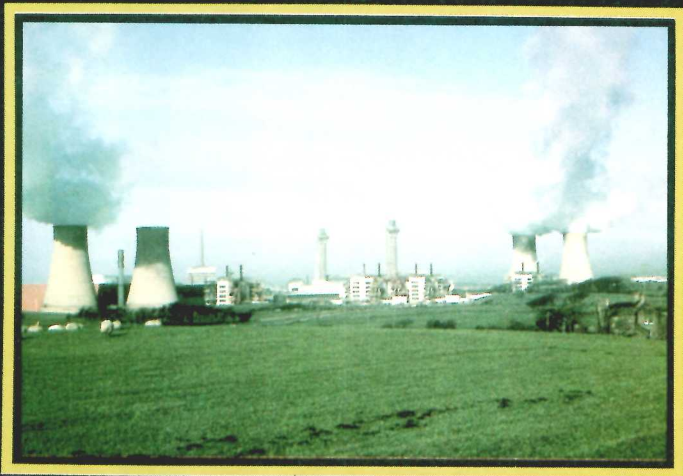
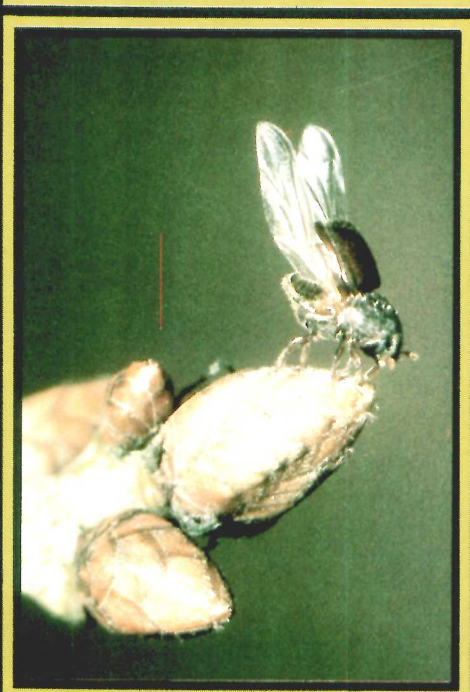
Natural Environment Research Council

Institute of Terrestrial Ecology





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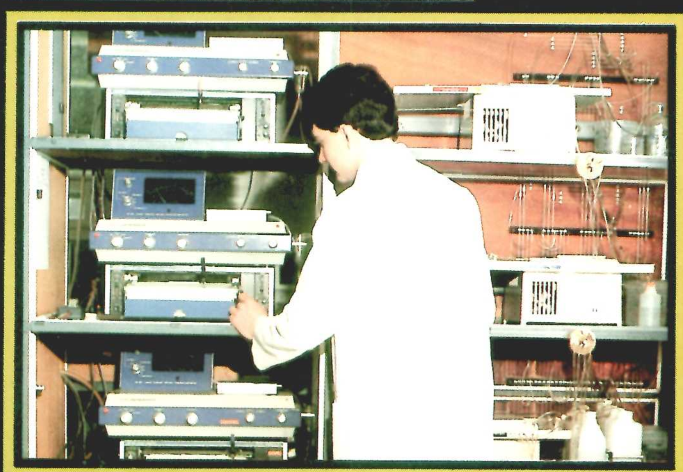

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Institute of Terrestrial Ecology
68 Hills Road
Cambridge
CB2 1LA
0223 (Cambridge) 69745

Cover photographs

Permanent pasture in the proximity of Sellafield reprocessing plant, Cumbria
(Photograph by Mel Tonkin)

Continuous flow analysis at Merlewood chemistry laboratories
(Photograph by A W Drury)

Scolytus intricatus on an oak bud
(Photograph by M G Yates)

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 14 sister institutes which make up the *Natural Environment Research Council*, spanning all the environmental sciences.

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

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

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

Contents

Introduction

INSTITUTE OF TERRESTRIAL ECOLOGY: THE FIRST 10 YEARS

In 1973, the transfer of the Conservation Branch of the Nature Conservancy to the Department of the Environment provided the opportunity for the Natural Environment Research Council (NERC) to complete its restructuring of a series of Institutes to cover the main fields of the environment. By creating the Institute of Terrestrial Ecology from the Research Branch of the Nature Conservancy, the Institute of Tree Biology and (later) the Culture Centre of Algae and Protozoa and the Bryophyte Section of the British Antarctic Survey, NERC added a major capability for research in the terrestrial and freshwater environment to the Institute of Geological Sciences (now the British Geological Survey), the Institute of Oceanography (IOS) and the British Antarctic Survey. This family of Institutes covering all aspects of the natural environment underlines the role of NERC in the planning of fundamental, strategic and applied research.

The formation of ITE coincided with the implementation of the so-called 'Rothschild Principle' under which research has been directly commissioned from NERC Institutes by Government departments and other agencies. This commissioning of research has had a critical influence on the history of ITE's development.

Objectives
The original objectives of ITE were defined by its first Director, Dr M W Holdgate, as follows:

> 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.

These objectives perhaps need some qualification and explanation. First, it is important to recognize the extent of ITE's remit. With the possible exception of the very small proportion of the land surface which is devoted to urban and industrial development, ITE's remit covers the whole of the rural area of Britain, and is not confined to the relatively small area (30%) devoted to semi-natural vegetation. Thus, ITE is concerned with the implications of past, present and future policies for agriculture and forestry, as well as with the impact of recreation and sport on wildlife.

The ITE objectives have recently been redefined so as to give increased emphasis to the distinctive function of the Institute within NERC:

> To assess the ecological consequences of past, present and future policies for managing the terrestrial environment.
>
> To investigate the interaction of organisms with each other and with their environment and to elucidate the processes which determine change in ecological systems.
>
> To integrate conclusions from research in order to predict the behaviour of ecosystems under a wide range of options for management.

Requirements of ecological research
The characteristics of the scientific research necessary to fulfil the objectives defined above are broadly 3-fold. First, ecological research, and especially research related to the effects of policies for the rural environment, is essentially long term in nature, and usually encompasses 5 years or more of carefully planned and integrated survey, experimentation and modelling. Second, the research is necessarily multi-disciplinary, requiring the active participation of a wide range of biologists, as well as that of chemists, physicists, mathematicians, computer scientists, statisticians and, sometimes, historians, economists and sociologists. Third, the investigations necessary for ecological research frequently have to be conducted over a wide range of geographically-dispersed sites. For all of these reasons, strategic ecological research needs to be directed and co-ordinated by an Institute, although many of the component projects can be delegated or sub-contracted to universities and other centres within the central concept of the main programme.

Even more important, however, is the efficient use of the scarce resources available for ecological research of this kind—scarce both in terms of the numbers of scientists available with the appropriate skills, and in terms of the expensive equipment which is necessary to determine biological, physical and chemical characteristics in the field, and to evaluate and interpret the interactions of these characteristics. As an NERC Institute, ITE has a well-tried system of project plans defining the objectives, methods and criteria for all research projects. These plans enable the research to be conducted with the maximum of efficiency in the use of both resources and equipment. They also ensure that projects are terminated when they have reached the end of their usefulness, so that resources can be reassigned to new work. ITE represents the largest group of terrestrial ecologists in Europe under strong and efficient management. Furthermore, as members of the NERC family of

Institutes, ITE scientists remain independent of the policy-advocating departments and agencies, and so can give unbiased advice on scientific problems of the terrestrial environment. The fact that all ITE staff have signed the Official Secrets Act also ensures that problems of national or regional sensitivity can be tackled without fear of involvement with environmental pressure groups.

Development

Since its formation in 1973, ITE has been under almost continuous reconstruction so as to improve the efficiency of the Institute and to make it more capable of meeting its objectives.

At the time of its formation, ITE had staff at 12 different locations in the UK. Progressively, and as funds have become available for the construction of new accommodation, or the modification of existing accommodation, the number of separate sites has been reduced, and, by the end of 1984, ITE will have 7 locations. Considerable thought has been given by ITE management, as well as by 2 NERC Visiting Groups, to the optimum number of sites to be maintained within ITE, and the long-term strategy has been fixed at 6 locations. The principal reason for this dispersion of the research stations is that ITE is essentially a field research organization, so that it is necessary for its scientists to have ready access to experimental and survey sites. Indeed, it is one of the strengths of the Institute that it is able to undertake research economically in almost any part of Britain from one of its research stations, thus greatly reducing the cost of the research itself. From the Banchory Research Station, near Aberdeen, for example, ITE scientists are able to work on a wide range of sites in the Scottish Highlands, as well as having easy access to the Orkneys and Shetlands for monitoring the environmental effects of oil exploitation in the North Sea. Similarly, the Merlewood Research Station provides a vital working base for the Lake District, North Pennines and the Borders, as well as ensuring convenient access to the Cumbrian coast to enable radionuclide deposition to be monitored. Each of the research stations provides similar examples of efficient access, and ITE's system of management has been especially adapted to cope with, and, indeed, take advantage of, this dispersal of resources.

The original organization of ITE was based on a matrix system designed partly to break down the near autonomy that existed in its component parts. Since that time, ITE management has been modified progressively to place greater emphasis on integrated programmes of research, and to co-ordinate the many separate projects at the research stations. Total numbers of staff increased towards the end of the 1970s, mainly in response to an increasing Commissioned Research programme, but have subsequently declined because of the NERC policy of reducing staff complements; ITE has lost 15% of its staff in this way during the last 3 years.

Collaboration

ITE is part of a much wider community of scientists with particular interest in the terrestrial and freshwater environments, and therefore collaborates actively with scientists in universities and research institutes. Collaboration, through teaching, external examination of MSc and PhD theses and joint supervision of post-graduate students, is maintained with over 50 universities in the UK. Although none of the ITE stations is on a university campus—except for the Edinburgh Laboratories on the Edinburgh Science Park of the Bush Estate—the regional distribution of ITE research stations makes for easy collaboration, and for exchange of visits between ITE staff and university research workers. Because of the facilities that they can provide, ITE stations are popular as locations for post-graduate research, a trend which is encouraged by ITE management.

ITE also belongs to a family of NERC Institutes, and, through this family, is able to take advantage of new developments in many different fields of science, for example in remote sensing, digital cartography, computing and biotechnology. Close links also exist with several of the research stations of the AFRC, and particularly with those that have strong environmental and ecological interests, and paradoxically especially those which are most under threat in the recent AFRC economies.

Overseas collaboration is also very strong. Ever since the development of the International Biological Programme (IBP) in the mid-1970s, which generated a great deal of practical co-operation between scientists in many different countries, active research collaboration has continued. The UNESCO Man and the Biosphere Programme (MAB), while in no way to be regarded as a successor to IBP, has also stimulated co-operation, perhaps especially with countries which were not actively involved in the earlier programme. Research contacts in China, Egypt, the Sudan, West and East Africa, and India have been particularly stimulated through MAB, and ITE is playing a central role in the training of ecologists from these countries, and is retaining a strong commitment to ecological studies in the countries concerned. Increasingly, ITE is joining with British consultants in competing for contracts in overseas countries, and is thus helping to provide ecological expertise for environmental projects.

Achievements

The list of ITE's achievements since its formation in 1973 is too long to be given in full here. One principal area of achievement has been in the field of environmental pollution. Much of the early work on the pathways of organic pollutants had been done by ITE staff prior to the formation of ITE. Since 1973, however, carefully integrated toxicological and physiological research, particularly on birds, has revealed the complex mechanisms by which organic and inorganic pollutants are incorporated into animal tissues, as well as the conditions under which sub-lethal doses of pollutants begin to have harmful effects on animals, through changes in breeding, behaviour or response to external stimuli.

ITE was the first research organization to establish sampling stations in the rural environment for the whole range of chemicals which are now known to be implicated in 'acid rain'. Partly as a result of ITE's work, the ecological effects of acid inputs to the environment, and the linking of those effects to geochemical cycling, are beginning to be understood. Work on soil processes has helped to provide a link between pollution and the equally complex cycles of nutrients in terrestrial ecosystems. Similar work has also established the pathways of fluorine through terrestrial systems.

In response to the Seventh Report of the Royal Commission on Environmental Pollution, ITE has established an expertise in the measurement of the deposition of radionuclides, and the tracing of their pathways through ecological systems. These studies are currently proving to be vital in establishing the deposition and dispersion of radionuclides around the Sellafield reprocessing plant.

ITE has established a system of land classification which is firmly based on ecological theory, and the land classes defined by this system are now proving to be invaluable in measuring landscape change resulting from agricultural and forestry policies in the rural environment. The same system is currently being used to provide estimates of land use potential derived from ecological relationships between primary productivity and physical and chemical environmental characteristics. For example, this system has been used to assess the potential forestry production of the UK and to determine the likely distribution and location of any increased area of forest made necessary by future difficulties in importing wood and wood fibre. ITE studies of the potential for the production of plant biomass in the UK have also indicated the feasibility and importance of this source of renewable energy under a wide range of future energy scenarios.

Finally, ITE studies of plant and animal organisms have provided essential information for the management of rural environments. Studies of the dynamics of fox populations, for example, have shown that the methods proposed to control and eradicate rabies, if it is introduced into Britain, are impractical; the same studies have indicated a range of feasible options for the control of this disease. Studies of red and roe deer in forests have helped to define the extent to which these animals can be maintained in conifer forests without unacceptable levels of damage to the trees. Badgers, otters, grey squirrels and rabbits are all examples of animals for which new knowledge of practical value has been obtained through ITE research, while, in the much larger field of invertebrate animals, the value of butterflies and moths as indicators of ecological change has been demonstrated and exploited in a series of applications. Studies of plant organisms and communities have also played an important part in the prediction of ecological change resulting from proposed policies or management of rural areas. The survey and monitoring of the distributions of organisms provide a basis for the identification of change in the environment. The mapping schemes of the Biological Records Centre, for example, contain information on the distribution and status of more than 8000 species.

The future

There is a pressing need for a great deal more work for an ecological Institute concerned with the terrestrial and freshwater environment. Indeed, many of the current environmental problems are so serious, and have such far-reaching consequences for society, that the resources devoted to terrestrial ecology will need to be expanded rather than simply maintained at the present level. The complex problems of acidic inputs to the environment, with their possible effects on plants, soils and fresh waters, interacting in equally complex ways with the natural processes of geochemical cycling, represent one example of an area which demands a multidisciplinary, multi-site and long-term research strategy, backed by practical research under strong scientific management of the kind provided by ITE. Public concern about the deposition and dispersion of radionuclides from facilities like Sellafield is almost certain to intensify—again, the impartiality of ITE scientists is an essential element in the response to that concern. Even more recently, concern has been expressed about landscape change resulting from the intensification of agriculture during the last 20 years, and this concern will undoubtedly interact with any proposals to increase the area devoted to forests, whether in the uplands or the lowlands, to meet projected shortages of wood and wood fibre.

In the years immediately after ITE's formation in 1973, Government departments showed a willingness to commission ecological research, but most of the research which was commissioned was relatively short term, ie of less than 5 years' duration. Very few Government departments or agencies appear to be willing to look further than 5 years in order to anticipate environmental problems and to commission research to ensure that adequate scientific advice is available to answer such problems.

With the recession of the last few years, even less research has been commissioned in the terrestrial and freshwater environments. What little research has been commissioned has been for very short projects of 2 years or less. These changes have placed even more emphasis on the importance of the strategic research which has been done by NERC

Institutes like ITE, despite the loss of income which has followed from the recession and the reduction in commissions by departments.

How large ITE should be in the future is an interesting case to argue. Inevitably, some of that argument must rest on the importance which is attached by society in general to the kinds of problems which have been outlined above. During the late 1970s, there was some indication that society had become rather less concerned with environmental problems in the face of apparently more immediate social and economic problems that followed in the wake of recession. More recently, there has been a resurgence of interest in ecological and environmental problems, triggered by local and regional concerns for individual and public health and amenity. Placing a value on those concerns is more difficult. The total cash expenditure of ITE, at today's prices, is about £4.5 million a year. A comparison can be made with the costs of the operations which contribute directly to the environmental problems themselves. The amount spent on fertilizers by the agricultural industry in 1982, for example, was estimated to be £800 million, a sum of which ITE's annual expenditure is only a little more than 0·5%: the amount spent by the agricultural industry on pesticides and herbicides is included in the £969 million attributed to 'miscellaneous expenditure' for the same year. By these standards, or indeed any other, the cost of NERC's ecological research in the terrestrial environment is miniscule, and, indeed, inadequate by comparison with the scale of the problems.

J N R Jeffers
Director

Research reports

FOREST AND WOODLAND ECOLOGY

The effects of clear-felling plantation forests

During the period of rapid afforestation in upland Britain, the attention of ecologists and soil scientists was concentrated on the effects of planting. Now that many of the older plantings are maturing, it is time to examine what will happen as a result of harvesting.

The effects of forest clearance vary widely from place to place, and have been studied in many parts of the world. Because plantations in British conditions differ from those elsewhere, they might be expected to respond differently to clear-felling. In Britain, upland forests show little response to nitrogen fertilizers but very often respond to phosphorus—in marked contrast to coniferous forests in most northern regions, where nitrogen is the main limiting nutrient. Another major difference is related to the length of the rotation: trees in Britain are felled after about 55 years, compared with 80–120 years or longer in more continental regions.

Immediate effects of clear-felling

Although British upland forests differ widely from forests in most other parts of the world, the immediate effects of clear-felling can be expected to be the same. Qualitatively, we already know much about such effects (Table 1), but their magnitude and their significance for future forest crops are uncertain. For example, rapid mineralization of nitrogen has been observed in some North American forests after clearance, but not in others, with mineralization generally being greater in broadleaved than in coniferous forests (Vitousek 1981). British coniferous forests can be expected to behave like American coniferous forests rather than broadleaved forests, but, even so, this assumption needs to be substantiated.

A collaborative multidisciplinary project

In 1980, the Forestry Commission (FC) and ITE embarked on a multidisciplinary study of the effects of clear-felling. The aim was to examine a wide range of ecosystem processes, notably nutrient budgets, the carbon budget, rates of decomposition of organic matter, regrowth of vegetation, soil aeration, and the effects of differing felling practices on growth of second, third, etc, rotations. Collaboration between the organizations is close. The FC, equipped with the manpower and resources to make large-scale field trials, is interested primarily in the performance of future forest crops, and, in particular, how tree growth may be affected by differing harvesting practices and fertilizer regimes. ITE, in contrast, is interested primarily in the ecological processes that lead to differences in crop performance and ecosystem function.

Table 1. Inter-relationships between causes and effects, direct and indirect, following clear-felling

Causes	Effect	
	0	Clear-felling operations
0	1	Removal of tree canopy
0	2	Local compaction of soil
0	3	Local disturbance of litter layer
0	4	Input of slash to forest floor
1	5	More light on forest floor
1	6	Greater temperature variation
1	7	More water reaches forest floor
1	8	Stumps and roots begin to die
1	9	Litterfall ceases
1	10	Tree roots cease to absorb water
8	11	Tree roots cease to absorb nutrients
3,5,6	12	Buried seeds germinate
2,7,10	13	Soil wetter, at least in winter
7,10	14	Runoff and/or percolation increase
6,13	15	Rate of decomposition changes
9	16	Forest floor loses mass
11,16	17	Mineralized nutrients dissolve
17	18	Nutrient redistribution or loss
5,12	19	Ground vegetation re-establishes
19	20	Voles increase

The effects of clear-felling

At present, forest managers are interested in the possibilities of whole-tree harvesting, in which all above-ground parts of trees are removed from site, leaving only stumps in the ground, a procedure contrasting with normal harvesting in which only stems are removed, leaving leaves and branches to rot *in situ*. It has been estimated that, in 50 year old Sitka spruce on a good site, 24% of the above-ground dry matter and 70% of the nitrogen are in branches and leaves (Carey 1980). Thus, whole-tree harvesting results in a relatively small gain in usable fibre (and, at current prices, often not even usable), in exchange for a relatively large drain on the nutrient capital of the site. In spite of these disadvantages, a few sites are already being whole-tree harvested, because, on difficult terrain, contractors sometimes prefer to remove whole trees to the roadside, before chopping off the branches and tops.

Clear-felling experiments

Two main experimental sites, in Kershope and Beddgelert Forests, have been developed to study effects of clear-felling. Both are planted with Sitka spruce (*Picea sitchensis*). Kershope Forest on the Scottish border has been the subject of a major FC study of soil water and oxygen regimes (Pyatt & Smith 1983). During 1982–3, the trees were clear-felled by normal harvesting methods. Linking with hydrological work by FC, ITE has collaborated by measuring the chemical constituents of throughfall, stem flow, soil water and ditch water. The site is ideally suited to chemical budgeting studies because

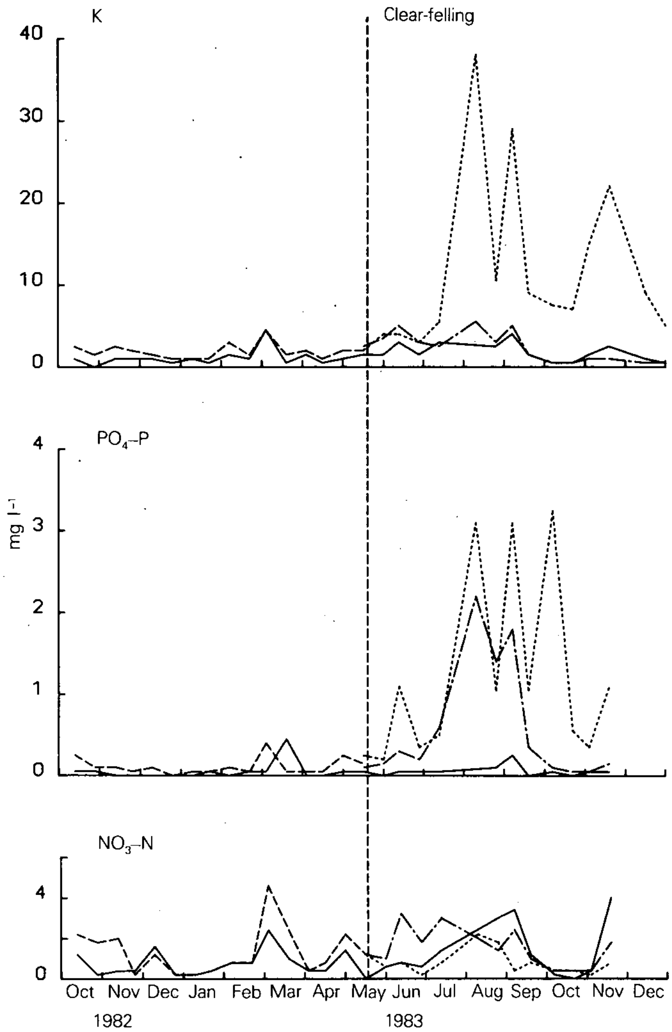

Figure 1 Effects of different clear-felling procedures on the composition of water samples from organic horizons of soil that had been planted with Sitka spruce

———— *control plot with trees left standing*
------ *treatment A, trees cleared according to standard practice*
.... *treatment B, plots cleared by normal harvesting*
—·—·— *treatment B, plots cleared by whole-tree harvesting*

the subsoil is impervious to water, so that incoming precipitation is lost either by evaporation or by overland flow through ditches. The ITE study began several years before clear-felling and will continue for several years afterwards. It should lead to a detailed understanding of the chemical response to this management practice, both at the scale of the whole site and at the scale of individual soil horizons.

Interest in the Beddgelert Forest, North Wales, centres on the resultant differences after whole-tree, compared with normal, harvesting (Plate 4). The experimental layout consists of 4 plots, each of 0·64 ha, and each of which is split to test the 2 harvesting treatments. Two plots were harvested in 1983, 2 in 1984. The site is fenced to exclude sheep.

In addition to the 2 main experimental sites, 3 more sites are being used to follow effects of normal clear-felling, the research emphasis being on the growth of vegetation, performance of young trees, soil oxygen status, and rates of litter decomposition.

Changes in dissolved chemicals

When a forest is cleared, soil changes are most immediate and most intense at the surface. In the few months that have elapsed since clear-felling in Beddgelert Forest, chemical changes in water sampled from the surface organic horizons have been large (Figure 1). For nitrogen and potassium, the broad effects could have been predicted from general ecological knowledge. Nitrogen is present in organic matter mainly as insoluble proteins, and is not rapidly released by decomposition. Forest litter at the time of the tree harvest is capable of immobilizing nitrogen, as well as releasing it. Thus, though one sink for inorganic nitrogen (tree roots) has been removed from the system, another (the litter itself) remains. There is no reason to expect a rapid change in dissolved inorganic nitrogen in conifer litter; an increase is to be expected in the years that follow, but not at once.

Potassium, on the other hand, is at the other extreme of mobility from nitrogen. In living plant tissues, it is almost all stored in solution, and it is readily leachable, especially from moribund tissues. Thus, there is little potassium in the dead organic matter on the forest floor. The large release of the element after normal harvesting is derived from debris being leached by rain. In the absence of debris, where whole-tree harvesting was practised, the concentrations of potassium were not augmented.

The most interesting response is that of phosphorus. Concentrations of dissolved phosphate were appreciably increased after both whole-tree and normal harvesting. These increases cannot be attributed to fresh debris: they must therefore be derived from organic matter already present on the forest floor.

Changes in vegetation

As yet, there has been little time for plants to recolonize the experimental plots since clear-felling, though many seedlings have germinated. Indeed, the most marked early effect of clearance on ground vegetation is the smothering effect of slash from normal harvesting. However, numerous seeds of sedge (*Carex binervis*) and gorse (*Ulex gallii*) germinated in the 3 months after clear-felling. These seeds are known to survive long periods of burial in forest soil, and those germinating on the plots would be at least 40 years old.

The experimental plots were clear-felled too recently to provide any indication of medium-term differences between whole-tree and normal harvesting. However, we have data from 2 plots nearby. On one of

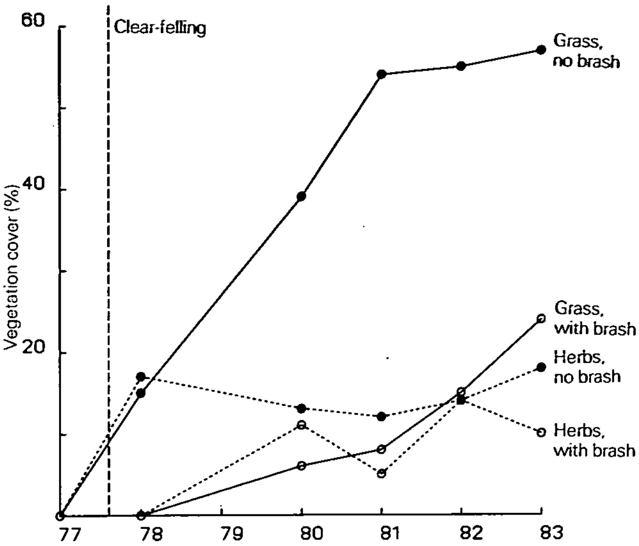

Figure 2 Effects of normal clear-felling (○) of Sitka spruce and simulated whole-tree harvesting (●) on the subsequent growth of grasses (——) and herbs (....)

these, slash was removed by hand to simulate a whole-tree harvest; on the other, slash was left in place, as in a normal harvest. The difference between the 2 treatments is clear (Figure 2). Whole-tree harvesting permitted much more rapid establishment of grass cover, which could conceivably be beneficial to the next forest rotation if it prevented the loss of nutrients from the site. On the other hand, grasses compete with the roots of young trees, and may pose a weed problem.

Changes in decomposition

In the plots in Beddgelert Forest, the mass of decaying organic matter on the forest floor (L, F and H horizons) amounts to 17 tonnes ha^{-1}; annual litter-fall is about 3 t ha^{-1}. Thus, litter takes, on average, about 6 years to decompose under standing crops. This relatively long timescale is potentially advantageous to following crops. Provided that decomposition does not markedly accelerate after clearance, then many nutrients stored in the forest floor will be retained until a new crop can make use of them. Clear-felling not only alters the physical environment of the forest floor, it adds numerous new materials to be decomposed. On the surface, there is debris formed as a result of felling, at least after normal harvesting. In the soil, roots, stumps and mycorrhizas and hyphae of mycorrhizal fungi begin to decay. Death of roots and stumps can be quite slow, although they rapidly stop functioning as a powerful nutrient sink. In June 1983, medium-sized roots (2–5 mm diameter) of Sitka spruce were sampled, from under a standing crop, and buried in litter bags in a clear-felled area. Five months later, some of these roots were still alive; others were dead.

The main effect of these new materials on the rate of decomposition of other organic matter is probably physical. The lack of response to chemical amendment was shown clearly in a pot experiment done at ITE, Bangor. Litter bags of forest floor organic matter were buried in damp silica sand in pots. Pots were watered with nutrient solutions with, and without, the major nutrients N, P and K. The rate of evolution of carbon dioxide from the pots was used as a measure of rates of decomposition, which responded strongly to changes in temperature, dropping by a factor of 2 from one day to the next as a cold front came through. However, after 6 months, there was no difference attributable to the added nutrients.

If chemical changes have little effect, then temperature and moisture are the 2 main factors that should control decomposition rates. In a cool, wet climate with frequently overcast skies, moisture and temperature will change only moderately as a result of clear-felling. Therefore, changes in rates of decomposition should not be large.

This prediction is being tested empirically. Decomposition rates are being measured in the field using litter bags, CO_2 evolution and a standard substrate (cotton cloth), which is dug into the ground to see how fast it rots.

Other changes

So great is the effect of clear-felling that all components of the ecosystem can be expected to change. Populations of voles *(Microtus agrestis)* rapidly increase. Where there is some slash (branch debris), voles may be sufficiently protected to graze, even when the overall amount of vegetation is still small. Within 3 months of clear-felling in 1983, it was noticeable that the grass *Deschampsia flexuosa* appeared to be untouched, whereas the superficially similar *Festuca ovina* was consumed almost to the roots. Unpalatability to voles could well account for some of the success of *D. flexuosa* as a colonist in cleared areas.

FC colleagues are measuring changes in soil aeration and soil temperature. They will also assess the performance of the next rotation in relation to the 2 felling treatments. ITE, in extending its own studies, is collaborating with CNRF, Nancy, France, and with colleagues at Rothamsted Experimental Station, Harpenden, Herts, to examine the effect of harvesting operations on soil structure and porosity.

M O Hill, M Hornung, D F Evans, P A Stevens, J K Adamson and Shirley A Bell

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Dispersal of the oak bark beetle (*Scolytus intricatus*)

Studies on the oak bark beetle *(Scolytus intricatus)*, reported in previous ITE publications (Yates 1981a, b), have been concerned with the beetle's potential as a vector of oak wilt disease and its population biology. It was apparent from these studies that an understanding of the dispersal behaviour of *S. intricatus* was needed to assess the beetle's ability to disperse and locate new hosts (recently dead or dying oak). The beetle's mobility is also an important feature in assessing its potential as a vector of the disease.

During the summer of 1983, an experiment was done to investigate the beetle's pattern of dispersal from old to new logs in an open grass field, on the southern edge of Monks Wood NNR, Cambridgeshire. Oak logs containing pre-emergent adult *S. intricatus* were treated with a solution of radioactive orthophosphate (^{32}P), at the rate of 6·7 mCi m^{-1}, and placed at the centre of 5 concentric circles, of radii 10 m, 16·6 m, 27·5 m, 45·7 m and 75·8 m, around which fresh cut oak logs, each 2 m in length, were placed vertically 15 m apart (Figure 3). As the beetles emerged from the treated logs, they became marked with ^{32}P which allowed their identification when recaptured.

At one or 2 day intervals from 3 June, when the logs were treated with ^{32}P, to 6 July, all *S. intricatus* found on the fresh cut logs were removed and inspected for radioactivity in the laboratory. Figure 3 shows the total numbers of marked and unmarked *S. intricatus* caught on each log during this period. A total of 2761 beetles emerged from the ^{32}P treated logs during the experiment. If it is assumed that the logs on the circumference of each circle intercepted the flight of the marked beetles in direct proportion to the fraction of the circumferences occupied by the logs, the number of marked beetles expected to be caught would be 3·9% of the total number emerging. Therefore, of the 2761 beetles, 108 were expected, compared with 111 beetles (4%) actually caught. The similarity between these proportions suggests that the beetles dispersing from their emergence sites only detected new logs over a short distance.

The pattern of distribution of marked beetles between logs on each concentric circle (Figure 4) is such that

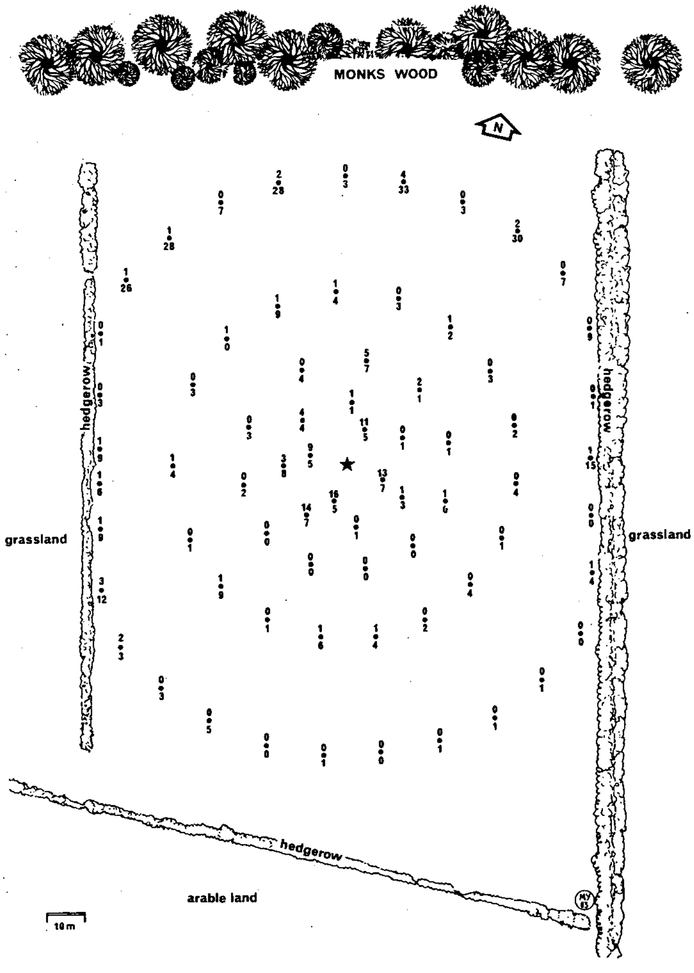

*Figure 3 The layout of host logs (●) and the position of the source of ^{32}P marked oak bark beetles (indicated by *). Numbers above each log are the total numbers of marked beetles caught, those below are numbers of unmarked beetles*

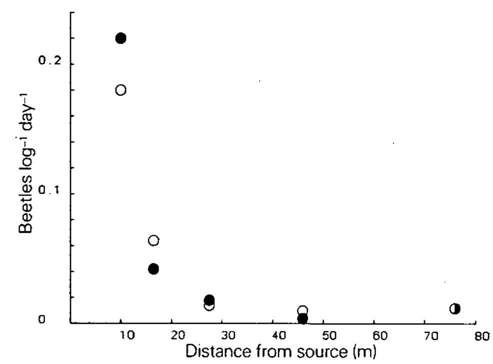

Figure 4 Numbers of ^{32}P marked male (●) and female (○) oak bark beetles caught per trap per day on logs at different distances from the source of marked beetles

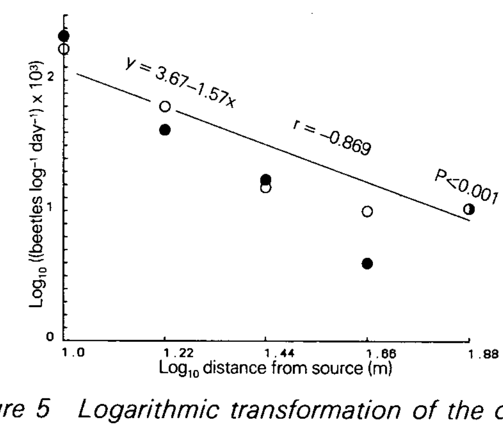

Figure 5 Logarithmic transformation of the data in Figure 4, showing the near linear decline in numbers of marked male (●) and female (○) oak bark beetles, caught at different distances from their source

69·5% were captured on logs on the perimeter of the circle of 10 m (radius) from the central emergence site, while 18·7%, 5·6%, 2·5% and 3·7% were taken on logs at distances of 16·6 m, 27·5 m, 45·7 m and 75·8 m respectively. A logarithmic transformation of this pattern (Figure 5) indicates that the decline is almost linear and that males and females dispersed similarly.

Monks Wood was considered to be the most likely source of unmarked *S. intricatus*, so it is not surprising that over half were caught on logs nearest Monks Wood (Figure 3). On the other hand, all but 10 of the 70 logs had been found by unmarked beetles by the end of the experiment. The fall-off of marked beetles with distance from their sources suggests that some beetles moved up to 0·35 km. This estimate will depend upon a number of factors, such as the number of days during which temperature and wind speed are suitable for flight, but it gives some idea of the beetle's powers of dispersal. In comparison, the large and small elm bark beetles *(S. scolytus* and *S. multistriatus)*, that transmit Dutch elm disease, may disperse to distances of about 1 km and 10 km, respectively.

M G Yates

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Competition in tree stands

In forestry, there is a special need to understand the process of inter-tree competition in monocultures because it has a marked bearing on genetic improvement and management.

For genetic improvement, individual tree selections have to be made among mature trees within closed stands in which competition, as well as environmental heterogeneity, can obscure inherent differences among genotypes. The reason is that competition is a spatial neighbour-dependent process. Consider a mixed-genotype stand in which inherently vigorous genotypes are randomly (not uniformly) dispersed. Then, in some parts of the stand, these vigorous genotypes will be immediate neighbours, and so some will eventually be suppressed, and possibly die. Conversely, in other parts of the stand, some of the less vigorous genotypes will have equally unvigorous neighbours, so that some will grow large.

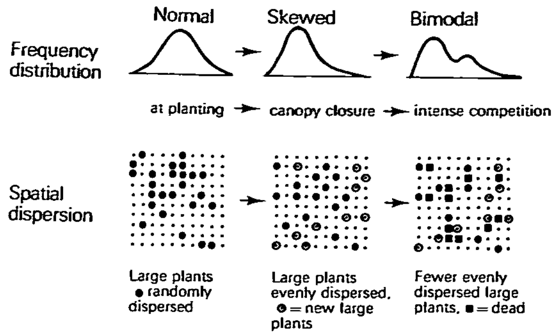

Figure 6 Changes in the frequency distribution of plant size (top row) and the spatial distribution of large plants (bottom row) within populations in which there is progressively greater competition among individuals for evenly dispersed resources of light, water and mineral nutrients. These changes were predicted using models (Ford & Diggle 1981) and they were found in tea plantations (Cannell et al. *1977) and in stands of Sitka spruce and lodgepole pine (Cannell* et al. *in press)*

After a period of intense competition, the outcome will be that large trees are progressively more uniformly, or evenly, dispersed and mortality is also uniformly dispersed (Figure 6). Thus, the spatial, non-genetic, competition process will obscure differences among genotypes in stands, and all the big trees will not be inherently the most vigorous. This may, indeed, be one of the reasons why phenotypic selection for vigour within tree stands has not been very effective.

Having selected superior phenotypes, their genotypes are evaluated by comparing the growth of their variable (outbred) progenies. The progenies can differ in initial size, in their abilities to 'capture' the site before canopy closure, in their competitive ability after canopy closure, and in their ability to form stands with rapid rates of stem wood production per unit area of ground. The relative importance of these attributes needs to be evaluated in order to quantify genetic gain (Cannell 1979).

Earlier studies of spatial competition in mixed-genotype stands of tea in Kenya led to a revised selection procedure being recommended to increase the chances of selecting bushes that would produce high-yielding clonal stands (Cannell *et al.* 1977). Similarly, it was shown that spatial competition processes occur in closely planted stands of Sitka spruce *(Picea sitchensis)* and lodgepole pine *(Pinus contorta)* (Cannell *et al.* in press), and work on progeny testing suggested that many progenies that grow vigorously as widely spaced individuals are not outstanding in terms of wood production per unit area of ground after canopy closure (Cannell 1982). Current work on identifying the ideal tree characteristics for maximum production per hectare in closed stands has concentrated on the analysis of

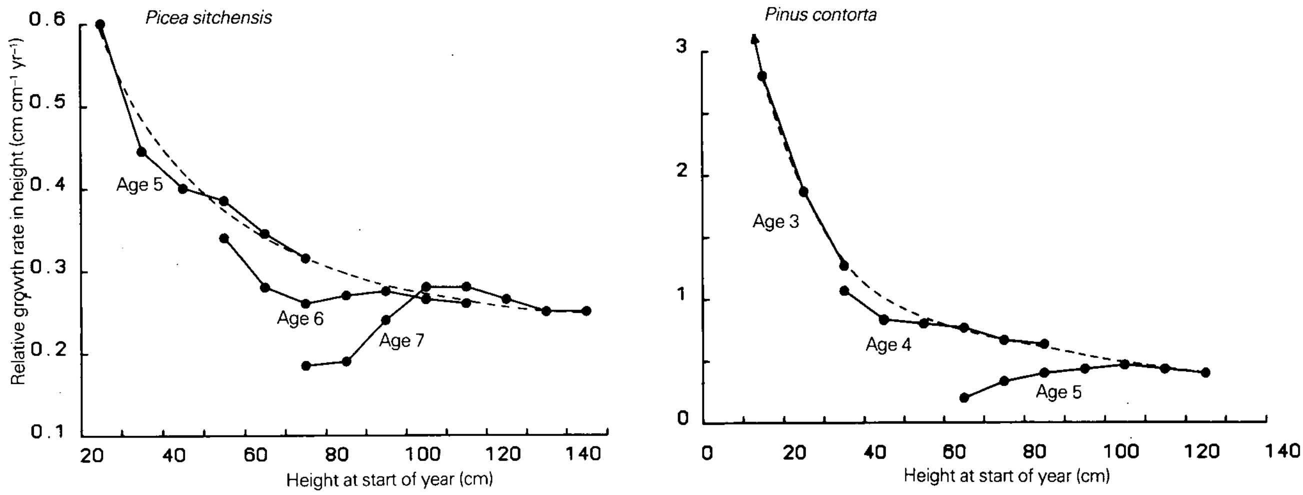

Figure 7 The mean relative growth rate in height of young trees of Sitka spruce and lodgepole pine, each grown at 14 cm spacing in nursery plots (Cannell et al. *in press). The dashed lines mark the expected relative growth rates of trees in the absence of competition. At age 5 (Sitka spruce) or 3 (lodgepole pine), there was little inter-tree competition, but at greater ages (6–7 Sitka spruce, 4–5 lodgepole pine) there was increasing inter-tree competition, and the small trees had lower relative growth rates than expected. A similar pattern was found in mature Sitka spruce in the forest (Ford 1979)*

vegetatively propagated (genetically uniform) clones of Sitka spruce with contrasting branching characteristics. Clonal propagation began in 1979, and nursery plots of single or mixed clones have been planted annually since 1981.

The importance of inter-tree competition in forest management is readily apparent. Foresters usually plant many more trees per hectare than they want at the final harvest. Inter-tree competition suppresses weeds, inhibits branching, encourages self-pruning, decreases branch and hence knot size, decreases stem taper, decreases ring widths and increases wood density, thereby improving many of the quality aspects of the timber. However, competition also decreases the growth rate per tree and the size obtained by individual boles, and there is a severalfold difference in the value of small 'roundwood' and large 'sawlog' boles. Foresters attempt to optimize the quality/bole size balance by periodically thinning the stands, a procedure which also provides saleable yield.

In Britain, the decisions on how many trees to plant and how severely and often to thin them are further complicated by the fact that heavily-thinned stands are more likely to blow down, ie are susceptible to 'windthrow'. Indeed, because of persistent gale damage, many forests are now left unthinned, and so will produce mostly low-value roundwood. This situation is clearly unsatisfactory, and has prompted new ideas on how best to manage competition in forest stands (Ford 1980). In order to test these ideas, forest experiments have begun to examine the effects of novel planting and thinning regimes on wood quality and stem wood volume production.

Meanwhile, substantial steps have been made to understand the process of inter-tree competition by developing theoretical models (Ford & Diggle 1981) and by examining the growth of trees in the forest (Ford 1979) and in closely planted nursery plots (Cannell *et al.* in press) (Plate 18). Distinctive changes in population structure have been identified. First, small trees have much lower relative growth rates than expected, compared with trees of a similar size not subject to competition (Figure 7). Second, as competition increases, the frequency distributions of tree size become negatively kurtotic (more spread), with tendencies toward negative skewness (right-skewness) or bimodality. Third,

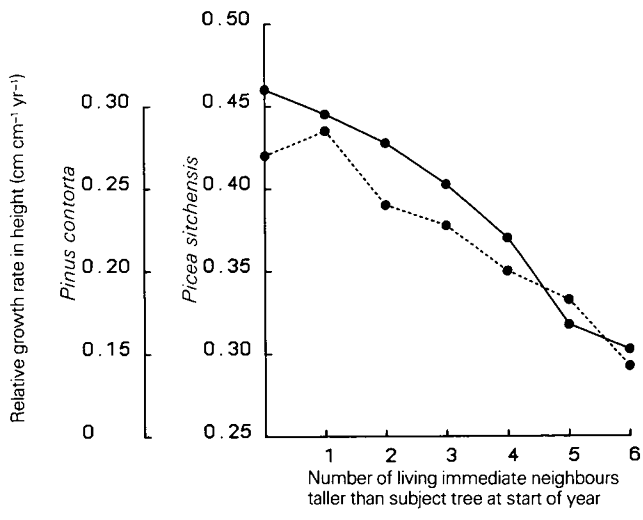

Figure 8 The relative growth rates in height of young trees of lodgepole pine (———) and Sitka spruce (---) during a year of intense inter-tree competition, showing strong neighbour-dependent growth. The trees were 14 cm apart and grew from about 100 cm to 140 cm tall during the year (Taken from Cannell et al. *in press)*

although mortality may occur in clumps at first, mortality occurs evenly over the plots as competition intensifies, ie dead trees are uniformly, not randomly, dispersed. Fourth, the trees most affected by their competitive status (ie whose growth is most affected by the size of their neighbours) are those of intermediate size. Fifth, even with intense inter-tree competition in nursery plots, competition is restricted mainly to immediate (first-order) neighbours. Sixth, competition between trees is overwhelmingly one-sided, big trees suppressing smaller neighbours, but the small neighbours having little effect on the big trees. Seventh, the competitive status of a tree is diminished by all immediate neighbours taller than itself, and not only by those that overtop it by a certain amount (Figure 8). Finally, competition accounts for up to 25–35% of the variation in tree size within tree stands.

These fundamental studies of competition suggest numerous ways in which forest planting and thinning methods could be modified to attain specific harvest objectives (eg wood, pulp or sawlog timber) and have led to practical tests on a larger scale.

M G R Cannell, E D Ford and P Rothery

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The defecation frequencies of red deer in different habitats

The 'faecal accumulation method' was identified about 50 years ago, by North American wildlife biologists, as a means of detecting differences and trends in the abundance of large herbivorous mammals living in habitats where it was difficult or impossible to make direct counts, eg deer in thick woodlands. On the assumption that the defecation rate of a single species would be relatively constant, it was argued that differences in rates of accumulation of faecal material at different sites and periods of the year could be interpreted as differences in population density or site occupation. It was also appreciated that it would only be possible to estimate actual population densities (or site occupation in animal days ha^{-1}) from faecal accumulations, if the actual defecation rates of different herbivores were known. To facilitate these measurements, sample plots are first cleared of existing faecal material, and then, after an appropriate interval, revisited to measure the accumulations of new material, the interval being short enough to minimize natural losses, but long enough to maximize gains. With the exception of those species producing a scattering of semi-liquid dung, for which volumes or weights may be the only practicable measurement, the simplest approach is to count numbers of separate deposits. Fortunately, most large herbivores produce distinct groups of faecal pellets which can be counted readily. However, the applicability of this method depends on the availability of reliable information about defecatory behaviour. Does the frequency of defecation change seasonally, and is it altered by the type of forage?

A priori changes associated with changing seasonal nutritional demands would be expected, and also changes associated with the quality of available forage, but are these variations significant, and can they be assessed? To test these possibilities, the faecal output of red deer *(Cervus elaphus)* was studied using fenced enclosures with known numbers of deer in 3 contrasting habitats. Site 1, a deer park (14 ha and 20–29 red deer) with herb-rich grassland at Kinlochewe, Ross-shire, was selected as an example of a nutritionally rich habitat; it had been used formerly for livestock farming (dairy cattle), and the present deer stock was clearly performing well on its lush grassland. Site 2, part (26 ha and 47 deer) of Glensaugh experimental deer farm, Kincardineshire, was chosen as an example of a dry upland heath, dominated by *Calluna*, with a nutritionally poorer (more fibrous) type of forage. To create a study site with red deer in a very poor quality habitat, some red deer were introduced into a woodland restoration enclosure (6 increasing to 8 deer in 18 ha), on rough hill ground on the Beinn Eighe National Nature Reserve, Kinlochewe, Ross-shire. This enclosure (Site 3) was dominated by a wet *Molinia* heath, and, although partly planted with Scots pine (12–14 years old, 1–3 m tall), it was clear that the deer fed mainly on ground vegetation. Site 1 had the most digestible forage, Site 3 the least, with Site 2 being in between.

Accumulation rates of faecal deposits, associated with known numbers of deer, were measured on

Table 2. Defecation frequencies (=numbers of faecal deposits deer^{-1} day^{-1}) of red deer in 3 different habitats, with corrections for losses attributable to decomposition and incomplete searches

Study sites	Intervals between observations	Faecal deposits deer^{-1} day^{-1} (uncorrected) Mean ± SE	Correction factors for % deposits that disappeared	% deposits not observed	Faecal deposits deer^{-1} day^{-1} (corrected) Mean ± SE
1. Most digestible forage	22/3 –28/4/78 (37 days)	21·7 ± 2·0	5·0	0·5	22·9 ± 2·1
(grassland deer park	28/4 –24/5/78 (26 days)	26·3 ± 2·1	8·5	2·5	29·2 ± 2·3
Anancaun, Kinlochewe,	24/5 –28/6/78 (35 days)	30·1 ± 2·0	7·5	5·0	34·0 ± 2·3
Ross-shire)	28/6 –25/7/78 (27 days)	27·3 ± 1·6*	14·0	7·5	33·5 ± 1·9*
14 ha and 20–29 deer	25/7 –30/8/78 (36 days)	18·5 ± 1·5	17·5	9·5	23·8 ± 1·9
	30/8 –27/9/78 (28 days)	19·2 ± 1·2	11·5	10·0	23·5 ± 1·5
	27/9 –24/10/78 (27 days)	24·8 ± 1·9	8·5	9·5	29·4 ± 2·2
	24/10–12/12/78 (49 days)	18·2 ± 0·8	3·5	7·5	20·3 ± 0·9
	12/12– 1/3/79 (79 days)	13·1 ± 1·0	1·0	5·0	13·9 ± 1·1
	1/3 –26/3/79 (25 days)	18·0 ± 1·9	0	0	18·0 ± 1·9
	26/3 –25/4/79 (30 days)	17·8 ± 1·9	6·0	0·5	19·0 ± 2·0
2. Intermediate digestibility (upland heath, part of Glensaugh experimental deer farm, Kincardineshire) 26 ha and 47 deer	15/8 –16/9/78 (32 days)	20·4 ± 2·1	12·0	9·5	25·0 ± 2·6
3. Least digestible forage	6/5 –22/6/79 (47 days)	16·1 ± 2·2	0	2·5	16·5 ± 2·2
Molinia heath planted	22/6 –30/8/79 (69 days)	13·4 ± 1·9*	4·0	7·5	15·0 ± 2·1*
with Scots pine (Beinn	30/8 – 2/11/79 (64 days)	21·5 ± 2·1	5·0	9·5	24·7 ± 2·4
Eighe NNR,	2/11–10/1/80 (69 days)	18·0 ± 3·2	0	5·0	18·9 ± 3·4
Kinlochewe,	10/1 – 6/3/80 (56 days)	24·6 ± 3·3	0	0·5	24·7 ± 3·3
Ross-shire) an	6/3 – 8/5/80 (63 days)	20·5 ± 2·4	1·0	0·5	20·8 ± 2·4
enclosure of 18 ha	8/5 –16/7/80 (69 days)	23·9 ± 2·3*	4·0	5·0	26·1 ± 2·5
and 6–8 red deer	16/7 – 4/9/80 (50 days)	2·06 ± 2·6	6·0	9·5	23·9 ± 3·0*

* = Faecal deposits of young calves first detected, calves included in calculations thereafter

marked sample plots: at Site 1, 41 plots (each of 225 m²), were checked 13 times at approximately monthly intervals; at Site 2, one estimate was made after 4 weeks on 48 plots (each of 225 m²); while at Site 3, 60 plots (of 100 m²) were checked every 2 months for a period of 6 months. The longer interval between observations at Site 3 was adopted because decomposition was expected to be slower than at Sites 1 and 2. Each plot was searched carefully after first being divided into 1·5 m strips. Faecal deposits were counted and then removed; most were compact, but a small proportion were scattered, usually linearly. Deposits with less than 15 pellets were discarded as being either fragments of larger deposits or earlier remnants.

It was essential to find if natural decomposition and incomplete detection could seriously affect numbers of deposits counted per sample plot. To assess rates of decomposition, fresh deposits (usually 40–60 at a time) were placed at marked locations within each study site, and then checked periodically until none remained. As expected, with the most digestible forage, faecal deposits at Site 1 disappeared sooner than those at Site 3, the 'least digestible' site, especially in summer. In addition to the fact that there were more invertebrates than at Site 3, the deer at Site 1 tended to produce softer faecal pellets, a large proportion of them being amorphous during the summer. Elsewhere, most deposits consisted of drier pellets. On average, pellet losses ranged from nil to 17·5% (Table 2) between successive observations taken at intervals of 1 and 2 months. At one extreme, samples at Site 1 in July disappeared completely within 95 days; in November at Site 3, it took about 450 days for complete decay.

The ability to detect faecal deposits was assessed in short vegetation (easy to search), and in 'moderate' and 'difficult' locations where vegetation was up to, and over, 0·5 m, respectively. After one member of a team of 3 had distributed 1–9 groups of fresh pellets in each of 30 plots at each site, the second and third members of the team instituted a search. They found almost all (96%) of the deposits in short vegetation, 86% of those in vegetation of intermediate height, and only 76% on 'difficult' ground with tall 'ground vegetation'. Because the sample plots at the main experimental sites varied from 'easy to count' in late March (when the vegetation was shortest) to between 'easy' and 'moderate' in late September (relatively few plots were 'difficult'), it seems that few deposits were likely to be overlooked in late winter–early spring, but that up to 10% could be missed in late summer–early autumn. Correction factors for the different 1 or 2 monthly samples were calculated from these data. Although the effects of natural decomposition and incomplete detection were slightly out of phase, their combined effects were clearly much smaller during late winter–early spring than at other times of the year.

In calculating defecation frequencies (Table 2), calves were ignored until they were producing normal faecal deposits, ie from July onwards; for a couple of weeks after birth (mainly in June), calves produce soft, pale-coloured dung, much of which is eaten by their mothers, the remainder decomposing very rapidly. On average, deer seemed to produce more pellet groups per day in summer than in winter, this seasonal pattern being more distinct at Site 1 than at Site 3, possibly because intervals between successive assessments were shorter at the former site. The number of deposits of pellet groups averaged 20 $deer^{-1}$ day^{-1} in winter, and about 25 $deer^{-1}$ day^{-1} in summer, with a peak of over 30 $deer^{-1}$ day^{-1} around calving time. However, on occasions, the numbers of deposits were appreciably smaller than might have been expected, as happened between December 1978 and February 1979 at Site 1 where snow was followed by flooding, and again at Site 3 during May–August 1979, immediately after releasing deer on to the experimental site.

The observations made at Site 2–the 'moderate' site–in August–September 1978 gave estimates of defecation comparable with those from Sites 1 and 3 at the same time, ie 24–25 deposits $deer^{-1}$ day^{-1} in September. At Site 1, estimates of defecation derived from counts made at intervals of one month were directly paralleled by hourly observations of the defecatory behaviour of 2 tame hinds between late April and early July. These observations suggested defecation frequencies of 33 and 24 deposits $deer^{-1}$ day^{-1} for the different individuals (Mitchell *et al.* 1983), compared with averages of 29–34 deposits $deer^{-1}$ day^{-1} derived from the monthly surveys.

It seems that the frequency of defecation is greater in summer than in winter, a cycle that is presumably associated with the changing nutritional requirements of red deer, the summer peak being related to increased food requirements between late pregnancy and early lactation. Many species of deer are well known to have a smaller voluntary food intake during the least favourable part of the year.

Somewhat surprisingly, defecation frequencies at the same time of the year but in contrasting habitats were remarkably similar, suggesting that the conversion factors are widely applicable to a variety of habitats. However, the faecal accumulation method described in this report may provide more reliable estimates of red deer populations in winter than in summer, because faecal decomposition in winter is slower than during summer when the detection errors, particularly in rich habitats with tall ground cover, will also be larger.

Acknowledgements

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FRESHWATER AND MARINE ECOLOGY

Lamprey populations in the catchments of the Forth and Clyde estuaries

Lampreys belong to a small but important group known as Agnatha–literally, jawless fishes. They are quite distinct from all other fishes and have no lower jaws, the whole mouth being surrounded by a round sucker-like disc within which are horny teeth. The life cycle involves the migration of adults to spawning areas in running water, where they spawn in crude nests. The young are washed by currents to areas of sandy silt, where they burrow and spend the next few years. They are blind, the sucker is incomplete, and the teeth are undeveloped. They feed on organic particles and minute plants, such as diatoms. In the change from larval to adult form, the mouth develops into a fuller sucker with teeth, the skin becomes silvery and opaque, and the eyes develop fully. The adults then migrate downstream, usually to the sea where they are parasitic on fish. In some waters, lampreys are serious pests of commercial fish stocks. On reaching sexual maturity, the adult lampreys migrate into fresh water and back again to the spawning areas.

Studies of the ecology of lampreys are at present being carried out in the adjacent catchments of the Forth and Clyde estuaries. Both rivers have a high percentage of common watershed, but drain in entirely different directions and have other important differences. The 3 British lampreys–sea lamprey *(Petromyzon marinus)*, river lamprey *(Lampetra fluviatilis)*, and brook lamprey *(Lampetra planeri)*–all occur in both catchments. However, the sea lamprey seems to be relatively uncommon and the brook lamprey, though very common in many streams, is purely a freshwater species. The river lamprey is recorded as being frequent in the rivers of the Forth area and in its estuary, and it also occurs in the Loch Lomond area of the Clyde. Much of the present study has concentrated on this species.

The river lamprey is widely distributed in western Europe where it spawns in catchments of the Baltic, Atlantic and Mediterranean Seas (Maitland 1980). Several studies have elucidated the ecology of this species, but much more information is needed on its estuarine and sea phase. In addition, there is virtually no information on its feeding in fresh water anywhere in Europe.

Large numbers of river lampreys were obtained during the course of collecting fish entrained on the intake screens of power stations in the estuary of the River Forth (Maitland *et al.* 1980). These individuals varied considerably in size (Plate 8), and, from an examination of the contents of their intestines, many had recently been feeding. In view of the paucity of information on the estuarine periods in their life cycle, the current study concentrated on providing new data relevant to the timing of the downstream migration, the size at which parasitic feeding commences, the duration of estuarine parasitic feeding, the type of host and the relationship between size of prey and predator.

Samples were collected regularly during 1979, 1980 and 1981 from the intake screens of power stations in the estuary of the River Forth. Recently metamorphosed animals were common during the spring, while sexually maturing adults were abundant in the late summer and autumn. They were assumed to be lampreys at the end of their downstream and the start of their upstream migrations, respectively. The respective sizes of the presumed downstream and upstream migrants were 69–135 mm (0·2–2·8 g) and 200–361 mm (7·0–93·2 g). Smaller numbers of animals of intermediate size were collected during the summer and late autumn. Males were usually the predominant sex, with an average of 56·5% of the population in 1980–81. In all months, the mean weight and, with one exception, the mean length were greater for females than for males. The intestine frequently contained fish remains, especially muscle, bone and scales of herring and sprats, and thus the river lamprey seems to feed mainly on bony fishes in this estuary. An analysis of the size of scales in the intestines of lampreys of various body lengths indicates that there is a relationship between the size of host and predator. Comparisons with other studies of *Lampetra fluviatilis* emphasize the variability that exists in aspects of the biology of this species within and among populations.

In the Clyde catchment, work has concentrated on the unique population of river lampreys in the Loch Lomond system (Plate 1). This is the only system in the British Isles where lampreys are known to feed on fish in fresh waters. Whitefish *(Coregonus lavaretus)* are abundant in Loch Lomond and are frequently attacked by lampreys there. In all samples (totalling about 1000 whitefish) taken from different parts of the loch between 1951 and 1979, the incidence of lamprey scarring was high (26–50%), many times that of any of the other 14 species of fish in the loch. Multiple scarring was common. Small whitefish (<25 cm) were rarely scarred, whereas larger ones (>25 cm) frequently had been attacked. Scars occurred all the year round, but fresh wounds only in the summer—especially July and August (Plate 9). Almost all the scars occurred along the backs of the fish between the head and adipose fin, and above the lateral line, but there is little evidence that these attacks affected the growth or condition of the whitefish concerned. Lampreys do not appear to attack fish in fresh water in other parts of Great Britain, but parasitism has been recorded in a few lakes in Finland and Russia.

Plate 1 Lamprey studies are being carried out at Loch Lomond, seen here looking south-east, across Sloy hydro-electric power station, towards Ben Lomond)
(Photograph S V Mills)

The estuarine study has now been virtually completed and future research in the Forth area will concentrate on the populations of adults in the River Forth. In Loch Lomond, the work will concentrate on the spawning runs of adults in the tributaries to the loch, where it is hoped eventually to make population estimates.

P S Maitland, K East and K H Morris

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Eutrophication of Loch Leven

Fresh waters commonly become increasingly enriched with mineral nutrients, and lakes and rivers are each subject to this eutrophication process (Vollenweider 1968). The substances of most concern in this context are nitrogen and phosphorus, as both are essential for plant growth, and it is commonly the growth response by plants to the enrichment that causes problems. Thus, in standing waters in particular, the enrichment is shown by dense algal populations which may (directly or indirectly) affect man's use of the water for potable and industrial supply, as well as fishing and other leisure activities. Depending on the particular species of alga present, the growths may form the surface 'blooms' characteristic of many lakes on calm and especially warm days.

Records of algae collected from Loch Leven in south-east Scotland at the turn of the century (Bachmann 1906, 1907) suggest that this large shallow lake (4 m mean depth, 13 km² surface area) has been eutrophic for a long time. Moreover, dense blooms of blue-green algae in the loch were noted in 1937, when they were associated with poor trout angling returns (Rosenberg 1938), and on occasions during the 1950s and 1960s (Brook 1957, 1958, 1965). Fluctuations in the Loch Leven phytoplankton—monitored especially closely since 1968 (Bailey-Watts 1974, 1978, 1982)—show that the loch has remained eutrophic. However, it is only since the late 1960s that detailed chemical analyses have been made of Loch Leven water. Our understanding of the relationships between phytoplankton performance and nutrient concentrations in this loch has thus been developed from the analysis of the last 15 years' records.

Since 1968, it has been established that the major source of nitrogen to the loch is surrounding agricultural land (Holden & Caines 1974; Holden 1976). To increase the yields of improved grass for cattle and of grain crops, much of the catchment of the loch (70% of a total area of 145 km²—Smith 1974) has been heavily fertilized since the late 1950s. Runoff from the agricultural land has resulted in increases in nitrate concentrations in the inflowing streams. These increases have led to a rise of approximately 1 mg N l⁻¹ over the period 1970–1980 in the recorded winter (January–March) maximum concentrations in the loch itself (Figure 9).

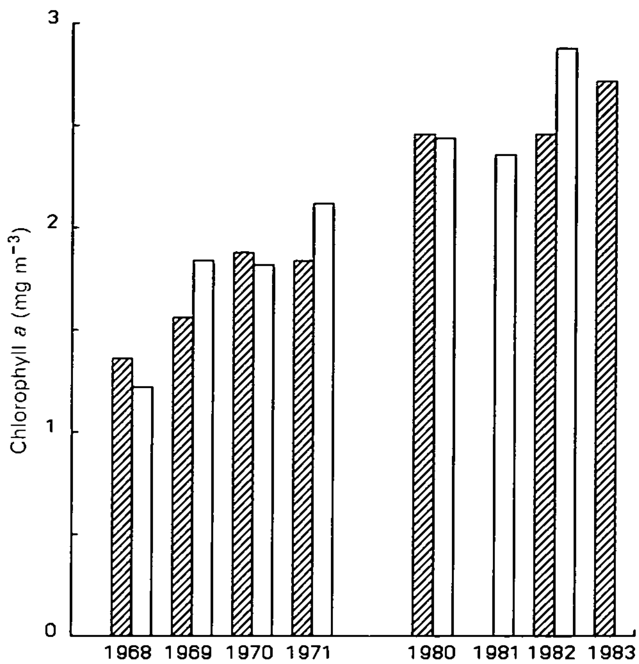

Figure 9 Contrasts in the winter maximum nitrate concentrations in Loch Leven between the periods 1968–71 and 1980–83 (1968–71 data from Holden & Caines 1974). Shaded columns refer to a sampling station near the outflow and unshaded columns to an open water site

Contrasting with nitrogen supplies, which enter the loch in a diffuse manner, most of the phosphorus reaches the loch at well-defined points (Plate 7). During the late 1960s, and up until 1972, some 65–70% of the total loading (>1·25 g P m⁻² yr⁻¹) was associated with a single point source, ie an outfall of woollen mill effluent (Holden 1976). By 1976, a considerable reduction in total phosphorus loading was effected by a change in the policy of the wool manufacturers for the disposal of their effluent. Thus, by 1976, the estimated total loading had been reduced to 0·7 g P m⁻² yr⁻¹ (values calculated from Holden & Caines 1974).

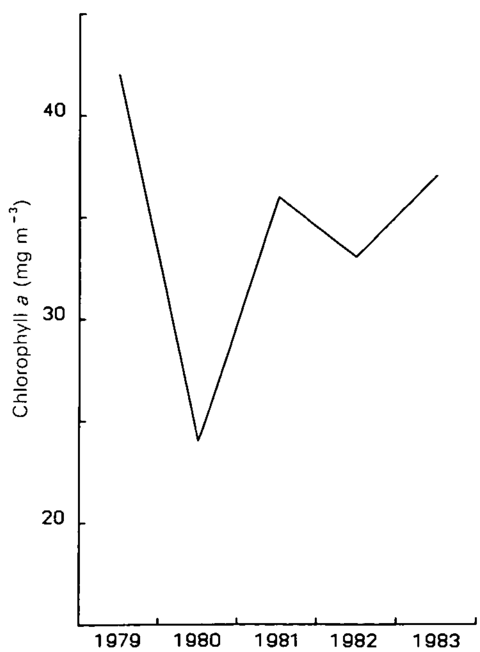

Figure 10 Mean phytoplankton biomass levels (expressed as concentrations of chlorophyll a*) in Loch Leven 1979–83*

Table 3. Algae dominating the phytoplankton of Loch Leven at the times of various biomass maxima, 1979–82

Season	Year 1979	1980	1981	1982
January–April	Unicellular centric diatoms	Unicellular centric diatoms	Unicellular centric diatoms	Unicellular centric diatoms
May–August	Cryptomonads and chrysoflagellates	Chrysoflagellates	Pennate diatoms, chrysoflagellates, unicellular and colonial green algae	Colonial blue-green algae and cryptomonads
September–December	Filamentous blue-green algae	Filamentous blue-green algae	Unicellular green algae, chrysoflagellates and unicellular centric diatoms	Unicellular and colonial green algae and colonial blue-green algae

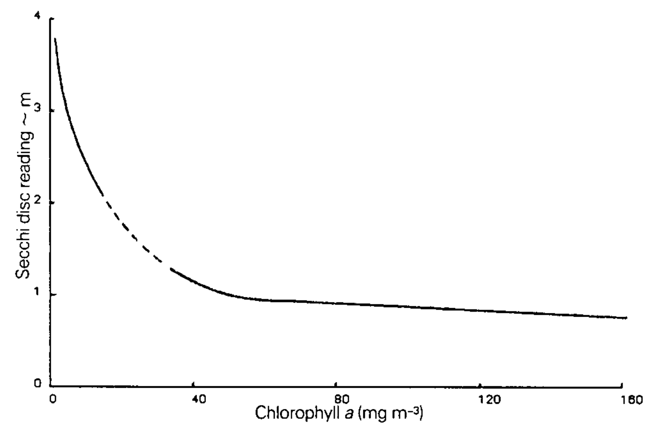

Figure 11 Line illustrating relationship between water transparency (expressed as Secchi disc reading) and phytoplankton biomass (expressed as chlorophyll a *concentration) in Loch Leven for 1980–83 (n = 130); dashed portion corresponds to the predicted decrease in pigment concentration if the phosphorus loading is reduced (see text)*

The eutrophication of Loch Leven over recent times can, therefore, be summarized as an overall increase in nitrogen loading and a general decrease in phosphorus loading. A desk study (Bailey-Watts 1983) suggests that the current total loading of phosphorus has changed little since 1976, and, at 0·8 g m^{-2} yr^{-1}, reflects an increase attributable mainly to the contribution in treated sewage as a result of population increases in the catchment area (see also Cuttle 1982).

Mean algal biomass had approximately halved over the period 1968–1976, during which time the loading changes referred to above took place, and annual mean chlorophyll concentrations of 36, 32 and 41 mg m^{-3} were obtained for the years 1977, 1978 and 1979 respectively (Bailey-Watts 1982). As Figure 10 shows, the pigment levels have remained fairly low since 1979. However, changes in algal species composition have continued throughout the period under review (Bailey-Watts 1974, 1978, 1982, unpublished data); Table 3 illustrates the range of dominant species recorded at the times of major crop maxima during 1979–1983 – the period of relative stability in terms of mean annual biomass.

Although current algal biomass levels are low compared to those recorded a decade ago, the general problems commonly associated with algal developments induced by eutrophication persist. At Loch Leven, these include (i) unsightly scums and odour associated with the collapse of occasional dense blooms of blue-green algae, (ii) poor water clarity, (iii) problems in treating water for downstream industrial purposes (paper making), (iv) limited coverage by submerged rooted vegetation, and (v) poor fishing. The recent desk study to assess the feasibility of further control of phosphorus inputs to the loch suggested that removal of phosphorus from sewage and trade effluent should be seriously considered; phosphorus in these effluents currently appears to represent over 60% of the total loading. Other work (Bailey-Watts – unpublished observations) suggests that some of the current densest phytoplankton crops are prevented from increasing further because of phosphorus shortages. The application to Loch Leven data of the findings of an OECD programme on chlorophyll–phosphorus relationships (Anon 1982) indicates that a further reduction in mean chlorophyll levels to about 15 mg m^{-3} might be expected. If this were the case, a marked increase in water clarity could result, even though no significant increase in water transparency has been found since mean chlorophyll levels were reduced from the earlier values of 1000 mg m^{-3}. The relationship between water transparency and pigment levels is complex (Figure 11), but a marked change in water transparency is observed over that part of the range of pigment concentrations of interest here.

A E Bailey-Watts and A Kirika

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Acid rain effects on river catchments in north-west England

There is increasing concern that acid precipitation may have deleterious effects on some fresh waters in Britain. In England, the Lake District region in the north-west is receiving much attention. Here, the rainfall is high (1000–4000 mm yr^{-1}) and its pH is low – the mean value for 1978–79 was 4·4 (Nicholson *et al.* 1980). The geology of much of the area is dominated by volcanic rocks with low calcium buffering capacities. Consequently, fresh waters tend to be acidic and often contain high concentrations of aluminium – a metal which is toxic to fish (Driscoll *et al.* 1980).

The North West Water Authority (NWWA) is investigating the chemistry and biology at approximately 100 river and lake-side sampling points throughout the Lake District. About 50 of these points are on the Rivers Esk and Duddon or their tributaries (Plate 5). NWWA has already reported some of its findings (Prigg 1983). It has noted the absence of fish from stretches of river where it had expected to find some, and is also concerned about fish mortalities which have occurred in the Rivers Esk and Duddon in recent years, usually after periods of heavy rain.

The Freshwater Biological Association (FBA) is also studying the area (NERC 1983). Its studies of a number of freshwater tarns and lakes and of rainfall (Sutcliffe *et al.* 1982) have led it to conclude that there has been no evidence for acidification of the waters studied over recent years. Nevertheless, the FBA is continuing its studies, concentrating on high altitude lakes and tarns, which are more likely to be affected by acidification, and on the chemistry of aluminium and its complexes, which are particularly relevant to the toxic effects on fish.

A research project has been started, in collaboration with the above organizations and others working on similar topics in the UK, to explore several related avenues of research.

1. Water samples are being collected from many of the NWWA sampling points along the Rivers Esk and Duddon, with the assistance of NWWA staff. Analysing the samples for different soluble aluminium compounds will give some indication of the possible toxic effects of this metal on fish in these rivers, as some aluminium compounds are much more toxic to fish than others (Driscoll *et al.* 1980).

2. The acidity of precipitation is being studied, using rain collectors, with the aim of identifying acid deposition 'episodes' (Fowler & Cape in press) and relating these to the continuous pH monitoring records of the NWWA from the Rivers Esk and Duddon.

3. Sediments collected from tributaries of the Esk and Duddon are being analysed for a range of toxic metals, to determine if metals other than aluminium may affect the biology of these rivers.

4. Using computing methods previously applied to land classification studies in ITE (Bunce 1979), an attempt is being made to classify catchments, currently sampled by the NWWA, into different

types. The present classification is based upon data from Ordnance Survey, geological, soil and rainfall maps. Already we are able to relate some catchment characteristics to the chemical and biological data which the NWWA has collected.

5. The information gathered will facilitate the selection of some catchments for more detailed study. Such studies may make use of catchments with different soil types or geologies. Studies will certainly focus attention upon the effects of vegetation and land use on the acidification of streams, as it is already known that afforestation can lower the pH of stream water (Harriman & Morrison 1982).

K R Bull and Jane R Hall

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Water temperature—an important factor in rotifer ecology

Rotifers are small, multicellular invertebrates, 100–200 µm in length, which occur in large numbers in almost every freshwater environment—lakes, ponds, temporary pools, and even in garden water-butts. In spite of their abundance, the biology of these animals is not well documented and there is little information on the factors which control their populations. In January 1977, an intensive study of rotifer ecology was initiated as part of the on-going plankton monitoring programme at Loch Leven, Kinross-shire,

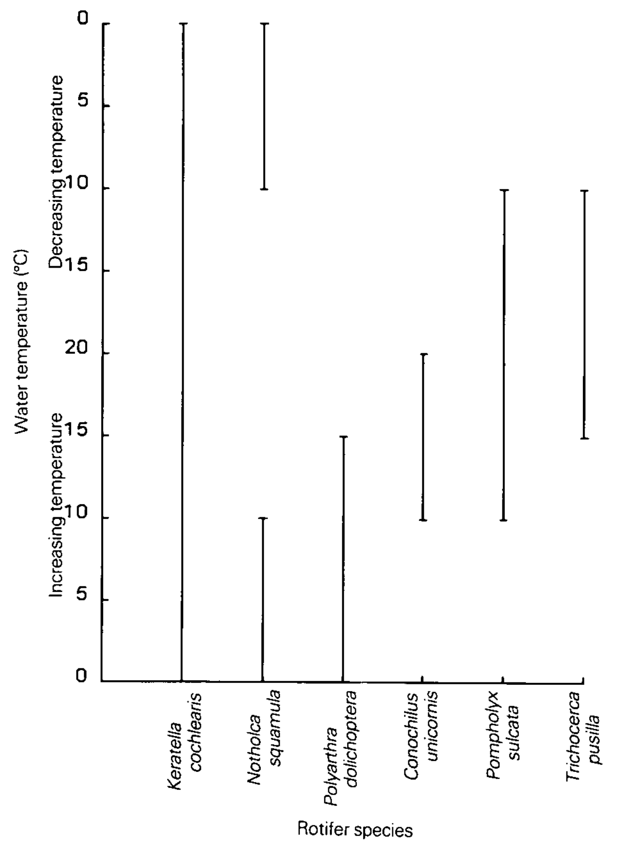

Figure 12 Preferred temperature ranges of the dominant rotifer species in Loch Leven

Scotland (Bailey-Watts *et al.* 1983). Here, rotifers form an important part of the plankton community, reaching population densities in excess of 6000 individuals per litre during the summer months.

Like all cold-blooded animals, rotifers are greatly affected by the temperature of their environment. Our work at Loch Leven has indicated that many species show a well-defined range of temperature preference, outside which they are unable to maintain a viable population (May 1983). These animals are known as stenotherms. Preferred temperature ranges recorded for the dominant species in the loch are shown in Figure 12. While *Keratella cochlearis* achieved high population densities over the whole range of temperatures recorded, other species showed a more limited range of temperature preference. For example, *Notholca squamula* and *Polyarthra dolichoptera* appeared to be cold stenotherms, occurring only in winter and early spring when temperatures were low. In contrast, *Conochilus unicornis, Pompholyx sulcata* and *Trichocerca pusilla* were absent unless the water temperature rose above 10°C.

Loch Leven is shallow, well-mixed, and generally of uniform temperature throughout. As the temperature of the loch changed through the seasons, ranging from 0·8°C in winter to 22°C in summer, each rotifer species established a population while

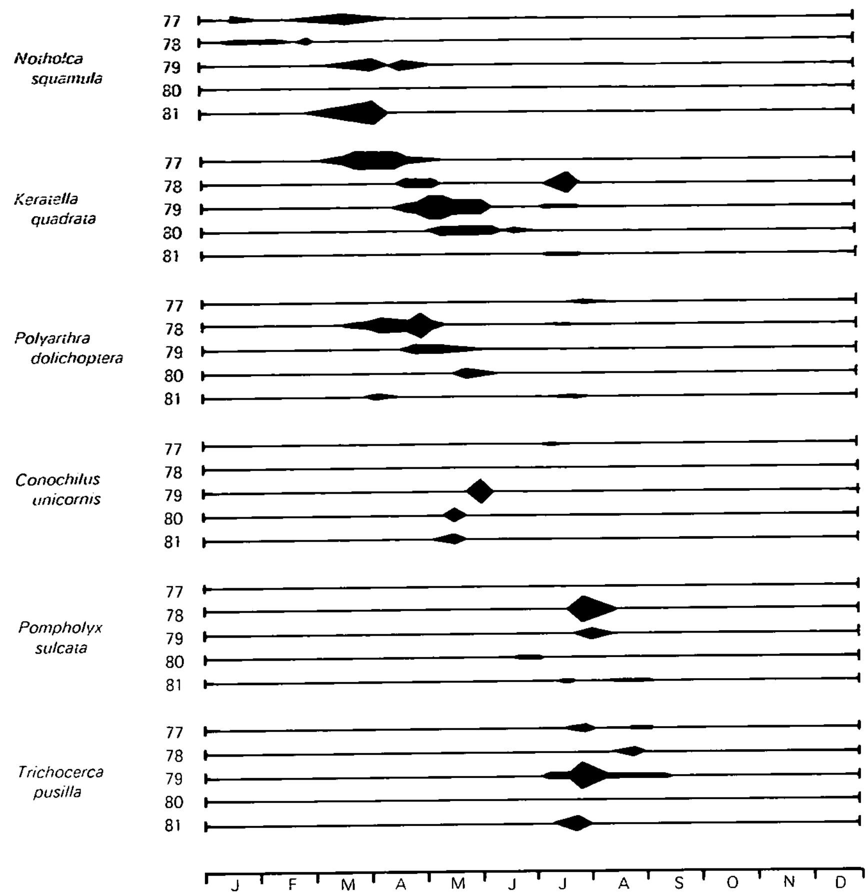

Figure 13 Seasonal succession of the dominant rotifer species in Loch Leven (1977–81). Species abundance is proportional to the height of the shaded areas

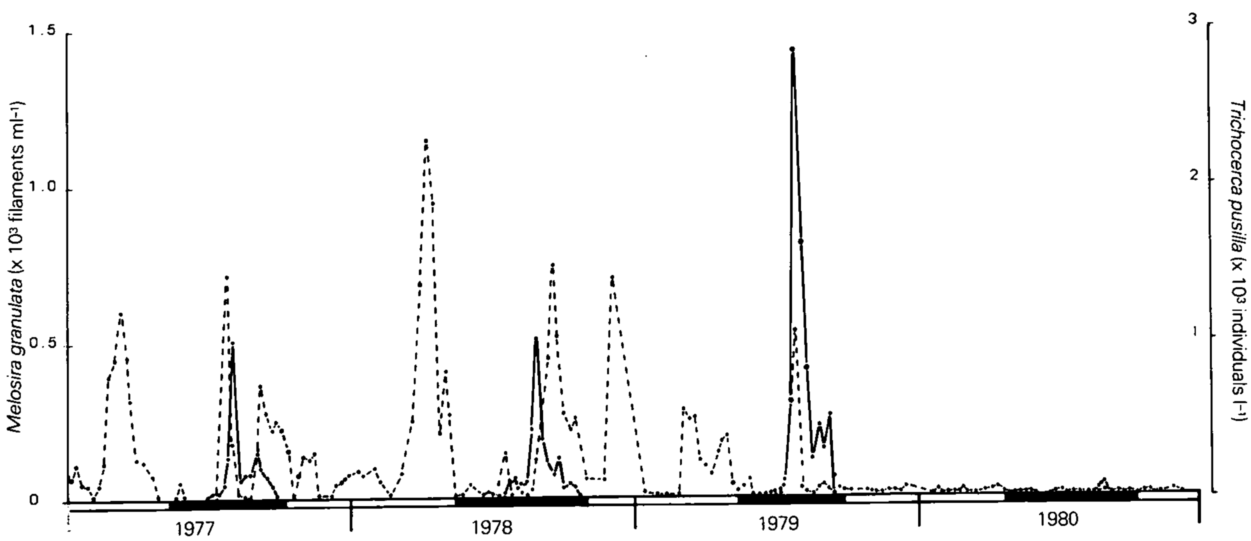

Figure 14 Seasonal variation in the population of Trichocerca pusilla *(——) in relation to the density of* Melosira italica *(....). The shaded areas indicate the periods during which the water temperature was above 10°C*

the thermal conditions were favourable. When unfavourable conditions returned, resting eggs were laid and the species disappeared. The overall effect of this mechanism was a marked seasonal succession of rotifer species throughout the year (Figure 13). The winter species *Notholca squamula* and *Polyarthra dolichoptera* disappeared as the water warmed during May. The colonial rotifer *Conochilus unicornis* made a brief appearance in early summer, and was followed by the warm water species *Pompholyx sulcata* and *Trichocerca pusilla,* occurring from June to October. As the water temperature fell again in autumn, these warm stenotherms disappeared, and winter forms began to re-establish themselves.

The thermal limitations to rotifer population growth, outlined above, are an important consideration in our study of grazing interactions in the field situation. A direct comparison of rotifer densities with the abundance of potential algal food species may be misleading, unless the animals' temperature requirements are taken into account. For example, the rotifer *Trichocerca pusilla* only occurred in Loch Leven during the summer months, although its algal food, *Melosira granulata* (data kindly supplied by Dr A E Bailey-Watts), was also common in spring and autumn (Figure 14). This is because *T. pusilla* cannot establish a population in spring and autumn, when temperatures are below 10°C, despite an abundance of food. However, Figure 14 shows that, within its range of temperature preference, the abundance of this rotifer was closely related to food availability.

The species specific responses to changing water temperature described above have the net effect of temporal segregation within the rotifer community. The adaptive significance of this mechanism is probably avoidance of competition in an environment where spatial separation is almost impossible. There is evidence of this in Loch Leven, where the rotifers *Notholca squamula* and *Trichocerca pusilla*, which both feed on *Melosira granulata*, are separated in time by their thermal requirements.

Linda May

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REHABILITATION OF DISTURBED ECOSYSTEMS

Effects of treatments on succession in a limestone quarry

The use of Clipsham Quarry on the oolitic limestone in Leicestershire for studies on primary succession was outlined by Park and Davis (1982). The study of seedling demography reported there provided insight into some of the limiting factors for plant establishment and growth. However, it did not consider the longer term development of species-rich communities which are often such a striking feature of disused chalk and limestone quarries. For this purpose, 2 contrasting areas of the quarry floor at Clipsham, about 40 m apart, were chosen. The first (A) had a very sparse and largely ephemeral vegetation with a cover of less than 10%. The second (B) had a more established and very species-rich vegetation, but still had about 80% bare ground. Historical evidence suggested that the latter area, at least, had probably been undisturbed by human agencies for 40 years, since work finished in the quarry.

Vegetation cover and species richness

In 1980, area B was divided into 72 one metre square plots separated by 0·5 m guard lanes. Half of the plots (one chosen at random from each adjoining pair) were surveyed in late May, early July and early September. Altogether, 80 species were recorded over the year, together with measures of rooted frequency and vegetation cover, using a quadrat frame divided into 25 units. Species richness in July ranged from 22 to 41 m^{-2} and cover from 7% to 60%, with means of 30·4 m^{-2} and 21·4% respectively (Table 4).

Table 4. Vegetation cover, species richness and total rooted frequency on the floor of Clipsham Quarry (area B) in May, July and September 1980. Means and standard errors for 36 plots

	% cover	Species m^{-2}	Rooted frequency m^{-2}
May	16·3 ± 1·7	27·6 ± 0·7	151·6 ± 6·7
July	21·4 ± 2·3	30·4 ± 0·7	176·9 ± 6·9
September	19·9 ± 2·1	27·8 ± 0·6	152·6 ± 5·1

Two patches of closed vegetation about 60 cm × 60 cm in the plots were apparently used as rabbit latrines. Examination showed that these patches contained slightly more species than the mean for comparable areas in 17 adjacent plots. This result suggested a subtle balance between eutrophication encouraging development of vegetation, on the one hand (Green 1972), and the suppression of competitive species by grazing, on the other (Grime 1973).

Many factors may limit vegetation development on a quarry floor. The more obvious ones that could apply at Clipsham are illustrated in Figure 15 with some of their interactions. The principal constraints were thought to be low rainfall, low levels of plant nutrients, the shallow and often stony soil, and rabbit grazing. Seed input might also be limited, partly because of rabbits. The alleviation of a major constraint could set up a chain reaction which would accelerate vegetation development, eg addition of fertilizers→more soil organic matter→more water retention→greater nitrogen availability (Lloyd & Piggott 1967). The result could be a too rapid development of vigorous competitive species at the expense of diversity. On the other hand, the effect might still be imperceptible or temporary if another limiting factor quickly came into operation.

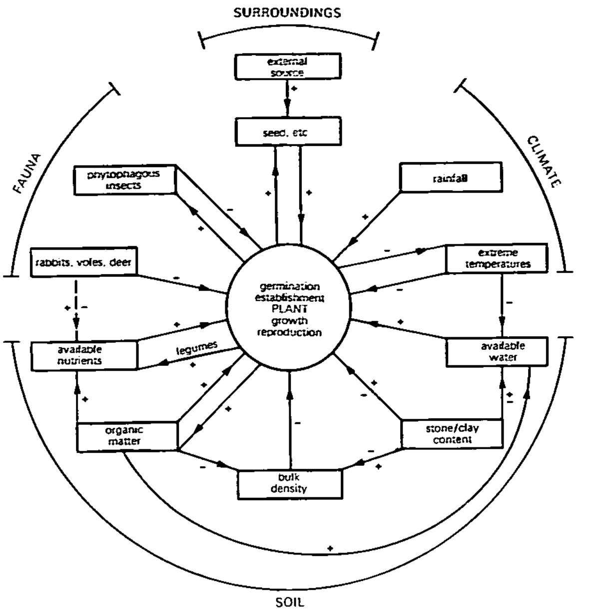

Figure 15 Constraints on succession in a limestone quarry at Clipsham. Arrows with + or − indicate positive and negative effects of factors on plant growth, interactions between factors, and feedback mechanisms

To test these hypotheses, a factorial experiment was set up in area A, with 4 replicates of 8 treatments. The existing vegetation was progressively eliminated with herbicide during 1980, and 3 treatments applied singly and in combination, as shown in Table 5. Wire mesh cages were used to prevent rabbit grazing, though microclimate or seed dispersal might also be affected. The sowing of the grass *Brachypodium sylvaticum* and legume *Lotus corniculatus* was intended to test whether there were limitations on seed input into the area. Small numbers of *L. corniculatus* already occurred in area A but there was no *Brachypodium sylvaticum*, though both were common in the quarry as a whole. Percentage cover and rooted frequencies of all vascular species were recorded in the same way as in area B described above.

Table 5. Treatments applied in factorial experiment to accelerate vegetation development on bare ground at Clipsham (area A). Four randomized blocks

Treatments							
0 (Control)	C	S	F	CS	CF	SF	CSF

C = cages, applied 20 January 1981
S = sowing of *Brachypodium sylvaticum* and *Lotus corniculatus* in March 1981
F = fertilizers N P K Mg, applied March and May 1981, and April 1982

Effects of treatments on cover

The control plots regained their original cover of about 5–7% during the second season 1982, and maintained the same levels in 1983. The other 7 treatments showed early and increasing effects on

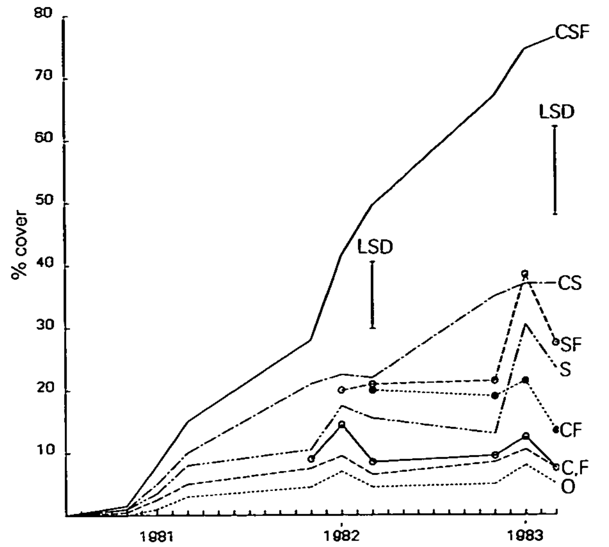

Figure 16 Effects of factorial combinations of cages (C), sowing (S) and fertilizers (F) on percentage cover 1981–83. Some lines are omitted in 1981 and 1982 for the sake of clarity

cover such that, by the end of 1982, all 2-factor treatments (CS, CF, SF) were ranked above 1-factor treatments, while the combination of all 3 factors gave much the most rapid increase (Figure 16). In 1983, only the sowing treatments gave further increases, with CSF continuing to promote cover dramatically, so that by September 1983 it reached 76·3%.

Effects on flowering

There was a highly significant increase in the number of species flowering in the caged, as compared with uncaged, treatments in the second half of 1981 and in May 1982. Fertilizers also enhanced flowering in May and July 1982. In July 1983, flowering was recorded for each 20 cm × 20 cm unit in the plots. Analysis of results showed that all treatments receiving one or more factors significantly enhanced flowering, compared with controls (Figure 17). However, when the contributions of *Brachypodium sylvaticum* and *Lotus corniculatus* in the sown plots were subtracted from the totals, it appeared that sowing merely replaced the beneficial effects of cages and fertilizers on other species.

Effects on species richness

The overall plot mean for numbers of species rose each year from 22·25 in 1980 to 29·6 in 1983. Thus, after 3 years, treatment effects on species richness in the plots were indistinguishable.

Effects on rooted frequency

The contributions of the 2 sown species were subtracted from the total rooted frequencies before analysis of the data to avoid giving undue bias to the S treatments. Rooted frequency values were subject to marked seasonal variations as a result of the appearance and death of short-lived individuals: after the dry summer of 1983, nearly all plots had lower species densities than in September 1981. Of

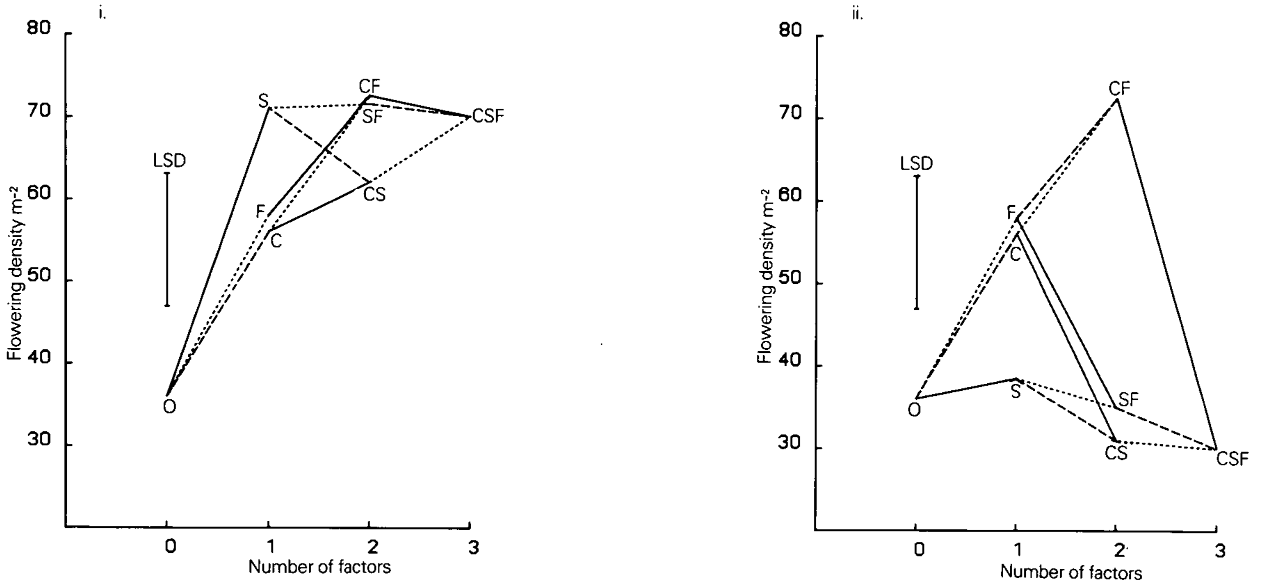

Figure 17 Effects of factorial combinations of cages (C), sowing (S) and fertilizers (F) on mean levels of (i) total flowering density, (ii) flowering density minus sown species, in July 1983

the 3 factors, only sowing produced a consistent trend in the progressive reduction of rooted frequency compared with unsown plots. Cages and fertilizers sometimes acted in the same direction and sometimes in opposition to each other, so that the combined effect of all 3 factors was largely unpredictable. Among the 8 treatments, only CF produced a significantly higher rooted frequency value than controls, while CS and CSF significantly reduced rooted frequency (Figure 18).

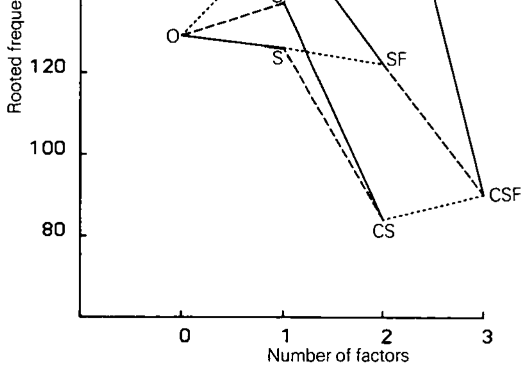

Figure 18 Effects of factorial combinations of cages (C), sowing (S) and fertilizers (F) on mean levels of rooted frequency (minus sown species) in July 1983

Conclusions

Three years is too short a period to observe the full effects of these treatments on plant succession. Because of the feedback mechanisms suggested earlier, there might well be long term trends which were masked by short term variations. Nevertheless, it is clear that all 3 factors—plant nutrients, rabbit grazing and seed input—were limiting plant succession on the quarry floor at Clipsham. The alleviation of either of the first 2 constraints had only marginal benefits for increased plant cover, but the introduction of *Brachypodium sylvaticum* and *Lotus corniculatus*, and especially their combination with either cages or fertilizers, produced a rapid and marked increase in cover in an area which normally supported 5–8% vegetation. That plant growth was still limited was clearly shown by the dramatic increase resulting from the combination of all 3 factors. The CSF treatment produced about a 10-fold increase over control plots, and at least twice as much as any single or 2-factor treatment (Figure 16).

Rapid increases in cover did, however, suppress the frequency of unsown species in the plots (Figure 18). This suppression has not (yet) affected total species richness, as there was still enough bare ground for the germination of many species, even if they could not long survive the competition for resources from established individuals. The best treatment for promoting total rooted frequency was the combined use of cages and fertilizers. This treatment produced 20% cover after 3 years, which was about that seen on area B as a result of natural succession over 40 years. However, the relative frequency of species in the 2 areas was quite different, and the longer term effect of preventing rabbit grazing in area A could produce vegetation with a very different structure and composition. There is clearly much scope for manipulating the course of succession in such early seral communities.

B N K Davis and Christine Brown

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Selection of trees for planting derelict land

(This work was largely supported by Department of Environment funds)

Derelict and disturbed sites commonly present an inhospitable environment to trees used in land rehabilitation; poor establishment and slow subsequent growth are often the result. Factors which combine to inhibit growth include substrate compaction, waterlogging and drought, nutrient deficiencies, and the presence of toxic substances. The relative importance of each factor varies both between and within sites.

Adequate tree performance depends upon good site preparation and the use of appropriate species (Broad 1979). While extensive site preparation is undoubtedly important and capable of producing substantial improvements in growth, at least in the short term, it should be remembered that a tree is a long-lived crop with an extensive root system—the alleviation of chemical and physical problems associated with the surface layers may enhance growth of herbs and young trees, but may contribute little towards providing suitable conditions in the long term for mature trees. After planting, opportunities for further site amelioration are considerably restricted.

It is against this background that attempts have been made to select 'within-species' variants tolerant of the difficult conditions prevailing at reclaimed sites, the aim being to develop clones for amenity use rather than timber production. Good selections should permit successful tree planting with a possible reduction in the amount of site preparation necessary.

Species being investigated include silver and hairy birch *(Betula pendula* and *B. pubescens)* and common and grey alder *(Alnus glutinosa* and *A. incana)*. Birches are commonly the predominant species where derelict land is colonized naturally: alders rarely occur as volunteer species on derelict ground, but they often perform well when planted.

As the primary objective of this work was the reclamation of deep-mined colliery waste, selections were made of 'superior' trees among those which had either naturally colonized waste, or had been successfully planted. Cuttings were collected from these trees, rooted under mist in a heated glasshouse, and then used as 'mother plants' for the production of containerized clonal stocks for trials. Chemical and physical characteristics of the sites of origin were determined.

Twelve trials have been initiated, 7 on colliery waste (mostly unameliorated), with the remaining 5 on a range of other 'difficult' sites (2 on motorway sites and one each on a disused railway siding, a domestic refuse dump and on foundry sand); these sites had all been subjected to normal reclamation procedures. The extension of trials from colliery waste, for which the clones were originally selected, to other sites was implemented so as to determine the range of substrates for which the clones might be of use.

So far, 25 clones have been incorporated into these trials in which 2 types of 'controls' have been used for comparison—(i) containerized stock grown in the same conditions as the selected material, either from commercially obtained seed, or cuttings from mother plants obtained from such seed, and (ii) bare-rooted stock obtained commercially (the type of stock generally planted when reclaiming derelict sites). Assessments are being made of survival, height, stem diameter and form. Although amenity rather than timber production is the aim, a small tree makes no visual impact, so rapid growth is important.

Trials have been established for a maximum of 5 years, so assessments can only be made on the basis of a few years' performance—the relevance of these observations to performance in the longer term remains to be seen.

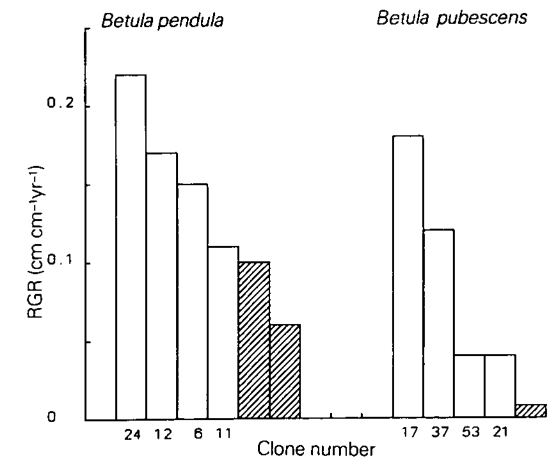

Figure 19 Performance of selected (□) and unselected (▨) clones of birch (Betula spp.) over the 4 years since planting on burnt colliery waste at Goreglen, Midlothian. (Performance assessed as height increment (cm) between planting and the end of the 4th growing season, expressed per unit initial height (RGR cm cm^{-1} yr^{-1}))

As an example, the performance of selected and unselected birches in a trial on burnt colliery waste in Midlothian is illustrated (Figure 19). This waste had been regraded, but only a limited amount of fertilizer or limestone was applied to the test area (pH 6·6 with relatively low levels of N and K). Non-destructive assessments have been, and are being, made at the beginning and end of each growing season. The mean height relative growth rate (RGR $cm\,cm^{-1}\,yr^{-1}$) of the best clone is 27 times greater than that of the worst, with clones 24, 17 and 12 growing significantly faster than the other clones; the performance of the unselected controls has been relatively poor. Comparison of growth data from a number of trials suggests that clone 24 is a consistently good performer. RGR of control material is comparatively low on all the colliery waste trials, but is similar to that of selected material on the motorway and rubbish dump sites. The trials on these sites, however, are more recently planted and assessments over a longer timespan are desirable.

Julia Wilson

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Germination of *Juncus trifidus* on bare soil, moss and gravel surfaces

Seedlings of *Juncus trifidus* are rare on moss-covered surfaces but relatively frequent where the soil has a thin surface layer of gravel. This study examines the reasons for this curious distribution.

Open *Juncus trifidus* heath occupies extensive tracts of the highest ground in the Cairngorm mountains (Plate 23). The cover of the *Juncus* tussocks is characteristically sparse (frequently less than 40%), the remaining ground being rock, bare soil, gravel or soil thinly colonized by mosses and lichens. Ingram (1958) noted that 'it is rarely that seedlings are found' and 'germination may be common only in particular years'. However, *J. trifidus* is an important seed producer on exposed high ground; in fine summers, the seeds can be freely produced and are usually of high viability. The random distribution and age structure of tussocks indicate that reproduction is primarily by seed and not vegetative (Pryor 1984).

Seedlings seem to be uncommon in most years, but were relatively numerous in 1980 on Cairn Lochan.

Medium gravel (particles 4·1–8 mm) was the most frequent type of surface colonized, but fine gravel (particles 2–4 mm) had the largest proportion of seedlings (Table 6). Bare soil had slightly more seedlings than would have been expected from a random distribution, and fine gravel about 3 times as many as expected. No seedlings were found on coarse gravel (particles 8·1–12 mm); the coarse gravel formed a deeper layer than the fine or medium gravel, and this might have inhibited seedling establishment. There were no seedlings on lichen surfaces, and only a single specimen was found growing amongst moss. Fine gravel was clearly more productive of seedlings than bare soil, medium gravel or coarse gravel, and moss and lichen surfaces were apparently unsuitable.

Some of these differences might have been attributable to a shortage of seed, or to unsuitable subsurface soil, so a trial was conducted at Glas Maol to compare germination of *J. trifidus* on pots of identical soil, which were bare, had previously been colonized by the moss *Dicranum scoparium*, or were surfaced with a shallow (8 mm) layer of gravel (particles 3·4–6·4 mm). In each case, seeds were placed on the supposed original soil surface. Results were similar to observations on Cairn Lochan, with larger numbers of seedlings on gravel than on bare soil or moss (Figure 20). In subsequent growth over 12 months, seedlings on gravel were larger, produced more leaves, and survived better than on bare soil or moss.

One of the effects of a layer of gravel is to reduce the rate of water loss from the surface (Bayfield 1983). To examine germination in relation to surface moisture loss, seeds of *J. trifidus* were placed on

Table 6. Relative frequencies of colonizable surfaces in an area of 30 m^2 at Cairn Lochan, and observed and expected numbers of seedlings

	Surface frequency (%)	Seedlings observed	Seedlings expected	Depth of gravel (mm)
Bare soil	15	30	20	0
Fine gravel	15	67	20	8
Medium gravel	37	31	48	12
Coarse gravel	9	0	11	23
Mosses	9	1	12	0
Lichens	15	0	19	0

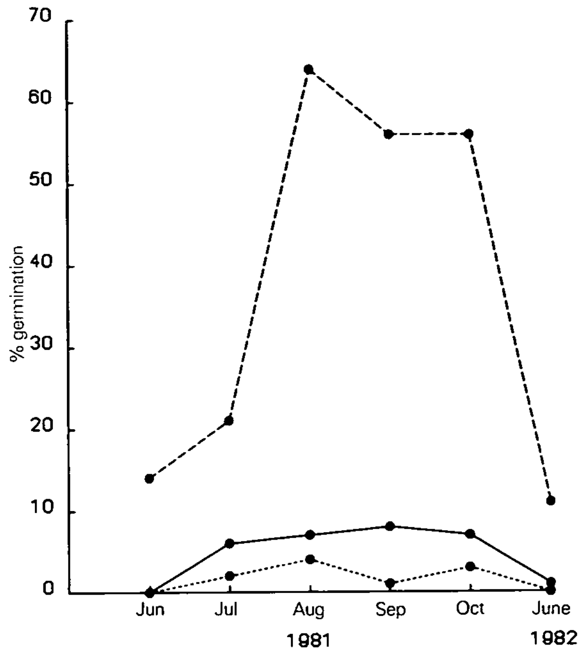

Figure 20 Percentage germination and survival of Juncus trifidus *seedlings on pots of soil with bare soil (____), moss (....) or gravel (----) surfaces at 900 m on Glas Maol, Scotland*

sheets of wet filter paper in a wind tunnel (Weatherley & Barrs 1959), and exposed to a range of water loss rates by means of screens to modify the wind blast. Germination appeared to be almost linearly related to water loss (Figure 21).

In addition to its effect on moisture loss, a layer of gravel can reduce evaporative cooling and also affect radiation reflectance. For example, in a moderate (2·5 m s^{-1}) wind in the wind tunnel, the surface temperature of moist bare ground was 16·2°C, but 17·9°C under 8 mm of gravel, and 18·8°C at the gravel surface. The proportion of reflected radiation

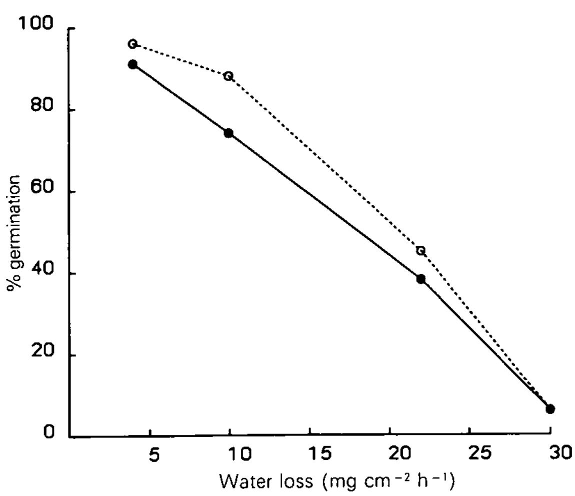

Figure 21 Effects of rates of substrate water loss on the germination of Juncus trifidus *after 7 (●) and 15 (○) days in a wind tunnel (wind speed 2·5 m s^{-1}, 20·5°C, 300 µE, 56% RH; water loss was varied by means of screens to reduce wind speed)*

from the bare soil (a mixture of peat, sand and compost) was 14% and that from gravel 23%. The greater reflectance by gravel might benefit seedlings if light was limiting to growth. However, Ludwig and Harper (1958) found poorer germination of maize on light soils than dark, apparently because of the greater radiation absorption, and consequently higher temperature, of the dark surface. In windy environments, however, soil temperature increases from incident radiation are probably less important influences on germination than temperature losses through evaporative cooling, except in the absence of wind, or when the soil surface is dry.

Moss surfaces also have a mulching effect on moisture loss, but without the apparent benefit to seedling germination seen with gravel. A germination trial in the wind tunnel, sowing seeds on to bare soil, gravel and moss surfaces, again demonstrated that germination was best on gravel surfaces, but the reduction in water loss (21 mg cm^{-2} h^{-1} from gravel pots, compared with 34 mg cm^{-2} h^{-1} on bare soil) was only slightly less than from the moss (24 mg cm^{-2} h^{-1}), which had the poorest germination of the 3 surfaces (Table 7).

Table 7. Percentage germination of seedlings on soil, gravel and moss surfaces after 7 and 20 days in a wind tunnel, and the corresponding rates of moisture loss from each surface

	Bare soil	Gravel	Moss
7 days	20	61	17
20 days	46	79	34
Water loss rate (mg cm^{-2} h^{-1})	34·1	21·1	23·6

Why is germination so poor on moss surfaces? Bayfield (1983) has found that there can be severe local drying of the surface soil under moss colonies, but a more likely explanation in the present experiments was poor seed–moisture contact. The soil surface under moss carpets is usually densely covered and permeated by moss rhizoids. Moisture in the vicinity of the soil surface is mainly held in capillary spaces in and between rhizoids, and in the capillary spaces of stems and leaf axils. Seed–moisture contact is thus poor and may not always be adequate for germination. Further work is being done to examine this possibility in more detail.

This report shows that there are important differences in the suitability of surface types for germination and early growth of *J. trifidus*. It is likely that similar phenomena occur in lowland habitats, but these effects are particularly pronounced in the harsh environment of open *J. trifidus* heath.

*N G Bayfield and P J Pryor**

* NERC CASE student, University of Aberdeen

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MANAGEMENT OF NATURAL AND MAN-MADE HABITATS

Herbicidal control of weeds on nature reserves, with special reference to lowland heaths

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

Many people interested in conservation are surprised to learn that nature reserves may have a weed problem, but many of the routine management practices on nature reserves involve some aspect of weed control. In some situations, weeds are controlled for convenience, eg to keep rides and firebreaks clear of vegetation, but, in most instances, weeds are controlled for scientific reasons, usually to prevent, or reverse, the process of succession. This control occurs on reserves where the management objective is to conserve those communities which in most cases are maintained by the intervention of man. In the past, these communities were maintained by a combination of grazing (natural and agricultural), burning and cutting—practices which prevented succession to a climax community. However, in the last 40 years, and for a variety of reasons, these forms of management have often been abandoned, with a rapid invasion by weeds as a result. The conservation of such communities poses 2 problems:

1. the need to keep good representative areas of the vegetation weed-free—ie succession must be prevented;
2. the need to control existing weed problems, and then restore the original community—ie succession must be reversed.

At present, several types of communities are at risk; for example, lowland heaths are being invaded by bracken *(Pteridium aquilinum)* and/or birch *(Betula* spp.), chalk downland is being colonized by hawthorn *(Crataegus monogyna)*, and dune grasslands are being invaded by sea buckthorn *(Hippophaë rhamnoides)*.

Cutting is the most generally accepted means of controlling weeds on nature reserves, but it is not necessarily effective in reducing weed infestations because some species recover quickly after a cutting treatment; for example, deciduous trees and shrubs can resprout from cut stumps within one year. Moreover, cutting is rarely effective first time; it usually needs to be repeated frequently or at intervals covering a fairly long timespan. For successful control, bracken needs to be cut either annually for 5–6 years, or 2–3 times per year for 3–4 years.

Cutting and other manual methods of weed control have been superseded to a large extent in agriculture, horticulture and forestry by the use of herbicides, but the potential use of these chemicals for nature conservation has not been fully appreciated. However, if the concept of weeds in nature reserves surprises conservationists, the prospect of using herbicides to control these weeds may be positively alarming. Should this be so? Can herbicides not be used in a rational manner, to help manipulate the vegetation of nature reserves towards the desired objectives?

The use of herbicides for nature conservation is, of course, completely different from the more conventional uses. When managing crops, there is usually only one non-target species, the crop, and all other plants can be considered as weeds. In contrast, on nature reserves, there is usually only one target species, the weed, and, ideally, all other species, the non-targets, must be left undamaged. Therefore, before using herbicides on nature reserves, it is essential to know the answers to the following questions.

1. What is the most appropriate herbicide to eliminate the target weed without damaging the non-target species?
2. Can the potential risks of using herbicides be reduced by changing the methods of application?

Choice of herbicide

When considering the control of weeds on lowland heath nature reserves, it is essential to use selective herbicides, ie herbicides that affect some plant species more than others, killing some species, damaging others to varying degrees, and leaving other species unaffected. It is vital, therefore, to know the spectrum of activity of available herbicides on the different species found on lowland heaths, a problem that is intensified by our incomplete knowledge of the amounts of herbicide likely to reach non-target species. In some locations, this uncertainty may not matter, for example in areas completely dominated by weeds, which have excluded the desirable vegetation. Nevertheless, even in this situation, care must still be taken to minimize spray drift. If there are interesting plant communities beneath the target weeds, then the amounts, and hence effects, of herbicides likely to reach the non-target understorey must be assessed—a difficult task depending on the density, size and form of the target species, weather on the day of spraying, spraying techniques used, and the skill of the operator.

Table 8. Herbicide treatments applied to *Calluna* and grass heaths

Treatment	Product	% active ingredient	Recommended application rate of product	Treatment rate of product
*Ammonium sulphamate	Amcide	100	Spot treatment of scrub 1 :5–1 :1 w :vol Total weed removal 500–1000 kg ha^{-1}	150 kg ha^{-1}
Asulam	Asulox	40	11·2 l ha^{-1}	11·2 l ha^{-1}
Glyphosate	Roundup	36	2–6 l ha^{-1}	5 l ha^{-1}
Hexazinone	Velpar (wettable powder)	90	2–3 kg ha^{-1}	3 kg ha^{-1}
Fosamine ammonium	Krenite	48	6–10 l ha^{-1}	10 l ha^{-1}
Picloram	Tordon 22K (salt)	24	2–8·5 l ha^{-1}	9 l ha^{-1}
2,4,5-T	Trioxone 50	50	1–3 l ha^{-1}	3 l ha^{-1}
Tebuthiuron	Spike pellets	20	30–45 kg ha^{-1}	45 kg ha^{-1}
Triclopyr	Garlon 4 (ester)	48	2–6 l ha^{-1}	6 l ha^{-1}

* Ammonium sulphamate was applied at the lowest concentration recommended for spot treatment of scrub (1 :5 w :vol), but at a lower application rate (150 kg ha^{-1}) than that recommended for total weed removal

Although little is known about the amounts of herbicide likely to reach non-target vegetation, the worst possible effects can be deduced by screening the understorey vegetation with herbicides applied at the rates recommended for controlling the weed species. In this type of experiment, damage to non-target vegetation is likely to be over-estimated, because, in practice, some, if not substantial, amounts of herbicide should be intercepted by the target species.

Screening trials have been done on 2 types of lowland heath, a *Calluna (C. vulgaris)* heath and a grass heath. At each site, 9 herbicides (Table 8) were applied at manufacturers' maximum recommended rates, and their subsequent effects on the non-target vegetation were monitored over a period of one year. Quantitative assessments of damage were made; at the *Calluna* site, 25 *Calluna* shoots were sampled, while, at the grass heath site, 20 cm ×20 cm sub-quadrats of ground vegetation were clipped. In both instances, the samples were separated into live and dead tissue, and damage expressed as the proportion of the sample killed. At the grass heath site, the percentage of rooted frequency of all species was also noted.

Asulam, fosamine ammonium and 2,4,5-T did not significantly damage the non-target vegetation on the *Calluna* and grass heaths. Triclopyr damaged *Calluna* to an unacceptable degree, but did not damage grass heath vegetation; the other herbicides, ammonium sulphamate, hexazinone, glyphosate, picloram and tebuthiuron caused unacceptable damage, and should not therefore be used for conservation purposes with conventional sprayers, or, in the case of tebuthiuron, by broadcast pellet application.

Techniques for applying herbicides

Herbicides rejected because of likely damage to non-target species may nevertheless still be used if their application can be restricted to target species. The most commonly used direct application method for controlling birch is to paint the stumps after cutting. This painting is usually done manually, but it is possible to cut and apply the herbicide in one operation, eg using hypo-hatchets, and specially modified secateurs, chain saws and brush clearers (Christensen 1984; Evans 1980; Jones & Morgan 1978; Kossuth *et al.* 1978; Peevy 1972).

Recently, rope-wick applicators have been developed for the direct application of herbicide, and have been found useful for some conservation tasks. There are 2 types—those held in the hand for small-scale tasks, and tractor-mounted versions (Plate 10) which are especially useful where there is a height difference between target and non-target species. The height of the bar carrying the rope-wick is set above the non-target species, but below the height of the target species. In this way, only target plants are smeared with the herbicide solution.

Birch control

Foliar sprays of selective herbicides and direct applications of a range of herbicides, selective and non-selective, were tested for the control of birch on lowland heaths.

The 3 selective herbicides which caused least damage to native heath vegetation, fosamine ammonium, 2,4,5-T and triclopyr, were sprayed to a mixed stand of birch and *Calluna*, each herbicide being applied:

i. to birch saplings
ii. to birch saplings which were cut the following year
iii. to birch regrowth produced as a result of cutting one year earlier.

When applied to saplings, all 3 herbicides greatly reduced their survival, fosamine ammonium being the

Table 9. Effects 2 years after applying fosamine ammonium, 2,4,5-T and triclopyr on densities of birch and *Calluna*, measured as numbers (n) of plants m^{-2} ($\log_e n+1$ plants 4 m^{-2} in brackets)

Species	Untreated	Treatment (applied 1979) Fosamine ammonium 4·8 kg ai ha^{-1})	2,4,5-T (1·5 kg ai ha^{-1})	Triclopyr (2·9 kg ai ha^{-1})	Tukey's HSD
Birch					
Established saplings	20	0	0	1	
	(4·401)	(0)	(0)	(1·059)	(0·634)
Damaged saplings	0	0	7	3	
	(0)	(0)	(3·327)	(2·606)	(0·520)
Seedlings	7	54	24	0·5	
	(3·370)	(5·376)	(4·752)	(1·099)	(1·462)
Calluna					
Established plants	12	8	11	3	
	(3·870)	(3·443)	(3·772)	(2·628)	(1·228)
Seedlings	4	6	64	1	
	(2·800)	(3·147)	(5·548)	(0·231)	(1·762)

Table 10. Effects of applying herbicides to birch regrowth produced after cutting on the densities of birch and *Calluna*, measured as numbers (n) of plants m^{-2} ($\log_e n+1$ plants 4 m^{-2} in brackets)

Species	Untreated	Treatment (cut 1979, herbicides applied 1980) Fosamine ammonium (4·8 kg ai ha^{-1})	2,4,5-T (1·5 kg ai ha^{-1})	Triclopyr (2·9 ka ai ha^{-1})	Tukey's HSD
Birch					
Stumps producing new regrowth	16	0	1	1	
	(4·157)	(0)	(0·549)	(0·621)	(1·036)
Seedlings	9	4	2	3	
	(3·591)	(2·920)	(2·247)	(2·463)	(1·462)
Calluna					
Established plants	12	56	22	17	
	(3·903)	(5·411)	(4·502)	(4·246)	(1·228)
Damaged plants	0	3	0	0	
	(0)	(2·669)	(0)	(0)	(0·614)
Seedlings	83	10	80	8	
	(5·806)	(3·737)	(5·770)	(3·443)	(1·762)

most effective (Table 9). However, the loss of saplings following the application of 2,4,5-T and fosamine ammonium was compensated by the emergence of enhanced numbers of seedlings, 24 m^{-2} and 54 m^{-2}, compared with 7 m^{-2} in the untreated plots. In contrast, triclopyr significantly decreased seedling emergence. The density of established *Calluna* was affected neither by fosamine ammonium nor by 2,4,5-T treatment; it was, however, reduced by triclopyr, so confirming the results of the screening trials. Unlike the other herbicides, triclopyr also reduced the numbers of *Calluna* seedlings.

While birch saplings can be controlled by herbicide sprays, this method, by itself, is unacceptable in most nature reserve areas because of the unwanted presence of dead trees. Where spraying was followed a year later by cutting, these dead trees were eliminated. However, a few of the saplings treated with 2,4,5-T and triclopyr, but not fosamine ammonium, produced new regrowth after cutting.

When birch regrowth, produced as a result of cutting one year earlier, was sprayed with herbicide, fosamine ammonium proved to be most effective, with a complete kill of birch stumps (Table 10). Where 2,4,5-T and triclopyr were applied, a few individuals survived treatment. Unlike sprays applied before cutting, those applied to regrowth caused no significant effect on the densities of birch seedlings after one year. After spraying the birch regrowth, some *Calluna* plants were found to be damaged and a few were killed. However, one year later, numbers of undamaged *Calluna* plants had increased to pretreatment densities, either because damaged specimens had recovered, or because numbers had been augmented by recruitment from the seedling pool.

Although fosamine ammonium, 2,4,5-T and triclopyr will reduce birch infestations when applied either to saplings or to regrowth, with only a small risk of damage to non-target vegetation, the risks can be reduced further by applying herbicides to cut stumps. In a further trial, 7 herbicides (selective–fosamine ammonium, 2,4,5-T and triclopyr; non-selective–ammonium sulphamate, glyphosate, hexazinone and tebuthiuron) were applied to birch stumps immediately after cutting. All herbicides, except tebuthiuron, which was applied around the stumps in pellet form, were applied by paint brush. Additionally, crystals of ammonium sulphamate were also applied to cut stumps. Some of the herbicides applied by painting were tested in water and oil-based carriers, and some were examined at a range of concentrations; all treatments were applied in autumn, spring and summer. The entire range of herbicides tested reduced birch regrowth from cut stumps in at least one season of the year, and a summary of successful treatments is shown in Table 11. Although direct application of herbicides to target species reduces risk of damage to the non-target understorey, risks can be reduced further by the direct application of a selective herbicide (eg fosamine ammonium, 2,4,5-T and triclopyr).

The direct application of herbicides to cut stumps gives reserve managers a greater degree of flexibility than spraying of foliage, because controlling birch by cut stump treatment can be done at any time during the year. Obviously, foliar spraying of herbicides can only be done when the leaves are present during the summer.

Bracken control

The second species posing weed problems on lowland heaths is bracken. It can be controlled by several herbicides, including the selective herbicide asulam, and the non-selective dicamba and glyphosate

Table 11. A summary of successful herbicide treatments to cut birch stumps; herbicides shown below successfully killed or suppressed regrowth production

Selective herbicides

Season of application	Fosamine ammonium	2,4,5-T	Triclopyr
Autumn	50% in water	5% in oil	5% in oil 10% in water
Winter	10% in water	5% in oil	5% in oil 10% in water
Spring	10% in water	5% in oil	5% in oil 10% in water
Summer	10% in water	5% in oil	5% in oil 10% in water

Non-selective herbicides

Season of application	Ammonium sulphamate crystal	Ammonium sulphamate 40% w:vol	Glyphosate	Hexazinone pellets 5%	Hexazinone pellets 20 g stump^{-1}
Autumn	×	×	5% in oil 10% in water	×	√
Winter	√	√	5% in oil 10% in water	√	√
Spring		√	5% in oil 10% in water	√	√
Summer	√	√	5% in oil 10% in water	×	×

Table 12. Effects of applying asulam (4·4 kg ai ha^{-1}) in 1978 on the standing crop of dry bracken (g m^{-2}) in the 5 succeeding years. Treatment means ± standard errors, and the % reduction compared to untreated means are presented

Site	Treatment	1978 pre-spraying	1979	1980	Year 1981	1982	1983
Calluna heath	Untreated	594 ± 45	398 ± 70	420 ± 40	437 ± 40	524 ± 26	520 ± 42
	+asulam	593 ± 40	1·2 ± 1·1	15·2 ± 11·6	25·7 ± 14·2	181 ± 71	124 ± 77
	% reduction	—	99·7	96·4	94·1	65·4	76·2
Grass heath	Untreated	414 ± 48	638 ± 92	472 ± 49	575 ± 116	809 ± 115	715 ± 159
	+asulam	447 ± 36	7·3 ± 5·3	14·8 ± 8·4	82 ± 33	321 ± 53	505 ± 126
	% reduction	—	98·8	96·9	85·9	60·3	29·4

Table 13. Effects of applying asulam (50% asulox product) in 1981, using a rope-wick applicator, on the density of bracken fronds (fronds m^{-1}) in the following 2 years

Treatment	1981 (pre-treatment)	1982	1983
Untreated	5·1	2·7	5·6
One pass of applicator	5·8	0·6	0·9
Two passes of applicator	4·9	0·1	0·1
LSD ($P<0{\cdot}05$)	2·6	1·8	3·2

(Fryer & Makepeace 1978). However, as asulam did not damage heath vegetation in the screening trials, further investigation was restricted to the use of asulam on dense bracken at 2 sites: a *Calluna* heath and a grass heath. At both sites, asulam gave good bracken control (99% reduction) in the year after spraying (Table 12). Thereafter, there was a recovery, notably at the grass heath site, where there was a 30% reduction in the standing crop of bracken after 5 years, compared with a 70% reduction at the *Calluna* heath. In addition to reinvasion by bracken, the conservationist is faced with the problem of restoring native heath vegetation which has been suppressed, probably by the large accumulations of bracken litter (Plate 11).

Asulam, in addition to being applied in conventional foliar sprays, has been sprayed on bracken foliage using newly developed ultra low volume (ULVA) sprayers. This type of sprayer uses the same amount of herbicide for a given area, but requires only 5–20 litres per hectare of diluent, compared with the large volumes (200–1000 l ha^{-1}) required for conventional sprayers. As ULVA sprayers are also lighter, and less cumbersome to use than conventional sprayers, they may be used increasingly in the future for conservation purposes. In trials of this type of equipment, the standing crop of bracken was less than 1% of that in the untreated plots in the year after spraying. This reduction persisted for at least a further year.

It is also possible to apply herbicides directly to bracken fronds, using a rope-wick applicator. After applying asulam (50% asulox in water) by this means to scattered bracken invading a grassland nature reserve, there was a significant reduction in frond density (Table 13), with no visible signs of damage or scorch marks. Making 2, instead of one, pass of the applicator did not significantly affect the outcome.

These results indicate that bracken can be controlled effectively by asulam, whether applied as a foliar spray or by rope-wick applicator. However, as yet, glyphosate, a non-selective herbicide, is the only herbicide recommended for general use in these applicators; further research on the suitability of using asulam, a selective herbicide, should be extended to consider the use of lower concentrations than tested previously (ie <50% asulox).

Conclusions

Potentially, herbicides have an important, and increasing, role in the control of weeds in nature reserves. However, before herbicides are used for conservation purposes, their effects on a range of target and non-target species must be explored, and an appropriate method of application chosen. If a herbicide does not damage non-target vegetation in screening trials, then it can be used with confidence in the field. However, the range of acceptable herbicides is increased by using a direct method of application. Together, the correct choice of herbicide and method of application will minimize greatly the risks to the non-target vegetation which is to be conserved.

Despite these improvements in our understanding of herbicide use for nature conservation, it is clear that herbicides will never be the sole panacea for vegetation management, especially if succession has proceeded and there is already a dense weed problem. It may be possible to eliminate the weeds, but positive steps will be needed to restore and maintain the desired plant communities. In this respect, the use of herbicides is a complement to the existing techniques of vegetation management, eg grazing, cutting and burning (Lowday 1984; Marrs 1984a, b). A word of caution, however, is necessary—the deductions made in this report are based on observations made in 2 habitats, *Calluna* and grass heaths. While it would be foolish not to extrapolate to other sets of weed problems, investigations in other communities maintained by man are needed urgently.

R H Marrs and J E Lowday

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Native and naturalized species of plants as renewable sources of energy in Great Britain

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

Contract reports to the Department of Energy have surveyed the productivity and extent of British vegetation (Callaghan *et al.* 1978), and suggested scenarios for the production of significant quantities of fuel by direct combustion, thermal conversion to flammable gases or liquids, anaerobic digestion to methane gas and fermentation to ethanol. Subsequent reports focused on the exploitation of natural vegetation as a source of biofuels (Lawson *et al.* 1980; Callaghan *et al.* 1981), and have selected highly productive species which could be established in plantations as 'dedicated energy crops'. Other species have been identified which, although less productive, already cover sizeable areas and could be harvested as 'opportunity energy crops' with little disturbance to existing patterns of land use.

The current study is concerned with 3 promising candidates as energy crops—bracken *(Pteridium aquilinum)*, cordgrass *(Spartina anglica)* and Japanese knotweed *(Reynoutria japonica)*—and has tested the ability of these species to sustain yields when harvested once a year on the same date, but under 3 different harvesting rotations (ie treatment Y1 = harvested in 1980, 1981, 1982 and 1983; Y2 = harvested in 1981 and 1982; and Y3 = harvested only in 1982) (Plate 13). The seasonal variation in yield was assessed by harvesting on one of the 4 dates representative of the development of the species. Each treatment received 4 fertilizer applications (0, 0·5, 1 and 2 t ha^{-1} of Fisons 'Regular' 20:10:10 NPK granules).

Plantations of Japanese knotweed have taken 4 years to develop yields approaching those in natural communities, but increased planting densities of up to 25 rhizome pieces m^{-2} produce a closed canopy and high yield more rapidly.

Yields of the 2 'opportunity crops' differed due to annual weather variations by up to 37% in bracken and 81% in cordgrass. Low yields were observed in 1982, particularly from the repeatedly harvested plots, because the removal of surface litter allowed unusually heavy spring frosts to damage the young growing buds. This effect was especially observed with bracken (Figure 22).

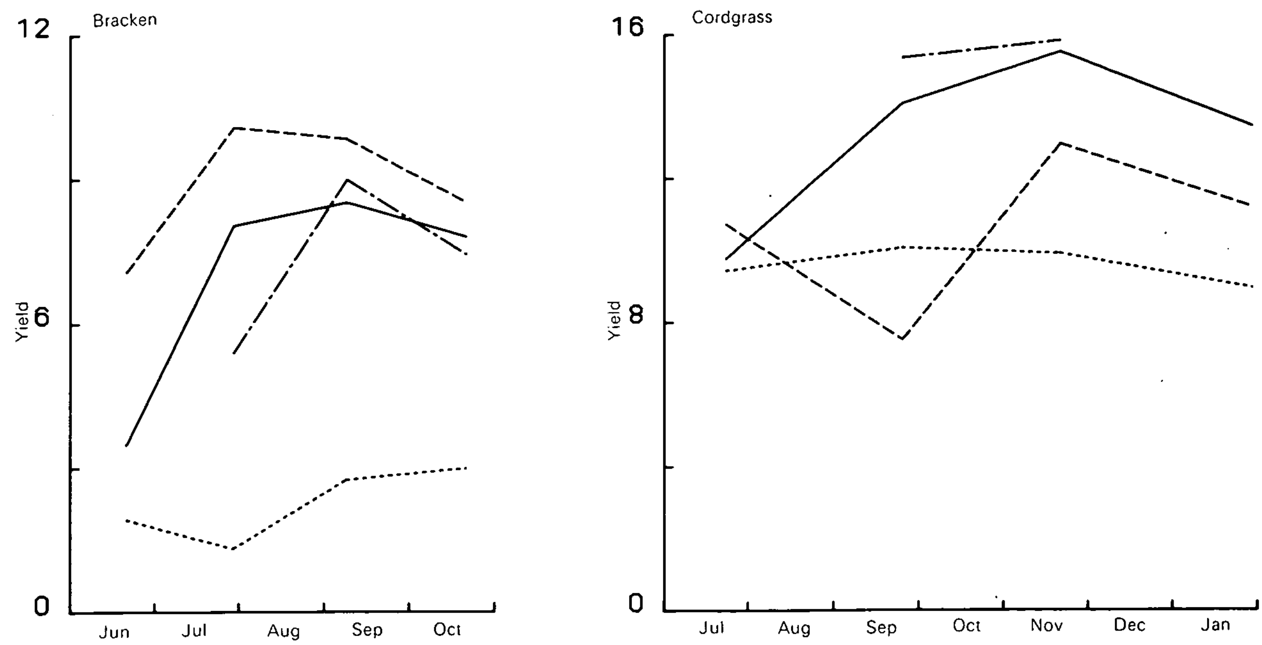

Figure 22 Mean yields (t ha^{-1} yr^{-1}) from 4 successive years of harvesting natural stands of bracken and cordgrass, with 4 harvests through the growing season (——) 1980, (– – – –) 1981, (. . . .) 1982, (–.–.–) 1983

Table 14. Costings per dry tonne of bracken (20 GJ or 3·4 barrels oil equivalent) assuming yields of 6 t ha^{-1} yr^{-1} for direct burning and gasification, and 9 t ha^{-1} yr^{-1} for anaerobic digestion

	Direct burning £	Gasification to methanol £	Anaerobic digestion to methane £
Fertilizer costs	6·00	6·00	14·00
Cutting and collection	13·00	13·00	12·80
Densification	26·23	8·00	?
Storage (1 year)	2·00	6·00	32·00
Transport (20 km)	3·00	3·00	12·00
Conversion costs	0·00	44·70	38·75
Total cost	50·23	80·70	109·55
Conversion efficiency	75%	50%	45%
Total cost per GJ produced	3·34	8·07	12·17
Price per GJ of conventional fuel	1·58[a]	4·56[c]	2·94–5·50[e]
	3·43[b]	10·02[d]	8·90–9·85[f]
Price per barrel oil equivalent	19·77	47·77	72·06

Where a = price of coal to large industrial users
b = price of coal to domestic users
c = price of pre-tax motor spirit
d = price of post-tax motor spirit
e = price of natural gas at 80–800 therms yr^{-1}
f = price of propane assuming 14–47 kg cylinders

Note that transport and storage costs are not pro-rata because:
i. less densification is required for gasification than direct combustion, with a consequent increase in bulk
ii. summer biomass harvested for anaerobic digestion contains a lot of water, thereby increasing both volume and weight

The effects of repeated harvesting depend on weather and the season of harvest. Bracken harvesting in spring and early summer depletes yields in subsequent years, while later harvests have less effect on the vigour of the plant because its nutrients and food reserves have already been, in large measure, translocated to below-ground perennial storage organs.

Natural vegetation, by definition, is not cut routinely, and optimum harvesting cycles have yet to be defined. Periodic rest years may have to be introduced to allow rhizomes to recover from the likely depletion of their reserves, but average peak yields of 7·6 t ha^{-1} and 13·6 t ha^{-1} have been sustained from bracken and cordgrass respectively after 4 years of annual harvesting, and there is no evidence of a continuous decline.

Tests have demonstrated the technical feasibility of producing combustible pellets from senescent bracken. Preliminary results indicate that this pelletized fuel is also financially viable, but that anaerobic digestion, alcoholic fermentation and thermal conversion to methanol are not yet economic prospects (Table 14). Further investigation is required of the possible co-generation of food, fuel and fibre, which may alleviate fears over land use competition and increase the financial attractiveness of biofuels.

T V Callaghan, G J Lawson, R Scott and Alison M Mainwaring

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Impacts of agricultural land drainage on wildlife

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

The Nature Conservancy Council has commissioned ITE to assess the impact of agricultural land drainage on wildlife communities. Land drainage is intended to upgrade the quality of farmland and, therefore, to encourage higher food production. Because its primary aim is to change the soil water regime, land drainage constitutes 'one of the sharpest points of conflict with conservation'.

Because most drainage schemes take place on existing farmland, rather than on areas newly reclaimed for farming, the agricultural industry has tended to under-rate the impact of its work on wildlife. Spokesmen for the industry have often overlooked the fact that the schemes are intended to destroy the very artefacts of the farming landscape that have, up to now, been so outstanding for their wildlife interest. The biological interest of the Somerset Moors, for example, does not reside in the primeval relicts of natural plant and animal life—none survives—but rather in the abandoned peat cuttings, ditches (rhynes) and pastures that have been created during the various phases of agricultural drainage and reclamation. If the experience of the Romney Marsh is any guide, the scope for transforming the surface and under-drainage of a wetland is now so considerable, and the impact of more intensive forms of grassland management and of cultivation is so extensive, that few, if any, refuges for pasture and pasture–dyke species may survive.

There are 4 priorities for research, namely:

i. to record the chronology and extent of changes in drainage regime;
ii. to record changes in the pattern of agricultural land use and management;
iii. to record changes in the wetland communities, and selected plant and animal species within those communities;
iv. to identify the reasons for changes in biological interest, where observed.

Despite the many publications on land drainage, and a great deal of active research, there is comparatively little information on changes in field drainage and ditching on specific tracts of land. For the first time, ITE has been able to plot the incidence of some of these schemes for the period 1940–79 over extensive areas of countryside, namely the Romney Marsh and Pevensey Levels, the Somerset Moors and Levels, and the Misson Levels on the Humberside/Nottinghamshire/south Yorkshire border. It is estimated that about 60% of the Romney Marsh, 30% of the Misson Levels, and 10% of the Somerset Levels and Moors have experienced the direct effects of tile drainage schemes.

Drainage is intended to increase the productivity of existing grass or ploughed land, or, in an increasing number of instances, to prepare the way for the conversion of long-established grassland to arable production. The precise relationship may vary both in time and place. In parts of the Romney Marsh, tile drainage was regarded in the late 1960s as a way of ensuring that potato crops could be lifted in wet autumns. This view encouraged improvements to arterial drainage which, in turn, made possible the ploughing of land that had previously only been suitable for grass.

The availability of historical information on the distribution and abundance of wildlife species varies widely between localities. Among the sources used are published Flora, the field notes and specimens of

Plate 2 i. Old Romney prior to improved drainage. Air view (June 1956) of village, looking south-east. The pastures within and around the moat (TR 033254) can be seen on the left of the photograph. Patches of rush are visible on the right (Crown copyright reserved)

ii. Old Romney at the time drainage was taking place. Air view (June 1956) of village, looking north-west. The moat and pastures are visible upper right. The drainage scheme in foreground has a herring-bone pattern of tiles, and involves straightening of existing dykes (June 1958) (Crown copyright reserved) naturalists, and further field work. ITE has used a stratified random sampling approach to its surveys. The length of ditch is measured in representative areas of each soil type, and sites are allocated in proportion to the total population of ditches (ie calculated total lengths of ditches in the entire area of each soil series). The sites are located using random grid co-ordinates and 100 m samples recorded, examining both bank and water. Other sites are chosen where earlier site-specific data are available. All the information is subjected to TWINSPAN as a means of classifying the vegetation types and identifying correlations between environmental factors and vegetation samples. It is essential that a proportion of sites is visited on more than one occasion, so as to ensure that conclusions are not based entirely on a 'single frame' in the ever-changing 'picture' of the individual ditches.

The kind of change taking place in the Romney Marsh may be illustrated by reference to the old moat (TR 033254), north of the village of Old Romney (Plate 2). An almost contemporary air photograph confirms that, when Dr Francis Rose visited the site in September 1959, the moat and surroundings were intensively-grazed pasture, with extensive patches of rush (almost certainly *Juncus inflexus).* The grasslands were converted to arable after being under-drained in the 1960s (G Finn-Kelcey, pers. comm.), and they now mainly support wheat crops. The species list compiled by Dr Rose in 1959 suggests that the moat supported a characteristic pasture-dyke flora, made up of low-growing, light-demanding plants, associated with waterlogged soils or water margins. They included *Myostis scorpioides, Galium palustre, Lycopus europaeus* and *Nasturtium officinale.* When the water table was lowered, and the pasture ploughed in 1960s, these species were probably displaced by tall emergents. When surveyed in September 1981, the moat had been colonized by species of reed swamp and coarse, marshy vegetation, namely *Calystegia, Solanum* and *Salix atrocinerea.* The local rarities, *Wolffia* (a member of the duckweed family) and *Ceratophyllum submersum* (spineless horn-wort), had disappeared from the species list. A further visit in 1983 showed little change from 1981.

Taking the Romney Marsh as a whole, there has been an increase in the distribution and abundance of 25 vascular plants, as recorded over the last hundred years. The increase may, however, be more apparent than real; there was considerable taxonomic confusion over many of the species. Those which experienced a real increase were either introductions or species that could not tolerate grazing. Available records also suggest that 70 species experienced a reduction over the same period. Of these natives of shallow pasture ditches, unpolluted open water, or wet unimproved coastal pastures, over half are now thought to be extinct.

J O Mountford and J Sheail

Leafhopper populations on the Park Grass Experiment, Rothamsted

The Park Grass Experiment to test the effects of fertilizers on permanent meadow grassland is a well known agricultural experiment in Britain. It began as an agricultural trial, but is now of much wider interest and importance to a variety of biological disciplines, notably ecology. Established in 1856 on a 3·24 ha level field near Rothamsted Manor, Harpenden, Herts, the experiment has been maintained with only minor modifications ever since. There are 20 numbered plots, with plots 4 and 11 being split (Figure 23). Plots 1–13 were established in 1856 to test the effects of organic manures, mineral fertilizers and nitrogen as ammonium sulphate. Plots 14–17 were added in 1858 to test nitrogen applied as sodium nitrate. Acidification caused by successive applications of ammonium

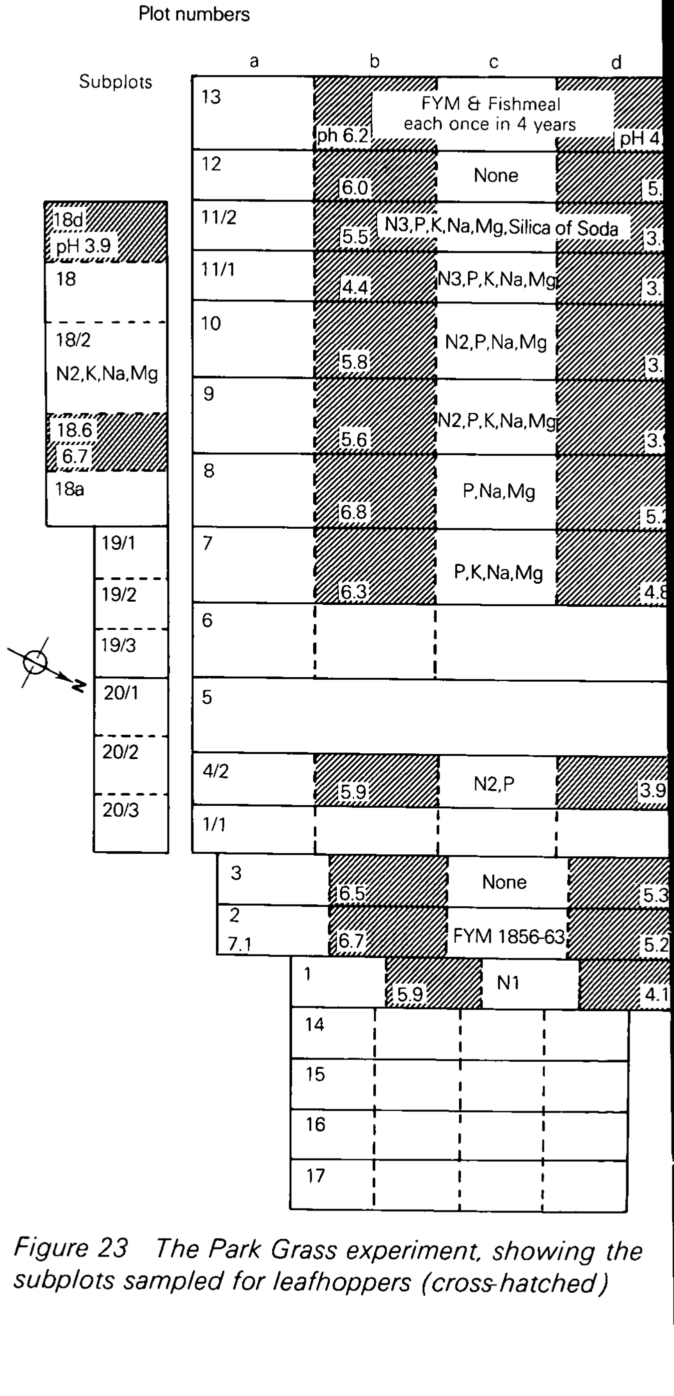

Figure 23 The Park Grass experiment, showing the subplots sampled for leafhoppers (cross-hatched)

sulphate led to the imposition of a differential liming programme which was formalized in 1965, when each plot was divided into 4 subplots (a–d), with the aim of establishing soil pHs ranging from pH 4 in the 'd' subplots to pH 7 on the 'a' subplots.

Through the Lawes Agricultural Trust and staff at the Rothamsted Experimental Station, permission was obtained to sample leafhoppers (and other insects) from a selection of the unreplicated experimental plots in 1977 and 1978. Although the plots are large by botanical standards (maximum 0·2 ha), they are small for studies of animals. Five samples were taken in 1977 and 1978 at about fortnightly intervals from (i) 14 July–8 September 1977 and (ii) 3 August–25 September 1978. Ten plots, 1, 2, 3, 7, 8, 9, 10, 12, 13 and 18, and 3 split plots, 4/2, 11/1 and 11/2, were included, the samples being restricted to 'b' and 'd' subplots. Areas of 1·1 m² of grassland were sampled with a D-Vac insect net.

Because of their agricultural origins, the Park Grass plots are cut (harvested for hay), usually in June, a treatment that produces a uniform sward structure but which reduces the abundance of leafhoppers (Morris 1981). The most abundant species was *Psammotettix confinis*, which was found on every subplot; it accounted for 56% of the leafhoppers (Auchenorhyncha) and was particularly abundant on subplot 1(d), where numbers reached 833 m^{-1} on 8 September 1977. In contrast, the maximum density on the same day on subplot 1(b), which was less acid, was only 41 m^{-1}. While large numbers of *P. confinis* have been found on other subplots, eg 18(d), the great abundance on subplot 1(d), which is persistent (Dr L R Taylor, pers. comm.), has not been explained. Other widespread species of leafhoppers included *Aphrodes serratulae, Deltocephalus pulicaris, Arthaldeus pascuellus* (but in small numbers), *Euscelis incisus, Macrosteles laevis* and *M. sexnotatus, Hyledelphax elegantulus* and *Javesella pellucida*. While *Doratura stylata* was caught on 20 subplots in 1977 (a total of 194 individuals), it was found on only 7 in 1978 (15 individuals); *H. elegantulus* and *J. pellucida* were more abundant in 1978 than 1977.

A total of 47 species of leafhoppers was recorded, but several of these species were restricted to individual specimens possibly having strayed from trees and/or tall herbs. More than 10 individuals were recorded, over the 2 years, of 21 species, 14 of which are multivoltine (ie they produce more than one brood per year). When the leafhopper fauna of the non-calcareous Park Grass was compared with those of 4 established calcareous grasslands, which included unmanaged (control) plots (see pp 40–41), it was found that the number of univoltine species was significantly smaller ($\chi^2 = 8{\cdot}5$, $P < 0{\cdot}01$), a reflection of the effects of cutting for hay.

Although it is known that nitrogen availability is an important factor affecting the abundance of Auchenorhyncha (Waloff 1980), the effects of nitrogenous fertilizers are difficult to assess on Park Grass, primarily because the effects of N and other nutrients are confounded, and secondarily because of the lack of replicate main plots. However, differential liming in subplots 'b' and 'd' has produced some distinct effects. On average, more leafhoppers were collected from the more acid 'd' subplots than from the nearer neutral 'b' subplots. In contrast, numbers of species and diversity were greater on the neutral, than on the acid, subplots (Table 15). Differences were larger and more obvious in 1977 than in 1978.

Table 15. Mean numbers m^{-2} of leafhoppers trapped in 1977 and 1978 from subdivisions of the Park Grass plots at Rothamsted. Subplots 'b' were treated with more lime than subplots 'd'

Leafhopper species	1977 Near neutral subplots 'b'	1977 More acid subplots 'd'	1977 Significant difference between 'b' and 'd'	1978 Near neutral subplots 'b'	1978 More acid subplots 'd'	1978 Significant difference between 'b' and 'd'
Neophilaenus lineatus	0·8	0·2	Signif	0·5	1·3	NS
Aphrodes serratulae	6·7	2·2	Signif	5·0	1·2	Signif
Deltocephalus pulicaris	9·2	10·4	NS	5·1	12·5	Signif
Psammotettix confinis	28·5	290·2	Signif	7·5	79·3	Signif
Euscelis incisus	15·2	4·8	Signif	14·3	4·4	Signif
Streptanus aemulans	0·5	0	Signif	0	0·1	NS
Macrosteles laevis	5·0	3·8	Signif	9·5	6·1	NS
Hyledelphax elegantulus	5·0	0·8	Signif	13·8	2·1	Signif
Javesella pellucida	4·5	0·7	Signif	18·8	8·3	Signif
Total number of leafhoppers including unlisted species	105	334	NS	114	169	NS
Numbers of species	13·2	9·0	Signif	12·4	10·7	NS
Diversity	2·55	1·49	Signif	2·48	2·02	NS

Twenty-nine per cent of the variation in species diversity was attributable to pH ($P < 0{\cdot}01$), but 44% of the species in which only a single individual was recorded were omitted. Numbers of *Euscelis incisus, Hyledelphax elegantulus* and *Javesella pellucida* were significantly larger in the neutral, than in the acid, subplots. In contrast, numbers of *Psammotettix confinis* were much larger in the acid subplots.

It remains to be seen how the occurrence of leafhoppers is related to the botanical composition of the different Park Grass plots. In the meantime, by producing soil pHs ranging from 3·7–6·8, the application of lime and other fertilizers has created a diverse and interesting array of leafhoppers, despite the impoverishment caused by hay-making.

M G Morris and R Plant

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Colonization of sown calcareous grasslands by leafhoppers (Hemiptera, Auchenorhyncha)

The destruction and alteration of areas of semi-natural lowland grassland by agricultural intensification have focused attention on their recreation; in a more general context, the reconstruction of ecosystems has been identified as one of the important problems for conservation in the future (Bradshaw 1977). In April 1973, a field experiment was established at Royston, Herts, to examine the colonization of 2 different sown grasslands by invertebrate animals. There was established chalk grassland about one km away.

Four replicate plots of 2 different seed mixtures were arranged in a randomized block design, each plot measuring 30 m × 30 m. Mixture A, of coarse grasses, contained *Dactylis glomerata, Festuca arundinacea, Phleum pratense* and *Lolium perenne*. Mixture B of fine-leaved grasses included *Festuca rubra, F. ovina, Poa pratensis, Agrostis tenuis* and *Cynosurus cristatus*. Before the swards were consolidated, the occurrence of invertebrates was assessed with pitfall traps (May–September 1973). Between 20 September 1973 and 10 December 1975, the plots were sampled with a D-Vac insect net. Although Heteroptera (plant bugs), like Auchenorhyncha (leafhoppers and froghoppers), were identified to species, only the latter, the more abundant group, are considered in this report.

The most numerous first colonists on both grassland types were the well-known opportunistic species *Macrosteles laevis, M. sexnotatus* and *Javesella pellucida*. The last of these species had established a breeding population by September 1973 on both types of grassland. In both 1974 and 1975, the second generation, but not the first, was significantly more numerous on the coarse grassland A than on the finer sward B. *M. laevis* and *J. pellucida* (though not *M. sexnotatus)* were more abundant in 1974 than in 1975, suggesting that by this time these first colonists were already at a disadvantage compared with later ones.

Apart from a few overwintering species, adult leafhoppers are not usually abundant in grasslands until July; they are then often numerous until November, persisting even until December. At Royston, mean species diversity was consistently higher on mixture A than on B for the latter half of the year. Mean species richness (number of species recorded) was also generally higher, though not consistently so, on grassland A (Figure 24). Numbers of species were generally larger in 1975 than in 1974.

The establishment of populations of different species was very variable. Some species characteristic of only one type of grassland were well-established in 1974: *Cicadula persimilis* and *Zyginidia scutellaris* on the coarse grassland A, and *Paluda adumbrata* on the fine-leaved grassland B. Other species were much more numerous in 1975 than 1974: *Stenocranus minutus* and *Mocydia crocea* on grassland A, and *Deltocephalus pulicaris* on B. A few species occurred in rather small numbers, but, in aggregate over the 2 years 1974 and 1975, were significantly more abundant on one particular grassland type: for example, *Crimorphus albomarginatus* and *Dikraneura variata* on B, *Neophilaenus lineatus* on A.

Species that produce only one brood per year (univoltine) were not always the later, or the less abundant, colonists, when the 2 years are compared, eg *N. lineatus*. Others, such as *S. minutus*, were markedly more numerous in 1975 than in 1974, but this also applied to several of the species that have 2 broods (bivoltine), such as *D. pulicaris*. With totals of more than 10 individuals being trapped, 8 univoltine and 11 multivoltine species (2 or more broods) were regarded as breeding. These numbers were compared with those occurring among established faunas of calcareous grasslands at (i) Barton Hills, Beds (Morris 1971), (ii) Aston Rowant NNR, Oxon (Morris 1973), (iii) Castor Hanglands, Cambs (Morris 1981a, b), and (iv) Old Winchester Hill NNR, Hants (unpublished). At these established sites, mean numbers of breeding species were $34{\cdot}25 \pm 4{\cdot}07$, with mean numbers of univoltine and multivoltine species of $14{\cdot}25 \pm 1{\cdot}97$ and $20{\cdot}0 \pm 1{\cdot}87$ respectively; there were no significant site effects. However, numbers of breeding species were significantly smaller at Royston (19,

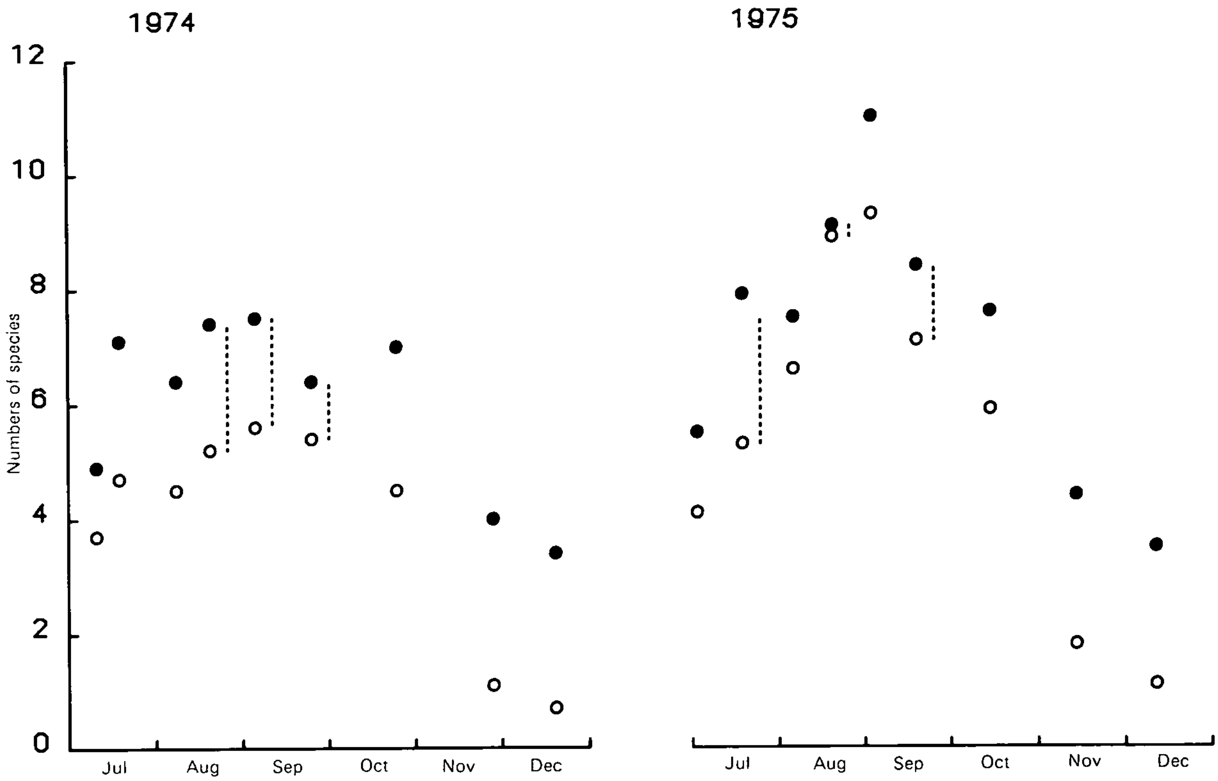

Figure 24 Mean numbers of species per standard sample in sown grassland at Royston, Herts, July–December 1974 and 1975
●, grassland A (coarse); ○, grassland B (fine)
A and B values joined by dotted lines are not significantly different

$\chi^2 = 6{\cdot}79$, $P < 0{\cdot}01$), as were numbers of univoltine species (8, $\chi^2 = 7{\cdot}20$, $P < 0{\cdot}01$). As numbers of multivoltine species at Royston and the established sites did not differ significantly, the poverty of the breeding fauna at Royston is attributed to the lack of univoltine species.

Despite this poverty of species compared with established chalk grassland, the experimental grasslands supported many more species within 3 years of sowing than occur on ryegrass leys (Morris & Rispin 1980).

M G Morris

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SURVEY AND MONITORING

Vegetation dynamics in Lake Ichkeul, Tunisia

Lake Ichkeul is a brackish lake basin, 16 km long, 10 km wide, in Tunisia. Fresh water is supplied by 5 rivers, primarily during winter, but the lake is connected to the sea by a channel, *via* a saline lake (Bizerta). Salinity in Lake Ichkeul varies with season, the water being fresh at the end of winter but, with net flows from the sea during the summer, it later becomes strongly saline. The salinity and its duration vary yearly according to the wetness of the seasons. These, in turn, affect the extent and annual biomass of aquatic macrophytes and of marsh vegetation surrounding the lake.

The Tunisian government plans to dam the freshwater rivers to provide stored water supplies. The scheme will undoubtedly have an impact on the lake salinity and the vegetation composition. As the lake is a major winter wildfowl refuge for European birds, the EEC is funding an impact assessment by University College London (UCL) (Hollis *et al.* 1983). ITE is contributing by providing an historical perspective, examining aerial photographs and other existing remotely sensed imagery, and is looking at the dynamics of the dominant marsh species *Scirpus maritimus* and one of its main competitors *Scirpus litoralis*. The information from these studies, together with other survey and experimental data, will enable us to model past vegetation dynamics relative to hydrology. Extrapolation of the results will help UCL to predict the impact of reductions in freshwater supply to the lake, and make recommendations for possible schemes to minimize the ecological impacts (Hollis 1983).

Changing vegetation patterns 1948–1983

Vertical aerial photographs of Lake Ichkeul had been taken in winter 1948–9, summer 1963, and winter 1974. From 1975, Landsat has collected regular multispectral scanner data over the site. This series of images of the area contributes the background data to the environmental impact assessment by UCL.

The photographs were mapped using a Stereo Zoom Transfer Scope to provide accurate transfer of outlines on to copies of topographic maps at 1:14 000 scale. Thirteen types of vegetation were recognized on the summer 1963 photographs (Plate 3), including, especially, *Scirpus maritimus* and *Scirpus litoralis* marshes, *Phragmites australis* beds, and *Potamogeton pectinatus* in the lake itself. Winter photographs showed less vegetation, due to the partial submergence of marsh vegetation and breakdown of *Potamogeton*. Photointerpretation was checked in the field in 1983, so as to ensure the accuracy of the map data.

The photographs showed aspects of man-made changes to the marshes and their drainage, in particular highlighting former cultivation patterns, management of drainage by straightening channels, embanking to form canals, and cutting new channels redirecting flows for marsh reclamation. The construction of bridges and a pipeline crossing the outflow of Lake Ichkeul may also have changed the lake hydrology. Such changes will be considered when assessing the nature of hydrologically based changes in the marsh vegetation.

Phragmites australis is tall enough to emerge above the winter flood level and remains visible on all aerial photographs. It forms a nearly continuous ribbon some 30 m wide, fringing most of the lake except the north-eastern shoreline. The maps show that it has advanced at rates varying up to 17·4 m yr^{-1} between 1949 and 1963, but more typically the rate of advance is between 0·5 and 1·0 m yr^{-1}. The rate between 1963 and 1974 has perhaps slowed, with less extensive areas of rapid colonization, but the analysis of the changing patterns of *Phragmites* requires further attention before factors controlling its spread are understood. As the species represents the primary colonizer in marsh formation, and so sets the pace of marsh encroachment on the lake, its dynamics may be very important to an understanding of what will happen in the changed hydrological regime after the dams have been completed.

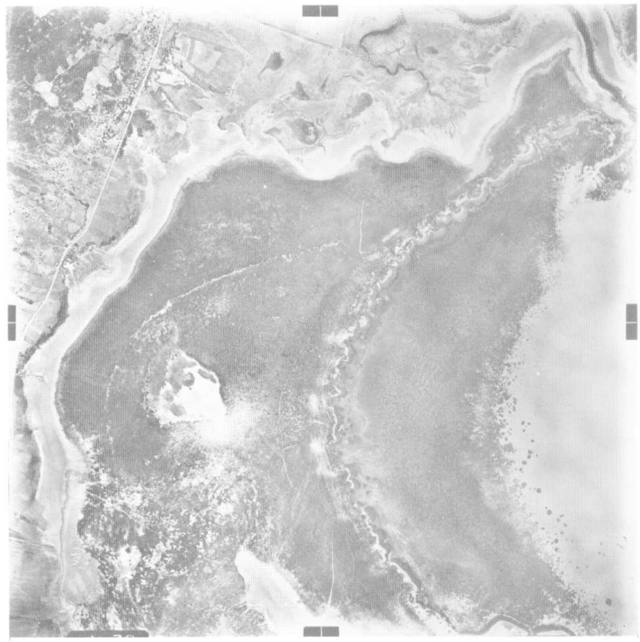

Plate 3 The Melah marsh, Lake Ichkeul, summer 1963. The photograph shows, from west to east: road, agricultural land, bare mud, Scirpus *marshes, as far as the bare mud behind the crescents of* Phragmites, *and then* Potamogeton *growing out into sediment-laden lake water. This transect, as described, runs about 4 km from road to open water*

The vegetation outlines shown on the maps will be digitized, together with contour information shown on the topographic maps, to help model the relationship between vegetation type, topographic level and submergence. The photographically derived data provide a useful comparison for checking with the outlines of vegetation as seen on Landsat imagery, which continues the sequence of coverage where the photographs finish.

Cloud-free Landsat scenes of the area were numerous and the extent of their use was more limited by cost and time constraints than by availability. The imagery was analysed on a GEMS image analysis system. Although scenes were obtained for all seasons to show the annual cycles of change, the study concentrated on mid-summer (typically June) imagery which showed the marshes after floodwater had receded, but before summer drought had set in. By June, the *Potamogeton* in the lake had grown almost to its full extent in area.

Geometrically corrected scenes were used for analyses, including trials of a range of contrast stretches, principal component analyses and arithmetic manipulations, but, in practice, a simple auto-linear stretch provided excellent clarity, quite adequate for the detection, for example, of *Scirpus* marshes, bare ground, open water, and *Potamogeton* (Plate 15).

Eight classes were identified in a supervised classification of the scenes, using the GEMS software (Plate 16). Of 20 scenes obtained for the period 1975–82, 12 were analysed using the 'CLASSIFY' software. These provided cover for each of the years from 1975 to 1982 inclusive, with 1977 imagery analysed for each season.

The record of annual changes in vegetation patterns provides a valuable opportunity to relate these functions to the broad range of climatic and hydrological data collected at Lake Ichkeul since 1952.

The extent of actively growing *Scirpus* varies markedly with season, reaching a maximum when lake level drops in May–June, decreasing again, as soil moisture deficits increase, in July–August.

Potamogeton cannot be successfully detected remotely until June–July when the water level is low. Superimposed on this seasonal factor affecting the area surveyed is a strong variation between years (Figure 25). The regression of the area of *Potamogeton*, as calculated from pixel counts, on several variables quantifying freshwater supply, lake level and salinity in current and preceding seasons suggests that the level of the lake at the time of the survey is the most useful predictive variable. The regression

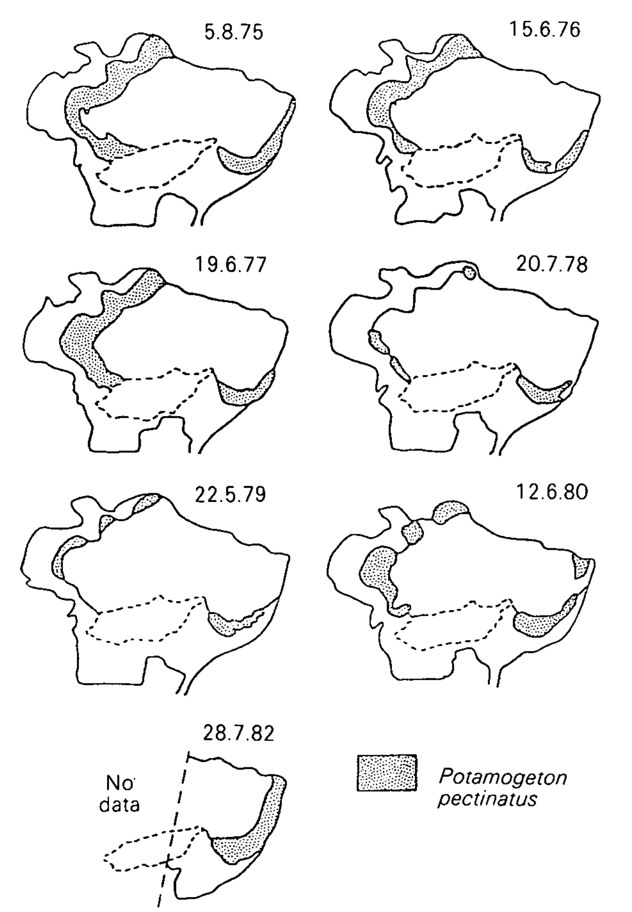

Figure 25 Maps from Landsat images showing annual variations in the areal extent of Potamogeton pectinatus *in Lake Ichkeul*

of the residuals from this regression against the other parameters suggests a further improvement due to a measure of the average salinity during the preceding winter (November–March). The combined regression accounts for 93% of the variability in the area of *Potamogeton*.

From these relationships, it is possible, using available hydrological data, to calculate the likely past annual extents of *Potamogeton*. The result for 1963 (11·3 ha), compared with the actual value measured from air photographs (10·8 ha), is very close. Further comparison has been possible for August 1973 using a Skylab photograph, 20·5 ha being measured against 13·9 ha predicted; this comparison is less satisfactory, perhaps because the actual date of the photograph remains unknown, resolution is poor, and because geometric distortions of the print, due to tilt, were not accurately corrected. Further analysis will allow the 1983 extent, as measured in the field, and values for future years, as they become available, to be used in testing the effectiveness of the model and its value in predicting changes following dam construction.

Field sampling in 1983 of biomass measurements of *Scirpus* and *Potamogeton*, and simultaneous readings made using a hand-held radiometer show an apparently close relationship between reflectance and standing crop, which suggests that it may be possible to assess standing crop by using Landsat radiometric data. It will be necessary to obtain the 1983 Landsat MSS imagery of Ichkeul before more definite conclusions can be made, and further field sampling is likely to be required in future years. However, if possible, the collection of biomass information from remotely sensed imagery will be valuable in assessing food resources for wildfowl.

The results of the vegetation analyses have already been compared with existing ornithological data, and interesting relationships appear to exist between the changing extents of the 2 major food species, *Scirpus maritimus* and *Potamogeton pectinatus*, and the numbers of herbivorous birds present in the lake, with an apparent upper limit of winter numbers based on the previous summer's vegetation growth.

Vegetation dynamics in the Scirpus marshes

Over 650 ha of the marshes surrounding Lake Ichkeul are dominated by *Scirpus maritimus*, a halophytic, rhizomatous sedge which is characteristic of shallow, saline wetlands (Lieffers & Shay 1982). The tubers of this species form the main food source for the greylag goose *(Anser anser)* which overwinters at Ichkeul. As any decline in *S. maritimus* may decrease the value of the site as a goose feeding ground, we need to predict how the hydrological changes to the lake are likely to affect the population of *S. maritimus* either directly through inundation or indirectly through grazing and competitive interactions with other marsh speces, particularly *Phragmites australis* and *Scirpus litoralis*.

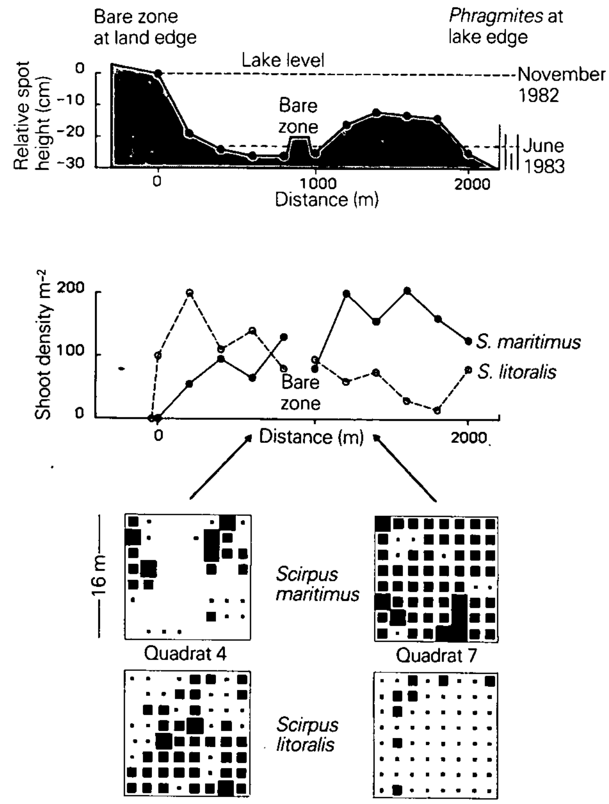

Figure 26 Transect across the Melah marsh, Lake Ichkeul, showing the distribution of Scirpus maritimus *and* Scirpus litoralis. *Two examples of the 1982 distribution pattern of the 2 species within permanent quadrats are also shown. Shoot density of each species within each 2 m × 2 m sub quadrat given by:* □, *none;* ⊡, *>0;* ▣, *>120 m^{-2};* ■, *>240 m^{-2}*

In most of the marshes, *S. maritimus* occurs in almost monospecific stands, but, in the 230 ha of the Melah marsh to the western end of the lake (Plate 3), it co-exists with a second species, *Scirpus litoralis.* To examine both the existing patterns of vegetation and changes that may occur in future years, a transect of 11 16 m×16 m permanent quadrats has been laid across the Melah (Figure 26). Over the marsh, there is a gradual change in species composition from 100% *S. litoralis* in a narrow 50–100 m band at the landward edge, up to almost 100% *S. maritimus* near the lake. This pattern is only partly consistent with the hypothesis that *S. litoralis* can colonize deeper water and tolerate higher salinities than *S. maritimus.* In addition, the small-scale distribution patterns of the 2 species within the marsh vary in a way that is unlikely to be explained by simple environmental variation, but may provide insight into the dynamics of colonization and growth in the past.

In some areas of the marsh, the 2 species occur in fairly discrete patches. These patches occur mostly, but not exclusively, near areas of open water and are probably the result of recent, almost simultaneous, colonization by both species. In other areas, where *S. litoralis* is ubiquitous, patches of *S. maritimus* may be the result of more recent invasion into established stands of *S. litoralis* (eg quadrat 4 in Figure 26).

Eventually, the extensive rhizome system of *S. maritimus* should enable this species to spread completely through the *S. litoralis,* giving an area with a relative homogeneous distribution of the 2 species (eg quadrat 7 in Figure 26). An alternative hypothesis of *S. litoralis* invading into stands of *S. maritimus* cannot be totally rejected, but it is less consistent with observed patterns of vegetation. Therefore, it seems likely that, if the present conditions prevail, the Melah marsh will become increasingly dominated by *Scirpus maritimus.* Records from the permanent quadrats in future years will be used to test this hypothesis.

The effects of changes in water depths and salinity on the growth of the 2 species, and the competitive interactions between them, are currently being investigated experimentally in glasshouse experiments at University College London and in field experiments at Ichkeul. This information, together with the field data on the rates of colonization and patch expansion, will be synthesized into a model of *Scirpus* dynamics. This model should not only explain the existing pattern of *Scirpus* distribution, but should also enable predictions to be made about future changes in response to changes in the lake hydrology.

Further analyses of field and remote sensing data, combined with continuing experimental and field survey work, will help to refine the model being derived in the environmental impact assessment of dam construction at Lake Ichkeul. Furthermore, as each of the 6 dams comes into operation successively over a number of years, it will be possible to observe the predictive value of the model, refining it as necessary.

Finally, it is hoped to suggest appropriate engineering works, including the possible construction of a sluice on the outflow and a dyke to isolate parts of the lake, combined with appropriate hydrological management to release freshwater supplies, which will minimize the ecological impact of the dam construction scheme.

*R M Fuller, T W Parr and A C Stevenson**

* University College London

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Mapping the forests of Bhutan: a practical approach to quantifying resources in remote and inaccessible areas

Duk Yul, land of the thunder dragon, Buddhist Kingdom of Bhutan, lies in the eastern Himalaya between China (Tibet) and India, where it borders Sikkim, West Bengal, Assam and Arunachal Pradesh. In 1972, it became a member of the United Nations (UN), although it is still considered to be a protectorate by, and of, the Indian Government.

With UN membership, the hitherto closed borders have begun to open, and there is an increasing input of foreign aid through the United Nations Development Project (UNDP), Helvetas (a privately funded Swiss aid organization), the British Government Overseas Development Agency (ODA), as well as various organizations concerned primarily with health. India, which has a large military presence in Bhutan, is financing road building and hydro-electric schemes, and contributing considerable other expertise. Nevertheless, Bhutan is concerned that progress should 'preserve the ancient religious and cultural heritage ... and achieve the essential balance between the values of the past and the innovations of the present' (Jigme Singye Wangchuk 1979).

The land covers approximately 47 000 km² and rises from 200 m to almost 8000 m within the meridians of 88°45′ and 92°, and the parallels of 26°45′ and 28°30′N latitude. Bhutan is inadequately mapped. A reliability diagram published by the United States Army Corps of Engineers (1956) classifies as 'good' the mapping of less than 30% of the country. On the relevant 1 :1 000 000 aeronautical chart (DMAAC 1978), Bhutan is left partially blank. Indian Ordnance Survey maps have been prepared, but these are classified for security reasons, and their coverage and degree of accuracy are unknown. More recently, the World Bank (1982) has published a 1 : 2 500 000 map from Landsat imagery. Contours are not given, and the author's experience is that superimposed features (tracks, settlements) are not always correctly located.

Botanical information about Bhutan is increasing and 'sufficient collections now exist to make the production of a checklist and Flora possible'. These collections are documented by Grierson and Long (1983) who are preparing the Flora, which will also include the material they collected during their visits to Bhutan in 1975, 1979 and 1982.

Few ecological studies have been made, although almost 20% of the land area has been declared a nature reserve. Much of this land is in the 'Great Himalaya', above the permanent snow-line, although a number of smaller reserves have been set up to protect subtropical forest in the southern foothills. The best known of these is the Manas Game Reserve, which is contiguous with the Manas Sanctuary in Assam (Jain & Hajra 1975). Dago Tshering and Varnham (1979) state that 'more than two thirds* of Bhutan is covered with valuable forests. At lower altitudes, Sal is plentiful†; in the central belt, the hills are cloaked with oak‡ which gives way in the higher reaches to conifers, pine, fir, spruce and larch'.

Fischer (1976) describes the economy, which is almost entirely rural, as 'archaic in ... (the) methods and techniques of soil utilization, which, in Central Europe, may have been practised towards the end of the early middle ages'. Agriculture, animal husbandry and forestry are integrated to provide livings which are not far above a subsistence level. Valley bottoms and more gently sloping land are terraced for the cultivation of rice, wheat, maize and millet. Some orchards have been planted. Elsewhere, shifting agriculture is practised. Yak, buffalo and cattle, and Chinese yellow (buffalo) and dzo (yak) crosses are herded. Forest and open lands are used for grazing, and the pressure of such may have an adverse effect on tree regeneration. In a Lamaistic Buddhist country, which is averse to killing, herd populations are not strictly controlled. Domestic timber felling, coupled with poor regeneration, has led to areas of deforestation and serious soil erosion near settlements. Above 3500 m, where yak are pastured during the summer months, much *Abies* and *Rhododendron* forest has been burnt and cleared.

Although the population is, at present, low (officially 1·3 million, but informed estimates suggest a figure closer to 0·8 million), improved medicine will lead to a rapid increase, and deforestation and erosion may become as severe a problem as it is in Nepal (Numata 1983). The consequences are loss of usable land and a probable increase in flooding in the Brahmaputran plain and delta.

In 1969, the Royal Government of Bhutan established a Forestry Department with a remit to protect and manage the forests and to develop an export industry in timber. 'Priority is being given to survey and demarcation ... and to the most up-to-date methods of harvesting and reforestation' (Dago Tshering & Varnham 1979).

A preinvestment survey of forests was undertaken by the Indian Government between 1975 and 1981. The results are classified information, and the survey was based on aerial photographs taken during the 1950s, which are also classified and therefore not

* The preliminary research described suggests that the figure for closed and partially closed forest is nearer 45%.

† Sal *(Shorea robusta)* is not a common plant in Bhutan. 'Sal forest ... is absent, although sal occurs as scattered trees in the Sharbhang district' (Grierson & Long 1983).

‡ This is the most densely populated part of Bhutan, where agriculture is widespread and soil erosion has become a problem.

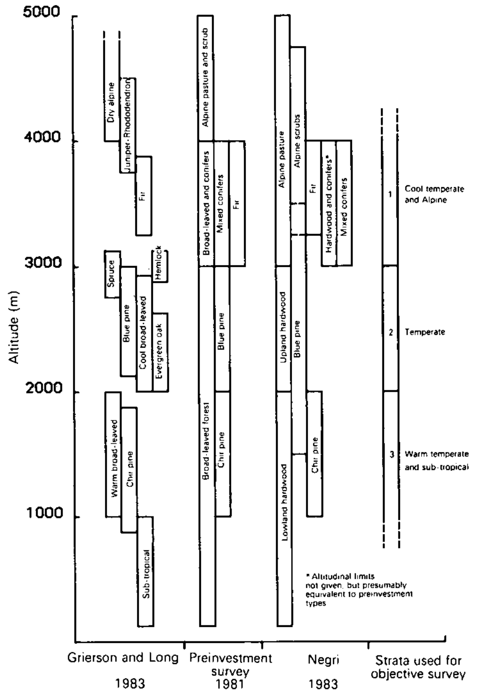

Figure 27 Existing vegetation classifications and sampling strata (see text for details). There is sufficient agreement between existing classifications to indicate appropriate altitudinal strata

available for inspection. Natural and semi-natural vegetation was subjectively grouped into 7 very broad types distinguishable on the aerial photographs (Figure 27). The distribution of each type was plotted, and the area covered calculated. These figures were modified (Figure 27) by Negri (1983), and replotted using visual assessment of a false colour composite Landsat image of Bhutan.

With the assistance and interest of the Bhutanese Forestry Department, ITE has undertaken a resource mapping project, in which it is hoped to achieve a considerable improvement in accuracy. It is intended to produce an objective classification of the forests, dependent on a random stratified survey. The distribution and calculated area of each defined class will be plotted against digital Landsat information, using the image analysis facilities available at Thematic Information Services, NERC Swindon.

Data collection

Prior to visiting Bhutan, 3 Landsat images, covering more than 90% of the country, were obtained from the National Aeronautic and Space Administration (NASA). These were selected for clarity, low cloud and snow cover. Using the I²S image analysis system at TIS, a supervised classification was prepared of the reflectance properties in an area covering western Bhutan. Ten classes were defined, with the following general distribution characteristics.

1. Snow, cloud, unclassified
2. High SW facing slopes
3. High NE slopes
4. Central SW slopes
5. Central NE slopes
6. Central valley bottoms
7. Low NE slopes
8. Low SW slopes
9. Low valley bottoms
10. Plains

These characteristics were compared with 3 vegetation classifications given by Grierson and Long (1983), the preinvestment survey (Government of India 1981) and Negri (1983). Other descriptions have been prepared (given in Grierson & Long 1983), but these depend on data and observations made from outside Bhutan. All 3 classifications shown (Figure 27) are subjective. The first was drawn from field observation, although the preinvestment survey classification was constrained by what could be distinguished on aerial photographs. The third classification was made without the benefit of field work. The consensus shows 3 broad forest zones (Figure 27), coincident with thousand metre altitudinal limits and approximately corresponding with the high, central and low areas defined with the Landsat classification. The zones are:

1.	< 2000 m	warm temperate and subtropical
2.	2–3000 m	temperate
3.	> 3000 m	cool temperate and alpine

The tree line occurs between 4000 m and 4300 m.

A stratification was prepared by combining the predominant aspects (NE 251°–70°; SW 71°–250°) shown on the Landsat classification (although it is recognized that this is partly an artefact of the sun-synchronous orbit of the satellite) with the altitudinal zones, to give a total of 6 strata. Almost all valley bottoms of significant area are cultivated, and not of sampling interest in the present project. It was proposed to distribute samples for vegetation survey as far as possible in 3 areas—west, central and east (Figure 28), corresponding to existing road and track systems, in order to include climatic variation consequent on changing longitude.

Proportionally distributed sites were located using randomly selected altitudes and aspects. Because of inadequate mapping, and a constraint that each site should occur within an homogeneous area of at least 250 m × 250 m (ie clearly identifiable on a Landsat image with pixel resolution of 79 m × 56 m), sites could not be pre-located. Instead, a number of possible sites were selected which fell within the area expected to be covered each day, and were located with altimeter and compass. Travel was difficult, often confined to rough footpaths, and largely by foot, pony or, occasionally, yak. The terrain and density of forest were such that it was seldom possible to sample opposing slopes, which resulted in a sampling bias towards south-western aspects. Where a jeep could be used, long delays caused by landslides were experienced. A poor diet (rice, chillies and

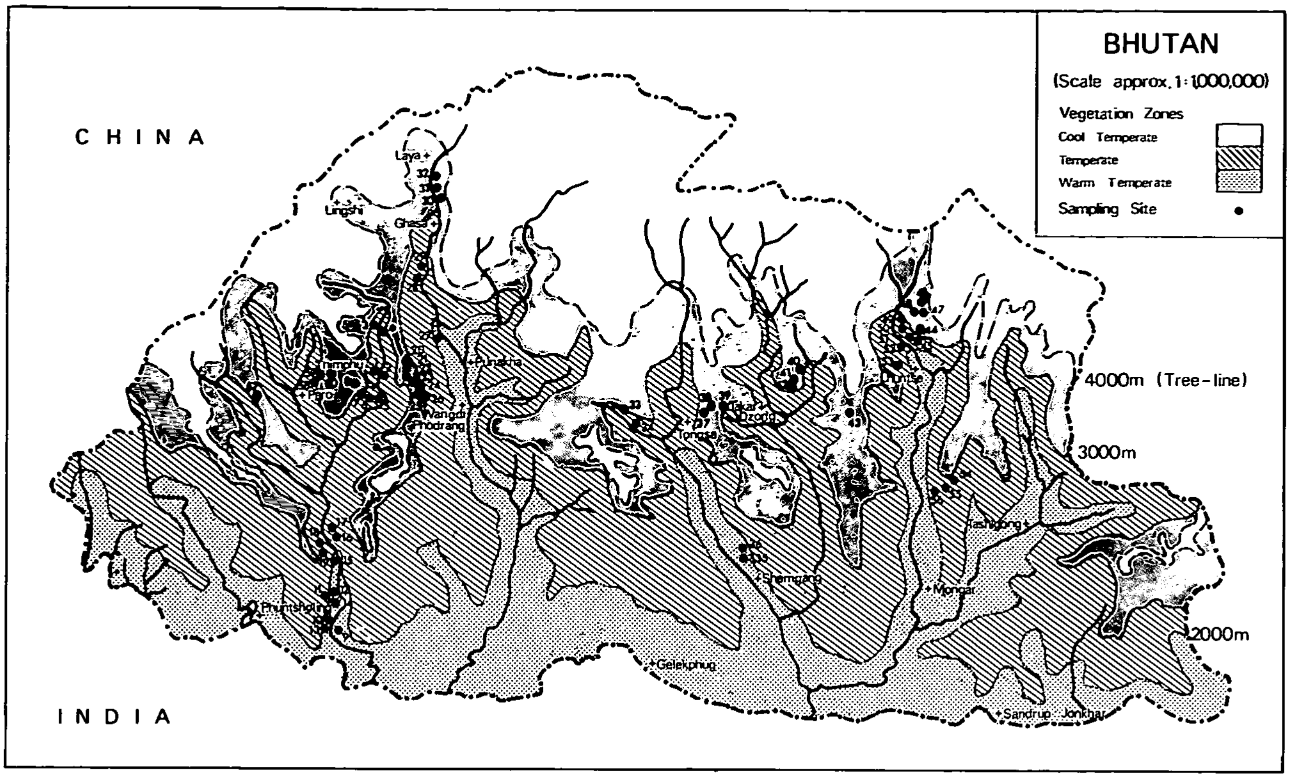

Figure 28 Vegetation sampling sites in Bhutan. The approximate distribution of 60 sampling sites within 3 altitudinal strata is shown

yak-butter tea), human parasites (leeches, fleas and bed bugs), the monsoon at lower levels (preventing adequate sampling of subtropical areas) and the need to acclimatize above 3500 m all contributed to sampling difficulties.

At each site, 3 10 m^2 quadrats were distributed along a level 100 m transect. Woody species were recorded and coded, and voucher samples were taken. The identification of these species has been kindly checked by A Grierson and D Long, and specimens are lodged at the Royal Botanic Gardens, Edinburgh. A collection of some 500 species was made. Cover, tree height and diameter, disturbance and regeneration were recorded, and descriptions were written about each quadrat.

Soil samples were taken and slopes measured. Bhutanese foresters were trained to assist with the work, and information was collected from a total of 60 sites (Figure 28; 180 quadrats). Twenty-five sites were recorded in each of the temperate and cool temperate strata (Figure 27). One transect was placed above the tree line (4100 m) and the remainder were recorded from subtropical and warm temperate areas, where additional sampling is needed.

Analysis

A preliminary numerical classification of the data is being prepared. With the help of a superimposed grid (underlying Plate 17), sites have been located on one Landsat image, and the range of spectral values will be calculated for each defined vegetation class. Assuming spectral differentiation, the classes will be plotted on the image, and the area covered by each class summed. A correction for slope will be made, and, using collected tree height and diameter data, the forestry resource will be estimated.

A further visit to Bhutan is planned to check the conclusions of this survey and to collect additional data.

I am grateful to the Forestry Department, Royal Government of Bhutan, for their help with this project.

Caroline Sargent

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Butterflies in the British Isles: a new data base

The Biological Records Centre's data base on the occurrence of butterflies in the British Isles contains ¼ million records. The data base was compiled from records contributed to a BRC recording scheme for macro-Lepidoptera organized by John Heath, and which ran from 1967 to 1982. More than 2500 recorders, mainly amateur naturalists, contributed records during the project. Most of the records date from the period of the project, but, in order to gain a broader picture of distributional changes with time, many earlier records were incorporated from the personal notebooks and diaries of recorders, museum and private collections, and publications.

During 1982–83, BRC processed the information on butterflies from the project and set up a computer file containing the following information for each separate record.

1. Species code	Generic and specific epithets combined; a dictionary file is used to convert this code to either a scientific binomial, a vernacular name, or both
2. Country code	England, Wales, Scotland, Northern Ireland, Eire, Channel Islands
3. Grid reference	National Grid or Irish National Grid, to 100 metre square where available
4. Date	Day, month and year, where available
5. Recorder's or literature code	A dictionary file is used to convert this code to names and initials
6. Source code	Field record, museum collection or published record
7. Altitude	In feet
8. Locality code	A dictionary file is used to convert this code to a place name

This computer file was used, in July 1983, to fulfil the original objective of the recording scheme—to produce distribution maps for each species. The 64

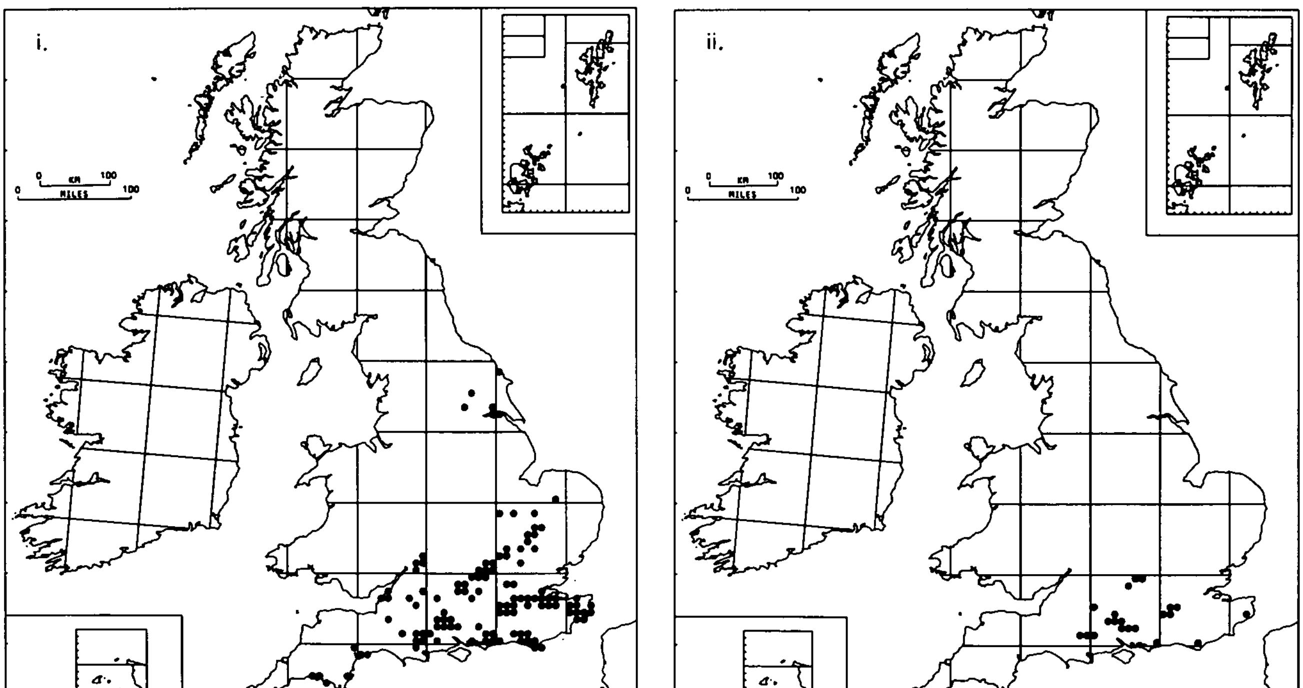

Figure 29 Distribution of the silver-spotted skipper (Hesperia comma), *summarized by 10 km squares of the National Grid*
i. All records up to 1969
ii. All records from 1970 onwards

Plate 4 Experimental plot in Beddgelert Forest immediately after clear-felling. The plot is square, and has been split between 2 felling treatments, whole-tree harvesting and normal harvesting (Photograph P A Stevens)

Plate 5 Dodknott Gill: a tributary of the River Esk draining a small catchment on the slopes of Harter Fell in Eskdale, Cumbria (Photograph K R Bull)

Plate 6 Part of the guillemot colony on the Isle of May (Photograph M P Harris)

Plate 7 Part of the township of Kinross on the west bank of Loch Leven: much of the phosphorus entering the loch does so in the form of industrial effluent and treated sewage effluent from Kinross and neighbouring townships (Photograph A E Bailey-Watts)

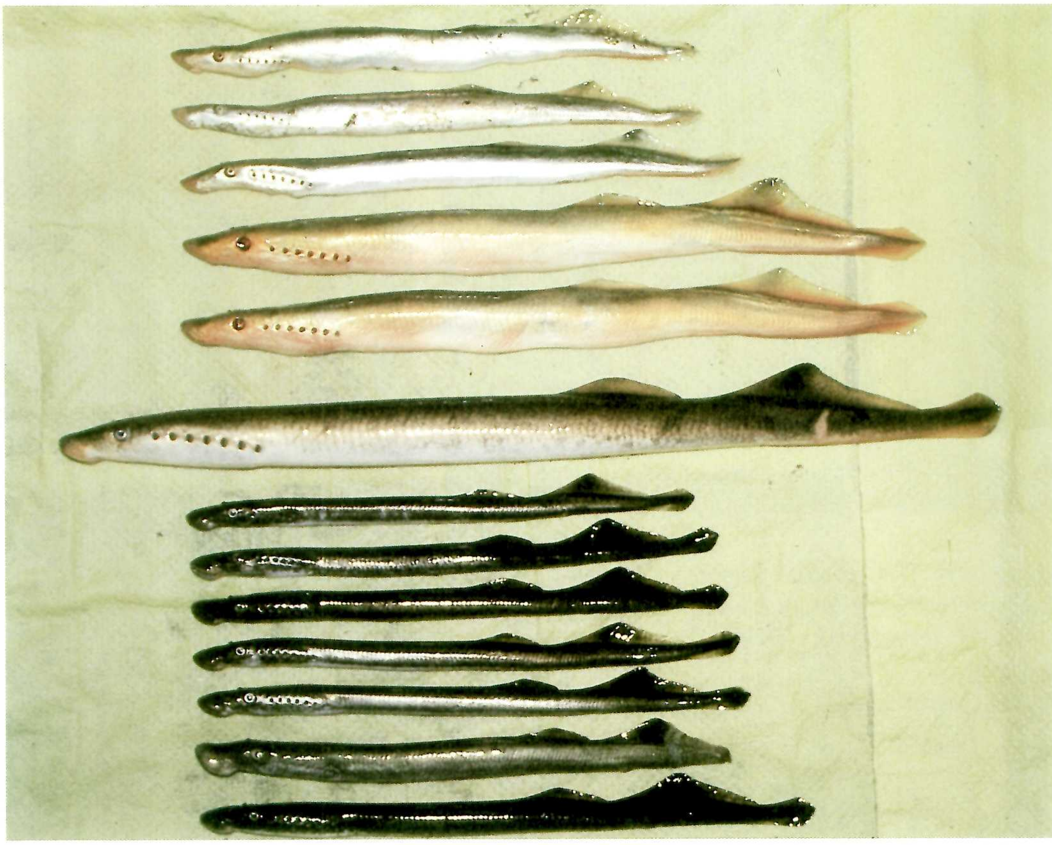

Plate 8 Examples of river lampreys showing variation in form: top 5 specimens – feeding animals from the Firth of Forth; 6th from top – Forth upstream adult migrant; bottom 7 specimens – Lomond upstream adult migrants
(Photograph K East)

Plate 9 Typical large (scaled paper in mm) lamprey wound found on powan in Loch Lomond in late summer
(Photograph K H Morris)

maps produced form the basis of *The atlas of butterflies in Britain and Ireland* (Heath *et al.* in press), which combines distributional information with the results of ecological work done elsewhere in the Institute.

The data base on butterflies has applications which are wider than the production of distribution maps. Data can be sorted and listed in 2 basic forms.

1. *All the records of one species*
   Although this format is analogous to a distribution map, it provides additional information on frequency of observation or recurrence in an area, site names and recorders.

2. *All the records from a geographical unit*
   It is possible to list all the records from a square of the National Grids (ie from 100 km square to 100 m square), from a biological (Watson/ Praeger) vice-county or from a country.

Within these basic forms, it is possible to select records further, for example by years (eg only records since 1970), by months, by recorders or by source codes, in response to particular requests.

Although work on this data base is still continuing, its usefulness to research workers and those concerned with conservation and land use planning has already become apparent: listings of records for several species and from 3 vice-counties have already been produced in response to requests from both within and outside ITE.

Developmental work on the production of lists of records from named sites is continuing. This work is being done under contract to provide the Nature Conservancy Council with information on species occurring on statutory conservation sites.

A longer term use of the BRC data base is to monitor changes in the distribution of species. This monitoring will involve continual updating of the data base and assessing changes with, for example, 10-year intervals between survey periods. Even now, it is possible, using the historical information already in the data base, to demonstrate the reduction in range of species, such as the silver-spotted skipper *(Hesperia comma)* (Figure 29). This small, quick-flying butterfly was never common in Britain, but it is now much less widespread than formerly. A recent survey (Simcox & Thomas in Heath *et al.* in press) revealed only 53 breeding colonies in 33 localities. It is a species associated with grazed calcareous grassland, especially on steep south-facing slopes. Loss of breeding sites (since 1960) was attributed to agricultural improvement of pasture (20%), ploughing (6%), and afforestation and urbanization (15%) Remaining losses were thought to be due to a decline in grazing, both by domestic stock and rabbits.

In future, as other detailed data bases are compiled, it will be possible to use them to compare the changes in occurrence of species in different but interdependent groups, or changes in species occurrence in relation to environmental changes.

P T Harding and Dorothy M Greene

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AIRBORNE POLLUTANTS, INCLUDING RADIONUCLIDES

Episodicity and acid rain deposition

Rainfall acidity for individual sites or across a region is often expressed as the annual mean H^+ concentration, weighted by the rainfall quantity. Similarly, the deposition of pollutants in rain, or by dry deposition, is generally reported as an annual flux to the ground. These annual amounts, however, conceal considerable variation between events. For example, H^+ concentrations in rain typically span 3 orders of magnitude, from 1000 $\mu eq\ H^+\ l^{-1}$ to 1 $\mu eq\ H^+\ l^{-1}$ (pH 3·0–6·0). The range of variation in concentrations of other ions is similarly large. Interest in deposited acidity is primarily motivated by its potential to cause damage, and the properties of individual events may be more important than annual average values in any consideration of effects.

Acidity deposited in precipitation (rain, snow, etc) has been widely assessed from analyses of H^+ concentrations, but these measurements are subject to a range of random and systematic errors (Fowler & Cape 1984). The gases SO_2 and NO_2 are absorbed directly by the ground and/or vegetation, a process known as dry deposition. Solution and oxidation of dry deposited SO_2 and NO_2 yields acidity (aqueous oxidation from $S^{(iv)}$ to $S^{(vi)}$ yields $2H^+$ for each SO_2 molecule), so that acid deposition at the surface includes contributions from both wet and dry deposition. While the concept of dry deposited acidity is important in defining net inputs to a catchment, or for that matter other surfaces, the acidity generated, particularly on foliage, following dry deposition cannot be measured directly because sites of sorption and reaction occur both on, and within, leaves and stems. Other gases, eg HNO_3, contribute to total deposited acidity, but, to offset these acidic gases, the alkaline gas NH_3 may also be dry deposited, neutralizing one H^+ per NH_3 molecule.

Rainfall is episodic by nature and daily monitoring data for 5 years at ITE Bush show that volumes of rain in each event are well described by a log-normal distribution with a median of 2·5 mm (Figure 30).

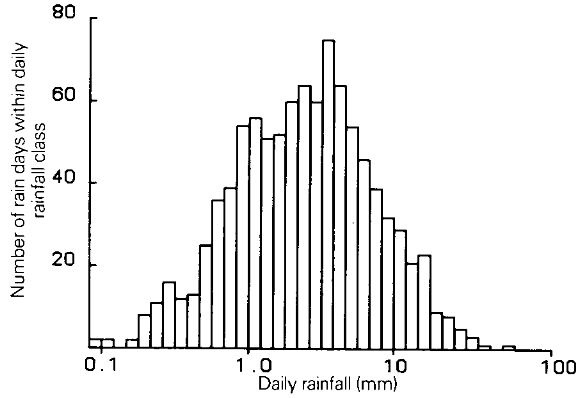

Figure 30 Frequency distribution of daily rainfall at Bush, Midlothian (1977–1981)

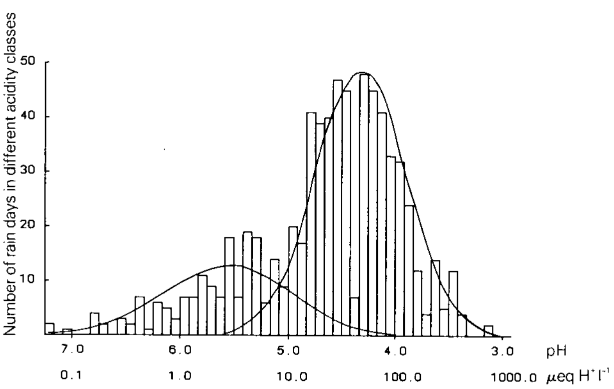

Figure 31 Frequency distribution of the daily amounts of wet deposited acidity at Bush, Midlothian (1977–1981)

The upper 30% of rain is contributed by only 5·6% of rain days, corresponding to an average of 10 days each year when rain amounts exceed 16 mm. Acidity deposited shows a greater episodicity, with 30% of the annual deposit contributed by 2·7% of events (an average of 5 days per year, Figure 31).

Although our knowledge of rainfall chemistry for the UK is based largely on weekly or monthly collections from limited daily measurements, rainfall acidity has been shown to be highly episodic in Cornwall (Irwin & Keddie 1983), Oxfordshire and Nottinghamshire (Barrett *et al.* 1983). It is likely that episodicity is a characteristic of wet deposited acidity throughout the UK.

Deposited acidity is the product of rain amount and H^+ concentration; the frequency distribution of H^+ concentration (pH) in rain events (Figure 32) is poorly described by a single log-normal distribution. It may be better described as 2 overlapping distributions, one containing the majority (75%) of events with a median pH of 4·29, and the other containing the remaining 25% of events, with a median pH of 5·57. Some insight into the reasons for the observed distribution of acidity may be gained by examining the extremes of the observed acidities. Events with

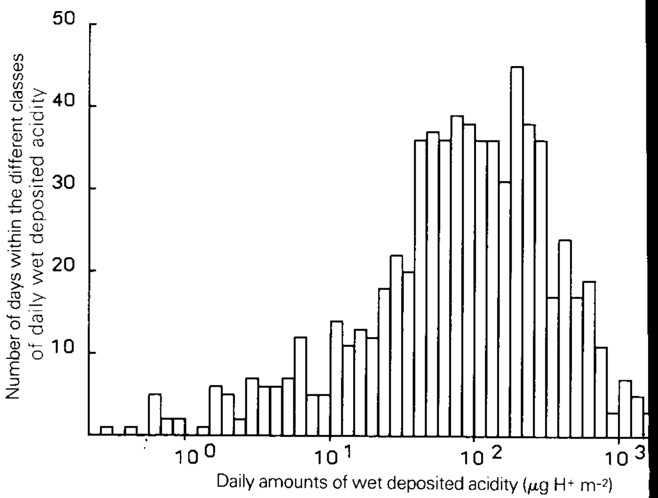

Figure 32 Frequency distribution of pH in daily collections of precipitation at Bush, Midlothian (1977–1981)

acidities exceeding 100 µeq $H^+ l^{-1}$ ($pH < 4$) are typically associated with low wind speed, smaller amounts of precipitation, poorer visibility and larger concentrations of (i) SO_4^{2-} in precipitation, (ii) SO_4^{2-} in particulate matter, (iii) SO_2 in air, than events with less than 10 µeq $H^+ l^{-1}$ ($pH > 5$).

The 2 classes of events at the Bush Estate each contain characteristics that appear to be linked to meteorological conditions, as has been found at Banchory in Scotland (Nicholson *et al.* 1980a) and Brookhaven, New York, in North America (Raynor & Hayes 1982). The quantity of pollutant in a given air mass is influenced by its trajectory and speed over the ground (Smith & Hunt 1978). Back-trajectories of air associated with precipitation events at Bush Estate were constructed for all the events with acidities greater than 100 µeq $H^+ l^{-1}$, approximately 20 events in each class (Fowler & Cape in press). Low-level winds (surface geostrophic) at 6-hour intervals for a 48-hour period were used for this exercise, and positions close to sites of measured vertical profiles of wind speed and direction (from radio-sonde ascents) allowed the estimated wind speed and direction to be checked against measured values. In general, trajectories associated with the most acid events had traversed a major source area in the UK or continental Europe before reaching central Scotland, so confirming observations made earlier by Nicholson *et al.* (1980a). The mean wind speeds along these trajectories were also 40% smaller than in the <10 µeq $H^+ l^{-1}$ class. Back-trajectories associated with 'clean' precipitation generally showed larger wind speeds along mainly North Atlantic trajectories, with only a short path over central Scotland.

Figure 33 shows how rainfall quantity, SO_4^{2-} in rain, SO_4^{2-} in particulate matter, SO_2 concentrations in air, wind speed and visibility vary with pH at Bush Estate. The consistent trends evident for each of

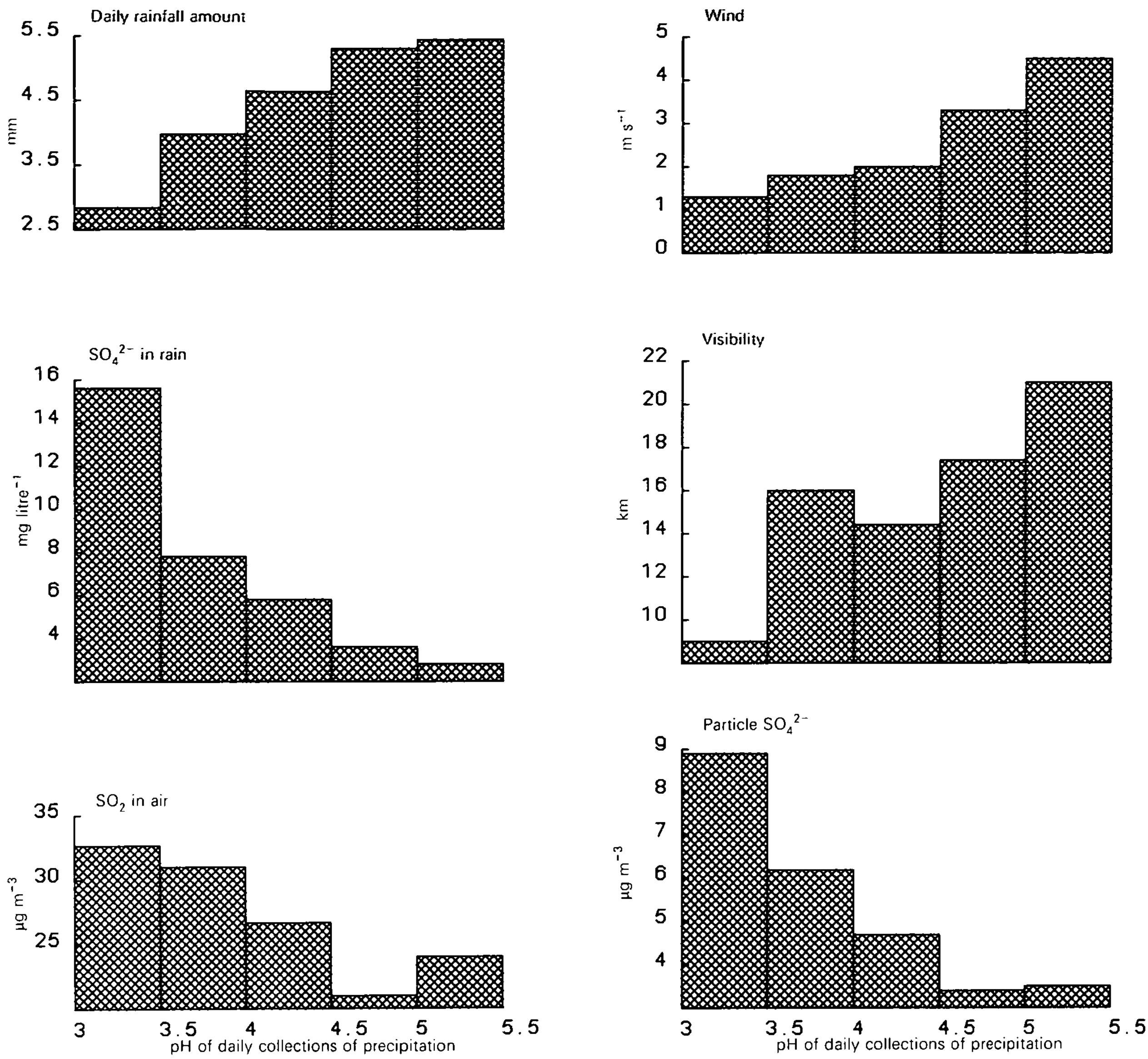

Figure 33 The relationship between pH of daily collections of precipitation and (i) rainfall amount, (ii) concentrations of SO_4^{2-} in rain, (iii) atmospheric concentrations of SO_2, (iv) mean daily wind speed at 2 m, (v) visibility, and (vi) atmospheric concentrations of particulate SO_4^{2-} (Bush Estate, Midlothian) (1977–1981)

these variables support the view that the most acid events represent the upper tail of a distribution of acidity in rain; they do not form a separate group of events with properties that would not be anticipated from a description of the statistical properties of event distribution. This predictability is an important characteristic of rainfall acidity which may not, however, be shared by events with extreme concentrations of gaseous pollutants. From 3 years of continuous monitoring of SO_2, NO, NO_x and O_3 at Devilla Forest in central Scotland, the largest expected 10-minute gas concentration in a year would be in the order 200–400 ppbv for SO_2 or NO_x (600–1200 µg SO_2 m^{-3}, 400–800 µg NO_2 m^{-3}) (Nicholson *et al.* 1980b). However, the occurrence of events with large concentrations of SO_2 and NO_x was not adequately predicted from a log-normal distribution that seemed adequate for the bulk of the data (Fowler & Cape 1982). Alternative methods of predicting their occurrence (return times) based on extreme value statistics (EVS) provided values that differed significantly from those predicted from log-normal distributions (LND); LND predicted larger peak values of SO_2 and O_3 than EVS. In contrast, EVS predicted the larger peak values for NO_x (Table 16).

Rates of dry deposition also show large short-term variability (Fowler & Cape 1983), even though the process is often treated as a constant over large regions and for periods of a year (Galloway & Whelpdale 1980). Episodicity of dry deposition arises from variations in gas concentrations and deposition velocity. The episodicity attributable to variations in gas concentrations is of the same order as that found for rainfall (Fowler & Cape in press), ie 30% of annual

Table 16. Maximum expected gas concentrations (ppbv) for 10-minute samples at Devilla Forest (central Scotland), calculated from extreme value statistics (EVS) or assuming that pollution events are log-normally distributed (LND)

	1 year		2 years		5 years		10 years		20 years	
	EVS	LND	EVS	LND	EVS	LND	EVS	LND	EVS	LND
SO_2	240	370	260	430	300	520	320	590	350	680
O_3	130	450	160	510	220	600	280	680	350	760
NO_x	310	290	380	320	490	370	580	400	690	440

dry deposited SO_2 accumulated during 10% of the year. In practice, the episodicity of dry deposition will be larger because variations in deposition velocity may occur independently of variations in gas concentrations. Changes in deposition velocities are coupled closely with physiological properties of vegetation, whether grasses, cereals or forests, and particularly with stomatal behaviour; they are not generally related to changes in air concentrations of SO_2. The episodicity of dry deposition therefore contains a systematic component caused by diurnal changes in stomatal opening and a random component caused by changing air concentrations of SO_2. In practice, the episodicity of dry deposition may be similar to that of wet deposition (for deposited acidity or sulphate), but it may prove difficult to quantify precisely.

The episodicity of deposited acidity described in this report refers to direct deposition to land surfaces. In practice, however, rain is usually intercepted by plant canopies before reaching the soil. As a result, its chemical properties will be influenced by interactions in, and on, the vegetation (Nicholson *et al.* 1980c). On reaching the ground, the modified rain is subject to a further set of interactions as it percolates through soil to reach freshwater courses, these interactions now being the subject of intensive soil chemistry and freshwater ecology research.

D Fowler, J N Cape and I A Nicholson

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Changes in rainfall chemistry and uptake of sulphur dioxide by wet surfaces

Most measurements of the uptake of pollutant gases by plants have been made in dry conditions, but surface wetness may be very important if there are interactions between the chemical composition of rain, gases in the atmosphere and leaf surface chemistry. These processes must be better understood to interpret what happens when plants are exposed to air pollution.

The chemical composition of rain falling through a polluted atmosphere changes as pollutant gases dissolve, or are released from solution. Equilibrium may be established before rain reaches the ground, in which case there will be no net removal of a pollutant gas near the ground. Where sources of pollutant gases are close to ground level and there is a decreasing gradient in concentration from the ground upwards, falling rain may decrease ground level concentrations by dissolving gases, without equilibrium being achieved before reaching the ground. Situations of this sort are shown by decreases in gas concentrations during or immediately after periods of rain (Martin in press). The chemical composition of rain just before it reaches the ground (or vegetation) is therefore determined by the material originally present in rain clouds and that collected (or released) while falling. In some circumstances, soluble gases could be released from falling rain if concentrations of pollutant gases were greater at a distance from the ground than near ground level, for example in the plume from a chimney.

When rainwater reaches a surface (soil, water or vegetation), its chemical composition changes. In soil, the ions present in rain participate in the chemistry of the soil solution and may undergo a variety of ion exchange processes and reactions. Even on a relatively inert man-made surface, there is the likelihood of a change in composition. In dry weather, surfaces accumulate deposits of gases and particles which may subsequently be dissolved by rainwater. This form of contamination may be very important for continuously-open rain collectors (Fowler & Cape 1984). When rain falls on the surface of a plant, 2 additional processes occur: there may be a net gain of material from plant tissues (leaching) and there may be modifications in chemical composition as a result of ion exchange. The overall result of surface deposits, leaching and ion exchange may be measured in the chemical composition of throughfall (rain which has fallen through vegetation). Earlier studies by ITE (Nicholson *et al.* 1980) showed significant enhancement of sulphate and hydrogen ion concentrations in throughfall collected beneath Scots pine growing in moderately polluted air, but it was not possible to separate the relative contributions of the 3 processes.

The rate of uptake of sulphur dioxide by a rain-wetted Scots pine canopy has been measured using an eddy correlation method (Fowler & Cape 1983). The rate of uptake during rain, expressed as a deposition velocity (v_g), was seen to be very small relative to that which would be predicted for pure water, suggesting that rainwater was close to equilibrium with gaseous sulphur dioxide before reaching the canopy. However, uptake was greater than in dry conditions, implying that chemical reactions were occurring at the wetted surface. The solubility of sulphur dioxide in water is controlled by solution acidity (Cape in press), so that direct transport of sulphur dioxide through the layer of water to the leaf surface would decrease as acidity increased. As sulphur dioxide in solution is oxidized to sulphate, the resulting increased acidity would restrict further uptake of the gas. The observed steady rate of uptake during rain suggests that some neutralization of acidity was possible through ion exchange processes. A simplified picture of the processes occurring at a wetted leaf surface is shown in Figure 34, while the changing rates of uptake of sulphur dioxide to a Scots pine forest during an 18-hour period with rain are

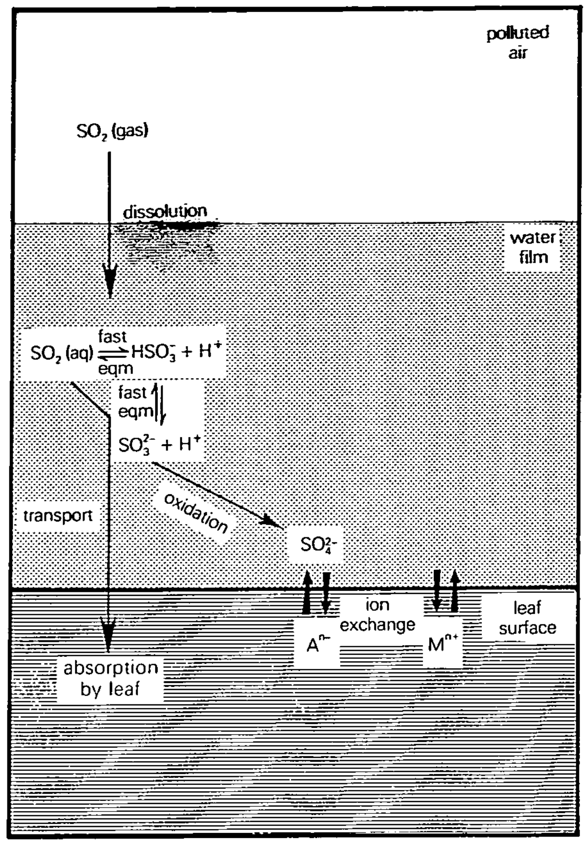

Figure 34 Chemical processes involved in the uptake of sulphur dioxide gas by rainwater on a leaf surface, showing net fluxes to and through the surface

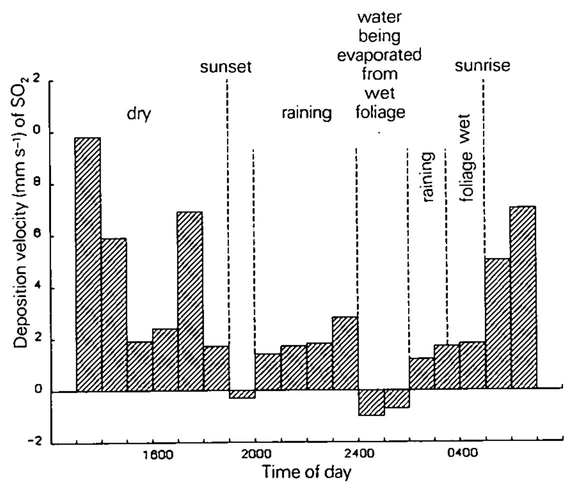

Figure 35 The rate of uptake of SO_2 (expressed as a deposition velocity, v_g), measured above a Scots pine canopy in central Scotland (21–22 April 1982) during wet weather

shown in Figure 35. The decreased uptake (expressed as deposition velocity, v_g, mm s^{-1}) from 1300–1900 hours was caused by the closure of stomata, which are the major sink of sulphur dioxide in dry conditions during day-time. Rain started falling between 2000 and 2100 hours and continued until about midnight. During this period, SO_2 uptake was steady, at about 2 mm s^{-1}. The rain stopped at midnight, and water was evaporating from the canopy until 0200 hours, when it appeared that sulphur dioxide was being released from the wet canopy (rates of uptake <0), either in response to smaller gas concentrations or as water evaporated. At about 0200 hours, it started to rain intermittently for an hour or so, and rates of SO_2 uptake began to increase from 0500 hours, as it became light and stomata opened.

Observations of this sort are being augmented by studies of the chemical composition of surface water, in the hope of being able to interpret the sequence of events that has been described. The theoretical background to these observations may also be of relevance to the transport and uptake of carbon dioxide, another acidic gas.

J N Cape and D Fowler

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Radionuclides in terrestrial ecosystems

(This work was largely supported by Department of Environment funds)

Since the development of atomic weapons and nuclear power stations, much effort has been devoted to assessing radiation doses to man from routine or accidental releases of radionuclides into the environment. A major source of artificial radionuclides in west Cumbria is the Sellafield reprocessing plant located on the coast (BNFL 1981). Some radionuclides are emitted as aerosols, but most low-level waste is discharged via a twin pipeline which extends 2·1 km into the Irish Sea. Until recently, most of the studies associated with Sellafield discharges have been concerned with survey and routine monitoring of the concentrations of radionuclides in fish and intensively managed agricultural crops, but attention is now being widened to include less intensively managed habitats.

ITE, on contract to the Department of the Environment, has recently been studying the fate of radionuclides that are deposited on the area surrounding the Ravenglass estuary. Some of the radionuclides emitted via the pipeline from Sellafield are carried to the Ravenglass estuary, approximately 7 km south of Sellafield, in association with sedimentary material. During high tides, the salt marshes of the estuary are covered by water carrying diluted radioactive effluent and a suspension of contaminated particulates, some of which are deposited as the tide recedes, particularly on vegetation. As a consequence, the deposits of artificial radionuclides on these salt marshes are considerably larger than on any other grazed pasture in the United Kingdom. ITE's studies are concerned with:

1. the concentration and spatial distribution of radionuclides in grazed and ungrazed salt marshes;
2. root uptake of radionuclides by plants from contaminated silt,
3. radionuclides in contrasting types of coastal pasture;
4. uptake and inland transfer of radionuclides by birds feeding in the estuaries and salt marshes at Ravenglass;
5. incorporation of radionuclides by sheep grazing on an estuarine salt marsh.

Detailed investigations of the dynamics of radionuclide movement from pasture to animals are required for models which are used to predict radiation doses arising from the release of radioactivity into the environment. The enhanced concentrations of radionuclides on the salt marshes in the Ravenglass estuary provide an opportunity to investigate the transfer of radionuclides to grazing animals in field conditions. To this end, the incorporation of radionuclides by sheep grazing on salt marsh on the western, seaward, side of the River Irt has been studied. The radionuclide content of sheep tissues was measured and the daily intake of radionuclides by sheep was estimated. The latter was difficult because sheep frequently grazed other areas of heathland adjacent to the salt marsh with very different and smaller radionuclide contents. Hence, regular samples of all grazed areas had to be combined with frequent observations of grazing behaviour, to obtain estimates of the daily intake of radionuclides. The total area likely to be grazed by the experimental sheep was subdivided into a number of areas, based on the concentration of radionuclides, vegetation types and sheep grazing ranges. Observations on the grazing behaviour of the sheep established that there was a considerable difference in their grazing habits between summer and winter. Over 75% of grazing in June, July and August took place on the salt marsh, as opposed to less than 25% in December and January.

There were also considerable seasonal differences in the radionuclide content of the salt marsh vegetation. Peak concentrations of radionuclides were found in vegetation in late winter/early spring, after

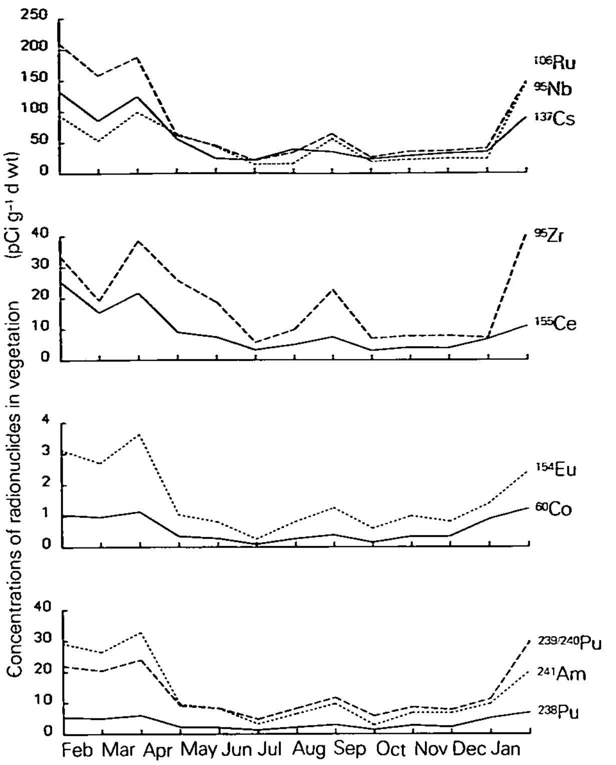

Figure 36 Seasonally changing concentrations of 10 radionuclides in part of a salt marsh on the seaward, western side of the River Irt, Cumbria

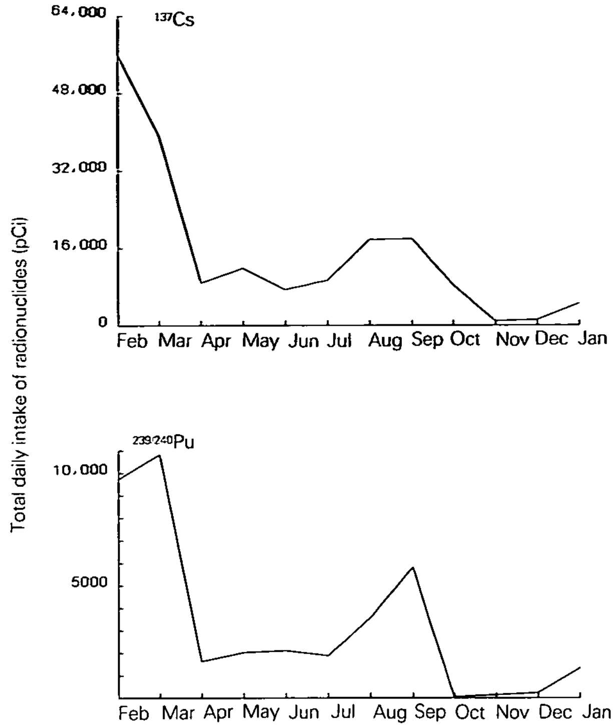

Figure 37 Seasonally changing daily intake of ^{137}Cs and $^{239/240}Pu$ by sheep grazing a salt marsh on the seaward, western side of the River Irt, Cumbria

which the concentrations of all radionuclides dropped markedly (Figure 36). The radionuclide content of the vegetation on non-inundated areas was less varied; there was no obvious seasonal pattern. The most abundant radionuclides on the salt marsh were ^{106}Ru, ^{137}Cs and ^{95}Nb, which, together with ^{95}Zr, ^{134}Cs, ^{144}Ce, ^{60}Co, ^{154}Eu, ^{238}Pu, $^{239/240}Pu$ and ^{241}Am, formed the main radionuclide content of the vegetation. The concentrations of ^{137}Cs in samples of salt marsh vegetation taken from a control area on the Humber estuary were at least 2 orders of magnitude smaller than those in the River Irt salt marsh.

The mean daily intake of radionuclides calculated for each month, assuming a daily intake of one kg dry weight, was highly variable (Figure 37). The intake depends on (i) the number of days that the sheep grazed the different vegetation types within their range, and (ii) the radionuclide concentrations found in those vegetation types. In February 1982 (when the concentrations of radionuclides were largest), the total radionuclide intake was at its maximum, even though the sheep spent less time on the salt marsh than in the summer months.

Initially, one ewe was analysed to identify the pattern of radionuclide distribution in different tissues. On the basis of this work, selected tissues (liver, lung, kidney, muscle and bone) were analysed from (i) a ewe and a lamb, one month after lambing in May 1982, and (ii) 3 ewes and 3 lambs in September 1982 when the lambs were being sent to market. As a 'control', the tissues of a draft ewe, brought in from Swaledale in the Yorkshire Dales for restocking, were analysed.

Tissues of the sheep accumulated different radionuclides disproportionately. ^{137}Cs was distributed relatively uniformly throughout most of the soft tissues of the sheep; this finding is consistent with the metabolic model adopted by the International Commission on Radiological Protection (1979). However, there were some tissues with consistently larger (eg kidney) or smaller (eg bone, adipose tissue) concentrations of ^{137}Cs than average.

Most of the body burden of the transuranic radionuclides (^{238}Pu, $^{239/240}Pu$ and ^{241}Am) was associated with the fleece and other external tissues of the sheep. Because of the relatively low absorption of the transuranic elements in the gut of many animals (Harrison 1982), their concentrations in tissues in contact with the environment are far greater, because of physical contamination, than those of internal tissues. The principal internal tissues containing transuranic elements were the liver and skeleton (Figure 38). Occasionally, gamma-emitting radionuclides other than ^{137}Cs and ^{134}Cs were detected in certain tissues; for example, ^{60}Co was detected in liver and kidney, ^{95}Nb in bone, kidney and once in a liver, and ^{106}Ru in the kidneys of the lambs sampled in September 1982.

In the animals sampled in September 1982, tissue concentrations of ^{137}Cs were consistently larger in

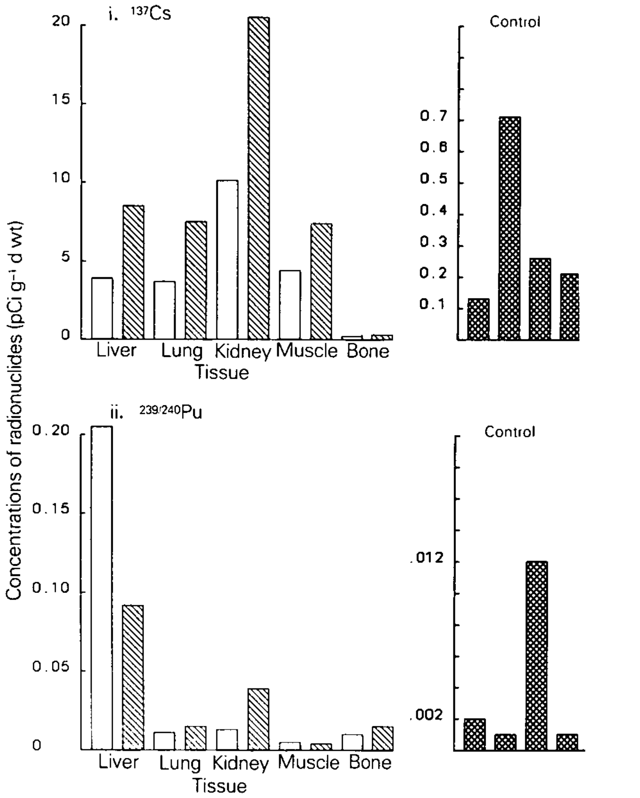

Figure 38 Concentrations (means ± SE) of (i) ^{137}Cs and (ii) $^{239/240}Pu$ in selected tissues of sheep that had grazed a salt marsh on the seaward, western side of the River Irt, Cumbria, and a 'control' ewe from the Yorkshire Dales

□ *Ewes, September 1982* ▧ *Lambs, September 1982* ▩ *Control ewe*

the lambs than in the ewes (Figure 38), even though the lambs had grazed the area for a much shorter period of time. This finding implies that there are more differences in the ^{137}Cs metabolism of lambs than ewes.

Transfer coefficients, which assume that the concentrations of radionuclides are in equilibrium, were calculated for ^{137}Cs.

Transfer coefficient = C/I

where C = concentration of radionuclides in tissue (fresh wt)

I = daily intake of radionuclide

The transfer coefficients for muscle in ewes and lambs, calculated for the September samples using the August estimates of mean daily intakes, were $6{\cdot}4 \times 10^{-2}$ day kg^{-1} (SD $3{\cdot}3 \times 10^{-2}$), and $1{\cdot}1 \times 10^{-1}$ day kg^{-1} (SD $5{\cdot}6 \times 10^{-2}$) respectively. Despite their dependence on estimates of daily intake, these transfer coefficients are very similar to that of $1{\cdot}2 \times 10^{-1}$ day kg^{-1} derived by Ng *et al.* (1979).

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

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Fluoride in the prey of barn owls (*Tyto alba*)

Most of the fluoride that vertebrates take from the environment is incorporated into their skeletons. Large loads can result in a variety of skeletal disorders (Franke 1979), and those that impede locomotion may increase a prey species' vulnerability to predation. Because small mammals trapped in the vicinity of the aluminium reduction plant on the Isle of Anglesey sometimes have extremely large concentrations of fluoride in their bones (Walton 1982), it was decided to check if they were taken selectively by their barn owl predators. Barn owls in Anglesey, North Wales, consume a preponderance of short-tailed voles *(Microtus agrestis)* and common shrews *(Sorex araneus)* whose bones can be recovered from the pellets that owls regurgitate at the roosts.

The fluoride contents of the skulls of voles taken by barn owls were compared with the contents of skulls of voles trapped mechanically near owl roosts. Collections of both types were made at 2 sites—(i) a control site (Llangaffo, 22 km from the Holyhead reduction plant) where bone fluoride concentrations were relatively small and below those that would produce skeletal disorders, and (ii) a contaminated site (Holyhead A, 0·9 km south of the reduction plant) where large bone fluoride concentrations could be expected. In the event, the concentrations of fluoride in skulls collected at Holyhead A were about 10 times larger than those in skulls from Llangaffo (Tables 17 & 18).

Average concentrations of fluoride in skulls of trapped voles were less in September than in March when the vole populations consisted entirely of animals born the previous year. By autumn, animals born the previous season will have died and been replaced by current season progeny. While the concentrations of fluoride in the skulls of predated voles were sometimes larger than in those of trapped animals, the evidence suggests that barn owls do not selectively consume voles with large concentrations of fluoride. In other words, voles with large amounts of fluoride were no more at risk than those with smaller amounts.

Table 17. Fluoride in the skulls of short-tailed voles *(Microtus agrestis)* trapped near owl roosts

Collection periods	Holyhead A 1979	Holyhead A 1980	Llangaffo 1979	Llangaffo 1980
	Concentrations of fluoride μg g^{-1} ± standard error			
March	2190 ± 108 (20)	[1630 ± 153]* (13)	257 ± 15 (18)	146 ± 8 (20)
September	1660 ± 158 (16)	1580 ± 232 (20)	111 ± 13 (20)	117 ± 13 (20)

* Voles trapped in January and April 1980
Numbers of observations in parentheses

Table 18. Fluoride in the skulls of short-tailed voles *(Microtus agrestis)* taken from the pellets of barn owls

Collection periods	Holyhead A 1979	Holyhead A 1980	Llangaffo 1979	Llangaffo 1980
	Concentrations of fluoride μg g^{-1} ± standard error			
January–March	3150 ± 278 (42)	1590 ± 398 (16)	147 ± 13 (20)	158 ± 18 (33)
April–June	2420 ± 252 (49)	1360 ± 202 (23)	125 ± 11 (50)	133 ± 13 (15)
July–September	804 ± 129 (46)	650 ± 124 (20)	184 ± 10 (33)	107 ± 10 (17)
October–December	843 ± 119 (50)	—	95 ± 10 (26)	—

Numbers of observations in parentheses

Common shrews accumulate larger concentrations of skeletal fluoride than voles (Andrews *et al.* 1982). In April 1980, common shrews trapped at 6 locations close to the aluminium reduction plant had skull mean fluoride concentrations ranging from 2392 μg g^{-1}, at a sheltered location, to 10 120 μg g^{-1} immediately windward of the reduction plant. Skulls extracted from pellets of owls, that could have hunted the 6 sites, averaged only 2230 μg fluoride g^{-1}, evidence again suggesting that barn owls do not preferentially select prey with large concentrations of fluoride.

A G Thomson

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PLANT PHYSIOLOGY AND GENETICS

A simple method for the cryopreservation of trypanosomes of the subgenus *Schizotrypanum*

Low temperature preservation of trypanosomes was first investigated systematically by Polge and Soltys (1957), reviewed by Walker (1970) and standardized by Lumsden *et al.* (1973). Their methods were based on the use of glycerol (at 7·5 or 10% v/v) as cryoprotectant, and slow cooling to −40°C or below, before transfer either to solid carbon dioxide (−79°C) or liquid nitrogen (−196°C). Thawing at about 37°C was recommended for retrieval. These methods were developed primarily for trypanosomes of the subgenus *Trypanozoon*, and for these organisms they gave acceptable survival. Preservation of other subgenera, especially *Schizotrypanum* (which contains the important South American pathogen of man, *Trypanosoma cruzi)*, was less satisfactory. Although survival of some organisms was usually achieved, the proportion of viable cells was often unacceptably low. Also, careful control of cooling rates required either specially constructed apparatus or the laborious addition of pieces of solid CO_2 to a methanol bath. Routine methods, such as placing the material in an insulated container inserted in the neck of a Dewar vessel containing liquid N_2, though convenient, resulted in variable and rather unpredictable cooling rates, which may have contributed to the variable proportions of viable cells. The purpose of this work was to develop a simple method for the cryopreservation of species in the subgenus *Trypanozoon*, reproducibly giving an acceptable level of survival. The test organism used, *Trypanosoma dionisii*, was originally isolated from the common British bat *(Pipistrellus pipistrellus)*; unlike the related *T. cruzi*, it is not a pathogen of humans (see Baker & Pennick, pp 78–80).

Trypanosoma (Schizotrypanum) dionisii dionisii, strain CCAP 1981/13, was grown at 28°C in Grace's Insect Tissue Culture Medium, supplemented with 30% v/v foetal bovine serum (Pennick & Paul 1983); cultures were about one week old when used, with a population predominantly of epimastigotes. A 2-step method of cooling was used to freeze the cells into liquid nitrogen. With this technique, best considered as interrupted rapid cooling, freezing occurred during an initial period of rapid cooling to a constant holding temperature. After maintenance at this subzero temperature, the sample was further cooled rapidly by plunging into liquid nitrogen. This method has several practical advantages: it is simple, requires no specialized controlled cooling rate equipment, and low concentrations of cryoprotective additives are effective.

Because few unprotected trypanosomes recovered from −196°C, it was decided to investigate the addition of compounds which reduce cellular freezing injury, so-called cryoprotectants. Preliminary experiments demonstrated that glycerol was a more effective cryoprotectant for trypanosomes than either dimethyl sulphoxide or methanol. Therefore, it was used in all further experiments, the final concentration of glycerol being one molar; to allow intracellular accumulation of this compound, the cells were exposed to glycerol for 15 minutes at 20°C before freezing. Suspensions of cells, 0·5 ml aliquots in polypropylene tubes (Nunc cryotubes, 1·5 ml capacity), were then placed for different times (5–60 min) in a constant temperature alcohol bath, maintained at −15°C, −20°C, −25°C, −30°C, or −35°C, before being either thawed directly, or plunged into liquid nitrogen and then thawed; some tubes were immersed directly in liquid nitrogen. After thawing (by immersion in a water bath at 37°C), viability was determined by a most probable number assay, using microtitre plates containing supplemented Grace's Insect Tissue Culture Medium.

There was no significant recovery when suspensions directly immersed in liquid nitrogen were thawed. After freezing at −15°C or −20°C, without subsequent cooling to −196°C, recovery was over 80%. Survival following freezing at −25°C, −30°C or −35°C decreased steadily as the duration of exposure to these temperatures increased, with recovery from −35°C being much less than from −25°C and −30°C.

When cells were immersed in liquid nitrogen after pre-freezing at −15°C or −20°C, there was no significant survival. After pre-freezing at −25°C or −30°C for different times before immersion in nitrogen, survival increased with time up to 10 or 15 minutes, and thereafter decreased. At all times, mean survival rates were higher after pre-freezing at −30°C than at the other temperatures tested.

Conclusion

Based on the results cited above, a standard technique with the following steps was adopted.

1. Addition of glycerol to unimolar concentration (≡ca 7·5% v/v)
2. Equilibration at ca 20°C (room temperature) for 15 minutes
3. Immersion in an alcohol bath maintained at −30°C for 15 minutes
4. Plunging directly into liquid nitrogen.

Using this technique, recovery, after thawing at 37°C, averaged 35%.

Julie Tansey and G J Morris

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Gibberellins and male cone initiation in lodgepole pine

Inability to induce forest trees to flower is a major constraint on tree breeding and forestry practice. Coniferous species in the Cupressaceae and Taxodiaceae are the first group where reliable stimulation has been achieved, applications of gibberellic acid (GA_3) to large or small trees inducing many male and female cones in a wide range of environmental conditions (Longman *et al.* 1982; Longman & Manurung 1982). In the Pinaceae, however, which contains many of the world's commercially important softwoods, GA_3 seems to be rather ineffective, although reproductive stimulation has been reported with a mixture of 2 other gibberellins, GA_4 and GA_7. A series of glasshouse and growth cabinet experiments with lodgepole pine *(Pinus contorta)* is in progress, testing the effectiveness of $GA_{4/7}$, and identifying interactions between hormonal and other inductive treatments. Research on flowering in small, potted plants has been made possible by developing (i) clones of rooted cuttings from 'highly reproductive' selections and (ii) a miniaturized injection system for small volumes of gibberellin solution.

This report describes an experiment designed to address 2 specific questions: (i) does injection of

$GA_{4/7}$ increase the number of male buds formed in glasshouse conditions, and, if so, how does the response depend on dose and clone; and (ii) how long-lasting are the effects of injection?

Five individual trees aged between 8 and 16 years were selected on the basis of repeated production of many cones of one or both sexes. Cuttings from the 5 clones were rooted in 1977 under mist propagation, and then grown in pots in the nursery. In March 1981, 60 plants, now approximately 0·6–0·9 m tall, were moved to a glasshouse without supplementary lighting or heating. In mid-June, when height growth for the year was largely completed, equal numbers of plants of each clone were assigned to 3 treatments and received: (i) 10 microlitres of alcohol (control), (ii) 0·9 mg $GA_{4/7}$ mixture (courtesy of ICI Ltd) in 10 microlitres of alcohol, or (iii) 8·1 mg $GA_{4/7}$ in 90 microlitres of alcohol. A single injection hole was used in treatments 1 and 2, while 9 holes per tree had to be made in treatment 3, because the hormone could not be concentrated into a smaller volume of solvent. In late September of the same year (year 1), the plants were returned to the nursery, where they remained in a randomized layout. Assessments of cones initiated in years 1 and 2 were made after they emerged in late spring of years 2 and 3.

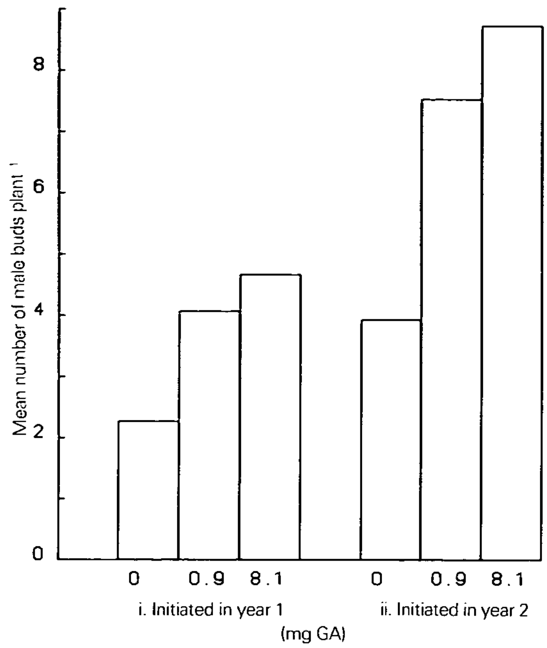

Figure 39 Effects of gibberellin on male cone initiation in lodgepole pine. Mean numbers of male buds (excluding those containing both sexes) initiated per plant in years 1 and 2, after injection with 0, 0·9 or 8·1 mg $GA_{4/7}$ per plant in year 1

Overall, gibberellin injection significantly increased numbers of male buds in year 1, about twice as many being formed as in the control trees (Figure 39 i). No significant difference was found between the 2 doses of $GA_{4/7}$, in which 25–30% of all buds formed male cones. The numbers of male buds were strongly influenced by clone, as in previous results with female cloning (Longman 1982). Clone no. 7, for instance, averaged 10 male buds per tree, summed over treatment, while clone 3 formed only one male bud for every 4 trees. Clones 3 and 4 formed no male clones without $GA_{4/7}$.

Although the trees received no further hormone or glasshouse treatment, the influence of the previous year's $GA_{4/7}$ injection was even more marked in year 2 (Figure 39 ii), with a pronounced stimulation for the first time in clones 3 and 4. Overall, treated plants produced more than twice as many male buds as the controls, bringing their proportions of buds which were male to 40–50%. As before, there was no significant difference between doses. Clonal variation was much less marked in the second year, with clone 7 producing on average only twice as many male buds as clone 3.

These results confirm that substantial stimulation of coning by gibberellin treatment can be achieved in the Pinaceae. They also suggest that no further significant increase in the number of male buds occurs in these conditions, even when the lower dose is multiplied 9-fold. Further enhancement may be possible, however, when more information has been obtained on clonal variation, on dates or stages of development when treatments are optimally effective, and on interactions between more than one stimulatory factor (Wheeler *et al.* 1980). Because the threshold for stimulation of male cones may well lie below 0·9 mg $GA_{4/7}$ (Figure 39), it may be appropriate to test smaller doses, more closely related to the lower concentrations of endogenous gibberellins that have been found in reproductive shoots in the Pinaceae (Kopcewicz *et al.* 1977).

The clear indication that male bud initiation can be stimulated more than a year after injecting trees with $GA_{4/7}$ is an important development. It is not yet clear whether this reflects an unusually long retention of hormone in an unmetabolized form in the wood, or whether the cells in the main apices of the buds have been induced, such that they transferred a tendency to produce male cones to their subsequently formed lateral short shoot apices. Instances of apparent carry-over into the second year have been observed for male cones in another experiment with $GA_{4/7}$ injected into lodgepole pine, and with injections of GA_3 in leyland cypress (male cones) and coast redwood (female cones). Delayed effects of this sort, when properly understood, may provide extra seed crops without a second treatment, perhaps even in the strongly vegetative genotypes of greatest interest in forestry.

K A Longman and Jan McP Dick

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Timber density of Sitka spruce

Tree growth in the United Kingdom is more rapid than in most other European countries. However, foresters are becoming increasingly aware that fast grown timber may have low wood density and therefore low mechanical strength, attributes that may seriously limit the purposes for which the timber can be used. Of particular importance is the decrease in wood density which occurs as tree growth accelerates in the early years after planting, because the timber which grows then may form a weak central core in the harvested log. However, there is considerable variation in timber density between trees, and so it is possible that individual trees with high density timber could be selected as breeding stock or for clonal propagation. To investigate this possibility, a study was made of the density of timber produced by 7 clones of Sitka spruce *(Picea sitchensis)* during their first 7 years of growth (Cannell *et al.* 1983). The clones had been selected at random from provenance trials throughout the United Kingdom and were planted on mineral soil at a lowland site on the Bush Estate, Midlothian, where tree growth is rapid.

There were substantial differences between clones in the production of stem wood over the 7 years; the maximum weight was 2·7 times the minimum. There was a tendency that clones which produced the greatest timber volume also produced timber of lowest specific gravity ($r^2 = 0{\cdot}30$). The annual timber volume production of all clones increased progressively over the 7 years, whilst wood density decreased as a linear function of the logarithm of annual timber production (Figure 40). Interestingly, those clones with the densest timber in the early years also had the greatest rate of decrease in timber density ($r^2 = 0{\cdot}94$). This finding poses a difficulty for devising a selection procedure for high timber density in Sitka spruce, because clonal rankings change with age. Furthermore, Figure 40 suggests that, if a trial were planted on a site of low productivity where growth was slow,

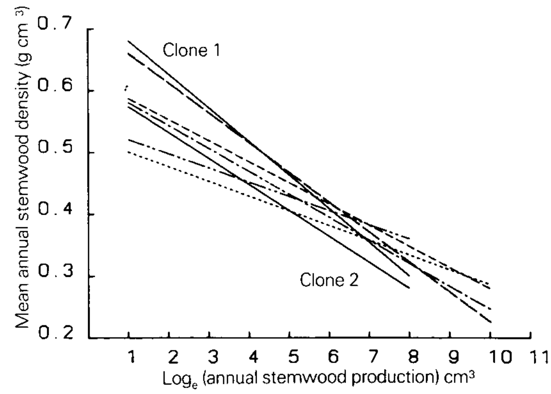

Figure 40 Calculated regression of mean annual stem wood density on log_e (annual stem wood production) which increased progressively over the first 7 years of growth of each of 7 clones of Sitka spruce grown at Bush Estate, Midlothian. The relationship for each clone was calculated from the analysis of 3 trees and the regression accounted for between 72% and 95% of the variation. Stem wood density was estimated gravimetrically as g dry weight/unit volume of dry material. Contrasting clones 1 and 2 were used for further detailed studies (see Figure 42)

then the ranking of clones for timber density might not be the same as that found on sites with faster growth rates. The variation found between clones shows that it may be possible to increase timber density through tree selection and breeding. However, this variation is complex, particularly in the relationship between growth rate and density.

A study was made of the ways in which the component processes of wood formation varied in 2 contrasting clones (see Figure 40), as growth rates increased and timber densities decreased. The wood of Sitka spruce comprises cells known as tracheids, their formation involving 4 sequential biological processes. Thin-walled cambial cells (Figure 41) repeatedly divide to produce a radial file of cells. These then expand, their walls thicken, and they become impregnated with lignin. The structure of the wood formed in successive years at the base of each tree was examined by scanning transverse sections, 10 µm thick, of each complete annual ring with a Quantimet image analyser. With this instrument, measurements were made of the number of cells and the projected cell wall area in defined fields of view under a microscope.

For both classes, the cross-sectional area of wood increased progressively from year to year (Figure 42 i), though with clone 2 making substantially more growth than clone 1. The number of cells produced each year in a radial band 800 µm wide (Figure 42 ii) increased rapidly for both clones to a value of 9000 at year 4, after which it stabilized over the next 3 years for clone 1, but decreased gradually for clone 2

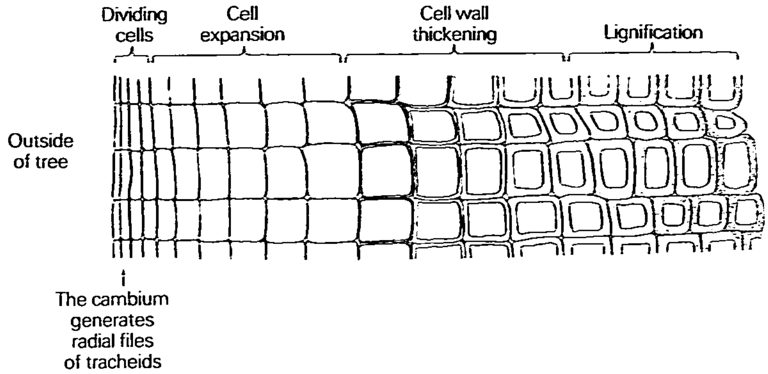

Figure 41 Diagrammatic representation of the historical stages in wood formation in Sitka spruce

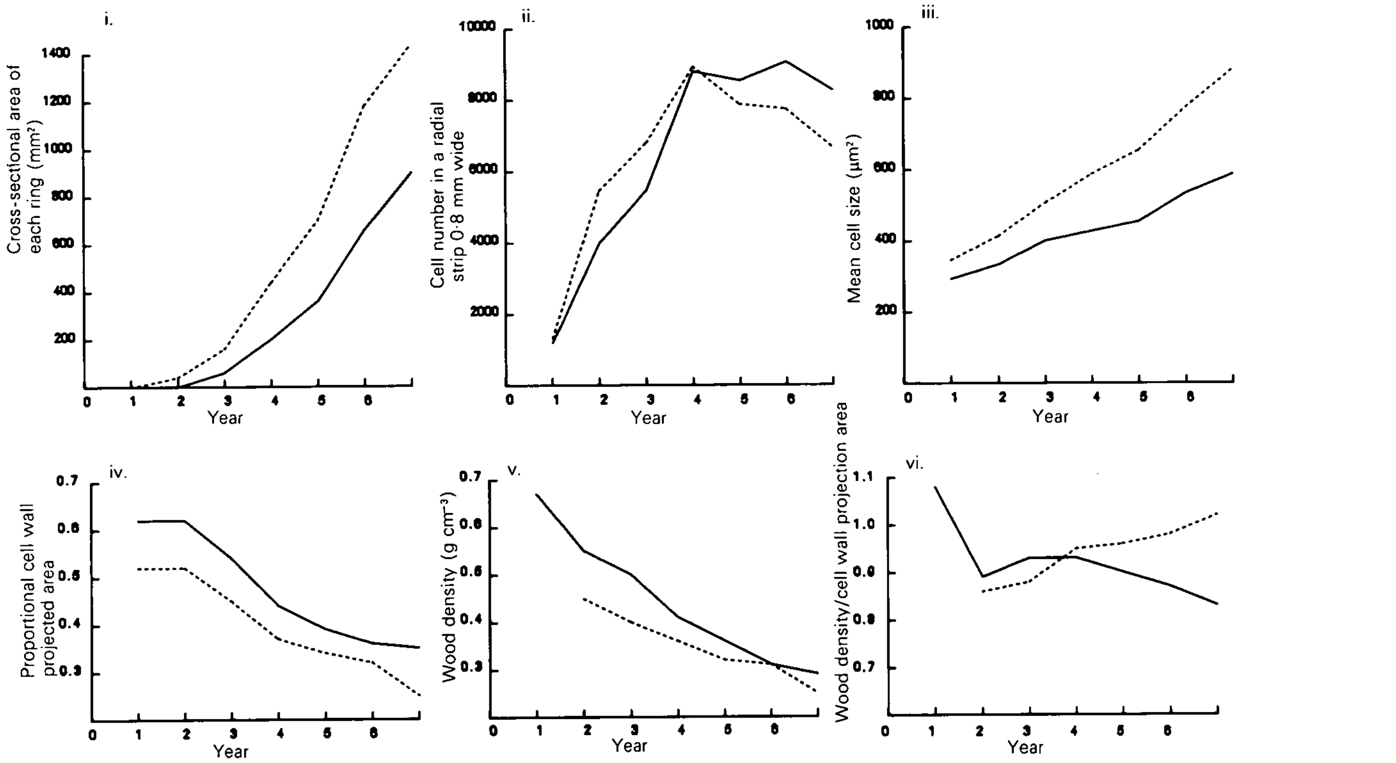

Figure 42 Wood properties of the first 7 successive annual rings produced at the base of the tree for each of 2 clones of Sitka spruce: _____ clone 1, _ _ _ _ _ clone 2 (see Figure 40). Data are means for 3 trees: (i) cross-sectional area of each annual ring; (ii) cell number in a radial strip 0·8 mm wide; (iii) mean cell size; (iv) cell wall projected area; (v) wood density measured volumetrically; (vi) apparent cell wall density measured as the ratio of wood density : cell wall projected area

despite this clone producing the larger cross-sectional area of wood. The difference in cell number was more than compensated by a difference in mean cell size (Figure 42 iii): although both clones showed an almost linear increase, that for clone 2 was 1·8 times larger than that for clone 1.

As would be expected with these large differences in cell size, the projected area of cell wall of clone 1 was always greater than that of clone 2 (Figure 42 iv). The projected area of cell wall decreased at the same rate for both clones over the 7 years of growth, but, in contrast, the annual decline in density was more rapid for clone 1 than clone 2 (Figure 42 v), density being assessed as the weight in grams per unit volume of timber in cubic centimeters measured by volumetric displacement. The lumen space of each cell is empty, and so a comparison can be made of the density of cell wall material as the ratio of density to cell wall projected area, which increased gradually over the 7-year period for clone 2 but decreased for clone 1.

These results show that the component processes of wood production, while forming juvenile wood of Sitka spruce, vary between clones and years. Although there was a decrease in wood density in both clones as growth rates increased, changes in

(i) cell size and (ii) cell wall density did not have identical patterns. The physiological bases for these differences are being investigated, with the objective of designing selection criteria for trees which will maintain high timber density when growth rates are rapid.

E D Ford and R H F Wilson

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ECOPHYSIOLOGY AND POLLUTION IN ANIMALS

Environmental control of breeding in birds

In mid and high latitudes, where climate changes seasonally, there is a great evolutionary pressure for birds, as with other animals, to breed at the best time of year for the survival of their young. As a bird raising a brood of nestlings has to find very much more food than usual, the best time of year to breed tends to be when the food on which the young are fed is most abundant. For this reason, insect-eating birds, for example, tend to breed earlier than seed-eaters. At Monks Wood, most of the work on control of the timing of breeding has been done on the starling *(Sturnus vulgaris)*, which has a markedly restricted breeding season. It feeds its young mainly on leatherjacket larvae, which are abundant during May. Environmental factors, such as food availability, which determine when a species breeds, are called 'ultimate factors'.

Birds, therefore, time their breeding so that the young hatch when food becomes abundant. However, a long sequence of events has to precede hatching. Birds have to pair, defend a territory, and build a nest. There are also parallel physiological changes. The gonads of both sexes have to grow and mature; eggs have to be ovulated, fertilized, laid and incubated. These events can take a considerable time. It is therefore important that the birds begin the breeding cycle in advance of the time when food becomes abundant. Ultimate factors are therefore inappropriate cues to time the onset of breeding, and so birds use other environmental cues as 'proximate factors' to indicate when breeding will shortly be practicable. Such proximate factors need bear no direct relationship to the ultimate ones, but must change in a predictable way during the year, so that they can accurately reflect the date. The environmental variable which changes most predictably during the year is day length, and this is the proximate factor used by nearly all species of birds which have so far been investigated from mid and high latitudes.

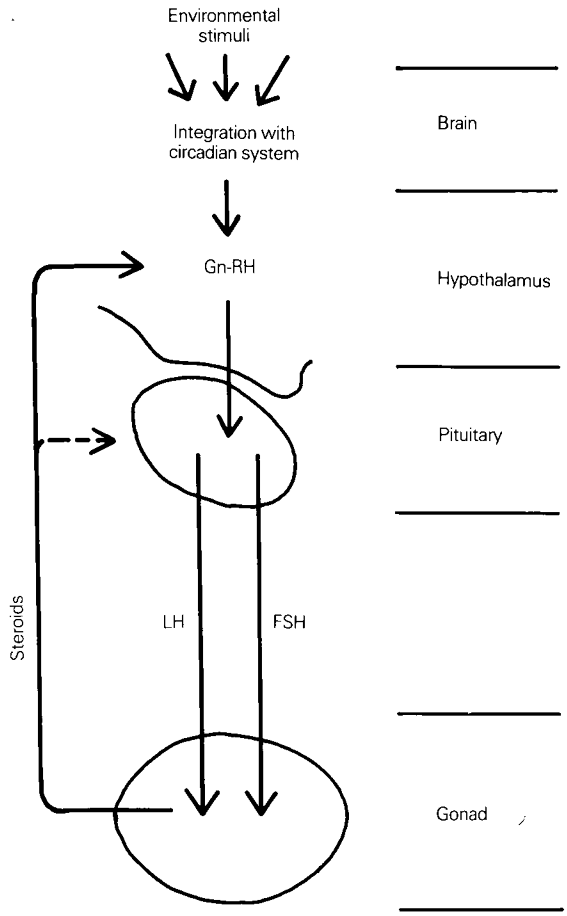

Figure 43 A schematic diagram illustrating basic components of the neuro-endocrine mechanism, through which changes in the environment, particularly day length, cause growth of the testis or ovary

The use of day length to time the onset of breeding—called photoperiodism—has been studied extensively in birds during the last few decades, particularly since the advent of radio-immunoassays which can be used to measure very small amounts of hormones in blood plasma. The principal mechanisms involved are illustrated schematically in Figure 43. Birds can measure day length accurately. They do this not by measuring elapsed time since dawn, an 'hour glass' model, but by using a system of circadian oscillators. When a bird experiences a 'long day', the information is perceived and integrated in the brain, causing neurosecretory neurones in the hypothalamus to secrete a peptide hormone, gonadotrophin releasing hormone (Gn-RH), which is carried in portal blood vessels to the pituitary gland. This system is quantitative, ie the longer the day length, the larger the response. The Gn-RH stimulates cells in the pituitary gland to synthesize and release gonadotrophic hormones, luteinizing hormone (LH) and follicle stimulating hormone (FSH). These hormones are carried in the blood to the gonads where they promote growth and maturation. LH, in particular, also stimulates interstitial cells in the gonads to synthesize steroid hormones, and these modulate the production of Gn-RH and gonadotrophins by negative feedback in the hypothalamus and pituitary.

In wild birds, the gonads are generally at their smallest and least active in winter. They start expanding in early spring; their growth accelerates with further increases in day length, until the maximum size is attained at the appropriate time of year.

It is crucial that the onset of breeding is accurately timed. It is equally important that breeding finishes before environmental conditions become unfavourable. For most species of birds, breeding ends well before autumn, and it is therefore inappropriate simply to wait for short day lengths to inhibit breeding. Instead, most birds enter a state of photorefractoriness. Although long day lengths stimulate birds initially to become sexually mature, birds become refractory to the stimulatory effect after a certain period of exposure and the gonads regress spontaneously. Exposure to a period of short day lengths is then necessary before birds again become photosensitive. Unlike the photoperiodic response at the beginning of breeding, little research has been done on photorefractoriness. Over the last 3 years, this problem has been studied in a joint research programme between ITE at Monks Wood and the Department of Zoology at the University of Bristol.

At the outset, we needed to know the changes in plasma levels of reproductive hormones in free-living starlings during the year and at different stages of breeding. Birds were caught in mist nets, or, during breeding, in nest boxes. A record was kept for each pair so that the reproductive state of each bird caught was known. Blood samples were taken from all birds, and plasma was assayed for LH and gonadal steroids. Plasma levels of prolactin were also measured: this is another peptide hormone produced by the pituitary gland, and for many years has been thought to be responsible for causing broody behaviour in birds. Figure 44 shows the results obtained for males. As expected, LH levels were highest early in breeding and during nest building, and prolactin was highest later, during incubation. When expressed as monthly means (Figure 45), highest LH levels corresponded to maximum testicular weight, during April, when most birds were in the early stages of breeding. Prolactin was highest in May, when most birds were in the later stages of breeding. Results for females were similar.

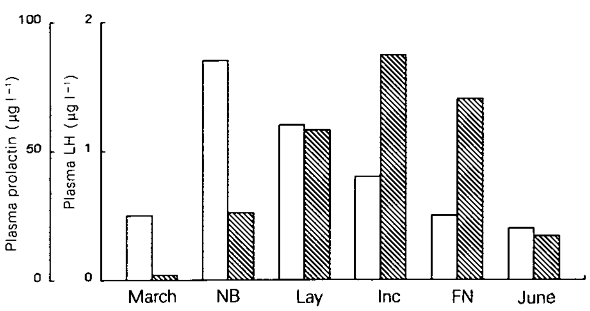

Figure 44 Changes in plasma concentrations of LH (open bars) and prolactin (cross-hatched bars) in free-living male starlings through March, nest-building (NB), laying (LAY), incubation (INC), feeding nestlings (FN), and after breeding in June

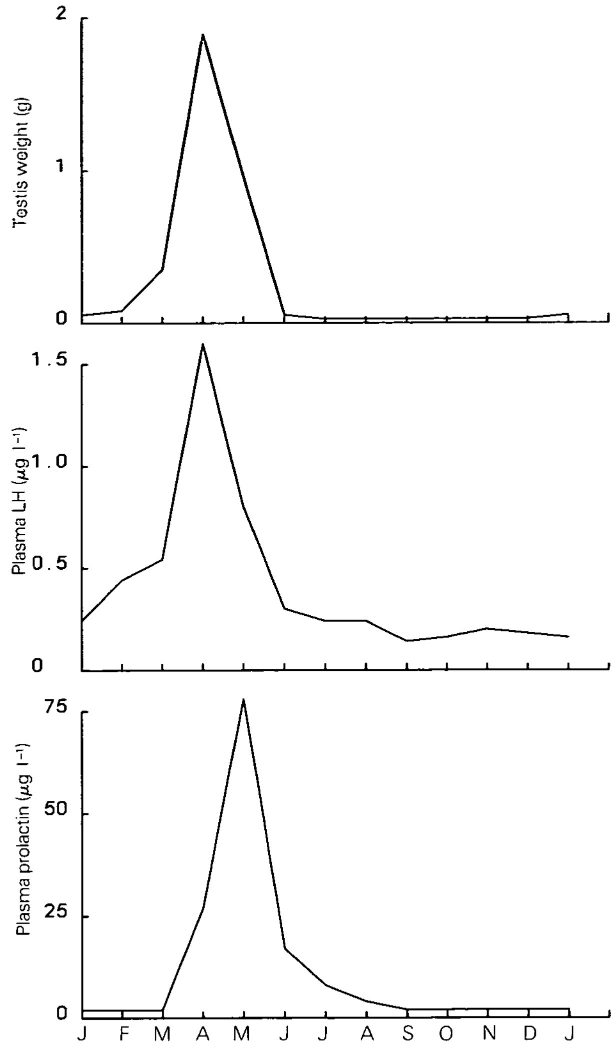

Figure 45 Changes in testicular weight and plasma concentrations of LH and prolactin in free living male starlings during the year

Although these findings were expected, in the sense that they corresponded to the appropriate stages of breeding, we found exactly the same pattern of seasonal changes in LH and prolactin in captive birds held in outdoor aviaries, where there was no breeding activity. In other words, annual cycles of both hormones appeared to be driven by simple environmental cues. Although it had been known for many years that LH levels increased as a result of increasing day length, and decreased at the onset of the photorefractory state, an increase in prolactin levels in non-breeding birds had not previously been recorded. Moreover, prolactin levels increased at the same time as LH levels decreased. These results suggested that prolactin secretion may also be under photoperiodic control, but requires a longer day length than LH, and that it was associated in some way with the onset of photorefractoriness.

Another experiment was done to test this hypothesis. Four groups of starlings were transferred from outdoor aviaries into light-tight boxes during December. They were kept initially under a lighting schedule of 8 hours light and 16 hours darkness per day (8L:16D) and then each group was transferred to either 18L:6D, 13L:11D, 11L:13D, or kept on 8L:16D for 13 weeks. Blood samples were taken every week and assayed for LH, FSH and prolactin, and testis size in males was measured frequently.

Testis size increased most rapidly in birds on 18L:6D (Figure 46), but these birds quickly became photorefractory: testis size began to decrease between 2 and 4 weeks. Testis size also increased rapidly in birds held on 13L:11D, but these birds did not become photorefractory until 6 weeks.

Under 11L:13D, testis size increased slowly and these birds did not become photorefractory. Other studies have shown that starlings can be held indefinitely on 11L:13D without becoming photorefractory. Finally, on 8L:16D, there was only very slight testis growth.

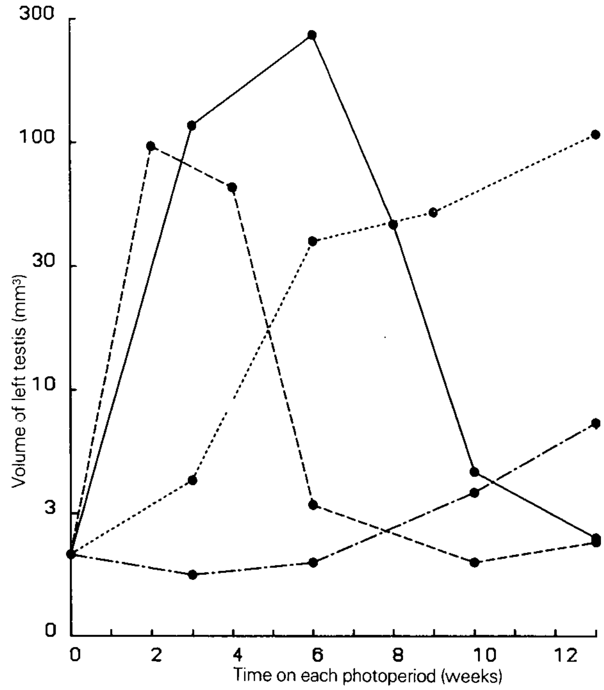

Figure 46 Changes in volume of the left testis in male starlings after transfer from 8 h light:16 h darkness (8L:16D) to 18L:6D (●----●), 13L:11D (●——●), 11L:13D (●·····●), or kept on 8L:16D (●–·–·●). Note that volume is plotted on a log scale

These changes in testis size reflect changes in plasma gonadotrophins (Figure 47). Under 18L:6D and 13L:11D, plasma LH and FSH increased equally rapidly. Under 18L:6D, they decreased after 1 and 2 weeks respectively, and had returned to initial levels by 4 weeks. Under 13L:11D, there was also a decrease in LH levels after one week, but this was probably due to negative feedback by gonadal steroids. The decline to initial values began at about 6 weeks, corresponding to the decline in testis size. Under 11L:13D, there was an immediate, but only slight, rise in LH levels which was maintained throughout 13 weeks.

Prolactin levels increased immediately in the 18L:6D group, but more slowly in the 13L:11D group. In both cases, prolactin levels were increasing rapidly as birds became photorefractory, ie after 3 and 6 weeks respectively. In birds on 11L:13D, which did not become photorefractory, there was no increase in prolactin levels. These results therefore seemed to support the hypothesis that increased prolactin secretion is associated with the onset of photorefractoriness, and that it is under photoperiodic control, requiring a longer day length than gonadotrophin secretion. More recent results, however, have shown that prolactin secretion is not under direct photoperiodic control.

An early theory to explain photorefractoriness suggested that the gonads themselves became refractory or 'exhausted' after a certain time. This theory was disproved because injections of gonadotrophins caused gonadal growth in photorefractory birds, and the pituitary gland did not become exhausted because injections of Gn-RH had the same effect. A more recent theory suggested that increasing day length in some way increased sensitivity of the hypothalamus to the negative feedback effect of gonadal steroids, thus suppressing gonadotrophin secretion and causing gonadal regression. This is an unlikely explanation, as plasma levels of gonadal steroids are themselves very low during photorefractoriness. Nevertheless, we tested this possibility by keeping intact and castrated starlings in an outdoor aviary throughout one year, taking regular blood samples and assaying them for LH and prolactin. In intact starlings, LH showed the same pattern as before, with levels increasing during spring to a peak in early May, then decreasing rapidly as birds became photorefractory (Figure 48). In castrated starlings, LH levels were much higher than in intact birds during spring (because there were no gonadal steroids to suppress LH secretion), but they decreased at the same time to levels indistinguishable from those in intact birds. LH levels increased again during autumn as photorefractoriness was broken by short days. Castrated birds therefore do become photorefractory, and so steroid feedback is not involved. Prolactin levels again increased at the onset of photorefractoriness and were identical in intact and castrated birds.

In another study, castrated starlings were given testosterone implants to suppress LH secretion completely. Again, birds became photorefractory, and changes in prolactin levels were the same as in intact birds. These results suggest that, whatever change

Plate 10 Tractor-mounted rope-wick applicator; this apparatus carries a concentrated solution of herbicide flowing through the rope-wicks, which smear the chemical on to the target weeds
(Photograph N Turner, Hectaspan Ltd)

Plate 11 Effects of asulam one year after application to a dense stand of bracken; the deep litter layer left after treatment prevents colonization by desirable species
(Photograph J E Lowday)

Plate 12 Root systems being teased out intact from the forest
(Photograph J D Deans)

Plate 13 Harvesting cordgrass in January. This is a productive and invasive species of coastal mudflats, and would therefore provide an energy crop without displacing agriculture or forestry
(Photograph R Scott)

Plate 14 Harvesting winter barley from open top chamber plot in Glasgow as part of the air pollution study
(Photograph I S Paterson)

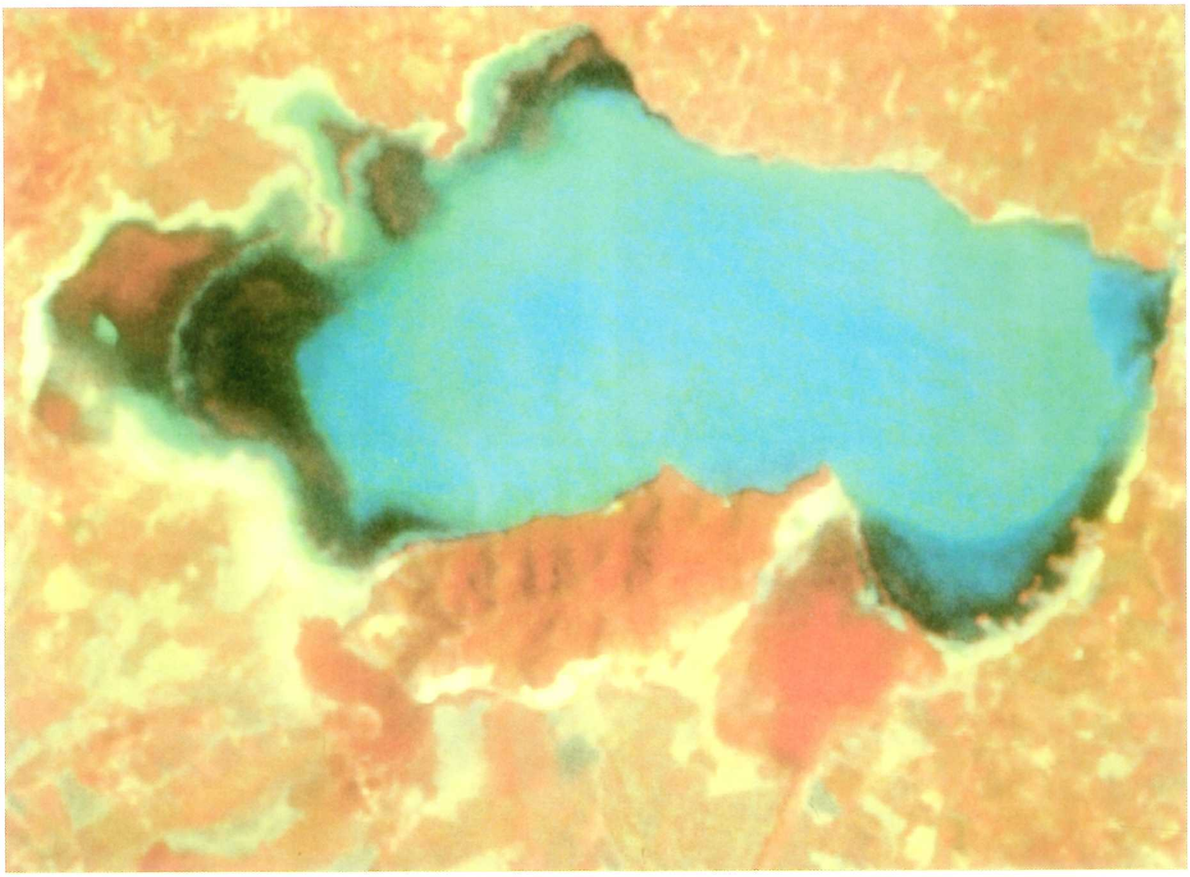

Plate 15 Lake Ichkeul, June 1980: an auto-linear sketch of Landsat bands 4, 5 and 7

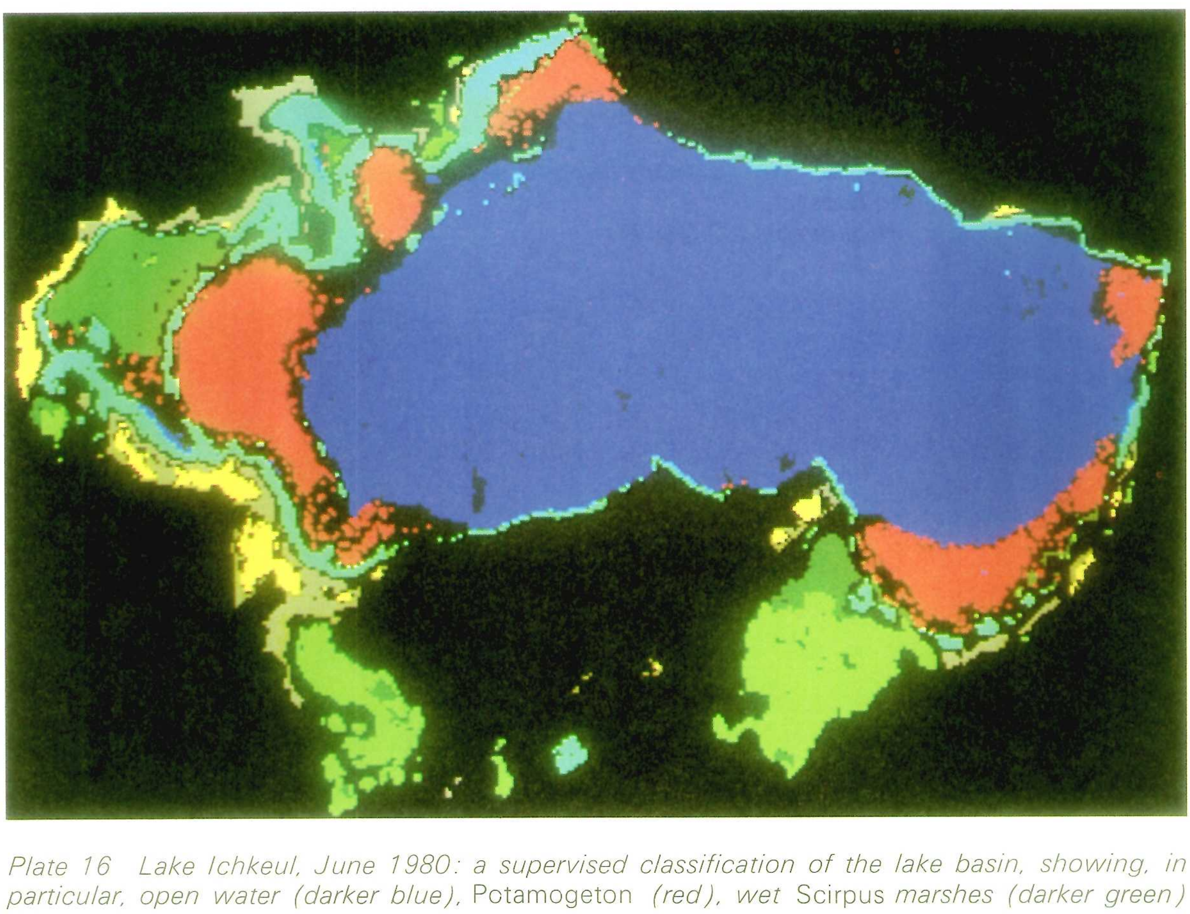

Plate 16 Lake Ichkeul, June 1980: a supervised classification of the lake basin, showing, in particular, open water (darker blue), Potamogeton *(red), wet* Scirpus *marshes (darker green) and drier* Scirpus *marshes (light green)*

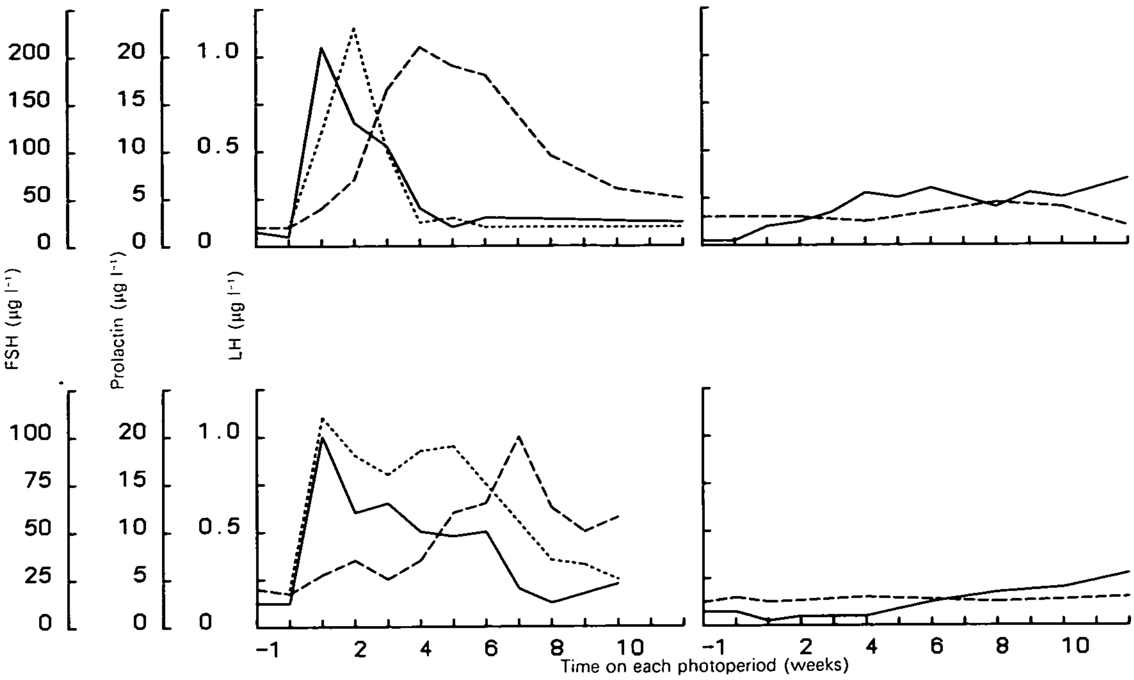

Figure 47 Changes in plasma concentrations of LH (———), FSH (······) and prolactin (– – – – – –) in male starlings after transfer on week 0 from 8 h light : 16 h darkness (8L : 16D) to A, 18L : 6D; B, 13L : 11D; C, 11L : 13D; or D, kept on 8L : 6D

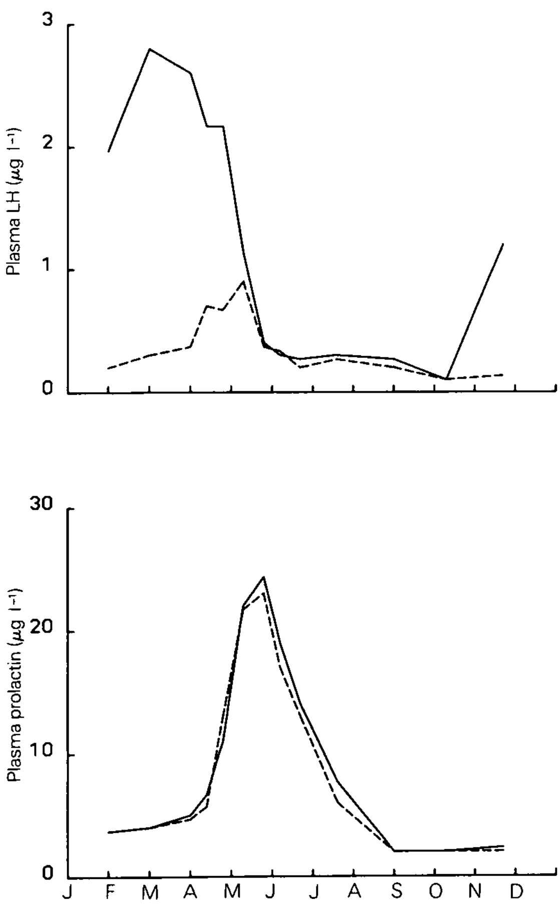

Figure 48 Changes in plasma LH and prolactin concentrations in intact males (– – – – – –) and castrated males (———) held in outdoor aviaries during the year

causes photorefractoriness, it must occur in the hypothalamus, or higher in the brain. To confirm this theory, we have recently managed to measure Gn-RH content of the hypothalamus from starlings at different stages of a photo-induced gonadal cycle. As expected, Gn-RH content increased as birds became sexually mature after transfer to long day lengths, but, when they became photorefractory, not only did Gn-RH content decrease, but it decreased to levels significantly lower than in non-photostimulated photosensitive birds at the beginning of the experiment. Pituitary contents of LH, FSH and prolactin were also measured and changes reflected those found previously for plasma levels. Pituitary prolactin content showed particularly dramatic changes. It has been known for a number of years that the thyroid gland must be involved in the onset of photorefractoriness, because thyroidectomized starlings do not become photorefractory.

When such birds are transferred to long day lengths, the gonads grow and remain large. We have recently begun a series of experiments to investigate the role of the thyroid. The first of these showed that thyroxine (one of the hormones produced by the thyroid gland) increases in birds transferred to photoperiods long enough to induce photorefractoriness. The second experiment confirmed that thyroidectomy prevents refractoriness. Testicular width in intact starlings increased after transfer to long day lengths, then decreased as they became photorefractory (Figure 49 i). In starlings from which the thyroid glands had been removed, it also increased, but then

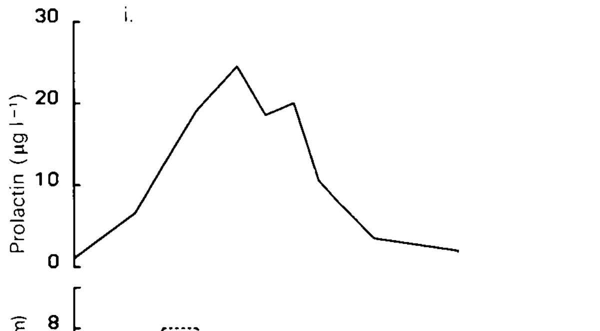

Figure 49 Changes in testicular width and plasma prolactin concentrations in (i) intact and (ii) thyroidectomized starlings after transfer from 8L:16D to 16L:8D

remained large (Figure 49 ii). Prolactin levels increased in intact birds, as before, but in birds without thyroid glands there was no increase in prolactin after transfer to long day lengths. Again, therefore, there was an association between prolactin levels and the onset of photorefractoriness. Another experiment showed that hypothalamic Gn-RH content in chronically photostimulated, thyroidectomized starlings was greater than in intact birds which had become photorefractory. When thyroidectomized starlings, held on long day lengths, were treated with thyroxine, they became photorefractory; so did intact starlings held on 11L:13D (which normally causes gonadal growth but does not induce photorefractoriness). These results suggested that thyroid hormones caused photorefractoriness. However, it turned out to be more complex. The effect of thyroxine treatment depends on the stage of the gonadal cycle at which the treatment is administered. When we gave thyroxine to birds during photoinduced gonadal growth, it had no effect. When given to photosensitive birds on short day lengths, it appeared to stimulate gonadal growth. One possibility, therefore, is that thyroxine precipitates the next stage of a gonadal cycle. In other words, it acts as a long day.

However, these few experiments concerning the thyroid are very recent and were carried out with few birds. The conclusions are therefore tentative and further experiments are being done to investigate the problem further.

A Dawson

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Alkyl lead and essential metals

If pollution is to be controlled, then we must (i) detect the effects of pollutants as soon as possible, (ii) understand the mechanisms by which pollutants cause harm, and (iii) define the lowest concentration of pollutant which has an effect on the biological system under study. Biochemical changes in tissues are one way of studying all 3 of these aspects of pollution, as biochemical changes in cells and tissues may be detected long before effects on the whole animal become apparent. For various reasons, changes in the concentrations and amounts of essential metals in tissues could be a convenient and economical way of monitoring the effects of pollutants on an animal's subcellular biochemistry. ITE has begun to evaluate this possibility by measuring the levels of 3 essential elements (zinc, iron and copper) in tissues of birds that had been exposed to 2 alkyl lead compounds—triethyl and trimethyl lead.

Both the metal concentration (mg metal kg^{-1} dry tissue) and the metal load (µg metal) of the pectoral muscle, liver, kidney and bone have been determined. Earlier studies on these birds (Osborn *et al.* 1983) suggested that changes in the essential metal status of these tissues might be expected in birds suffering from alkyl lead poisoning. However, it is not certain which metals would be affected, and what would be the influence of the tissue weight changes that occurred in birds dosed with alkyl lead.

Zinc was the least affected of the 3 essential metals. Although the observed changes in concentration could be biochemically important, there were few that could not reasonably be explained by changes in tissue weight.

There were marked effects of alkyl lead treatment on the copper and iron status of several tissues. Both concentrations and organ loads of these metals changed in ways which could not be accounted for by changes in organ weight. Changes in copper and iron were most apparent in bone, where increases of between 60% and 200% occurred in both concentrations and loads. Presumably, these increases were the result of increased haemopoiesis (blood cell production) in the bone marrow. Evidence for increased haemopoiesis had been observed in earlier work (Osborn *et al.* 1983), but could not be quantified. These changes in essential metals provide a quantitative measure of the effect on blood production, and make further work possible. In contrast to the increase in bone copper and iron, muscle copper and iron concentrations were about 20% lower than was expected from the loss of muscle weight, and this finding could indicate that biochemical aspects of muscle function were impaired even before weight loss itself rendered the muscle useless for flight. Effects on iron in liver and kidney were difficult to determine, as the changes seen could not easily be separated from the natural seasonal variations in iron concentrations. Effects on copper metabolism in liver were greater than could be explained by changes in liver weight, loads increasing by 120–170%. This result may suggest that the liver's storage role in essential metal physiology has been altered by alkyl lead treatment.

The data are now being analysed to see whether the ratios of essential metal concentrations were altered by alkyl lead. Ratios of the concentrations of essential metals may provide a better guide to the 'health' of a tissue than the concentrations of any one metal. In this respect, the differential effect of alkyl lead treatment on zinc and copper may be especially important, as concentrations of these 2 metals seem to be kept in constant ratio in bird liver, even through periods of major physiological change (eg breeding, moult and over-winter survival). Any departure from the usual copper:zinc ratio would provide a firm indication that normal biochemical processes had been adversely affected.

In a broader context, it is interesting that alkyl lead compounds affect copper and iron metabolism, because swans poisoned by inorganic lead compounds also had altered copper and iron concentrations (Simpson *et al.* 1979). Possibly, disturbance of copper and iron metabolism is a fundamental aspect of the toxicology of lead compounds in birds. If so, it is possible that inter-family differences in copper and iron metabolism could explain the differing susceptibility of various types of birds to lead poisoning.

D Osborn and Wendy J Young

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Study of an expanding sparrowhawk population

In the years around 1960, sparrowhawks *(Accipiter nisus)* were almost eliminated from large parts of Britain, following the widespread introduction of certain pesticides in agriculture, notably aldrin and dieldrin. Since that time, the uses of these chemicals have been progressively restricted, residues in wildlife specimens have declined, and the sparrowhawk has partly recovered and recolonized areas from which it had disappeared. One such area is Rockingham Forest in Northamptonshire, which has been re-occupied since about 1978. ITE has studied the development of this population, partly for comparison with stable populations elsewhere in Britain, which became re-established 10–15 years earlier.

Occasional birds were seen in the Rockingham district from the early 1970s, and 3 nests were found in a large study area in 1979, extending between the towns of Corby and Oundle. Since then, the population has expanded rapidly, with 16 nests found in the same area in 1980, 23 in 1981, 42 in 1982 and 53 in 1983 (Table 19). The increase was too rapid to result entirely from high survival of locally produced young, and must have been due partly to immigration, probably from western areas where the species had recovered earlier.

The pattern of recolonization has proved interesting, for pairs have not settled at random throughout the study area, but have concentrated, first, in particular woods (up to 5 pairs per wood), and only later spread to other woods. For the first few years, all the nests were in conifer stands, and only in the last 2 years did some pairs breed in broadleaved stands. By 1983, the conifers were still occupied to a much greater extent than the broadleaved areas, and a further expansion is predicted largely in the latter.

Table 19. Numbers and success of sparrowhawk pairs found breeding in the Rockingham Forest area, Northants, 1979–83

	1979	1980	1981	1982	1983	Overall
Number of nests found	3	16	234	42	53	137
Number which produced young	3	10	8	16	24	61
Mean number of young produced per nest	—	1·8	1·5	1·7	1·4	1·5

Table 20. Proportion of yearlings (Y) and adults (A) among breeding sparrowhawks in Rockingham Forest (increasing population) and south Scotland (stable population). Records from different years are combined

	Numbers of males		Numbers of females	
	Y	A	Y	A
Rockingham Forest	19 (33%)	38	32 (26%)	92
South Scotland	52 (18%)	242	132 (15%)	726
Significance of difference between areas	$\chi^2=6{\cdot}3$, $P<0{\cdot}01$		$\chi^2=7{\cdot}7$, $P<0{\cdot}01$	

A striking feature of this expanding population was the high proportion of first-year birds among those breeding. Such birds have a distinct brown plumage, so they are readily separated from older birds, which have adult plumage and are mainly grey-blue in colour. The proportion of yearling males in the breeding population varied between 30% and 40% in different years, and the proportion of yearling females varied between 19% and 32%. These figures compared with overall means of 18% for males and 15% for females in a more stable population in south Scotland. The difference between areas in this respect was highly significant statistically (Table 20). It may have resulted either because of higher survival through the first year in the expanding population, or because a greater proportion of individuals were breeding at a young age. In south Scotland, many birds delayed breeding until their second or third year.

Analysis of unhatched eggs collected from the Rockingham population confirmed that residues of aldrin and dieldrin were low. On the other hand, residues of DDE (from the insecticide DDT) were relatively high, shell thinning was marked, and breeding success was poor, with a mean production of 1·4–1·8 young per nest in different years (Table 19). Evidently this population has expanded, despite continued poor breeding associated with DDE contamination. It was presumably the improved survival of adults, resulting from declining aldrin/dieldrin levels, which has allowed the expansion, together with continuing immigration. In general, less than half the breeding birds which were trapped had been ringed as local nestlings, so the remaining breeding birds had been raised outside the study area.

As this population has grown, sparrowhawks have been seen increasingly in areas to the east. However, there still remains a large section of East Anglia in which the species has not yet recovered. This region includes much of Lincolnshire and Cambridgeshire, and parts of Norfolk, Suffolk, Essex and Kent. The area includes some of the most intensely arable farmland in Britain, where pesticide use has always been heavy. If the use of the persistent chemicals can be kept low, however, it will probably only be a matter of time before this region, too, will be recolonized.

I Newton and I Wyllie

Growth of pregnant wild rabbits in relation to litter size

In domestic rabbits, there is a direct relation between litter size and birth weight of individual young (Breuer & Claussen 1977). The resources available for growth during gestation, which may be independent of litter size, are divided roughly equally between the young in a litter. This study investigated the pattern of investment in the growth of litters during gestation for European wild rabbits *(Oryctolagus cuniculus)*.

Three adult female and 3 adult male wild rabbits, which had been captured locally, were placed in each of 6 enclosures (80 m × 80 m) at Monks Wood Experimental Station, fed on natural pasture, and allowed to breed freely. At weekly intervals from March to August, the body weights of all females were measured. Litters were located, and the number of young counted, usually within one day of birth. The date of conception was calculated from the date of birth, assuming that gestation lasted 30 days.

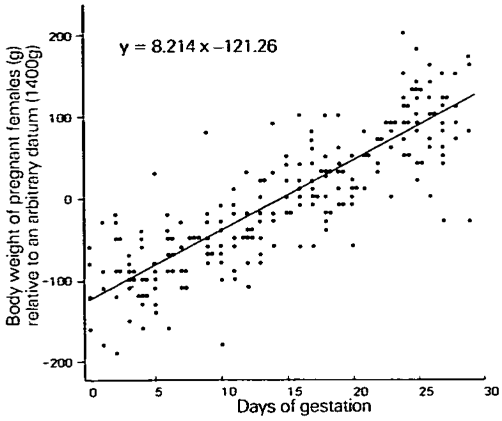

Figure 50 Scattergram plot of all recorded weights from female wild rabbits during pregnancy (n = 211). The mean weight of females during pregnancy was given the value of zero, so that the weight changes could be compared in different individuals. A linear model was fitted to these points and the equation of the best-fit straight line, derived by least squares regression, is given

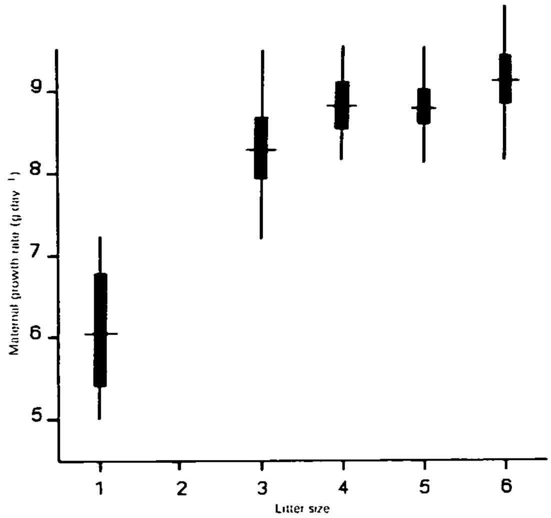

Figure 51 Growth rates of pregnant female wild rabbits according to the litter size at birth. Growth rates were calculated by fitting a linear model to the plots of female weight with time through gestation. 95% confidence limits (▬) and the variance (——) on the estimated growth rates are given

Twenty-nine litters, containing 101 individuals, were collected on day 1 post-partum and estimates of nose-to-tail length, wet weight, dry weight, and lean dry weight of the individuals were obtained.

Body weight of females increased as pregnancy progressed and declined sharply at parturition. Growth of females during gestation was described in empirical terms by expressing all the growth curves of pregnant females relative to their means. This calculation was possible because weight measurements were taken at regular intervals during gestation, and weight increase was fairly constant, so that the arithmetic mean was close to the mean at the mid-point in gestation. By setting all mean weights during gestation to equal zero, a scattergram of weights in relation to the stage of gestation for all recorded pregnancies was produced (Figure 50). On average, females gained 8·2 g day^{-1} during gestation (SD = 0·378 g, n = 211). Mean litter size was 4·16 (SE = 0·19, n = 56), which is not significantly different from the mean litter size of a wild population (Wood 1980), with a range of 1–6 young. In contrast to domestic rabbits, litter size did not influence the size of young at birth (Table 21). Sex ratio at birth was not significantly different from 1 :1 and was not influenced by litter size. Figure 51 shows the growth rates of females which produced litters of different size, calculated in the same way as the overall growth rate of pregnant females (Figure 50). Females producing 2 young were not included in Figure 51 because of insufficient data. In spite of the size of young being independent of litter size at birth (Table 21), female weight gain during gestation was indirectly proportional to litter size (Figure 51). It is unlikely that foetal resorption will have influenced this relationship significantly.

These results suggest that females invest the same amount in tissue growth during pregnancy for all but

Table 21. Relationship between litter size and various measurements of new-born wild rabbits. The overall means ($\bar{X}$) and standard errors of the means (SE) are given

	Litter size											
	1		2		3		4		5		6	
	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE
Nose–tail length (mm)	124·25	8·240	115·25	2·418	117·26	1·333	122·38	2·250	114·00	2·130	119·06	1·352
Wet weight (g)	40·20	5·789	30·84	1·732	35·92	1·455	38·01	1·870	32·72	1·487	38·84	1·124
Dry weight (g)	8·12	1·394	5·79	0·352	6·94	0·319	7·78	0·371	6·40	0·389	7·68	0·292
Lean dry weight (g)	6·43	1·175	4·52	0·293	5·46	0·246	6·13	0·253	5·07	0·267	6·16	0·192
Number of new-born in sample	4		8		27		8		35		18	

the smallest litters, and that this growth is partitioned between maternal growth and foetal growth. Females having large litters would gain less in terms of maternal tissue growth during gestation. Because lactation is a time of high energetic stress in rabbits, nutrients stored during gestation may form an important source of nutrients during lactation. Nutrient storage occurs in some other mammals during gestation (Dewar 1969), and could influence the neonatal survival and growth of young from litters of different sizes, as nutrient storage will be small when litters are large.

Selection for a high reproductive rate in domestic rabbits may have meant that most resources are channelled into foetal growth, whereas, in the wild counterpart, where nutrient availability is less predictable, greatest reproductive success may be achieved through the partitioning of resources between foetal growth and storage for later use in lactation.

I L Boyd

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PLANT POPULATION ECOLOGY

Taxonomy of sub-antarctic mosses – *Tortula*

Mosses form a major part of the tundra-like vegetation of the Antarctic and sub-Antarctic. Ecological studies including this group have been hindered by an inadequate taxonomic and nomenclatural framework. These inadequacies are largely due to shortcomings in the work of 19th century botanists who first described many of the region's plants. They had a very narrow species concept and did not appreciate the extent of variation now known to occur within many species of plants. As a result, many taxa were described which differ from each other only in minor respects, and modern checklists, which are based on these descriptions, perpetuate the same mistakes. To remedy this situation, taxonomic revisions of moss genera are being prepared, using the large and important herbarium of the British Antarctic Survey, with the aim of producing a new manual to the moss flora of South Georgia, which revises, describes and identifies each species in a dichotomous key, enabling biologists to make their own determinations. South Georgia, a sub-Antarctic island lying on the Scotia Ridge between Tierra del Fuego and the

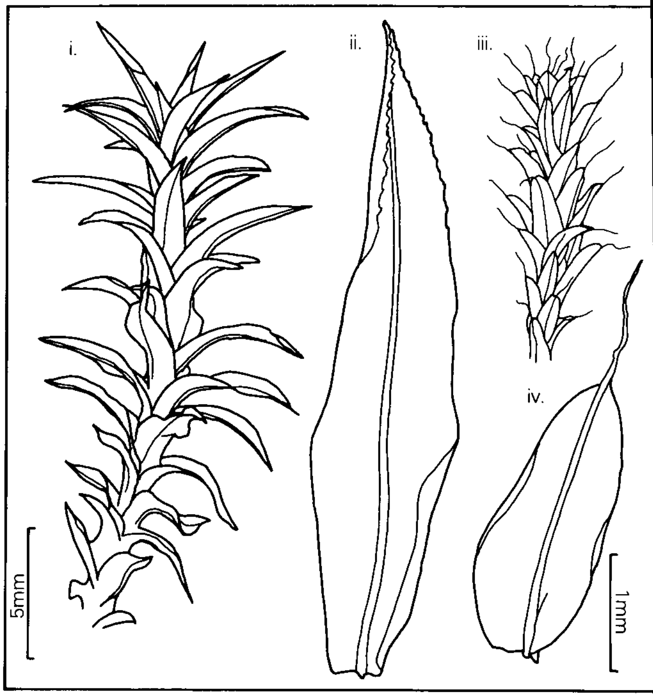

Figure 52 Two moss species belonging to the genus Tortula *from the sub-Antarctic island of South Georgia. (i) Stem of a non hair-pointed species,* T. robusta*; (ii) Leaf of* T. robusta*; (iii) stem of a hair-pointed species,* T. princeps*; (iv) leaf of* T. princeps*. Scales: left for stems, right for leaves*

Antarctic peninsula, has been chosen for this study as many Antarctic species can be found there growing luxuriantly and producing sporophytes. In more southerly latitudes with severer climates, the same moss species have stunted growth and do not produce sporophytes.

Species of *Tortula* are among the island's most abundant bryophytes. A recent study has divided the genus into 8 species which can be placed conveniently in 2 groups, depending on the presence or absence of a hair-point at leaf apices (Figure 52). Among the non hair-pointed species, *T. robusta* forms an association with a rosaceous shrub, *Acaena*, which dominates much of the island's steep scree slopes, while *T. arenae* and *T. fontana* are characteristic of wetter habitats, eg stream-sides, flushes and base-rich bogs. *T. saxicola*, by contrast, is a drought-tolerant species found particularly on coastal rocks. Altogether, the non hair-pointed group includes 7 species and one variety which growth experiments have shown remain distinct in identical environments. The hair-pointed group consists of a single polymorphic species, *T. princeps*, whose taxonomy has posed many problems. It is a cosmopolitan species which is extremely variable on South Georgia. Multivariate analysis, however, supports the decision to regard it as having 3 separate varieties.

World-wide, *Tortula* is a fairly large genus consisting of about 200 mainly temperate species, with some occurring in the tropics at high altitudes, while others extend into polar regions. A few species are cosmopolitan, but most appear to be limited to either northern or southern temperate zones. In the northern hemisphere, many *Tortula* species have hair-pointed leaves and are remarkable because of their adaptation to extreme drought; they are probably advanced in an evolutionary sense. In the south, the hair-pointed group appears to be much less diverse: on South Georgia, hair-pointed species are in a minority. Of the non hair-pointed species, 5 form a distinct group which has not yet been recognized taxonomically. The species concerned have dentate leaves and basal marginal cells which are elongated instead of quadrate, a combination of characters which appears to be unique to the southern hemisphere. One member of this group has the smallest chromosome number known in *Tortula*, which suggests that it is primitive. In addition, the greater morphological diversity of the genus as a whole in the southern hemisphere indicates that this area may be its original centre of distribution. If it is true that the southern hemisphere moss flora contains ancient species, how many of these relicts occur in the Antarctic? It has been suggested that they would probably survive on isolated sub-Antarctic islands, while disappearing elsewhere because of unfavourable climate and/or competition. In the event, this proposition is not supported by the distribution of *Tortula* species. Not only are all 8 South Georgian species present in southern South America, but the flora of the latter also includes closely related species which are not found on South Georgia. Similarly, the Antarctic flora consists of 3 species which are also found in both central South America and on South Georgia. Antarctic and sub-Antarctic *Tortula* floras could thus be explained by long distance dispersal from South America along the islands of the Scotia Ridge. If this were the case, the relicts would be centred in southern South America. However, the Antarctic and sub-Antarctic possess one endemic taxon of *Tortula*. These plants, previously referred to the species *T. conferta*, appear to be an extreme modification of *T. princeps*, and are regarded as a distinct variety which probably evolved quite recently. The status of Antarctic and sub-Antarctic floras may be resolved when further genera have been revised. In this connection, the distribution of the genus *Andreaea*, with its montane species, promises to be particularly interesting.

P J Lightowlers

AUTECOLOGY OF ANIMALS

The wood white butterfly

In the 1979 ITE Annual Report, an interim account was given of a PhD study by M S Warren on the distribution and ecology of the wood white butterfly (*Leptidea sinapis*). The PhD work was successfully completed (Warren 1981), but the study has been continued to provide sufficient data for the identification of key factors determining annual fluctuations in the main study population, and to try to establish the causes of longer term trends in numbers. The study area is a conifer plantation managed by the Forestry Commission, and there is a likelihood that, in future, management of rides will be modified to take into account the requirements of the wood white butterfly.

The wood white, at this site, normally has one generation a year, although there may occasionally be a very small second emergence. The flight period is long, usually from late May until the end of July; overwintering is in the pupal stage. There are several leguminous food plants, but the study population was mainly found on *Lathyrus pratensis*, which is very abundant along the ride edges.

On the basis of 3 years of study, Warren suggested that annual fluctuations were largely caused by variation in the number of eggs laid, which was, in turn, caused by the weather during the flight period. This suggestion has been largely confirmed; cool or wet weather during the flight period results in fewer eggs being laid, and also appears to increase the mortality of very young larvae. Warm, dry weather results in more eggs, better survival of young larvae, and higher numbers of adults the following year.

The analysis of life table data of invertebrates, by k factor analysis, has largely been concerned with the analysis of annual changes. It could be argued that studies on species of conservation interest should be equally, or perhaps more, concerned with longer term population trends caused by habitat change. In order to investigate the role of habitat change, the study area has been subdivided, and changes in the abundance of butterflies in time and space have been examined in relation to the shade provided by the conifers and to the availability of suitable food plants.

The annual fluctuations, determined by the previous year's weather, were very similar over the whole area, but the long term (7 year) trends have varied greatly. Open rides which initially were scarcely used by the butterflies have become more suitable, while rides which initially had optimal conditions have become too shaded.

Food plants were abundant in all but heavily shaded rides, and the increased use of rides by the butterflies was not related to any increase in the abundance of *Lathyrus*. Larvae transferred to *Lathyrus*, in a ride which was not used for oviposition, survived well, suggesting that the suitability of rides was not related to the quality of their food plants. It seems more likely that the distribution of the adults, and of favoured areas for oviposition, depends directly on the varying conditions for adult flights provided by areas with different shade and shelter. The fact that, in very warm and still conditions, the females moved into, and laid eggs in, more open areas tended to confirm this view.

The wood white would not normally be expected to survive throughout the life of a conifer plantation of uniform age. In the study area, the plantations are not even-aged, but a large proportion of the trees are of a similar age, and it seems that, in the absence of special management, the wood white will not survive. If such special management, ie the widening of a limited number of rides and the rotational cutting of the scrub growth of their edges, is practised, it is hoped that monitoring of the butterflies will continue in order to assess its success.

E Pollard

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Demographic model of red grouse cycles

Cycles in the abundance of common vertebrate herbivores, such as voles, lemmings, hares and grouse, are a marked feature of boreal forest and tundra biomes, and have been remarked upon for hundreds of years. Cycles in animal populations do not have an invariant period; rather, one observes a statistically significant tendency for fluctuations in numbers to be repeated at intervals which are more regular than would be expected by chance. Not all populations of 'cyclic' species actually show cycles, but shooting bags of red grouse *(Lagopus l. scoticus)* from north-east Scotland from 1850 onwards do show a clear 6-year periodicity (Williams 1974), and any explanation of their fluctuations in numbers has to account for this periodicity.

A very long run of data is required to satisfy statistical criteria which show that a population does cycle. Furthermore, in real populations, there are always causes of fluctuations which act in addition to any underlying cyclic process. From the statistical point of view, these extra causes may simply be regarded as 'noise', but, to the population biologist interested in cycles, they pose a severe problem. In a typical study, he may be able to study only one or 2 fluctuations; how can he tell whether a decline observed during such a study is typical of cyclic fluctuations or merely a result of some other, extraneous, process?

One approach is to build a mathematical model of the studied fluctuation, and see whether extrapolations of it into the future show cyclic behaviour. One must be very careful to make the model completely empirical, and to use it entirely on observed data; it is only too easy to make a model fulfil expectations by incorporating unverified assumptions.

A major fluctuation in the numbers of red grouse at Kerloch Moor in Kincardineshire has been studied by ITE from 1969 to 1977 (Watson & Moss 1980). The data showed the characteristics of a cyclic-type fluctuation, in that there was a delayed density dependent relationship between spring numbers and major population losses in subsequent years. The main loss, and the one best correlated with changes in spring numbers, occurred over winter, and was due largely to emigration. Losses from emigration also occurred during spring and summer, and were correlated with winter losses; it was concluded that the decline in numbers during 1973–77 was a result largely of emigration occurring at all seasons.

A mathematical model has been built which mimics the Kerloch fluctuation, and predictions from it are now being tested in a new study area, Rickarton. Winter losses have not been included in the model, because it would have been necessary to know the subsequent spring density, and it would be no test of the model to predict a value already known. Earlier variables were therefore sought which were correlated with changes in spring numbers. The main variable is the chick production ratio, which is calculated for each sex separately and is the number of young in the area in August, divided by the number of adults in spring. It incorporates not only variations in brood size, but also losses of hens and chicks emigrating in spring and summer.

The chick production ratio was correlated with densities in previous springs—most strongly 2 years back—and, when this empirical delayed density dependent relationship is incorporated and the model run far into the future, a cycle results. Predictions made so far at Kerloch and Rickarton have proved satisfactory.

The essence of the model is that a decline from high densities occurs due to massive emigration following high densities. The question now being studied at Rickarton is whether this mathematical description actually reflects the biological processes involved. If so, it should be possible to stop or markedly reduce emigration, and the consequent decline in numbers, by removing birds from an experimental population and keeping its density fairly low. The experiment is now in its second year. Food quality has remained high and parasite burdens low, so these possible complications can be discounted so far. In both 1982 and 1983, more birds emigrated from the control area than from the experimental area; these are hopeful signs that population processes are being affected by the experiment.

A Watson and R Moss

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Monitoring winter attendance of guillemots at breeding colonies

Guillemots *(Uria aalge)* (Plate 22) now return to the breeding colonies bordering the North Sea in early October, prior to breeding in April and May the following year. This return is much earlier than formerly (Taylor & Reid 1981). The work described here aims to monitor the amount of time guillemots spend at the colonies. It is part of a larger study documenting how well a seabird species can perform in apparently extremely favourable conditions, as a base-line against which future change can be assessed.

Until recently, it was thought that guillemots seen at colonies during the winter were either non-breeding birds or birds from other colonies coming ashore at colonies near their wintering areas. However, ITE studies of marked birds show that most, if not all, of these birds bred at the colonies in the previous season. They spend the night at sea and come to the colonies just as it is light enough to see. Numbers present increase rapidly to a peak soon after sunrise, and then gradually decline. Some birds stay all day in February and March, but only occasionally from October to January. Food must be easily obtainable to allow these individuals to spend such a long time ashore, and colony attendance may provide a measure of food availability.

Colony attendance is monitored using a Kodak Analyst time-lapse camera focused on defined areas of the colony. These cameras have been modified to expose a single frame of Kodachrome Super 8 film every 30 minutes. A set of 4 HP2 batteries lasts at least 2 weeks, and a film 7 weeks, so that running expenses are low. Counts of the birds present on the developed film are made using a zoom binocular microscope fitted with a variable light source. Birds visiting the colony for less than 30 minutes could be missed, but direct checks showed that this happened rarely, and only when very few birds were present. Pictures are taken day and night, with dawn defined as the time of the first picture when it is possible to determine whether or not guillemots are present.

Figure 53 shows data from a typical winter at Fowlsheugh, Kincardineshire. Guillemots return in October, visit regularly during November, rarely (if at all) in December, infrequently in January, and regularly in February and March. Then, a cycle commences of a few days' presence alternating with a few days' absence, typical of the pre-breeding period.

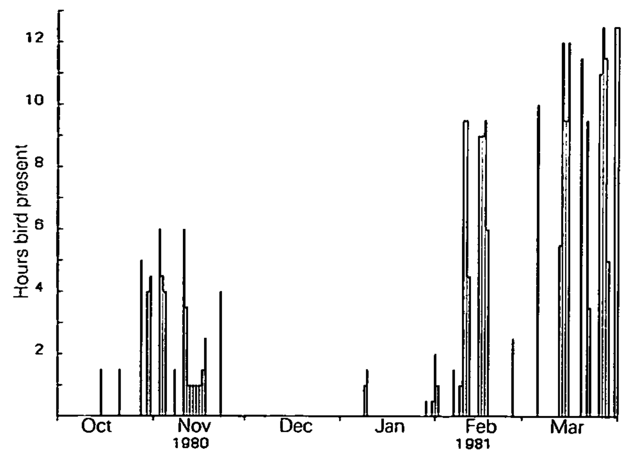

Figure 53 Colony attendance of guillemots at Fowlsheugh during the 1980–81 winter, as shown by time lapse photographs every 30 minutes

Differences occur between colonies, birds at the Isle of May, Fife, for example, normally visiting daily during October. Preliminary analysis suggests that there is no direct link between weather and colony attendance. Food availability seems the most likely controlling factor.

In February 1983, about 10 000 guillemots and 20 000 other auks were washed ashore dead on the east coast of Britain. These birds were not oiled and analyses of tissues at Monks Wood indicated that neither organochlorine insecticide nor metal levels were high enough to have contributed to their deaths (D Osborn, pers. comm.). It appeared to be a natural event, and Blake (in press) concluded that food shortage was probably the major factor in the death of the auks. During the 1982–83 winter, cameras were in place at the colonies at Fowlsheugh, Isle of May (Plate 6), and St Abb's Head, Berwickshire, allowing events to be followed prior to the wreck. Guillemots returned to the 3 colonies in October 1982, and birds were present on many days until early January 1983. Their visits then became erratic, with only a few birds coming ashore for a short time after dawn. This had also happened in early 1981 and 1982. However, no guillemot was seen on photographs taken at any colony from 26 January to 19 February 1983 (Figure 54). Over this period in 1981 and 1982, the ledge photographed at Fowlsheugh (the only one studied in those winters) was occupied for totals of 6600 and 2600 bird hours, respectively. Obviously, something different happened in 1983. By the end of the first week of February, dead and dying auks were being washed ashore (Mead & Cawthorne 1983), some 10–15 days after the colonies had been deserted. Guillemots returned on 20 February, numbers increased rapidly, and some birds soon spent all day on the ledges. The wreck had no significant lasting effect on the breeding population—for example, that on the Isle of May increased by 5% between 1982 and 1983—or on breeding the following summer (Harris & Wanless

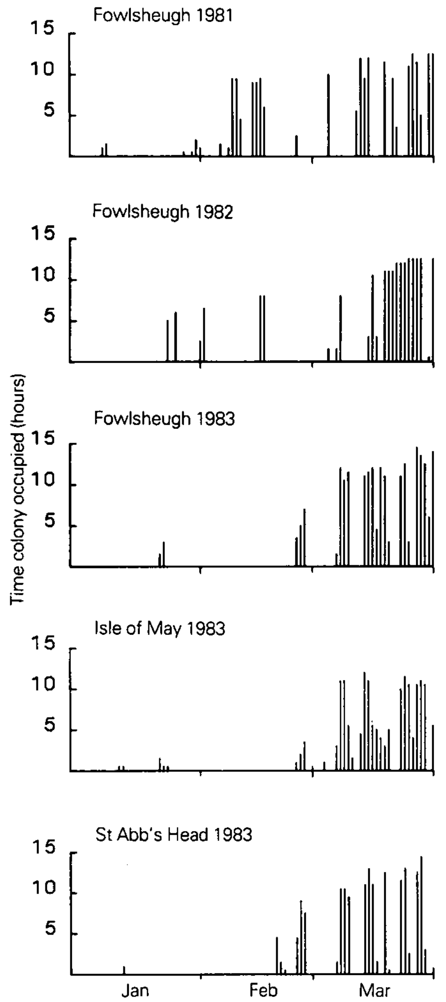

Figure 54 Colony attendance of guillemots at 3 east Scottish colonies in January–March

in press). Photography was a good method of detecting when guillemots were stressed, even before birds started to be found dead, and when the subsequent mortality was at a level which did not affect the breeding population.

Presumably, birds which spend time at the colonies during the winter gain some advantage over those which do not. An attempt is now being made to follow winter attendances of individual guillemots to determine what, if any, are these advantages.

M P Harris

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Breeding behaviour in the common toad

In 1982, on Portland, Dorset, a population of common toads *(Bufo bufo)* began its breeding migration from the overwintering sites to the spawning pond during periods of warm (>4°C), wet nights in late January–early February. The numbers arriving at the spawning pond slowly increased to a maximum during late February–early March, and then slowly declined, so that spawning was over by late March. A similar migration pattern was also observed in 1981 and 1983, and periods of cold, dry weather halted toad movements in all 3 years.

Males which arrived at the pond at the start of the breeding period stayed for 18·3 ± 0·96 days, whilst those that arrived later, during the period of peak arrivals, stayed for only 5·2 ± 0·24 days. Females which arrived early stayed for 6·4 ± 0·81 days, whilst those which arrived later stayed for 3·0 ± 0·08 days. Females left the pond immediately after spawning, whereas the males stayed.

Most females (88–94%) arrived at the pond already paired with a male. These males were significantly larger than those males which arrived at the pond unpaired. Once in the pond, intensive fighting over females occurred between males, and resulted in those males which successfully spawned with a female being significantly larger than those which did not. Although large males were more successful at obtaining and spawning with a female than small males, no assortative pairing by size was found.

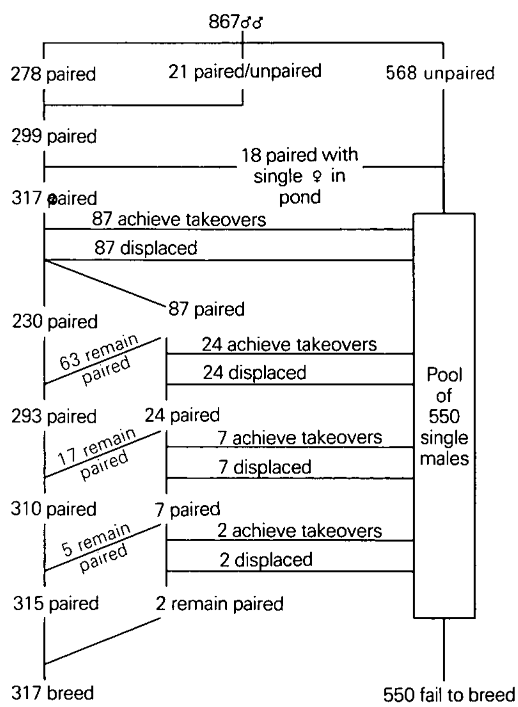

Figure 55 Flow diagram showing male spawning success in the common toad

The intense competition between males over females was the result of an imbalance in the sex ratio (♂:♀), which was 2·7 in the overall breeding population, but varied between 2·5 and 12·7 in the pond on any particular day. The probability of a paired male in the pond losing his female to another male in a fight was relatively constant (P=0·725), and independent of the number of previous fights (Figure 55). Although the mean probability of an unpaired male obtaining a female over the whole breeding period was 0·075 ± 0·002, this figure varied between P=0·043 ± 0·004, at the start of the period, to P=0·092 ± 0·003 at the end. The low probability value observed for the start of the breeding period may well explain why males which arrived early stayed longer.

Some single males left the pond on 'sorties', possibly in search of unspawned females. Although some of these males returned paired with a female, the majority did not. The probability of a single male obtaining a female on a 'sortie' was 0·0847 ± 0·0011, which is not significantly different from the probability of obtaining a female within the pond. This is evidence that a spatial evolutionary stable strategy existed between the pond and an undefined area surrounding it, such that the expectation by an unpaired male of finding a female at either site was equal.

C J Reading

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ANIMAL SPECIES INTERACTIONS AND COMMUNITIES

Song birds in some semi-natural pine woods in Deeside, Aberdeenshire, in 1980–83

Very little information is available on the numbers or habitat preferences of song birds in different types of Scottish woods. Bird territories were mapped in 4 pine stands in Glen Tanar (selected partly because they were representative, but also for ease of access), and their densities were compared with characteristics of the vegetation. It is hoped eventually to be able to provide advice on woodland management, based on the results.

ITE was particularly interested in the general proposition put forward by MacArthur and MacArthur (1961) that the diversity of species of song birds, called 'Bird Species Diversity' (BSD), was highly correlated with 'Foliage Height Diversity' (FHD). This is a measure of the complexity of the vertical distribution of live and dead vegetation from the ground to the top of the canopy. Both indices are estimated by the Shannon index (Shannon & Weaver 1949). ITE also wished to test the more specific relationship which Moss (1978) proposed for Scottish woods, viz BSD = 0·962 + 1·089 × FHD.

The pine woods

All pine stands studied had similar underlying soils and ground floras (Type 27, Bunce 1982), so that variation in soil type could be discounted in comparing the effects of different profiles.

Three of the stands (A, B and C) were in areas of native pine woods and had probably regenerated naturally. The fourth (D) was a young wood, with some trees planted in 1946 (and others regenerating more recently), only 5–9 m high (Table 22). In these pine woods, deciduous trees were so few as to be negligible. The ground vegetation was mainly *Calluna* and *Vaccinium*, often relatively tall and on big hummocks in A. Areas A, B and C were on gentle slopes, whilst much of D was steep hillside.

Methods

The study plots varied in size from 8·9 ha to 15·7 ha. Each plot was marked in a grid of 40 m × 40 m squares, to aid locating birds for mapping. Bird populations were assessed using the Common Bird Census (CBC) technique of the British Trust for Ornithology. The bird censuses were done between March and mid-June. Each plot was visited by the same observer, on at least 15 early mornings in all years.

Our territory scores for the commoner species (eg chaffinch) are considered to be minimum estimates. For species with little song, when simultaneous registrations were rare, decisions on territory boundaries were necessarily subjective and somewhat arbitrary. Siskin territories were counted, although these birds were usually absent in early spring, because they song flighted in May. Crossbills, which were not obviously territorial in Glen Tanar in spring, were excluded from the counts (though their presence was noted), as were other birds such as wood pigeon, wood cock, game birds, and birds of prey, whose behaviour made them difficult or impossible to census by CBC methods.

The basic methods described by Moss (1978) were modified to measure vegetation profiles, and the proportion of ground covered by vegetation was recorded in sample plots of 10 m × 10 m from ground level to the top of the canopy, with height classes 0–0·25 m, 0·25–0·5 m, 0·5–1 m, 1–2 m and thereafter according to the presence of canopy, to the nearest metre. Whole stand (overall) profiles were calculated as a weighted average (proportionally, by relative area) from the individual plot profiles. Figure 56 shows profiles for the 4 woods.

Table 22. General features of the pine stands studied in Glen Tanar

Stand	Age (years)	Altitude (masl)	Average density (stems/ha)	Modal height (m)	Top height (m)	FHD*	Notes
Drum (A)	150–240	300–340	25	12–15	19	0·97	Old pine wood: regenerated naturally
Allachy (B)	150–240	250–280	100	15	20	1·08	Old pine wood regenerated naturally
Gairney (C)	140	250–280	200	17	21	1·12	Old pine wood: possibly regenerated after fire
Strone (D)	35	180–240	1500	7	9	0·83	Young plantation, some regenerated naturally

* Foliage Height Diversity (see text)

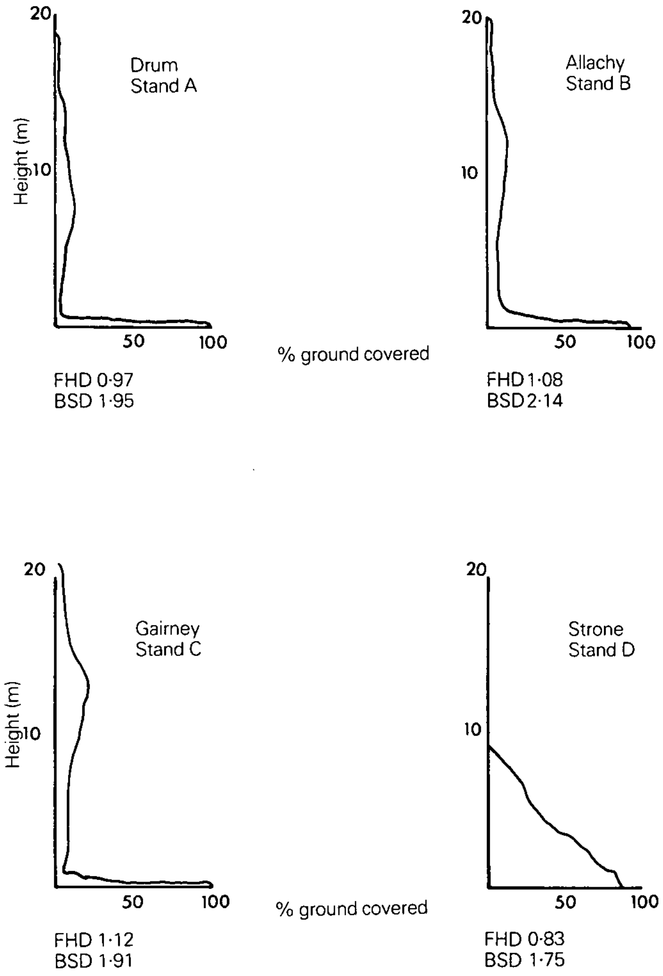

Figure 56 Whole-wood vegetation profiles (weighted average) for the 4 stands studied in Glen Tanar

Results

1. Total numbers of territories and numbers of species in 1980–83 (Table 23)

The mean territory scores (density/10 ha) varied from 30·4 ± 2·8 (SE) in one of the old pine woods to 42·5 ± 5·2 in the young plantation. In general, within any wood, the range over the 4 years was almost as great as, or greater than, the differences between woods (eg 25·5–52·5 at C, or 27–50 at D).

The numbers of bird species tended to be inversely related to overall numbers of bird territories. Stand B, in the old Caledonian forest, had fewest territories, but most species (11 species in at least 3 years, 12 in 2 or more years). By contrast, D, the young plantation with the highest mean score for territories, had only 5 species in 3 years, and 6 in 2 years. High scores at D were due to high densities of a few species in the shrub layer, notably robin (range 10·5–14 territories) and willow warbler (6–14·5 territories). A and C were intermediate in both overall numbers of territories (37·1 ± 4·6 at A, 37·9 ± 5·7 at C) and species (8 and 9 species in 3 and 2 years at both sites).

2. Numbers of individual species

In the 3 mature pine woods, chaffinch was the most common bird (with, on average, 12·3 territories/10 ha), with wren (8·2 territories/10 ha) and coal tit (4·3 territories/10 ha) next; most other species were low in numbers.

In the young plantation, while chaffinch numbers were fairly high (7·8), robin and willow warbler were more numerous (13·5 and 10·6). Goldcrests (4·1) were also more common than in the other woods. Wren numbers (3·8) were consistently lower than in the mature woods. So, too, were coal tits (2·5), with the exception of a surprisingly high score (6·0) in 1983. The siskin, an irruptive species, had high numbers in all woods in 1981, but markedly lower densities in all other years—this may be related to the cone crop, but 1981 was a 'good' year for many other birds in Deeside.

3. Bird diversity in relation to habitat

Foliage height diversity was calculated using Moss's (1978) height bands. Numbers of territories show no strong relationship to FHD. Numbers of species and BSD tended to increase with FHD (Tables 22 & 23), but data are only available from 4 stands and these are not sufficient to calculate a significant regression between BSD and FHD. If these data are compared with Moss's (1978) regression, 3 of the 4 stands lie within the 95% confidence limits of the

Table 23. Densities/10 ha of territories, numbers of species and Bird Species Diversity (BSD) of song birds in the pine stands studied in Glen Tanar 1980–83

	Number of territories	Mean $\pm$ SE	Number of bird species	BSD	BSD aggregate over all 4 years
Drum (A)					
1980	33·0		7	1·66	
1981	44·0	37·1 $\pm$ 4·6	9	1·95	1·98
1982	26·0		8	1·73	
1983	45·5		9	1·97	
Allachy (B)					
1980	23·5		9	1·84	
1981	33·0	30·4 $\pm$ 2·8	12	2·09	2·14
1982	28·5		12	2·15	
1983	36·5		11	2·14	
Gairney (C)					
1980	25·5		5	1·27	
1981	52·5	37·9 $\pm$ 5·7	10	2·04	1·91
1982	34·0		9	1·87	
1983	39·5		9	1·71	
Strone (D)					
1980	27·0		5	1·43	
1981	50·0	42·4 $\pm$ 5·2	7	1·78	1·75
1982	45·0		7	1·61	
1983	47·5		6	1·68	

regression, but only one stand (B), one of the old pine stands, lies on or just above the regression line. The fourth stand (C), which has the highest FHD (1·12), has a BSD of 1·91, which is a much lower value than the lowest limits predicted by Moss's equation. From the data available, it appears that bird populations in the Glen Tanar pine woods are generally less diverse than would be expected from Moss's regression. Looking at individual woods, certain anomalies are apparent. From Figure 56, it would appear as if B should have a similar bird fauna to A, with C being more diverse. FHD (Table 22) indicates that the order of bird diversity should be A < B < C. Instead, the actual order is C < A < B. However, a comparison of the profiles of recognizable habitats within each wood (see Figure 57) and the occurrence of individual species suggest trends which may help answer this apparent anomaly.

1. The willow warbler occurred at A and B (but not at C). In both woods, it was associated with areas of juniper, which was absent at C. The area of juniper required was not great (in B < 0·1 ha, but supporting 3 willow warbler territories).
2. Both mistle thrush and tree pipit appeared to frequent tall trees with few low branches, adjacent to gaps or open areas with low vegetation, and present in B and C, but not to the same extent in A.
3. In both A and B, robins were found in areas of mixed cover, and, like the willow warbler, these required only small areas for territory (about 0·3 ha). Such small areas of mixed cover were not available in C, and hence robins were usually absent or scarce.

Moss (1979) related density of some species in even-aged plantations to the height of the trees. If the species common to Moss's study are compared to our study, the following points emerge.

1. Our results agree with those of Moss in the conditions showing a peak density of willow warbler. At D, the highest density of these warblers was in an area with a top height of 5–6 m, exactly corresponding to Moss's results. Our data, however, indicate that the critical factor was not the canopy height *per se*, but the amount of green cover between 1–3 m, which was greatest in young conifer plantations like D.
2. Our data for the wren in coniferous woods broadly agree with Moss's, although the densities were generally higher in the Glen Tanar pine woods.

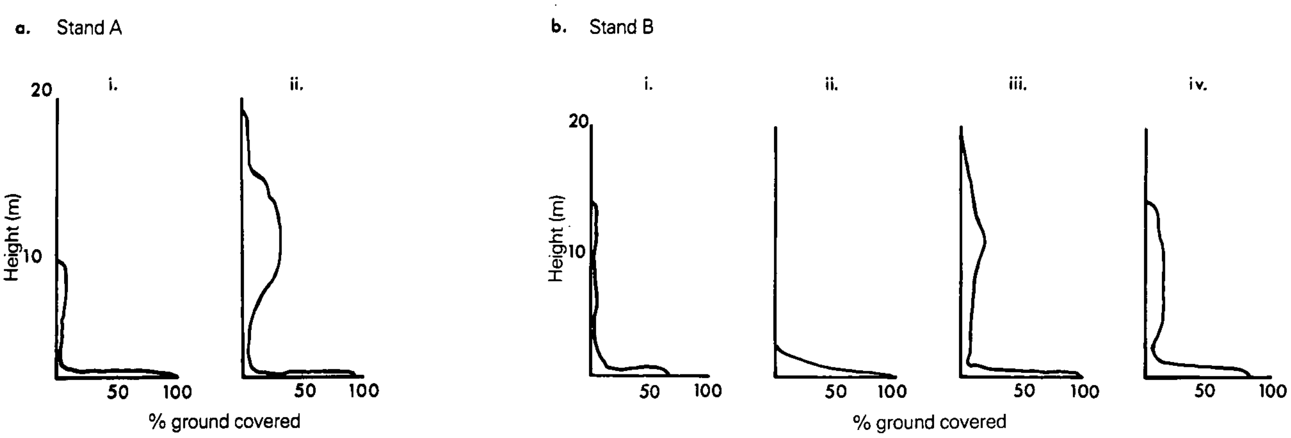

Figure 57 Vegetation profiles of recognizably distinct habitats within 2 of the mature pine stands
a. Drum (Stand A): (i) open areas, (ii) denser pine
b. Allachy (Stand B): (i) recent clearings, (ii) old clearings, (iii) pine areas without juniper, (iv) pine areas with juniper

However, the relation with top height is again likely to be indirect, reflecting, in this case, the amount of dead branches and other cover on the ground.

3. Chaffinch and coal tit also show a general agreement, but, like the wren, numbers were generally higher in Glen Tanar than in Moss's woods.
4. Our data for robins show a very different pattern from Moss's, with a clear peak in the young stand at D.
5. For goldcrest, our data show a completely opposite trend to Moss's, with highest numbers corresponding to lowest stand height. However, goldcrests in D tended to concentrate in a block of taller trees, and perhaps this species needs both height and a dense canopy to reach maximum numbers.

All the above points indicate that the presence of individual species is likely to depend on the presence of a minimum amount of suitable habitat, and that the diversity of possibly very small patches of different habitat types, and their spatial distribution on the ground, is likely to be at least as important as the overall (average) structural diversity of a stand in determining bird diversity. At C, there was only a single distinct profile type (Figure 56). At A, there were at least 2 (Figure 57a), and at B, 4 (Figure 57b), and these are in the order of bird diversity in these 3 woods. At D, the young plantation, on the other hand, there were at least 3 distinct profile types, but lower BSD and fewer species than in any of the older woods, and this reduced diversity did correspond with a much lower FHD.

Conclusions

The overall numbers of birds found in the Glen Tanar pine woods were higher than those generally found in pine plantations. Numbers were, moreover, approximately equal to, or a little lower than, semi-natural pine in Speyside (Moss 1978). The Speyside pine wood had a profile similar to the mature Glen Tanar pine woods. Plantation profiles are usually simpler than those of natural woodland.

A major difficulty in dealing with whole-wood profiles of heterogeneous woods, like most of those in Glen Tanar, is that the single profile may conceal a variety of different smaller-scale profiles. The data from Glen Tanar suggest that, when studying birds in semi-natural, non-uniform woods, rather than simply comparing the overall FHD with BSD, it might be better also to examine the number of distinct profile types in the wood. For example, although the numbers of bird territories and BSDs in the Glen Tanar pine woods were equal to, or slightly lower than, those in some other semi-natural pine woods, the number of species tended to be slightly higher. Additional species appear to be encouraged by a suitable scale of pattern within a wood, including a variety of different profiles, preferably in fairly small blocks. Our main conclusion confirms and expands the ideas being tested—namely, a wood with a large number of fairly small, discrete patches of different habitat types will contain more bird species, though not necessarily more birds, than either a wood of uniform mixture or one with only large-scale aggregations. The data being collected from other types of woods tend to confirm this conclusion.

Acknowledgements

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D Jenkins, D D French and J W H Conroy

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Characterization of trypanosomes from bats

Bats in many temperate and tropical countries are commonly infected with protozoan parasites of the genus *Trypanosoma*. Members of this genus are common parasites of a variety of vertebrates (see Baker 1982), and a few are notorious pathogens—including the causative organisms of African human sleeping sickness, nagana and related diseases of livestock in Africa and elsewhere, and Chagas' disease of man in South America. The parasite causing the latter disease, *Trypanosoma cruzi*, is classified in the subgenus *Schizotrypanum*; apart from one unsubstantiated report from *Mus musculus* in Egypt, all other known species of this subgenus are restricted to bats. Until fairly recently, the subgenus *Schizotrypanum* (with the exception of *T. cruzi)* had been little studied and its taxonomy was confused. However, starting with a note by Bafort *et al.* (1970), there has been an upsurge of interest in the subgenus, and it is now clear that it comprises at least 6 distinct species or subspecies, in addition to *T. cruzi*. There is a 2-fold interest in studying this group of organisms—first, because of their close relationship with an important human pathogen, for which in some respects they may serve as useful laboratory models (Baker & Selden 1981), and, second, because of their relationship with their bat hosts. There is no evidence of any overtly harmful effect exerted by these parasites on infected bats, but it is becoming increasingly recognized that trypanosomes may affect their hosts in rather subtle ways (eg by immunosuppression) and that the delicate balance between host and parasite may be upset, in favour of the parasite, by a variety of stresses, including concurrent infections with other organisms and probably other, as yet unrecognized, events. Like other species of trypanosomes, they can be studied and characterized in various ways and at various depths. Most superficially, and traditionally, they have been characterized morphologically—as revealed by light and, more recently, electron microscopy. In addition, a range of more fundamental characters can be measured, included under the so-called 'molecular taxonomy', involving study of gene products (antigens, polypeptides, enzymes) and—ultimately—the genome itself (deoxyribonucleic acid or DNA), in various ways.

Methods

Acquisition of Helena Laboratories cellulose acetate electrophoresis (CAE) equipment at the Culture Centre of Algae and Protozoa has enabled determinations to be made of isoenzyme profiles from several strains of trypanosomes isolated from bats. The species examined include the following members of the subgenus *Schizotrypanum*—*T. (S.) dionisii dionisii* (5 strains) and *T. vespertilionis* (4 strains) from England and *T. (S.) dionisii* breve (2 strains) from France; *T. cruzi marinkellei* (7 strains) from South and Central America; *T. hedricki* (4 strains) and *T. myoti* (3 strains) from Canada; and 3 strains isolated from bats in Portugal, of which one may represent a different subgenus (see below). Large-scale cultures have been grown (lately in Grace's medium; see Pennick & Paul 1983), and suitable extracts prepared for this purpose, as well as for DNA buoyant density determination in collaboration with the Molteno Institute, University of Cambridge, and polypeptide 'fingerprinting' by sodium dodecylsulphate-polyacrylamide gel electrophoresis (SDS-PAGE; see Taylor *et al.* 1982), in collaboration with the London School of Hygiene and Tropical Medicine.

Results

Overall, the results have largely confirmed the classifiction arrived at as a result of previous work based on morphology, DNA density and preliminary isoenzyme electrophoresis; Figure 58 summarizes some of the results obtained by the 2 electrophoretic techniques. The grouping into 'peptidemes', on the basis of SDS-PAGE, fits reasonably well with previous distinction into species and subspecies (based on morphology and DNA buoyant density). However, one subspecies *(T. c. marinkellei)* comprises 2 peptidemes (nos 7 and 8), and, conversely, 2 morphologically distinct taxa—*T. d. breve* (from

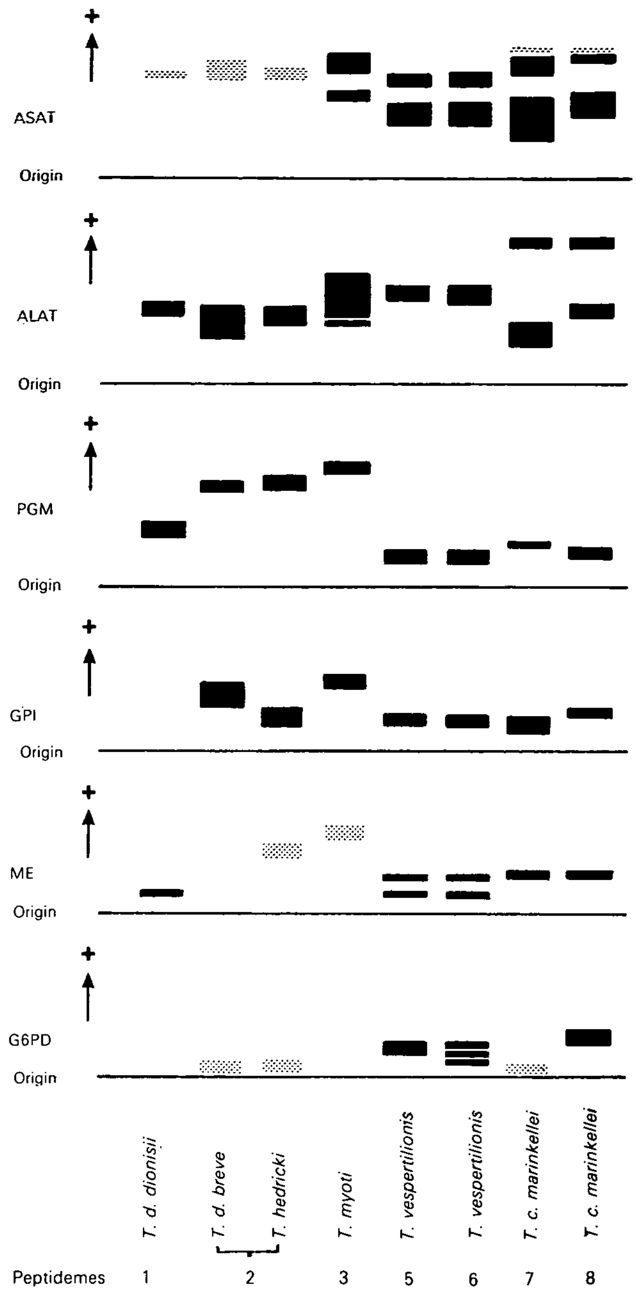

Figure 58 Isoenzyme patterns obtained by electrophoresis of extracts of 6 species or subspecies of chiropteran trypanosomes, belonging to 7 different peptidemes
ALAT = Alanine amino transferase (E.C. 2.6.1.2)
ASAT = Aspartate amino transferase (E.C. 2.6.1.1)
G6PD = Glucose-6-phosphate dehydrogenase (E.C. 1.1.1.4)
GPI = Glucose phosphate isomerase (E.C. 5.3.1.9)
ME = Malic enzyme (E.C. 1.1.1.40)
PGM = Phosphoglucomutase (E.C. 2.7.5.1)
(Modified from Taylor et al. *1982)*

southern France) and *T. hedricki* (from Canada)—belong to the same peptideme (no. 2). This similarity is perhaps reflected in the rather similar banding patterns shown by 4 of the 6 enzymes studied by CAE from these 2 taxa, though—like all 6 taxa included in the Figure—they could be distinguished enzymatically and by DNA buoyant densities. Heterogeneity of *T. c. marinkellei* is indicated not only by its peptideme composition but also by minor differences in CAE banding patterns of some enzymes (eg ALAT and G6PD). Preliminary examination of the Portuguese strains by DNA measurement and isoenzyme CAE suggests that one (M50) may represent a distinct taxon; this is supported by its nutritional requirements for *in vitro* culture. Unlike the other chiropteran trypanosomes of the subgenus *Schizotrypanum*, which are maintained at the Culture Centre, M50 will not grow in Grace's tissue culture medium containing 30% v/v foetal bovine serum (Pennick & Paul 1983), unless supplemented with 10% v/v of a rabbit erythrocyte extract. Furthermore, its morphology *in vitro* appears rather different and is being checked by electron microscopy. The ultrastructure of its kinetoplast does not conform to the '2-layered' structure characteristic of other strains of the subgenus *Schizotrypanum* (Mühlpfordt 1981), and it is possible that this isolate belongs to a different subgenus–perhaps *Megatrypanum*, the only other subgenus so far recorded from bats (Baker 1973; Baker *et al.* 1981).

Acknowledgements
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J R Baker and N C Pennick

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Greater horseshoe bat–food and foraging behaviour

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

The greater horseshoe bat (*Rhinolophus ferrumequinum*) (Plate 21) has declined rapidly in abundance and distribution throughout its range in the Palaearctic from Britain to Japan. In some areas of northern Europe, the Middle East and Japan, it is already extinct, and everywhere it is considered as an endangered species. In Britain, the greater horseshoe is no longer found in over 50% of its former range of a century ago, and its numbers are believed to have declined by about 99% in that time (Stebbings 1982a).

Results have been gathered on the present and past distribution of the species in Britain, and on the population dynamics of 2 of the 6 British colonies. Emphasis has been given to investigating the relative importance of the large number of roosts which are occupied seasonally (100–200 per colony), as it is likely that only a few key sites can be protected in a conservation programme. It was discovered that some populations, occupying large areas, have suddenly declined. Remedial timber treatment using Lindane, in a building used by bats as a nursery roost, is known to have killed most of one colony in 1953, and so pesticides could have been implicated in these declines. Nursery colonies are particularly vulnerable, because almost all breeding females gather in a single site for parturition. Greater horseshoe colonies may occupy a home range of up to 2000 km^2.

Having found that certain roosts were crucial to the survival of a colony, we wished to know what the bats eat, whether or not they are selective feeders, and where they forage. It was possible that some of the declines might be attributable to changes in land use, leading to changes in availability of food.

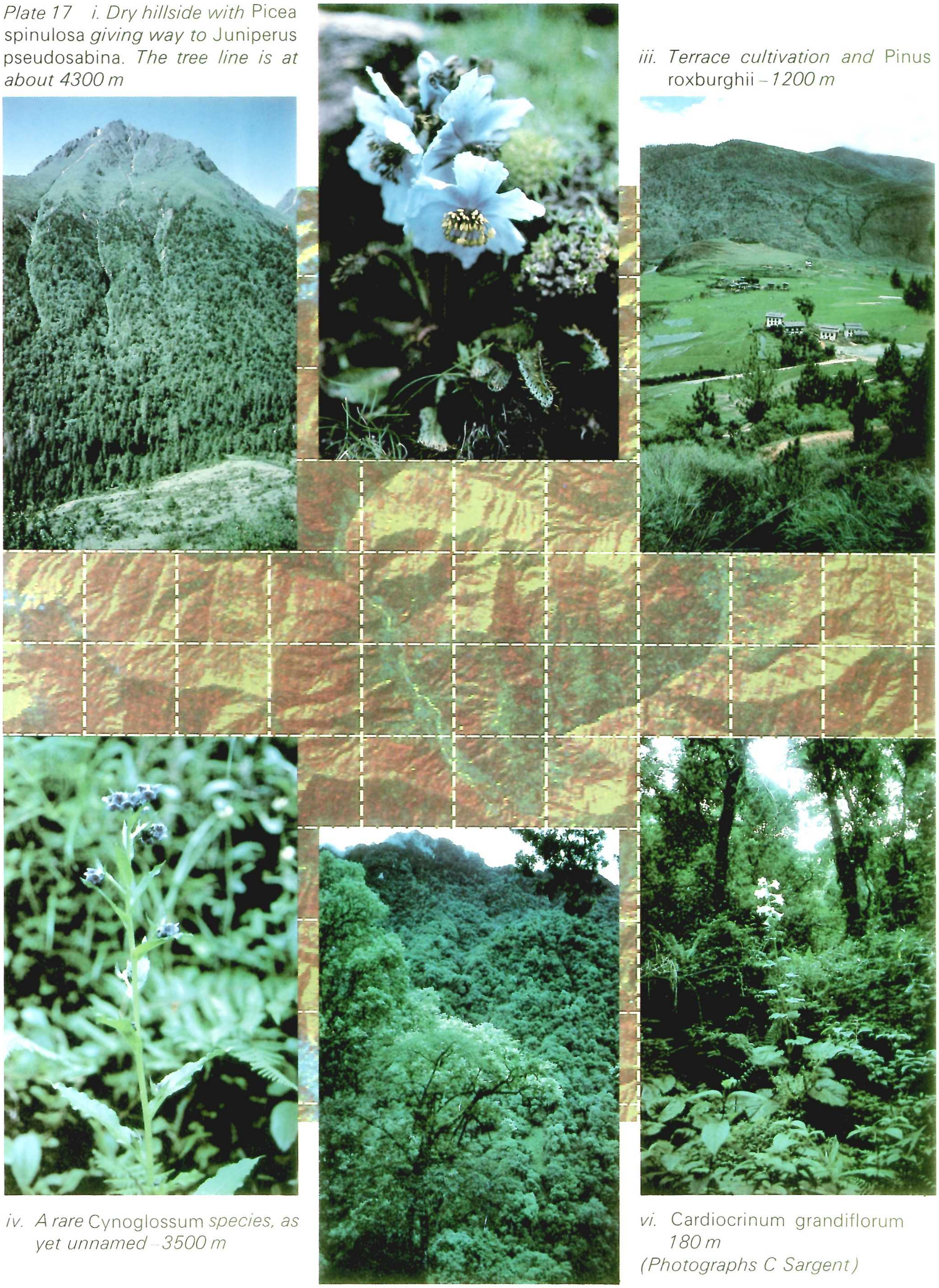
Discovering where bats feed was partially solved by attaching small radio transmitters to them. Greater horseshoes are small (15–30 g), highly mobile animals, which, from mark/recapture experiments, were known to fly 30 km from their day-time roosts in a night. Transmitters averaging 2·0 g in weight when stuck to a bat, and with a 10–15 cm trailing whip aerial, could be detected at ranges of up to 3 km on the ground, or 8 km from an aircraft flying at 300–400 m altitude. However, in woodland, range of detection was often reduced to 300 m. Transmitters dropped off the bats after about 10 days (Stebbings 1982b).

In settled weather, individual bats followed similar routes on successive nights, but patterns changed seasonally. Each night, bats typically moved over a range of habitats, spending longer in some than others, and usually reaching 7–10 km distance from

Plate 17 i. Dry hillside with Picea spinulosa *giving way to* Juniperus pseudosabina. *The tree line is at about 4300 m*

ii. Meconopsis horridula *– 5000 m*

iii. Terrace cultivation and Pinus roxburghii *– 1200 m*



iv. A rare Cynoglossum *species, as yet unnamed – 3500 m*

v. Quercus castanopsis *forest – 2800 m*

vi. Cardiocrinum grandiflorum *180 m*
(Photographs C Sargent)

Underlying, a ratioed Landsat image of central Bhutan (Bumthang) showing grid used for site location. Scale 1 : 250 000

Plate 18 Views of (i) Sitka spruce and (ii) lodgepole pine plots, showing differences in branching habit. The Sitka spruce are 7 years old and the lodgepole pine 5 years old. Lodgepole pine shows more plasticity in its response to close spacing
(Photographs M G R Cannell)

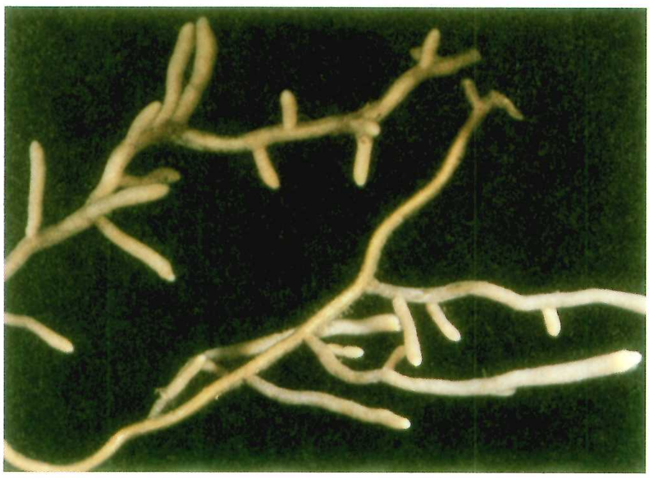


Plate 19 Roots of Sitka spruce showing mycorrhizas formed with:
(i) Laccaria *sp. and*
(ii) Paxillus involutus
(Photographs J Wilson)

a roost. It is thought likely that a longer time spent by a bat in one habitat probably indicates the presence of a more abundant food supply there. Sudden changes in weather altered the bats' flight patterns, with bats preferring woodland at any time when it was cold, windy or raining.

Radio tracking showed that, following hibernation, bats fed mostly in riparian woodland in April and May, gradually spent more time over permanent unimproved pasture in June, and were almost exclusively over pasture in July and August, following parturition and during lactation. As autumn progressed, they returned to woodland.

A quantitative picture was obtained of what the bats ate by examining bat droppings containing the crushed indigestible remains of insects. These results were partially quantified by experimental feeding trials using the major prey items. Simultaneous insect sampling in all the various habitats enabled production of an index of food availability, and this was related to known bat activity obtained from radio tracking. Several insect species were included in the diet at any one time, with one large species usually dominating.

In spring, the large cockchafer beetle *(Melolontha melolontha)* (up to 1·0 g) forms 30% (of total dry mass) of prey. At this time, bats are low in weight and gestation begins in adult females. After parturition and during lactation, the large yellow underwing *(Noctua pronuba)* and the drinker moth *(Philudoria potatoria)* constitute about 40% of their diet, and in autumn, prior to hibernation, dung beetles and, particularly, dor beetles *(Geotrupes* spp.) (about 0·8 g) are most important (33%).

Throughout the year, tipulids form 5–18% of the greater horseshoe's diet, and other insects that assume varying importance seasonally include dung beetles (*Aphodius* sp.), ichneumons (*Ophion* sp. and *Netelia* sp.), and caddis flies (*Limnephilus* sp. and *Stenophylax* sp.).

Greater horseshoe, being one of the largest British bats, shows a preference for large insects, over 25 mm in length, and no insects smaller than 5 mm long were eaten. There are indications that the abundance of large insects may have declined substantially with habitat change. Cockchafers require about 4 years to complete their larval stage, feeding on roots in pasture. Much of this habitat has been ploughed up or 'improved', sometimes with pesticide spraying specifically to kill these beetles. Similarly, high densities of large moths were once found over permanent unimproved pasture. In spring, when nights are predominantly cold, woodland provides the only important feeding habitat. Felling and fragmentation of woodland have considerably reduced the potential foraging areas.

It seems likely that these habitat changes will have reduced the abundance of large insects at times crucial to the bats (eg at the end of hibernation, during gestation and lactation), and hence the breeding success of the greater horseshoe may have been affected. Work is continuing to investigate this possibility.

R E Stebbings, H R Arnold and Nicola Davies

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CYCLING OF NUTRIENTS

The phosphorus economy of lowland heathland

The cycling, sources and losses of nutrients in natural and semi-natural ecosystems have received considerable attention by ecologists and other environmentalists during the past years. They are of particular importance in understanding the overall functioning of ecosystems where nutrients are in short supply, and should figure prominently in any discussion of management.

Studies done by workers in north-west Europe have examined heather-dominated ecosystems with respect to organic matter production, litter accumulation, decomposition, and inputs and losses of nutrients. At Furzebrook, these studies have been concentrated upon the dry heathland in southern England, where the vegetation dominated by *Calluna vulgaris* grows on free draining, low nutrient status soils developed upon Bagshot Sands of the Hampshire Basin. Studies have been made of organic matter production (Chapman & Webb 1978; Chapman *et al.* 1975a), the production and accumulation of litter (Chapman *et al.* 1975b), and root production and organic matter accumulation in soils (Chapman 1979).

While attempts have been made to relate organic matter production and litter accumulation to soil and climate at a number of sites (Chapman & Clarke 1980), a satisfactory synthesis of southern heathland production and nutrient data remains to be achieved. When describing nutrient budgets for lowland heath – an exercise that raised more questions than answers – Chapman (1967) found that the phosphorus budget was particularly critical, because inputs and losses to the system were finely balanced. In an attempt to

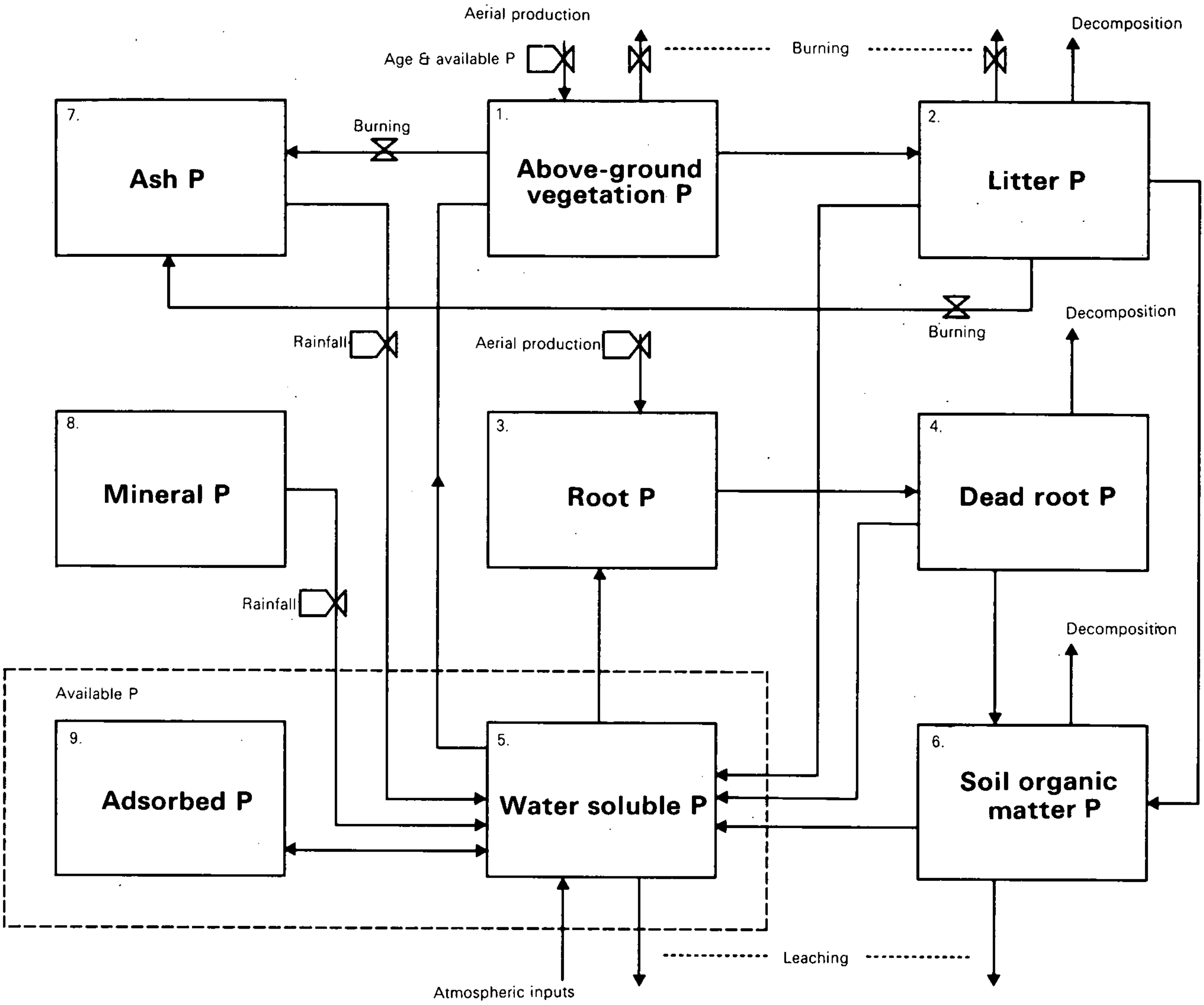

Figure 59 Organization of heathland nutrient cycling model

resolve the role of phosphorus, and hopefully other nutrients, it was decided to construct a computer model that would allow examination of nutrient cycling within *Calluna* ecosystems, and which could draw upon data obtained from the Studland dune heath series (Chapman 1979).

The organization of the model is shown in Figure 59. It is intended primarily for use with *Calluna* heathlands subject to periodic burning, but the design is such that it only needs minor alterations for use with other types of vegetation. In the first version, organic matter production was used as the input to the model and the requirement for phosphorus uptake from soil available-P was calculated. However, because there were, at times, insufficient amounts of soil available-P, the model required additional inputs. These were supplied as required; the amounts were not much larger than normal annual inputs from the atmosphere. In the process of development, however, the improved and more generally applicable version of the model is 'driven' by organic matter production, the latter being regulated by soil available phosphorus. It thus differs from the model described by de Jong and Klinkhamer (1983).

The regulation of organic matter production by soil available-P was analysed by Chapman and Clarke (1980). Their analysis additionally suggested ways in which rainfall and temperature might be incorporated into future versions of the model, so helping to give the model wider geographical applicability.

The present model attempts to examine the behaviour of heathland by considering only production, phosphorus, and, to some extent, rainfall, but organic matter production, and therefore the economy of other nutrients, is controlled by other, additional, factors; future versions of the nutrient cycling model should attempt to involve the interactions, although over-sophistication should not be sought too soon. At the same time, it is necessary to be aware of the possible shortcomings of undue simplification.

The simulation shown in Figure 60 started from conditions that exist on sandy beaches; it then pur-

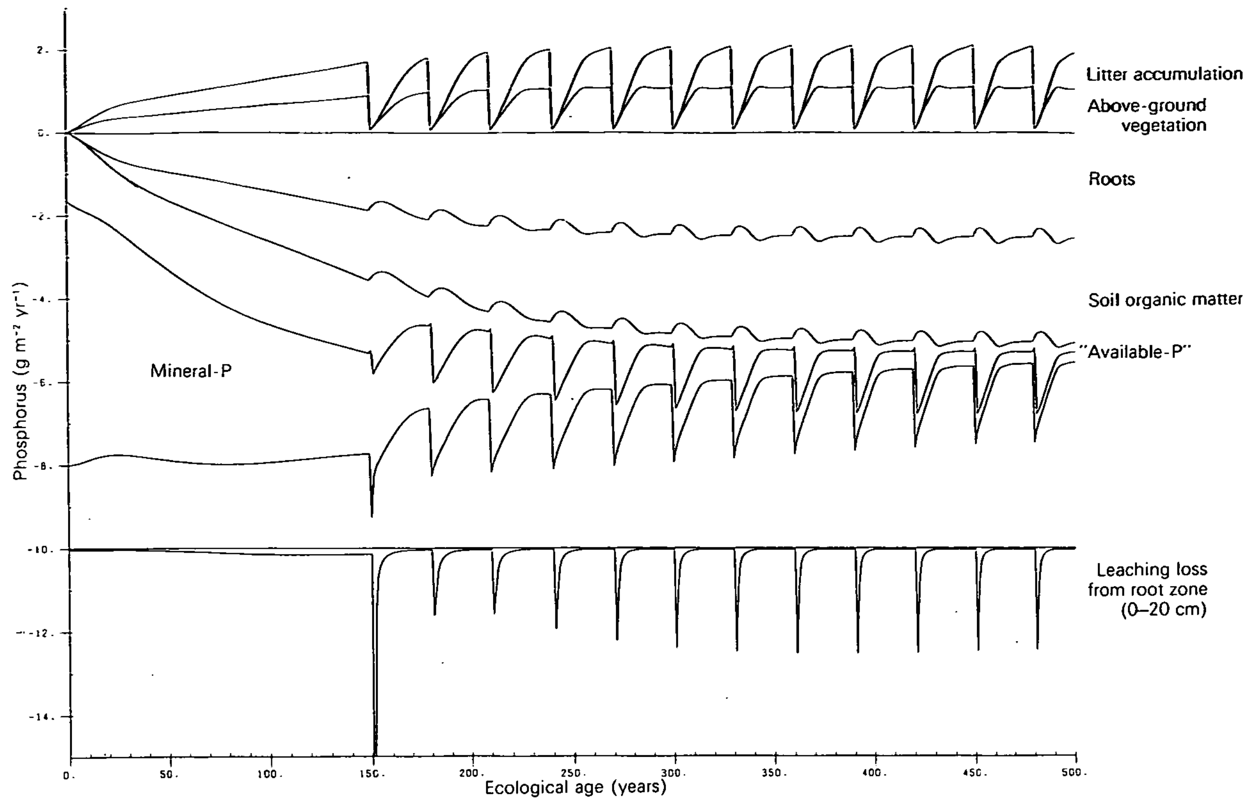

Figure 60 Computer simulation of phosphorus distribution in a Calluna*-dominated dune-heath ecosystem, starting from beach conditions and subject to burning at 30-year intervals from an age of 150 years onwards*

ports to simulate the development of a heathland-soil system. In the event, the results bear a good resemblance to observations of dune ridges at Studland, where a time series of soils exists with ages ranging from zero to about 400 years, and to older heathland soils with an age of about 3000 years, but this is hardly surprising remembering that the model was derived from data from Dorset heathlands and the Studland dune heaths. The model predicts a number of features, such as the magnitude of phosphorus losses (in the organic and inorganic phases) at different stages of the fire cycle. It also suggests that the concentrations of available soil-P under stands of heather of different ages should differ. For the future, it will be interesting to use the model to predict amounts of soil organic matter and the extent of leaching losses in heathland sites in Dorset and the Scottish uplands.

The model can be manipulated to simulate the impacts of management practices such as ploughing, mowing and the application of herbicides. Furthermore, these predictions can be compared with reality. Continued ploughing has been simulated and compared with conditions existing upon firebreaks of different ages. These comparisons provide both agreement and disagreement, and it is by such manipulation and development that both the model and an understanding of the heathland system can be improved.

Models, albeit in their development stage, used in this way can provide information about the possible effects of disturbing heathland soil, whether by ploughing or the burial of pipelines, or attributable to restoration after mineral extraction or road construction. They also have their uses when applied to different types of ecosystems, and can highlight fundamental differences between them.

S B Chapman

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The impact of land improvement on streamwater chemistry

The streamwater chemistry of a series of first and second order catchments in mid-Wales has been monitored as part of a geochemical cycling study. The catchments are located in the headwaters of the River Wye on the eastern slopes of the Plynlimon massif, about 400 m above sea level, and within the Institute of Hydrology's Plynlimon experimental catchment. They are underlain by Silurian and Ordovician shales and the dominant soils are stagnopodzols. While most retain their semi-natural vegetation, 2 of the catchments have been improved. Catchment C7 was ploughed, treated with magnesium-rich limestone, and reseeded some 40 years ago: C17 was surface cultivated and then treated with magnesium-rich limestone and compound fertilizer, prior to reseeding some 10 years ago, since when 'maintenance' additions of lime and fertilizer have been applied.

The concentrations of most solutes are higher in the drainage from improved than from unimproved catchments (Table 24). The increased calcium concentrations in the improved catchments reflect the solution of added lime; it is interesting that this increase is still detectable in stream C7 40 years after the lime additions. Solution of the magnesium-rich limestone could also explain the increased magnesium concentrations. It is surprising, however, that the concentrations of magnesium have increased more than those of calcium. There may be preferential retention of calcium in the soils or increased release of magnesium from the weathering of chlorite, a magnesium-rich mineral which occurs in the soils. The larger silica concentrations almost certainly reflect the increased solution of silica from soil minerals, possibly as a result of changed soil conditions, physical and chemical, following cultivation and liming.

Both streams from improved catchments have significantly larger nitrate concentrations than the unimproved catchment. In the C17 catchment, this effect could be attributed to the solution and loss of artificial fertilizers, but, in catchment C7, to which fertilizers were not applied, the larger concentrations reflect increased nitrate production *in situ*. Similarly, the raised sulphate concentrations in C17, compared to C2, could be related to the solution of sulphate contained in artificial fertilizers, but another explanation is needed for catchment C7. In this instance, oxidation of localized sulphide mineralization in the bedrock may be producing groundwater with relatively large sulphate concentrations, a suggestion to some extent confirmed by the large concentrations of sulphate at low flows in C7, compared with C17 and C2. Solution of chloride from potassium chloride fertilizer applied to catchment C17 can explain the small but significant increase in chloride concentrations in that catchment. The slightly larger concentration of sodium in the same stream could also be derived from fertilizers. The concentrations of chloride and sodium were virtually identical in catchments C7 and C2, probably reflecting an overall control by the concentrations in precipitation.

There were no significant differences between the potassium concentrations in the 3 streams. Fertilizer potassium repeatedly added to catchment C17 must be utilized very efficiently or any excess, which enters solution, must be fixed in clay or mica lattices, thus preventing loss to drainage waters.

Differences in stream pH are inconsistent. The stream draining mini-catchment C17 shows the expected increase in pH, as a result of liming, but C7 is more acid than the unimproved catchment drainage. The more acid groundwater in catchment C17 is thought to mask any effect due to liming. Although differences in water chemistry have apparently resulted from the pasture improvement, they are small and are unlikely to damage freshwater communities. The increased nitrate concentrations are appreciably below the maximum acceptable concentration of 11 mg l^{-1} identified for drinking waters by the World Health Organisation. Phosphate, the other major concern to the water industry, remained at concentrations below the limit of detection (0·02 mg l^{-1} P) throughout the study, and is therefore unlikely to create problems for water treatment.

M Hornung and B Reynolds

Table 24. Mean concentrations (mg l^{-1}) of solutes in streams draining improved and unimproved mini-catchments at Plynlimon

Mini-catchment	Na	K	Ca	Mg	Si	NO_3-N	SO_3-S	Cl	HCO_3*	H*	pH
Unimproved											
C2	3·1	0·10	1·1	0·7	0·8	0·07	1·6	5·0	53	5·4	5·27
'Improved'											
C17	3·6	0·11	1·6	1·8	1·6	0·28	2·2	5·8	100	0·8	6·12
C7	3·1	0·13	1·6	1·6	1·4	0·18	3·2	4·9	45	14·8	4·83

* H ion and HCO_3: µeq l^{-1}

Growth in the 'field' of Sitka spruce transplants after being inoculated with sheathing mycorrhizal fungi

In recent years, interest in sheathing mycorrhizas has been renewed as it becomes increasingly evident that inoculating tree seedlings with sheathing mycorrhizal fungi may markedly improve the growth and establishment of forest transplants (Moser 1958; Marx 1980). However, the extension of a very considerable body of evidence from laboratory experiments in highly controlled conditions to conditions in forest plantations has often led to unexplained failures, with many sheathing mycorrhizal fungi selected in laboratory tests appearing to be ineffective in plantations. Recent observations of the succession of mycorrhizal toadstools and earth-fans associated with an ageing stand of birch (*Betula* spp.) seem to provide an explanation for some of the failures (Last *et al.* 1983; Mason *et al.* 1983). Whereas fungi associated with both young and older trees formed mycorrhizas with equal facility on seedlings growing in sterile (axenic) conditions, only the fungi associated with young trees stimulated mycorrhiza formation on seedlings grown in *unsterile* soils. This difference suggests that the probability of controlling mycorrhizal development in unsterile conditions is likely to be greater when fungi (early-stage) associated with young trees are tested than when late-stage fungi, associated with old trees, are used. In testing this

Table 25. Effects of inoculating Sitka spruce transplants with different isolates of sheathing mycorrhizal fungi on heights (cm) at the end of the first (1982) and second years (1983) after planting into peat or peaty gley soils at Wealside, Hexham

Inoculation treatments at transplanting	Site type: Peat, End of 1st year	Peat, End of 2nd year	Peaty gley, End of 1st year	Peaty gley, End of 2nd year
1. Inoculated with:				
Paxillus involutus,				
i. isolate PI 16	13	25	15	25
ii. isolate PI 32	16	31	14	23
Laccaria isolate 003	17	33	16	24
2. Uninoculated controls	11	24	9	15
LSD (P=0·05)	2	6	4	5

Table 26. Effect of inoculating Sitka spruce transplants with different isolates of sheathing mycorrhizal fungi on root development at the end of the first year (1982) after planting into peat or peaty gley soils at Wealside, Hexham

Inoculation treatments at transplanting	Numbers of root fragments	Numbers and % (in brackets) of root fragments with mycorrhizas	Numbers and % (in brackets) of mycorrhizas attributable to inoculant fungus
Peat			
1. Inoculated with:			
Paxillus involutus			
i. isolate PI 16	438	74 (17)	35 (47)
ii. isolate PI 32	547	180 (33)	179 (99)
Laccaria isolate 003	641	187 (29)	185 (99)
2. Uninoculated controls	378	19 (5)	NA
Peaty gley			
1. Inoculated with:			
Paxillus involutus			
i. isolate PI 16	560	194 (35)	189 (97)
ii. isolate PI 32	457	157 (34)	156 (99)
Laccaria isolate 003	367	74 (20)	74 (100)
2. Uninoculated controls	434	40 (9)	NA

NA = Not applicable

hypothesis, seedlings of Sitka spruce were inoculated with different isolates of *Laccaria* sp. and *Paxillus involutus* before being transplanted into peat and peaty gley soils at Wealside, near Hexham, Northumbria.

At the end of the first year, after inoculation and transplanting, seedlings inoculated with *Laccaria* sp. or *Paxillus involutus* isolate 32 were significantly taller than the uninoculated counterparts at the peat site (Table 25). These benefits were maintained during the second season, with transplants inoculated with *Laccaria* finishing 36% taller than the uninoculated controls. Whereas growth was improved by isolate 32 of *Paxillus involutus*, the other isolate (16) of this fungus did not stimulate height growth.

On examining the roots, it was found that the *Laccaria* isolate and *Paxillus involutus* isolate 32 increased numbers of root fragments and mycorrhizas per plant, with virtually all the mycorrhizas being attributable to the respective inoculant fungi (Plate 19). In contrast, isolate 16 of *P. involutus*, which seemed unable to resist competition from naturally occurring fungi, had a relatively small effect on numbers of mycorrhizas per plant, and virtually no effect on root system size as gauged by numbers of root fragments per plant (Table 26).

At the second site, a peaty gley, the response to *Paxillus involutus* isolate 16 was markedly different—the height increases attributable to this fungus were just as large as those attributable to *Laccaria* and to the other *P. involutus* isolate (32). They all significantly increased heights by about 76% and 57% in the first and second years after transplanting, respectively. However, these benefits were associated with markedly different effects on root growth. Whereas all 3 fungi prevented the development of mycorrhizas by other fungi, *Laccaria* sp. had little or no effect on numbers of root fragments and mycorrhizas (Table 26).

Two years after transplanting, the results of this trial, done with the ready co-operation of the Economic Forestry Group, show that, with the rational selection of inoculant fungi, substantial improvements in tree growth can be obtained from controlled inoculations with sheathing mycorrhizal fungi. They also show that *Laccaria* sp. and *Paxillus involutus* isolate 32 were able to resist competition from other fungi in peat and peaty gley soils, whereas *P. involutus* isolate 16 was more sensitive to competition.

F T Last, P A Mason and Julia Wilson

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Soil changes through afforestation

Because the United Kingdom imports about 92% of the timber that it uses, a considerable expansion of the afforested area appears to be inevitable (CAS 1980). A study of the effects of tree species on soils is, therefore, timely and of practical importance because it is desirable to be forewarned of changes likely to result from the establishment of trees. It should then be possible to direct those changes by selecting the most suitable tree species for conserving and improving soil fertility, an aspect of particular importance to poor marginal land where most of the expansion is likely to occur.

To gain an insight into the effects of trees on soils, Ovington (1953, subsequent papers) examined soil conditions in 1951 in plots planted with different species (Table 27). The soil at Bedgebury is a compact, silty clay, with imperfect drainage; that at Abbotswood is a fairly coarse sandy loam; and at West Tofts a sandy soil overlies chalky boulder clay.

Table 27. Species studied by Ovington at Bedgebury, Abbotswood, and West Tofts, and resampled in 1974

Site	Species	Date planted
Bedgebury, Kent National Pinetum	*Pinus nigra*. var. *maritima* (Ait.) Melv.	1934
	Picea abies Karst.	1932
	Chamaecyparis lawsoniana (A. Murr.) Parl.	1931
	Tsuga heterophylla (Raf.) Sarg.	1929
	Thuja plicata D. Don	1930
	Pseudotsuga menziesii (Mirb.) Franco	1931
	Larix eurolepis Henry	1929
	Quercus petraea (Matt.) Liebl.	1931
	Quercus rubra L. sec du Roi	1931
	Nothofagus obliqua (Mirb.) Blume	1930
Abbotswood, Gloucestershire Forest of Dean	*Larix decidua* Mill.	1906
	Picea abies Karst.	1905
	Pinus nigra var. *maritima* (Ait.) Melv.	1906
	Abies grandis Lindley	1928
	Fagus sylvatica L.	1913
	Quercus robus Linn.	1905
	Castanea sativa Mill.	1905
West Tofts, Norfolk Thetford Chase	*Pseudotsuga menziesii* (Mirb.) Franco	1930
	Pinus nigra var. *maritima* (Ait.) Melv.	1930
	Larix leptolepis (Sieb & Zucc.) Gord.	1930
	Alnus incana (L.) Moench.	1930
	Betula alba (nomen ambiguum)	1930

Ovington's observations suggested that surface soils under conifers tended to be more acid than those under hardwoods (Ovington 1953). At Bedgebury, the surface soil of 3 of the 4 hardwood plots had more total nitrogen than that in the coniferous stands, but the overall difference between hardwoods and conifers was not significant at Abbotswood (Ovington 1956). At all 3 sites, the amounts of extractable soil phosphorus tended to be larger where conifers had been planted. Ovington found no evidence to suggest that afforestation affected amounts of extractable magnesium, but afforestation accelerated the losses of extractable calcium from the surface mineral soil (Ovington 1958).

With this background, members of the Forestry Commission (FC) and ITE resampled Ovington's plots in 1974. The new data showed that the 3 sites represent a range of soil conditions. Bedgebury and Abbotswood had similar mean pH and contents of total nitrogen, extractable potassium and magnesium at all depths, but amounts of extractable phosphorus were smaller at Bedgebury than at Abbotswood. There was little change of pH with depth at either site. In contrast, West Tofts soils had higher pH which increased with increasing depth. They also had larger amounts of extractable calcium and phosphorus, but smaller amounts of organic matter, total nitrogen and extractable potassium.

The only species planted at all 3 sites was *Pinus nigra*. Under that species, from 1951 to 1974, there were significant increases in pH below 10 cm at Bedgebury, while the very large increases below 25 cm at West Tofts suggest that, at the 1974 sample locations, the chalky boulder clay was close to the surface. At all 3 sites, there were significant decreases in extractable magnesium in the top 30 cm and of extractable calcium between 5 and 20 cm (Figure 61). Extractable potassium increased significantly below 25 cm at Bedgebury, and below 15 cm at Abbotswood, but the increases at West Tofts were not statistically significant.

Amounts of total nitrogen under *Pinus nigra* decreased significantly at all depths at Abbotswood, at all depths except 0–5 cm at Bedgebury, but only at 15–20 cm depth at West Tofts (Figure 61). There were also decreases in the amounts of total nitrogen where the other 17 tree species were planted; at Bedgebury and Abbotswood, broadly similar decreases in total nitrogen occurred at all depths except 0–5 cm. In this surface layer at Bedgebury, there was a gain under *Larix leptolepis*, whereas there were significant decreases under *Quercus robur*, *Fagus sylvatica*, *Castanea sativa*, and *Abies grandis* at Abbotswood. Changes in total nitrogen were generally smaller at West Tofts, except for the increase at 0–5 cm under *Alnus incana*. At Bedgebury, there were significant decreases in the amount of extractable calcium in the top 5 cm of soil under *Pseudotsuga menziesii*, *Nothofagus obliqua*, and *Quercus rubra*; soil at greater depths under most species showed a decrease in extractable calcium content. At Abbotswood, there were significant decreases at 0–5 cm depth under all species except *Larix decidua* and *Picea abies*, at 5–10 cm under all species except *Larix decidua* and *Fagus sylvatica*, at 15–20 cm under all species, at 25–30 cm under *Picea abies* and *Castanea sativa*, and at 45–50 cm under all species except *Quercus robur* and *Larix decidua*. At West Tofts, there were significant decreases only under *Alnus incana* and *Larix leptolepis* (0–5 cm). There were significant decreases in extractable magnesium at most depths under all species at all sites.

Changes in pH were not consistent. At Bedgebury, pH both increased and decreased from 1951 to 1974, depending on species and depth. There were significant increases at all depths under *Quercus petraea* and at all depths except 0–5 cm under *Pseudotsuga menziesii* and *Nothofagus obliqua*. There were fewer significant changes in pH at Abbotswood, but all species were associated with a significant decrease at 0–5 cm, and all except *Abies grandis* at 5–10 cm. At West Tofts, there were significant decreases under *Alnus incana* down to 20 cm.

Amounts of extractable potassium increased at many depths under most species at all 3 sites, the most significant increase occurring between 15 and 50 cm at Bedgebury and Abbotswood. Apart from large decreases in extractable phosphorus under *Larix decidua* at Abbotswood, at all depths, changes in extractable phosphorus were not consistent.

The changes in soil properties between 1951 and 1974 were often inconsistent, the interpretation being made difficult by the lack of adequate replication. Furthermore, many of the differences between coniferous and deciduous species found by Ovington were not found in 1974. In trying to find an ecological interpretation for the differences between 1951 and 1974, it is useful to recognize 2 groups of variables: (i) those concerned directly with the quality and quantity of soil organic matter (loss-on-ignition, total nitrogen, extractable phosphorus) and with changes in these variables attributable to soil organisms, and (ii) elements of the soil exchange complex (eg extractable potassium, calcium, magnesium, and sodium) which can be removed by leaching and replaced by weathering of soil minerals, and, in the surface soil, by litter decomposition and mineralization.

Bearing in mind our reservations about the statistical design of the samples, and the fact that many of the changes occurred inconsistently at one or a few depths, it is possible to rank the species very crudely by the magnitude of changes in the groups of variables concerned with soil organic matter and the elements of the soil exchange complex. The higher a

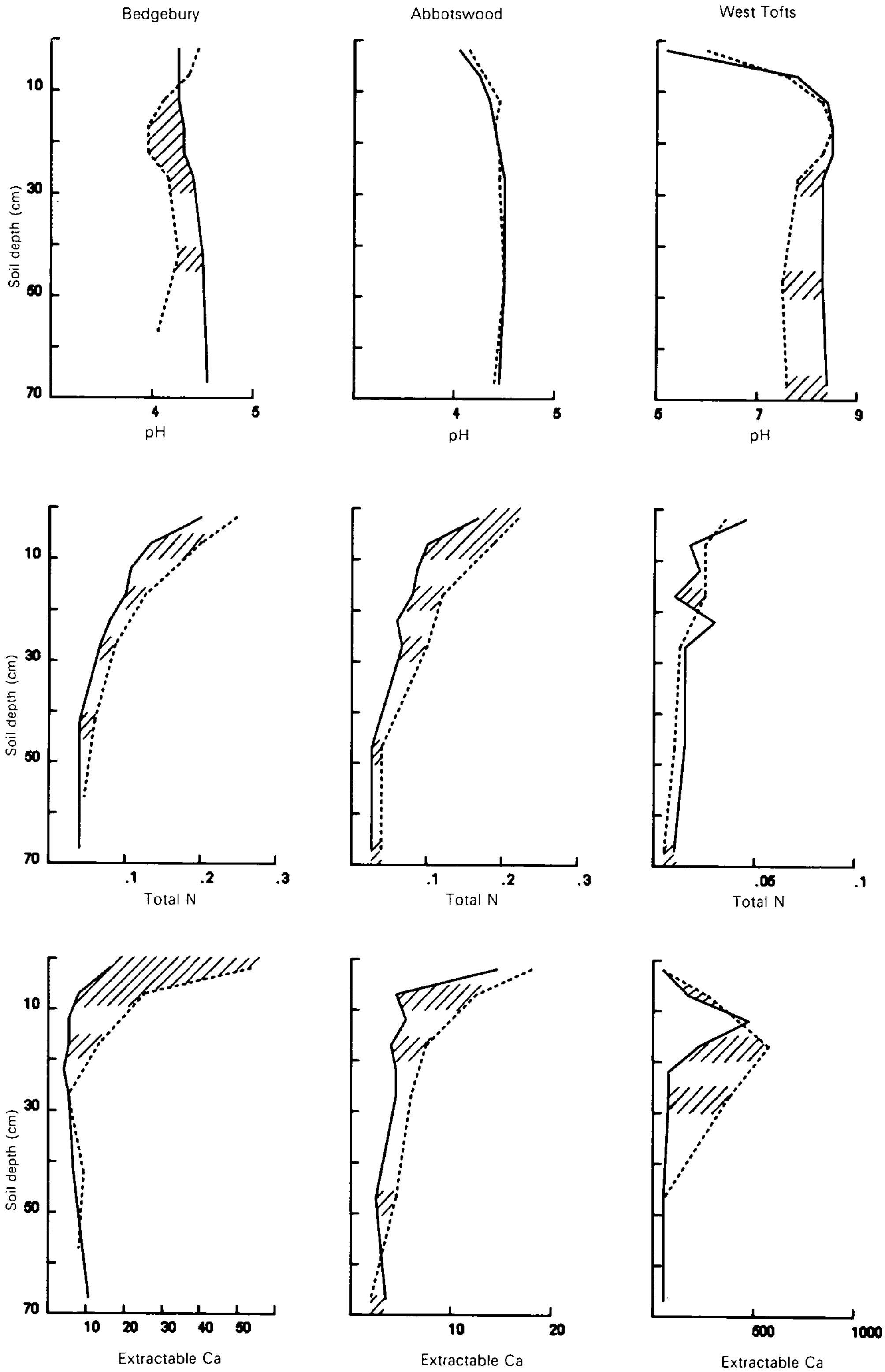

Figure 61 Changes in soil profile properties under Corsican pine between 1951 (-----) and 1974 (———) at 3 sites in southern England. Differences in pH, total nitrogen and extractable calcium that are significant at $P < 0{\cdot}05$ are shaded

species in these rankings, the greater have been the leaching losses and decrease in pH. These criteria are usually inversely related to changes in total nitrogen and extractable phosphorus.

At Bedgebury, the ranking of the species is: *Pinus nigra* > *Quercus rubra, Pseudotsuga menziesii, Nothofagus obliqua* > *Tsuga heterophylla, Chamaecyparis lawsoniana, Thuja plicata* > *Quercus petraea* > *Larix eurolepis* > *Picea abies*. The position of *Pinus nigra* relative to the other species is consistent with other published data, which show that *Pinus nigra* litter is low in calcium, potassium, magnesium, and phosphorus relative to that of broadleaved trees and other conifers (Gloaguen & Touffet 1976). Ovington (1953) noted that the accumulation of surface organic matter was greatest under *Pinus nigra* and *Picea omorika* (the latter was not resampled in 1974). Also, *Quercus rubra* litter is usually low in calcium and fairly acid (Bard 1946; Plice 1934; Petch 1965). Duchaufour and Bonneau (1961) found that leaching and acidification, under 26-year old *Pseudotsuga menziesii*, were accelerated relative to the original oak-hornbeam forest, and the pH had decreased by 0·5 unit. *Pseudotsuga menziesii* has a low rate of return of minerals to the soil in litterfall (Gloaguen & Touffet 1976), but it does not cause as severe soil deterioration as generally occurs under spruces (Noirfalise & Vanesse 1975). The position here of *Picea abies* may appear to be somewhat at variance with its reputation for occurring on very poor and acid soils, but it may be one of the species whose effect on soils depends upon the soil parent material, although other site factors may also be important (Saly 1980).

At Abbotswood, the approximate ranking is: *Quercus robur* > *Fagus sylvatica* > *Abies grandis* > *Castanea sativa* > *Pinus nigra* > *Picea abies* > *Larix decidua*. The position of *Pinus nigra* at Abbotswood contrasts with that at Bedgebury and elsewhere.

At West Tofts, the ranking is: *Alnus incana* > *Larix leptolepis* > *Pinus nigra* > *Pseudotsuga menziesii* > *Betula alba*. Larch is often regarded as a beneficial tree species, with a nutritious, easily-decomposed litter. However, the evidence in the literature is somewhat contradictory, and the effect of larch may depend to some extent on local conditions, and species (*L. leptolepis* or *L. decidua*). According to Bonnevie-Svendsen and Gjems (1957), humus conditions under larch generally appear to be 'more favourable' than those under Norway spruce or Scots pine. Acidification of soil and leaching of calcium have been observed under alder species by other workers (eg Crocker *et al.* 1955).

It is clear that different tree species have different effects on soils, and that these effects may depend on local conditions. Changes in amounts of nitrogen, phosphorus, potassium, calcium and magnesium serve to illustrate these generalizations, but how are the changes brought about? For the future, a greater emphasis on soil processes is required.

P J A Howard and Doreen M Howard

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LAND RESOURCES AND LAND USE

Evaluation of remote sensing as an aid to the study of ecological change

Remote sensing from aircraft or satellites using digitally recording sensors is rapidly becoming a routine tool for land resource inventory and monitoring. These techniques are particularly attractive, and have been widely used in areas where land resource records are sparse, where access is difficult, and where land cover is relatively homogeneous and thus susceptible to treatment using data at the comparatively coarse spatial resolutions which have hitherto been available.

These conditions do not apply in the United Kingdom, or in much of western Europe. The area is well mapped, and the complexity and variability of the natural and semi-natural vegetation cover present formidable problems in the use of low resolution remotely sensed data for vegetation community mapping. As a result, remote sensing has not been widely used for ecological applications in Britain. Nevertheless, if some of the problems of interpretation and classification can be overcome, remote sensing offers significant advantages over conventional ground survey methods, particularly where comprehensive coverage of large areas or regular resurvey for monitoring purposes is required.

Paradoxically, because low resolution remote sensing produces a highly integrated picture of vegetation

Plate 20 Multi-band hand-held radiometer in use in the field
(Photograph K C Walton)

canopies, ecologists are presented with a novel means of studying ecosystem dynamics from a holistic viewpoint. Hitherto, remote sensing has always been exploited as a means of mapping pre-determined land cover classes. Anomalies in the remotely sensed data have always been explained as shortcomings in the methodology. There is a strong case for a departure from this approach, for seeking order in the remotely sensed data without preconceptions, and *then* looking for ecological explanations.

In addition to these applications in resource inventory and monitoring, there is evidence (Curran 1983) which suggests that multispectral sensors can yield quantitative information on ecosystem parameters such as green biomass, soil moisture status, susceptibility to stress, etc.

Remote sensing in ITE

ITE is undertaking a programme of work to explore these various possibilities. The use of remote sensing for synoptic survey of natural and semi-natural ecosystems and for monitoring change is being evaluated in upland areas in mid-Wales and in lowland areas in East Anglia. Various sources of imagery are being investigated, including both satellite and aircraft systems. The work includes fundamental research into the problems of classification of multispectral imagery for purposes of vegetation community mapping, and is intended to lead to the development of an integrated land cover survey methodology, drawing upon the combined resources of ground survey, aerial photography, and digital remote sensing from aircraft and satellites.

In parallel with this work, research is being undertaken into relationships between vegetation dynamics (eg canopy composition and condition, phenology) and reflectance characteristics. This research will link the results of an intensive programme of field observations, including measurements of radiance using a ground-based radiometer (Plate 20), with airborne multispectral imagery. Once the fundamental canopy reflectance relationships are better understood, the research will be extended to explore the feasibility of detecting and quantifying subtle pressures on vegetation communities from factors such as water stress, sublethal levels of pollution, or grazing.

Upland inventory

Early work in ITE on ecological applications of remotely sensed data was carried out using Landsat Multispectral Scanner (MSS) imagery in a test area, 20 km × 20 km, in mid-Wales, centred on Dolgellau (Figure 62). This area was selected for several reasons: (i) it falls within the Snowdonia National Park, where an extensive vegetation survey was undertaken by ITE in the late 1960s; (ii) it includes a smaller area considered in more detail in a recent study of land use change in upland areas (Ball *et al.* 1982); (iii) it is a region with a considerable diversity of ground cover, where most upland structural vegetation types are encountered; finally, Landsat images are available which are acceptably free of cloud cover (by no means a trivial consideration in

Figure 62 Location of the 20 km × 2 km upland test area in mid-Wales

Table 28. Upland vegetation classes

Level 1	Level 2	Level 3
Woodlands	Coniferous Deciduous Other	Coniferous Deciduous Mixed Scrub
Heaths	*Calluna* *Vaccinium*	*Calluna* *Calluna/Vaccinium* *Calluna/Trichophorum* *Calluna/Ulex* *Calluna/Pteridium* *Vaccinium*
Grasslands	*Molinia* *Nardus* *Agrostis* *Pteridium* *Ulex*	*Molinia* *Molinia/Juncus* *Molinia/Eriophorum* *Nardus* *Nardus/Juncus* *Nardus/Festuca* *Nardus/Festuca/Juncus* *Agrostis* *Agrostis/Festuca* *Agrostis/Festuca/Juncus* *Agrostis/Festuca/Nardus* *Pteridium* *Pteridium/Agrostis/Festuca* *Pteridium/Calluna* *Ulex*
Wetlands	*Eriophorum* *Juncus*	*Eriophorum* *Eriophorum/Juncus* *Juncus*
Summits/cliffs/screes	Summits/cliffs/screes	*Rhacomitrium* Screes/bare rock/*Nardus* Ungrazed hedges
Lakes	Lakes	Lakes

planning remotely sensed studies of upland areas in Britain).

The first step was to encode the existing vegetation maps in digital form to provide 'ground truth' for interpreting, classifying and evaluating the satellite imagery. A 50 m square grid was superimposed on the 1:25 000 vegetation maps, and each cell was assigned the appropriate vegetation code (Table 28). Coding was carried out using a digitizing tablet, linked to the PDP-11/34 computer at ITE Bangor. Subsequently, image analysis was performed using the NERC International Imaging Systems I^2S Model 70, located in Swindon.

The hierarchical coding system used to describe vegetation community types permits an evaluation of the imagery at 3 levels of sophistication; in practice, work has so far concentrated on the coarsest level of discrimination. Initial interpretation and classification made use of an image acquired in May 1977. Subsequently, additional suitable imagery has become available, although, interestingly, all the available scenes which are acceptably cloud free cover the same period in late spring–early summer. For this reason, it has not been possible to exploit seasonal canopy differences to distinguish vegetation types using multitemporal techniques.

Using standard software available on the I^2S system, ground control points were identified in the Landsat images which enabled them to be digitally magnified and registered to the National Grid. The resultant images comprised 400×400 picture elements (pixels), directly equivalent to the 50 m square sampling grid used in digitizing the vegetation maps. Thus, it is possible to overlay the thematic maps exactly upon the satellite imagery.

Several approaches were taken in classifying the Landsat imagery, using the available ground truth data. The entire 400×400 pixel digitized vegetation map (6 classes) was used as a training set for a supervised classification. This was followed up by unsupervised classification of the Landsat scene using cluster analysis. Visual inspection of the results suggests an encouraging degree of consistency between the classified images and ground truth (Plates 24 & 25). However, more rigorous pixel-by-pixel examination of classification performance indicates major discrepancies between the satellite interpretations and the vegetation maps.

Investigation of these discrepancies by reference to other map sources and through field visits indicated that there are inaccuracies in the vegetation maps, to some extent due to changes in land cover between the time of the vegetation survey and the Landsat overpass.

The supervised classification was repeated, this time based on training areas specified interactively, which were known to represent unambiguously the map classes of interest. The statistics of these training sets suggest that Landsat-MSS is capable of separating at least the 6 broad land cover classes without difficulty (Figure 63).

Since beginning the study, further data sources have become available. These include large-scale stock maps of Forestry Commission plantations in the area, and aerial photographs at 1:20 000 scale, contemporary with one of our Landsat-MSS scenes and covering much of the region of interest. Furthermore, in 1983, NERC acquired 11-band multispectral imagery at 10 m square resolution from an aircraft-mounted scanner, covering Coed-y-Brenin in the north-west sector of the test area. These airborne MSS data are currently being explored for geological and hydrological applications, but are also available to ITE. It is thus clear that there is an extensive data set available for experimental purposes, covering this part of upland Wales.

It is therefore proposed to completely revise the vegetation maps, using the aerial photographs as the principal source of information and resolving any uncertainties by field visits to the area. By this means, it is planned to compile an accurate map of vegetation over the entire 20 km × 20 km area, using 1975 as the base date. This map will be used to improve and extend procedures for upland vegetation inventory and as a base-line for studies of the use of remote sensing for monitoring change in land cover.

Monitoring land cover change

Change in rural land use is a topical and important issue in environmental planning, and is not easy to

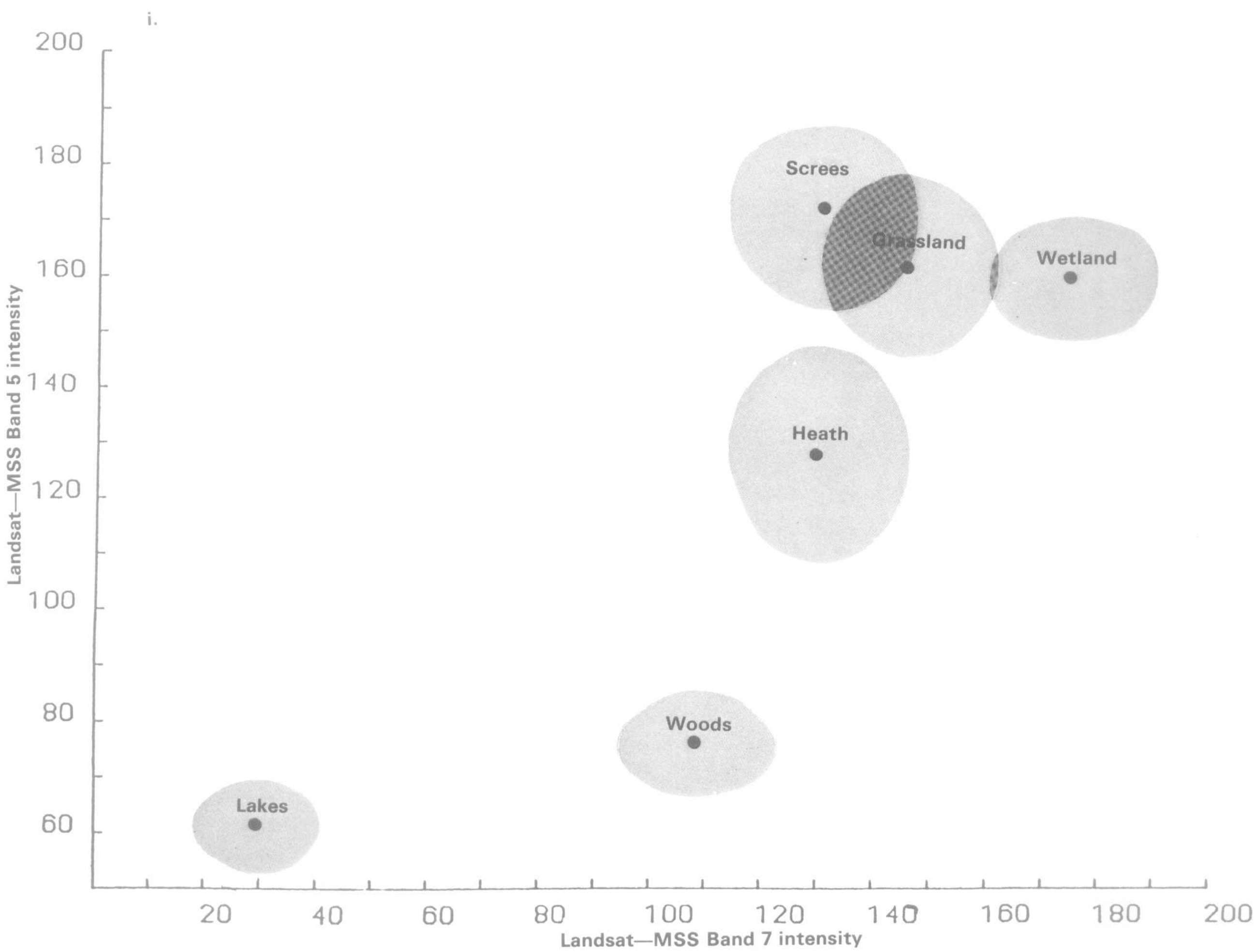

Figure 63 i. Separability of land cover classes using Landsat MSS bands 7 and 5

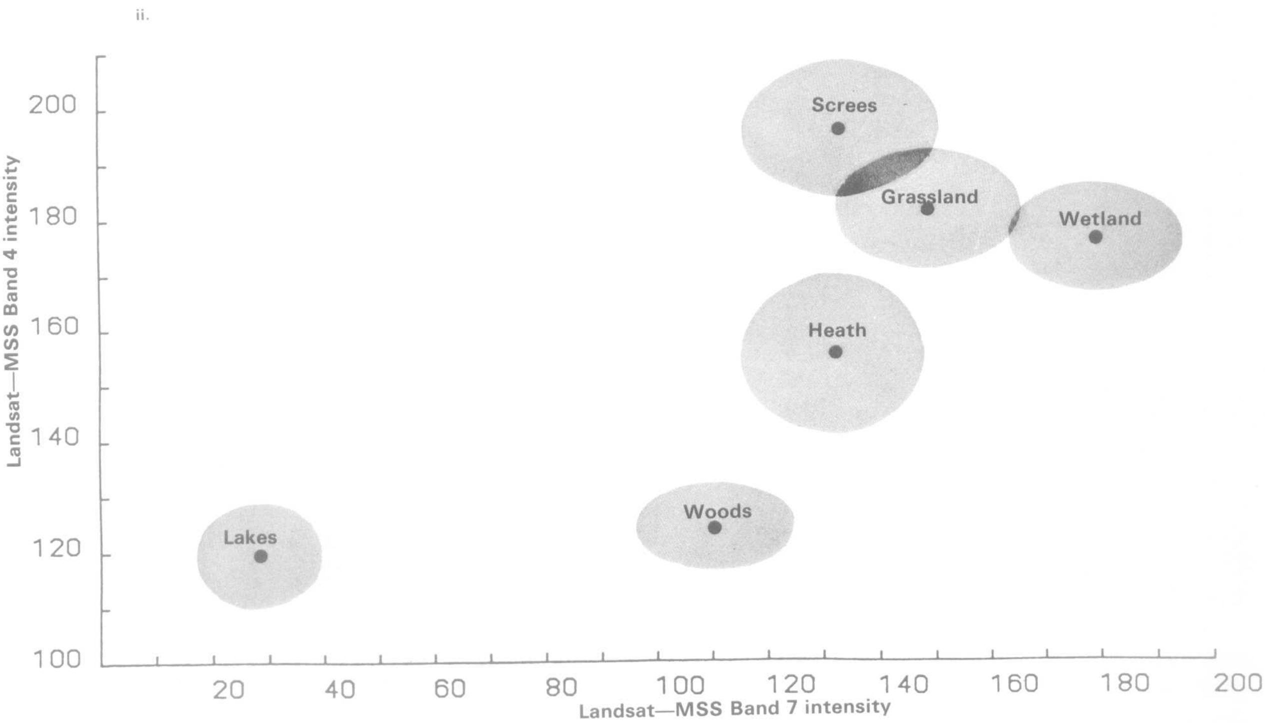

Figure 63 ii. Separability of land cover classes using Landsat MSS bands 7 and 4

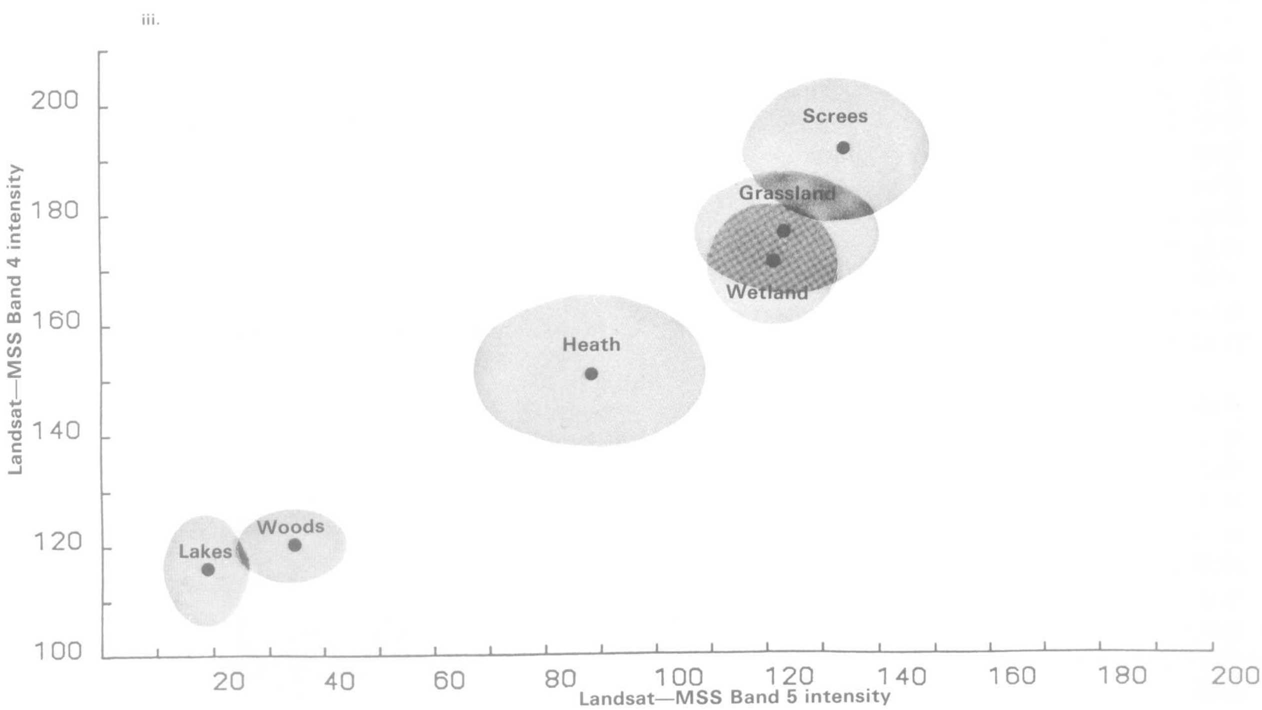

Figure 63 iii. Separability of land cover classes using Landsat MSS bands 5 and 4

detect or quantify at regional or national scales. One of the claims of advocates of satellite remote sensing concerns its potential for routine monitoring of land cover and detection of change. Our experience in Wales suggests that monitoring of change in areas of high cloud cover over timescales of less than 5 years presents difficulties, as suitable imagery often does not exist. Over longer periods (say 5–10 years), images are more reliably available. It was not sensible to embark upon a detailed evaluation of the use of remote sensing for monitoring change in upland Britain until we were sure that the technique is capable of distinguishing the land cover types of interest. Nevertheless, a preliminary evaluation study

Table 29. Lowland vegetation classes

Water bodies	
Reed fen	Uncut, very wet transitional habitats between swamp and dry fen
Reed and sedge	A cutting fen with a standing crop of reeds and/or sedges
Cut fen	Recently cut fen
Carr	Alder/willow, wet and usually growing as shrubs with multiple stems
Woodland	Usually oak/alder
Pasture	Flood-plain pasture
Arable	
Bare soil	Mainly ploughed

was considered to be worthwhile. Woodland was selected as a land cover class whose distribution within the test area is known with some certainty, so that training areas can be selected readily.

A supervised classification of Landsat MSS images from 1975 and from 1982 was performed, and the results are presented in Plate 26. Precise quantitative estimates of the areal extent of such changes are possible by counting pixels in the appropriate cover classes. In this example, there is an apparent net increase in mature forest canopy of 1072 ha (2·7%). Although this figure is not inconsistent with Forestry Commission records for this period, it does represent something of an over-simplification. For example, an apparent increase in forest cover may be the result of canopy closure, rather than new planting. Similarly, a reduction in cover may be the result of either thinning or felling. Further field work is necessary to identify the precise nature of the changes registered by the classification. More sophisticated image analysis will be necessary to identify fresh plantings at an earlier stage in their development.

Lowland inventory

A similar evaluation of remotely-sensed classification of lowland vegetation has been undertaken, based on an area in the Norfolk Broads. ITE has compiled maps of natural and semi-natural vegetation of the entire Broads Authority area by interpretation of aerial photographs (Fuller 1982). NERC commissioned a campaign of airborne multispectral scanner flights during the summer of 1982, and one of the areas covered was a 10 km × 4 km swathe including Barton Broad and the valley of the Rivers Ant and Bure (Plate 27). The airborne scanner recorded in 11 wavebands, with a ground resolution of 10 m square. In addition to the overall aim of investigating methods of vegetation survey using multispectral data, the campaign was intended to simulate high resolution satellite imagery from Landsat Thematic Mapper and the French SPOT satellite systems, which will shortly be routinely available.

The study examined the ability of the imagery to detect and distinguish 9 broad lowland land cover classes (Table 29). Initial results were promising, confirming that the improved radiometric resolution of Thematic Mapper will be of considerable help in vegetation classification. The extra bands in the photographic infra-red appear particularly useful in differentiation.

Quantitative evaluation of classification performance was difficult because of problems in registering the digital aircraft data with the maps. There is evidence to support literature claims (Forshaw *et al.* 1983) that improved spatial resolution does not invariably lead to increased classification accuracy, because within-class variance tends to be greater in high resolution imagery. It appears that new and more sophisticated classification algorithms are required to handle this imagery satisfactorily.

R M Fuller, R J Parsell and B K Wyatt

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CHEMICAL AND TECHNICAL SCIENCES

The historical development of analytical chemistry in ITE

Quite a high proportion of the research carried out in the Institute, and earlier by the research branch of its predecessor, the Nature Conservancy, has depended on the measurement of chemical characteristics at some stage in the investigation. Indeed, the need for a chemistry contribution became so urgent that an analytical chemistry service was established to cater for research requirements.

In the earliest days, there was always an emphasis on the needs of conservation. Examples of such investigations that needed analytical support include: (i) limiting conditions for *Primula farinosa*, (ii) effects on chalk grasslands of the removal of rabbit grazing pressures in the early days of myxomatosis, (iii) the examination of food plants to determine which attracted specific insects. Some requirements were rather more urgent. There were occasions when it was thought that activity outside a nature reserve or special site might affect the ecosystem balance within the site. For example, there was once concern about the penetration of farm slurry into a nature reserve. In such cases, it was often possible to provide a quick answer by applying appropriate chemical tests.

There was a thin division between conservation-type research and that which was concerned with understanding ecosystems, a topic which also became popular in the first decade of the Nature Conservancy. The approach of Professors Tansley and Pearsall in the understanding of ecosystem processes and mechanisms strongly influenced the work of many of the earlier NC scientists. Studies on nutrient cycling, litter decomposition and soil formation were prevalent, especially at Merlewood, Edinburgh and Bangor. Rather more comprehensive was the research looking at the full ecosystem balance sheet, such as that pioneered by Dr J D Ovington. He concentrated on woodlands, and his work led to the establishment of a long-term study into tree mixture growth and its effect on soils at Gisburn, Yorkshire, which is still attracting attention today. The ecosystem cycling and productivity approach reached its peak under the International Biological Programme in the late 1960s. This Programme gave birth to a cluster of experiments in selected woodland and upland sites in the UK (notably Meathop Wood, Moor House and Snowdon). In these experiments, all components of the ecosystem were systematically examined so that the processes and transfers could be understood in relation to each other, and productivity figures obtained. Without chemical data, much of this work would have had little value.

The incorporation of the Institute of Tree Biology, Edinburgh, into ITE in 1972 strengthened another research area which had only been pursued in preliminary studies by the NC research branch. This led to more attention being paid to physiological aspects, and potential applications, especially in the culture of trees.

Parallel studies on freshwater ecosystems were started in Edinburgh on the IBP site at Loch Leven. Even though the conditions contrast markedly with terrestrial ecosystems, the approach and research philosophy are basically similar, and, here again, the chemical input has been essential in the studies.

Research development at Monks Wood in the 1960s followed a different route. There were 2 main threads which needed chemical support at this station. In one area of work, interest centred on the effects of toxic chemicals on wildlife, and work there concentrated on looking at the extent of, and the reasons for, this damage. The work later developed into a search for ways of mitigating the effects of these pesticides, and research, still being carried out, involved looking much more into the mechanisms involved. The other research emphasis at Monks Wood was concerned with conservation problems in the agricultural lowlands, and the need to meet some of the pressures of intensive farming.

By studying toxic chemicals in the environment, Monks Wood started a train of research which has incorporated other pollutants and now involves staff at 5 of the 7 ITE stations. Work at Bangor started in 1969 on possible damage to plant and, later, animal life by fluoride emissions from an aluminium smelter on Anglesey. In the early 1970s, ITE was drawn into the problems of atmospheric pollution, and a research programme was established to study the effects of gaseous pollutants, notably sulphur, nitrogen oxides and ozone, on tree health and growth. The most recent of the major pollutant studies has been the one concerned with radionuclides entering the terrestrial environment. The involvement of the Institute in this research area was stimulated by the Parker inquiry into emissions from Windscale in 1978, and practical work commenced in 1980.

In the last decade, there has been much more emphasis on land use and on the effects of land management on soil and its associated plant communities. One major project is a study into the effects of clear-felling conifer plantations, now being carried out at sites in Gwynedd and Cumbria. Apart from the obvious interest in such aspects as drainage, erosion, and changes in flora and fauna, the possible changes in soil chemistry may be of considerable importance. Another project with similar chemical requirements is concerned with geochemical cycling processes. These projects have necessitated the collection of soil leachates and other waters over many months before and after felling. Such long-term studies confront the analyst with the need to handle large numbers of samples, often arriving at regular time intervals. Because of the heterogeneity of natural ecosystems, statistical techniques must be used when designing experiments and surveys, and these techniques often generate more samples than the analyst can process easily.

This review has only mentioned a few of the many studies carried out over the last 25 years or so involving analytical chemistry. Furthermore, it does not mention the more unusual analyses, eg nitrogen fractionation in grouse droppings, composition of coelomic fluid of earthworms, polyphenol levels in relation to palatability tests, minor elements in deer antlers, or energy changes in decomposing litter. The main requirement in most of these studies has been to determine the concentration of nutrient elements. Potassium, calcium, magnesium, phosphorus and nitrogen are frequently determined, but requests have frequently been extended to the essential trace nutrient elements, and to an examination of different forms of those elements. Various organic fractions and physical tests are needed less frequently, but, because of their complexity, the time required for development and analysis may be just as great.

The development of analytical chemistry services over the last 25 years has coincided closely with the revolution in analytical methodology and instrumentation which has occurred over the same period. Before the middle 1950s, there had been remarkably little change in most analytical chemistry techniques since the early years of the century. New reactions and reagents had been described regularly, but most of the methods were essentially volumetric or gravimetric in nature. The only precision instrument possessed by many chemical laboratories would be the analytical balance, although this item of equipment has now changed beyond recognition, from a weighing machine that depended on the manual addition of individual weights, to current instruments with top pan loading and instant read-out. Indeed, many models can now be linked to a laboratory computer.

Very few commercial laboratory measuring instruments were available in the 1950s. A few pH meters were coming into use—large boxes full of bulky electronic components and with 2 fragile electrodes. Some powerful analytical systems were installed in the larger soil laboratories; for example, the Macaulay Institute had pioneered the use of optical emission spectrometry since the 1930s, but not many laboratories had the expertise to run them or could afford such massive installations. Probably the most widely used analytical instrument available in the UK at this time was the Spekker absorptiometer, which was used for colorimetric tests. This instrument was quickly followed by the EEL filter flame photometer. The principles of flame photometry had been established by Lundegardh in 1928, but, until the EEL model came on the market, determinations of potassium and sodium were long and laborious gravimetric procedures. Almost overnight, this flame photometer made it possible to process relatively large numbers of samples for these elements. With the introduction of more stable and sensitive electronic and optical systems, both the filter absorptiometer and flame photometer gave way to double-beam, monochromator instruments. Models for automatic sample presentation and also recorder attachments came later. More recently, the introduction of the thermal atomiser attachment has pushed the sensitivity of flame methods almost to the practical limit.

Probably the 2 instruments which have made the biggest impact in the analysis of ecological materials have been the atomic absorption spectrophotometer and the gas-liquid chromatograph, which became widely used in the early 1960s. The application of atomic absorption was very rapid following its discovery by Walsh in 1955. At first, atomic absorption systems were developed as an adjunct to flame spectrophotometers using large, expensive, purpose-made hollow cathode lamps, but they were soon replaced by dedicated instruments. The gas-liquid chromatographic technique was first described in 1941, but commercial instruments were not available until much later. Its use in ITE is another example of the development of the instrument matching the need. The toxic chemicals research group at Monks Wood was in the forefront of research into the effects of organic pesticides, and was quick to make use of the gas-liquid chromatograph separation techniques for the measurement of these pesticides and their residues.

These instruments have been continually improved and are still in regular use in ITE, but there are other instruments, eg the polarograph, which at first appeared to have considerable potential as analytical instruments in ecology, especially for the essential minor elements, but which have to some extent been overtaken by other developments. Atomic absorption developed so rapidly as a powerful element technique that the polarograph was soon displaced in routine use. It does, however, still have a great deal of value as a research instrument. One electroanalytical technique which has proved to be of value is anodic stripping voltammetry, which will measure different ionic forms, and this has been used in ITE for the measurement of the pollutant, trialkyl lead.

With some techniques, it is possible to make direct measures on the original dry material. X-ray fluorescence spectrometry is one example. For ecological purposes, however, with its mix of analytical requirements, including soil extracts, plant digests and waters, 'wet' techniques still have to be used. These methods have been improved, so that many of the stages are now partly automatic, and even preliminary dilution, reagent addition, standard addition and other early treatment steps can be done automatically. In automated discrete and flow analysers, the full sequence, including sample presentation, reagent addition, and colorimetric recording, can be done automatically. In some laboratories, many routine instruments can be connected to a laboratory computer, which will process sample and standard readings. In more sophisticated systems, the labora-

Plate 21 A greater horseshoe bat
(Photograph R E Stebbings)

Plate 22 A bridled form of the guillemot
(Photograph M P Harris)

Plate 23 Open Juncus trifidus *heath at 1200 m on Cairn Gorm, Scotland*
(Photograph G R Miller)

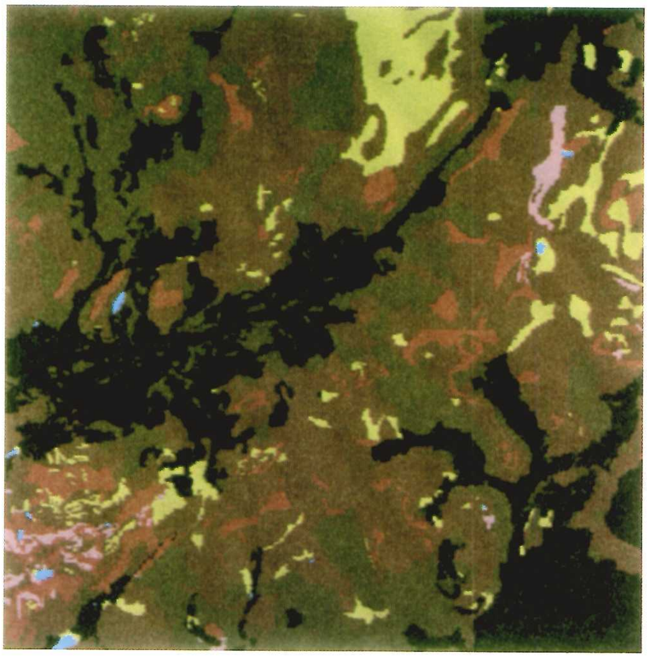

Plate 24 Vegetation base map of Dolgellau test area, used as 'ground truth'. Colour code: black – unsurveyed areas (mainly agricultural grassland); dark green – woodland; light green – wetland; red – heathland; brown – grassland; purple – scree; blue – lake
(Photograph NERC Thematic Information Service)

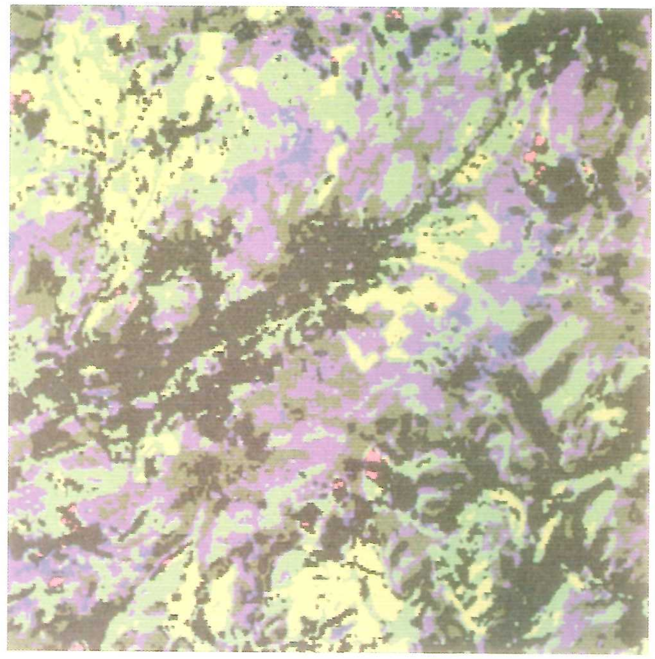

Plate 25 Supervised classification of Landsat-MSS image of the Dolgellau test area. Colour code: black – unsurveyed areas (mainly agricultural grassland); light green – woodland; mid-green – wetland; dark green – heathland; purple – grassland; blue – scree; pink – lake
(Photograph NERC Thematic Information Service)

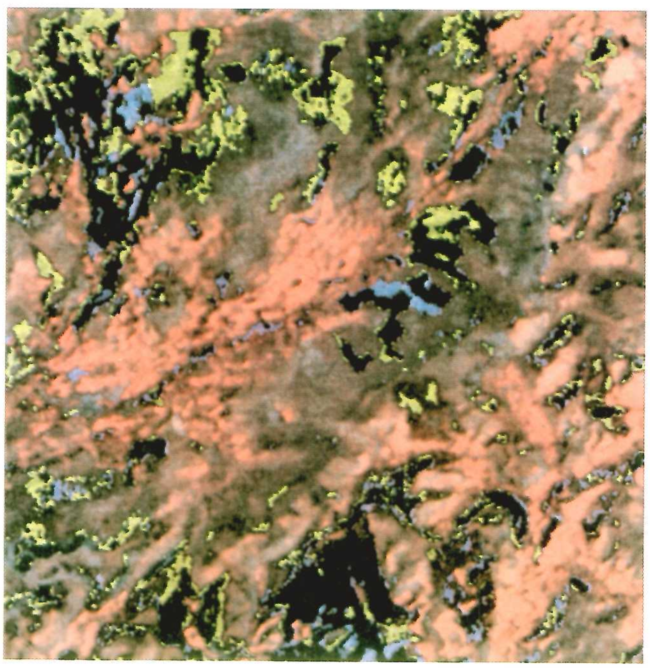

Plate 26 Changes in forest cover in mid-Wales detected using Landsat-MSS imagery. Green areas indicate increase in mature forest canopy from 1975 to 1982. Blue areas indicate reduced mature canopy. Black areas are classified as woodland in both 1975 and 1982 scenes
(Photograph NERC Thematic Information Service)

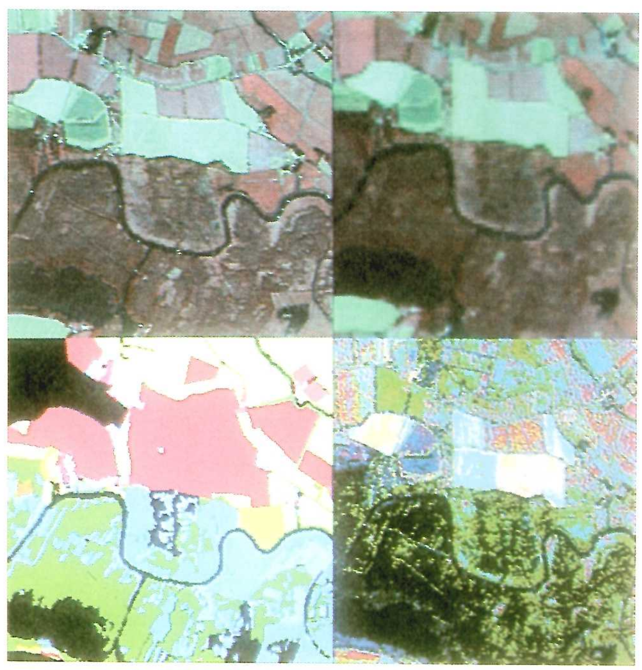

Plate 27 Airborne multispectral imagery of the Bure valley. Source image at $10\,m^2$ resolution (top left). Simulated Landsat TM image at $30\,m^2$ resolution (top right). Vegetation base map (bottom left). Classified multispectral image (bottom right)
(Photographs NERC Thematic Information Service)

tory computer will feed back and control the introduction of the sample into the analytical system.

There are few signs of instrumental development levelling out. Over the last few years, completely new instrumental systems have been introduced. Examples include the ion analyser (suitable for continuous measurements of cations and anions), the IC plasma analyser (a spin-off from atomic absorption), and flow injection (a variant of continuous flow analysers).

One may ask how far these changes have aided the study of plant nutrition. The field worker has benefited, in that he can design complex factorial experiments knowing that the modern laboratory can handle many more samples in unit time. He is no longer compelled to provide relatively bulky samples because sensitive equipment allows smaller sample weights to be acceptable, if the material is sufficiently homogeneous. The analyst, too, is not burdened with time-consuming methods, but, while the time 'saved' in adopting an automated method will free an operator to carry out additional tasks, it less often shortens the absolute time required to complete a varied analysis of a given sample. The final data are more precise and less subject to operator error, but one crucial criterion—accuracy—has perhaps changed the least. The old gravimetric method could be quite accurate in the hands of a skilled analyst. Modern techniques may have brought the result closer to the 'true' value, but they have also opened the door to a variety of interference problems that volumetric and gravimetric techniques never encountered. An important key to accuracy lies in the effective control of interferences, and this problem is still met regularly in the analytical laboratory.

It has been suggested that, with the increased use of computer-controlled automated analytical systems, the need for the analytical chemist will gradually disappear. This is conceivable in some industrial laboratories handling only a narrow range of sample types and analytical methods. In ITE, however, the problems of keeping various instruments running successfully for such a wide range of sample types and compositions and controlling chemical interferences continue to keep the analysts fully occupied. Furthermore, in ecology, certain manual methods are still needed which are difficult to automate; for example, lignin and cellulose have to be determined by gravimetric procedures, crude fat and soil exchange methods still depend on extraction techniques, and loss on ignition is still the simplest way of measuring organic matter. It is likely that the analytical chemist will still be playing a vital role in ITE's research in 25 years' time.

S E Allen

Chemistry

Flow injection analysis

Flow injection analysis (FIA) is a recent development in continuous flow analysis, with the potential for very high sample throughput. A system has been assembled from basic components to explore the application of this technique for ecological samples. In this system, the sample is injected directly into a carrier stream in which controlled dispersion occurs. For example, a low dispersion manifold could be used for pH or ion-selective electrode measurement, medium dispersion for colorimetric determinations, and high dispersion for titrations. The main interest initially was to compare the performance of FIA colorimetric methods with standard Auto Analyzer methods. Auto Analyzer methods typically operate at 60 samples per hour, with a delay of up to 30 minutes between sample uptake and reaching a steady state. In FIA, the flow dynamics are much more controllable, and the reaction does not go to completion. This enables throughput rates of up to 300 samples per hour to be achieved.

Fast chemical reactions are relatively simple to apply to FIA, and the indirect colorimetric method for chloride is an example of such a method, where dramatic improvements in sampling rates can be achieved without loss of sensitivity. However, reactions which require elevated temperatures to speed up the process, such as in nitrogen and phosphorus methods, need further study, especially for the low level determinations in natural water samples. The few FIA documented methods for phosphorus using the molybdenum blue method were initially too insensitive for water analysis. A modified method using a catalyst (potassium antimony tartrate), a larger sample volume and a higher reaction temperature has been developed for water samples and acid digests, although further tests are required to evaluate the routine operation of this method. However, the indophenol blue method for ammonium–nitrogen in acid digests has proved more difficult to adapt to FIA.

The simplest form of analyser consists of a small pulse-free peristaltic pump, an injection valve, 0·5 mm internal diameter tubing, perspex connectors and a flow through detector. Automation of the system is being considered using a commercial sampler with an output device to trigger a servomotor which drives the injection valve.

A P Rowland

Engineering

Equipment for exposing plants to controlled concentrations of airborne pollutants

Four exposure chambers were required to expose plants to 2 pollutant gases, singly and in combination,

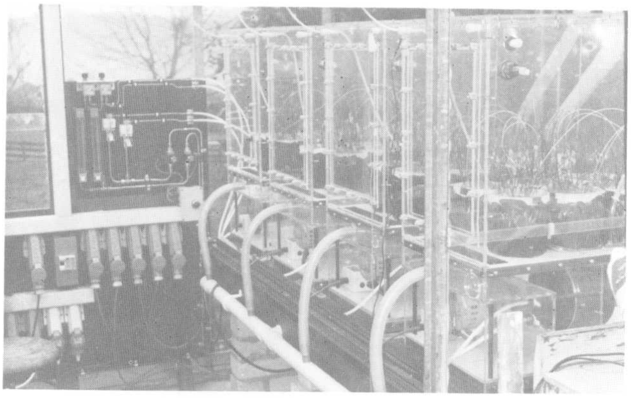

Plate 28 The sophisticated gas flow control system built to expose plants to concentrations of airborne pollutants
(Photograph G H Owen)

and to provide one control chamber with no pollutant additions. The design of the chambers had to take into account a number of criteria: the most important was to have sufficient air movement in the chamber to keep boundary layer resistances around the leaves of plants at a low level comparable to those expected on plants growing under field conditions. Air and gases in the chambers had to be changed about once each minute to ensure that pollutant gas concentrations would not be depleted and to maintain a near ambient level of carbon dioxide. Each chamber had to accommodate up to 30 plants in 3 inch pots. Means of introducing air and gases into the chambers and ports for sampling and monitoring the contents were also required.

The chambers were constructed from acrylic sheet. Each has a total volume of 185 litres and the air was circulated by a built-in fan with externally mounted motor drive. Each chamber was provided with adjustable baffles to regulate the air circulation and was fitted with a number of gas inlet and sampling ports. Air in the chambers is removed by an exhaust system discharging to the atmosphere, and replacement air is supplied through a carbon filter pack at a rate sufficient to produce one change per minute. A removable front panel gives access to the compartment housing the plants.

A sophisticated gas control system was built up from commercially available precision pressure regulators, flow controllers, flow meters and safety valves (Plate 28). The pipework was engineered in stainless steel and Teflon. The chambers and gas flow controls were installed in the glasshouse at Bangor, and a hydrogen supply line was fitted to allow the operation of an air monitor.

G H Owen and C R Rafarel

Vegetation/root washing machine

There has been a demand from several projects within ITE for a machine to wash organic matter and other debris from various substrates, eg soil from small root structures, clay from vegetation, humus material from woven fabric. In addition, a more automated method was required for size separation of small quantities of aggregates, root fragments, fungal hyphae or other substances. These washing or sorting operations would normally involve a spray of water from a hosepipe or other smaller hand-spraying equipment. To save labour, increase the throughput and standardize treatments, a washing machine was devised (Plate 29).

Experiments showed that better washing or sorting action occurs if a spray or jet of water penetrates the substrate at an angle other than vertically above. This angle results in more efficient waste removal and reduces blockage of a mesh screen if used to support the substrate. Rotating the spray through an angle up to 120 degrees proves even more effective for sorting, breaking down balls of soil, and keeping meshes free from blockage. It was therefore decided to use an array of adjustable water jets with an oscillating swing through 100–110 degrees. A clear acrylic (Perspex) box, 600 mm × 600 mm × 430 mm deep, was constructed to contain this apparatus. Several sieve trays of various mesh sizes could be stacked

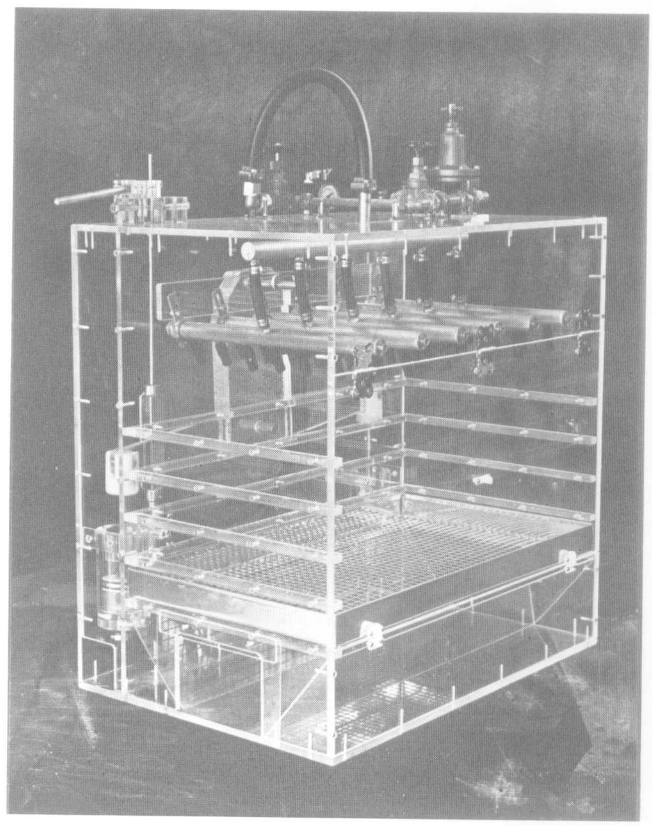

Plate 29 Water-powered machine devised for washing vegetation and root samples
(Photograph D G Benham)

below the array of jets for sorting applications. The 42 spray nozzles can be adjusted between a mist spray and a coarse water jet. They can also be turned off individually to conserve water and to maintain water pressure to nozzles in use. A pressure regulator prevents nozzle damage from excessive pressure.

The apparatus was designed to rest on a domestic sink draining board so that waste water drained down the sink via a sediment trap. Motive power to drive the nozzles slowly from side to side was provided by a novel design of a water-powered beam-engine integral in the back of the apparatus.

Operation of this power source is proving trouble-free, and costs nothing, provided that there is a head of water.

D G Benham

SYSTEMS ANALYSIS AND BIOMETRICS

Review of Programme on Systems Analysis and Biometrics

Objectives of the Programme

1. Provision of advice on the design, analysis and interpretation of ITE research, and on the systems analysis and modelling of ecological processes.
2. Development of research on statistical methods and systems analysis relevant to ecology, and identification of the principal areas in which such research should be concentrated.
3. Encouragement of training in statistical methods, systems analysis and computing for ITE staff, particularly through the use of checklists, case studies and programmed learning techniques.
4. Communication of information on new developments in the broad field of statistical methods and systems analysis, derived from attendance at meetings of learned societies and from published papers, through information networks and computer-based expert systems.

Provision of advice

The efficiency of ITE's research depends to a large degree on the availability of sound advice on the design of experiments and surveys and on their subsequent analysis and interpretation. Similarly, as more members of ITE's staff begin to use modelling and simulation techniques as an integral part of their research, advice on the efficient use of models and on their verification, validation and sensitivity analysis is necessary. It is characteristic of this type of advice that it must be available quickly when the need has been recognized by the Project Leader or by his Head of Station or Programme Leader. If such advice is not readily available, the scientist frequently makes his own choice of methods and proceeds to a stage in the research at which it is difficult, if not impossible, to change the basic approach. As far as possible, therefore, ITE must ensure that there is sufficient expertise at each of the stations to ensure that Project Leaders can obtain a quick response to a request for advice. This constraint leads directly to the conclusion that ITE's statistical and systems analysis expertise must be dispersed, with at least one expert in these fields at each of our stations.

It is, however, impossible to ensure that the whole range of expertise in statistical methods and in systems analysis will be available at every station, and the function of the local advisor may be to refer the Project Leader to a colleague at another station who has particular experience or expertise, and may therefore be able to provide better and more up-to-date advice. The existence of an ITE programme on statistical methods and systems analysis assumes an Institute-wide provision of service, drawing on the most relevant expertise through a series of direct links between colleagues. There will also be occasions when advice should be sought from outside ITE, and the principal function of the ITE advisor will then be to direct the Project Leader to the appropriate expert, and, possibly, to act as an interface between the ecologist and the external expert, who may have little or no knowledge of ecology.

The most important advice is that on the design of experiments and surveys, and a priority must therefore be given to this aspect of the advisory function. If experiments and surveys are well designed, their subsequent analysis can also be efficient and properly directed towards the defined objectives of the project. If the initial design is bad, no amount of subsequent advice will enable the ecologist to rescue the results, beyond a frequently abortive attempt to squeeze something of value from the research, even though the defined objectives are not attainable. In deploying the relatively scarce resources of statistical advice, therefore, priority must be given to Project Leaders seeking advice on the design of their experiments and surveys.

Priority having been given to such design, advice and practical help with the analysis of data and with the modelling of ecological processes and populations remain essential functions of ITE's limited number of experts in biometrics, statistics and systems analysis. The range of expertise in these fields among ITE's scientists is extremely variable, but very few of these scientists have sufficient expertise to analyse data effectively, even though they may be reluctant to admit this fact. Making sure that appropriate advice is sought, and, having been sought, taken, is therefore an important facet of research management, involving Heads of Stations, Assistant Directors and the Director, but also senior staff. Ideally, we should be able to forecast the need for advice from the project plans, and more attention is currently being given to the identification of future requirements for statistical advice when project plans are reviewed and approved, and by the more deliberate involvement of biometricians in the review process. Computing requirements also need to be forecast, partly so as to ensure that the appropriate experience and advice is available from within ITE.

Research
Research on statistical techniques and on systems analysis will frequently arise from the direct involvement of ITE's biometricians and systems analysts with individual projects. Such research will usually result in joint papers with ITE colleagues, and may also result in an independent paper by the biometrician in a statistical journal. Obviously, such collaboration is to be encouraged, and ITE's research projects should provide a fertile breeding ground for new ideas in statistics and systems analysis. Not all of the statistical research done by ITE, however, necessarily arises in this way. A significant proportion of ITE's statistical research should be planned by the biometricians, and should arise from their knowledge of the current state of the art. The opporunities to combine theory and practice are perhaps unique in institutes like ITE, and we must therefore make the best use of those opportunities.

To some extent, the choice of active research topics must depend on the expertise and interests of individuals, but there is much to be gained from a planned programme of research which harnesses such interests and expertise, particularly if the programme is related to the needs of present and future research projects. Broad areas of statistical research relevant to ITE interests include the following:

i. development of appropriate techniques for the analysis of data arising from pollution surveys and experiments, including radionuclides, where the statistical distributions are markedly non-normal;
ii. selection of multivariate techniques for defined purposes in ecological studies;
iii. deterministic and stochastic modelling of ecological processes related to management and policy options, and the interaction between economic and ecological submodels;
iv. development of expert and information systems through the use of microprocessor-based graphics.

Within these broad areas of research, there is a wide range of individual topics: examples include environmental assessment, monitoring and prediction, the analysis of spatial patterns, characterization of functional relationships, time series analysis, robust methods of estimation, and compartmental analysis. The list is probably endless, and selection of appropriate topics needs to be discussed with the broader statistical community so as to make the best use of ITE's slender resources.

Statistical training
Attempts have been made in the past to provide training in basic statistics in-house, but with only marginal success. The preparation of training courses is time-consuming and demands expertise which is not readily available within ITE. There is also little evidence that the benefits to the participants are sufficient to warrant the costs of preparing and running the courses. Good external courses are available, at a cost, especially at the Civil Service College, and ITE should take advantage of such courses wherever possible and appropriate. Within ITE, training should be concentrated on the preparation of programmed learning techniques using microprocessors, on the development of checklists to guide the use of statistical and computing methods, and on the publication of a series of case studies which ITE staff can use as examples to guide the conduct of their own work.

Communication of information
There is obviously a need for improved communication of information about statistical, systems analysis and computing techniques within ITE, both between members of staff with expertise in these fields, and from the experts to the less expert members of ITE. Information from books, papers and reports needs to be more widely disseminated, and information derived from attendance at meetings of appropriate learned societies should be more readily available to ITE as a whole. Increasingly, the development of computer-based expert systems incorporating the latest ideas and techniques can be expected to help fulfil this need. Such systems will also provide a medium for the sale of techniques developed within ITE.

J N R Jeffers

Simulation of the structural root system of Sitka spruce

Over large areas of upland Britain, windthrow seriously limits the size of trees which can be grown and so reduces the economic value of forest plantations. For trees to resist windthrow, it is important that their structural roots should be evenly distributed around the stem (Deans & Ford 1983). However, visual examination of root systems (Figure 64) gives the impression that root growth is haphazard, particularly when a comparison is made with the above-ground branching structure of the tree. The latter develops in a regular and systematic manner, which can be described by simple mathematical rules governing the relationship between shoot growth and branch production, and the angles and azimuths at which branches grow (Cochrane & Ford 1978). A joint investigation between ITE and the Department of Statistics, University of Edinburgh, examined the

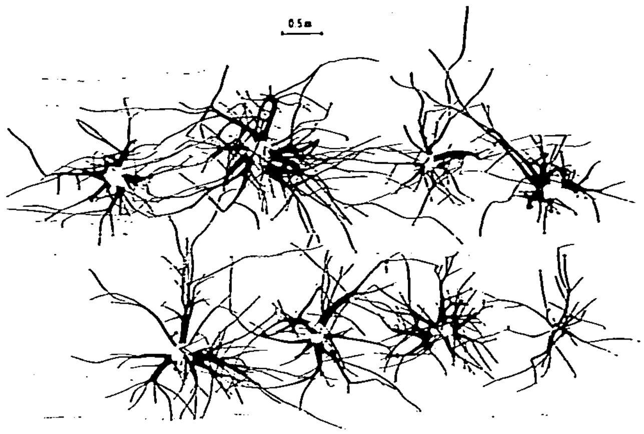

Figure 64 In situ *plan view of the root systems of 8 Sitka spruce 16 years old, Moffat Forest, Dumfriesshire. The soil, a peaty gley, had been ploughed with a single mouldboard spaced furrow plough before planting and the dotted lines indicate the position of furrows*

extent to which the growth of the root system of Sitka spruce *(Picea sitchensis)* could be described by similar rules.

Root systems were extracted carefully by hand from the soil and their orientation noted (Deans 1983) (Plate 12). They were transported to the laboratory and bolted below an aluminium framework fitted with a plumb-bob (Henderson 1981). With the apparatus, the length of each root segment and the position of each branching point, bend, fork and proliferation were measured on 4 complete root systems, and partial information taken from 3 other systems.

Statistical analyses of these measurements were made (Henderson *et al.* 1983a). First-order roots tended to be regularly distributed around the main stem. The orientation of all root segments was determined by their initial direction, either from the main stem or where they were formed as laterals, and by changes in direction at bends or branching points which tended to be alternatively clockwise and anticlockwise. Lateral branches subtended larger angles from their parent roots than the angles between the 2 arms of a root fork. Irrespective of the length of a root segment and the number of laterals arising from it, the points of origin were evenly distributed along the segment (Figure 65), and these appear as distinct bands of root origins separated by clear zones. The angles of lateral roots were generally more steeply downwards than those of their parents.

A simulation model was developed (Henderson *et al.* 1983b), which assumes that a root system consists of a number of first-order roots arising at the tree stem, a number of second-order roots originating on first order, and so on. The foundations of the model are statistical distributions, fitted individually for each order of roots for the occurrence of lengths of root segments, branching frequencies from these segments, and growth directions. In addition, it was found necessary to make special provision for the deviation of roots when they encountered the soil surface, naturally occurring boundaries between soil horizons of markedly different penetrability to roots, and the artificial boundary at the ditch made by ploughing at forest plantation.

Simulated root systems, eg Figure 66 i, seemed very similar in structure to the observed patterns of excavated roots (Figure 64), although the rigorous and exhaustive comparison of branching systems with complex shapes remains a problem. However, we were able to increase our understanding of the relative importance of different components of the root branching process by varying parameters from the values estimated from the data.

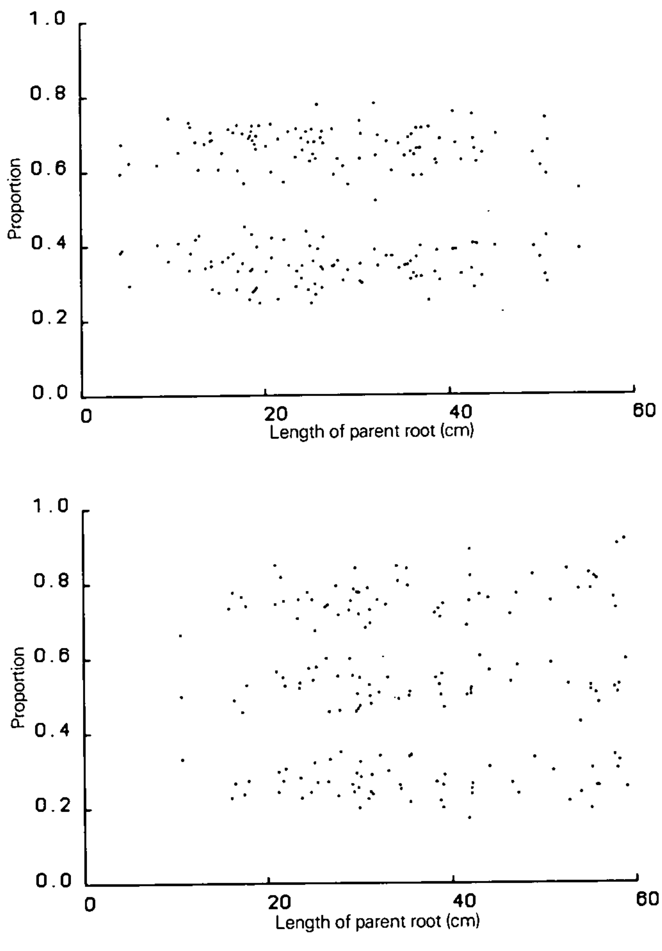

Figure 65 The distribution of lateral root origins, expressed as proportions of parent root length, for root segments of different total length: (i) for root segments with only 2 laterals, (ii) for root segments with only 3 laterals

For each relationship, a variance had been estimated, and it was these parameters, especially those governing root directions, which most influenced rooting patterns when they were varied. When all variances were set to zero, unrealistic, isotropic rooting patterns were produced which included neither sparsely nor densely occupied regions (Figure 66 ii). Note that, with all variances taken as zero, then all roots of the same order have the same number of bends and branching points and that these always alternate clockwise and anti-clockwise. The simulated root systems had either an anti-clockwise (Figure 66 ii) or a clockwise twist, depending upon the direction of the first bend and the first lateral on each first-order root. When the variances of the azimuth distributions were increased, the simulated systems were also unrealistic because correlation between root directions before and after bends or lateral branching was low. Many roots then turned backwards towards the stem, reducing the outward spread and causing the central region to become very densely occupied (Figure 66 iii).

In the model, the first-order roots are almost regularly spaced around the stem, with small deviations from perfect regularity. When the variance of the deviations

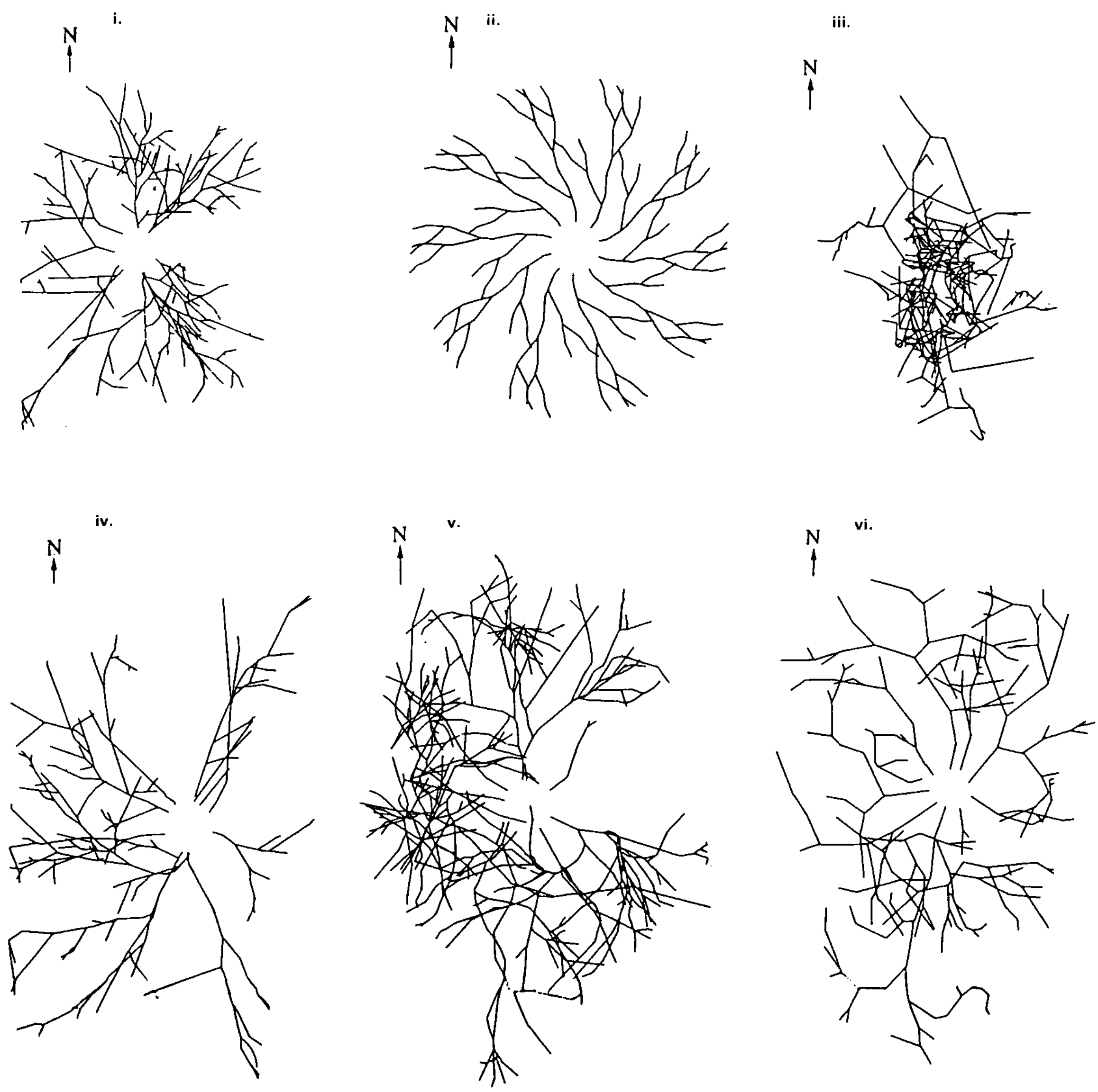

Figure 66 Structural root systems of Sitka spruce simulated under various conditions:
i. with all model parameters as fitted from the data
ii. with the variance of each modelled relationship set to zero
iii. with all variances twice their estimated values
iv. with the variance of the deviation of first-order root spacing around the stem set to 0·30 (radians)^2 rather than the fitted value of 0·07 (radians)^2
v. with bending and branching rates twice that of the fitted data
vi. with successive directional changes of roots set at random rather than with an alternate clockwise/anti-clockwise sequence

was allowed to increase, the simulated patterns became unconvincing, with larger sparse regions than the excavated systems (Figure 66 iv). When the parameters which determined the frequency of bending and branching were increased, root paths became irregular and very densely occupied regions were found in the simulations, although sparse regions could also occur (Figure 66 v). The tendency for azimuth changes to be alternately clockwise then anti-clockwise was necessary to produce rooting patterns similar to those observed. If direction changes were assumed to be independent of previous changes, then a high frequency of roots formed loops and turned back towards the stem (Figure 66 vi).

This work suggests that the structural root system of Sitka spruce does have an ordered morphology. Root growth is not entirely random and, in particular, the variances of angle and azimuth changes at bends and of new roots at forks are low. This ensures that roots grow outwards, away from the stem, with few roots forming loops. It is also important that lateral branches subtend large angles and azimuths to their parents and so occupy separate soil regions. We suggest that there is natural variation in the biological processes which comprise root growth, and that further work is necessary to see if genetic variation exists which could be exploited to produce a regular development of the root system. However, the most important sources of variation, and particularly those which may disrupt the all important directional patterns of root growth, are the natural and man-made obstacles in the soil, particularly the ridge and furrow system caused by ploughing.

E D Ford and J D Deans
(in co-operation with R Henderson and E Renshaw, Department of Statistics, University of Edinburgh)

References

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Deans, J. D. & Ford, E. D. 1983. Modelling root structure and stability. *Pl. Soil*, **71**, 189-195.

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Henderson, R., Ford, E. D., Renshaw, E. & Deans, J. D. 1983a. Morphology of the structural root system of Sitka spruce. 1. Analysis and quantitative description. *Forestry*, **56**, 121-135.

Henderson, R., Ford, E. D. & Renshaw, E. 1983b. Morphology of the structural root system of Sitka spruce. 2. Computer simulation of rooting patterns. *Forestry*, **56**, 137-153.

Post-fledging survival of young puffins in relation to early growth

Studies of several bird species (eg Manx shearwater, great tit, pied flycatcher and herring gull) have shown that young fledging early in the breeding season survive better than those fledging late. Also, in the Manx shearwater and Cape gannet, heavier young at fledging have a higher survival rate than light young. However, studies on other species (eg oystercatcher and guillemot) have failed to find such an effect. In puffins, the influence of fledging date and growth on post-fledging survival has been examined using data from a detailed study on the Isle of May NNR, Fife, carried out by Dr M P Harris.

In each year, 1974, 1975, 1977–79, at least 40 chicks were ringed in their burrows and then weighed every 4 days until near fledging when they were weighed daily. Information on subsequent survival was obtained by catching puffins in nest burrows and by mist-netting in 1976–82. Birds seen again are termed returners, while those not seen again are called non-returners and include birds which died and those that survived but were not caught subsequently. Non-returners and returners were compared in terms of the various parameters of the growth curve: (i) mean hatch date; (ii) mean weight at fledging; (iii) mean age at fledging; (iv) mean date of fledging; (v) mean peak weight; (vi) mean age when peak weight was attained; (vii) mean weight at 4-day intervals. Peak weights and ages were obtained from individual growth curves using quadratic interpolation on the observed peak weight and weights either side.

For a particular growth variable, the observations formed a 2-way cross-classification of years and type of bird (returner/non returner). The main statistical problem was the imbalance in the data with unequal numbers of birds in each class. Overall differences between returners and non-returners were tested, after allowing for annual variations, using a 2-way additive model with year and group effects estimated by the method of fitting constants. More complicated effects involving a variable difference were investigated by testing for interaction of years and type of bird, but none were found. This result is ecologically relevant because effects of early growth on subsequent survival might only be apparent in relatively poor years.

Estimated growth curves and overall differences between returners and non-returners are shown in Figure 67. The maximum overall difference in weight occurred at 33–36 days when returners were an estimated 4 g (SE = 5 g) heavier. The difference is not, however, statistically significant. No consistent differences in growth curves over the 5 years were observed. Similarly, no differences between specific growth parameters were detected. The estimated

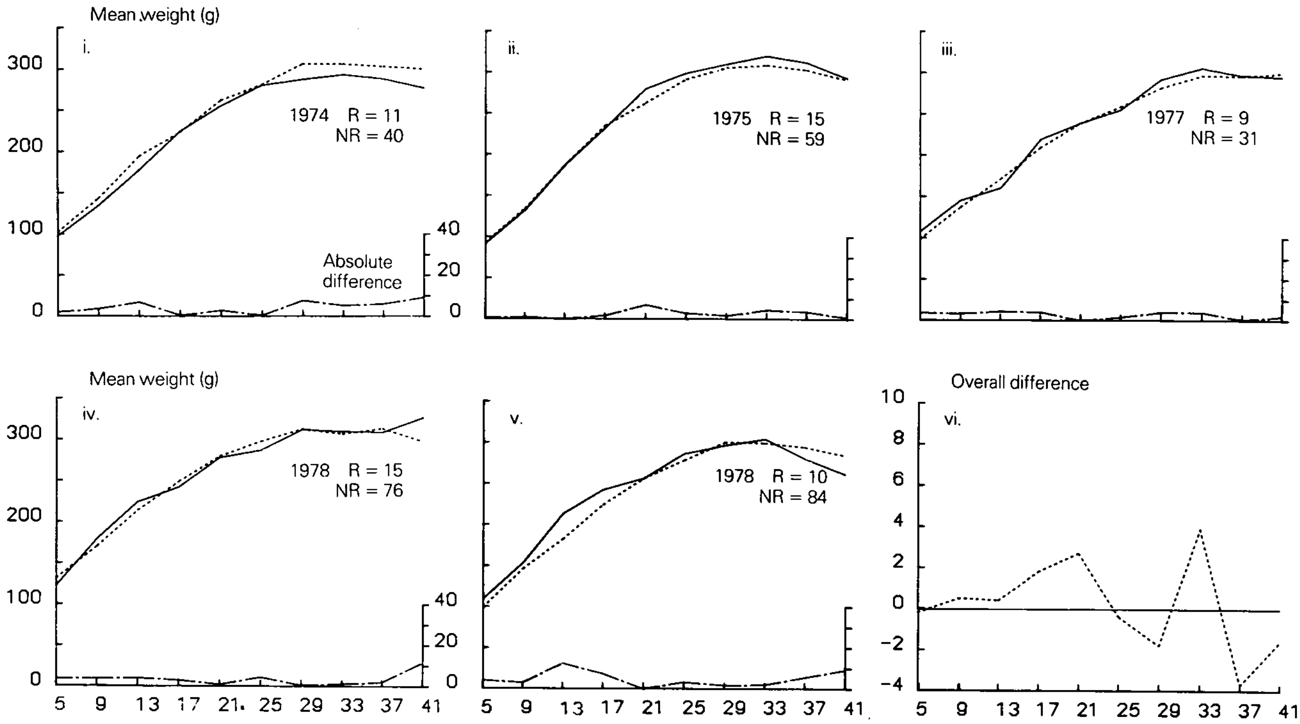

Figure 67 Mean weights of returners (——) and non-returners (. . .) at 4-day intervals. The absolute difference (—.—) is given, but note the different scale. Figure 67 (vi) shows the weighted average of annual differences returner minus non-returner ± SE (horizontal line = no difference)

values, returners minus non-returners, were as follows:

Peak weight (g)	−3·6 (SE = 3·8)
Age at peak (days)	0·1 (SE = 0·7)
Fledging weight (g)	−2·7 (SE = 3·9)
Age at fledge (days)	−0·1 (SE = 0·5)
Fledging date (days)	0·2 (SE = 0·7)

A more refined approach which allows for the contamination of the non-returners group by those survivors which evaded retrapping has been developed and is currently being applied to the data. It seems unlikely, however, that the conclusion of no demonstrable effect of early growth on subsequent survival will be affected.

P Rothery

Use of statistics in the Journal of Ecology

The sceptical attitude of the public to statistics is healthy and well-founded. Disraeli's famous aphorism is all too often exemplified in the popular media. Sadly, too, scientific papers are not above criticism. A number of recent studies on the use of statistics in scientific journals ranging from fisheries, medicine, ornithology, physiology and zoology have all shown that there is much scope for improvement.

Statistical methods are being used more and more. For example, in a review of the papers appearing in the first 50 years of the Journal of Animal Ecology, Taylor and Elliot (1981) showed the marked increase in the percentage of quantitative papers which included a statistical test. This was close to zero in the early volumes, but has been as high as 100% since Volume 47 appeared in 1981. The trend in ecology reflects a more general increase, and this raises difficulties for editors trying to safeguard against the misuse of statistics in their journals. The problems of statistical presentation of information in biological journals were discussed by biologists and biometricians at the 129th Ordinary Meeting of the Biometrics Society in December 1981. At that meeting, a review of the use of statistics in the Journal of Ecology was presented by P Rothery. The findings, summarized below, were far from satisfactory.

The survey covered the 58 papers appearing in a recent year of the Journal. Papers with one or more author in common were grouped into 48 studies, 32 of which contained some sort of statistical analysis. Papers were scrutinized, and abuses of statistics and the types of error committed were recorded. Occasions where statistical methodology could have been used more effectively were also documented and some suggestions for improvement were put forward.

Deficiencies were detected at both the design and analysis stages, the former being more serious as they are more difficult or even impossible to rectify once the observations have been collected. Out of the 32 studies, 75% could be criticized for one reason or another. Nineteen per cent of studies were deficient at the design stage; examples were lack of replication, biased sampling, and inappropriate bulking of samples. Forty-four per cent of studies contained errors in applying a statistical technique; examples were disregard for statistical independence, failure to allow for pairing or blocking in the data, and misuse of linear regression. Nineteen per cent of studies would have benefited from more use of statistics in fitting non-linear models, analysing proportions, model discrimination and the examination of variance heterogeneity.

The main conclusion from the survey is that, like many other journals, there is a need to improve the use of statistics in the Journal of Ecology. Ideally, this would be achieved by closer collaboration between the biologist and the biometrician in the design, analysis and interpretation of the study. The fact that so many errors were found in published papers calls for more careful scrutiny at the refereeing stage, but, while worthwhile, this is not a completely satisfactory remedy.

As a follow-up to this work, papers submitted to the Journal of Ecology are regularly refereed for their statistical content by P Rothery. So far, 24 papers have been scrutinized. Shortcomings ranged from the very serious—one study advocating a potentially misleading methodology—to relatively minor matters of presentation such as reporting spurious precision (mean = 2058·47, SE = 69·421).

In over 75% of papers, it was possible to make worthwhile suggestions for improvement in terms of description of design and analysis, the application of a statistical technique, or the presentation of results.

P Rothery

Reference

Taylor, L. R. & Elliot, J. M. 1981. The first fifty years of the Journal of Animal Ecology – with an author index. *J. Anim. Ecol.*, **50**, 951-971.

General properties of predictive population models in red grouse

Analyses of grouse shooting bags covering many decades have shown that bags exhibit cycles, that is a tendency for fluctuations to recur at intervals more regular than random, usually with a period of 6 years but in some areas as low as 4 and in others as high as 10.

A more recent analysis of a long run of population data from a detailed demographic study on Kerloch Moor in north-east Scotland led to empirical models which retrodicted past observed numbers successfully and gave reasonably good predictions for future numbers on a new study area (Watson *et al.* in press). A model for cocks produced regular oscillations which were slowly damped with a period of 9 years. The model embodied 2 intrinsic time-lagged components, but contained no extrinsic factors, such as harsh weather or predation, which occur naturally and result in poor breeding. In trying to reconcile the modelled oscillation at Kerloch with the irregular fluctuations in grouse bags and the variation in cycle length from area to area, general properties of the Kerloch model were studied, and in particular the effect of the sporadic occurrence of poor breeding was explored.

For the ith year, let Y_i be the natural logarithm of the population size in spring, S_i be the proportion of birds surviving over winter, and r_i the chick production ratio (ie the number of full grown cock chicks on the area in August divided by the number of adult cocks in spring). The relationships reported by Watson *et al.* (in press) are:

$$\log (1 + r_i) = 2{\cdot}84 - 0{\cdot}50\ Y_{i-2} \qquad (1)$$

and

$$\log S_i = 0{\cdot}29 - 0{\cdot}18\ Y_{i-1} \qquad (2)$$

which together produce the Kerloch model:

$$Y_{i+1} = 3{\cdot}13 + Y_i - 0{\cdot}18\ Y_{i-1} - 0{\cdot}50\ Y_{i-2} \qquad (3)$$

The irregular occurrence of poor breeding was mimicked by imposing poor years at random on the model. In a normal year, the chick production ratio was determined by equation 1, but in a poor year a reduced value was used. The effect was studied by imposing poor breeding, first, on average once in 5 years, and, second, on average once in 3 years. In these poor years, the chick production ratio was either fixed at 0·2 young cocks per spring cock or made variable at 0·1 or 0·2, with a probability of 0·3 and 0·7 respectively. For these 4 possible combinations, runs of 100 years were generated with 10 replicates. Each run was analysed by calculating both serial correlations and intervals between successive large peaks, excluding minor spikes which went up or down for only one year.

The results were similar for all 4 analyses, and those for variable poor breeding one year in 5 are given in Figure 68, which shows (i) one of the 10 replicates together with the unperturbed series; (ii) the correlogram for the original model run for 100 years with no poor breeding, together with the average serial correlations for the 10 replicates; and (iii) the pooled histogram of times between successive large peaks.

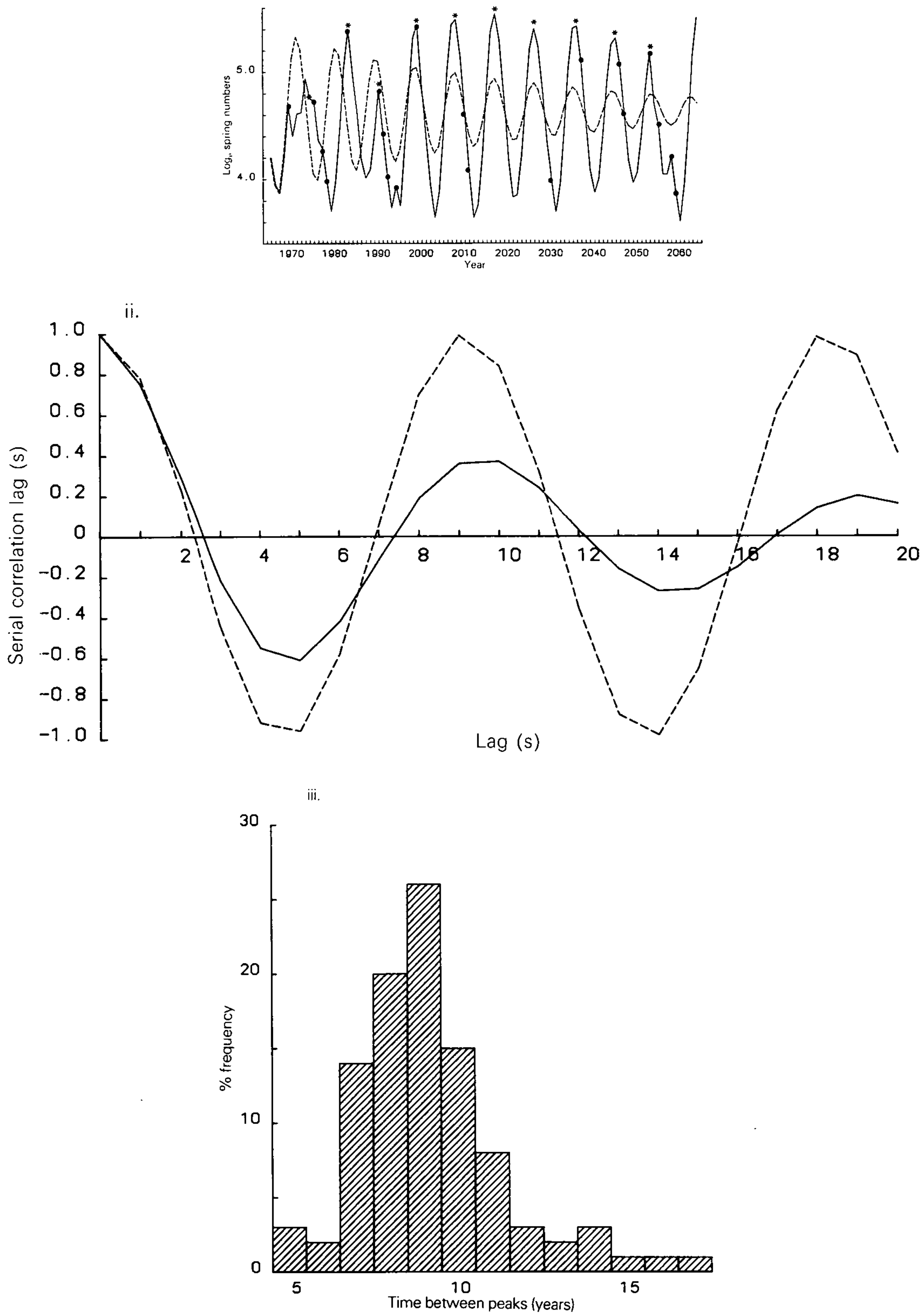

Figure 68 The effect of variable poor breeding occurring at random one year in 5 and producing 0·1 and 0·2 young cocks per spring cock, with probabilities of 0·3 and 0·7 respectively

i. ‑‑‑ undisturbed series

—— a typical perturbed run of 100 years

● indicates a poor year

** indicates a major peak*

ii. ‑‑‑ serial correlations for the undisturbed series

—— averaged over 10 perturbed runs

iii. histogram of the time between successive major peaks, pooled over the 10 runs he obvious damping of the undisturbed series was ot apparent in any of the perturbed sequences vhere the cycles were sustained by the environ- nental noise. The average correlogram was damped, s expected, but its turning points at 5, 9–10 and 4 years show that randomly occurring poor breeding ad no major effect on the modelled cycle length. he same conclusion is drawn from the histograms f the interval between successive large peaks, which aried between 5 and 17 years, with a modal value f 9 years and a mean of 9·2.

hanges in the cycle length of the oscillations can e achieved by altering the slope coefficients in quations 1 and 2. However, even quite large varia- ions in parameter values about the observed ones roduced relatively small changes in cycle length rom 8–10 years. Shorter periods, from 4–6 years, an be produced, but involve reducing the time lag n the model from 2 years to one.

Finally, it must be stressed that, although the models describe aspects of the form of the observed fluctu- ations, they do not establish underlying mechanisms. One possible cause of population cycles, postulated from detailed observations at Kerloch Moor, is changes in spacing behaviour and consequent rates of emigration at different densities and phases of the cycle. Present work is aimed at finding whether manipulations of current density alter spacing behaviour and if subsequent densities are as predicted by the model.

P Rothery

Reference

Watson, A., Moss, R., Rothery, P. & Parr, R. A. In press. Demographic causes and predictive models of population fluctuations in red grouse. *J. Anim. Ecol.*, **53**.

CULTURE CENTRE OF ALGAE AND PROTOZOA

General report

1. The collection

(Elspeth A Leeson, R. L. Swirski, Ann Asher, N C Pennick, Sheila F Cann and J P Cann)

Following the decision of NERC to increase the charge for cultures to the full economic cost, and to cease charging a reduced rate to educational estab- lishments in the UK, the numbers of orders for cultures declined markedly. In the first 2 months after imple- menting this decision (September and October 1983), only 248 cultures were sold, compared with 1141 in the same period of the previous year, a reduction of 80%. It is expected that sales will decline further as universities and schools have time to make alternative arrangements. This reduction has enabled more effort to be expended on the continuing process of improving the quality of material in the collection (see also Section 4.3 below). The number of axenic strains in the collection is now about 450, some 30% of the total holding. Some protozoa require food organisms and so cannot be made axenic.

Careful, selective 'culling' of uncharacterized and poorly documented material has led to the discarding of about 200 strains. The 35 strains of Bryophyta and the single angiosperm, *Wolffia*, have also been removed, and 12 strains of amoebae known or sus- pected to be human pathogens have been transferred to the London School of Hygiene and Tropical Medicine. On the other hand, about 90 new strains of well documented organisms of actual or potential genetic value have been added to the collection.

It is planned to establish a panel of honorary con- sultants, each expert in one or more fields of the Centre's interests, to advise on matters pertaining to the improvement of the stock, on acquisitions and deletions, and on research activities. Already the Centre has benefited from advice and visits by Mr G H M Jaworski, of the Freshwater Biological Association, and Professor A E Walsby and Ms Annette Bees, both of the University of Bristol.

2. Cryopreservation

(G J Morris, Glyn C Coulson and Ann Asher)

The genetic lability of organisms maintained by serial subculture *in vitro*, where they are subjected to intense selection pressures often entirely different from those experienced in nature, is well recognized. Because of this, increasing effort is being expended on achieving successful cryopreservation of the Centre's holdings, as this form of maintenance is the most stable available. However, this valuable asset is attained only if organisms are not subjected to drastic selection during the hazardous processes of freezing and thawing; it is thus the Centre's policy to rely on cryopreservation only when at least 50% of the preserved population is subsequently viable. Using a modification of the two-step freezing process developed previously, Dr Morris successfully cryo- preserved 142 strains of Cyanophyta (blue-green algae) during the year. A further modification of the process for use with trypanosomes is reported on pages 57–58.

In collaboration with a visiting worker, Dr B J Finkle (US Department of Agriculture), the efficiency of high molecular weight compounds such as hydroxy- ethyl starch (HES) and polyvinylpyrrolidone as cryoprotective additives, either singly or in combi- nation with conventional cryoprotectants, has been investigated using a cell wall-less mutant of *Chlamydomonas reinhardii* (strain CCAP 11/32 cw 15^+) as test organism. Preliminary results suggest that HES is a good protectant.

3. Data and information

(D F Spalding, Ann Asher and Geraldine Day)

Coding of book, journal and offprint references has continued and key-punching of 10 000 has been completed. The data have been transferred to magnetic tape storage on the IBM 3081D mainframe computer at the University of Cambridge Computer Laboratory. Computerized data on the naming and culture of nearly 2000 strains were set up in 1982, data on lost strains being omitted for the time being.

CCAP is also involved with other systems: we are collaborating with the Department of Trade and Industry in the creation of a UK biotechnology data base; and Mrs Asher represented CCAP at the European Culture Collection Curators Organization meeting in Paris, at which the feasibility of setting up a computerized EEC information system for micro-organism culture collections was discussed.

Meanwhile, we are incorporating archival data on lost strains and filling gaps in the information on our other strains as far as possible. Cumulative list of amendments to the 4th edition of the *CCAP Lis of strains* have been produced, including new entrie for about 200 mutants of *Chlamydomonas moewus* and *C. reinhardii*, new media, about 250 withdraw strains, 90 acquisitions and changes in method o maintenance.

4. Research

Some of the Centre's research work is describe elsewhere in this Report (pp 57–58, 78–80); othe projects are summarized briefly here.

4.1 Cryobiology

(G J Morris, K J Clarke, Elspeth A Leeson anc Glyn C Coulson)

Investigations of the biophysics and biochemistry o the effects of cold stress on unicellular algae, anc the mechanisms whereby certain algae tolerate sub-zero temperatures under natural conditions, are continuing. The cellular response defined as 'cold shock

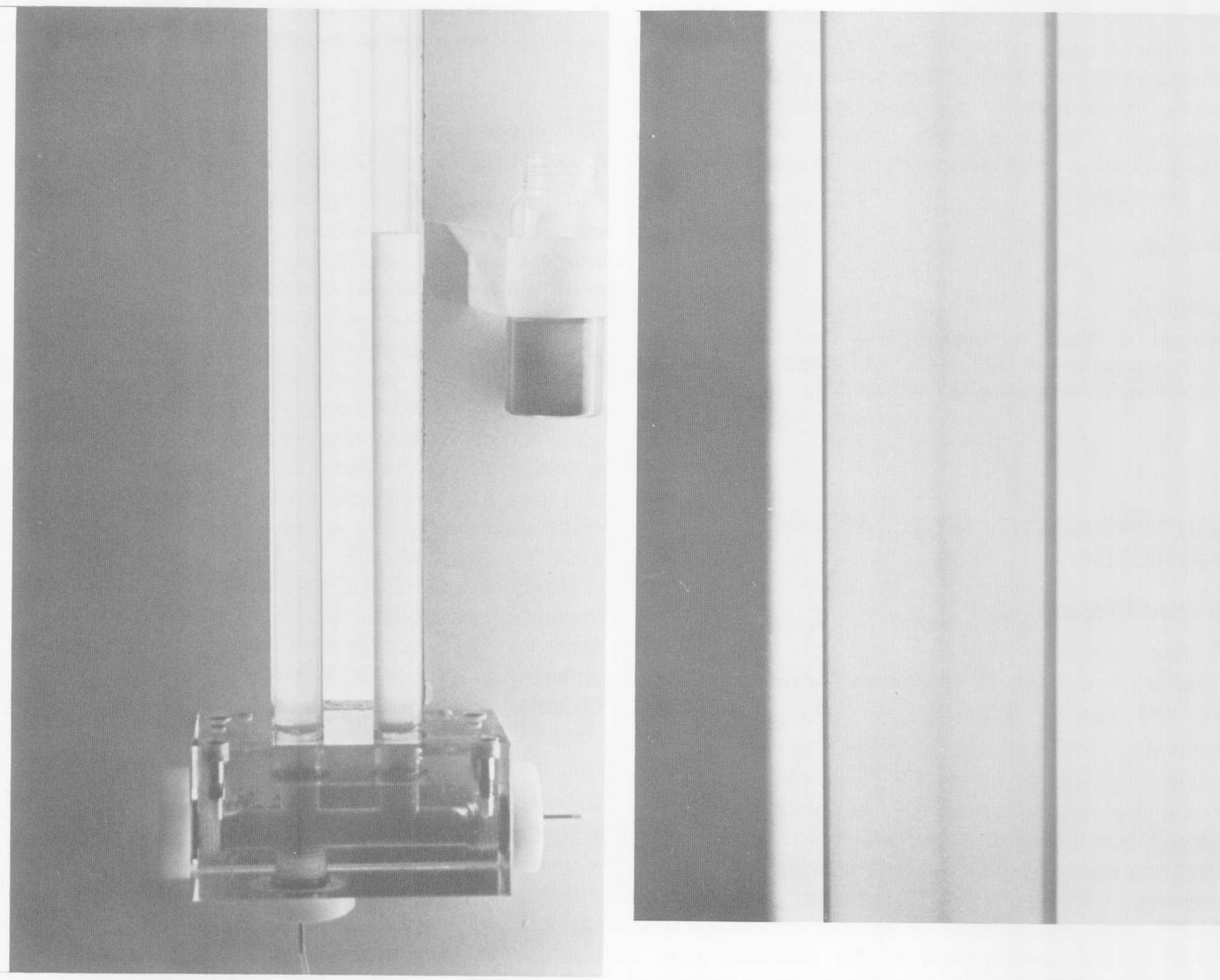

Plate 30 i. Apparatus for gyrotactic focusing of unicellular flagellates under joint influence of gravity and vorticity

ii. Enlarged section of part of glass column: the protists constitute the dark vertical central band (Photographs Prof J O Kessler, University of Arizona) s more widespread than previously thought; all cell ypes may be sensitive to it, if cooling is rapid enough nd the final temperature attained sufficiently low. Cold shock' and conventional 'chilling injury' may epresent extremes of a continuum and a unified ypothesis to account for both in terms of the ucleation patterns accompanying thermotropic vents within cellular membranes has been deve-oped.

Vork has commenced on a project to investigate the ffects of long-term preservation methods on the iability and stability of micro-organisms of industrial mportance, under contract with the Department of rade and Industry.

4.2 Taxonomy

F C Page is developing and applying a new approach o the taxonomy of naked, free-living amoebae (gymnamoebae). The present stage of work on marine species has been completed with the publi-cation by ITE of *Marine gymnamoebae* (Page 1983) and the preparation of 2 papers on new genera. In collaboration with the Institute of Cytology in Leningrad, light- and electron-microscopic and non-morphological characters (including nucleo-cytoplasmic compatibility of heterokaryotes produced by nuclear transplantation, serological reactions, nuclear DNA content and generation time) are being evaluated as taxonomic characters of large, *Amoeba proteus*-like organisms. In October, Dr Page visited Leningrad to work on this project with Dr Lydia V Kalinina and Dr S Yu Afon'kin. At the other end of the size spectrum of free-living gymnamoebae, Dr Page and Dr R L Blanton (University of Georgia, USA) are investigating the possible relationship between acrasid unicellular 'slime moulds' and small *Gymnamoebia*. Dr N B S Willumsen (Denmark) spent a week working with Dr Page.

Dr H Preisig (University of Zurich) once again visited CCAP to continue his collaborative study (with K J Clarke) on colourless flagellates, and Dr Margaret A Harper (Victoria University, Wellington, New Zealand) is analysing collections of diatoms from geological specimens.

4.3 Fluid dynamics and motile protists

Professor J O Kessler (University of Arizona), a Fulbright Fellow visiting the Cambridge University Department of Applied Mathematics and Theoretical Physics, is collaborating with N C Pennick and J P Cann to extend his practical and theoretical studies on the interaction between swimming behaviour of protists and imposed hydrodynamic forces. Two aspects are being investigated.

i. Gyrotactic focusing: when certain flagellated cells exhibiting asymmetric internal mass distribution are oriented jointly by gravity and the spatial variation of velocity (vorticity) of the fluid in which they swim, they tend to accumulate in specific regions. This effect can be used to concen-trate and separate cells (see Plate 30).
ii. Fibrous plug cell concentration: this simple tech-nique utilizes negative geotaxis and/or positive phototaxis to induce cells to swim upwards from a mixed or contaminated culture, through a fibrous plug (eg cotton wool), into clean medium. By this means, *Dunaliella parva* was separated from a fungal contaminant, and *D. tertiolecta* was separated from a mixture with *Chlorella marina*, and also concentrated from $0{\cdot}4 \times 10^6$ cells cm^{-3} to about 1×10^7 cells cm^{-3}.

4.4 Ecological parasitology

Over 700 blood samples have been collected as part of a continuing longitudinal study of *Hepatozoon* infection in *Sciuris carolinensis* (Baker & Kenward 1982); the data will be analysed with respect to sex, age and distribution of host. Prevalence of the infection is high (ca 80%), and developmental stages (schizonts) of the parasite have been found in the lungs of infected squirrels.

R A Gardner, a NERC CASE student jointly supervised by Professor D H Molyneux of Salford University, Dr R E Stebbings and Dr J R Baker, is studying the impact of parasitic infections on bat populations. He has evidence that at least one, *Babesia microti*, may be directly harmful by inducing anaemia. The development cycles of 2 species of *Trypanosoma*, which commonly infect bats in Britain, are also being studied (see also pp 78–80).

J R Baker

References

Baker, J. R. & Kenward, R. E. 1982. A protozoan blood parasite of squirrels. *Annu. Rep. Inst. terr. Ecol. 1981*, 105-106.

Page, F. C. 1983. *Marine gymnamoebae*. Cambridge: Institute of Terrestrial Ecology.

Projects

listed by Programmes as at 31 December 1983

The listing by Programmes also shows the numbers of other Programmes in which the project appears.

1 Forest and woodland ecology
2 Freshwater ecology
3 Rehabilitation of disturbed ecosystems
4 Management of natural and man-made habitats
5 Survey and monitoring
6 Airborne pollutants, including radionuclides
7 Plant physiology and genetics
8 Ecophysiology and pollution in animals
9 Plant population ecology
10 Autecology of animals
11 Animal species interactions and communities
12 Cycling of nutrients
13 Land resources and land uses
14 Chemical and technical sciences
15 Systems analysis and biometrics

Key for symbols against project numbers

@ Nature Conservancy Council contract
\+ Department of Environment contract
£ Other outside contract
! PhD or other student project
S Visiting worker project
* Project proposal not yet approved by Management Group

1. Forest and woodland ecology, the integrated effects (botanical and zoological) of woodland and forest management practices

Programme Leader: F T Last
Core Group: D Jenkins, E D Ford, A H F Brown

1	Semi-natural woodland classification	R G H Bunce	1		
9	Monitoring at Stonechest	J M Sykes	1		
17	Meathop Wood IBP study	J E Satchell	1		
61	Variation in growth of birch and sycamore	A F Harrison	1		
88	Plant establishment in shrubs	J Miles	1		
90	Birch on moorland soil and vegetation	J Miles		(1)	12
137	Sparrowhawk ecology	I Newton		(1 8)	10
246	Physical environment, forest structure	E D Ford	1	(7)	
359	Fibre yield of poplar coppice	M G R Cannell		(1)	7
367	The Gisburn experiment	A H F Brown		(1)	12
389	Management effect in lowland coppices	A H F Brown	1		
417	Silvicultural systems—N Ireland experiment	A H F Brown	1		
454	Monitoring of woodlands	J M Sykes	1		
463	Age class of amenity trees	J E Good	1		
479	Red deer in production forests	B W Staines	1	(10)	
483	Scottish deciduous woodlands	R G H Bunce		(1)	5
517	Primary productivity in woodlands	J N R Jeffers	1		
528	Red deer populations in woodland habitats	B Mitchell	1		
549	Monitoring in native pinewoods	J M Sykes	1		
568	Subcortical fauna in oak	M G Yates		(1 11)	10
574	Potential for fuel cropping in upland Wales	D I Thomas	1		
606	Grey squirrel damage and management	R E Kenward	1	(10)	
625£+	Effects of clear-felling in upland forests	M O Hill		(1)	12
633	Water level and vegetation change—Kirkconnell Flow	J M Sykes	1		
636	Song bird density and woodland diversity	D Jenkins		(1)	11
711	Tree growth and climate	A Millar		(1)	7
721	Dry matter in forests: world review	M G R Cannell	1		
746	Grazing in woodlands	T W Ashenden	1		
758*	Effects of grazing on woodland vegn diversity	J Dale	1		
773	Silviculture of respacing Sitka spruce	E D Ford	1		
793	Ecotypic variation in oak	M W Shaw	1		
794	Rhododendrons in Snowdonia	M W Shaw		(1)	4
820	Regional aspects of forest dynamics in Europe	P Ineson	1	(12)	
839	Assessing pressures at Pipar, Nepal	N Picozzi	1		
852*	Impact of herbivores on vegetation in pinewoods	J M Sykes	1		
862	Population ecology of pine beauty moth	A D Watt		(1)	10

2. Freshwater ecology, with special reference to synoptic limnology and the interactions between flora and fauna

Programme Leader: J P Dempster
Core Group: I Newton, P S Maitland, I R Smith

116	Freshwater survey of Shetland	P S Maitland	2	(5)	
117	Freshwater survey of Great Britain	P S Maitland	2	(5)	
123	Zoobenthos at Loch Leven	P S Maitland	2		
124	Distribution and biology of fish in GB	P S Maitland		(2)	5

289	Residues and effects of pollutants	F Moriarty		(2)	8
481	Monitoring and chemistry of aquatic pollutants	K R Bull	2	(8)	
527	Long-term changes in zooplankton	L May	2	(11)	
577	Predation of freshwater zooplankton	D H Jones	2	(11)	
584	Nutrient loading, phytoplankton and eutrophication	A E Bailey-Watts	2	(5 11)	
585	Diatom ecology	A E Bailey-Watts	2		
586	Freshwater phytoplankton periodicity	A E Bailey-Watts	2		
609+	Biological classification of UK rivers	D Moss	2	(5)	
642	Physics of freshwater systems	I R Smith	2		
644	Breeding success and survival in the common toad	C J Reading		(2)	10
676	Ecology of lampreys in Loch Lomond	P S Maitland		(2)	10
694	Zooplankton communities in freshwater lakes	D H Jones	2	(11)	
698	Zooplankton population dynamics	L May	2	(11)	
705	Impact of barytes mine project	P S Maitland	2		
739	Life history of the common frog	C P Cummins		(2 10)	8
765	Ecology of the heron	M Marquiss		(2 8)	10
797	Effects of acid rain on fresh water	K R Bull		(2)	6
833	Fish farms: mass balance and pollutants	I R Smith	2		
837£*	Fish populations and acid precipitation	P S Maitland		(2)	6
847*	Hydroclimate in rivers and lakes	I R Smith	2		
863	Fourth international rotifer symposium	L May	2		
866*	Aerial remote sensing of Lochs Leven, Lomond, Tay	A A Lyle	2	(5)	
870*	Mixing and spatial variation in lakes	I R Smith	2		
871*	River condition scale	I R Smith	2		

3. Rehabilitation of disturbed ecosystems, and creation of biologically rich habitats from scratch

Programme Leader: J P Dempster
Core Group: B N K Davis, T C E Wells

102	Mountain vegetation populations	N G Bayfield	3		
242@	Establishment of herb-rich swards	T C E Wells	3		
265	Regeneration on lowland heaths	S B Chapman		(3)	4
360£	Tree planting on opencast sites	J E Good	3		
408+	Arboriculture: selection	F T Last	3		
500	Recolonization by spiders on Hartland Moor	P Merrett		(3 4)	11
511	Landscaping at Swindon	F T Last	3		
567	Coastal dune management guide	D S Ranwell	3		
690	Plant succession in a limestone quarry	B N K Davis	3		
693	Plant species establishment in grassland	L A Boorman	3	(4)	
707	Plant establishment in woodland	L A Boorman	3	(4)	
726	Restoration of heathland vegetation	R H Marrs		(3)	4
819£	Creation of butterfly habitats on landfill site	B N K Davis	3		
834£*	Revegetation after disturbance	J Miles	3		
848	Mosses and indigenous plant litter in bare ground	N G Bayfield	3		
859£	Restoration of heathlands	N R Webb	3		

4. Management of natural and man-made habitats, but excluding forests and disturbed sites, effects of management, including grazing, cutting ... on plants, animals and soils

Programme Leader: F T Last
Core Group: M G Morris, M D Hooper, C Milner

78	Management of sand dunes in Wales	D G Hewett	4		
89	*Calluna-Molinia-Trichophorum* management	J Miles	4		

92	Grazing intensities causing change	D Welch	4	
95	Importance of dung for botany change	D Welch	4	
148	Soil erosion on Farne Islands	M Hornung	4	
158	Community processes (physiology)	D F Perkins		(4 7) 12
227	Sheep grazing on chalk grass flora	T C E Wells	4	
228	Effect of cutting on chalk grassland	T C E Wells	4	
230	Grassland management—invertebrates	M G Morris	4	(11)
243	Scrub succession at Aston Rowant NNR	L K Ward	4	
265	Regeneration on lowland heaths	S B Chapman	4	(3)
296	Scrub management at Castor Hanglands	L K Ward	4	
374	Sand dune ecology in East Anglia	L A Boorman	4	
457	Grazing models	C Milner		(4) 15
467	Roadside studies	T W Parr	4	
500	Recolonization by spiders on Hartland Moor	P Merrett		(3 4) 11
573+	Amenity grass—stage 2	M D Hooper	4	
599	Bracken and scrub control on lowland heaths	R H Marrs	4	
602	Modelling sports turf wear	T W Parr	4	(15)
634	Field plot survey—Monks Wood	R Cox	4	
650	Amenity grass irrigation	M D Hooper	4	
665	Coastal management	D S Ranwell	4	
666	Coastal publications	D S Ranwell	4	
674£	Plant species for energy in Great Britain	T V Callaghan	4	
693	Plant species establishment in grassland	L A Boorman		(4) 3
703	Vegetation change at Dungeness and Orfordness	R M Fuller	4	
707	Plant establishment in woodland	L A Boorman		(4) 3
718@	Impact of land drainage on wildlife	J Sheail	4	
726	Restoration of heathland vegetation	R H Marrs	4	(3)
744	Effects of grazing in Snowdonia	M O Hill	4	
769£	Bracken biofuel potential for energy in Wigtown	T V Callaghan	4	
772	Japanese knotweed control	R Scott	4	
776	Long-term studies of vegn change at Moor House	R H Marrs	4	
794	Rhododendrons in Snowdonia	M W Shaw	4	(1)
796	Poole harbour salt marshes	A J Gray	4	
835£	ITE/UCL EIA Lake Ichkeul: plant demography	T W Parr		(4 15) 9
836£	ITE/UCL EIA Lake Ichkeul: remote sensing survey	R M Fuller		(4) 5
838£	Sizewell ecological survey	D S Ranwell	4	
853£	Falkland Islands airport ecology impact	J Miles	4	(5)
858£*	EIA of drainage schemes	M D Hooper	4	

5. Survey and monitoring of plant and animal distributions and abundance

Programme Leader: J P Dempster
Core Group: P S Maitland, M O Hill, B K Wyatt

116	Freshwater survey of Shetland	P S Maitland		(5) 2
117	Freshwater survey of Great Britain	P S Maitland		(5) 2
124	Distribution and biology of fish in GB	P S Maitland	5	(2)
132	Monitoring in the Cairngorms	A Watson	5	
165	N Wales bryophyte recording	M O Hill	5	
181@	Birds of prey and pollution	I Newton		(5) 8
204@	Assessing butterfly abundance	E Pollard		(5) 10
208@	Botanical data bank	C D Preston	5	
209@	Vertebrate recording schemes	H R Arnold	5	
232	Butterfly studies at Porton Range	M G Morris	5	
309	Phytophagous insects data bank	L K Ward		(5) 11

340	Survey of Scottish coasts	D S Ranwell	5	
405	Fauna of pasture woodlands	P T Harding		(5) 11
406	Distribution and ecology of non-marine Isopoda	P T Harding	5	
424	Ecological survey of Britain	R G H Bunce		(5) 13
466	Ecology of railway land	C M Sargent	5	
469	Scottish invertebrate survey	R C Welch	5	
470	Upland invertebrates	A Buse		(5) 11
483	Scottish deciduous woodlands	R G H Bunce	5	(1)
529	Biological data bank	D M Greene	5	
534	National land characterization	D F Ball		(5) 13
557@	Terrestrial and freshwater invertebrate surveys	P T Harding	5	
565	Bibliography of Shetland	N Hamilton	5	
566	Islands: biogeographic analysis	N Hamilton	5	
584	Nutrient loading, phytoplankton and eutrophication	A E Bailey-Watts		(5 11) 2
591	Terrestrial Environment Information System	B K Wyatt	5	(15)
609+	Biological classification of UK rivers	D Moss		(5) 2
615	Heathland invertebrates	N R Webb		(5) 11
656@	Marine invertebrate recording schemes	H R Arnold	5	
657	Biological Records Centre—general	P T Harding	5	
671	Analysis of BRC data	G L Radford	5	
684	Mapping broadland vegetation with aerial photos	R M Fuller	5	
743	Railway resource monitoring	C M Sargent	5	
751	National survey of fluoride in predatory birds	D C Seel		(5) 6
760£	EEC ecological mapping	B K Wyatt		(5) 13
761£	EEC remote sensing	B K Wyatt		(5) 13
771	Chemical data bank (Monks Wood)	K R Bull		(5 8) 14
774	Long-term trends in upland vegetation	J Dale	5	
795	Standard procedures for recording data	D M Greene	5	(15)
799	Dutch elm disease resurvey	J Wilson	5	
806	Assessment of LANDSAT value for land use	B K Wyatt		(5) 13
807	Ecobase	B K Wyatt	5	
822	Landsat classification and vegn survey of Bhutan	C M Sargent	5	(13)
836£	ITE/UCL EIA Lake Ichkeul: remote sensing survey	R M Fuller	5	(4)
850£	Pembrokeshire NP air photo interpretation	D F Ball	5	(13)
853£	Falkland Islands airport ecology impact	J Miles		(5) 4
866*	Aerial remote sensing of Lochs Leven, Lomond, Tay	A A Lyle		(5) 2

6. Airborne pollutants, including radionuclides, their pathways through and effects on terrestrial ecosystems

Programme Leader: F T Last
Core Group: S E Allen, I A Nicholson, D F Perkins

160£	Fluorine pollution studies	D F Perkins	6	
380	Monitoring of atmospheric SO_2 at Devilla Forest	I A Nicholson	6	
426	Preparation of sulphur review document	I A Nicholson	6	
452	Study of precipitation	J W Kinnaird	6	
453	SO_2 dry deposition in Scots pine forest	I A Nicholson	6	
491	Radiochemical development	J A Parkinson		(6) 14
524	Fluoride in predatory mammals	K C Walton	6	
525	Fluoride in predatory birds	D C Seel	6	
526	Biological monitoring in Forth Valley	B G Bell	6	
553£+	Radionuclide pathways	S E Allen	6	

556	Estimation in acid rain	K H Lakhani	6		
669	Interaction of grazing and air pollution	T W Ashenden	6		
710	Airborne pollutants and Scots pine	J N Cape	6		
751	National survey of fluoride in predatory birds	D C Seel	6	(5)	
753	Fluoride and magpies	D C Seel	6	(10)	
756	Fluoride pathways in invertebrates	A Buse	6		
790£+	Effects of polluted atmospheres on crops	I A Nicholson	6		
791	Effect of acid rain on Sitka spruce	D Fowler	6		
797	Effects of acid rain on fresh water	K R Bull	6	(2)	
809	Fluoride toxicology	D Osborn		(6)	8
829!	Physiological effect of SO_2 and NO_x on silver birch	E Wright	6		
830	Rainfall acidity and gas transport	J N Cape	6		
837£*	Fish populations and acid precipitation	P S Maitland	6	(2)	
841	Gisburn project	I A Nicholson	6		
845£*	Effects of acid rain on vegetation in Wales	T W Ashenden	6		
849!*	Distribution of radionuclides in soils	F R Livens	6		

7. Plant physiology and genetics, responses of native and introduced species to environmental factors

Programme Leader: F T Last
Core Group: M H Unsworth, T V Callaghan

158	Community processes (physiology)	D F Perkins		(4 7)	12
245	Genetics of *Betula* nutrition	J Pelham	7	(9)	
246	Physical environment, forest structure	E D Ford		(7)	1
266	Root dynamics of *Calluna vulgaris*	S B Chapman		(7)	12
359	Fibre yield of poplar coppice	M G R Cannell	7	(1)	
410	Tundra plants (bryophytes)	T V Callaghan		(7)	9
447	Freshwater and marine amoebae	F C Page	7		
449	Preservation of cultures	G J Morris	7		
512	National collection of birch	J Pelham	7	(9)	
575	Regeneration and growth of bracken rhizomes	R E Daniels		(7)	9
674£	Plant species for energy in Great Britain	T V Callaghan		(7)	4
702	Selection of frost-hardy trees	M G R Cannell	7		
711	Tree growth and climate	A Millar	7	(1)	
717	Birch variation and environmental differences	J Pelham	7	(9)	
748	Temperature limits of growth for Chlamydomonas	E A Leeson	7		
750	Domestication of tropical hardwoods	R R B Leakey	7		
767	Formation of cones by lodgepole pine	K A Longman	7		
770	Evaluation of conifer clones and progenies	M G R Cannell	7		
785	Cultivation of freshwater algae	E A Leeson	7		
786	Cultivation of marine algae	N C Pennick	7		
787	Cultivation of free-living protozoa	J P Cann	7		
801	Radial growth of Sitka spruce roots	J D Deans	7		
805	Effects of mycorrhizas on assimilation	E J White	7		
815	Control of wood density in Sitka spruce	E D Ford	7		
816	IUFRO Conference 1984: trees as crop plants	M G R Cannell	7		
831	Modelling of transpiration in Sitka spruce	R Milne	7		
842!	The physiology of cones in *Pinus contorta*	C J Couper	7		
851£*	Viability and stability of industrial macro-organisms	G J Morris	7		
861	Characterization of sheathing mycorrhiza	A Crossley	7		
865*	Mycorrhizal toadstools in coniferous planting	J Wilson		(7)	12

8. Ecophysiology and pollution in animals, covering broadly the same fields as the former Subdivision of Animal Ecology

Programme Leader: J P Dempster
Core Group: I Newton, R Moss

129	Red grouse and ptarmigan populations	A Watson	(8) 10
137	Sparrowhawk ecology	I Newton	(1 8) 10
181@	Birds of prey and pollution	I Newton	8 (5)
199	Avian reproduction and pollutants	S Dobson	8
255	Ecology of *Myrmica* species	G W Elmes	(8 10) 11
256	Protein electrophoresis	B Pearson	8
262	Digestive enzymes	A Abbott	8
289	Residues and effects of pollutants	F Moriarty	8 (2)
393	Isolation effects in butterfly populations	J P Dempster	(8 10) 11
444	Endocrine lesions in birds	S Dobson	8
455	Heavy metals in avian species	D Osborn	8
461@	Puffins and pollutants	M P Harris	8 (10)
481	Monitoring and chemistry of aquatic pollutants	K R Bull	(8) 2
559	Ecology of reproduction in the wild rabbit	I L Boyd	8
624	Population genetics	P J Bacon	(8) 10
630	Stress in birds	A Dawson	8
697	Pesticides and wildlife: historical perspective	J Sheail	8
728	Kestrels in farmland	A Village	(8) 10
737	Population genetics of *Pardosa monticola* spiders	R G Snazell	8
739	Life history of the common frog	C P Cummins	8(2 10)
759+	Chemicals in the terrestrial environment	S Dobson	8
763£	Data profiles on chemicals	S Dobson	8
765	Ecology of the heron	M Marquiss	(2 8) 10
771	Chemical data bank (Monks Wood)	K R Bull	(5 8) 14
809	Fluoride toxicology	D Osborn	8 (6)
810	Lead poisoning in birds	M C French	8
811	Foraging and reserve storage in red and-grey squirrels	R E Kenward	8 (11)
812	Grouse aviary	R Moss	8 (10)

9. Plant population ecology: the biology of individuals and populations, including a consideration of gene flow

Programme Leader: F T Last
Core Group: S B Chapman, A J Gray

82	Seed produced by montane plants	G R Miller	9
225	Population studies on orchids	T C E Wells	9
245	Genetics of *Betula* nutrition	J Pelham	(9) 7
269	Autecology of *Gentiana pneumonanthe*	S B Chapman	9
295	Survey of juniper in N England	L K Ward	9
346	Genecology of grass species	A J Gray	9
365	Competition between grass species	H E Jones	9
410	Tundra plants (bryophytes)	T V Callaghan	9
411	Taxonomy of bryophytes	B G Bell	9 (7)
508	Botanical variation in elm	J N R Jeffers	9
512	National collection of birch	J Pelham	(9) 7
575	Regeneration and growth of bracken rhizomes	R E Daniels	9 (7)
576	Isoenzyme studies in *Sphagnum*	R E Daniels	9
649	Demographic genetics of *Agrostis setacea*	A J Gray	9
717	Birch variations and environmental differences	J Pelham	(9) 7

742	Population fluctuations in annual legumes	C D Preston	9
775	Ecology of Arctic alpines in Snowdonia	C Milner	9
783	Interactions between mosses and vascular plants	N G Bayfield	9
835£	ITE/UCL EIA Lake Ichkeul: plant demography	T W Parr	9(4 15)
846*	Influence of events on population growth	I R Smith	(9 10) 15
857*	Rare grass species	A J Gray	9

10. Autecology of animals, with particular reference to population management for conservation and pest control

Programme Leader: J P Dempster
Core Group: I Newton, E Pollard, A Watson

54	Red deer ecology on Rhum	V P W Lowe	10
67	Prey selection in redshank	J D Goss-Custard	10
104	Distribution and segregation of red deer	B W Staines	10
111	Population dynamics of red deer at Glen Feshie	B Mitchell	10
129	Red grouse and ptarmigan populations	A Watson	10 (8)
130	Management of grouse and moorlands	A Watson	10
131	Golden plover populations	A Watson	10
137	Sparrowhawk ecology	I Newton	10(1 8)
193	Stone curlew and lapwing	N J Westwood	10
202	The Roman snail	E Pollard	10
204@	Assessing butterfly abundance	E Pollard	10 (5)
255	Ecology of *Myrmica* species	G W Elmes	(10 11) 8
273	Ecology of *S. magnus* and other mites	N R Webb	10(11)
291@	Population ecology of bats	R E Stebbings	10
292@	Specialist advice on bats	R E Stebbings	10
386	Behaviour and dispersion of badgers	H Kruuk	10
393	Isolation effects in butterfly populations	J P Dempster	(10) 11
400	The large blue butterfly	J A Thomas	10(11)
403	The black hairstreak butterfly	J A Thomas	10
404	The brown hairstreak butterfly	J A Thomas	10
441	Oystercatcher and shellfish interaction	J D Goss-Custard	(10) 11
442	Ecology of capercaillie	R Moss	10
461@	Puffins and pollutants	M P Harris	(10) 8
479	Red deer in production forests	B W Staines	(10) 1
499	Taxonomic studies for mammalian autecology	V P W Lowe	10
509	Wood white butterfly population ecology	E Pollard	10
543	Population ecology of the red squirrel	V P W Lowe	10
568	Subcortical fauna in oak	M G Yates	10(1 11)
606	Grey squirrel damage and management	R E Kenward	(10) 1
624	Population genetics	P J Bacon	10 (8)
644	Breeding success and survival in the common toad	C J Reading	10 (2)
660	Adonis blue populations	J A Thomas	10
676	Ecology of lampreys in Loch Lomond	P S Maitland	10 (2)
687	Radio location and telemetry development	T Parish	10
692	Goshawk population dynamics	R E Kenward	10
709	Techniques for rearing the large blue butterfly	J C Wardlaw	10
715£	Shetland otters	D Jenkins	10
722	The habitat ecology of the spider *Eresus niger*	P Merrett	10
728	Kestrels in farmland	A Village	10 (8)
734	Estimation of seabird numbers	M P Harris	10
735	Oystercatcher population dynamics	M P Harris	10
739	Life history of the common frog	C P Cummins	(2 10) 8

753	Fluoride and magpies	D C Seel	(10) 6
764£	Habitat requirements of black grouse	N Picozzi	10
765	Ecology of the heron	M Marquiss	10(2 8)
777	Estimation of population parameters	K H Lakhani	(10) 15
789	Food resources limitation in orange-tip butterfly	J P Dempster	10
808	Effect of food on home range size in otters	H Kruuk	10
812	Grouse aviary	R Moss	(10) 8
818	Increasing guillemot populations	M P Harris	10
828	Rabbit foraging, dispersal and mortality	R E Kenward	10
846*	Influence of events on population growth	I R Smith	(9 10) 15
860*	The ecology of trypetid flies on burdock	N Straw	10(11)
862	Population ecology of pine beauty moth	A D Watt	10 (1)

11. Animal species interactions and communities, including studies of the interactions between species (eg competition, predator/prey) and between fauna and their habitats (eg effects of area and isolation)

Programme Leader: J P Dempster
Core Group: M G Morris, J D Goss-Custard, H Kruuk, D Jenkins, J R Baker

230	Grassland management—invertebrates	M G Morris	(11) 4
252	Hartland Moor NNR survey	A Abbott	11
255	Ecology of *Myrmica* species	G W Elmes	11 (8 10)
270	Distributional studies on spiders	P Merrett	11
309	Phytophagous insects data bank	L K Ward	11 (5)
370	Exp. reduction of inter-species competition in ants	B Pearson	11
393	Isolation effects in butterfly populations	J P Dempster	11 (10)
400	The large blue butterfly	J A Thomas	(11) 10
405	Fauna of pasture woodlands	P T Harding	11 (5)
407	British Staphylinidae (Coleoptera)	R C Welch	11
441	Oystercatcher and shellfish interaction	J D Goss-Custard	11 (10)
470	Upland invertebrates	A Buse	11 (5)
500	Recolonization by spiders on Hartland Moor	P Merrett	11(3 4)
527	Long-term changes in zooplankton	L May	(11) 2
568	Subcortical fauna in oak	M G Yates	(1 11) 10
569	Insect fauna of *Helianthemum* and *Genista*	B N K Davis	11
577	Predation of freshwater zooplankton	D H Jones	(11) 2
584	Nutrient loading, phytoplankton and eutrophication	A E Bailey-Watts	(5 11) 2
612	Analysis of common birds census	M D Mountford	11
615	Heathland invertebrates	N R Webb	11 (5)
621	Models of rabies epidemiology	P J Bacon	(11) 15
636	Song bird density and woodland diversity	D Jenkins	11 (1)
641	Invertebrate fauna of *Nothofagus* and *Quercus*	R C Welch	11
694	Zooplankton communities in freshwater lakes	D H Jones	(11) 2
698	Zooplankton population dynamics	L May	(11) 2
708!	Structure of spider communities on heathland	P J Hopkins	11
723	Characterization of Trypanosomes from bats	J R Baker	11
724	Protozoan parasites of wild British animals	J R Baker	11
811	Foraging and reserve storage in red and grey squirrels	R E Kenward	(11) 8
821*	Modern agriculture and wildlife	T Parish	11
826	Invertebrate fauna of native and introduced broadleaves	R C Welch	11

827	Weevil study	M G Morris	11
854£	Competition between red and roe deer in forests	M Hinge	11
856	Agricultural symposium	D Jenkins	11
860*	The ecology of trypetid flies on burdock	N Straw	(11) 10
867!*	Parasitic diseases of bats	R A Gardener	11

12. Cycling of nutrients: the movement and utilization of nutrients

Programme Leader: F T Last
Core Group: O W Heal, M Hornung, J Miles

90	Birch on moorland soil and vegetation	J Miles	12 (1)
153	Mineralogical methods	A Hatton	12
158	Community processes (physiology)	D F Perkins	12(47)
266	Root dynamics of *Calluna vulgaris*	S B Chapman	12 (7)
364	Early growth of trees	A F Harrison	12
367	The Gisburn experiment	A H F Brown	12 (1)
431	Soil change through afforestation	P J A Howard	12
438	Ecology of *Mycena galopus*	J C Frankland	12
589	Microbial characteristics in soils	P M Latter	12
594+£	Geochemical cycling	M Hornung	12
625£+	Effects of clear-felling in upland forests	M O Hill	12 (1)
645	Effects of soil chemistry on decomposition	D D French	12
654	Status of mycorrhizas in the soil ecosystem	J Dighton	12
695	Effects of mycorrhizas on tree growth	F T Last	12
712	Organic matter quality and tree growth	O W Heal	12
714	Role of forest vegetation in pedogenesis	P J A Howard	12
738!	Effect of altitude on grassland at Moor House	J C Hatton	12
820	Regional aspects of forest dynamics in Europe	P Ineson	(12) 1
824	Nitrogen and phosphorus cycling in forest soils	A F Harrison	12
865*	Mycorrhizal toadstools in coniferous planting	J Wilson	12 (7)

13. Land resources and land uses, habitat characteristics, their inter-relations and value in site assessments and resource management

Programme Leader: F T Last
Core Group: J N R Jeffers, O W Heal, D F Ball

2	Meteorological factors in classification	E J White	13
4	Soil classification methods	P J A Howard	13
163	Ordination and classification methods	M O Hill	13
377	Historical aspects of environmental perception	J Sheail	13
424	Ecological survey of Britain	R G H Bunce	13 (5)
471	Soils of Upper Teesdale	M Hornung	13
534	National land characterization	D F Ball	13 (5)
541	Marginal land in Cumbria	C B Benefield	13
554	Cumbria land classes and soil types	J K Adamson	13
561	Soil fertility	M Hornung	13
700+	Ecological guidelines for locational strategies	G L Radford	13
745	Land availability for wood energy plantations	R G H Bunce	13
747£	Highland region land classification	R G H Bunce	13
760£	EEC ecological mapping	B K Wyatt	13 (5)
761£	EEC remote sensing	B K Wyatt	13 (5)
781	Land use changes of chalk aquifers	R M Fuller	13

806	Assessment of LANDSAT value for land use	B K Wyatt	13 (5)	
822	Landsat classification and vegn survey of Bhutan	C M Sargent	(13)	5
844£	Potential for wood production on coal measures	R G H Bunce	13	
850£	Pembrokeshire NP air photo interpretation	D F Ball	(13)	5

14. Chemical and technical sciences, as a service to ITE

Programme Leader: J N R Jeffers
Core Group: S E Allen, M Hornung, I H Rorison

484	Chemical technique development	D Roberts/ P Freestone	14
485	Chemical support studies	S E Allen	14
486	Engineering development	G H Owen	14
487	Microprocessor development studies	C R Rafarel	14
489	Glasshouse and nursery maintenance	R F Ottley	14
490	Photographic development	P G Ainsworth	14
491	Radiochemical development	J A Parkinson	14 (6)
771	Chemical data bank (Monks Wood)	K R Bull	14(58)
788	Electron microscopy of algae and protozoa	K J Clarke	14
804	Effect of changing environment on plant growth	E J White	14
832	Operation of the Rivox field site	R Milne	14
864*	Sunday Telegraph magazine article	J A Parkinson	14

15. Systems analysis and biometrics

Programme Leader: J N R Jeffers
Core Group: C Milner, M D Mountford, E D Ford

306	Statistical analysis of spatial patterns	P Rothery	15	
307	Index of eggshell thickness	P H Cryer	15	
376	Statistical training	C Milner	15	
402	Biometrics advice to NERC	M D Mountford	15	
434	ITE computing services	C Milner	15	
457	Grazing models	C Milner	15 (4)	
503	Development of systems analysis	J N R Jeffers	15	
518£	UNESCO MAB Information System	J N R Jeffers	15	
591	Terrestrial Environment Information System	B K Wyatt	(15)	5
602	Modelling sports turf wear	T W Parr	(15)	4
610	Computerization of CCAP records	D F Spalding	15	
613	Computerization of ITE/NERC costing procedure	M D Mountford	15	
621	Models of rabies epidemiology	P J Bacon	15(11)	
663	Estimation of abundance of populations	M D Mountford	15	
699	Checklist of computer programs	D K Lindley	15	
754£	Development of bilateral link with IES, Khartoum	J N R Jeffers	15	
777	Estimation of population parameters	K H Lakhani	15(10)	
780	Use of statistics in Journal of Ecology	P Rothery	15	
795	Standard procedure for recording data	D M Greene	(15)	5
802£	MAFF environmental sampling in west Cumbria	D K Lindley	15	
825	Statistical consultancy in ITE	M D Mountford	15	
835£	ITE/UCL EIA Lake Ichkeul: plant demography	T W Parr	(415)	9
846*	Influence of events on population growth	I R Smith	15(910)	
868$*	Training in computing and statistics	L Li	15	
869*	Graphics for general publications	C Benefield	15	

Staff List 31 December 1983

Institute of Terrestrial Ecology Directorate

Director		
CSO	Mr Jeffers, J. N. R.	Merlewood Research Station Grange-over-Sands Cumbria LA11 6JU (04484) 2264-6, 3826
EO	Mrs Ward, P. A.	
PS	Mrs Delve, J.	
Assistant Director		
DCSO	Prof Last, F. T.	Bush Estate Penicuik Midlothian EH26 0QP (031 445) 4343-6
PS	Mrs Hogg, A. H.	
Assistant Director		
DCSO	Dr Dempster, J. P.	Monks Wood Experimental Station Abbots Ripton Huntingdon PE17 2LS (048 73) 381-8
PS	Mrs Stocker, B. J.	
Institute Secretary		
PRIN	Mr Brown, E. J.	68 Hills Road Cambridge CB2 1LA (0223) 69745-7

Institute of Terrestrial Ecology
68 Hills Road
Cambridge
CB2 1LA
0223 (Cambridge) 69745-7
Telex 817201

Headquarters

Head of Station
Institute Secretary

Prin Mr Brown, E. J.

Administration

SEO Mr Collins, R. T.
HEO Mr Clapp, E. C. J.
EO Mr Easterbrook, M. J.
EO Mrs Harvey, C. L.
CO Mrs Chambers, E. M. (PT)
CO Miss Dickerson, A. S.
CO Mrs Rumbelow, R. J.
CA Mrs Hannay, A. E. (PT)
CA Miss Jackson, S.
SP/T Mrs Cowling, M. J. (PT)

Scientific

PSO Mr Mountford, M. D.
SSO Mr Cryer, P. H.
SSO Mr Rothery, P.

Institute of Terrestrial Ecology
c/o University of East Anglia
School of Biological Sciences
University Plain
Norwich
NR4 7TJ
0603 (Norwich) 56161

Scientific

PSO Dr Ranwell, D. S.
ASO Mr Storeton-West, R. L.

Institute of Terrestrial Ecology
Monks Wood Experimental Station
Abbots Ripton
Huntingdon
PE17 2LS
048 73 (Abbots Ripton) 381-8
Telex 32416

Head of Station

SPSO Dr Hooper, M. D.
CO Mrs Wood, H. M. (PT)

Administration

HEO Mr Abbott, L. F.
CO Miss Atkinson, L.
CO Mrs Cowan, E. (PT)
CO Mrs Purdy, M. I.
CO Mrs Weller, S. M.
CA Miss Allen, D. A.
SP/T Miss Abblitt, J. M.
SP/T Mrs Glover, P. R.
SP/T Mrs Stokes, J.
CLNR Mrs Bell, K. C. J. (PT)
CLNR Mrs Chance, M. E. (PT)
CLNR Mrs Ennis, S. (PT)
CLNR Mrs McDowell, J. (PT)
CLNR Mrs Schietzel, P. E. (PT)
BAND 10 Mr Farrington, T. F.
BAND 8 Mrs Wade, E. E. C. (PT)
BAND 6 Mr Farrington, D. T.
BAND 4 Mr White, W. F. (PT)

Scientific

SPSO Dr Newton, I.
PSO Dr Boorman, L. A.
PSO Dr Davis, B. N. K.
PSO Mr Lakhani, K. H.
PSO Dr Moriarty, F.
PSO Dr Pollard, E.
PSO Dr Sheail, J.
PSO Dr Welch, R. C.
PSO Mr Wells, T. C. E.
SSO Dr Bull, K. R.
SSO Dr Dawson, A. S.
SSO Dr Dobson, S.

SSO	Mr French, M. C.
SSO	Mrs Greene, D. M.
SSO	Mr Harding, P. T.
SSO	Dr Kenward, R. E.
SSO	Dr Marrs, R. H.
SSO	Dr Osborn, D.
SSO	Dr Stebbings, R. E.
SSO	Mr Westwood, N. J.
HSO	Mr Arnold, H. R.
HSO	Dr Boyd, I. L.
HSO	Mr Cummins, C. P.
HSO	Mr Freestone, P.
HSO	Mr Frost, A. J.
HSO	Mr Fuller, R. M.
HSO	Ms Hanson, H. M.
HSO	Mr Parish, T.
HSO	Dr Parr, T. W.
HSO	Mr Preston, C. D.
HSO	Dr Sargent, C. M.
HSO	Dr Village, A.
HSO	Mrs Welch, J. M.
HSO	Mr Wyllie, I.
SO	Miss Brown, M. C.
SO	Miss Cox, R.
SO	Mr Eversham, B. C.
SO	Mr Greatorex-Davies, J. N.
SO	Mrs Haas, M. B. (PT)
SO	Mrs Hall, M. L. (PT)
SO	Miss Harper, R. J.
SO	Mr Lowday, J. E.
SO	Mr Mountford, J. O.
SO	Mr Plant, R.
SO	Mr Yates, M. G.
SO	Mrs Young, W. J.
ASO	Mrs Bibby, T. J.
ASO	Mrs Gore, D.
ASO	Miss Hall, J. R.
ASO	Mr Howe, P. D.
ASO	Mr Leach, D. V.
ASO	Mr Myhill, D. G.
S/PHGR	Mr Ainsworth, P. G.
P&TO3	Mr Snapes, V. W.
ALIB	Mrs King, J.

Institute of Terrestrial Ecology
Merlewood Research Station
Grange-over-Sands
Cumbria
LA11 6JU
044 84 (Grange-over-Sands) 2264-6
Telex 65102

Head of Station

SPSO	Dr Heal, O. W.
PS	Miss Duncan, H. R.

Administration

HEO	Mrs Foster, E.
CO	Mrs Coward, J.
CO	Mrs Coward, P. M.
CO	Mrs Holgate, A. (PT)
SP/T	Mrs Wilson, M. (PT)
TYP	Miss Benson, C.
TYP	Mrs Couch, T. E.
TYP	Miss Jackson, D.
TYP	Mrs Kay, C. G. (PT)
CLNR	Mrs Burton, E. (PT)
CLNR	Mr Casey, M. (PT)
CLNR	Mrs Pearson, V. (PT)
BAND 8	Mr Foster, P. L.
BAND 4	Mr Lethbridge, R.

Scientific

SPSO	Mr Allen, S. E.
PSO	Mr Brown, A. H. F.
PSO	Dr Bunce, R. G. H.
PSO	Dr Callaghan, T. V.
PSO	Dr Harrison, A. F.
PSO	Mr Howard, P. J. A.
PSO	Mr Lindley, D. K.
PSO	Mr Lowe, V. P. W.
PSO	Mr Sykes, J. M.
SSO	Dr Bacon, P. J.
SSO	Mr Grimshaw, H. M.
SSO	Dr Horrill, A. D.
SSO	Dr Ineson, P. *(Research Fellow)*
SSO	Miss Latter, P. M.
SSO	Mr Millar, A.
SSO	Mr Parkinson, J. A.
SSO	Mr Quarmby, C.
SSO	Mr Roberts, J. D.
HSO	Mr Barr, C. J.
HSO	Mr Benefield, C. B.
HSO	Mr Benham, D. G.
HSO	Dr Dighton, J.
HSO	Miss Hamilton, N. M.
HSO	Dr Howard, B. J.
HSO	Mrs Howard, D. M.
HSO	Mrs Howson, G. (PT)
HSO	Mr Lawson, G. J.
HSO	Mr Rowland, A. P.
HSO	Mr Scott, R.
SO	Mr Adamson, J. K.
SO	Mr Coward, P. A.
SO	Mrs Kennedy, V. H. (PT)
SO	Miss Robertson, S. M. C.
SO	Mrs Shaw, F. J.
SO	Mr Smith, M. R.
SO	Miss Whittaker, H. A.
SO	Mrs Whittaker, M.
ASO	Mr Briggs, D. R.
ASO	Mrs Gardener, C. L.
ASO	Miss Grove, J.
ASO	Miss Hodgson, A. L.
ASO	Miss Jewell, S. E.
ASO	Mrs McClure, C.
ASO	Mrs Mainwaring, A. M.
ASO	Mrs Poskitt, J.
ASO	Mr Woods, C.
ASO	Mrs Zirkel, S. M. (PT)
LIB	Mr Beckett, J.
	Dr Frankland, J. C. (C/T PT)
	Dr Jones, H. E. (C/T PT)

Institute of Terrestrial Ecology
Furzebrook Research Station
Wareham
Dorset
BH20 5AS
09295 (Wareham) 51518-9, 51491
Telex 418326

Head of Station

SPSO	Dr Morris, M. G.
PS	Mrs Perkins, M. K.

Administration

EO	Mr Currey, R. J.
CO	Mrs Jones, M. C. (PT)
SP/T	Miss Weller, R. A.
CLNR	Mrs Fooks, N. M. (PT)
CLNR	Mrs Parker, I. (PT)
BAND 8	Mr Parker, B. D.

Scientific

PSO	Dr Chapman, S. B.
PSO	Dr Elmes, G. W.
PSO	Dr Goss-Custard, J. D.
PSO	Dr Gray, A. J.
PSO	Dr Merrett, P.
PSO	Dr Ward, L. K.
PSO	Dr Webb, N. R. C.
SSO	Mr Clarke, R. T.
SSO	Dr Daniels, R. E.
SSO	Dr McGrorty, S.
SSO	Dr Thomas, J. A.
HSO	Mr Abbott, A. M.
HSO	Mr Pearson, B.
HSO	Dr Reading, C. J.
HSO	Mr Snazell, R. G.
SO	Mr Rispin, W. E.
SO	Mrs Wardlaw, J. C. (PT)
ASO	Ms Benham, P. E. M.
ASO	Miss Durell, S. E. A.
ASO	Mrs Jones, R. M.
ASO	Mr Rose, R. J.

Institute of Terrestrial Ecology
Bush Estate
Penicuik
Midlothian
EH26 0QB
031 445 4343-6
Telex 72579

Head of Station

SPSO	Dr Unsworth, M. H.
PS	Miss Thomson, L. S.

Administration

HEO	Mr Smith, I. C.
CO	Mrs Campbell, A. M. (PT)
CO	Mrs Shields, S. E. (PT)
SP/T	Mrs Wilson, E. (PT)
TYP	Miss Aitchison, C.
TYP	Mrs Thompson, M. (PT)
CLNR	Mrs Mowat, E. A. M.
BAND 4	Mrs Innes, D. S. (PT)

Scientific

PSO	Dr Cannell, M. G. R.
PSO	Dr Ford, E. D.
PSO	Dr Longman, K. A.
PSO	Mr Pelham, J.
SSO	Mr Bell, B. G.
SSO	Dr Cape, J. N.
SSO	Mr Deans, J. D.
SSO	Dr Fowler, D.
SSO	Dr Leakey, R. R. B
SSO	Dr Marquiss, M.
SSO	Dr Mason, P. A.
SSO	Dr Milne, R.

SSO	Dr Watt, A. D.
SSO	Mr White, E. J.
HSO	Dr Crossley, A.
HSO	Mr Murray, T. D.
HSO	Mr Ottley, R. F.
HSO	Dr Sheppard, L. J.
HSO	Mr Smith, R. I.
HSO	Dr Wilson, J.
SO	Miss Dick, J. M.
SO	Mr Harvey, F. J.
SO	Mr Ingleby, K.
SO	Mr Leith, I. D.
SO	Mr Lightowlers, P. J.
SO	Mr Munro, R. C.
SO	Mr Wilson, R. H. F.
ASO	Mrs Halcrow, A.
ASO	Mrs Murray, M.
P&TO4	Mr Elphinstone, G. B.
P&TO4	Mr McCormack, J. W.
ALIB	Miss Scoular, L. M.

Institute of Terrestrial Ecology
78 Craighall Road
Edinburgh
EH6 4RO
031 552 5596-9

Administration

CO	Mrs Adair, S. M.
SP/T	Mrs Wilson, M. S.

Scientific

PSO	Dr Maitland, P. S.
PSO	Mr Smith, I. R.
SSO	Dr Bailey-Watts, A. E.
SSO	Mr East, K.
SSO	Mr Jones, D. H.
HSO	Dr May, L.
SO	Mr Kirika, A.
SO	Mr Lyle, A. A.
SO	Mr Morris, K. H.

Institute of Terrestrial Ecology
Banchory Research Station
Hill of Brathens
Glassel
Banchory
Kincardineshire
AB3 4BY
033 02 (Banchory) 3434
Telex 739396

Head of Station

SPSO	Dr Jenkins, D.
SP/T	Mrs Burnett, L. M. (PT)

Administration

EO	Miss Pirie, A.
CO	Mrs Barron, M. A.
TYP	Mrs Allan, E. J. P.
TYP	Mrs Andrews, P. A.
CLNR	Mrs Griffin, M. D. (PT)
BAND 8	Mr Griffin, C.

Scientific

SPSO	Dr Watson, A.
PSO	Dr Harris, M. P.
PSO	Dr Kruuk, H.
PSO	Dr Miles, J.
PSO	Dr Miller, G. R.
PSO	Dr Mitchell, B.
PSO	Dr Moss, R.
PSO	Mr Nicholson, I. A.
PSO	Dr Staines, B. W.
SSO	Dr Bayfield, N. G.
SSO	Mr French, D. D.
SSO	Mr Kinnaird, J. W.
SSO	Mr McCowan, D.
SSO	Mr Parr, R. A.
SSO	Mr Paterson, I. S.
SSO	Mr Picozzi, N.
SSO	Mr Welch, D.
HSO	Mr Conroy, J. W. H.
HSO	Mr Cummins, R. P.
HSO	Mr Young, W. F.
SO	Mr Catt, D. C.
SO	Mr Scott, D.
ASO	Mr Glennie, W. W.
ASO	Miss McPherson, M.
ASO	Mr Trenholm, I. B.
P&TO4	Mr Morris, J. A.

Institute of Terrestrial Ecology
Bangor Research Station
Penrhos Road
Bangor
Gwynedd
LL57 2LQ
0248 (Bangor) 364001-5
Telex 61224

Head of Station

SPSO	Dr Milner, C.
PS	Mrs Lloyd, A. C.

Administration

EO	Mrs Owen, B. J.
CO	Miss Owen, D. E.
CO	Mrs Owen, M.
CO	Mrs Pritchard, J. E. (PT)
SP/T	Miss Jones, H. A.
TYP	Miss Roberts, M. E.
CLNR	Mrs Jones, J. F. (PT)
CLNR	Mrs Stedmond, L. A.
BAND 4	Mr Wilson, J. N.

Scientific

PSO	Dr Ball, D. F.
PSO	Mr Hill, M. O.
PSO	Dr Hornung, M.
PSO	Dr Perkins, D. F.
PSO	Mr Radford, G. L.
PSO	Mr Shaw, M. W.
PSO	Dr Wyatt, B. K.
SSO	Dr Ashenden, T. W.
SSO	Dr Buse, A.
SSO	Mr Dale, J.
SSO	Mr Evans, D. F.
SSO	Dr Good, J. E. G.
SSO	Mr Hewett, D. G.
SSO	Mrs Jones, V.
SSO	Dr Moss, D.
SSO	Mr Owen, G. H.
SSO	Mr Rafarel, C. R.
SSO	Dr Seel, D. C.
SSO	Mr Thomas, D. I.
SSO	Mr Walton, K. C.
HSO	Mr Bell, A. A.
HSO	Miss Hatton, A. A.
HSO	Mr Millar, R. O.
HSO	Mrs Neep, P.
HSO	Dr Reynolds, B.
HSO	Mr Stevens, P. A.
HSO	Mr Thomson, A. G.
HSO	Mr Williams, W. M.
SO	Mrs Bell, S. A.
ASO	Mr Hughes, S.
ASO	Mr Williams, T. G. (C/T)
P&TO4	Mr Hughes, G.

Institute of Terrestrial Ecology
Culture Centre of Algae and Protozoa
36 Storey's Way
Cambridge
CB3 0DT
0223 (Cambridge) 61378

Head of Station

PSO	Dr Baker, J. R.

Administration

EO	Miss Moxham, M. J.
CO	Mrs Day, G. M. (PT)
SP/T	Mrs Connell, C. (PT)
C/TKR	Mr Yorke, D. A.
CLNR	Mrs Yorke, M. J. (PT)

Scientific

SPSO	Dr Page, F. C.
PSO	Dr Morris, G. J.
SSO	Mr Clarke, K. J.
SSO	Mr Spalding, D. F.
HSO	Mr Pennick, N. C.
SO	Mrs Asher, A. (PT)
SO	Mr Cann, J. P.
SO	Mrs Coulson, G. E.
SO	Mrs Leeson, E. A.
ASO	Mrs Cann, S. F.
ASO	Mrs Winters, L. C.

Publications

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Customer	Project number	Project title
Nature Conservancy Council	181, 461	Birds and pollution
	204	Butterfly monitoring scheme
	208/9/11, 557, 656	Recording of data on individual species
	242	Creating attractive grassland
	291/2	Population ecology of bats
	718	Effects of drainage on wildlife
	776	Moor House data analysis
	852	Impact of herbivores on woodland
	—	Advice and services
Department of the Environment	408	Arboriculture
	553	Radionuclides
	609	Biological classification of UK rivers
	625 (pt)	Upland management and water quality (joint FBA/IH)
	700	Ecological guidelines for locational strategies
	759	Biological effects of chemicals in the environment
	790, 837	Acid deposition on soils and plants
Department of Industry	851	Effects of long-term preservation on micro-organisms
Ministry of Agriculture, Fisheries and Food	802	Environmental sampling in west Cumbria
Ministry of Defence	834	Gruinard Island decontamination assessment
Central Electricity Generating Board	838	Ecological survey of Sizewell
National Coal Board	360	Tree planting study
		Vegetation overburden mounds
Anglian Water Authority		Holme dune study
Severn & Trent Water Authority	858	Soar Valley improvement scheme
Essex County Council	819	St Osyth conservation scheme
Building Design Partnership	853	Falkland airport survey
Laurence Gould Consultants	858	Environmental study of River Ray drainage scheme
		Environmental study of Thames drainage scheme
English China Clay Company	859	Furzeyground restoration scheme
Dartington Trust	844	Wood production on Culm measures
Shetland Oil Terminal Environmental Advisory Group	715	Otters at Sullom Voe
Welsh Office	160 (pt)	Fluorine pollution
	594, 625 (pt)	Upland management and water quality
	845	Acid rain in Wales
Dyfed County Council	850	Pembrokeshire National Park
European Commission	160 (pt)	Fluorine pollution
	553 (pt)	Radionuclides
	625 (pt)	Land management and water quality
	674	Native and naturalized species for energy production
	760	European mapping
UNESCO	750	West African hardwoods
UNEP	763	Chemical data profiles

UNEP/FAO		Senegal Sahelian project
World Pheasant Association	764	Black grouse studies

Expected level of income from commissioned work for the financial year 1983/84

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	773

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