(3) UNEP/MAB integrated project on arid lands

This project in which the Subdivision has taken part advising on biometrics and mathematical modelling is a component of the UNEP strategy in relation to arid lands and grazing land ecosystems and is closely related to the UNEP preparations to tackle the problems of desertification. IPAL has been established as a project with the stated intention of extending its operations throughout the arid zone but initially the project has been established and is operational in Kenya. It was to the Kenya project that the initial year's efforts were confined.

In order to assist the long term and immediate objectives of the IPAL project, it was necessary to analyse the current projects and sub-projects to examine their suitability in biometrical and experimental design terms; this has been done and recommendations made. In addition, however, it was felt useful to develop three mathematical models which would not attempt to describe the study area fully, but highlight major features of relevance to the implementing of ecologically sound strategies within this particular arid region. The three models developed aim to

(i) describe the movement of the nomadic tribes of the area and their stock over the study area in response to rainfall, water availability and the constraints of transport;

(ii) provide estimates of potential off-take of camels and sheep for sale in order to decrease the dependence of the nomadic tribes on livestock and to increase their financial viability; and

(iii) describe the vegetation of the area and relate it to environmental factors.

This project continues and the final report will be produced in 1978.

C. Milner

Projects

listed by subdivisions as at 8 February 1978

KEY

Station code

1 Monks Wood Experimental Station
2 Merlewood Research Station
3 Colney Research Station, Norwich
4 Furzebrook Research Station
5 Edinburgh (Bush)
6 Edinburgh (Hope Terrace)
7 Banchory (Brathens)
8 Banchory (Blackhall)
9 Bangor Research Station
10 Cambridge
11 NERC
12 Cambridge CCAP
13 c/o UIV, Oxford

Project status

* Ph.D. student supervised by ITE
† Paid for by external contract
‡ Supported by Nature Conservancy Council
§ Supported by Department of Environment

VERTEBRATE ECOLOGY SUBDIVISION

			code
54	Red deer ecology on Rhum	V.P.W. Lowe	2
59	Taxonomy of the red squirrel	V.P.W. Lowe	2
67	Prey selection in redshank	J.D. Goss-Custard	4
68	Dispersion in waders	J.D. Goss-Custard	4
104	Distribution and segregation of red deer	B.W. Staines	7
106	Red deer food studies	B.W. Staines	7
109	Annual cycles in Scottish red deer	B. Mitchell	7
111	Population dynamics of red deer at Glen Feshie	B. Mitchell	7
116	Freshwater survey of Shetland	P.S. Maitland	6
117‡	Freshwater synoptic survey	P.S. Maitland	6
123	Zoobenthos at Loch Leven	P.S. Maitland	6
124	Fish distribution and conservation	P.S. Maitland	6
134	Shelducks at Aberlady Bay	D. Jenkins	7
136	Hen harrier study in Orkney	N. Picozzi	8
137‡	Sparrowhawk ecology	I. Newton	6
138‡	Puffin research	M.P. Harris	7
159	Upland bird project	D.C. Seel	9
209‡	Amphibians and reptiles survey	H. Arnold	1
210‡	Mammal distribution survey	H. Arnold	1
291‡	Population ecology of bats	R.E. Stebbings	1
292‡	Specialist advice on bats	R.E. Stebbings	1
322	Dispersal of otters	D. Jenkins	7
325‡	Carrion-feeding birds in Wales	I. Newton	6
363	Dispersion of field voles in Scotland	N. Charles	6
386	Behaviour and dispersion of badgers	H. Kruuk	7
391	British mammals — the red fox	V.P.W. Lowe	2
420	Intraspecific variation in the Polar bear	V.P.W. Lowe	2
430	Dynamics of a mute swan population	D. Jenkins	7
439	Red deer on the Isle of Scarba	B. Mitchell	7
441	Oystercatcher and shellfish interaction	J.D. Goss-Custard	4
442	Ecology of capercaillie	R. Moss	8
460	Interaction of gulls and puffins	M.P. Harris	7
461‡	Puffins and pollutants	M.P. Harris	7
479	Red deer in production forests	B.W. Staines	7
498*	Wildcat studies	L.C. Corbett	7
499	Classification of Cervidae	V.P.W. Lowe	2
524	Fluoride in predatory mammals	K.C. Walton	9
525	Fluoride in predatory birds	D.C. Seel	9
528	Red deer in woodland habitats	B. Mitchell	7
543	Population ecology of the red squirrel	V.P.W. Lowe	2
545‡	Study of Lochs Morar and Shiel	P.S. Maitland	6
546†	Study of Lochs Lomond, Awe and Ness	P.S. Maitland	6
555	Ecology of Craigroyston Woods	N. Charles	6
560	Red data book on vertebrates	H.R. Arnold	1

INVERTEBRATE ECOLOGY SUBDIVISION

			code
65	Invertebrate population studies	S. McGrorty	4
66	Variation in strandlines	S. McGrorty	4
161	Littoral fauna of Llyn Peris	A. Buse	9
162	Freshwater gastropods in North Wales	A. Buse	9
185	Effect of urbanisation	B.N.K. Davis	1
188	Woodland invertebrates	R.C. Welch	1
201	The white admiral butterfly	E. Pollard	1

202	The roman snail	E. Pollard	1
204‡	Assessing butterfly abundance	E. Pollard	1
205	Invertebrates in hawthorn hedges	E. Pollard	1
211‡	Lepidoptera distribution maps scheme	J. Heath	1
212‡	Odonata distribution maps scheme	J. Heath	1
213	Orthoptera distribution maps scheme	J. Heath	1
223	European invertebrate survey	J. Heath	1
229	Ecology/taxonomy of Spanish Hemiptera	M.G. Morris	4
230	Cutting experiment (Coleoptera)	M.G. Morris	4
231	Barton Hills grazing experiment (Coleoptera)	M.G. Morris	4
232	Butterfly studies at Porton Range	M.G. Morris	4
233	Cutting experiment (Hemiptera)	M.G. Morris	4
234	Grassland management by fire	M.G. Morris	4
236	Invertebrate populations in grass sward	E. Duffey	1
241	The fauna of box	L.K. Ward	1
243	Scrub succession at Aston Rowant NNR	L.K. Ward	1
255	Ecology of *Myrmica* species	G.W. Elmes	4
256	Protein electrophoresis	B. Pearson	4
261	Caste bias in *Myrmica* eggs	B. Pearson	4
262	Digestive enzymes	A. Abbott	4
270	Distributional studies on spiders	P. Merrett	4
273	Productivity of *S. Magnus*	N.R. Webb	4
274	Physiology of soil fauna	N.R. Webb	4
277	Moth collection by light trap	N.R. Webb	4
278	Spider populations on heather	P. Merrett	4
295	Survey of juniper in N. England	L.K. Ward	1
296	Scrub management at Castor Hanglands	L.K. Ward	1
309‡	Phytophagous insect data bank	L.K. Ward	1
345	Spiders in East Anglian fens	E. Duffey	1
400	The large blue butterfly	J.A. Thomas	4
403	The black hairstreak butterfly	J.A. Thomas	4
404	The brown hairstreak butterfly	J.A. Thomas	4
405‡	Fauna of mature timber habitat	P.T. Harding	1
406	Non-marine Isopoda	P.T. Harding	1
407	British Staphylinidae (Coleoptera)	R.C. Welch	1
414	Hartland Moor spider survey	P. Merrett	4
423*	Predator/prey relations on heathland	A.M. Nicholson	4
450	Ecology of pseudo-scorpions	P.E. Jones	1
469‡	Scottish invertebrate survey	E. Duffey	1
470	Upland invertebrates	A. Buse	9
474	Breckland open ground fauna	E. Duffey	1
500	Spiders on Hartland Moor NNR	P. Merrett	4
509*	Wood white butterfly population ecology	M. Warren	4
519	*Myrmica sabuleti* and *M.scabrinodis*	G.W. Elmes	4
527	Long-term changes in zooplankton	D.G. George	6
547	Study of the genus *Micropteryx*	J. Heath	1
557	Other distribution maps schemes	J. Heath	1
568	Subcortical fauna in oak	M.G. Yates	1

ANIMAL FUNCTION SUBDIVISION

			code
178‡	Causes of seabird incidents	R.K. Murton	1
179‡	Heavy metals in waders	P. Ward	1
181‡	Birds of prey and pollution	A.A. Bell	1
182‡	Aquatic herbicides	H.R.A. Scorgie	1
183	Frogs and pollution	A.S. Cooke	1

193	Stone curlew and lapwing	N.J. Westwood	1
199	Avian reproduction and pollutants	R.K. Murton	1
289	Pollutants in freshwater organisms	F. Moriarty	1
413	Breeding biology of the cuckoo	I. Wyllie	1
436*	Social behaviour of thrushes	A. Tye	1
444	Endocrine lesions in birds	S. Dobson	1
455	Heavy metals in avian species	D. Osborn	1
456	Heavy metals and metabolism	D. Osborn	1
459	Shell formation and pollution	A.S. Cooke	1
473	Metal residues in birds of prey	A.A. Bell	1
475	Pollution and starling nutrition	P. Ward	1

GROUSE AND MOORLAND ECOLOGY

			code
129	Red grouse and ptarmigan populations	A. Watson	8
130	Management of grouse and moorlands	A. Watson	8
131	Golden plover populations	A. Watson	8
132	Monitoring in the Cairngorms	A. Watson	8
510*	Caecal threadworm and red grouse	G.R. Wilson	8

HEATHLAND SOCIAL INSECTS

			code
252	Hartland Moor NNR survey	M.V. Brian	4
253	*Tetramorium caespitum* populations	M.V. Brian	4
258	Degree of control by queen ants	M.V. Brian	4
259	Larvae and worker communication	M.V. Brian	4
263	Worker ant activity	M.V. Brian	4
370	Inter-species competition in ants	M.V. Brian	4
371	Male production in *Myrmica*	M.V. Brian	4

PLANT BIOLOGY SUBDIVISION

			code
2	Meteorological factors in classification	E.J. White	2
73	*Puccinellia maritima*	A.J. Gray	4
81	Plant production, grazing and tree-line ecology	G.R. Miller	7
82	Seed produced by montane plants	G.R. Miller	7
100	Trampling effects on montane grasslands	N.G. Bayfield	7
102	Mountain vegetation populations	N.G. Bayfield	7
158	Community processes (Physiology)	D.F. Perkins	9
160	Fluorine pollution studies	D.F. Perkins	9
208‡	Botanical data bank	F.H. Perring	1
215	Biological information network	F.H. Perring	1
246	Physical environment, forest structure	E.D. Ford	5
247	Physiology of flowering	K.A. Longman	5
248†	Physiology of root initiation	K.A. Longman	5
249	Morpho-physiological differences	M.G.R. Cannell	5
265	Regeneration on lowland heaths	S.B. Chapman	4
266	Root dynamics of *Calluna vulgaris*	S.B. Chapman	4
269	Autecology of *Gentiana pneumonanthe*	S.B. Chapman	4
329	Response of Scots pine	E.J. White	2
346	Genecology of grass species	A.J. Gray	4
359	Fibre yield of poplar coppice	M.G.R. Cannell	5
410	Tundra plants (bryophytes)	N.J. Collins	5
411	Taxonomy of bryophytes	S.W. Greene	5
412	Genecology of *Racomitrium*	B.G. Bell	5
437†	Further ecological studies on the Wash	A.J. Gray	4

451	Analysis of S. Georgian graminoids	T.V. Callaghan	2
493	Physiological life cycle of mosses	N.J. Collins	5
506	Viruses of trees	J.I. Cooper	11
507	Ecologists' flora	E.M. Field	5
536	Autecology of *Orchis militaris L.*	L. Farrell	1
552	Carbon as a renewable energy resource	T.V. Callaghan	2

PLANT COMMUNITY ECOLOGY SUBDIVISION

			code
1	Semi-natural woodland classification	R.G.H. Bunce	2
6	Scottish native pinewood survey	R.G.H. Bunce	2
9	Monitoring at Stonechest	J.M. Sykes	2
13	NW England commercial forest survey	M.W. Shaw	2
14	Tree girth changes in 5 NNR'S	A.D. Horrill	2
48‡	Asulam effects on three upland pastures	A.D. Horrill	2
50	Defoliation of oak seedlings	M.W. Shaw	2
55	Establishment of trees at Moor House	A.H.F. Brown	2
70	Management of sand dunes in East Anglia	L.A. Boorman	3
72	Salt marsh management	D.S. Ranwell	3
74	Sand dune stabilization	D.S. Ranwell	3
75	Control of *Spartina*	D.G. Hewett	9
76	Mature shingle beach vegetation, Sussex	D.G. Hewett	9
77	Cliff vegetation methods	D.G. Hewett	9
78	Management of sand dunes in Wales	D.G. Hewett	9
92	Grazing intensities causing change	D. Welch	7
93	Assessing animal usage in N.E. Scotland	D. Welch	7
95	Importance of dung for botany change	D. Welch	7
121	Phytoplankton productivity	M.E. Bindloss	6
163	Ordination and classification methods	M.O. Hill	9
165	N. Wales bryophyte recording	M.O. Hill	9
187	Vegetation history from opals in soils	M.D. Hooper	1
191	Forest management studies	A. Millar	2
225	Population studies on orchids	T.C.E. Wells	1
227	Sheep grazing on chalk grass flora	T.C.E. Wells	1
228	Effect of cutting on chalk grassland	T.C.E. Wells	1
242‡	Re-establishment of chalk grassland	T.C.E. Wells	1
318	Peat hydrology	A.J.P. Gore	1
340‡	Survey of Scottish coasts	D.S. Ranwell	3
360†	Trees on industrial spoil	J.E. Good	9
362	Ecological survey of Cumbria	R.G.H. Bunce	2
364	Early growth of trees	D.R. Helliwell	2
367	The Gisburn experiment	A.H.F. Brown	2
369§	Sulphur content of tree leaves and bark	J.W. Kinnaird	7
374	Sand dune ecology in East Anglia	L.A. Boorman	3
377	Environmental perception studies	J. Sheail	1
380§	Monitoring of atmospheric SO2	I.A. Nicholson	7
381	Plankton populations in Loch Leven	D.G. George	6
383	Shading effect on *Primula vulgaris*	D.R. Helliwell	2
388	Rusland Moss NNR survey	J.M. Sykes	2
389‡	Management effect in lowland coppices	A.H.F. Brown	2
392§	Amenity grass cultivar trials	A.J.P. Gore	1
417	Silvicultural systems	D.R. Helliwell	2
424	Ecological survey of Britain	R.G.H. Bunce	2
426	Modelling of sulphur pollution	I.A. Nicholson	7
428†	Vegetation management in country parks	T.C.E. Wells	1
435	Ecology of *Sorbus aucuparia*	C.J. Barr	2

452§	Foliar leaching and acid rain	J.W. Kinnaird	7
454‡	NCC monitoring of woodlands	J.M. Sykes	2
463	Age class of amenity trees	J.E. Good	9
464	Populn, competn and genetics of grasses	M.J. Liddle	1
465‡	Stanford PTA	M.D. Hooper	1
466‡	Ecology of railway land	J.M. Way	1
467	Roadside experiments	J.M. Way	1
483‡	Scottish deciduous woodlands	R.G.H. Bunce	2
495†	Soil acidification	A.J.P. Gore	1
497‡	Macrophyte studies	A.E. Bailey-Watts	6
539‡	Phragmites 'dieback' in Norfolk Broads	L.A. Boorman	3
549‡	Monitoring in native pinewoods	J.M. Sykes	2

SOIL SCIENCE SUBDIVISION			*code*
4	Soil classification methods	P.J.A. Howard	2
8	Radiocarbon analysis of wood humus	A.F. Harrison	2
17	Meathop Wood IBP study	J.E. Satchell	2
21	Decomposition in Meathop Wood	O.W. Heal	2
22	Fungal decomposition of leaf litter	J.C. Frankland	2
23	Soil temperature in Meathop Wood	K.L. Bocock	2
27	Fungal biomass of Meathop litter and soil	J.C. Frankland	2
29	Phosphorus circulation	A.F. Harrison	2
30	Biomass and decay of *Mycena* in Meathop Wood	J.C. Frankland	2
32	Moor House IBP study	O.W. Heal	2
33	Vegetation decomposition at Moor House	O.W. Heal	2
40	Woodland organic matter decomposition	P.J.A. Howard	2
45	Tundra biome IBP study	O.W. Heal	2
52	Biological studies of *Glomeris*	K.L. Bocock	2
61	Variation in growth of birch and sycamore	A.F. Harrison	2
87	Vegetation potential of upland sites	J. Miles	7
88	Plant establishment in shrubs	J. Miles	7
89	*Calluna-Molinia-Trichophorum* management	J. Miles	7
90	Birch on moorland soil and vegetation	J. Miles	7
140	Weathering and soil formation, Whin Sill	M. Hornung	9
148	Soil erosion on Farne Islands	M. Hornung	9
153	Mineralogical methods	A. Hatton	9
154	Field recording of profile data	M. Hornung	9
245	Genetics of *Betula* nutrition	J. Pelham	5
358	Earthworm production in organic waste	J.E. Satchell	2
368‡	Afforestation effect on the uplands	M.O. Hill	9
384	Benthic microalgal populations	S.M. Coles	3
398	Upland land use	O.W. Heal	2
431	Soil change through afforestation	P.J.A. Howard	2
432	Effect of birch litter on earthworms	J.E. Satchell	2
438	Ecology of *Mycena galopus*	J.C. Frankland	2
471	Soils of Upper Teesdale	M. Hornung	9
521*	Mathematical modelling in Cumbria	I.D. Bishop	2
522§	Ecology of vegetation change in uplands	D.F. Ball	9
533	Podzolic soils	P.A. Stevens	9
534	National land characterisation	D.F. Ball	9
541	Marginal land in Cumbria	C.B. Benefield	2
553	Radionuclide contamination of ecosystems	K.L. Bocock	2
554	Cumbria land classes and soil types	J.K. Adamson	2
561	Soil fertility	M. Hornung	9

NORTH WALES ECOLOGY			*code*
168	Sheep population studies	R.E. Hughes	9
170	Arctic/alpine vegetation survey	R.E. Hughes	9
171‡	Bracken control with Asulam	R.E. Hughes	9
172	Vegetation change with grazing	R.E. Hughes	9
173	Past land use in N.W. Wales	R.E. Hughes	9
174	Snowdonia vegetation map	R.E. Hughes	9
175	Herpetological studies	R.E. Hughes	9

DATA AND INFORMATION SUBDIVISION			*code*
44	Information handling and retrieval	D.K. Lindley	2
47	Shetland modelling	C. Milner	9
118	Lake hydraulics	I.R. Smith	6
119	Physical limnology	I.R. Smith	6
216	Register of NNRs	G.L. Radford	9
217	Species recording	G.L. Radford	9
218‡	Event recording	G.L. Radford	9
219‡	Data processing for BTO	D.W. Scott	1
221‡	Data processing for Wildfowl Trust	D.W. Scott	1
302	Population growth and regulation	M.D. Mountford	10
303	Method of cluster analysis	M.D. Mountford	10
304	Estimation of quantiles	M.D. Mountford	10
306	Spatial process and application	P. Rothery	10
307	Index of eggshell thickness	P.H. Cryer	10
308	Data from multi-compartment systems	P.H. Cryer	10
310	Polluted watercourses survey	D.F. Spalding	10
311	Data definition and validation	D.F. Spalding	10
313	Seals research	M.D. Mountford	10
314	Wytham Wood survey	M.D. Mountford	10
365	Competition between grass species	H.E. Jones	2
375	Theoretical models of diet selection	P. Rothery	10
376	Statistical training	C. Milner	9
402	Biometrics advice to NERC	M.D. Mountford	10
421	Management information system development	D.I. Thomas	9
433	Data transmission network	D.F. Spalding	10
434	ITE computing services	C. Milner	9
457	Grazing models	C. Milner	9
458	Shetland publication	C. Milner	9
494	Computing facilities at Hope Terrace	I.R. Smith	6
496	Data processing services at Monks Wood	D.W. Scott	1
514	British birch publication	A.S. Gardiner	2
529	Biological data bank	D.W. Scott	1
530	Laser scan mapping system	D.W. Scott	1
531	Statistical & computing advice, Furzebrook	R.T. Clarke	4
532	Statistical research, Furzebrook	R.T. Clarke	4
548	Leaf-shape analysis of European birch	A.S. Gardiner	2

CHEMISTRY AND INSTRUMENTATION SUBDIVISION			*code*
62	National plant nutrient survey	H.M. Grimshaw	2
378	Chemical data bank	S.E. Allen	2
481	Sphagnum 'moss bag' monitoring	K.R. Bull	1
482	Chemistry of aquatic pollutants	K.R. Bull	1
484	Chemical technique development	J.A. Parkinson	2
485	Chemical support studies	M.C. French	1

486	Engineering development	G.H. Owen	9
487	Field logging systems	C.R. Rafarel	9
488	Data interface systems	D.G. Benham	2
489	Glasshouse and nursery maintenance	R.F. Ottley	5
490	Photographic development	C. Quarmby	2
491	Isotope development studies	S.E. Allen	2
512	National collection of birch	A.S. Gardiner	5
523*	New Forest soil characteristics	H. Whittaker	2

DIRECTORATE

			code
393	The swallowtail butterfly	J.P. Dempster	1
408§	Arboriculture: selection	F.T. Last	5
503	Development of systems analysis	J.N.R. Jeffers	2
504	Markov models	J.N.R. Jeffers	2
505	Ecology of Outer Hebrides	J.N.R. Jeffers	2
508	Botanical variation in elm	J.N.R. Jeffers	2
511	Landscaping at Swindon	F.T. Last	5
515†	Alternative energy sources	J.N.R. Jeffers	2
516	Forest management for energy	R.C. Steele	10
517	Primary productivity in woodlands	J.N.R. Jeffers	2
518†	UNESCO MAB information system	J.N.R. Jeffers	2
526†	Monitoring in Banff and Buchan	F.T. Last	5

CULTURE CENTRE FOR ALGAE AND PROTOZOA

			code
445	Marine flagellates taxonomy	J.H. Belcher	12
446	Freshwater flagellates taxonomy	D.J. Hibberd	12
447	Freshwater and marine amoebae	F.C. Page	12
448	Colourless flagellates taxonomy	E.M.F. Swale	12
449	Preservation of cultures	G. J. Morris	12

LIST OF PROJECT PROPOSALS FOR APPROVAL BY MANAGEMENT GROUP 8.2.78

537	Water relations and photosynthesis in mosses	N.J. Collins
540	Training in systems analysis	D.K. Lindley
542	(Sandwich student project)	D.S. Ranwell
551	Overseas liaison activities	J.E. Satchell
556	Estimation in acid rain	K.H. Lakhani
558*	Fauna/mycoflora relationships	K. Newell
559	Ecophysiology of the rabbit	D.T. Davies
562	Data processing services at Merlewood	D.K. Lindley
563	*Betula carpatica tortuosa*	A.S. Gardiner
564	British Hydracarina — mainly of mosses	N. Hamilton
565	Bibliography of Shetland	N. Hamilton
566	Islands: biogeographic analysis	C. Milner
567§	Polluted atmospheres and leaf surfaces	D. Fowler
569	*Heliantheum* fauna	B.N.K. Davis

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Publications

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