Natural Environment Research Council

Institute of Terrestrial Ecology

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> The cover shows clockwise from the top: Puffin. Photograph M. D. Harris; Red deer calf. Photograph B. Mitchell; Dorset heath. Photograph S. B. Chapman; Female Shield bug on juniper. Photograph L. K. Ward; Common gill fungus. Photograph J. K. Adamson.

The Institute of Terrestrial Ecology is a component body of the Natural Environment Research Council

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Ecology and the management of the British environment

Introduction

In last year's Annual Report, we discussed the role of ecology in policy making. Specifically, we argued that, because ecology was a multi-disciplinary science, uniquely capable of analysing the ways in which plants and animals are distributed, associated in communities, and related to factors in the environment, it has an important part to play in determining the choices we make about the management of land. Principles we now describe as 'ecological' have been applied in agriculture and forestry for a long time, while the conservation of wild life is a more recent activity equally dependent on ecological understanding.

Several developments in the past year demand a response from ecologists. Government has published a Cabinet Office paper on future world trends, suggesting what will happen, on the largest scale, to environment and humanity in the next few decades.*

A new Centre for Agricultural Strategy in the University of Reading has begun to examine how new policies to increase food production at home may affect the farm lands of Britain. Forestry policy continues to excite considerable attention within a rapidly changing economic framework. Ecologists and planners have embarked upon a series of discussions, one of which, in the form of a specialist workshop, was held at ITE's Monks Wood Experimental Station early in 1975. A report of this workshop was published in the British Ecological Society Bulletin†; it was criticised by some who believed that it was too greatly influenced by the concepts of the industrial society with which contemporary planners have, of necessity, to deal. In the autumn of 1976, the British Ecological Society is convening further discussion on the way in which ecologists and planners should work together.

Because of these events, all of which indicate how important it is for ecologists to make a thoughtful contribution to discussions about the wise use of the environment, it was decided to preface this second ITE Annual Report with a consideration of some of the principles and constraints that influence the planning and management of environmental resources.

We would emphasise at the outset that we are here discussing ecology in its original sense, as a scientific discipline and not in the more generalised, popular, (and often vaguer) sense of a philosophy, way of life of quasi-religious dogma. For us, ecology is a scientific study of how the patterns of life which we see in the world today have come into being, and one

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which, through analyses of these patterns and through detailed research which explains their causes, endeavours to predict the changes that are likely if the present processes in the world continue, or if they are perturbed in different ways by man. Like any other branch of science, ecology demands successive phases of activity. Description (or the acquisition of data) must be followed by analysis to determine what appears to be related to what and therefore suggest possible causes. As a result of this analysis, prediction should both formulate hypotheses which can be tested experimentally and lead to application in terms of social policy. The aim of this whole exercise is to guide the ways in which people modify (or protect) their environment so that they do not unwittingly damage elements of it on which they depend or which they cherish, and to enable them to make choices which ensure that they live in the best of attainable worlds.

MAN WITHIN THE ECOSYSTEM

As any doctor knows, despite the most sophisticated of medical technologies, human individuals remain very much the victims of their physiology and genetics. We have learnt to protect people from the diseases that would unquestionably have killed them centuries, if not decades, ago, but all our medical skills do not make us immune from senescence or environmental stresses of extreme heat or cold which, if they catch us unprotected on the mountains or in the deserts, can kill us just as swiftly and certainly as they did our scantily-clad ancestors millennia ago.

Similarly, despite his industrial and urban civilisation, man should not, indeed cannot, think of himself as being apart from the constraints of the environment. As our scientific and technological society becomes more sophisticated, we grow less tolerant of the upsets that the force of nature can cause. Our ancestors may have accepted such disturbances as Acts of God: our contemporaries are more likely to blame scientists for failing to foresee them! One of the great values of ecology as a science is that it is concerned with the total situation in which man finds himself. Ecology is a science of inter-relationships and inter-dependences. It teaches us some salutory truths which are all too readily forgotten in the derived and secondary world of the city and industry.

First among these truths is the fact that all animal life, including our own, depends entirely upon the process of photosynthesis by which green plants harness the energy of the sun and produce the basic foods on which animal life depends. Those green plants are equally vital for the renewal of atmospheric oxygen upon which all animals depend for respiration. Hidden in the soil, in the swamps and in the sea, the

^{*} Cabinet Office 1976. Future World Trends. HMSO.

[†] Holdgate, M. W. and Woodman, M. J. (1976) Bull. Br. Ecol. Soc. 6: 4, 5-14

tiny micro-organisms we collectively label 'the decomposers' play a similarly essential part in recycling the waste products and dead remains of plants and animals back to the nutrient pools on which the living plants draw.

We are learning all the time of unsuspected elements in these basic processes. For example, the continued production of methane gas in swamp land deprived of oxygen appears to be important in checking the rise in the levels of oxygen in the air which would occur if the photosynthetic processes of plants went on uncompensated. If oxygen levels rose by 5 to 10 per cent above the present value, cornfields might regularly take fire in a storm of summer lightning and even forests might burn, thereby creating devastating instabilities in the world, but at the same time applying a brake to the continued evolution of oxygen. In such ways, the checks and balances of complex ecological systems, involving large numbers of species operating at many 'levels', are an indispensable regulator, giving stability to atmosphere, soil and other vital components of the environment.

Much has been made, in recent years, of the relationships between the species diversity of ecological systems and their stability in the face of environmental perturbations. Just how far this relationship is real is a matter of debate, and the debate has produced a voluminous literature which at least shows that the relationship is not simple. Different kinds of ecological system vary in their resilience under the stress of physical and chemical disturbance, and in their resistance to invasion by additional species of plant and animal. Despite these uncertainties, however, it remains true that green plants, herbivores, predators, decomposers. and the organisms that, in turn, consume those decomposers are all indispensable components of any ecosystem that is to be balanced and capable of sustaining agriculture, forestry, wild life or human life.

Another basic lesson for man from ecological science is that no organism increases in its numbers indefinitely and unhindered. Population limitation is a universal fact of nature. Man throughout his evolutionary history has had his numbers limited by processes which include competition for space, shortage of food, hostile interaction with his fellow humans, disease, and possibly (although probably to an unimportant extent) predators. Although great wars and their aftermath have taken their toll, in Britain we have largely escaped from these regulatory processes for a period of some centuries through the development of a technological civilisation, and, most recently, through the special versions of that technology which we term 'medicine'. Nonetheless, in many parts of the world famine, disease

or warfare still devastate communities which have not yet attained a certain level of development or which are particularly exposed to severe environmental stress. The enormous increase in human numbers in recent years places increasing demands on our technology to keep ahead of the natural regulators, not in order that human populations can continue increasing so much as to permit them to be brought into a new and socially determined balance with the environment while there is still sufficient space and food. The natural limiting factors are unpleasant in operation and incompatible with the social values of any modern society. It follows that societies now need to work to evolve voluntary systems for containing the numbers of mankind and thus to eliminate the operation of these regulators from the future scene.*

In Britain, it may be easy to be complacent about some of these issues. Like a small number of other developed countries, we appear to be moving towards population stability. The standard of living, medical care and nutrition are high. In contrast, many nations with standards of living which we would consider intolerable are experiencing growth in their populations at rates which are outstripping the benefits being brought by their development. The grave imbalances of the world are real, and ecologists in Britain, as much as ecologists elsewhere, need to be prepared to devote their skills to helping to solve the associated problems.

THE APPLICATION OF ECOLOGY TO LAND MANAGEMENT IN BRITAIN:

The challenge

Within the overall responsibility of the Natural Environment Research Council for the sciences of the environment, staff of the Institute of Terrestrial Ecology are chiefly concerned with contributing, as ecologists, to the wise management of the natural resources of the land in this country.

Apart from marginal adjustments along the coast, the area of Britain is fixed. Within this limited and densely populated area, however, rapid changes are taking place in the way in which the land is used. Land is being withdrawn from rural to urban uses at a rate of about 50 thousand acres a year. Forestry and private woodland is taking land from agriculture (mainly upland grazing) at an even faster annual rate. The total loss from agriculture to other uses is running at about 140 thousand acres a year. Yet, despite this loss, increasing concern about the need to grow food

* Report on the State of the Environment 1976. 4th Meeting of the Governing Council of the United Nations Environmental Programme, Nairobi. at home is manifest. How long can the trends, which have been accepted as inevitable, be tolerated? Will it be necessary to restrict the expansion of towns into green field sites, consequently increasing the concentration of development within existing city boundaries? How far can agriculture, on a shrinking acreage, nonetheless produce more food?

Planning and land management

As last year's report indicated, many areas of land can be devoted either to agriculture, forestry, wild life conservation, urban and industrial development, mineral exploitation, recreation, or any combination of these activities. The decision as to which particular configuration of land management to employ for a given area constitutes planning in its broadest sense. As the workshop we held at Monks Wood emphasised, this is a different kind of planning from the statutory version operated by central and local government, which is mainly concerned to control changes in certain broad categories of land use, and with marginal adjustment in the expansion of urban development into the countryside. There are many important land use changes that lie outside planning processes; among these, for example, is the replacement of one kind of agricultural system or one type of woodland by another; even the change from an existing industrial development to one that may be more polluting or more hazardous because new processes with larger capacities are substituted, is only half caught in the planner's net (though it may well be caught by the Health and Safety Commission or the Alkali and Clean Air Inspectorate).

Nevertheless, the planning procedures in Britain do provide a way of influencing the use of the natural resources of the land. Ecologists are intellectually attuned to this kind of operation because, like planners, they are concerned with the relationships between sectors and components of the environment and the ways in which the modification of some of the many variables lead to predictable outcomes. It is not, therefore, surprising that ecologists are seeking increasingly to assist the planners by making their special expertise available.

In Britain, planning is undertaken at two levels (or three if the special powers of the Secretary of State for the Environment and his counterparts in Wales and Scotland to call in and themselves determine particularly important developments, and to lay down the guidelines for planning at all levels are taken into account). At the county level in England and Wales, or the regional level in Scotland, local authorities are responsible for strategic planning, embodied particularly in structure plans. These indicate the broad zonation of land use which is proposed for wide tracts of our

environment. Naturally these structure plans are anticipatory; that is, they look at the situation as it is now, in advance of any specific proposals, and they attempt to secure the future by guiding the developer to the areas in which he would be welcomed. At the district level, planning is a more responsive process; it is concerned with deciding whether actual applications for development should be approved and with ensuring that such development takes place in the most desirable way.

At both levels, the planner needs to know about the natural resources of the area of environment with which he is concerned, and to be able to predict how they will be affected by possible changes in the pattern of land use. To gain such knowledge both *surveys*, describing existing situations, practices and trends, and *experiments*, probing into the interactions of components of the system and their responses to environmental factors are necessary. NERC is well placed to gather and supply both kinds of information.

The survey of environmental patterns and resources

There are many kinds of environmental survey. Geological surveys tell us of the distribution of mineral resources, and also something of the costs of different kinds of engineering in different regions. Hydrological surveys define the pattern of water run-off, and incidentally underline drainage problems that will be encountered by building in different kinds of setting. Soil surveys give information about the potential fertility of the land. Surveys of agricultural potential define where we can most usefully raise particular crops, while similar evaluations are important in improving the distribution and productivity of forestry. General ecological surveys of flora and fauna are important, because much of our stock-raising is done on pastures comprised of plants native to this country, and because the ecologists can provide a background to the work of other specialists in the understanding of environmental processes and the potential for change. The ecologist is also able to predict the likely effects of development on wild life, natural beauty and amenity, much of which is controlled by biological factors.

The surveys that describe such resources can be done in many ways. At their simplest, they are subjective: an ecologist sitting on a hillside can provide a coherent description of the country spread out below him, and explain a good deal about its soil and its history. More critical and numerically more reliable surveys involve some form of sampling and measurement that allows us to make statistically valid statements about the frequency with which various types of plant and animal communities occur, and the kinds of relationships these communities have with factors of the environment. Such objective surveys are uniquely able to relate the observations of different people at different times and allow us to state quantitatively the degree of change taking place from one period to another, thereby enabling us to make extrapolations into the future. Modern methods of ecological survey have increasingly focused on relatively rapid and inexpensive ways of undertaking objective surveys, designed from the outset to give the level of resolution required by the purposes for which the information is to be used. Such surveys need take no longer than the more superficial and descriptive approach and have the advantage that they are more readily repeated and interpreted.

There is little point in the collection of data for their own sake. Indeed, it is a defect of environmental scientists that they are far too prone to collect data, acquiring masses of information which are then difficult to analyse and may be redundant. This tendency is clearly wasteful. The kind of survey to be undertaken must be decided after considerable thought has been given to the questions the survey is designed to answer. On what kinds of question are ecologists likely to be consulted?

First, there are questions of a descriptive character: what is the pattern of soil, vegetation, fauna and biological productivity over a tract of countryside, and to what variables does the pattern relate? To answer such questions, objective descriptive surveys, followed by analysis to establish correlations, will clearly be needed. These can be done fairly fast, for the methods are fairly well proven even though they will doubtless be improved. A further series of questions may, however, be superimposed on those simply requiring broad descriptions. These include questions of trend: how fast and in what direction is this pattern changing, and in response to which variables? Such questions are more difficult to answer instantaneously, for the observation of change demands repeated measurements over a period of time that relates, in a meaningful way, to that over which the prediction is required. If we have to start from scratch, repeated surveys, spaced out over a decade or more may be needed - a procedure that is of little use to a planner confronted with urgent policy decisions. Sometimes, however, we are fortunate in already having time-series of observations of certain components of the environment which, related to the detailed analysis of the patterns that we can derive from general surveys today, may help us suggest probable directions of change. Experience, too, of changes in one place may allow predictions in another which is shown by survey to be comparable.

A third group of questions may be addressed to the scientist but stem from the value judgments society places today, and may place tomorrow, on components of the environment: which are the areas of land richest in wild life? Where are new combinations of wild life most likely to emerge? Where are rare species concentrated? What areas particularly display specified combinations of features like ancient trees, broad and fertile park-lands or cliffs rich in birds? Yet other questions relate to the options for management: what are the alternative configurations that nature tends to produce in an area and that human management can produce with the injection of varying degrees of effort and expense? what mix of high-yielding agriculture, productive forestry, rich wild life, mineral exploitation, urban development and outdoor recreation can be attained in a particular area? Finally, there are questions relating to the ways of achieving the desired pattern: how does one maintain the character of an area of our environment?

A few decades ago, many people held to the belief that nature managed itself and that one should not interfere with those parts of the countryside set aside as nature reserves. This is now well-known to be a false belief: left to itself, the chalk grassland over the southern downs slowly reverts to scrubland and then to forest, and heathland likewise moves toward woodland. One kind of tree replaces another, and the insects and the plants of the forest floor associated with different kinds of woodland slowly evolve towards their respective climax assemblages. In the urban environment, where we are often dealing with soils that have been modified by agriculture and then modified again by industrial activity, it is even more necessary to look critically at the environment before predicting the kind of management needed to create a particular landscape, or even to grow a particular selection of trees for amenity. These are all issues with which the ecologist must be concerned. There is already considerable experience among ecologists, in ITE and in Universities, in answering this kind of question.

The experimental approach

Surveys, especially when their repetition allows trends to be established and the penetrating analysis of correlations suggests cause, can help us to predict what is going to happen in the future under various alternative systems of management, and if the natural environment changes in various ways because of climatic and other cycles. But experimental science also has a contribution to make. Mathematical associations between the elements described by a survey may suggest inter-dependences and causes, but experiment is needed to establish the basis of the process being observed.

There are many major issues relating to land use in Britain today which need to be explored in this way. Some are of no immediate concern to ITE, but our expertise in upland ecology is highly relevant. The hill country accounts for nearly a third of the surface of Britain, most of it is pasture, which, because of altitude, waterlogging and high rainfall, coldness of the soil or a history of depletion of nutrients through mis-management, yields a very small part of our food resources. The pasturage is composed of wild plants, and the nutrient fertility in these, as indeed in all soils, depends on microbes, fungi and invertebrates about whose management we know virtually nothing.

Substantial experimental programmes are exploring the processes in these systems. Such research has demonstrated that the fertility of some of the poorer heather moorlands of Scotland can be enhanced if they are allowed to remain under closed-canopy birch woodland for perhaps fifty years : other research on the soil fauna may indicate ways in which it could be manipulated more positively to improve productivity. The International Biological Programme, on the study site at Moor House in the north Pennines of England, indicated that less than a tenth of one per cent of the energy fixed by the plants in a year was consumed by the sheep that are man's chief yield from this particular environment. That study site was on the most unproductive bog land and much of the sun's energy falling on it was being accumulated as a 'sub-fossil fuel' in peat, which was, however, not being used. What are the options for the management of such land? Can we increase livestock productivity and, indeed, centre much of our meat production on the uplands, thereby using the lowlands for intensive plant food production, which, if we were also to change our eating habits, would certainly materially increase the amount of our diet we derive from home-grown resources? Alternatively, would it be more economic to change (as is indeed happening over large areas of southern Scotland) such upland areas to commercial forestry, bearing in mind the economic and other values of timber as a raw material? Should a first rotation of Sitka spruce be followed by a second of the same species? What are the management options open to us? What kind of countryside would they produce? What is the effort involved in each option? These are examples of the kinds of issue to which we need to respond.

Development control and the assessment of 'environmental impact'

The ecological information derived from survey, analysis and experiment is deployed not only as a foundation for strategic, anticipatory planning at the regional or county level but in the more immediate control of individual developments, done especially at district level, and responsively as plans are formulated. At this level, both planners and ecologists are concerned with 'environmental impact' in its wide sense. The planner is especially concerned with industrial and urban developments. Sometimes these developments will occur in land previously rural in character. Sometimes they will occur within a city boundary, replacing pre-existing development. Habitat changes can be brought about in all cases, through the physical modification of the environment by removing soil, altering drainage patterns, or changing topography and through the emission to air or water of chemicals which influence, in turn, the suitability of the region as a habitat for various kinds of plants and animals. Both kinds of impact evidently affect the attractiveness of the area in visual terms to people living in it or going there for recreation. Environmental impact assessment is a way of examining, in advance of a development, the likely changes that the development will cause, and consequently guiding it to the most suitable site or constraining it to the optimal degree. The British planning process already contains the equivalent of environmental impact assessment procedures, and ways of improving their effectiveness are being considered by the Departments concerned. It is not our purpose here to argue the advantages or disadvantages of particular systems of assessment, but to point out that ecological evaluations will be needed as a part of any such examination.

The basic surveys and impact predictions of the ecologist and the prescriptions for managing the environment to various desired ends are rarely simple and the results may need interpretation if they are to be used by the professional planner (whose own professional judgments also commonly need translation if they are to be understood by ecologists). One role of the ecologist in this situation, therefore, going beyond his role as a gatherer and analyser of data, is to interpret his specialist scientific knowledge for the benefit of the planner. Specialists in agriculture, forestry, wild life conservation or landscape planning similarly provide interpretations (the Nature Conservancy Council is making a particular effort here), but these commonly cover parts of the total ecological field and are undertaken from specific points of view. Such interpretations are complemented by the broad analyses of the general ecologist, and this is a contribution which ITE, with colleagues in Universities, must make.

The response of ITE

Faced with these challenges, ITE in collaboration with the other Institutes of NERC, is developing a research

strategy aimed at providing the scientific base for the application of ecology in the management of the nation's environmental resources. We naturally wish to work closely with our colleagues in nature conservation, agriculture and forestry who are themselves well advanced with similar strategies. The Institute is also well aware of the priority given to enlightened land management in developing countries, many of which are bringing into intensive use ecologically sensitive areas and are also encountering problems of pests and diseases of a kind no longer seen in Britain. Several of our scientists are working on such problems with the support of the Ministry of Overseas Development.

There are two particular requirements within an organisation faced with such problems. The first is to increase the numeracy of our research workers - which does not mean a predisposition to amass vast quantities of data only capable of analysis by a large computer! Ecological disciplines, on the other hand, are increasingly benefiting from the adoption of mathematical skills in the design of sampling and experimental schemes, the analysis of environmental systems and processes, and the development of models which allow the implications of our logical analysis to be tested alongside the real world. Ecological surveys must be designed so that statistical tests can assess the reliability of the patterns they describe. As problems become increasingly complex and understanding of the world deepens, so the need for numerate ecologists will undoubtedly also increase. Our second requirement is to develop a capacity to manage and to integrate complex, multi-disciplinary projects, for the range of expertise needed for the solution of these problems is vastly greater than that commonly addressed in our universities and other academic institutions - or in ITE's research stations in the past.

A wide range of types of work could be undertaken within the Institute's subdivisions, but the limits of manpower and resources necessitate a selective approach. For example, the Subdivision of Soil Science may have, as its broad objective, improvement in the management of the soil resources of the nation, but, within this broad strategy, some immediate tactical objectives are needed, and this is why work is at present concentrated on upland soils and the way in which the micro-flora and fauna of the soils respond to changes in land use. Similarly, within the Subdivision of Plant Community Ecology, attention is being focused on community processes and competitive interactions, while in the Subdivision of Plant Biology, the genetically controlled variation and physiology of primary producers, and their ecological response to competition and grazing are themes of major interest.

The overall objective of ITE is to respond to the changing demands on the ecologist by studying ecological problems relevant to the reduction of economic margins in our national land management. A start has already been made in this area, for example in the research that has been done on how communities of diatoms affect the rate of accretion of sediment in the Wash, and how the whole complex estuarine ecosystem determines the rate of reclamation of salt marshes for agriculture, a process which has been steadily edging forward into this wide bay, nearly half of which has been reclaimed since Saxon times.

In the coastal zone generally, the economics of land management are very much to the fore, and can be greatly affected by ecological understanding. Sand dunes provide natural barriers to sea surges around substantial mileages of the soft coasts of England and Scotland. In East Anglia, there are places where only a narrow bar of dunes stands between inhabited and farmed land and the sea, and there have been occasions when this fragile barrier has been breached, as most recently in the east coast floods of 1953. The strength of such a barrier depends on the power of the grasses which bind the dunes, and the extent to which sand is available to accrete to the fixed dunes of the systems, drawing upon areas further along the coast.

Collaboration between physiographers and botanists is fundamental to understanding how to maintain a viable and stable dune bar, and this understanding in turn has implications for the use of the dunes for public recreation which can bring erosion. New and more vigorous dune-building grasses could almost certainly be bred, just as more vigorous crop plants have been bred, at a cost which is trivial compared with the costs of coast protection.

Similarly, ecological research can enhance our understanding of the impact of pollutants on ecological systems and consequently help us adjust the economic margins of our pollution control policy. A good deal of work has already been done by ITE on how wild bird and invertebrate populations are affected by exposures over long periods to low doses of pollutant. The new research in the Subdivision of Animal Function is aimed at elucidating in detail how the physiology of birds and other organisms is affected by various processes. New work on the impact of air pollution by sulphur oxides and other gases and of acid rain on forest growth and production and on processes within the soil will similarly improve our understanding of pollution and its effects. There will also be implications for the national programme of monitoring and surveillance. Finally, a national survey of ecological systems, in which the variability in environmental conditions and associated vegetation is being assessed objectively may, if sufficiently sensitive, be the first stage of a series of studies to characterise the national environmental resource more fully than has hitherto been attempted.

In Section III of this Report, accounts of individual research projects have been grouped in a way that reflects this spectrum of interest and response. The first sections include a series of reports on survey. Following sections deal with the performance of

species and with processes within ecosystems, and there are then accounts of research on how land use changes and the release of toxic substances to the environment affect plants and animals. The projects described are only a few among over 300 in which the Institute is currently engaged, as the Project Register (Section IV) reveals. Taken as a whole, the potential contribution of the Institute to the themes discussed in this Introduction is evident.

M. W. HOLDGATE Director

The international role of ITE

The world's scientists today are concentrated in the developed countries of the temperate zones. Yet the major environmental problems of the world spread much more widely, and many are most acute in tropical developing countries. The kinds of contribution ecologists can make in Britain are equally – or even more – needed overseas, and while scientists like those in ITE, employed by Government, must centre their activities in this country, it is natural that they are interested in the needs of the wider world.

There are positive gains for British ecologists from working overseas since familiarity with widely different soils, terrain, climates and plant and animal communities gives a broader understanding of the subject. Hot or cold deserts, or the rain forests of the tropics, are selfevidently unlike anything the British ecologist can find in his home country. In these islands, virtually the whole landscape has been altered by human impact, and while few parts of the world are truly 'natural' in the sense of presenting the pre-human condition, many places overseas are far closer to this situation than can be found here. Work overseas thus widens the ecologist's horizons, and confronts him with different and pressing problems, and he is a better scientist for the experience.

There are four ways in which ITE ecologists participate at the international level. First, they may undertake individual research projects abroad as a natural extension of their work, with ITE support or through collaboration with overseas Universities and Foundations. Second, they may participate in programmes arranged by bilateral negotiation with overseas Agencies or Governments, often (though not invariably) through the Ministry of Overseas Development. Thirdly, they may become involved in multi-national programmes organised by international Committees or organisations. Finally, many visitors from other countries come to ITE stations for differing periods, some on sabbatical leave and some for training. These visits are often valuable in establishing contacts which may be developed by our own staff.

Two projects on the genetics, physiology and propagation of West African forest trees, are based respectively at Ibadan, Nigeria, and ITE's Bush laboratory near Edinburgh; they are supported by the Ministry of Overseas Development. Dr K. A. Longman and Dr R. R. B. Leakey are leading the research, done at Bush which is under Professor F. T. Last's overall guidance. The work employs ITE's expertise in gene conservation and growth regulation in trees. It is seeking to conserve the range of variation found in an important timber tree, *Triplochiton scleroxylon*, by the production of vegetative cuttings in which precocious flowers are then induced: already flowers have been produced on two year-old cuttings instead of waiting about 40 years for trees to mature. The 'generation time' is thus shortened dramatically, breeding programmes can be speeded up, and at the same time the techniques, perfected for vegetative propagation, allow the immediate multiplication of plants with desirable attributes.

During 1975 ODM also supported Dr P. Maitland, Dr A. E. Bailey Watts and Mr I. R. Smith who formed a team advising on fisheries in Malawi. The Royal Society supported Dr S. W. Greene's participation in an international survey of vegetation in Patagonia in the southern summer of 1975/76 - an example of the first kind of international activity listed above in that it was a logical extension of Dr Greene's previous research in the Antarctic and Sub-Antarctic, and led to the discovery in the Magellanic forests of Chile of a moss species previously believed to be confined to the Antarctic (see Section III). Such projects follow work on bat and swiftlet conservation in Sarawak by Mr R. E. Stebbings and on Eared doves in Argentina by Dr R. K. Murton, described in the 1974 Report, and on the conservation needs and possibilities in Mauritius and the Seychelles by Mr J. E. A. Proctor in the same period. In 1976, two officers are expected to undertake field work in India for the International Union for the Conservation of Nature, developing a scheme for surveying and recording habitats in the nature reserves established to protect tigers. The range of these projects says something of the versatility expected of an ecological Institute today.

There are some areas in which ITE staff are actively co-ordinating international research. The Biological Records Centre (BRC), which was one of the first centres to be established in the world to collect systematic information on the distribution of plants and animals, is active on a European scale. Dr F. H. Perring of the BRC has played an active part on the Committee for Mapping the Flora of Europe, and Mr J. Heath has been a leading member of the Committee of the European Invertebrate Survey: the BRC has also contributed to the European Ornithological Atlas Committee. All these schemes are direct developments of the initiative established within BRC, and link the work of the Centre to that in other parts of Europe. In the same way, members of BRC have influenced developments of similar mapping schemes in Australia, New Zealand, Canada and the United States.

There are many (some may say too many!) scientific and professional societies and associations, many of which are international in their outlook and coverage. Care is needed in choosing which are appropriate for support from ITE staff. In the non-Governmental field most of the leading organisations are Unions or Committees of the International Union or Scientific Unions (ICSU). ITE staff are participating in the work of the International Union of Biological Sciences (IUBS), the International Association for Ecology (INTECOL), and the Scientific Committee on Problems of the Environment (SCOPE). In the past, there was a major commitment to the International Biological Programme (IBP), run by a Special Committee of ICSU (SCIBP). Outside ICSU, members of the Institute have participated in the work of the International Union for the Conservation of Nature and Natural Resources (IUCN) (of which the United Kingdom Government is a member), the International Union of Forest Research Organisations (IUFRO) and the Soils Working Party of the Council of Europe. In 1974/75 two working parties of IUFRO met in Edinburgh for discussions of processes in forest canopies and physiology and tree improvement, organised by Drs E. D. Ford and M. G. R. Cannell respectively. Members of staff have also taken an active part in the work of several United Nations agencies, including the UN Environmental Programme (UNEP), UNESCO, the Food and Agriculture Organisation (FAO) and the United Nations Development Programme (UNDP).

The International Biological Programme played a major part in the development of new approaches to ecology (even though these led, with hindsight, to the recognition of how that programme could have been better planned!). Within ICSU, world environmental problems are now the concern of the Special Committee on Problems of the Environment (SCOPE). The Director of ITE, Dr M. W. Holdgate has been a member of the steering committee of SCOPE (which met twice at ITE's Monks Wood Experimental Station in 1975/76) and is joint editor of its Report to the 1976 General Assembly of ICSU, while Mr J. N. R. Jeffers is a member of an international committee for the SCOPE project on simulation modelling. British scientists, including many now in ITE, made major contributions to the IBP projects in the Productivity Terrestrial (PT) section of the programme concerned with woodlands, grasslands and tundra, and also to the Conservation Terrestrial (CT) section. At Loch Leven, in Scotland, staff based in Edinburgh worked alongside colleagues from Government and Universities in a main site study in the (Productivity Freshwater) PF section. The need to link work on British sites with that in other countries led to much collaborative work with scientists overseas : indeed, one of the principal advantages of IBP was that it brought scientists who had hitherto been working in isolation together, and defined the ecological similarities between widely separated areas. ITE

scientists played a particularly important role in the international synthesis of the Tundra project: Mr A. J. P. Gore in initiating the co-ordination of research and the comparative analysis of data, followed by Dr O. W. Heal as one of the Chairmen of the Tundra Biome Steering Committee. UNESCO's Man and the Biosphere (MAB) programme is a major programme of research and development which is, in some respects, a successor to IBP. It seeks to identify and assess changes in the biosphere, examine the structure, functioning and dynamics of ecosystems, study the interrelations between ecosystems and social and economic processes and develop the necessary technique for measuring change in the environment. As a result, it is hoped that world-wide environmental research will become more coherent, that simulation and modelling will be promoted as tools for environmental management and that environmental education will also be improved.

The scientific approach of the MAB programme involves the analysis of ecological systems and studies of interactions between man and the environment. The information collected is being integrated over various spatial levels, and modelling techniques which allow quantitative predictions are included. The programme is, therefore, a major initiative to solve many of the ecological problems which are of international significance. Mr J. N. R. Jeffers, the Deputy Director of ITE, is the UK delegate to the International Coordinating Council of MAB and represents the UK at the meetings of this Council. Several members of ITE staff have played major roles in the expert panels and working groups of the individual projects of MAB, and have helped to develop the fourteen major projects of the programme. ITE has made a particular contribution to the development of systems analysis and modelling as a foundation for research within MAB as a whole (Mr J. N. R. Jeffers was the Chairman of the Expert Panel on Systems Analysis and Modelling which did this work). In the UK, ITE is the lead agency for Project 2, on the ecological effects of different land uses and management practices on temperate and mediterranean forest landscapes, and Project 6, on the impact of human activities on mountain and tundra ecosystems. A monograph on Man and Environment in the Tristan da Cunha Islands, of which Dr M. W. Holdgate is joint author, is being submitted as a case study for Project 5 on the rational use of island ecosystems. The Institute expects to mount major programmes of research within Projects 2 and 6 and possibly 14, while continuing to provide a basic input of expertise and advice on systems analysis, for the programme as a whole.

Another form of international participation is through the reception in Britain of colleagues from overseas. Many visitors come to our stations, particularly at Monks Wood, Merlewood and Edinburgh, each year and a full catalogue is out of place here. As an example: at Edinburgh Dr P. Hannah of the University of Vermont spent 1974/75 studying the varying abilities of different birch seedlings and seedlots to utilise fertilizers, Dr J. H. Warcup (Waite Institute, Adelaide, Australia) investigated the factors influencing the formation of beneficial mycorrhizas, and Drs C. Matieri and Kanda of the Argentine and Japan respectively studied the herbarium collection of Antarctic bryophytes.

The most productive international work, scientifically and personally, is probably that which takes individual scientists to situations in which they can investigate significant ecological problems in partnership with

colleagues from the countries they are visiting, and the interest of such work is enhanced if the problems being studied are clearly important to the management of the land or freshwater and the living systems they support. The diverse expertise of ITE is clearly applicable in many parts of the world where ecological problems are acute. It is the policy of NERC to make this expertise available to Governments and Agencies who seek to avail themselves of it, provided that these demands can be met without sacrifice of tasks of higher priority, and resources are available to support the research. This Report provides sufficient evidence of the range of skills within the Institute, and it is to be hoped that ITE staff will continue to participate in the future in overseas studies that will both benefit them as scientists and contribute to the solution of the world's pressing environmental problems.

The research of the Institute in 1975

Introduction

Section I of this Report described how ecologists contribute to planning and to the management of land. It indicated the need for knowledge at several levels and demonstrated that information may need to be gathered in steps that form a logical sequence.

That sequence often begins with survey, to establish the pattern of distribution of habitats, species and communities. Such surveys need to be designed to answer questions and to avoid the trap of amassing vast quantities of data of doubtful relevance. This Section illustrates this point by commencing with six contributions on different aspects of survey methodology, followed by nine reports on surveys of habitats and six investigations of species distribution and taxonomic variation.

Such studies may themselves provide important knowledge of how the performance of animals and plants varies from place to place and why, but very often these are matters that need to be explored further by experiment. Examples of the kind of detailed investigation required are provided in the subsequent parts of this Section, which deals with the performance of species, including trees and their associated fungal mycorrhiza, plants on coasts and mountains and the population dynamics and ecology of ants, butterflies, birds and deer.

An understanding of ecosystem processes is equally vital to the interpretation of the patterns revealed by survey, and there are seven accounts of work on such matters. These lead on to a series of reports of research on the effects of land use practices (including conservation management) on plant and animal species and communities.

Man also affects environment and living organisms through the release of chemicals, that is, pollution. This year only six of the many ITE projects on pollution are reported, because a number of studies are only just beginning. The six accounts do, however, reveal the breadth of the field. Finally, the diversity of work in special sections and services of the Institute is exemplified by the accounts of the sub-divisions of Chemistry and Instrumentation, and of Algal and Protozoan Culture.

Methods of survey and environmental characterisation

SYNOPTIC REVIEW OF FRESHWATER ANIMALS AND ECOSYSTEMS IN GREAT BRITAIN

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

There is no objective account of the number of, or range of variation in, freshwaters in this country nor of the organisms which inhabit them. Such a study is an essential preliminary to projects attempting to classify freshwater ecosystems, assess their conservation value or predict the impact of many kinds of human interference. The current work is designed as a series of independent studies which together form the basis of a major synoptic review of British freshwater ecosystems. The preliminary desk studies fall into three categories:

(1) Data banks of physical information on British freshwater. A major index covering all standing waters on 1:250,000 maps has already been completed and reported on (see *ITE Annual Report 1974*, pp. 62–64).

(2) Coded check lists of all organisms occurring in freshwaters in Britain. These will provide a firm basis for recording and analysing data concerning any species of plant or animal in Great Britain.

(3) A survey of the literature on freshwaters or freshwater organisms in Great Britain. It is intended that this will provide a basis for assembling or analysing available data related to freshwater ecosystems in this country.

The preliminary draft of the coded check list, which excludes Protozoa but includes all other freshwater animals from sponges to mammals, has been thoroughly revised for publication. It consists of three sections:

(1) An explanatory introduction including tables indicating the major groups covered, the number of species in each and the literature sources for that part of the list.

(2) The coded check list itself which covers just over 3,800 species.

(3) A bibliography listing the major identification keys and recent taxonomic reviews of all the groups concerned.

The checklist is organised in such a way that each species can be represented by a unique 5-digit code, thus establishing a standard and relatively easy basis for handling species lists, etc., numerically. The format of the list is quite simple and the numbers meaningful taxonomically. The first two columns (and their appropriate digits) represent the equivalent of phyla and classes or orders respectively. The 3rd and 4th columns give families and genera, while the 5th column includes specific names and authorities. The numbering system is sufficiently flexible to be able to distinguish full identifications to species level from those left at family or genus.

The increasing numbers of surveys of aquatic animals being carried out by freshwater ecologists in many parts of the country, especially by those working in the field of water supply, pollution prevention, fisheries and conservation, mean that the acceptance of a common check list, particularly a coded one, is becoming more and more desirable. It is suggested that the present one is extensive and versatile enough to meet the needs of almost all freshwater ecologists in the British Isles. The bibliography included with the list (114 references) will allow those anxious to identify animals in any group easy access to the main keys available.

A draft check list of higher plants (405 species) has also been produced and consideration is being given to a list of Algae. This will obviously require considerable effort since it may include about 8,000 species.

References to relevant papers in most of the major journals have been extracted for the bibliography. The criteria for including any paper in the system are that it must refer to a freshwater site in the British Isles and/or to an animal species included in the coded check list. Relevant journals are being searched from their inception up to 1970. It is intended to rely beyond this date on one or more of the various abstracting systems available. The bibliography is being organised and held initially on an author index and a content punch-card index system.

P. Maitland K. East K. H. Morris

CLASSIFICATION OF VEGETATION BY INDICATOR SPECIES ANALYSIS

Indicator species analysis, developed within ITE, is one of very few methods of classification that, being programmed for computer, can handle really large sets of data. Since its publication by Hill, Bunce and Shaw (1975) it has been successfully applied to several situations and as a result, its reliability and ease of interpretation have been confirmed. It has become apparent during the last year that classifications can often be much improved by incorporating quantitative, as well as qualitative data because lists of the presence and absence of species may not contain adequate information. The method has been applied to several sets of quantitative data describing upland vegetation, producing results which closely agree with earlier published descriptions. Paradoxically, the success of the method has revealed a new problem: how to ensure that subsequent analyses do not always have to return to first principles, but instead can build on existing knowledge. For example, the analyses all confirm that the main distinction in upland areas is between heath vegetation on the one hand, and grassland on the other. Now that this is known there is little value in allowing new and possibly different lines of demarcation to be drawn between heath and grassland by each subsequent analysis. New methods of analysis must allow the user to have greater control over the details of his classification including a greater ability to incorporate existing knowledge.

M. O. Hill D. F. Evans

Reference

Hill, M. O., Bunce, R. G. H. and Shaw, M. W. (1975) Indicator species, a divisive polythetic method of classification, and its application to a survey of native pinewoods in Scotland. *J. Ecol.*, **63**, 597–613.

PLANT INVENTORIES IN WOODLANDS

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

The managers of enterprises require inventories of their stock from time to time. For the rational management of areas such as National Nature Reserves these should provide comprehensive descriptions of existing vegetation which are periodically brought up to date. Several of these inventories have been prepared under contract to the Nature Conservancy Council, principally in woodlands but also in habitats which may be reverting to woodland or becoming woodland for the first time.

The methods used were designed to comply with a number of criteria. First, samples should be taken objectively to avoid bias when deciding on representative or typical areas. Second, to enable temporal variation to be studied, sample areas must be easily and confidently relocated on subsequent occasions. Third, samples taken on the first occasion should be as large as practically possible to minimize constraints on the choice of sampling methods to be used in the future.

At Kirkconnell Flow NNR, Kirkcudbrightshire, a lowland raised mire being colonized by birch and Scots pine, these criteria were met by the use of a permanently marked, randomly-sited systematic grid with intersections at 100m (Plate 1). Species occurring in 159 sample plots of 200m² were recorded and subsequent analyses classified the sample plots into eight groups. A dichotomous key, based on this classification and on indicator species, was used to extend the sample by determining the affinities of a second series of plots taken on a superimposed lattice of samples. The combined samples indicated that the differing plant assemblages were arranged in concentric zones. A central zone occupies one-third of the Reserve's area and is dominated by Eriophorum vaginatum and Calluna vulgaris in almost equal amounts; bog species such as Andromeda polifolia, Oxycoccus palustris, Drosera rotundifolia, Narthecium ossifragum and several Sphagna are also common in this, the wettest part of the area. Within this matrix, colonization by Scots pine has reached various stages of development which are associated with changes in the balance of species, and by the presence of more shadetolerant species such as Vaccinium myrtillus. Bordering the central zone is an area which has been disturbed in the past by peat cutting or fire, or by both. It is dominated by Calluna vulgaris and hydrophilous species are generally absent. In this zone, Scots pine commonly forms an open canopy beneath which birch saplings and seedlings are locally frequent. Further from the central zone woodland development is more advanced with both Scots pine and birch forming stands over 15m high and with a ground flora containing common woodland plants such as Dryopteris dilatata, Oxalis acetosella, Polytrichum formosum and many Sorbus aucuparia seedlings.

To study in detail the recruitment, growth and mortality of Scots pine and birch, 40 sample plots were selected using strata based on the first stage vegetation survey. This sample has shown that the relationship between the ground flora composition and numbers and sizes of seedlings, saplings and trees is reasonably predictable but the dynamics of succession (rates of change) need to be verified.

J. M. Sykes A. D. Horrill

A METHOD OF ASSESSING THE ABUNDANCE OF BUTTERFLIES

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

There is a need for a simple method of recording the abundance of butterflies in nature reserves and similar places so that changes from year to year can be assessed. A method, based on transect counts, has been developed at Monks Wood over the last three years.

The recording method consists of a regular walk along a transect. All butterflies encountered within prescribed limits are recorded. Counts are made only if certain minimal weather conditions are met, and the aim is to complete at least one each week from April to September inclusive.

The studies in Monks Wood, using several recorders, suggest that the method is reliable in the sense that counts are repeatable. Different recorders produce similar counts and the data indicate that variations in weather conditions, within the recommended limits, are not of great importance. It remains to be demonstrated that the index of abundance obtained is closely related to population size but studies in greater depth on two species strongly suggest that this is so.

Several National Nature Reserve wardens have been using the recording method during 1974 and 1975, fitting in counts when convenient in the normal course of their work. A few amendments to the recording instructions have been made as a result of this pilot trial, but there were no major problems.

The method was designed primarily for detecting year to year trends. In addition it is expected that the data will provide information on various aspects of the ecology of butterflies, on habitat requirements and on the effects of management on populations within reserves.

Examples are given (Figure 1) of counts made in Monks Wood for the Large skipper Ochlodes venatus (Br. and Grey), wall Lasionmata megera (L.) and ringlet Aphantopus hyperantus (L.), illustrating some of the striking changes which have already been observed. *E. Pollard*

ESTIMATION OF SOIL TEMPERATURES FROM METEOROLOGICAL DATA

Soil temperature is influenced by air temperature and other aspects of climate, by the exposure of the soil which is strongly influenced by vegetation cover and type, and by soil characteristics, particularly mineral, organic matter and water content and density. Temperature affects a wide variety of soil biological, chemical and physical properties and hence its estimation is a necessary part of many ecological studies. Unfortunately, detailed measurement is time-consuming and expensive so, with the help of Mr J. N. R. Jeffers and Mr D. K. Lindley, we have examined ways of estimating soil temperatures from the kinds of meteorological data which are often available.

Soil temperatures, measured over three years within the IBP Woodland site at Meathop Wood, south Cumbria, were compared with meteorological data from outside the wood. Six types of mathematical relationship were established between weekly mean soil temperature at 0cm and 50cm soil depth and meteorological variables. These relationships involved :

(a) linear regression of soil temperatures on air temperatures

(b) multiple regression of soil temperatures on different combinations of up to 14 meteorological variables

(c)–(f) four ways of relating soil and air temperature data using harmonic (Fourier) analysis (Bocock *et al.* 1974).



Figure 1 Mean weekly counts of three species of butterfly on the Monks Wood transect. Index values are given for each generation, the Wall having two generations a year, the others only one.

Relationships (a)–(f) were then used to estimate soil temperatures for 67 individual weeks spread over the three-year recording period and also for 12 other weeks from the following year. Estimated soil temperatures were then compared with actual recorded soil temperatures for the selected weeks and the precision and accuracy of the six ways of estimation were then compared. It was concluded that:

(i) for both soil depths, mean air temperature was the most important estimator of mean soil temperature, although changes in air temperature during the previous one to three weeks also had significant effects. Day length and total flow of wind were significant estimators of temperature at 0cm and 50cm respectively but surprisingly none of the rainfall variables, which influence soil moisture, were important,

(ii) for weeks within and outside the three year recording period soil temperatures estimated using linear regression were appreciably more variable than those estimated by multiple regression (Figure 2),

(iii) estimates were usually more precise for soil depths of 50cm than for 0cm.

(iv) best estimates for the 12 weeks outside the main recording period were about 0.5° C high but nevertheless they were within about 1.5° C of the expected values, about the same as best estimates for within the recording period (Figure 2),

(v) the differences between methods other than linear regression were not significant, so the choice between the predictive relationships (b)–(f) is largely a matter of convenience.

K. L. Bocock J. K. Adamson

Reference

Bocock, K. L., Lindley, D. K., Gill, Christine, A., Adamson, J. K., and Webster, J. A. (1974) Harmonic analysis and synthesis: basic principles of the technique and some applications to temperature data. *Merlewood R and D paper* No. 54, 29 pp.

PLANT ISOENZYMES AND THE CHARACTERISATION OF PLANT POPULATIONS

When studying how plant species are adapted by natural selection to local environments, interpretation is often restricted by lack of knowledge about the genetical structure of the populations occupying such environments. The physical form of the surviving plants





Figure 2 Observed weekly mean woodland surface soil temperatures (0°C) compared with temperatures predicted from (a) linear regression of soil temperature on air temperature.

(b) multiple regression of soil temperature on five

regressor variables (air temperature, changes in air temperature during the previous one, two and three weeks, and day length).

Weeks within the three year recording period denoted by black dots, and weeks outside by stars.

can usually be studied and from such observations inferences can be made about the type of selection which might have operated on individuals in the population to produce the observed range of variation. For example, in order to discuss whether a very homogeneous dwarf prostrate population of the grass *Puccinellia maritima*, contrasting markedly with a nearby population which includes tall erect plants is likely to have been produced by selection, it is first necessary to know something about the inter-relations of the individuals it comprises. At one extreme they could all be the same individual which has spread by vegetative means to occupy a large area; at the other extreme they could all be genetically distinct.

Usually the analysis of genetic variation in plant populations involves a long, complex programme of collateral (side by side) cultivation and cross-breeding, in which measurements of morphological characters are made to estimate their heritability and variability in different environments. However, the recognition that some enzymes exist in multiple molecular forms (termed isoenzymes) and that these can be distinguished by the technique of electrophoresis, has made the process easier. Although their appearance may differ with the type, age and pretreatment of plant tissues, isoenzymes usually separate on electrophoresis into distinct bands which can be distinguished by specific staining (Plate 2). This technique does not dispense with the need for cross-breeding which in most instances has shown that the presence of isoenzymes is genetically controlled.

Most known isoenzyme polymorphisms involve simple gene systems with, for example, 2 bands each being produced by alleles of the same locus, although multiple allelism is commonly found and heterozygotes may have 'hybrid' bands mid-way between the two homozygous parental bands.

Irrespective of such details, the fact that the different isoenzymes are genetically controlled makes them valuable in inferring the structure of species. For example, the fact that morphologically similar plants are not the same individual can be established (although the converse, that they are the same individual, cannot be proved directly) and in this way the relatedness of individuals in a local population can be estimated. Further, in species which are habitually both self and cross fertilised, hybrids can be identified by the appearance of paternally-derived bands. Thus the degree of outbreeding and inbreeding in both artificial and natural populations can be assessed. It is also possible to calculate allelic frequencies for a whole range of populations and to consider the effects of positive assortative mating, selection, inbreeding, population size and migration on the genetic constitution of these populations.

A. J. Gray

Survey of habitats

CLIFF VEGETATION IN SNOWDONIA

The ungrazed cliffs of Snowdonia are refuges for native plants and their flora has considerable scientific interest. They harbour elements of arctic and alpine origin as well as those whose distribution is continental or oceanic in western Europe. Additionally there are species which are common to the mountains of Britain and also those of lowlands, including woodland. Recent studies have sought to determine the composition and distribution of communities containing arctic and alpine species and to relate these to environmental features including soil nutrient status.

The vegetation was described in terms of groups of stands of similar species composition. These were not discrete but were instead subjective divisions of the vegetational continuum derived by ordination (Hill 1973). The seven groups (A--G) form a series from heaths and acidic grasslands to vegetation of more base rich situations (Plate 3); they distinguish habitats modified by the activities of sheep from those which are inaccessible. In the heaths and acidic grasslands (Group A) Agrostis canina, Vaccinium myrtillus and Deschampsia flexuosa were prominent. Agrostis tenuis/ Festuca ovina grassland rich in bryophytes (Group B) was widespread as was the related A. tenuis/F. ovina grassland (C) containing a range of lowland grassland species, e.g. Plantago lanceolata, Trifolium repens and Achillea millefolium. Six arctic-alpine species, e.g. Oxyria digyna and Saussaerea alpina were occasionally present. Habitats highly modified by sheep were typified by Agrostis tenuis grasslands (D) including lowland grasses, Poa annua, P. pratensis and P. trivialis; they did not contain species with arctic-alpine affinities. In less accessible sites there was herb-rich vegetation (E) with a variety of species including Agrostis tenuis, Festuca ovina and F. vivipara and up to 14 arctic-alpine species. The vegetation of steep slopes, clefts and ledges (Group F) included Oxyria digyna, Saxifraga oppositifolia, Sedum rosea, Silene acaulis, Carex atrata, Dryas octopetala, Lloydia serotina and Potentilla cranzii among the 25 species of arctic-alpine affinities which were recorded. Dominantly arctic-alpine vegetation (Group G) containing such species as Saxifraga oppositifolia, Sedum rosea, Woodsia alpina and Poa alpina was found in habitats isolated from grazing (Plates 23-28).



Plate 1 Vertical aerial photograph of Kirkconnell Flow National Nature Reserve (1967) showing the location of 159 permanent sample plots at the intersections of a 100m grid. Reproduced from the Ordnance Survey aerial photograph with the permission of the Controller of Her Majesty's Stationery Office (Crown copyright reserved).



Plate 2 Isoenzyme banding patterns revealed by acrylamide gel electrophoresis of esterase obtained from eight morphologically similar individuals of Puccinellia maritima. Note at least six distinct bands. Photograph A. Gray.



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Plate 3 Occurrence of 7 vegetation groups, including some with arctic–alpine affinities, in locations with differing amounts of available phosphate and exchangeable calcium found on the cliffs of Snowdonia (Vegetation groups A–G are described in the text, see page 16; size of circle indicates relative abundance).



Plate 4 Vertical aerial photograph of Culbin Shingle bar (1967). Reproduced from the Ordnance Survey aerial photograph with the permission of the Controller of Her Majesty's Stationery Office (Crown copyright reserved).



Plate 5 Gull roost area on the newly accreted western end of the Culbin Shingle Bar. The development of vegetation in the sandy hollows contrasts with the sparse growth on adjacent shingly ridges. Photograph *R. Fuller.*



Plates 6/7/8 Specimen trees of three provenances of Pinus contorta showing inherent variation in height, growth and branching habit. The trees are all 9 years old and growing at the same forest site (from Cannell, 1974).



Plate 9 Developing bud of Picea sitchensis, viewed from above in summer, after the scales have been removed. Numerous needle initials surround a large central apical dome. The scale bar is 0.5 mm long.



Plate 10 The same, in autumn, when the dome is smaller and less active. The scale bar is 0.5 mm long.



Plate 11 The same as seen in winter, with all the needles for the next year preformed in the bud. The scale bar is 0.5 mm long.

Photographs M. Cannell.

Plate 3 illustrates how the occurrence of these vegetational groups is influenced by amounts of exchangeable calcium and available phosphate occurring in soils. Species with arctic and alpine affinities were prominent mainly in ungrazed situations on steep slopes, ledges or clefts, where soils, derived mainly from a basic volcanic rock, pumice tuff and with relatively large amounts of calcium and phosphate, sometimes tended to be seasonally wet.

Clearly this kind of information is only indicative of the major environmental features influencing the distribution of species. Experimental work in which, for instance, the chemical factors of the soil are varied is a necessary development, so that more precise statements can be made concerning the circumstances which will ensure the future survival of this unique constituent of our flora.

R. E. Hughes J. Dale Jane Lutman A. Thomson

Reference

Hill, M. O. (1973) Reciprocal averaging: an eigenvector method of ordination. *J. Ecol.* **61**, 237–49.

SURVEY OF MATURE TIMBER HABITATS

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

Mature and over-mature deciduous trees support populations of many rare or uncommon species of invertebrates, especially Coleoptera (beetles) and Diptera (flies). The really old trees and decaying fallen trees suitable for these species, while common in natural forest, do not usually survive under normal woodland management. Many species of invertebrates associated with mature timber habitats in Britain have apparently declined recently or have been known only from a few well recorded localities such as Windsor Forest and Great Park, Berkshire; the New Forest, Hampshire; Moccas Park, Herefordshire, and Sherwood Forest, Nottinghamshire.

In response to a request from the Nature Conservancy Council an inventory has been compiled of areas likely to contain significant samples of the mature timber habitats favoured by these invertebrates. Nearly 400 areas are listed in the inventory which is derived from various sources including information from numerous entomologists and botanists. Many of the areas are also known to be of value for the conservation of the communities of lichens and bryophytes which are epiphytic on old deciduous trees.

Surveys were made of 45 areas in 1975, many of which were deer parks of medieval origin. Estimates were made of the species composition and age structure of trees and shrubs, the amount and distribution of dead wood and the regeneration or planting of trees and shrubs.

The management of the area was also examined, especially in relation to the removal of dead wood and old trees. Three management problems which could seriously reduce the conservation value were common to most areas visited. These were a discontinuous age-class distribution of the major tree species, or a complete lack of succession, the practice of progressive clearance of both living and dead old trees, and the clearance of fallen dead wood.

Having identified areas where these habitats may be particularly well represented it is possible to gain information about many from published records and from the collections and diaries of entomologists. To simplify the abstraction of records, a list of about 100 species of Coleoptera has been compiled with the cooperation of several entomologists. The species listed are associated with over-mature trees and dead wood, and many can be considered to be indicators of old forest areas in Britain.

P. T. Harding

STUDIES ON THE FAUNA OF JUNIPER

It is often said that in order to conserve a particular invertebrate fauna it is sufficient to protect the plant species with which it is associated. In these studies an attempt is made to understand how far this applies to the fauna of juniper, *Juniperus communis* L.

In the first part of the work, an inventory of the fauna was compiled from fieldwork and from the literature. In Britain 29 native species are reasonably specific to juniper as a food plant. One additional species is apparently extinct, while eight alien species have been introduced on ornamental *Juniperus* or other Cupressaceae. One of these has already been recorded on native juniper and others might spread to the wild species. Some predaceous and parasitic species may also be confined to the plant because they feed on herbivores specific to it. Knowledge of these groups is poor, but some 70 species have been recorded, most in southern England: three were new to the British list. It is certain that there are many more species which might be recorded with additional detailed work.

There is an abundant fauna which is not specific to the juniper. Many of these are associated with its abundant epiphytic lichens and algae, or overwinter in the shelter of the dense evergreen bushes. Several hundred species were recorded in southern England, and about 100 have been listed as common. For conservation the specific species are the most important, for they would be lost if the plant was destroyed on a site. Some of these species can also occur on ornamental Cupressaceae, but only the native sites will have the full fauna. Not all species will occur on any one site, for the distribution of each is super-imposed on that of the juniper.

Maps of the known distribution of all the phytophagous species have been prepared to show the regional differences in the fauna. There is striking contrast between northern and southern Britain, eight species being entirely northern and eight entirely southern. These distribution patterns are not static however, because some species are spreading to ornamental shrubs which have been planted in large numbers over recent years, while at the same time others are contracting in range as native junipers are lost.

In the second part of this work, the detailed variation of the specific phytophagous species on sites in southern England has been studied. Previous survey located all known juniper sites, and established that they were declining in number and size. Thus the fauna was expected to be affected adversely. The sites are discrete and can be seen as islands of food-plant in an otherwise hostile environment, and biogeographical theories of island biology can be applied to the results. A series of sites which differed in size and in other characteristics were visited on the North Downs (1968) and the Chilterns (1969). A total of 15 native species was recorded out of the possible regional total of 19, and as the size of the site declined so did the numbers of species. The species were not randomly represented, but sequentially, and the first to be lost were the three species feeding on the berries. The results were analysed using multiple regression techniques with the number of species as the dependent variable and the characteristics of the juniper sites as the independent variables. Site-size, as measured by the number of bushes, was most important. On the North Downs it accounted for 79% of the variation in the species number and on the Chilterns for 87%. The continuity of the site represented by the age of the oldest bush accounted for a further 9% of the variation on the North Downs. When the data were pooled to provide an approximation for the fauna of southern England, bush-number accounted for 77% of the variation, age of the oldest bush a further 5% and distance to the nearest other site with 100 or more bushes a further 4%. The great importance of site-size is demonstrated by these results, but the variation meant that it was difficult to give an exact estimate of the number of bushes needed to conserve the full fauna. Using the pooled data, however, very large sites with over 3,000 bushes are reasonably likely to support the 15 commoner species, while sites with 300 bushes have a probability of only about 0.05 of having all these species. The data also provide prediction equations for estimating the number of species on sites which have not been visited but whose important characteristics

are known. This information is available from the survey of all juniper sites in southern England carried out earlier. There were eighty six sites with over 50 bushes which might have much of the fauna present. The number of species were predicted for all these sites. There were four sites predicted to support 15 or more species, five with 14 species and twenty seven sites with 12 or 13 species.

Lena K. Ward K. H. Lakhani

SHETLAND

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

The survey of Shetland described in ITE Annual Report 1974 has been largely completed and has been drawn upon by NCC and the Sullom Voe Environmental Advisory Group (SVEAG). This group (made up of representatives of the oil industry, Local Authority, NCC, Countryside Commission for Scotland, and NERC together with two independent members) has published an Environmental Impact Statement for the Sullom Voe terminal and has advised the Shetland Islands Council and the developers on methods for minimising environmental damage. The Director of ITE, Dr M. W. Holdgate, represents NERC on SVEAG, with Dr H. T. Powell of the Scottish Marine Biological Association to cover marine ecology and monitoring.

Analysis of the results of the ITE survey has illustrated the considerable complexity of the Shetland environment. The archipelago is dominated by the influence of the sea although there is also considerable diversity inland. The Walls peninsula, hitherto unregarded by conservation bodies, has a large number of lochs and lochans set within an undulating peat-covered topography with distinctive characteristics. In contrast the higher hills around Ronas Hill have less peat and different topographic characteristics.

The vegetation of Shetland is dominated by the species of blanket bog. Ling heather, Cotton sedge and *Sphagnum* moss are widespread. There is, however, much small scale variation within the blanket bogs, which are almost always richer in species than their mainland counterparts. When the maritime vegetation and that of rock debris and eroded peat are considered together with the very species rich grasslands and hay fields, the considerable diversity of the Shetland vegetation is evident. The limited and carefully controlled industrial developments now going ahead are unlikely to impair this diversity significantly.

The archipelago abounds with lochs, lochans and streams. Most of the lochs of Shetland are less than 1 ha in extent and there are few large waterbodies. The highest concentrations of small lochans with their characteristic waterfowl are on the glacially eroded plateaux of North Roe and the Walls peninsula, where moderate sized rock basins are the predominant type. There are also many in areas of deep blanket peat, where peaty pools are the main type of waterbody. There are a few large lochs important for wintering waterfowl. The smaller lochans are usually acidic and their floras and faunas are of low species diversity whereas the larger lochs, occurring in areas of the more soluble sedimentary rocks, are often alkaline.

The Shetland coastline and shallow sub-littoral varies widely in its physical features, from extremely exposed rocky headlands to sheltered sedimentary beaches (which are however uncommon). The Shetland coast and seas have a rich flora and fauna, and some affinities with the Scottish west coast sea lochs. The richness is probably related to variability of substrate rather than to biogeographic factors.

The survey by NERC staff and their collaborators was drawn upon by SVEAG in writing the general account of the Shetland environment included in the Impact Statement, and was also used, together with information provided by NERC's marine Institutes and Universities, in planning the system for monitoring the impact of the industrial development. This is one direct product of the survey. Another comes through the extension of its methods of stratification sampling and analysis to a wider survey of Britain. Such methods appear valuable in reducing the time required for such large scale surveys, although the information content is reduced, and the broad surveys need to be supplemented by intensive examination of localised sites of especial interest. The data collected in Shetland are also undergoing further analysis, in conjunction with the NCC as customer for part of the survey.

ITE's Subdivision of Data and Information is also developing three types of mathematical model based on the data collected during the survey. The first, involving Markov processes is highly formalized but is expected to yield considerable insight into the changes to be expected in the Shetland environment. The second, involving the co-operation of economic analysts who have already produced models for Shetland, will attempt to integrate environmental with economic change, leading eventually to an integrated decision model. The third, using system dynamics will be less empirical, but will inevitably rely on less clear or formal relationships. Advice on this approach has been obtained from Canadian workers with experience in the use of models for predicting the environmental impact of major industrial development in wilderness areas.

It is the aim of these modelling projects to add further techniques to those available for environmental impact decision making. The Shetland survey provides a unique multi-disciplinary base for developing these techniques in a pilot trial in an important and interesting part of the United Kingdom.

C. Milner

THE CULBIN SHINGLE BAR AND ITS VEGETATION

The Culbin Shingle bar forms the seaward fringe of a 30 km² system of coastal dunes and shingle ridges on the Moray Firth between Findhorn and Nairn. At 55 ha the bar represents only a small part of the system, but after extensive afforestation it alone exhibits the natural plant successions to be found on the Culbin shingle.

The bar once formed part of a spit across the mouth of the River Findhorn but, breached in 1702, it has been carried south-westward towards Nairn by processes of erosion and accretion. Wind-blown sand from intertidal flats near Nairn forms dunes on the landward recurves of the shingle ridges (Plate 4).

A vegetation map of the bar was prepared from aerial photographs and together with ground surveys of topography, soil composition and plant communities it provides a baseline against which changes can be measured. Differences in species and cover abundance on ridges and in lows are considered attributable to the deposition patterns of wind-blown sand; laboratory experiments having shown that shingle holds more moisture if mixed with small quantities of sand (Figure 3). Because evaporation is decreased by a surface shingle 'mulch', the mixture also retains more moisture for longer than either pure shingle or sand. Windblown sand and litter are more readily trapped and accumulate in the lows, where the substantial amount of plant growth contrasts with its paucity on the ridges, an unusual situation contrasting with many shingle beaches where wave-borne fine material, deposited at the time of ridge formation supports vegetation whereas the lows remain bare. The pebbles of the Culbin shingle become encrusted by a black lichen. Rumex crispus colonises the shingle beach strandlines and, where finer material accumulates Silene vulgaris ssp. maritima and Cerastium atrovirens establish. As further sand is trapped Festuca rubra and Poa pratensis grassland develops and, in turn, is colonised by Festuca ovina as acidity increases. Shrub species including Calluna vulgaris and Empetrum nigrum subsequently invade this sward before Ulex europaeus and Sarothamnus scoparius establish themselves (Plate 5).



Figure 3 Effects of increasing proportions of sand in shingle mixtures on (a) field capacity and (b) subsequent water retention in pots kept under laboratory conditions.

The array of plant communities found on the Culbin bar illustrates the sequence of plant assemblages naturally colonising apposition shingle modified by the influx of wind-blown sand. It is one of very few examples in the UK.

R. M. Fuller

VARIATION IN BRITISH PEATLANDS

In the past attempts to classify peatlands in Britain have relied mainly on subjective assessments of floristic composition or have been based primarily on site morphology either by itself or in conjunction with estimated hydrological conditions or mean chemical composition of peat and peat waters. To improve this situation it was decided to carry out an objective analysis of the floristic composition of British mires and to attempt to relate the results to a similar analysis of environmental factors. A series of fifty six sites in Great Britain was chosen for sampling and at each of these 40 randomly located quadrats, $1 m \times 1 m$, were laid out and the presence of plant species within them was recorded. For analysis of results, however, those species occurring in 5 or fewer of the total 2,240 quadrats were discarded, leaving a total of 319 species.

Ordinations using the technique of reciprocal averaging (Hill 1973) and classifications using indicator species analysis (a derivative of reciprocal averaging) were performed for both site data and individual quadrat data. It was thought valuable to produce both ordinations and classifications, since the former would emphasise the continuous nature or otherwise of the variation found between sites of component plant communities whereas the classification could be expected to provide a means of separating different types of site or community, and thus help in the selection of areas which might require more detailed study.

Ordinations of whole sites showed a major distinction between nutrient poor (oligotrophic) sites with acid peats and water supplies derived solely from atmospheric precipitation, to nutrient rich (eutrophic) sites in which the peats are neutral and water is supplied mainly by run off from a surrounding catchment or by river flooding. Between the extremes there is a series of intermediate sites containing different proportions of a wide range of plant communities.

By successive division, sixteen readily interpretable groups were obtained from the classification of sites, these groups containing different proportions of the 26 end groups produced by classification of the individual quadrats. Whereas the site classification defines types of mire, the quadrat classification defines types of plant community (Figure 4).

At one extreme communities are found covering large areas of the most oligotrophic sites, e.g. group B. containing Calluna vulgaris, Trichophorum caespitosum, Racomitrium lanuginosum and Sphagnum tenellum, is the main component of site group 6 (oceanic raised and blanket mires of the north-west). Group T typifies the opposite extreme in which a community containing Cladium mariscus, Juncus subnodulosus and Phragmites communis is the major constituent of the highly eutrophic sites of site group 14 (the fens of Broadland and Anglesey). Intermediate groups, e.g. M, in which Sphagnum flexuosum, Erica tetralix, Vaccinium oxycoccus and Myrica gale are typical components, are found in smaller proportions within a large number of site groups. The analyses indicate that extreme sites contain large proportions of quadrats from few groups, whereas in the intermediate sites there are few quadrats within each of a large number of communities, indicating the high degree of heterogeneity of these sites, both in floristics and the factors controlling the distributions of individual species and communities of species.





When the performance of individual species was considered it soon became clear that species which grow together may be responding to entirely different environmental factors. For example, at a number of sites both Narthecium ossifragum and Phragmites communis were found growing together and showing a range of performance, as measured by height, flowering capacity and dry weight production although at times they may grow separately under very different conditions. At Roydon Common in Norfolk, the performance of N. ossifragum was found to be largely dependent upon the amount of oxygen to its root system. Elsewhere the supply of oxygen may be adequate but low levels of calcium in water tapped by the root system may be a limiting factor. At Roydon the amount of calcium appears to affect the performance of P. communis irrespective of water level whereas at other sites where calcium is abundant different factors control the performance of this species. The two species thus show considerable variation in the extent to which they utilise different ions dissolved in peat water so that although in some situations they may be growing in association they may not be strong competitors for mineral resources.

R. E. Daniels E. M. Field T. D. Murray

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MAN AND NATURE IN THE TRISTAN DA CUNHA ISLANDS The four volcanic islands of the Tristan da Cunha -Gough Island group were formed in association with the mid-oceanic spreading zone in the South Atlantic and lie 2,800km from South Africa and 3,200 from South America. They are all small, Tristan, the largest, being 12 km in diameter and 2,060 m high, and most are youthful (only Nightingale, the smallest and most eroded has yielded rocks dated at over 10 million years) : all display clear signs of recent volcanic activity. They are among the most isolated island groups in the world, and the only islands in the southern temperate zone whose native plants and animal communities remain substantially undisturbed by man. They have typically impoverished and disharmonic land flora and fauna, mostly derived from South America, which is upwind in the prevailing westerlies: among endemic species confined to the group are two flightless land rails, four other land birds and a number of flightless Diptera, Lepidoptera and Coleoptera. Very large populations of albatrosses, petrels and rockhopper penguins breed in the group, together with Elephant and furseals,

(which have recovered from near extinction a century ago). These features give the islands particular scientific interest. Visits in 1955/56, 1962 and 1968 and an extensive study of the literature have led to the publication of a monograph (Wace and Holdgate 1976) surveying the natural resources of the islands and the effects of several centuries of human impact.

The group was discovered by Portuguese sailors in 1505-6 and visited thereafter by the vessels of explorers and sealers. The only settlement ever made was on the largest island, Tristan, as a farming, fishing and sealing community. It was also used as a victualling station for whaling vessels. From its start in 1810, the population had grown irregularly to 264 at the time of evacuation in 1961 and in 1970 numbered 275 islanders and about 25 expatriates. Cattle, sheep, goats, pigs, donkeys, dogs, cats, and various poultry have been imported, and rats and mice were introduced by accident. The impact on the environment has been surprisingly localised to the coastal lowlands of Tristan, where a sward of mainly alien grasses has replaced the natural scrub and tussock grassland. Lack of fencing, poor control of stocking density and other mismanagement have lowered the fertility of the pastures: until recently the island subsisted largely on potatoes, with a few vegetables, and the produce of the sea.

Since 1948, a company based in South Africa has fished crayfish (*Jasus tristensis*) which is abundant around the islands. After the eruption in 1961–2, a harbour was built on Tristan, and islanders bring their catches to a new freezer. Standards of living have improved, and agriculture has been intensified.

Analysis confirms that the only significant exploitable natural resources of the islands are fish and crayfish, but farming on the lowlands of Tristan is capable of continued improvement. The islanders do not now depend on the traditional harvest of young Great shearwater (*Puffinus gravis*) from Nightingale Island, but this harvest has social value and is far below sustainable yield. There is little to gain from further overspill of agriculture or settlement onto the smaller islands of the group and hence conservation there is compatible with needs of the community, best met by intensive development of agriculture on the main island. New conservation ordinances have recently been enacted following ecological evaluation.

M. W. Holdgate (with *N. M. Wace*, School of Pacific Studies, Australian National University)

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ECOLOGICAL SURVEY OF THE LULWORTH RANGES. DORSET

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

The Ministry of Defence owns some 280,000ha of land in England, Wales and Scotland of which about half is used as firing ranges and for providing training facilities. Many of these areas are thought to be important for wild life conservation, a fact acknowledged in 1974 by the appointment by the Ministry of a Conservation Officer, part of whose job has been to establish a close liaison with organisations, societies, and people interested in wild life conservation.

In order to obtain details about the distribution and abundance of wild life on military land, the Nature Conservancy Council commissioned ITE to survey part of the Lulworth Ranges, Dorset. This included the 10.5km of coastline within the Dorset Area of Outstanding Natural Beauty along which the Ministry of Defence have recently marked out a footpath for public use (Plate 29).

Coastal habitats and the plant and animal associations of about 1,620ha of chalk, limestone and neutral grassland were surveyed and mapped. Studies were also made of former land-use and management in an attempt to explain the present day distribution of plant and animal communities.

Grasslands of 3 main types were distinguished :

(a) calcareous grassland on soils derived from the Chalk or Purbeck limestone in which Tor grass (*Brachypodium pinnatum*) was most abundant. In many areas, especially those burnt frequently, Tor grass formed dense stands in which few other species could survive; elsewhere, species-rich grasslands had developed in which Tor grass was less frequent, and other forbs and grasses were conspicuous;

(b) acid grassland and heath communities developed on drift deposits overlying the Chalk, including an unusual area of lichen-rich grassland;

(c) neutral grasslands on clay soils lying in the valley which separates the Chalk and Purbeck limestone escarpment.

Surveys of selected insect groups revealed that the Ranges had an outstandingly abundant and diverse fauna, especially of butterflies and grasshoppers. Among the butterflies, uncommon species such as the Lulworth skipper (*Thymelicus aceton*), Adonis blue (*Lysandra bellargus*) and Chalk hill blue (*Lysandra coridon*) were plentiful, especially on warm, south facing slopes. Of the 14 species of Orthoptera and Dictyoptera found on the Ranges, 3 are national rarities.

Ceperoi's ground-hopper (*Tetrix ceperoi*) was found only around seepages; the Long-winged cone-head (*Conocephalus discolor*) was common over one area of about 2ha, while the Grey bush cricket (*Platyceis denticulata*) was common on landslips and along the cliff-tops. Now that the sites of these rarities have been identified, special precautions can be taken to prevent the destruction of the habitat which is essential for their survival. Other fauna recorded during the surveys included 353 species of beetle, 67 species of spider, 112 species of moth and 29 species of Isopoda and Myriapoda.

Land-use studies indicated that with the exception of three small areas, the entire Chalk ridge had remained uncultivated in recent times, whereas most of the Purbeck limestone escarpment had been cultivated up to the late 1930s. It is not without significance that all of the floristically rich areas are confined to the uncultivated chalk escarpment while most of the previously cultivated areas on the harder limestones support coarse Brachypodium pinnatum grasslands. Another contributory factor in creating and maintaining floristic richness has been rabbit grazing, the location of commercial warrens in the seventeenth and eighteenth centuries on Little Bindon Hill probably creating the 'open' conditions which are still to be seen today. Photographs taken in 1911 reveal that scrub invasion in some areas had already begun before the Army took over the Ranges and that rabbit grazing was both intense and localised.

Data collected during the vegetation and insect surveys have been used to identify the most important areas for conservation on the Ranges; they also provide a base line from which changes in the future may be measured. Additionally, as a result of the survey, the management of the Ranges for wild life conservation can now be based not only upon a knowledge of the present distribution and abundance of species but also of past management practices which have been important factors in the development of the present plant and animal communities.

T. C. E. Wells

SURVEY OF SAND-DUNE AND MACHAIR SITES IN SCOTLAND

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

The coasts of northern Scotland have, until the last decade, been remote from major industry. Now, the exploitation of offshore oil and gas has brought pipelines, terminals and other developments to the region. The Nature Conservancy Council urgently needs information on habitats and vegetation so that the potential impact of these changes on conservation policies can be evaluated.

The Institute of Terrestrial Ecology has been given a three year contract to carry out a biological survey of more than 100 sites covering a total area of some 32,500 ha.

The specific objectives are to determine the nature and extent of habitats and the composition of the vegetation at each site so as to allow comparisons to be made between them. The presence of rare or localised plant species and some of the effects of human activities are also being recorded. A group of sites surrounding the Moray Firth was selected for priority attention in 1975/ 76 as these sites were considered most under threat from oil exploitation and related activities.

Sampling of large areas to meet the above requirement in a representative way presents many problems. The sites selected in the first year of the survey, 1975/76, varied in size from a quarter of a square kilometre to over 10km². They contain many species (243 were recorded on one site) and these often have to be identified from small heavily grazed specimens. A method was used in which sampling points were randomly pre-located within each site. The species of higher plants, mosses and lichens present, their approximate quantities (cover) and the most relevant habitat factors, e.g. topography, water table depth, organic matter content of the soil and signs of human interference were recorded at each sampling point. In all, 1,117 points were recorded in 28 sites by 4 teams of two people each working from May to September. Because it was considered that such methods would fail to locate rare or localised species, a separate survey was made by a single experienced worker using his knowledge of the likely whereabouts of such species. Data are being analysed in different ways to meet the stated objectives, but it is of interest to note that objective sampling has found no less and probably rather more localised species than the subjective sampling based on previous experience.

Analysis of the results indicates to the customer the level of detail that can be expected and how improvements can be made within the limits imposed by the staff and money available. For example by taking the total number of sampling points feasible in the current year (1976/77) a sampling system has been devised which will give allocations of sampling points proportional to the area of site; provide unbiased estimates of species frequency, cover values, proportions of habitats and vegetation types together with estimates of error; ensure even distribution of sampling points within a site and lastly, is straightforward to carry out in the field. This kind of information is also useful as a baseline against which change can be measured when further surveys, using comparable methods, are undertaken in future. The chief difficulty in interpreting the causes of the patterns described in the field and the changes that future surveys will reveal is likely to stem from the highly dynamic nature of important factors like salinity, water table fluctuation and sand movement. Some effects of these may be inferred from analysis of the data, but experiment will be needed if causes are to be established.

Discussions between NCC and ITE are proceeding as the details of analyses of the already extensive data set become available. Such exchange of information should not only provide results of practical value to the customer, but also help both parties to appreciate better the nature of the habitat under consideration.

D. Ranwell

Surveys of species distribution and taxonomy

ERICA CILIARIS AND ITS HYBRIDS IN DORSET *Erica ciliaris* L. (The Dorset heath) is one of the less common species of British heathers and forms a range of hybrids with *E. tetralix* L. It has a Lusitanian distribution occurring in north-west Morocco, the coastal regions of Portugal, Spain and France, the south of England and the west of Ireland.

The present distribution of the species, past changes so far as they are known, and its range of hybrids within south-east Dorset have been mapped using a 200 metre grid. By analysing nine morphological features of E. ciliaris - E. tetralix populations, individual plants can be placed into 'ciliaris', 'tetralix' or hybrid categories and each grid square can be classified according to a system based on the relative proportions of these components in each population. Each square on the map has also been categorized according to its predominant type of vegetation and χ^{2} analyses used to indicate statistical associations between types of population and vegetation. Positive associations between hybrid populations and peat communities have been interpreted in terms of the ability of seeds to germinate, establish readily and therefore change the population structure on wet Sphagnum surfaces, in contrast to the situation on drier communities where seedling establishment and change are more dependent upon intermittent factors such as fire and other disturbance. 'Ciliaris' populations also show an interesting positive association with tall vegetation, a factor that suggests greater competitive ability under such conditions because of a more upright growth form than is present in E. tetralix or many of the hybrids. 'Ciliaris' populations also appear to be associated with recent disturbance



Plate 12 Flower buds on the West African timber tree, obeche. Photograph K. Longman. From 'Tree Biology and Plant Propagation'. Comb. Proc. Int. Plant Propagators' Soc. 1976, Figure 7.



Plates 13/14 Accretion of mud in the Wash. After killing the invertebrates which graze the microalgae (left), there is accretion of mud on the surface (right). Photographs S. Coles.



Plate 15 Myrmica *ant eggs. Top left is normal bean-shaped reproductive egg; bottom right is Trophic egg. Photograph M. V. Brian.*



Plate 16 Myrmica ruginodis microgyne. *Photograph A. Abbott.*



Plate 17 Dartmoor. High and wet moor. Photograph N. Webb.


Plate 18 N. Dartmoor. High, wet, cold moor. Photograph G. Elmes.



Plate 19 N. Dartmoor. High, dry, cold moor. Photograph G. Elmes.



Plate 20 Morden National Nature Reserve. Low, warm heath. Photograph N. Webb.



Plate 21 Camber sand dunes, Sussex, 1967. Before stabilisation and restoration by local authorities. Photograph Meridian Airmaps Ltd.



Plate 22 Camber sand dunes, Sussex, 1971. After stabilisation and restoration by local authorities. Reproduced by kind permission of BKS Surveys Ltd.

such as banks, tracks and tree planting, probably due to greater production of viable seed than by the hybrids. The results have been interpreted in terms of an expanding rather than a diminishing distribution, which provides a satisfactory explanation for *E. ciliaris's* absence from apparently suitable sites in the area. Results from pollen analyses and macro-fossil research being undertaken by a member of Southampton University appear to substantiate this interpretation of the present distribution of *E. ciliaris* in Dorset.

E. ciliaris is a good example of a species which may require careful conservation following changes in land use and for which the ecologist needs detailed know-ledge about the structure and dynamics of its populations before he can predict with confidence the effects of various treatments or disturbances on its survival.

S. B. Chapman R. J. Rose

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PHLEGMACIUM SILVAMONACHORUM: A SPECIES NEW

TO THE WORLD LIST DISCOVERED AT MONKS WOOD Popular fungus forays traditionally convene in the autumn and, in the main, favour well known productive sites. Only the dedicated mycologists seek out the more unusual habitats and are able to organise their coverage throughout a large segment of the year. Even so, there are few experienced workers compared with the many sites of potential interest, so unusual discoveries are always a likely possibility. At first sight Monks Wood seems a poor locality in which to find many of the larger agarics and the impervious, often waterlogged, calcareous clay which covers much of the ground is not a good medium for hyphal growth. Nevertheless, J. P. Houlton (1973) produced an impressive species list for the wood and this list has since been considerably enlarged. A feature of Monks Wood is that several agarics, which have been infrequently recorded in other areas, are not uncommon, while the species association is somewhat unusual. Houlton noted Russula laeta as a possible first British record.

Flushes of agarics often appear in June or July with the summer rains while the late summer and autumn are frequently disappointing. However, this was not the case in 1974 and September witnessed a fine harvest of agarics. On 24 September N. J. Westwood and R. K. Murton found a clump of a large '*Cortinarius*' growing near the junction of Main and Badger Rides. This is a large and difficult genus which was segregated into several sub-genera by E. M. Fries. Examination of the

gross morphology immediately indicated something unusual for its obvious characters were evidently rather variable between young and old specimens, the pileus was oddly streaked and blotched and the spores rather roundish for the genus with a distinct brown ornamentation. Accordingly, D. A. Reid at the Royal Botanic Gardens, Kew was consulted and determined that we were dealing with a totally new species. Further searches during the ensuing ten days yielded three further clumps totalling about 15 specimens but no very immature individual. This was a little unfortunate since the gill colour at this stage is an important identification feature; however, sufficiently young specimens were found to establish that the gills are dark blue-grey with pale margins during early development. Regular searches throughout 1975 and early 1976 failed to reveal further examples - indeed 1975 was generally a poor season for fungi in the wood. The new species has been named Phlegmacium silvamonachorum in recognition of the Monks of Sawtry Abbey who in 1147 gave their identity to the wood previously known in the eleventh century as Ewingeswode (M. D. Hooper in Steele and Welch loc. cit.).

The Monks Wood *Phlegmacium* (Plate 30) is a large species, the mature pileus having a diameter of 4-16 cm, at first convex and then becoming flattened, and distinctly viscid when moist. At first there is a greyishlilac tinge to the pale brown cap but it soon becomes generally fawn coloured. A distinctive feature is that the cap is variegated with radial dark brown-blackish streaks and blotches which impart a dirty, apparently fibrillose, appearance, though there are no fibrils nor scales. The gills are up to 1 cm deep, at first blue-grey with a white margin, and becoming rusty brown at maturity. The stripe is 4-10cm high, up to 3cm thick with a swollen base, and is at first densely streaked the same colour as the cap though it becomes paler with age. A rusty-brown band comprised of the remnants of the cortina is seen round the lower portion of the stipe. The flesh is up to 2cm thick at the centre of the cap, mostly dirty white throughout, but sometimes greyish in the stipe, or with a slight lilac tinge in the base of the clavate portion; some specimens show a watery grey area at the apex of the stipe. There is no distinct smell and no chemical reaction to KOH, NaOH or NH₄OH. The cap is extremely bitter and unpleasant in young specimens but it becomes tasteless with age. There are no cystidia. The basidia measure $21-38 \times 7.5-9.0 \mu$ being sub-cylindric to clavate and often constricted near the apex and they are either colourless or contain a pale brown sap. The basidia are 4-spored and have a basal clamp-connexion and sterigmata up to 5 µ in length. Spores are either globose or sub-globose measuring $5.75-7.0\mu$ or are broadly elliptic to slightly almond shaped measuring $6.75-8.0 \times 5.75-7.0 \mu$, with a distinct brown ornamental wall (See also Plates 31, 32).

The habitat was amongst Dog's mercury (*Mercurialis perennis*) under a canopy of hazel (*Corylus avellana*), Silver birch (*Betula pendula*), oak (*Quercus robur*) and ash (*Fraxinus excelsior*) having a long history of coppicing. At present little can be said about the affinities of the new species. The bitter cuticle and round-ish spores suggest that it might be close to the *P. infractus* (Fr.) Wunsche group but these have dark rusty olive or sooty gills which is not the case in *P. silvamonachorum*.

D. A. Reid R. K. Murton N. J. Westwood

Reference

Houlton, J. P. (1973) Fungi pp. 100–117 *In Monks Wood, a nature reserve record*. Edited by R. C. Steele and R. C. Welch, The Nature Conservancy, Abbots Ripton.

THE CHEMICAL TAXONOMY OF SCOTS PINE AND ELMS

Scots pine

A pilot study has been made of the seasonally varying amounts of different monoterpenes in Scots pine. As expected, the relative proportions of different monoterpenes in shoots sampled from five trees remained more or less constant. Fifteen measurable peaks were consistently observed on chromatograms (GLC), although other peaks sometimes appeared; no attempt was made to identify the precise substances responsible for these peaks. Preliminary analyses indicated that the information obtained could be summarized by five significant components or axes. A series of graphic projections and cluster analyses highlighted considerable amounts of within-stand variation and suggested that the distribution of the differing monoterpenes was largely independent of geographical boundaries. Their occurrence was not associated with morphological features such as foliage colour, branch patterns, etc.

Elms

Using an electrophoretic method developed during 1974 leaves of twenty trees growing in Cambridgeshire and Essex and selected by Dr R. H. Richens (Commonwealth Bureau of Plant Breeding and Genetics) for their particular taxonomic interest, were investigated. Powdered extracts which were made at Monks Wood within two hours of field collection, were subsequently brought to Merlewood where peroxidase isozymes were determined. Two bands were common to every tree; five trees possessed either one or two additional isozymes. The few isozymes suggested that there was little variation but assessments of rates and intensities of staining added a further dimension to the analyses which may be a useful discriminant of variation.

A. S. Gardiner N. J. Pearce

THE DISTRIBUTION AND TAXONOMY OF ANTARCTIC BRYOPHYTES

In 1975/76 Dr S. W. Greene took part in an Anglo-Argentinian-Chilean botanical expedition to southern Patagonia sponsored by the Royal Society. One of the most startling discoveries of that expedition was that a moss, Sarconeurum glaciale was not uncommon on trunks or fallen logs of the deciduous southern beech Nothofagus antarctica, and less common growing on dry rocks. This study is but a part of the programme, which has as its main objectives the investigation of the nature and causes of variation in Antarctic bryophytes, studies of their distribution, and the naming of material for the ecologist. On the one hand the work involves extensive studies describing variation with the results being synthesised into descriptive accounts of taxa as part of a floristic treatment of the Antarctic bryoflora while on the other hand more intensive studies are being started to look more closely at intra-specific variation particularly in bipolar species.

Two species of *Campylopus, C. muricatus* and *C. nano-caudatus* have been examined and have been found to be synonymous with the common taxon *Chorisodontium aciphyllum. Campylopus nano-caudatus* was of particular interest as it was the only specimen from the first botanical expedition to South Georgia not destroyed in Berlin-Dahlem during the 1939–45 war. A reassessment of the genus *Dicranoweisia* for Signy Islands, South Orkney Islands, has also been completed.

Up to this date, *Sarconeurum* which has two species, *S. glaciale* and *S. tortelloides* has been the only moss genus thought to be endemic to Antarctic regions. *S. glaciale* is locally frequent although largely confined to Continental Antarctica with a few scattered localities on the Antarctic Peninsula, but is absent from the sub-Antarctic islands while *S. tortelloides* is known from only a few sites along the Antarctic Peninsula. The habitat in Patagonia contrasts strongly with the occurrence of *S. glaciale* on soil and gravel in dry situations on the Antarctic Continent. Moreover some of the South American material bore immature fruit, a condition unknown in Antarctica. Examination of material of *Tortula lithophila* and *T. pygmaea*, species reported by Dusen from southern South America around the turn of the century, has shown them to be synonymous with *S. glaciale* (Greene 1975). These findings tend to weaken the argument that *S. glaciale* is a relict species in Antarctica which survived the period of maximum glaciation for it would seem that only in Patagonia are conditions optimal for the completion of its life cycle.

The taxonomy group works closely with Argentinian bryologists. Dra. Hassel de Menendez spent 6 weeks with the group during July and August working on her revision of South Georgian hepatics while Srta. Matteri spent the winter at Edinburgh (Bush) working on several South Georgian moss genera.

A major reorganisation of the herbarium was carried out following the segregation of the Antarctic bryophyte collection (code name AAS) and its incorporation into the newly constituted austral cyptogamic herbarium (code name ACHE) which also includes rich material from southern South America and other parts of the Southern Hemisphere. The maintenance of these reference collections, now numbering some 15,000 specimens, and their development to include as great a range of material as possible is an essential back up component of the programme which facilitates the work on revisions and routine identifications. The computer based data bank of austral plant records is run in conjunction with the herbarium and now comprises a data base of some 50,000 plant records.

Collections from British Antarctic Survey biologists working on the Antarctic Peninsula have been identified including some interesting aquatic species of *Campylium* and *Dicranella* growing at considerable depths, i.e. 1–3m in fresh water lakes.

S. W. Greene D. M. Greene B. G. Bell J. D. Dolman

Reference

Greene, S. W. (1975) The Antarctic moss *Sarconeurum glaciale* (C. Muell.) Card. et Bryhn in Southern South America. *Br. Antarct. Surv. Bull.* Nos. 41 and 42, 187–191.

STATUS OF THE GREATER HORSESHOE BAT IN DORSET (This work was largely supported by Nature Conservancy Council funds)

In the 1950s and 1960s some amateur naturalists recorded substantial declines in numbers of Greater horseshoe bats in Britain. It was also known from historic records that its range had diminished considerably. These were the reasons why this species was given statutory protection under The Conservation of Wild Creatures and Wild Plants Act 1975.

This study involved searching 1300km² of Dorset and Wiltshire, looking for caves, mines, grottoes, cellars and roofs of large country houses and castles, in fact

all the likely places these bats may use as roosts. In some areas days were spent searching on foot every bramble-filled depression in many sq km in the hope of finding caves or mine adits – where often the entrance was barely large enough to allow anyone through. Such entrances may lead to several km of tunnel. It was often gratifying to find that in tunnels that had never been visited previously ringed bats were present which supported the view that almost every Greater horseshoe was known within the study area.

As the number of known occupied sites increased all were incorporated in a regular visiting programme so that all sites could be examined within a few days, which enables fairly accurate population estimates to be made.

From 1970–75 the Dorset population of Greater horseshoe bats (*Rhinolophus ferrumequinum*) consisted at most of only about 7% of the number alive in 1951. It was also likely that declines had occurred in the previous 20 years. The maximum number in 1975 appeared to be about 115 bats and they occupied a range of approximately 800 sq km.

In summer these bats live in roofs of large buildings where they give birth to a single young in July. Autumn and winter is spent in cellars and tunnels often 30 km or more from the breeding roost. The environmental conditions sought for roosting are chosen very precisely. The site selected is influenced by season, age, weight and sex of bat. During hibernation old adult females chose warm sites while juvenile males preferred cool areas, but all within the range $6 \cdot 0 - 11 \cdot 5^{\circ}$ C. In summer higher temperatures (in the range $15-25^{\circ}$ C) are required for these heterothermic animals to enable foetal development to proceed economically in terms of energy turnover. Prolonged cold weather in late June and early July not only prolongs gestation but can cause high mortality through lack of food.

The Dorset Greater horseshoe bats were studied intensively by several people during the 1950s. This initial study appears to have been a contributory cause to the decline but other factors included loss of suitable roosts, disturbance and killing by children and removing by collectors. The biggest known loss was to a breeding colony in 1952 when a roof was treated for woodworm infestation and hundreds of bats were killed accidentally.

The present study, which began in 1970, uses techniques designed to minimise disturbance and hence reduce mortality caused by the observer. Bats are marked individually in the autumn following birth. Sex-ratio at birth was assumed to be unity but at the end of weaning only 45% were males. The whole population



Figure 5 Numerical changes of males, females and combined total population of the Dorset Greater horseshoe bat (R. ferrumequinum). Three census points were selected for each year – mid February, late September and mid December. The upper line indicates the known number of Greater horseshoe alive during the present study period 1970–75.

The dotted line for the period February to September 1975 represents the predicted total alive at that time based on known births (51) in July in relation to patterns of previous years.

The middle two lines are the numbers of males and females showing trends of males increasing substantially and females declining slightly.

The bottom line shows the increasing percentage of males in the population.

averaged 40% males. Forty eight % of females and 33% of males survived the first year.

Males reach sexual maturity at 2–3 years and females at 3–4 years old. Maximum longevity for individuals of this population has exceeded 18 years although in Devon an individual over 22 years old has been recorded.

From 1970–75 the net increment in the Dorset population was about 3 bats per year. However this was due to much improved male survival (Figure 5) while the number of females appeared to decline.

In order to improve the status of this population, positive action is required to protect existing roosts and to provide more and greater variety of roosting sites. Further study should reveal the bats precise requirements and may make it possible to provide artificial roosts (See Plate 37).

R. E. Stebbings

RECENT CHANGES IN THE NUMBERS OF PUFFINS AROUND BRITAIN

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

The numbers of puffins (*Fratercula arctica*) at many British colonies have declined dramatically during this century. For some time it was thought that the decline was restricted to the more southern colonies but in 1970–1 it was realized that the far larger Scottish populations had also suffered. The present research is aimed at documenting population changes and determining possible causes for the decline.

Annual counts of burrows in permanently marked areas in seven Scottish colonies were started in 1972. These have shown that the past declines in these areas may have halted. This impression is supported by a survey of recent irregular counts at many other colonies. The few declines recorded between 1969–75 are mostly in the now very small colonies at the southern fringe of the species range (Figure 6). Whereas there have certainly been past declines, they have probably been somewhat exaggerated. There are now approximately 500,000 pairs of puffins in Scotland, 20,000–25,000 pairs in Ireland and 25,000 pairs in England and Wales. This compares to 4–5 million pairs elsewhere in the North Atlantic.

The main study on St Kilda showed that puffins were having difficulty in feeding their young in 1971, 1973 and 1974 but not in 1975. However, even in the latter year the young grew better if given additional food. Despite previous concern, contamination by pollutants appears not to be a cause of the decline. Present opinion





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is that some change in the marine environment may have altered the food supply of these birds. It may not be a coincidence that puffins seem to be coming upon better times just as the sea temperatures around Britain are falling after a long period of gradual warming.

M. P. Harris

Performance of trees

TOADSTOOLS, TREES AND MYCORRHIZA

Many different types of fungi form mycorrhizas with tree roots, including some that produce toadstool-like fruitbodies in the autumn. To support observations being made in the laboratory, where the roots of birch (Betula) species are inoculated with known strains of differing fungi, records were made of the field appearance of large fruit bodies associated with specified trees. In one instance their distributions were recorded within 0.5m, of replicate specimens of 4-year-old rowan (Sorbus aucuparia), birch (Betula verrucosa), pine (Pinus nigra and P. contorta) and alder (Alnus glutinosa and A. incana), planted on a reclaimed coal tip. Whereas Thelephora terrestris and the three times more numerous Paxillus involutus were associated equally with all tree species, other fungi were differentially distributed. Hebeloma crustuliniforme fruiting-bodies were only associated with B. verrucosa and Suillus luteus was restricted to Pinus spp., there being associations with 8 and 20% of the replicate trees of P. nigra and P. contorta respectively. Interestingly H. crustuliniforme, S. luteus, P. involutus and T. terrestris are all known to form mycorrhizas.

A second series of observations over the past three years have been restricted to collections of birch provenances (*B. pubescens* and *B. verrucosa*) grown on ITE experimental plots at the Bush Estate, south of Edinburgh. Whereas many *H. crustuliniforme* fruit bodies (215 per plant in 1975) have been associated with saplings from the southerly source (50°N) none has as yet appeared near to saplings from a more northerly latitude (66°N) which however, shed their leaves rather early in the late summer. In addition to numbers, fruit body sizes seem to be influenced by provenance. Like *H. crustulinforme* the less numerous *Thelephora terrestris, Laccaria laccata* and *Lactarius torminosus* were not randomly distributed.

Together these observations suggest that the occurrence of 'toadstools' is influenced by within-species variation in the tree host.

Taken with the observations from the slag heap, it is clear that fruitbody formation is strongly host-de-

pendent. But how can the occurrence of fruitbodies be interpreted in terms of mycorrhizal associations?

J. Pelham P. A. Mason

ROOT DISTRIBUTION IN A YOUNG SPRUCE PLANTATION

As part of a study investigating which aspects of the environment have most influence on the growth of a young forest, measurements have been made of the distribution, growth and activity of fine roots. Weekly soil cores were taken from May until the end of September in the eleventh year of growth of a plantation of Sitka spruce (*Picea sitchensis*). The growth of the fine root system is a continuous process although its components, the initiation of new apices, translocation of carbohydrates to the roots and root extension are not concurrent. The total concentration of roots was found to be the same at the end as at the start of the period but there were major fluctuations throughout the summer. For example distinct maxima were found:

(i) in the number of root apices per unit length of root in the pre-June period;

(ii) in the amounts of starch and soluble carbohydrate in roots during mid-June;

(iii) in root weight per unit soil volume during early July and

(iv) in root length per unit of soil volume in late July, with a second maximum in early September.

It was observed that two populations of fine roots occurred in the forest, one in the soil surface horizons, (i.e. amongst the fallen needles and the decomposing grass which had existed before the plantation canopy closed) and the other in the peat and mineral soil below. Of the two groups, the fine roots in the former had the greater mean diameter, more root tips per unit length, and higher concentrations. The surface regions contained greater concentrations of available nutrients and also played an important part in moisture uptake. Measurements with soil tensiometers showed that during summer the forest responded quickly to showers which dampened the soil surface. Removal of moisture from these regions increased rapidly whereas at the same time that from the lower soil horizons ceased.

Higher concentrations of fine roots were found both where soil had been disturbed by cultivation before planting and close to tree trunks. The disturbed soil regions had higher concentrations of available nutrients, but an explanation for the higher concentrations of fine roots near to tree trunks was not immediately obvious, particularly because the supporting root system was found to ramify from the trunks in all directions and usually at least as far as the nearest neighbour in the row. However, an investigation of the pattern of throughfall and stem flow during rain storms has indicated a distinct concentration of water deposition onto the soil around the base of the tree. This is greater than that found in older forests of the same or other species and may be attributed to the close arrangement of needles around the distinctly upward-angled branches which together act to conduct water from the edge of each tree crown towards the trunk.

D. D. Ford J. D. Deans R. Milne

Reference

Ford, E. D. and Deans, J. D. (in press). Growth of a Sitka spruce plantation: spatial distribution and seasonal fluctuations of lengths, weights and carbohydrate concentrations of fine roots. *Plant and Soil.*

FOREST TREE IMPROVEMENT: A PHYSIOLOGICAL ANALYSIS OF THE COMPONENTS OF GROWTH

Breeders in agriculture and horticulture are more and more basing crop selection on an understanding of the physiological basis of yield. Silviculturists and tree breeders lack this background information. To help fill this gap a study is being made of the physiological and morphogenic processes which underly the inherent natural variation found within species of forest trees grown for timber in Britain. Moreover, it is intended to work with tree breeders to discover how these processes are inherited, and so contribute in a meaningful way to present and future tree improvement strategies.

Three species are being studied: Sitka spruce (*Picea* sitchensis Bong Carr.), Lodgepole pine (*Pinus contorta* Torr. and Gray) and Black cottonwood (*Populus trichocarpa* Torr. and Gray). The first two account for about 50% and 20% respectively of the forest trees currently being planted by the Forestry Commission in Britain. All three are natives of western North America and provenances (seed populations) collected in different geographic zones differ in morphology and phenology.

Contribution of tree physiology

There are three reasons for seeking to understand why some trees are inherently capable of growing faster than others. Firstly, provenances which grow fastest in Britain are not necessarily those from situations elsewhere in the world with similar climates and, within stands, the largest individuals do not necessarily yield the fastest growing progenies. Secondly, tree breeders cannot select for final yield some 30–60 years after planting: instead they have to predict the growth of forests from the performance of seedlings or young trees. Thirdly, in advanced well-adapted breeding populations, crosses may usefully be planned on the basis of 'potential physiological complementation': that is, parents with differing desirable traits may be crossed. This has been done successfully in rice and wheat.

Growth analyses

Populations of trees have been grown and attempts have been made to account for differences in their rates of growth. Variation has been analysed among provenances, progenies or clones grown in glasshouse and nursery conditions at ITE's Edinburgh (Bush) laboratory and in the field by the Forestry Commission's Research Branch.

Northerly and montane provenances, which were photoperiodically adapted to stop increasing in height early each growing season, had relatively large root: shoot weight ratios by the end of each year. Thus, endof-year root: shoot ratios were correlated negatively with times of height growth cessation and positively with latitudes of origin. However, the following spring these differences in root:shoot ratio were 'corrected'. Northerly provenances, which spent the winters with relatively heavy root systems produced very little new root during the following spring 'flush' of shoot growth, whereas southerly provenances produced appreciable new root dry weight. It was concluded that there were no major provenance differences in the functional balance between the shoots as sources of carbohydrates and the roots as absorbers of nutrients. Endof-season differences in root:shoot ratio reflected inherent differences in the abilities of trees to produce new shoot growth. Roots were always able to grow provided photosynthates were available to them, whereas the period and amount of shoot growth was regulated by factors such as temperature and day length.

A visual survey showed that some types of Pinus contorta and Picea sitchensis were more profusely branched than others (Plates 6, 7, 8). A study was done to determine how closely branch and foliage development were linked to height growth, and to what extent there were inherent differences in branching pattern (Cannell 1974, 1976). It was found that slow-growing individuals of an otherwise fast-growing provenance could mimic members of an inherently slow-growing provenance. Although numbers of branches per unit length of shoot ranged from 0.25 to 0.35 per cm in different provenances of Pinus contorta and from 0.60 to 0.85 cm in Picea sitchensis, these differences accounted for only 8-16% of the variation in needle volume produced per tree, compared with 82-86% attributable to differences in height growth. That is,

if a tree grew greatly in height, it also produced proportionately more lateral branches, which were long, and in turn produced many sub-laterals. As with the studies of dry matter distribution, this investigation suggested that factors affecting shoot extension were of paramount importance.

Analyses of shoot apical growth

Studies of branching had stressed that trees which produce foliage and stem wood rapidly invariably produced long leaders. Other surveys confirmed that shoot length differences in *Pinus contorta* (and to a great extent in *Picea sitchensis*) were determined more by differences in numbers of needle-fascicles than by the extent to which the needle internodes elongated. Thus, the main criterion of 'success' was the ability to generate large numbers of needle fascicles. In mature north temperate pines, numbers of needle-fascicles are 'predetermined' within buds the year before shoots elongate (Plates 9, 10, 11).

Northerly and montane provenances were found to produce primordia (needles or cataphylls) earlier in spring than southerly provenances, suggesting differences in the 'heat sum' requirement to begin meristematic activity. The dates when bud development ceased were more closely related to latitude of seed origin, suggesting differences in photoperiod sensitivity. Among the pine provenances differences in total numbers of primordia formed were related to differences in maximal rates of initiation during the summer, whereas in spruce they were attributable to differences in the period over which needle initials were produced. By combining the prolonged periods of initiation of some provenances with the rapid rates of initiation of others, it seems possible to increase numbers of needles formed per year by up to 20 per cent. In some instances this would involve provenance crosses that would not previously have been considered worthwhile.

A study of *Pinus contorta* provenances showed that types which produced most primordia and hence potentially the longest shoots were those which developed the largest apical domes for the most prolonged periods during the preceding season. There is an analogy here with growth analysis concepts, there being a size component (apical dome size) and a rate component (apical dome relative growth rate). Those provenances which produced most initials were those that re-invested most of their new cells in new productive apical dome capital. Slow growing provenances were able neither to build up large apical domes in spring nor maintain large numbers of dividing cells at their apices during summer. Although their mitotic rates (and mean cell generation times) were probably similar to those of fast-growing provenances, they differentiated new primordia in spring and early summer at the expense of their apical domes.

It may be concluded that, in *Pinus contorta* the 'ideotype' is a tree which produces a large apical dome early in spring and maintains it until as late as possible in the autumn.

Analysis of branch growth

Although differences in branching habit are less important to yield than differences in height growth, they are of concern to silviculturists who seek a compromise between rapid foliage production and a narrow, sparsely-branched crown with small widely dispersed branches which will not produce large stem wood knots.

Branch buds formed on preformed shoots in April-May, when they begin to elongate and show green, only occur in the axils of some of the numerous needles on spruce. They are not randomly distributed but tend to be evenly spaced, at least on leaders. When the parent shoots elongate the buds become displaced relative to each other because the shoots expand more longitudinally than radially. (Figure 7). In this way, the branches can become arranged in whorls or staggered along the shoots. However, branch buds are almost always formed near the apex of the parent bud and form a terminal whorl when that parent bud elongates.

Performance of trees in stands

Earlier it was mentioned that large trees in stands do not always yield fast-growing progenies. This poses the question, familiar to field crop agronomists and breeders, of whether physiological characters favouring the growth of young, free-growing individuals, such as rapid foliage production and height growth, also favour dry matter production in assemblages of plants after canopy closure. The situation is complicated because spatial processes occur within competing stands which enable certain plants to grow more than their neighbours, irrespective of their genetic potentials as free-growing individuals.

To gain an insight into the nature of tree performance in closed stands a joint study is being done with Dr E. D. Ford (ITE, Bush) and Dr I. Forrest (Forestry Commission Research Branch, Bush) in which 2500 seedlings of *Pinus contorta* and *Picea sitchensis* were grown closely-planted in two 'mini-forests'. Of the 20 characters recorded after four years growth some



Plate 23 Saxifrage caespitosa. *Photograph R. Goodier.*



Plate 24 Saxifraga oppositofolia. *Photograph E. Roberts.*



Plate 25 Dryas octopetala. *Photograph E. Roberts.*



Plate 26 Lloydia serotina. *Photograph F. L. Taylor.*



Plate 27 Silene acaulis. Photograph F. L. Taylor.



Plate 28 Sedum rosea. Photograph J. Mylan.



Plate 29 Panoramic view of Tyneham valley, taken from the south-west corner of the car-park situated on the summit of Povington Hill. The chalk escarpment, which runs on an east to west axis, can be seen on the right hand side of the photograph. The Jurassic limestone ridge extends from Worbarrow Tout to Tyneham Great Wood. The distribution of bracken and gorse on Povington Hill (foreground) shows the extent of the superficial deposits overlying the chalk. The light green patch on Gold Down, and the purple brown patches on the same site and on Whiteway Hill mark the sites of fires, which occur regularly on the Ranges. Alms Grove wood can be seen in the middle foreground with the abandoned fields marked by thick hedgerows in the background. Photograph T. C. E. Wells.



Plate 30 Phlegmacium silvamonachorum Reid, Murton & Westwood Sp. nov. From an original watercolour by D. A. Reid of a fresh specimen collected at Monks Wood.



Plates 31/32 Phlegmacium silvamonachorum *photographed* in situ *at Monks Wood by R. K. Murton.* (*left*) *Young to middle-aged fruit bodies.* (*right*) *mature specimens.*



Figure 7 Computer simulations of elongating buds of spruce showing (a) all the needle primordia (compare with Plate 11), and (b) some of the basal needles which subtend lateral branch buds. Note that the branch buds are more or less evenly distributed on the unexpanded parent bud, but in this instance they become arranged in whorls as the shoot elongates.

(like height growth) are strongly affected by competition while others, like resin composition are not. The frequency and spatial distribution of plants with these characters, and the performances of individuals with respect to their neighbours, are being recorded. In this way, it is hoped to elucidate some mechanisms of competition within stands, and hopefully detect those characters which may enable conifers to convert environmental resources into dry matter efficiently within forests.

M. G. R. Cannell

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MAKING TREES FLOWER

Reliable control of flowering by forest trees has been sought for many years, because natural flowering and seed production is often sparse or unpredictable. Reproductive activity is generally completely lacking for the first 10 to 20 years of life, with the result that flowering material is very large and unsuited to experiments. The problems are increased by great variability, both genetical and environmental, in the morphology and timing of floral development.

Many of these difficulties have been overcome by using suitably treated vegetatively propagated clones which originated from selected flowering trees. In a number of species, flowers of both sexes have been induced in field and glasshouse experiments. The most striking results have been obtained with cypresses and sequoias by injecting small quantities of gibberellic acid. In *Cupressocyparis leylandii* (Leyland cypress), for example, a hybrid tree which produces no fertile seed, a single dose of one millionth of a gram is sufficient to stimulate male cones on an otherwise vegetative branch. One fiftieth of a gram can produce tens of thousands of male and female cones in a 6 metre high tree of *Thuja plicata* (Western red cedar).

A rare conifer *Metasequoia glyptostroboides* (Dawn redwood) known only from fossils until 1941, is propagated exclusively by cuttings in Britain where it forms no male and very few female cones. Flowers of both sexes have been induced in considerable numbers in glasshouses in Edinburgh, and as a result the first five 'home produced' seedlings have been raised. Whether these can in turn be induced to flower is not yet known, but early induction has been achieved in four other contrasting genera, before the seedlings were three years old. A variety of treatments were used, including rapid continuous growth, bark-ringing and hormone application, which has given some insight into the nature of the phase-changes which occur as trees become older.

Several of these successful approaches are being developed into practical techniques for the forester, arboriculturist and tree breeder and will, it is hoped, help towards plentiful supplies of seed and also the ability to utilise improved selections and create new forms or varieties of trees. Meanwhile fundamental investigations are continuing into the interactions of hormones, environmental and other factors governing the balance between reproduction and vegetative growth.

An important West African timber tree, *obeche*, is being studied in a Tree Improvement Scheme. In the tropical forest the flowers occur sporadically high up in the crowns, and may last for a few hours only. Frequent visits by skilled tree-climbers are required even for simple observations such as pollination, and it is therefore not surprising that virtually nothing is known of the species' reproductive biology.

Early in 1975, the feasibility of inducing flowering in less hazardous circumstances was unexpectedly demonstrated. One plant in a tropicalised glasshouse in Edinburgh produced four inflorescences, totalling 33 flower buds, less than a metre from the ground (see Plate 12). In subsequent experiments, it has been found possible to stimulate the first stage in the reproductive cycle, namely the formation of the characteristic lateral branchlets, by combining treatments which are effective in other species. If the formation and retention of flower buds on these shoots can also be achieved, a whole range of other studies could then be done in controlled conditions. Questions of this kind require urgent attention before conservation and utilization of the great gene resources of tropical forest become impossible.

K. A. Longman R. R. B. Leakey M. L. Edwards

Plant performance on coasts and mountains

GROWTH STRATEGIES WITH REFERENCE TO PUCCINELLIA

A distinction can be made between organisms adapted to unpredictable environments which subject them to high density-independent mortality, and others, from more stable habitats, showing greater competitive ability and able to resist density-dependent mortality factors. They are known respectively as r- and Kstrategies. In the build-up of a new population or the colonisation of a bare substratum there is a transition from environments favouring r-types, maximising growth not constrained by habitat resources to those favouring K-types, which exploit fully a share of the total resource for which they have had to compete. Generalisations are often made about characteristics of both types. These may be misleading because the effects of selection on a particular organism depend on its taxonomic affinities and the role in the ecosystem which it occupies. r/K categorisations can be made at all taxonomic strata, but the most illuminating studies of r- and K-guided selection have in fact been made at the intraspecific level.

Puccinellia maritima occupies a range of saltmarsh environments from bare intertidal mud to the midmarsh zones, being eventually replaced on high-level marshes by other species. At the pioneer stage there are few constraints on the growth of individuals, but mortality from physical causes may be high, denoting an r-environment. The species expands rapidly into the available space by vegetative means and by producing seed. On an undisturbed site in Norfolk this phase lasts about five years, when there is no longer bare ground to colonize. The marsh on this site shows a gradual seaward progression, and habitat zonation represents the temporal processes (this would be an over-simplification for most developing marshes). Puccinellia is a highly polymorphic species; growth form differences between individual clumps are conspicuous during the pioneer phase, and genetic differences have been confirmed by collateral growth trials and breeding tests. After the coalescence of clumps the plants enter a period of intense intraspecific competition leading to K, the maximum environmental capacity. Trials are in progress to look at the interactive effect of plants of different growth form and to compare total yield of pure and mixed stands.

In the absence of grazing, *Puccinellia* turf is invaded by other species, and replaced by *Halimione* marsh or the very species-rich 'general saltmarsh' community containing *Limonium* and *Armeria*. Grazed sites remain grassy, but *Puccinellia* is replaced at higher levels by other grasses. There is good evidence that in each instance selection acts on the original *Puccinellia* gene pool with only the best fitted forms surviving. For example on an ungrazed marsh at Holme Island, Cumbria, the intense selection against small plants leads to their absence in mature swards, though present in the pioneer populations (See Figure 8).

After the relegation of *Puccinellia* to a minor role by more competitive species, it appears that an opportunist strategy ensues for there is a reversion to an *r*-type existence in ephemeral gaps in the marsh vegetation. More information is required about the effect of the principal selection pressures on the genetic constitution of populations in these situations. In particular it is important to know if the genotype diversity seen late in the *r*-phase is actively selected, or if it merely represents a mixture of offspring from closely adjacent habitats containing distinct types. The use of isoenzyme 'fingerprinting' techniques (see Plate 2) should facilitate estimates of population diversity. Because effective seed dispersal range will affect the availability of seed for new sites, it will be measured,





the resultant values being linked with estimates of total seed production for different habitats, based on flowering spike size and number. In this way the generalities of the r-K concept will be tested and perhaps extended by the study of *P. maritima*, a highly flexible species subject to divergent ecological pressures during progressive changes in its environments.



BENTHIC MICROALGAE ON MUD FLATS

Studies on soft sediment shores generally assume that the particle size of the substrate is a major factor controlling the types of organisms present, and can be used as a direct indicator of the exposure of the area. Evidence from investigations in the Wash indicates that other factors may be more important in controlling the populations of organisms, and that the organisms themselves can radically influence the type of sediment present.

Three main zones can be generally recognised on the upper intertidal areas of the Wash: salt marsh, upper mudflats, and below these, sand flats. The salt marshes and mud flats are characterised by more or less continual accretion of fine sediments, whereas the coarser sediments on the sand flats show greater fluctuations, with generally no appreciable net gain.

Populations of benthic microalgae are more or less persistently high on the salt marshes and mud flats but low on the sand flats. This difference appears to be attributable to the grazing of numerous macroinvertebrates, especially Corophium and Hydrobia on the sand flats; the landward distribution of these invertebrates appears to be primarily limited by drought. The most abundant benthic microalgae are diatoms and filamentous blue-green algae, which are motile and produce copious mucus when moving through the sediment. It has been shown that this mucus is important in trapping and binding fine sediments. Accretion of fine sediments on salt marshes and mud flats can be stopped by artificially removing microalgae. Conversely, accretion of mud on sand flats can be induced by the removal of macro-invertebrates so allowing the development of large microalgal populations (see Plates 13, 14).

S. M. Coles

SEED PRODUCTION ON MOUNTAINS

The survival of any population, plant or animal, depends on its capacity to reproduce and to adapt to environmental gradients. This is especially true of mountain plants which often grow in unstable habitats with a harsh climate and poor soils. Studies began in 1974 on the production and germination of seed from a range of species throughout the Scottish Highlands including both obligate montane species found only above the tree-line and those which are facultative or more wide-ranging. The initial aim was to find how yield and the ability to germinate vary with the climate, altitude and latitude of the site of origin. Later, effects on seedling growth will be measured.

Calluna vulgaris, a widespread and important food plant of upland herbivores, is a good example of a facultative species. In the subcontinental climate of the Eastcentral Highlands it forms dense swards up to about 900m altitude and individual plants go well beyond 1000m; in the more oceanic West Highlands it is sparser, although still common below about 800m.

C. vulgaris produces copious seed where it is thriving, but seed production appears to decrease toward its geographical and upper altitudinal limits. In a good year, an average capsule of *Calluna* contains 26–30 seeds, but effective production is usually dependent upon less than 20 because a proportion are shrivelled and presumably aborted. In 1975, capsules at 300m in the eastern Highlands each contained about 14 fully developed seeds, nearly twice as many as at the same





altitude in the west (Figure 9). Indeed, there were as many seeds per capsule at 600m in the east as at 150m in the west. However, the differences lessened at higher altitudes because yields per capsule diminished at a faster rate in the east $(1.6 \text{ seed } 100m^{-1})$ than in the west $(0.8 \text{ seed } 100m^{-1})$. Seed production was also inversely related to latitude, particularly in the west. However the magnitude of the latitudinal effect depended on altitude, being negligible at 150m but progressively greater at higher levels until production was almost nil above 300m on Quinag in the far north-west.

These patterns of seed production are presumably to some extent determined climatically. Annual fluctuations have also been recorded and these may be a product of weather in different summers. For example during the warm and dry 1973 and 1975 seasons in the Cairngorms *C. vulgaris* set about 15 seeds per capsule at 300m and 2–5 at 900m. By contrast, the cool wet summer of 1974 yielded only 8 seeds per capsule at 300m and none above 600m. Thus it appears that *Calluna vulgaris* sets seed virtually every year at low altitudes in the eastern Highlands but it is likely that complete failure must occur frequently at high elevations, especially in the far north and west.

There is less detailed information about other species. Erica cinerea was found to be similar to Calluna vulgaris in producing fewer seeds with increase in altitude and latitude at the oceanic sites of the west. In Juncus squarrosus it was found that seeds tended to become scarce with increasing altitude and latitude at all sites. However Nardus stricta, Empetrum nigrum agg., Vaccinium myrtillus, V. vitis-idaea, and E. cinerea in the east showed little or no variation in the numbers of seeds produced between 300m and 900m but all set fewer seeds per capsule or berry in the west and all but two were less productive at high latitudes. The two exceptions, E. nigrum agg. and V. vitis-idaea, are arctic-alpine in their European distributions and in fact tended to yield more seeds per berry with increasing latitude.

G. R. Miller R. P. Cummins

ECOPHYSIOLOGY OF TUNDRA PLANTS

Tundra regions occupy about 15% of the earth's surface and are characterized by low species diversity, slow rates of organic turnover and marked conservation of energy. The balance of the ecosystems is so delicate that they can be irreversibly damaged by only minimal disturbance. Because of their general inaccessibility the potential of these ecosystems has been largely neglected. Yet their flora represents an important genetic resource which has arisen over thousands of years of selection by an extremely harsh environment and consists of individuals capable of withstanding such rigours as high winds, a limited or intermittent supply of water or nutrients and widely fluctuating diurnal temperature regimes.

Work that was formerly part of the International Biological Programme's Bipolar Botanical Project is being extended to investigate the patterns of growth and reproductive strategies which have evolved in tundra plants, particularly bryophytes, and which enable them to exist in harsh environments. During the summer of 1975 field investigations of photosynthetic strategies and the hormonal control of growth were made at Abisko, in Arctic Sweden.

Two main ways of maximising energy fixation by photosynthesis were found. First, in many species, all above-ground organs were photosynthetic and in some instances reproductive organs were not only self-supporting but also net exporters of photosynthate



Figure 10 The association of net photosynthetic rates in the moss Polytrichum alpestre and changing radiant flux densities and atmospheric temperatures. Results obtained with Antarctic material grown at 0°C during nights and 0°C to 5°C during the days. Dry matter gains occurred even at -5°C.

to storage tissue elsewhere in the plant. Secondly, adaptation of metabolic processes to environmental constraints was reflected in positive rates of net photosynthesis in exceptional conditions (Figure 10); many species of mosses were found to be able to sustain slow growth beneath snow. It was also found that many methods of energy conservation exist. For example tundra plants tend to be long-lived and vegetative reproduction leads to the formation of extensive clones, which consist of progressively older generations. Physiological continuity within these systems, and a division of labour between generations, short-circuits the cycle of death - decomposition - nutrient uptake thus reducing energy wastage. Such clonal systems in themselves resemble a miniature ecosystem, being almost self-sustaining units. A well developed transport and allocation system within such clones allows rapid remobilisation of energy early each spring for the production of assimilatory tissue, thus maximising energy fixation during the short tundra growing season, a capability of particular importance when it is realised that even at the beginning of the growing season the daylength is already decreasing.

Whereas the growth studies were based on short time scales which ranged from photosynthetic rates per minute to the life span of an individual plant, investigations of reproductive biology and survival probabilities have concentrated on population changes over much longer time intervals. By calculating agespecific probabilities of death and reproduction and determining their environmental controls it is hoped that the effects of disturbance or management treatments on population structure and stability may be predicted. When computer models of growth, based on field microclimate data which similate patterns of photosynthetic activity and dry matter accumulation throughout the lifetime of a species, are combined with models of population dynamics, estimates of yield and rates of production should be predictable over considerable time periods.

T. V. Callaghan N. J. Collins

Invertebrate performance and population dynamics

TROPHIC EGGS IN ANTS

In social Hymenoptera queens were until recently thought to stop worker egg laying completely. In ants this is true of some species but, as has been suspected for some time, it is not even remotely true for others. Tracer techniques have shown that queens of *Myrmica* induce workers to lay more eggs earlier, rather than later. Moreover, it has now been possible to show, normally using vital dyes, that egg laying by workers starts soon after egg laying by queens; only if there are no queens present do workers delay oviposition four or five weeks.

Not only is this so, but it has now been possible to demonstrate that the workers lay a different sort of egg if queens are present: a trophic egg. The normal reproductive egg (of queens or of workers) is bean shaped and rigid with a strong thick chorion, and is rich in protein: and it has developmental potentiality. The trophic egg of workers is flabby, has a thin cuticle, a white opalescent yolk containing more lipids than proteins and no developmental potentiality at all. When laid it is put with the other eggs in a cluster and serves as food for young larvae as they hatch. These larvae have sickle-shaped jaws that can lift up a section of the flabby skin and pierce it; the egg contents are then sucked out. Larvae cannot break into reproductive eggs owing to the rigidity of the cuticle and so most survive to produce larvae. Some trophic eggs may be fed to queens and larvae; they obviously constitute a rich concentrated store of nutrient.

Experiments are under way which aim to discover whether these eggs play a role in ant caste determination like that of royal jelly in honey bees. So far the evidence is that the eggs encourage female larvae to metamorphose prematurely into workers rather than grow into queens. However it is now known that even in the honey bee, worker-forming larvae are fed better than queen-forming ones for the first three days (on worker jelly) and only afterwards forced to undergo a restricted diet. Thus the resemblance may in fact turn out to be closer than at first appears (Plate 15).

M. V. Brian

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LARVAL RECOGNITION IN ANTS

Work has been carried out over the past few years with the aim of identifying the characteristics of larvae that enable worker ants to recognise them. It is known that they accept and nurse their own young (even those from other colonies) but usually reject those of other species. The test used was whether they retrieved dummy larvae from outside the nest as guickly as normal ones. With this in mind, larvae were deprived of their surface hairiness, of their surface chemistry by treatment in solvents, of their rotund shape by extracting some of their contents, or of their internal organs by replacing them with air or water. A series of such experiments showed that the most important, indeed the essential, feature in recognition is a lipid of high molecular weight, perhaps an ester wax or a steroid present in the cuticle just beneath the wax layer. Hairiness and rotundity, though not themselves essential, both reduce the time taken by workers to decide between a fake larva and a real one.

In addition to this general surface property it was discovered that larvae with the potentiality to grow into queens can be recognised by workers in spring by virtue of a liquid secreted on their undersurface in the forward and head region. This signal is only emitted for a short period in their total larval life but at a crucial phase of caste differentiation : just before the last opportunity to form workers instead of gynes. Hence in the presence of queens such larvae are suppressed by constant worker attack which brings on early metamorphosis and by dilution of the food which prevents adequate growth. In the absence of queens the same larvae are fed copiously and given absolute priority over small individuals so that they grow without hindrance into young queens.

Thus the complexity of communication and trophic organisation in quite a simple ant colony is considerable.

M. V. Brian

COMPARATIVE ECOLOGY OF MYRMICA SPECIES

The common red ants of the genus Myrmica, are well known to country-lovers, particularly for their ability to inflict a painful sting upon the unwary. In Britain there are seven species of Myrmica of which four are reasonably common and another two are ubiquitous; these are M. ruginodis and M. scabrinodis which can be found in every county of the United Kingdom. Colonies contain from fifty to several thousand workers depending upon the species and the genus is especially interesting because there are considerable variations in the numbers and types of queen present in colonies - even of the same species (see ITE report for 1974). Although each species seems to prefer a specific habitat type, there is a considerable overlap of range and when this occurs, particularly in M. scabrinodis and M. ruginodis, colonies compete for resources. Recent results suggest that the competition is for nest sites rather than food supply.

The differing potentials of the species to survive in different habitat types means that the numbers, size and distribution of *Myrmica* colonies will vary from site to site. This may well have a considerable effect on the invertebrate species that interact with *Myrmica*; for example, the Large blue butterfly research programme conducted by Dr J. A. Thomas suggests that the density, size and species structure of the *Myrmica* colonies at the breeding sites might be important in the survival of the caterpillars. Therefore, current work at Furzebrook is designed to investigate these natural

variations and to attempt to determine some of the factors that control them. (*M. ruginodis* -- Plate 16)

So far, comparative population data has been collected for all the British species and populations of M. scabrinodis and M. ruginodis have been compared in detail on several moorland sites. M. scabrinodis colonies have been collected from seven sites in southern England which can be grouped to form three habitat types. These are Calluna moor, represented by sites in Exmoor, Dartmoor and Dorset; grassy moor, in an abandoned field system on Bodmin Moor; and Lowland grassland at sites on calcareous and acid soils in Dorset. The average size of colonies found at these sites is given in Table 1 and there it is seen that Lowland grass sites support far bigger colonies than the Calluna moor. If the sites could be assessed qualitatively in terms of 'richness' the Calluna moor would be considered to be the 'poorest' site, the grassy moor the next and the Lowland grass the 'richest'. The concept of 'richness', defined as some arbitrary but integrated measure of the variety and abundance of plant and animal species present at the site, is unfortunately very subjective and difficult to quantify. but if it is possible to do so and then correlate the measure with the Myrmica population, the structure of Myrmica populations might provide a rapid method of comparing different moorland sites (Plates 17-20).

The populations of *M. ruginodis* colonies living in the same general habitat show differences between sites. Populations have been measured on three types of *Calluna* moor; first from high, dry, cold moors, secondly from more sheltered, boggy areas on Dartmoor and Exmoor and thirdly from a site on warm, sheltered Dorset heathland, protected by a low density of

Table 1 Mean number of individuals found in M. scabrinodis colonies collected from three types of habitat

	No. of colonies	Workers	Queens
Calluna moor	25	193	0·4
Grassy moor	12	275	1·1
Lowland grass	13	753	2·6

mature Scots pine. *M. ruginodis* has two types of colony that are separated by the size and numbers of queens they contain; the normal form usually has only one large queen and the other type has several small queens or microgynes (see *ITE 1974* report). Table 2 shows that although the colony populations of both forms vary between the sites in much the same way, the microgyne form is much more abundant on the colder moors than upon the warm Dorset heath. This suggests that the microgyne variety may be an adaptation to the poorer habitats that are found at the high levels on Dartmoor and Exmoor.

G. W. Elmes

ECOLOGY OF THE SWALLOWTAIL BUTTERFLY

Since the early 1950s, when the British swallowtail (*Papilio machaon britannicus*) became extinct at Wicken Fen, this subspecies has been confined to marshes around the Norfolk Broads. Here too, however, its abundance appears to be declining.

Since 1971, the ecology of this butterfly and of its food plant, Milk parsley (*Peucedanum palustre*), has been studied in an attempt to understand the causes for its recent decline in abundance in Norfolk, and of its extinction at Wicken (Dempster, King and Lakhani 1976). The possibility of re-establishing the butterfly at Wicken has also been studied. This research has taken the following three main lines. (See Plates 33–36.)

First, the survival of the young stages of the butterfly has been studied on a natural population in Norfolk, for comparison with survival of small numbers introduced at Wicken. This showed that there are three main periods of high mortality, first during early larval life, secondly during the fourth and early fifth larval stages, and thirdly, during the pupal stage. Invertebrate predators, particularly spiders, are the main cause of early larval losses, while birds are important predators of older larvae. Little is known about the causes of pupal mortality, but small mammal predators are likely to be involved. Survival at Wicken tended to be better than in Norfolk, because bird predation was not recorded there. It is likely that the very low numbers of caterpillars introduced to Wicken did not attract bird predation.

Table 2 Mean number of individuals and number of colonies of the two types of M. ruginodis from three moorland sites

	Microgyne type			Normal type		
	No. of colonies	Workers	Queens	No. of colonies	Workers	Queens
High, dry, cold moor High, wet, cold moor Low, warm heath	20 12 3	163 224 440	3 4 13	29 16 22	117 268 438	0.6 0.9 0.5

Larger numbers probably would have been fed on by birds, since the species feeding on *Papilio* in Norfolk are abundant at Wicken.

Before it became extinct, the swallowtail population at Wicken had persisted for at least 200 years in isolation. Repeated attempts to re-introduce the species to Wicken have failed, however, and this could be due to Norfolk butterflies now being sufficiently different from those which occurred at Wicken to be unable to persist there. The second line of work, therefore, undertook a comparison of the morphometrics of museum specimens from Wicken and Norfolk to see whether any indication of evolutionary change could be detected. This study showed that there were marked differences in the size and shape of butterflies between 1890 and 1920, but that these have become less marked in more recent times. These changes in size and shape of the butterfly appear to be linked with changes in its mobility. The final line of study was into the status and performance of the butterfly's food plant. This is a local species, restricted to fen habitats. At Wicken, the plants tend to be smaller, to produce less seed and to be shorter-lived than in Norfolk. These differences are not genetically determined, since plants from both areas performed equally well in a greenhouse at Monks Wood. At Wicken, there is a rapid turnover of plants and numbers are maintained solely by repeated cutting of the vegetation in which they are growing. In Norfolk, conditions are far more suitable for the plant and a low rate of production of seedlings is required to maintain plant numbers.

The butterfly selects mainly large plants, which have leaves exposed above the surrounding vegetation, on which to lay its eggs. Under the drier conditions found at Wicken suitable plants are at a very low density.

J. P. Dempster

Vertebrate performance and population ecology

DENSITIES AND BREEDING SUCCESS OF SPARROWHAWKS (This work was largely supported by Nature Conservancy Council funds)

The sparrowhawk (*Accipiter nisus*) is of interest because it suffered a widespread population decline in the nineteen fifties and 'sixties associated with the use of organo-chlorine pesticides in agriculture. With successive restrictions in the use of such compounds, the species has recently begun to recover, but in most areas it is still below its former strength. This project aims to find what is currently limiting the numbers and nesting success of the species in different parts of Britain.

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Sparrowhawks nest only in woodland of a certain structure, but hunt in other kinds of woodland and in other habitats. They use the same restricted nesting territories in different years. In 12 areas of Britain, territories were regularly spaced in continuous nesting habitat, but at different distances apart in different regions: from 0.5km in the Lower Solway Plain (Cumbria) to 2.1 km in Mar Forest (Aberdeenshire). The nearest neighbour distances were highly correlated with altitude (r = 0.911) and with soil productivity (r = 0.831). Comparing areas, territories became 0.1 km further apart for every 25 metres rise in altitude, or for every 0.36 point drop (on a 1-10 scale) in soil productivity. It is probable that these environmental factors influence the densities of the small song-birds (the main prey), and that sparrowhawks responded to these rather than to altitude or soil as such.

The major factor influencing breeding output in these areas was the organo-chlorine content of the birds and their eggs. Such compounds included DDE (the main metabolite of the insecticide DDT), PCB (industrial polychlorinated biphenyls) and HEOD (from the insecticides aldrin and dieldrin). Since 1947, when DDT first came into wide use in British agriculture, sparrowhawks have laid thin-shelled eggs, which are often broken, thus leading to reduced breeding output. In addition, many of the eggs which survive incubation fail to hatch because they are addled. Differences in the breeding output of sparrowhawks between the 12 study areas were highly correlated with the levels of certain organo-chlorine compounds in the eggs. DDE was important in causing shell-thinning and addling of eggs, while PCB also caused egg addling, and both compounds thereby contributed to reduced breeding success. HEOD was present in eggs only at low concentration and had at most a slight effect on breeding. In these areas the levels of DDE and HEOD in sparrowhawks eggs did not decline during the period 1971-75, but the levels of PCB declined significantly.

The index of eggshell thickness in the sparrowhawk, from 1870–present, is shown in Figure 11. Thin-shelled eggs have been laid from 1947, the period of widespread DDT usage in Britain. The graph is based on nearly a thousand clutches of eggs collected in all counties of Britain, and available in museum and private collections. Each point refers to one clutch, and is the mean of all eggs in that clutch which were examined.

In recent years many traditional nesting territories have been devoid of breeding pairs, and we are now trying to find how much the reduced breeding output is influencing adult numbers. It seems that in some areas populations are producing so few young that they can be maintained only by the immigration of surplus young



Plate 33 Milk parsley, food plant of Swallowtail butterfly.



Plate 36 Swallowtail butterfly adult.



Plate 34 Swallowtail butterfly V ph instar larva.



Plate 35 Swallowtail butterfly pupa. Photographs above by J. Dempster.



Plate 37 The Greater horseshoe bat (Rhinolophus ferrumequinum). Photograph R. Stebbings.



Plate 38 Cuckoo laying its egg in the nest of the Reed warbler, while throwing out the warbler's egg. Photograph I. Wyllie.



Plate 39 Red deer hind with her 2 month old calf. Photograph B. Mitchell.

produced by other less contaminated populations elsewhere. In yet other areas sparrowhawks became extinct in the late nineteen-fifties and still show no sign of re-colonisation. These are areas in eastern England where pesticide usage could be expected to be unusually heavy.

I. Newton M. Marquiss

CUCKOOS AND REED WARBLERS

Previous research into the breeding biology of the cuckoo (*Cuculus canorus*) has led to a number of theories, supported by varying amounts of evidence. These include:

(1) Adult cuckoos may be host-specific, each female laying eggs of unique colour and pattern in nests of one main host species. Edgar Chance (1940) showed that one female cuckoo returned annually for several years to the same breeding site where Meadow pipits (*Anthus pratensis*) were the usual hosts.

(2) The host-specificity of young cuckoos may be genetically determined usually for the species by which they were reared. Alternatively, young ones may be 'imprinted' on their fosterers.

(3) Adaptation of cuckoo eggs to match those of their hosts may have evolved through the discriminatory ability of the hosts. In other words, the hosts have rejected cuckoo eggs unlike their own. Baker (1942) has shown that the eggs of Asiatic and European forms of *C. canorus* tend to match the eggs of their hosts in size and colour.

(4) Female cuckoos may manipulate the breeding of their hosts by destroying unsuitable nests in order that repeat-nests become available for cuckoo eggs. Eggs are usually laid in the afternoons, at two-day intervals in nests where incubation has not begun (Chance 1940).

(5) The alternate-day laying sequence and the eggretaining ability of female cuckoos may be adaptations to produce partly incubated eggs. This is thought to give young cuckoos greater chance of survival on hatching, when the 'rightful' nest occupants are instinctively ejected. Research on the reproductive behaviour of cuckoos parasitising Reed warblers (*Acrocephalus scirpaceus*) at a study site near Monks Wood in Cambridgeshire was begun in 1975.

As adults look alike, it was necessary to catch and mark with wing-tags as many breeding birds as possible in order to investigate :



Figure 11 The index of eggshell thickness in the sparrowhawk, 1870–present.

(a) 'territorial' activities, including calls used by sexes, pair-formation, and territory sizes.

(b) breeding period in relation to that of the hosts' and the proportion of host nests parasitised.

(c) egg-laying procedure and host-nest predation by cuckoos.

(d) growth and survival of young cuckoos.

Initial results show that Reed warblers were the only known hosts: in 265 of their nests, 35 cuckoo eggs were laid. This suggests that cuckoos are, in fact, hostspecific. Only two eggs were deserted by the hosts but many disappeared before hatching, suggesting some discrimination by the hosts. There was some overlap of the egg-laying areas used by different female cuckoos, and males were observed to simultaneously occupy more than one female range during the season. An egg-laying area of one marked female was smaller than her total 'home-range'. Her nine eggs were the same in colour and pattern, and tended to be laid after mid-day at two-day intervals in nests with incomplete clutches, thus supporting Chance's findings.

Female cuckoos always laid directly into the nests by straddling the nest-cup. No other egg-laying method was recorded. Repeat-nests of previously predated Reed warbler nests were often cuckolded, and several observations of cuckoos robbing eggs or young from host nests indicated that some control over the host nests was exercised. The *actual* incubation period of cuckoo eggs was estimated at 12 days, and most hatched out in advance of the hosts' smaller eggs.

Future research will examine the possible hostspecificity of returning marked young cuckoos, assess the sizes of egg-laying areas and total home-ranges and make further detailed investigations of territorial and breeding activities. (Plate 38).

I. Wyllie

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THE ECOLOGY OF THE MEADOW PIPIT

Grassland covers about half the land area of the British Isles, and the Meadow pipit (*Anthus pratensis*) is one of the most widespread and numerous bird species in this habitat. In 1972–5 a pipit population was studied on a grassy mountain area in Snowdonia. One aim was to determine the numbers of birds present, and if this can be done accurately the Meadow pipit might be a useful indicator of the biological characteristics of this type of habitat and a monitor of changes caused by man.

During the winter, the Meadow pipit was absent from the mountains. The species emigrates to south west Europe, although some pairs probably remain in lowland and coastal areas of the British Isles. Birds returned in March, and took up home ranges mostly on sites occupied in previous years. The male declared himself and his range by means of a song-display flight. Within the range, both sexes spent about 90% of their time on the ground and conversely very little time in the air. Within this overall pattern there was variation both in the parts of the habitat utilised and in the activities of the sexes in successive stages of breeding. Prior to breeding (in April to August), the male spent 60% of his time on the level surface of the ground and 25% on elevated perching places such as rocks. When there were eggs in the nest, watching the range (followed by foraging), was his main activity. The female (who alone incubated) foraged nearly all the time (88%) she was away from the nest. When there were nestlings, which were fed by both parents, the male's main activity became foraging again.

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The rate of detection of any individual marked male was 29% of the number of days observation, while the rate of occurrence of song-displays was 8%; censuses of unmarked birds based on sightings or the occurrence of singing males seem likely to give underestimates of population size.

The numbers of resident males on the study site of 15 ha varied in different years from 11, when only 16% of the ground was unoccupied by range-holders, to 5 when 50% of the ground was apparently vacant. Despite these variations, range sizes remained much the same but showed large measures of overlap at higher population densities. Adults collecting food for their nestlings commonly transgressed previously defined range boundaries, suggesting that the prime function of the range is to disperse the birds and their nests, and so probably render them less liable to predation. Nest failures were numerous but in the remaining nests the survival rate of the young was high. The adults departed in about August, while the juveniles remained until October.

The grassland habitat on the mountains is largely maintained by grazing by sheep, but new economic conditions could alter this situation, for example, by introducing different grazing animals or a wholly different use of the land, namely, afforestation.

Information on the current status of the commoner animals could provide a basis for assessing the consequences of such changes.

D. C. Seel

FERTILITY AND FECUNDITY IN FEMALE SCOTTISH RED DEER

In northern Scotland, the Red deer (Cervus elaphus L.) is important both as a resource with meat-producing, sporting and aesthetic values, and as a habitat modifying factor. The importance of the animal as a resource together with the pressures of other land-use factors have encouraged relatively high population densities of Red deer in somewhat atypical habitat. The term deerforest may seem ecologically ironic in view of the fact that most present-day deer-forest land has only remnants of natural woodland, and it includes a great deal of land above the natural tree-line, but it is well known that the term in this context, means hunting ground and not woodland. Nevertheless, is it perhaps not surprising that Red deer on Scottish hill-land show lower rates of growth, smaller adult size, and lower reproductive output, than those deer living in the woodland or woodland-edge habitats more typical of the species in other countries. Understanding the causes of poor performance involves first describing the demographic properties of Red deer populations in terms of their sex and age constituents, and then relating variations in these to environmental influences and limitations. Much of the earlier work was concerned with the former, i.e. describing and comparing populations, and much remains to be done on how the deer respond to environmental factors.

Reproduction is clearly important both as a useful index of performance and as the main proximal influence on population turnover and cropping potential. Red deer are characterised by single births, and like other ungulates of the temperate zone they have a well defined annual breeding cycle. They mate in early autumn with gestation over the winter and spring and give birth in late May to late June in Scotland. In the most favourable environments, the birth rate may exceed 70 calves/100 hinds, but in Scotland it rarely exceeds 40 calves/100 hinds. Comparing the hinds in different populations indicates that the calving rate is affected by two factors which also tend to vary in parallel: the age at puberty and the proportion of sexually mature adults which fail to ovulate and conceive in a given year. At best, Red deer hinds become sexually mature as yearlings (at 1 year 4 months) and breed almost every year thereafter. In less favourable environments, as in Scotland, hinds tend to mature a year or more later and breed less frequently as adults. Typically in Scotland, some 30-35% of mature hinds fail to breed each year; hinds not supporting calves are called 'yeld' and hinds supporting calves, 'milk'. Yeld and milk hinds shot in late autumn and winter (during the early period of gestation) differ in weight, condition and pregnancy rates; yeld hinds tend to be heavier, in better condition, and have higher pregnancy rates than milk hinds. Except in the oldest age classes, yeld hinds show pregnancy rates of 90-95% compared with 50% or less in milk hinds. Thus there is a tendency for hinds to breed one year and fail the next, and there is little doubt that failure to breed is associated with the reduced weight and condition caused by the earlier pregnancy and current lactation. In fact, the studies have shown a number of different relationships between reproduction and body weight or condition. Whether and when a hind breeds in a given breeding season depends on her body weight or condition, and it is difficult to separate the latter two factors on account of their high correlation (Mitchell 1973; Mitchell and Lincoln 1973; Mitchell and Brown 1974). Hinds in good condition tend to ovulate and conceive early in the mating season, whereas those in poor condition tend to ovulate and conceive later or not at all. Thus high birth rates are associated with early breeding and in turn with high rates of individual growth. Low birth rates are associated with later breeding and lower rates of individual growth.

A mathematical model based on data from hinds at Glen Feshie (Mitchell and Brown 1974) shows convincingly the influence of various animal factors on fertility, and its predictions seem to fit the available data from other Red deer populations. Carcase weight, age, and whether yeld or milk, seem to influence fertility, in that order of importance. The carcase weight at which there is a 90% probability of breeding varies according to age, the minimum value being at 7 or 8 years of age. Yeld hinds seem to have a slightly higher probability of breeding than milk hinds of the same age and carcase weight. To achieve a 90% probability of breeding as yearlings, hinds must be about 55 kg in terms of larder carcase weights, i.e., weight of live animal minus alimentary tract (= $0.7 \times \text{live weight}$). This is seldom the case with Scottish yearling hinds; those at Glen Feshie (referred to in a previous report) weigh 35.9 kg on average and are not fertile whereas the few fertile yearlings found in some other study populations in Scotland are 50kg or more. (Plate 39).

The existence of appreciable proportions of yeld hinds in Scottish Red deer populations is presumptive evidence in favour of nutrition as the main proximal factor limiting performance; the animals are slow to recover from the effects of pregnancy and lactation in this environment, but it remains to be shown whether this is associated with forage quality, exposure or population density, or some combination of these. It would be useful for management purposes to know the extent to which performance could be improved by stock adjustment, habitat treatment or supplementary feeding.

B. Mitchell

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Ecosystem processes

THE PRODUCTION OF PHYTOPLANKTON AND THE LIGHT-CLIMATE OF LOCH LEVEN, KINROSS

Like that of other plants, the growth of phytoplankton depends on many external factors including light. However light penetration itself is influenced not only by suspended non-biological matter and dissolved coloured substances but also by the density of the phytoplankton crop. These interrelations were studied in the shallow (mean depth 3.9m) and nutrient-rich Loch Leven during the IBP study period.

Figure 12 shows seasonal changes at Loch Leven during 1971 in (a) phytoplankton population density, assessed as chlorophyll *a* (chl*a*) concentration, (b) the minimum vertical extinction coefficient over the visible spectrum (K min), (c) the euphotic depth (zeu), and (d) Secchi disc transparency.

Light extinction in the water column was highest in the blue and lowest in the orange spectral regions, a pattern typical of other turbid waters. The depth at which 1% of surface light was found (the euphotic depth) varied between 1.2 and 7.4m, and depended chiefly on phytoplankton crop density (measured as chlorophyll *a*). The increment in light extinction for unit increment in crop density indicated that the theoretical upper limit for chlorophyll *a* within the euphotic zone was *c*. 450mg/m². This value, which is higher than most published estimates from other waters, was sometimes closely approached in the loch and was one of the reasons for the high rates of gross photosynthetic productivity recorded (Bindloss 1974).

In many shallow waters wind-induced turbulence brings material from the sediments into suspension. This material competes for light energy with the phytoplankton and thereby reduces its productivity. Despite the shallowness and wind-exposed situation of Loch Leven there was no evidence of appreciable non-algal light extinction attributable to sediment disturbance. Any material which was disturbed during storms (when underwater light measurements could not be made) subsequently sedimented relatively quickly. In part, the nature of the sediments would favour this; in shallower, more-easily disturbed regions the sediment is a coarse-grained sand.



Figure 12 Phytoplankton production in Loch Leven

Dissolved coloured substances were a minor source of light extinction in Loch Leven; this situation contrasts with that found in many of the Shetland lochs examined during the ITE survey. These waters were often strongly coloured by dissolved humic material.

The rapid extinction of light in Loch Leven was reflected in the shape of the photosynthesis/depth profiles; these showed a narrow zone of optimum light and a sharp decrease of photosynthetic rate with depth. Productivity per unit area was shown to be related to the logarithm of the ratio between incident irradiance (I_0) and the irradiance (I_k) defining the onset of lightsaturation of photosynthesis. I_k increased with increase in water temperature, which in turn increased with increase in I_0 . A spring maximum in the ratio I_0/I_k is interpreted as due to a lag in the increase in water temperature with increase in I_0 .

It seems that the highest crop densities found in Loch Leven may be light-limited due to self-shading by the phytoplankton themselves. Poor light penetration may also explain the scarcity of submerged macrophytes in the loch during the study period (Jupp, Spence and Britton 1974).

M. E. Bindloss

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PLANKTON IN LOCH LEVEN

Since 1972 when changing methods of waste disposal decreased the phosphorus input into Loch Leven, there has been a conspicuous decrease in the biomass of microalgae. During the four years before 1972 seasonal maxima ranged from 190 to 259 mg chlorophyll a m⁻³; thereafter they have been fluctuating between 70 and 163. There have been accompanying differences in the species present. Thus, before 1972, the relatively small Cvclotella pseudostelligera, Oscillatoria redekei and Synechococcus and Steniella species predominated giving peaks, singly or in combination, in March, May and June. Since 1972 the peaks have changed to March, August, November and December and many specimens of the relatively large Melosira ambigua and Anaebaena spp. have been present. Throughout 1975 the pennate diatom Asterionella formosa Hass. was generally abundant with peaks of the small unicellular centric diatoms Cyclotella and Stephanodiscus in March, of the filamentous centric diatom Melosira (mainly M. ambigua (Grun.) Muller) in May and July, Diatoma elongatum Agardh. in June and the filamen-

tous blue-green Anabaena flos-aquae Breb ex Born. et Flah. in May and August.

Interestingly the decreased mean densities of phytoplankton have been associated with changes in the composition of the zooplankton. Whereas *Daphnia hyalina* var. *lacustris*, an herbivorous cladoceran, occurred infrequently before 1972, when the copepod *Cyclops strenuus* var. *abyssorum* (Sars) predominated, its numbers have since greatly increased. This observation suggests that changing concentrations of nutrients, in this instance forms of phosphorus, greatly influence the nature of the equilibrium between phytoplankton and zooplankton.

A. E. Bailey-Watts D. G. George

SECONDARY PRODUCTION IN ECOSYSTEMS

The remit for an invited paper for the First International Congress of Ecology, given by Heal and MacLean (1975), was to review information on secondary production (micro-organisms to mammals) in terrestrial ecosystems (tundra to tropics). There are many estimates of productivity of individual species especially of vertebrate herbivores and insects, but data are sparse or non existent for soil fauna, decomposer microflora and for complete trophic levels. With this limitation to comprehensive comparisons an alternative approach was adopted in which annual secondary production was predicted from the hypothesis that is a function of:

(i) the input from primary production;

(ii) the consumption, assimilation and growth efficiencies of the populations, these efficiencies being broadly characteristic of taxonomic group and food;

(iii) the organisation of heterotrophic into herbivore and saprovore subsystems, with recycling of organic matter confined to the saprovores (Figure 13).

Secondary production in any terrestrial ecosystem is thus the logical consequence of the combination of these factors.

Primary production varies greatly between ecosystems and has been reasonably well estimated at a range of sites; the secondary production was calculated for these sites and compared with observed values. There was broad agreement between observed and predicted values and an absence of obvious pattern of deviation in observed from predicted values for particular trophic levels or ecosystems. This agreement suggests that, despite major differences in species composition, most terrestrial ecosystems are similar in the organisation and efficiency of secondary production, with primary production being a major cause (possibly the major cause) of variation. Discrepancies between observed and predicted values can arise from large year-to-year variations in field populations, and from errors in field estimates and the model hypothesis. Further modification of the hypothesis is not possible until more data are available to test it critically.

The calculations emphasise the major role of the saprovore subsystem in energy and nutrient transformations. In a grazed grassland, about 14% of the energy in primary production passes through the herbivore subsystem with 86% passing through the dead organic matter and the saprovore subsystem. Production by litter and soil microflora is estimated to be 10²–10³ times greater than that of vertebrate herbivores. This production includes re-cycling of microbial production and brings into question the comparability of some estimates of production.

O. W. Heal (with *S. F. MacLean*, Institute of Arctic Biology, University of Alaska)

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SOIL PRODUCTION OF FUNGAL MYCELIUM

Fungi occur in soil as wefts of thread-like hyphae (mycelium), which grow, die and decay in cycles varying in length from a few days to several months. After three-quarters of a century of research, microbiologists are still only guessing at the total annual production of mycelium, although it is vital to soil fertility. The amount of mycelium present in a soil sample at a particular moment can be measured under the microscope, but this so-called standing crop can fall far short of production over a period of time. In continuing studies of the Common gill fungus, Mycena galopus annual production (P) of mycelium in the decaying leaves of a woodland soil in Cumbria has been estimated from measurement of net change in standing crop (ΔC) and allowing for mycelial decay (L), assuming that:

 $P = \Delta C + L$



Figure 13 A generalised trophic structure for terrestrial ecosystems with estimated efficiencies of ingestion. PP = primary production, DOM = deadorganic matter, H = herbivore, C = carnivore, S = saprivore,M = microbivore, V = vertebrate I = invertebrate, M = microbe, R = respiration. To determine this loss or decay rate, the fungal mycelium was 'labelled' in the laboratory by growing it on oak leaf discs lying on a nutrient medium, which contained a fluorescent chemical, Calcofluor White. When the fungus had absorbed this non-toxic dye, the discs were buried in a natural woodland habitat and examined at monthly intervals. Previous experiments had shown that the label was neither transferred to new growth, nor washed out by rain nor was it harmful to small animals which normally feed on mycelium. At each examination, some of the leaf discs were macerated and the length of fluorescing hyphae estimated from the number of hyphal intersections on a grid observed with a fluorescence microscope. Decay rate was then obtained mathematically by regression analysis of the form:

$$\log e \ \frac{(x_t)}{(x_0)} = a - bt$$

where, x_0 and x_t = lengths of hyphae present at time 'o' and 't' respectively.

These decay data were applied to measurements of the standing crop of *M. galopus*, growing naturally on decaying oak leaves in the same wood, when the minimum annual production of mycelium was found to be 0.5 kg/ha. This figure is about twice the maximum estimate for a standing crop and ten times the average weight of fruit bodies, that appear above ground (Hering 1966). It illustrates the disparity in woodlands between the aerial production of fruit bodies that can be readily seen and that production of teeming subterranean hyphae, where tree nutrients are 'prepared' by their activities.

J. C. Frankland A. D. Bailey (R. A. Kay, Liverpool Polytechnic, assisted with this project during a sand-wich course studentship)

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COTTON STRIPS AS INDICATORS OF CELLULOSE DECOMPOSITION IN SOILS

Cellulose constitutes about 70% of the organic carbon compounds in plants and is therefore an important component of the decomposition cycle. To compare the ability of microbes and microfauna in different soils to decompose cellulose a method widely used in the textile industry was adapted for ecological use in field studies during the International Biological Programme. The method consists of inserting cotton strips $(10 \times 30 \text{ cm})$ vertically into soil profiles. After retrieval, tensile strengths were measured across five sections of each strip, separated at 4 cm intervals, so estimating changes at different depths. Tensile strength depends on the breakdown of cotton cellulose and is less affected by soil contamination than are the alternative measures of dry weight or cellulose loss (Latter and Howson in press).

The use of a standard reproducible substrate minimises variability due to plant litter composition and allows the assessment of soil and climatic factors on decomposition. The method gives an integrated measure over periods of months and can be used in cold and temperate climates. Initial tests were made at Moor House NNR in the north Pennines where the time taken for a 50% loss of tensile strength varied from 30 days on *Festuca-Agrostis* grasslands with brown earths, to 170 days on blanket bog. On some polar sites, 50% loss is not reached for more than 10 years (Heal *et al.* 1974).

The method is also suited to the detection of major longterm effects of land use changes or fertiliser and other treatments, prior to more detailed studies. Such test methods can be easily replicated on sites over a wide area or with various fertiliser and other treatments with the advantage of simple collection and transport to a central laboratory for tensile testing.

P. M. Latter G. Howson

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MEAN RESIDENCE TIMES OF ORGANIC MATTER IN WOODLAND SOILS

The rate of decomposition of organic matter controls many soil characteristics, particularly fertility which is influenced by the recycling of bound nutrients, notably N, P and S. Consequently much attention has been given to this field of soil science. The field and laboratory methods most frequently used, namely weight loss and respiration of litter, have, however, concentrated on the more labile components. However, the turnover of more stable components is also important and needs to be studied before the fate of the total organic matter complement is understood.

Ideally the turnover of the labile and more stable components should be studied using similar techniques. This is being achieved by applying the classical radiocarbon dating technique to both the naturally introduced ¹⁴C, and ¹⁴C produced in the atmosphere by atomic weapons testing, so as to assess mean residence times of the fractions and total soil organic carbon complement.

Initial studies involved comparisons of soils from two contrasting Lake District oak woodlands. Their results have shown that (i) 'bomb ¹⁴C' has been incorporated into the organic matter and can be used to determine its mean residence time in surface soils and litters, (ii) there is excellent agreement for mean residence times for different sites within each woodland and (iii) there are significantly different mean residence time-depth patterns in the two woodlands. Further studies on soil organic carbon fractionated prior to ¹⁴C determination, indicate that in the two woodlands the mean residence times of fulvic acids are shorter than those of humins, with humic acid intermediate.

The results (Table 3) support the idea that the technique can be used to determine the turnover rate of total soil carbon and its fractions. The potential applications of the techniques are being examined in studies of soil humus in other Lake District woodlands, and of the influences of upland land use on soil organic matter, the latter by S. Ladyman, a NERC research student at the Radiocarbon Laboratory, East Kilbride.

A. F. Harrison (with D. D. Harkness, NERC Radiocarbon Laboratory, Scottish Universities Research Reactor Centre, East Kilbride)

THE EFFECTS OF BIRCH ON MOORLAND SOILS

It has been contended that past use of the uplands has resulted in widespread soil degradation, with lower fertility and increased acidity of the topsoil, and accelerated podzolization. There is some evidence that the growth of birch (*Betula pendula* and *B. pubescens*) may reverse these trends – though to what extent is unknown – thus increasing the capacity of sites to support other species and hence their value to man.

A project begun in late 1973 aims to identify the trends, rates, limits and causes of any effects associated with birch development on poor moorland soils. The approach was to examine changes in soil under first generation birch stands of different ages at each of thirteen sites, situated from Sutherland to north Yorkshire, where birch has invaded moorland. Soil

Table 3 Mean residence times of soil organic matter in two woodlands (i) Wintering Park with mor humus on
 Silurian slate and shale and (ii) Meathop Wood with mull humus on Carboniferous limestone with drift

	Litter layer Mean resider	Fermentation layer nce times in years	Mineral soil		
			0–5 cm	5–10 cm	10–15 cm
Wintering Park Meathop Wood	2–3† 	10–11 10–11	18–20 13–15	350 <u>+</u> 50* 17–19	380 <u>+</u> 50 420 <u>+</u> 50

• Times in the form $x \pm y$ are conventional carbon dates;

t, Times in the form x-y are derived by comparing bomb ¹⁴C enrichment values with the specific activities of carbon with atmosphere since c. 1950.

 Table 4 Chemical analyses of the top 15 cm of soil taken from sites near Cannich, illustrating the successional gradient from Callunetum to Betula pendula woodland

	Heather	17-year-old birch	26-year-old birch	69-year-old birch	LSD at 5% level
рН	4.3	5.0	5.1	4.8	0.3
Extr Ca (mg dm ⁻³)	202	399	402	726	274
Extr Mg (mg dm ⁻³)	95	92	110	168	19
Extr K (mg dm ⁻³)	119	89	134	118	32
Extr Na (mg dm ⁻³)	36	35	37	53	10
Extr P (mg dm ^{-3})	14.6	13.8	18.2	18-0	8.1
N mineralization after		,,,,,	102	100	01
$(ma dm^{-3})$	71	124	180	160	50
Total N (mg dm ⁻³)	3550	2660	3030	2080	53 750
Total P (mg dm ⁻³)	147	190	247	260	100
Extr Fe* (mg 100 g ⁻¹)	66	190	1360	1950	100
Extr Al* (mg 100 g ⁻¹)	190	—	550	650	180

* Soil from the bottom 10cm of the A horizon.

mineralogy, particle size distribution and buried plant remains are being examined to determine the degree of soil uniformity that existed over each site before birch colonization began, so that the present differences can effectively be interpreted as though the site were an experiment that had run over several years.

Measurements of pH, bulk density, loss of weight on ignition and available-water capacity are being made on the top 5cm of soil and of ammonium acetate extractable calcium, magnesium, potassium, sodium and hydrogen, 0.002 N sulphuric acid extractable phosphorus, total carbon, nitrogen and phosphorus, rate of mineralization of nitrogen on incubation, loss of weight on ignition, and bulk density on the top 15 cm. The degree of podzolization is being estimated by determination of 3% oxalic acid-extractable iron and aluminium down the profiles. At some sites studies are also being made on the decomposition of buried cotton strips and on earthworm abundance. Measurements made in studying the mechanisms of soil change under birch include description of developing birch root systems, the distribution of extractable bases down soil profiles and the tannin content of birch leaves. Changes in the ground vegetation under birch canopies are also being investigated.

As an example of the results being collected, Table 4 gives some soil chemical data from a site near Cannich (Grid ref. NH 325295). These results appear to indicate a trend towards depodzolization and increasing topsoil fertility under birch, but critical interpretation must await analysis of data from all the sites.

J. Miles

Effects of land management on vegetation and fauna

ASSESSMENT OF DUNE STABILISATION USING AERIAL PHOTOGRAPHS

In summer, Camber Sand Dunes on the Sussex coast are subject to intense recreational pressures, the results of which were assessed using aerial photographs enlarged to a scale of 1:12,000. With a 1 cm² overlay grid the extents of five vegetation categories – bare sand, intermittent tussocks, dense tussocks, turf and shrub – were separately assessed. Ground verification indicated that this procedure gave consistent underestimates of 'cover' which could be corrected mathematically.

Photographs taken from 1950 to 1967 (Plate 21) indicated that ground cover except by shrubs, was

seriously and progressively decreasing, and that sand was inundating roads and residential buildings behind the dunes. Shrub vegetation, including the prickly Hippophae rhamnoides, was understandably less subject to man-made damage. To correct the deteriorating situation a comprehensive programme of stabilisation and restoration was begun in 1967 by the local authorities. Using fencing, pedestrian access to the dunes was restricted to surfaced walkways, while the dunes themselves were recontoured to lessen wind erosion and then hydraulically seeded to aid stabilisation with a commercial seed mixture of Festuca rubra, Lolium perenne, Agrostis tenuis, Poa pratensis, Sarothamnus sp. and Trifolium repens. Photographs taken in 1971 (Plate 22) show that these measures reversed previous trends with a markedly increased percentage 'cover' affecting all vegetation categories. The results illustrate the value of an ecological approach to the maintenance of natural sea defences.

J. M. Pizzey

TRANSPLANTING ZOSTERA IN THE MUDFLATS OF NORFOLK AND SUFFOLK

Species of *Zostera*, the grass-wracks and eel grasses growing on inter-tidal mudflats, are important components of the diet of wildfowl. To safeguard the continuing survival of Brent geese when natural beds of eelgrass are eliminated by land reclamation, attempts were made to artificially establish *Zostera* beds using transplants.

In a preliminary trial turves $(22 \times 15 \times 10 \text{ cm})$ of Dwarf eel-grass (*Z. noltii*) were transplanted at Breydon Water, Norfolk in March 1972. They established themselves successfully in the first year, flowering and seeding, but after three years only 5% survived. In a second more extensive 'field' trial with 1,872 turves, survival two years after planting in 1973 was less than 1%, probably because the site was continually eroding with the creation of conditions favouring *Z. marina* var. *angustifolia* which grows in lower and wetter mudflat levels than *Z. noltii*.

Although these experiments and other tests using single offsets demonstrate that it is feasible to transplant *Zostera*, it seems site selection may prove to be overridingly important, *Zostera* being favoured by sites where accretion and erosion are finely balanced. These could possibly be created by engineering works done primarily for other purposes, e.g. the construction of trial reservoir impoundments in the Wash.

D. S. Ranwell

LAND-USE AND ITS EFFECTS ON THE CHANGING VEGETATION OF THE HUNTINGDON FENLAND: AN HISTORICAL STUDY

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

Areas of Holme Fen and Woodwalton Fen, in the former county of Huntingdonshire, were designated National Nature Reserves as a means of preserving the only remaining semi-natural communities in that part of the East Anglian fens. They are not, however, entirely representative of the original undrained fen: the raised mire species of Holme Fen NNR survive amid extensive birchwood, and the more acidic, upper layers of peat on Woodwalton Fen NNR have been largely removed by peat excavations. To help the interpretation of their present day wildlife communities, the Nature Conservancy Council commissioned a study in 1975-76 on the land-use history of the Huntingdonshire fenland, with special reference to the two nature reserves. The study identified the salient features of the undrained fenland environment in the eighteenth and early nineteenth centuries, the processes of drainage and reclamation, and the subsequent use and management of the reserve areas. (Plates 40, 41.)

The local topography of this south western part of the East Anglian fens encouraged the formation of an acidic *Sphagnum* bog in Woodwalton Fen and other areas close to the uplands of Oxford Clay overlain by boulder clay. Changes in the course of the river Nene led to the early development of a series of lakes, the largest of which was Whittlesea Mere. The depasturing of livestock in the drier summer months and the temporary cultivation of small tracts of fen may have encouraged further diversity in those areas most accessible to the settlements of the fen edge.

By the nineteenth century, experience elsewhere had shown the benefits of adopting a comprehensive scheme for the drainage and permanent cultivation of the fens. The necessary legislation was obtained for the Huntingdonshire fenland in 1844, and by 1850 the outfalls of the watercourses draining the area had been improved sufficiently to make it possible to drain the last shallow lakes and cultivate their beds and neighbouring areas. Once permanent drainage was assured by the installation of steam pumps, the luxuriant vegetation was destroyed and a layer of clay was spread over the bare peat. The process, called marling, helped to prepare the land for wheat, the only crop that was sufficiently remunerative to offset the high costs of drainage and reclamation.

It is not possible to compare the wildlife of the undrained and reclaimed fens in any detail because early naturalists tended to record only what was rare or distinctive. Nevertheless lepidopterists in the 1860s emphasised how the 'fenland forms of life' had given way to 'highland' forms, as the crops characteristic of the 'uplands' of Huntingdonshire were introduced to the greater part of the drained fen.

The process was not quite completed by the onset of the depression in wheat prices in the 1870s, and parts of the present-day reserves include fields which did not experience the full force of reclamation. The parts of Holme Fen NNR most remote from the main drainage channels may never have been ploughed, and the remainder soon reverted to rough pasture. From the 1870s spontaneous scrub growth was supplemented by the planting of birch and exotic species in order to form a pheasant covert. From 1904 bracken and brambles were also introduced, their subsequent spread being encouraged by the effects of continued improvements in the drainage of adjacent farmland. The installation of more powerful steam pumps, and subsequently diesel and electric pumps, countered the fall in land levels caused by peat shrinkage and wastage. Since 1952 the Nature Conservancy has attempted to sustain those species distinctive of the undrained fen, which had survived in the coverts of the otherwise intensively farmed fenland.

As the fenland was reclaimed, the neighbouring villages concentrated on the most marginal agricultural areas for their supplies of peat for fuel. Considerable quantities of turves were extracted from Woodwalton Fen during the late nineteenth and early twentieth centuries. A. J. Wilmott, writing in 1918, described how this played an important part in maintaining the fenland flora: not only did conditions remain damp, but the local clearance of vegetation benefited such species as *Viola stagnina*, the Fen violet.

This phase in activity ended when the area was acquired by N. C. Rothschild and later transferred to the Society for the Promotion of Nature Reserves in 1919. The protection of the distinctive fenland species from the depredation of the naturalist-collector and adverse changes in land use was successful, but the reserveowners did not at first realise how the cessation of regular peat cutting, grazing and haymaking, and the cleansing of watercourses, would lead to an invasion of the hitherto open grasslands and sedgebeds by carr. By 1931 the reserve was described as a 'dense impenetrable thicket of sallow bushes'. Thereafter efforts were made to check scrub encroachment and regulate water levels. Attempts to reintroduce the Large copper butterfly to the fenland (after an absence of almost a hundred years) stimulated this management work. The reserve, which was acquired by the Nature Conservancy in 1954, provides one of the earliest and

best documented examples of how problems of wildlife management were first identified and abated.

J. Sheail

REVEGETATION OF DISTURBED GROUND IN MOUNTAIN AREAS

In the last fifteen years there has been a substantial increase in out-door recreation in upland Britain. Some of these activities have resulted in the creation of new, and the deterioration of old, footpaths, and a varying amount of damage to vegetation and soils. In the Cairngorms there has been extensive penetration of remote areas by tracks bulldozed to give improved access for estate management and shooting. Ground disturbed by these activities can erode to leave a surface inhospitable to seedling establishment while the sediment removed may bury vegetation elsewhere.

Up to the tree line, natural colonisation of spoil by a wide range of native annual and perennial species can

be quite rapid, except where the surface material is very coarse or infertile, or where slopes are very steep. There is usually an adequate supply of seed from surrounding ground or in the soil, and seed may also be introduced on vehicular wheels, on human footwear, and in other ways. Above the tree line recolonisation becomes progressively slower with increasing altitude, attributable to the generally infertile soils and severe climate. On the highest ground few species grow and seed production of several is erratic or even non-existent: furthermore accidental introduction of seed is likely to be relatively infrequent.

Because of these difficulties it has been suggested that the scars on the upper reaches of some of our mountains may never heal. That this is probably an exaggerated view is illustrated by point quadrat data for plant cover on gently sloping road spoil along the Beinn a' Bhuird track, obtained in June 1975 nine years after its construction. Plant cover declined with altitude from about



Figure 14 (a) Effects of altitude on percentages of bare ground, rock and vegetational cover on gently sloping verges of the Beinn a' Bhuird track, nine years after its construction.



60% at 225m to about 33% at 1100m (Figure 14a). However, the cover at the highest altitude looked less than that recorded, mainly because of the raw unweathered appearance of the disturbed surfaces. On the surface of the track itself there was some colonisation at the lower altitudes but none higher up. From these data it is clear that some recolonisation of disturbed soil can occur, even at high elevations, but how long it would take to reconstitute completely a vegetation cover similar to what existed before the track was made is open to speculation. It might be 20 years or more and even if light disturbance were continuous it could be very much longer.

As a means of speeding vegetation recovery, trials have been in progress since 1968 of the advantages of using commercial seed mixtures on disturbed ground, for example on ski pistes and road margins. On Cairngorm different mixtures were sown above and below 610m between 1963 and 1968. Below 610m the mixture included a high proportion of rye-grass which was sprayed as a slurry with wood pulp whereas on higher ground, short or creeping varieties of grasses were used and the surface soil was stabilised after sowing by spraying with bitumen emulsion. Figure 14b shows that by 1972 the cover of grass at the highest altitude was around 42% and that it ranged up to about 67% at 610m. In fact most of this cover had been achieved in the first season.

A noteworthy feature was the presence of unsown species as for example mosses which in some instances covered nearly 50% of the ground surface. Mosses are known to be important colonisers of bare ground, but very little moss growth was observed on unseeded disturbed areas at Cairngorm, except in places where the ground was constantly damp. The vigorous growth of mosses in seeded ground may have been due in part to the fertilisers used or perhaps to shelter provided by the grass. Heather was another unplanted colonist and invaded the seeded areas below 720m, after five years covering nearly 30% of the ground at 425m. An increase in heather cover was usually accompanied by a decline in grass cover. Other indigenous species contributed comparatively little to the total plant cover except on the lower ground, but the number of species steadily increased between 1969 and 1974, from 7 to 29 at 700m, and 0 to 12 at 1100m. Thus seeding can be successful at least up to 1100m, and indigenous plants appear to invade gradually and replace the sown species.

In areas such as nature reserves it is usually thought undesirable to use introduced species for reseeding, especially as there is little evidence of just how long they may persist. For these situations it may be necessary to develop methods of seeding with indigenous species of flowering plants and perhaps bryophytes. Other techniques that have yet to be fully investigated include transplanting turves, and seeding partially disturbed ground to improve plant cover and increase resistance to further disturbance.

N. G. Bayfield

FACTORS AFFECTING RED DEER DISPERSION

Many Red deer management problems in Scotland are associated with deer movements and distribution. Particularly in winter, deer maraud on land used for forestry and hill-farming, and large numbers of deer are a conservation problem since they affect vegetational dynamics and succession. Work aimed at understanding the processes involved in deer distribution and movements (dispersion) started in 1970, mainly at Glen Feshie, Inverness-shire. Stags and hinds separate for most of the year and traditionally occupy different areas. The factors affecting this segregation were chosen as the main theme of study as a step towards a better understanding of the processes involved in deer dispersion generally. The emphasis was on winter dispersion, and the work initially concentrated on spacing and social behaviour with some later studies on feeding and shelter-seeking behaviour. The data are not yet fully analysed, but preliminary findings are as follows.

Segregation at Glen Feshie was not complete and its extent varied with the age or social class of stag, the younger, sub-dominant animals associating more with hinds than the adult dominants. The sexes mixed more during very bad weather, particularly when heavy snowfall covered the main feeding-areas. Group composition within the sexes was not random and groups tended to be biased towards either the young or old stags and either the lactating or non-lactating hinds. Even within groups, individuals associated more with those of a similar age, social class etc; young stags, for example were invariably found together, usually at the edge of the stag groups. (Plates 43, 44).

On the feeding areas there were more agonistic encounters per unit-time in mixed groups than those composed of predominantly one type of animal. All adult stags and most yearlings were dominant to hinds in direct encounters and stag-dominated groups were more likely to join hind groups than vice-versa.

Stags occupied the lower part of the valley, although at any one time they may have been at higher elevations than hinds. Young stags were found over a wider area than adults, and this range overlapped more with that of the hinds. The density of stags was about twice that of the hinds on their respective overall winter-ranges.



Plate 40 The mixed fen and carr communities of the Woodwalton Fen National Nature Reserve and surrounding arable fields on the south-west margins of the East Anglian fens. Photograph reproduced by kind permission of Dr J. K. S. St Joseph.



Plate 41 Shows land use around the site of the NNR from 1836–40, as indicated by the Tithe Commutation Surveys of the parishes of Holme, Ramsey and Woodwalton. The reserve-area and its vicinity at that time were covered by rough fen, although some cultivation was attempted on the higher ground and to the south of the drained site of Brick Mere.



Plate 42 'Vacuum net' sampling on experimental plot. Photograph H. Arnold.


Plate 43 Red deer. Group of resting stags, showing young animals at the periphery of the group. Photograph B. Staines.



Plate 44 Red deer. Mixed group of hinds with some young stags. Photograph B. Staines.



Plate 45 Sitka spruce on unflushed peat, two years after planting. Heavy application of phosphatic fertiliser has produced a luxuriant growth of Cotton grass (Eriophorum angustifolium) and Wavy hair grass (Deschampsia flexuosa), obscuring the ridges and furrows of the ground preparation.



Plate 46 Vigorously growing Sitka spruce four years after planting. Cessation of grazing has encouraged a tussocky growth of the Purple moor grass (Molinia caerulea).



Plate 47 Sitka spruce on peat, forty-five years after planting. Brashing and first thinning have recently allowed more penetration of light to the forest floor; bryophytes are beginning to increase. Modern methods of silviculture will produce a faster growing crop and a more uneven forest floor. Photographs by M. O. Hill.

Analyses of rumen contents showed that stags and hinds ate the same plant species, but that stags generally took more dwarf shrubs (mainly Calluna vulgaris) and less grasses and sedges than hinds in winter. Also, on Rhum as well as at Glen Feshie, hinds had higher quality food than stags throughout the year except in summer, and there was a suggestion that stags in winter compensated for poorer food by recycling more nitrogen, possibly to maintain a suitable environment for the rumen micro-organisms. Stags generally have lower fat reserves than hinds in winter and, since they live lower down the valley, it could be that they generally seek more sheltered areas in preference to those with better food. However, no consistent difference was found in the quality of shelter at sites where stags and hinds rested and fed. In fact, when conditions were very bad, hinds were invariably in better shelter. Possibly, if they are in better condition hinds can live over a wider area and move further to get both good food and, when needed, better shelter.

The interactions between the different environmental variables affecting the segregation of the sexes are undoubtedly complex. Obviously, more detailed analyses of the available data are needed before any firm conclusions can be drawn, but the evidence that animals of 'like-kind' associate within, as well as between, groups, and that there is more aggression in mixed groups may suggest that social behaviour is more important than differential habitat-selection in maintaining the segregation of the sexes. This breaks down only when other factors, such as food or shelter, become limiting, as in deep snow.

B. W. Staines

SHEEP AND CATTLE DENSITIES IN MEDIEVAL GWYNEDD

Effects of domestic grazing animals on the nature of the upland vegetation in Britain confuse those attributable to environmental factors, such as local rainfall and soil. It is known that the vegetation of the mountains of north-west Wales have been more severely altered by man's indirect activities during the past century than at any time since the medieval period, when populations of grazing animals were less dense. Estimates of numbers of grazing animals at different periods in time and their variation in relation to major ecological factors are thus a necessary part of studies of vegetational change.

Contemporary sheep densities during the summer are of the order of $2 \cdot 1-3$ adult animals per ha, but range between 0.5 and 18 adult animals per ha according to local environment (Hughes 1958; Hughes *et al.* 1975).

Analysis of medieval records enables approximate estimates of grazing densities to be given. Lands held by Cistercian foundations supported 0.10 adult sheep per ha but only 0.01 adult cattle per ha, a density which seems to have been standard for cattle over most of the upland grazings. On the mountain lands of Gwynedd generally the ratio of sheep to cattle was much less, from 1.6:1 to 2.1:1, implying that sheep were kept at a density of about 0.02 per ha (Hughes *et al.* 1973). Other studies of medieval farm economies in limited areas (Thomas 1968, 1974) show that lowland districts, as would be expected, carried higher densities of both sheep and cattle (0.02-0.05 and 0.02-0.04 per ha respectively) although their ratio of from 1:1 to 2.8:1 was similar to that found in the uplands.

Information of this kind, in addition to providing a baseline for assessing the continuing influence of man on the landscape, its vegetation and fauna, is also relevant to studies of economic history and of the nutrition of subsistence communities.

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EFFECTS OF CUTTING CALCAREOUS GRASSLAND ON INVERTEBRATE ANIMALS

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

Most grasslands must be managed if they are to survive. In the absence of management, grassland changes rapidly to scrub and eventually to woodland through the processes of succession. On many calcareous grasslands grazing by sheep or cattle is the traditional agricultural method of management, but for wildlife conservation mowing of grasslands has the advantage of not requiring the maintenance of stock. Cutting, like grazing, has the effect of lowering the mean height of the vegetation and reducing its biomass, but it is not selective and there are no effects of trampling or fertilisation. Experiments were undertaken at Castor Hanglands National Nature Reserve to determine the responses of invertebrate animals to contrasting annual cutting regimes. Cutting in May was compared with cutting in July, cutting in both May and July and with no cutting at all. In the main experiment, a randomised block design was set up on tall, unmanaged *Arrhenatherum* grassland in October 1970. There were four replicates of the four treatments, each plot measuring 16 × 12m, and the first cuts were made in May 1971.

Several groups of invertebrate animals were sampled, but emphasis was placed on Hemiptera, particularly leafhoppers (Auchenorhyncha). The animals in this group are all plant-feeders but in the main are known to be particularly affected by the structure, or architecture, of the vegetation, as well as by its floristic composition. Auchenorhyncha from the experimental plots were sampled using a 'vacuum net', i.e. by using a motordriven fan to create a partial vacuum to suck the insects into a collecting net. (Plate 42).

Results show that the richness and diversity of plots cut in July or in May and July are much lower than on similar plots cut in May only or not cut at all. Most leafhoppers become adult in August and September and are particularly vulnerable to a July cut. Some species overwinter in tall grassland and cannot survive on plots which are mown in July; regrowth of vegetation on plots cut in May is usually adequate for these plots to support overwintering populations of leafhoppers.

A few species of leafhoppers are able to exploit short, recently managed grasslands and some of these were found on the plots cut in July or in May and July. However, many species characteristic of tall grassland were eliminated from these plots. A few species which became adult in June or early July were reduced in numbers by the May cut and some individuals of these species survived on the plots cut in July only, as well as on the untreated plots. Most species recovered well from the May cut but several were reduced in numbers, though not so markedly as on the plots cut in July or in both months.

The results strongly support the conclusions reached from examination of the effects of grazing that rotational management of grassland will maintain a greater faunal richness than any one overall management treatment. Annual management is likely to eliminate some species, or at least to reduce their abundance. If nature reserves, or other areas, have to be cut annually the results show that midsummer cutting is particularly damaging. With leafhoppers a May cut is less damaging but since other insect groups would be approaching their peak in that period and would show an adverse reaction similar to that shown by the leafhoppers in July. Cutting between early spring and late autumn should be avoided if compatible with other management objectives.

M. G. Morris

EFFECTS OF AGEING PLANTATIONS OF SITKA SPRUCE ON THE SEMINATURAL VEGETATION OF SOUTH-WEST SCOTLAND

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

Large areas of upland Britain are now being transformed by large scale afforestation with conifers. Almost the only quantitative studies of the effects have been on birds. This paper outlines a project, under contract to the NCC, to investigate the effects on natural assemblages of plants. Work in 1975 was concentrated on the Southern Uplands of Scotland, an area that has been particularly heavily afforested in recent years (Figure 15). The research had two main aims : first to follow the effects of plantations of Sitka spruce (*Picea sitchensis*) on the former semi-natural vegetation, and second to investigate the value of forest roads, rides, streams, lakesides and walls in maintaining species diversity in forest environments.

Methods

The basic sampling units were 1 km squares of the Ordnance Survey National Grid. Only squares containing substantial proportions of coniferous plantation or of agriculturally unimproved land were regarded as relevant to the study. The total number of these squares in the study area was c. 1900, of which there was time to sample 65. To ensure that the range of variation was adequately assessed, a system of stratification was used, one square being sampled from each stratum. As a preliminary to the stratification, all eligible squares were classified using five criteria.

(1) Altitude at the centres of the 1 km Ordnance Survey squares (four classes, 0-230 m, 231-380 m, 381-460 m and 461-760 m above sea level).

(2) Steepness of the ground, assessed from contour densities on the map (three classes, 0-4, 5-9 and 9-25 sixteen-metre contour intersections per km).

(3) Proportion afforested (two classes, 0-30% and 31-100%).

(4) Nature of bedrock (two classes, granite and shale).

(5) Position east or west of the Ordnance Survey National Grid easting 28

In factorial combination the classes give 96 possible strata: in the event only 63 were represented. Additional strata reflecting forest age would have been desirable, but at the planning stage, planting dates were not available. Six replicate locations were sampled in each selected square. Most of these were systematically arranged to allow an unbiased assessment of the effects of afforestation; some, however, were specially placed in order to characterize the floristics of linear features such as roads, streams, rides, lake margins and walls.

Field records were made in quadrats 200m², using the system developed for the National Woodlands Classification by Shaw and Bunce (1971). The occurrence of plant species was recorded as were (i) diameters of trees at breast height, (ii) tree heights, and (iii) selected features of management and terrain. Soils were described in some detail from 30cm pits in the centre of each quadrat and samples from each horizon were collected for subsequent analyses.

Site characteristics

Since the formation of the Forestry Commission in the 1920s an increasing proportion of planting has been done on peat rather than good mineral soils. As a result, old and young plantings tend to be on different soils. Comparisons between planted and unplanted ground were vitiated because unplanted areas tended to be steeper and at higher altitudes. Techniques of site preparation have also changed, with deep ploughing, drainage and the use of fertilisers often modifying site characteristics to such an extent that conditions prevailing before planting were hard to assess.

To obviate these difficulties, it was decided to start by classifying the semi-natural vegetation. This classification was then used as the basis for a site classification which was used in turn to assess the effects of forest age on each site type.

Classification of semi-natural vegetation

The data were classified by Indicator Species Analysis (described elsewhere in this Report), modified to utilize quantitative information. 190 unafforested plots were assessed, the data being supplemented by those from 34 stands described in the literature. This analysis allowed the computer-generated classification to be related directly to existing phytosociological schemes such as those of McVean and Ratcliffe (1962), King and Nicholson (1964) and Birks (1975), at the same time biasing the classification slightly in the direction of the present study. The analysis generated 32 groups,



Figure 15 Study area in S.W. Scotland. Afforested areas shown as they were in 1973, although some had increased appreciably by 1975. The dotted line is the Ordnance Survey National Grid easting 28.

but many of these were similar and were therefore pooled to give a total of 19 groups. These groups provided a satisfactory description of the range of variation according to impressions gained from field experience, and, at the same time, closely agreed with vegetation types already described by other workers.

The area occupied by each vegetation type was estimated using a knowledge of the frequency of each stratum and of the frequency of the vegetation type within the stratum. Although some of the estimates were very imprecise, because of lack of information, it seems that:

(1) There is less vegetational variety on soils on granite than on shale: most *Molinia*-heather vegetation occurred on granite.

(2) Three vegetation types are exclusively western, two being characterized by an abundance of *Molinia;* the third is a high altitude association of matgrass (*Nardus stricta*) and bilberry (*Vaccinium myrtillus*).

(3) Bog cotton (*Eriophorum vaginatum*) tussock communities showed no particular geographical affinities.

(4) Matgrass (*Nardus stricta*) and Heath rush (*Juncus squarrosus*) communities cover a larger area in the east than in the west whereas communities with an intimate mixture of Sheep's fescue (*Festuca ovina*) and *Molinia* were strongly eastern.

Ordination of environmental data

After classifying the vegetation it was necessary to relate stands of vegetation to groups of selected environmental variables, choosing those that seemed likely to be affected by changing land use, e.g. slope, altitude and solid geology. This was done using multiple discriminant (canonical) analysis, which discovered combinations of environmental variables that identify sites with similar vegetation. The results were applied to afforested areas, making it possible to compare the ground vegetation of sites having similar environmental characteristics but at different stages (ages) of afforestation.

Vegetational changes in afforested areas

Species richness of unplanted stands naturally varied among the differing vegetation groups, but patterns of change, as Sitka spruce plantings aged, seemed to be similar. There was often a slight rise in species numbers immediately after planting, mainly attributable to invading lichens and bryophytes colonizing bare ground, e.g. on the sides of drainage ditches. Thereafter numbers progressively decreased for a period of *c*. 30 years; flowering plants being the most affected, whereas some shade-tolerant bryophytes, taking advantage of decreased competition, often increased to cover large areas of the forest floor. In the densest shade, however, even the shade-tolerant bryophytes were sometimes eliminated, although few plantations were without small areas where minimal light penetration allowed depauperate survivors to persist (Figure 16). In south-west Scotland, Sitka spruce plantations have been thinned from 30 or so years after planting, a practice that signalled an increase in species numbers with bryophytes remaining prominent and ferns sometimes appearing in quantity for the first time.

Different species of plants behave differently in ageing plantations of Sitka spruce. Heather at first increased when grazing and burning ceased, but, after c. 10 years it decreased, though patches persisted here and there where sufficient light penetrated the canopy. On the other hand, plants of open moorland, notably Bog asphodel (Narthecium ossifragum), Deer grass (Trichophorum caespitosum), matgrass (Nardus stricta) and fescue (Festuca ovina) decreased from the start, being superseded by heather (Calluna vulgaris), Bent grass (Agrostis canina and A. tenuis) and Molinia caerulea. Some species of ferns and bryophytes dilatata, Lophocolea cuspidata and (Dryopteris Plagiothecium undulatum) became conspicuous for the first time after thinning. (Plates 45-47.)



Figure 16 Mean numbers of plant species including bryophytes and lichens, within different age Sitka spruce plantations.

Some 10–15% of afforested areas remain unplanted, e.g. along linear features such as streams, rides and forest roads. Rides, though thickly vegetated, were often dominated by coarse grasses such as *Molinia caerulea*. Whereas stone walls supported only a few species that were absent from adjoining habitats, streamsides seemed to provide the habit for greatly increased numbers (Figure 17). Vegetation alongside forest roads was usually richer than in adjoining plantings but the effect was very variable, ranging from little or no increase along newly established roads, to a sixfold increase in two plantations more than 20 years old (Figure 18). Unlike rides, roads and their verges provide new habitats, gravel surfaces and exposed mineral soils, which become colonized by 'new' plants.

Conclusion

This study has already shown that the composition of the ground flora in afforested areas changes sequentially as plantations of Sitka spruce increase in age. Forest roads, like many streams, act as refuges for many



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SOIL EROSION ON THE FARNE ISLANDS

Introduction

The Farne Islands off the Northumberland coast are an internationally famous breeding station for sea birds and grey seals. They belong to the National Trust and are







Figure 18 Relation between numbers of plant species found alongside roads and numbers found in areas afforested with Sitka spruce for less than (\blacktriangle) or more than (\blacklozenge) 20 years.

managed as a nature reserve under the guidance of a local Committee. In the late 1960s the Committee, which was preparing a management plan for the islands, learnt that areas of bare and eroding soil had appeared on some of the islands. Figure 19 shows map of islands.

The present project was developed to:

(1) provide basic data on the soils for inclusion in the management plan;

(2) examine the extent, causes and processes of soil erosion; and

(3) investigate possible stabilisation and 'reclamation' measures for use on the eroding areas.

The soils

Apart from some very small areas of sedimentary rock, the islands are entirely composed of the very resistant quartz dolerite of the Great Whin Sill. Five islands (Inner Farne, West and East Wideopen, Staple Island and Brownsman) have remnant deposits of glacial drift. On West Wideopen and some of the drift-free islands there are also recent accumulations of sand and/or storm beach deposits. The main factors influencing the distribution pattern of the soils within the island group are the presence or absence of glacial drift, the texture (this varies from sandy loam to clay loam), thickness (from a few centimetres to 5 m) and degree of compaction of any such drift, and disturbance by man and animals.

Where drift is absent the soils are shallow humic rankers, usually between 15 and 30 cm deep, which have formed *in situ* from the accumulation of plant debris plus some addition of blown sand. Deeper soils have formed where glacial drift remains or where blown sand has accumulated. Most of these drift soils have peaty or humic surface horizons, which resemble the humic rankers, while the deeper horizons show signs of gleying.

A further group of drift soils also have peaty surfaces and subsoil gleying but are characterised by the development of a cemented horizon. This is up to 20 cm in thickness and begins at 20 to 50 cm below the surface. On some islands soils of this type are developed over the whole of the drift mass with the cemented layer forming an almost continuous sheet but on other islands they occur alongside gleys or gleyic brown earths. The cementing substance is a dark brown



Figure 19 The Farne Islands.

resinous material, largely composed of iron, aluminium and phosphorus, infilling cracks although in some instances it permeates the soil peds themselves. It seems likely that it is a complex iron aluminium phosphate, the iron and aluminium derived from the drift and the phosphorus from bird droppings. The cementation may be a relatively old feature, and it is therefore difficult to explain its formation in terms of variables which can be measured at the present day. Despite this, the cementation appears to be correlated with drift texture and with water table levels, and in some instances it corresponds with the upper surface of a highly compacted horizon. These soils are of great pedological interest and the type of cementation may be unique in Britain. The presence of the horizon is also important in the present ecology of the islands. It prevents or slows down percolation of surface water, it provides an effective barrier to rooting and when exposed by erosion it vegetates very slowly and is hard enough to form a distinct feature on slopes. The level of the upper surface of the cementation also determines the depth of soil available for puffin burrowing as the puffins are not able to penetrate it. The check on water percolation can also result in flooding of burrows during periods of very wet weather with consequent mortality amongst chicks.

Modification of soils by puffins, seals and man

The soils on most of the islands show evidence of modification by breeding birds (particularly puffins), seals or man. All the soil types outlined above have been burrowed by puffins. Except on a few steep slopes, burrowing is restricted to the peaty or humic surface horizons (or the whole thickness of the humic rankers) and in areas of dense burrowing, either formerly or at present, this has produced a characteristic modification of this part of the soil profile. Detailed investigation reveals that some areas with only scattered burrows at present had much larger numbers in the past. These disturbed soils have a sequence of surface layers which show a partial 'inversion' of the humus horizons. They also contain frequent buried feathers, fish and puffin bones, and plant material. The level of the former burrow floors is marked by large numbers of plant stems which were dragged into the burrows by puffins. (Plate 48.)

On islands utilised by seals the surface horizons commonly contain hairs from moulting pups and adults. Where there has been puffin burrowing in areas also used by seals, old surfaces can sometimes be recognised by their compaction and by layers of seal hair beneath material subsequently excavated by puffins.

Glevic brown earths on Inner Farne were cultivated over a long period and the effects of ploughing and digging are reflected in the profile morphology. The cultivated soils have also been manured and are now considerably less acid, with a surface pH of around 6.0 and calcium as the dominant cation. The humic horizons of the uncultivated soils, and of the rankers, are strongly acid (pH 4.0-4.5) and sodium and magnesium, probably from sea spray, are the dominant cations. The influence of the dense sea bird colonies and of the seals are shown by very high nitrogen and phosphorus levels in all soils.

Studies of erosion

Previous attempts to assess the rate of soil erosion involved measuring the rate of lowering of the surface relative to exposed boulders and rock outcrops or the tops of remnant tussocks of Sea campion (Silene maritima), or the comparison of surface levels inside and outside enclosures. These methods only gave a rough idea of the mean rate of lowering over a number of years. In order to obtain improved data covering shorter time spans and showing any variations in erosion from place to place various types and lengths of metal rod have been implanted as markers (erosion pins). Even these do not give a very precise measure of the rates of erosion, but they proved a considerable improvement on the earlier methods and highlighted the variations in the rates of surface lowering both within and between islands. On Staple Island the highest rates (2-3cm/annum) were found around the fringes of seal wallows while lower rates were found over a wider area of the north end of the island (also heavily used by seals) and there was little or no surface lowering over the southern part. On Brownsman the highest rates (1-2cm/annum) occur in the area of densest puffin burrowing. The results from West Wideopen show variations between the rates found in bare ground with few puffin burrows (< 0.5 cm) and bare ground with many, actively used, burrows (up to 2cm/annum). Vegetated areas of West Wideopen show little or no apparent surface lowering. In those parts of this island where the cemented horizon is close to the surface (i.e. at a depth of $< 25 \,\mathrm{cm}$), surface lowering at c. 2 cm/annum for a five to seven year period would reduce the thickness of the layers above the cement to a point at which they could no longer be used by breeding puffins.

Changes in the rate and character of the erosion throughout the year have been studied using simple sediment traps installed around the periphery of the soil-covered areas of West Wideopen, Staple Island and Brownsman. Marked seasonal variations in the amount and type of material being eroded have been revealed and the patterns also vary between islands. On West Wideopen the major erosion takes place between May and September or October and while wind and run-off transport are in evidence in the early summer the late summer erosion is dominated by run-off. Parts of Staple Island show a different pattern with erosion continuing into early winter and with this latter soil movement dominated by run-off; as might be expected the amount of soil moved in autumn and winter correlates with rainfall. The main soil loss on Brownsman is from around the densest part of the puffin colony. This reaches a maximum in early summer and wind transport seems to dominate; this latter reflects the flat nature of the site and the highly humic character of the surface horizons.

Although several tonnes of soil material are excavated annually by puffins on each of the main breeding islands the amounts moved from individual burrows varies both between and within islands, being influenced by the type and amount of vegetation cover, the nature of the surface soil, the thickness of burrow roofs and the amount of seal traffic. In well vegetated areas with relatively widely spaced burrows (and especially in areas with a Red fescue (Festuca rubra) derived humic surface mat) only a small amount of excavation is necessary each spring and this largely involves removal of dead vegetation. On bare ground in denser parts of the colonies burrow entrances may be partially, or even totally, infilled by eroding soil in autumn. Re-excavation the following spring is always more extensive than a removal of the infill. Where the cemented horizon is close to the surface thin unstable burrow roofs result and collapse frequently occurs, thus necessitating further excavation. Similarly, burrows in sandy textured materials collapse more readily than those dug in humic horizons with dense roof mats. In areas of high seal pressure most burrow entrances are infilled in the autumn by the ploughing action of the seals and a smaller proportion are actually collapsed. This again results in increased excavation by puffins. Much of the severe erosion on the Farne Islands is concentrated in the highly unstable areas.

In well vegetated areas the soil excavated by the puffins is largely retained in the system (although even these sites may only have a medium-term stability) but in bare ground some, if not all, is transported out of the system. The freshly dug soil is usually in aggregates but rainfall and trampling break these down. The comminuted material is readily transported by wind, rain splash or run-off, the relative importance of these depending on climatic factors and the soil texture/humus content of the debris. A large part of the spring and early summer erosion is a removal of some of this soil from the system. Some disruption of the actual surface may also take place and the late summer erosion seems to include burrow debris and actual surface material. In seal-free areas the bare surfaces restabilise in autumn.

The studies on the interaction between the puffins and the soils also require the distribution and density of the

breeding population to be monitored on each island. Attempts can then be made to correlate changes in these distribution patterns within the colony with alterations in the vegetation cover and in the intensity of erosion. The population work is carried out by the summer wardens employed by the National Trust and it overlaps similar work being carried out on the Isle of May (M. P. Harris, ITE, Banchory). Seventy birds ringed on the Farne Islands have been recovered on the Isle of May up to the end of 1975 and this suggests that the Farnes are a likely source of the immigrants which almost certainly account for a large part of the rapid growth of the Isle of May colony (Harris, in press). The influence of soil conditions on the time of breeding of puffins in the Farnes colony has also been investigated. In 1975 considerable differences in the time of laying were found both within and between islands. Analysis of available data showed that the most likely cause of this variation was soil conditions and in particular the time at which the burrowed horizon of the soil dried out sufficiently to allow burrow cleaning (Hornung and Harris, in press).

Breeding seals come to the islands in autumn, when the soils are usually very wet and standing water is present in the wallows. Movement of the seals about the surface causes puddling, especially around the wallows. The susceptibility of the saturated surface layer to removal by run-off in late autumn and early winter explains the continuation of the erosion on Staple Island into this period. In spring the surface dries out and stabilises until the following autumn. The amount of erosion and damage to vegetation is related to climatic conditions. In dry years only a hole around wallows is puddled and elsewhere a smoothed compressed surface is produced which is much more resistant to erosion. Wallows can develop in a number of situations but on the Farnes the commonest starting points would seem to be small hollows which have themselves resulted from puffin burrowing. The wallows expand as the walls retreat but their rate of growth seems to accelerate when an outlet channel develops. (Plates 49-51.)

The stabilisation and revegetation trials

Prior to the present project bare areas had already been unsuccessfully seeded with commercial seed mixtures. The present work on West Wideopen began with trials of various commercially available soil stabilisers including polyvinyl alcohols, bitumen materials and rubber latex. Four plots were treated with each material, one seeded and one unseeded on each of two slope angles. Ensuing changes in the surface were monitored photographically. The treatment was carried out during the spring as most of the erosion took place in the spring and summer. It soon became apparent that the



Plate 48 Part of the dense puffin colony on West Wideopen.

Plate 49 Seal wallows surrounding seal damaged areas.

Plate 50 Burrow entrance almost closed by eroding soil on West Wideopen.

Photographs by M. Hornung.



Plate 51 The cemented soil horizon exposed on West Wideopen.

Plate 52 Yorkshire fog (Holcus Lanatus) growing from 'seeded' areas below brushwood on West Wideopen.



Plate 53 Freshlylaid brushwood on bare ground which has been intensively burrowed on West Wideopen.

Photographs by M. Hornung.



Plate 54 Rich healthy growth of lichens covering bark of a sycamore tree in November 1970, a month before contamination began.



Plate 55 On the same tree and at the same point, five months later lichens are moribund or dead and exhibit marked chlorosis. The chlorophyll-containing algal component is visibly affected.



Plate 56 All lichens now dead (October 1972).



Plate 57 By October 1973 only a few dead remnants of a once rich lichen flora remain. Photographs R. O. Millar and D. F. Evans.





Plate 59 Bat detector. Photograph R. Mellor.





Plate 60 Thermogradient bars used in seed germination and seedling experiments. Photograph G. Owen.

bare surfaces and new growth would need to be protected from disruption by birds. The commercial stabilisers gave little protection although the bitumenbased materials were the best.

In the next stage of the trials a small initial experiment (by P. Hawkey, the National Trust Warden Naturalist for the Farne Islands), using brushwood, was developed and enlarged. The eventual method employed used two layers of brushwood laid on the surface at an angle to one another. As this technique clearly interferes with puffin burrowing the work was begun on bare ground with only scattered burrows so that few birds were affected. Some of the areas thus protected were 'seeded' with Yorkshire fog (Holcus lanatus) clippings spread on the surface; others were simply protected. By the summer following treatment the 'seeded' areas had a 100% vegetation cover. The 'unseeded' areas have developed c. 70% cover two years after the brushwood was laid. The earliest vegetation is dominated by Sea campion (Silene maritima) and chickweed (Silene media), but this is soon followed by annuals which are common on the island, e.g. nettle (Urtica dioica), hemlock (Conium maculata) and dock (Rumex obtusifolius).

The method is now being applied to areas with higher concentrations of used puffin burrows where the burrows have become highly unstable and erosion is severe. It will almost certainly involve disturbance and displacement of breeding puffins. In order to monitor these effects, as many as possible of the breeding adults in the experimental areas have been ringed and attempts are being made to recover them during the 1976 breeding season and to assess their breeding success. This work should show whether highly unstable areas can be 'reclaimed' while still in use by puffins. (Plates 52, 53.)

The results from this project are improving our understanding of part of the Farne Islands ecosystem and of the origin and significance of the soil erosion. The investigations have revealed the complex nature of the interactions of the breeding puffins and seals with the soils of the islands and with each other, and the way in which these interactions lead to, or aggravate, the erosion. Building upon the knowledge gained, and on subsequent field trials, successful reclamation techniques have been developed for the stabilisation and revegetation of one type of damaged ground.

M. Hornung

Toxic substances in the environment and their effects

BULB DIPPING AS A SOURCE OF MERCURY IN THE WASH Mercury is one of the heavy metals that causes most concern as a pollutant. It has no known biological functions. 'Minamata disease' demonstrated that some forms are very toxic, and amounts have increased in some parts of the world because of man's activities. Coastal waters tend to show significant degrees of contamination by mercury if rivers from industrialised areas enter them. It was therefore a matter for some surprise and interest when J. L. F. Parslow, then at Monks Wood, suggested from a survey that mercury levels increased, possibly 10-20-fold, in the livers of wading birds that spend the winter in the Wash. This conclusion was tentative, but it posed the question whether agricultural activities in England do contribute significant amounts of mercury to the environment. A limited survey was therefore made to test one specific possibility. Does the bulb-growing region south-west of the Wash cause much contamination of waterways by mercury? Mercurial fungicides are commonly used for dipping bulbs when they are lifted in the summer. Any suggestions of gross contamination were soon discounted. Superficial sediment samples taken from the Rivers Nene, Welland and Witham, and from some of the principal drainage channels, had a median value of 0.2µg mercury per gram of air-dried sediment. For comparison, the natural mercury content of soils, excluding those from mercury-rich areas, is about 0.1 µg per gram. However, there was some evidence of local high degrees of contamination. Sediment samples were taken from drainage channels near to five bulbdipping sites. Values for three sites were similar to those in the rivers, but were higher at the other two, with values of over 100 µg.g⁻¹ recorded at one spot.

Several points of general interest came out from this study. First, it was difficult to give meaningful values for mercury concentrations in the sediments: the greater the depth to which the sample was taken the lower the concentration. Such values should sometimes be regarded as indices. Secondly, most of the mercury that was retained by the channel sediments was found within a few hundred yards of the release point. It has been found for a range of pollutants that much is bound in the sediments, and the fate of pollutants in those sediments deserves much more study. Thirdly, aquatic molluscs may make useful monitors. For example Potamopyrgus jenkinsi contained 0.3 µg mercury per g fresh weight at a contaminated site, whereas from an uncontaminated river the value was only $0.02 \,\mu g$ per g. Some species of mollusc are relatively large, which is convenient for chemical analysis, they are relatively immobile, so that their pollutant concentrations relate to the site from which they are taken, and some species have a wide distribution. This particular study on mercury has now ended, but these and related topics are now being studied by the project group on pollutants in aquatic ecosystems.

F. Moriarty M. C. French

THE SULPHUR PROBLEM

The disastrous effects of the London smogs of the early '50s mainly on people with respiratory illnesses, emphasised the damage that could be done by airborne pollutants. Since that time, the levels of these particulate contaminants have been reduced by the greater use of oil, electricity, gas and smokeless solid fuels for domestic heating, and by changes in the design of chimneys (stacks) built for power stations and other industrial installations.

Because of concern for human health it is not surprising that measurements of air pollution have been concentrated in urban areas. Through the National Survey of Air Pollution, implemented by the Warren Spring Laboratory, we now have a picture of the concentrations of airborne sulphur pollutants likely to be experienced in such areas at different seasons. These pollutants have been shown to influence not only health and the erosion of stonework but also the occurrence of lichens and plant diseases. Black spot of roses, caused by *Diplocarpon rosae*, is less prevalent in polluted localities, and pollution usually decreases the variety of lichens colonising trees and stonework to the advantage of tolerant types such as *Lecanora conizaeiodes*.

If pollutants, notably sulphur compounds, can affect lichens and fungi in urban settings what is happening in rural areas, including those remote from sources of emission? Already we know from experiments done in controlled conditions that rye grass and species of *Pinus* can be damaged – but is it appropriate to extrapolate from these conditions to those actually occurring in the field? Are trees, remote from points of emission, damaged by the concentrations of sulphur pollutants actually found there? What happens to the 'sulphur' filtered from the atmosphere by trees and other plants together forming the vegetation component of forest ecosystems? Is it 'cycled' and in due course transferred to litter whose rates of decomposition are affected? On the other hand how much of the filtered sulphur is washed from foliage by rain to reach the soil in stemflow and throughfall? Does the sulphur-containing rain affect physical processes occurring in soil (e.g. cation exchange) and if it does, does this alter the composition of water draining into streams and rivers?

Ecosystems are complex organisations; studies of pollutants are also necessarily complex. There is evidence to suggest that mixtures of differing pollutants (sulphur dioxide, ozone and oxides of nitrogen) at normally non-toxic concentrations, together interact to cause extensive damage to plants. Further, chemical reactions may oxidise sulphur dioxide to sulphate and hence make rain acid. In a study of sulphur pollutants it is therefore necessary to consider their differing forms - gaseous sulphur dioxide, particulate (aerosol) sulphate and acid rain - also to be aware of the effects of other substances. Such a study must also recognise that sulphur is an essential element for plant growth. There is strong evidence suggesting that damaging sulphur deficiencies might have occurred in some areas of intensive agriculture had it not been for the deposition of airborne sulphur pollutants.

ITE has recently commenced a major new project in this area. The pathways of pollutant sulphur, in its differing forms, and its following fate and effects are being studied. An intensive investigation is centred on a forest in the Midland Valley of Scotland where equipment is being assembled to analyse simultaneously the atmospheric loads of sulphur dioxide, ozone and oxides of nitrogen, so as to obtain diurnal as well as seasonal patterns of change. Additionally amounts of particulate sulphate and acid rain will be measured. The information obtained will be used to design fumigation treatments applied to plants growing in controlled environment chambers. It will also serve as a measure of sulphur entering the sulphur cycle.

To gain experience of sampling procedures and analytical techniques, foliage of Scots pine, holly, birch and ash, growing in regions with different mean winter concentrations of sulphur dioxide, have been sampled. Whereas amounts of 'sulphur' washed from replicate batches of Scots pine, holly and birch were fairly consistent, those from ash differed excessively. Subsequent tests indicated that variation was minimised if surface sulphur was washed and collected from foliage immediately after it had been taken from trees. Not unexpectedly, amounts of surface sulphur increased with increasing mean concentrations of atmospheric sulphur dioxide.

Whereas similar amounts of sulphate-sulphur were found on foliage of Scots pine and holly, and on stems of holly, about four times as much was detected on stems of Scots pine. Larger sulphur accumulations were detected in dry, than in wet weather. It was noticeable that Scots pine growing in lightly polluted areas retained needles for three or more years, whereas those on trees in heavily polluted areas were lost after one year. *I. A. Nicholson*

AIRBORNE FLUORIDE AND LICHEN GROWTH

The emission into the atmosphere of potentially phytotoxic substances such as fluoride, in an area which has been, until recently, relatively free of contamination is of environmental concern, but it also presents a unique opportunity to study the effects of low level contamination on the growth of previously healthy plants.

The sensitivity of lichens to air pollution has been known since the mid-nineteenth century and since that time these plants have been increasingly used as indicators. Sensitive species decline in abundance towards the source of pollution until in areas of high pollution or close to the point of emission lichen 'deserts' develop where these plants are virtually absent.

Since 1970 the growth of lichens close to a new source of airborne fluoride in North Wales has been monitored. Lichens are composed of fungal and algal components which exist in close symbiotic relationship and they grow on a variety of substrata such as trees, rock outcrops, walls and buildings. To enable the growth of these slow growing organisms to be measured photographs of permanent, marked quadrats $(20 \text{ cm} \times 14 \text{ cm})$ have been obtained annually and, following examination in the laboratory, comparison has been made of the performance of individual species between affected and unaffected areas. As was to be expected quantitative data have shown that different species are affected at different distances from the source of emission. For example corticolous lichens (those found growing on trees) have been found to respond more rapidly than saxicolous lichens (those growing on rock surfaces) but within each group there is considerable differential sensitivity, the growth of some being slowed while others close to the source are eliminated. The extent of the effect has been increasing radially since the commencement of emissions and the concentration of fluoride in samples of lichens showing effects has also increased. Lichens with accumulated fluoride concentrations above about 50 ppm showed a marked deterioration although effects have also been observed below this level. (Plates 54-57.)

To date the emphasis of the work has been on relating the effects of fluoride to external and anatomical changes in the thalli. The work has now entered a more experimental phase in the hope of explaining the physiological processes which cause the ecological effects observed in the field. Rates of photosynthesis and respiration are being measured in lichens grown under controlled laboratory conditions. Simultaneously the pathway of fluoride and other substances in lichen communities is also being studied and the work is being extended to investigate its effects on other components of natural ecosystems.

D. F. Perkins V. Jones R. O. Millar P. Neep

COMPUTER MODEL TO SIMULATE MOVEMENT OF OIL AT SEA

The exploration for oil in the North Sea directs attention to the possible polluting effects of oil spillage. Sea-birds and birds of coastal habitats seem especially vulnerable. This study, carried out by Mr A. F. Gordon at Merlewood Research Station, sought to examine the likely patterns of dispersion of oil so that some measure of the risks could be assessed. Although the work was designed for use in furthering the understanding of oil movement at sea, the basic principles would apply to any study of movement and dispersion.

The oil which escaped from the Torrey Canyon was driven primarily by the wind. Tidal effects rarely result in more than a small net movement in the open sea and such effects mainly impose a cyclic, to-and-fro oscillation only. Observation shows that oil is driven on the sea-surface at some 3–4% of the wind speed. In the simulation, wind data were used in four ways: first, directly from previously recorded observations for the area concerned; second, from two probability distributions, one of wind speed and the other of wind direction but un-correlated with each other; third, from distributions of direction and speed in which the next most probable event was selected instead of a purely random selection from the different distributions; and fourth, from a probability matrix in which speed and direction were related. There are, however, relatively few distributions of the latter type available. The probability distributions of direction and speed were sampled using random numbers, and the values obtained were used to compute the distance and direction of movement of a point, representing the centre of an oil slick, across a matrix of points, representing an area of sea. Two types of simulation were examined, single path and continuous spill. The former traced the path of a single spillage and the latter examined the effects of chronic spillage such as a leaking hull or due to several minor accidents at a loading or unloading quay. Figure 20 illustrates an example of the results of the continuous spill model.

Trials were made to test the programmes, and their optional sub-routines, to simulate a range of real situations. The first of these used data from the *Arrow* disaster in February 1970. The tanker *Arrow*, grounded on a rock in Chedabucto Bay, Nova Scotia and oil leaked from her tanks for the next eight days. The continuous spill model was used to simulate the dispersal of oil, under a range of changing wind conditions, on to shores surrounding the Bay. Actual wind data for the

period from the nearby Canso automatic weather station were used to trace the paths of leaking oil. The results were compared with those obtained by using simulations based on probability distributions from the monthly meteorological returns. The agreement in terms of points at which oil struck the coast was fair, but the results emphasized the potentially widespread effects of such an accident in confined waters. The path of oil which escaped from the Bay and killed many birds on an adjacent shoreline was also followed, but data from Canso were inadequate to reflect the true path of this oil. Meteorological data on a larger scale are required for a satisfactory simulation of this type, although some information can be derived from surface pressure charts.

The second trial sought to examine effects of leakage from a pipeline serving a North Sea oil well. In general, this was the least satisfactory application because, in the real situation, leaks are most likely from the well-head itself. Obviously, the chances of oil pollution from such a source situated far out to sea under prevailing southwest winds are small on British coasts but threats to the coasts of European neighbours may be increased. Any oil discoveries in the western seas off the Irish coast would increase the probability of pollution of British shores from such a cause.

The third main trial was made from the Estuary of the River Tay. In this study, tide effects were introduced and, because of the high winter concentrations of wild duck in this Estuary, these were examined as potential victims of oil pollution. There have been several accidents in the Estuary and in February 1968 the *Tank Duchess* devel-



Figure 20 Three stages in the simulation of a continuous spill of oil from a fixed source.

oped a crack in her hull. Eighty-seven tons of oil were lost and about 1,300 birds killed. The oil remained moving about in the Estuary for some time. No attempt was made to simulate any particular accident in this case. The distribution of oil under wind and tidal influences, depended, apart from the point of spillage, very much on the time of spillage within the tidal cycle. Some attempt was made to allow for bird movement in relation to oil movement and certain localities of known bird aggregation were found to be particularly likely to receive moving slicks from potential points of origin within the Estuary.

It is concluded that further development of the model depends on accurately documented cases of spillage and their associated weather conditions. Complex combinations of probability distributions have not much improved the performance of models compared with simpler mechanisms although further attention to distributions linking direction with wind speed seems particularly necessary. The most useful applications of these models appear to be those which explore the implications of the siting of loading or discharging points in enclosed waters. Because of this, more attention has been paid in more recent work to the realistic simulations of the inshore effects of tidal oscillations.

A. J. P. Gore

EGG SHELLS OF HERONS (*ARDEA CINEREA*) EXPOSED TO ENVIRONMENTAL POLLUTANTS

Eggs collected from several heronries in Eastern England in the late 1960s and in the 1970s were found to have shells significantly thinner than those collected prior to 1946. In 1970, shells were on average thinner by 16%. A significant inverse relationship existed between shell thickness and egg residues of pp'-DDE. The fine structure of shells taken in 1973 was examined by an acetate peel technique. The thickness of the two main component layers of the calcified shell, the inner mammillary layer and the outer palisade layer, were both inversely related to egg residues of DDE and DDT-type compounds. A similar thinning of these layers was seen in shells produced by chickens treated with sulphanilamide to depress the availability of the egg shell carbonate fraction. Shell thinning in both instances was considered to be due to a decreased rate of shell formation. Shell strength was determined for the 1973 sample by a piercing technique. This demonstrated a significant inverse relationship between shell strength and egg residues. The relationship between thickness and strength was

strength = b (thickness) - a constant.

Thus any decrease in thickness leads to a proportionally greater decrease in strength. Incidence of egg shell

breakage was also monitored in the heronries and was found to be positively related to residues of DDE or dieldrin in intact eggs, i.e. the most contaminated colonies experienced the highest breakage rate. Eggs having shells thinner than 240 µm were found to be unlikely to survive incubation intact (mean thickness of intact egg shells in 1973 was 274 µm). Thin-shelled eggs that are lost during incubation should tend to have had high residues, so sampling intact eggs for the purpose of monitoring environmental pollutants can lead to a mean residue figure for a heronry that is much lower than the true mean. In the late 1960s, in the three main study heronries, more than half of the pairs broke their egg shells, probably because of a combination of shell fragility due to thinning and aberrant behaviour. Measuring shell thickness could be a rapid and economical bioassay of environmental levels of DDE.

Despite these various detrimental effects on reproduction, heron populations have not declined, perhaps because the birds relay if they lose their clutch. There are indications that egg residues of DDE and other organochlorines are diminishing, shell thickness is returning to normal and the incidence of shell breakage is decreasing.

A. S. Cooke A. A. Bell

TWO NEW POLLUTION PROGRAMMES AT MONKS WOOD

Throughout the 1960s pollution research in the old Nature Conservancy was concentrated on identifying, explaining and publishing the widescale and harmful effects certain persistant insecticides and industrial pollutants had on wildlife. The emphasis was primarily ecological, and physiological studies were restricted to fairly straightforward histological techniques. Research of this kind remains important to the NCC, which is commissioning studies at Monks Wood, but in addition ITE scientists are beginning to investigate the subtle and long term effects that sub-lethal doses of pollutants may have on the performance of individual species and populations, and a fuller understanding of physiological mechanisms is relevant to this theme. Two new programmes have recently started.

The first is concerned with pollutants in aquatic habitats. The study of any pollutant requires a knowledge of its distribution, movement and biological effects and some reliance has to be placed on laboratory experiments. Compared with most ecosystems, it is much easier to simulate aquatic habitats in the laboratory and, with this aim, a continuous flow system has been installed at Monks Wood. Local artesian water is saline, so tap water has to be deionized and then reconstituted to very strict tolerance limits before being distributed at controlled temperatures to a series of

aquaria containing the experimental subjects. In this way, freshwater molluscs and other animals can be exposed for long periods (6 months to 3 years) to very low concentrations of selected agents. Initial studies are being focused on two toxic metals (lead and cadmium) and one which is essential for life (zinc). By using atomic absorption spectrophotometers, electron probes and ion probes to measure heavy metal levels, it is possible to determine the rate of uptake of these foreign agents and the time and concentration at which steady states are achieved. One of Dr Moriarty's main concerns is the measurement of rate constants in different species and situations, so as to understand in detail why pollutants are distributed unevenly within organisms; such knowledge should also explain differences between species. This research is particularly important because we now appreciate that, in aquatic systems at least, the food chain concept does not explain the varying distribution of pollutants in organisms. In fact, knowledge of the relationship between exposure and uptake of a pollutant is fundamental to all our work.

Meaningful studies of the relationship between exposure and residue demand detailed chemical studies, because the form in which a chemical occurs greatly affects its intake; this remit is the responsibility of Dr K. Bull. It is essential to balance laboratory studies with field observations and these are being made on the Ecclesbourne River in Derbyshire, which has unusually high levels of lead, cadmium and zinc in its sediments. Laboratory experiments help in the interpretation of field observations and these in turn pose problems suitable for study in the continuous flow system. The major ecological input into the aquatic pollution group is being provided by Dr A. Scorgie, whose special concern is the effect of aquatic herbicides. Attention is centred on a new chemical, cyanatrin. Preliminary trials show that this agent is a particularly efficient herbicide at very low concentrations. Accordingly, if unnecessarily high application rates are employed there is a big risk that aquatic vegetation could be destroyed over a much wider area than was intended. This is partly a consequence of the very high diffusion rate of cyanatrin in water and unless sensible precautions are taken this poses a very real threat to those plants, and their associated fauna, which are valued by wildlife conservationists.

The second new programme involves Dr S. and Mrs B. Dobson, Dr R. K. Murton and Mr N. J. Westwood and is designed to understand how organochlorine compounds, particularly DDT and its metabolites, the polychlorinated biphenyls (PCB's) and dieldrin, cause abnormal behaviour and reduced reproductive success, including egg shell thinning, in birds. All animals exhibit diurnal rhythms of metabolism, including diurnal fat depo-

sition and annual cycles involving such periodic functions as gonad recrudescence, moult and preparation for migration. These circadian and circannual rhythms are linked by photoperiodic mechanisms to the environmental cycle of day and night and the uptake and mode of action of pollutants has to be viewed against this background. Furthermore, most of these rhythms depend on endocrine secretions and it is already known that organochlorine compounds interfere with thyroid and adrenal function. Accordingly, the critical measurement of plasma titres of various hormones is central to the programme and for this purpose we have recently installed automated gamma and beta scintillation counting facilities, thereby enabling sensitive and specific radioimmunoassay techniques to be employed. It is now possible to take plasma samples at one hour intervals throughout a 24hr cycle from birds the size of a pigeon. From each sample gonadotrophin, corticosteroid, thyroxin and androgen/oestrogen levels can be quantified. This means that for the first time the precise endocrine changes induced by a pollutant can be measured in both free-living and captive subjects.

R. K. Murton

Work of special subdivisions and centres

CULTURE CENTRE ALGAE AND PROTOZOA

Introduction

The Culture Centre of Algae and Protozoa became part of ITE in November 1975; after many years as an independent NERC Institute. It seems appropriate therefore to insert in this Report an account of the work of this internationally famous group.

CCAP traces its origin back half a century when Professor E. G. Pringsheim set up his culture collection in Prague. Cambridge University assumed responsibility for the collection in 1947 and retained it until 1970. when it was taken over and expanded into the Culture Centre of Algae and Protozoa by NERC. Culture collections play an indispensable role in microbiology by providing a source of authentic and documented material for teaching, research and many other purposes, including bioassay and the screening of pesticides and pharmaceutical products. More than half of the nearly two thousand strains maintained at CCAP have been the subject of at least one publication and about a quarter of the collection is of taxonomic type material. Several recent working parties have stressed the need for more taxonomic knowledge of the micro-organisms of soils and aquatic habitats of all kinds. Cultures play an important role as the basis for comparative studies and in the provision of uncontaminated material for nutritional, autecological and other studies.

Information

The value of a culture depends largely on the available data relating to the organism. CCAP, like other major collections, has become a centre of information and expertise, but problems of handling information have become acute. Steps are now being taken, aided by ITE's Subdivision of Data and Information, to apply computer techniques to these problems. Close liaison is being maintained with the World Federation of Culture Collections (WFCC) which aims to establish a single, world-wide data bank for all strains in culture, including bacteria, viruses, fungi, algae and protozoa. The WFCC has already produced a World Directory of Collections of Cultures of Micro-organisms which lists all the species, but not the strains in culture.

Preservation of cultures

For several years, it has been standard practice to maintain cultures of bacteria and other organisms by drying or freezing techniques which reduce the risk of mutation and other hazards inherent in maintaining active cultures. Progress in the preservation of algae and protozoa has been, and still is, largely sporadic, but, since the appointment of a cryobiologist in 1974, CCAP has taken the lead in methodical research in this field. The project has two objectives; first, to develop the methods and, second, to put these methods into regular use. So far, over 70 strains of Chlorella have been preserved in liquid nitrogen, with survival rates of over 60%-a much higher figure than that expected from lyophilised cultures of many bacteria. The ability of algal strains to withstand direct freezing has been shown to correlate so well with conventional taxonomic characters that it has already been used to confirm or contradict the identification of particular strains. Resistance to freezing also has ecological significance yet to be fully explored.

Research

Most of the research done at CCAP is taxonomic, often assisted by electron microscopy. The organisms involved are mainly pigmented or colourless flagellates which form a major portion of the biomass in aquatic habitats and which also occur in all kinds of soils. The other main taxonomic field is that of the naked amoebae, for which a comprehensive key to the freshwater and terrestrial species is now in the press. Our taxonomic work is directed to the abundant and widespread organisms and is directed to the scarcer forms only when scholarship demands. As well as crossing the conventional boundary between plant and animal, our researches frequently lead back and forth from freshwater to marine, and free-living to parasitic because either the one species or closely related species transgress these boundaries, which have been given undue importance by long-established interdisciplinary barriers separating, for example, botanists, zoologists and parasitologists.

Electron microscopy is an essential tool for much taxonomic study and even for the specific identification of some of our organisms. Many flagellates previously thought to be lacking in readily recognisable features are now known to be clothed in scales which are so small as to be beyond the resolving power of the light microscope. These scales are usually complex structures and quite specific in their pattern. Freeze-fracture techniques are being developed, partly to aid recognition of membrane damage due to freezing in the course of cell preservation, and partly to aid cytological investigation into problems such as the intracellular site of origin of extracellular scales. It is interesting to note that the apparatus involved is being developed for about a tenth of the cost of its commercially available counterpart.

Demand for cultures

Over the last four years, demand has been fairly steady at about 4,000 cultures per year. Three-quarters of these cultures go to universities and polytechnics, etc in Britain for teaching or research and over 10% go overseas, 27 countries being supplied in 1975. About 100 cultures go to government laboratories and a similar number go to industry in this country.

E. A. George

Subdivision of chemistry and instrumentation

THE ROLE OF THE SUBDIVISION

The Subdivision of Chemistry and Instrumentation was created to accommodate most of the technical staff who provide the essential background support for the Institute's research programmes. In a sense, this had produced an unnatural grouping of scientists and technicians, in some cases with little in common with each other. This factor, together with the problems arising from geographical separation and previous research connections have made it difficult to weld together a closely knit and effective Subdivision. Nevertheless, by the end of the first full year, considerable progress had been made, much to the credit of all the staff concerned.

Chemical sections

The chemical staff comprise the largest single component in the Subdivision, and, for historical reasons, are based entirely at Merlewood and Monks Wood, mostly in two analytical sections. The chemical laboratories at

Merlewood were established to provide chemical data on ecological materials in connection with the research projects of the then Nature Conservancy. Later, the work expanded to cover a variety of environmental topics and the section now employs a staff of eleven. The smaller Monks Wood unit arose out of the need to determine organic pesticides, and in particular organochlorines in avian materials. The distinction between the expertise and facilities at the two laboratories has continued to form the basis for their work and the intention is to make them fully complementary. As an example of this, the automated equipment of the Merlewood laboratories was considered more appropriate for the large demands made by the sulphur pollution projects, whereas the experience with gas chromatographic techniques developed at Monks Wood for the pesticide analyses led to them being applied in the examination of monoterpenes for taxonomic purposes.

The service provided by the two Analytical Sections is very extensive, and, during the course of a year, a large number and variety of samples and chemical characteristics are processed. Clearly, it is not practicable to list all these here but a few examples are given later to illustrate their variety. The service work is mostly associated with ITE projects, but the Analytical Sections do carry out direct contract work for external customers. These have included the Nature Conservancy Council, the Forestry Commission, universities, local authorities and even a foreign research institute. Samples are also sent in from other NERC institutes, notably from the British Antarctic Survey.

Engineering section

In contrast to the chemical staff, the engineers are distributed between several stations. This distribution is to some extent necessary to provide a construction and repair service at each station. However, there is a pressing need for a specialist engineering centre capable of producing the complex instrumental systems so often needed in modern research. Unfortunately, limitations in staff have made it difficult to arrange a structure which provides adequately for both the local and central engineering requirements. The result is a compromise, with a small specialist unit proposed for Bangor serving the whole of ITE, and an engineer at each of the three larger stations (Bush, Merlewood and Monks Wood). The smaller stations have, for the present, to depend on part-time or contract assistance. The work of all the engineering staff is co-ordinated by a recently-appointed Senior Engineer, Mr G. H. Owen.

Despite the organisational difficulties, the engineers have been able to meet most requests during the year,

Many of these are relatively simple jobs, but it has also been possible to tackle some major projects which have involved development and construction lasting several months. Some of these are described in more detail below.

Glasshouse and nursery unit

All the members of this unit are based at the Bush Laboratory where most of ITE's glasshouse and nursery facilities are located. Most of the research projects which require the support of the Unit's staff are also associated with the same station, a situation resulting from the role of the former Institute of Tree Biology. Since plant propagation and growth studies are essentially long term in nature, and a high capital investment is involved, the Bush laboratories are likely to remain as the principal centre for this type of work for the forseeable future. However, this concentration does not prevent smaller scale development at other stations and the appointment of Mr R. Ottley as Senior Nurseryman for ITE will encourage further development. It is also planned to make more use of the Bush nursery facilities for the benefit of staff elsewhere.

The considerable scale of the propagation and culture work does mean that the staff are committed to a great deal of general maintenance work involving watering, feeding, preparation of soil mixtures and beds, seeding and pricking out, checking the glasshouse ventilation and heating systems and the many other jobs associated with nursery work, some of it on seven days a week. A few of the experimental studies are summarised later.

Other technical functions

Apart from the principal support activities discussed above, there are other minor technical interests which are the responsibility of the Subdivision. One of these concerns the provision and use of scientific equipment in ITE. This task involves examining requests for new equipment, checking whether the needs can be met by redeploying existing equipment and generally ensuring the equipment is being used to its best advantage. The current economic situation has given fresh incentive to these activities. (Plate 58.)

Almost as an offshoot from the concern over efficient use of instrumentation a certain degree of coordination has been needed over radiochemical facilities. Four of the stations were equipped for experiments with radiochemicals, and at two of them (Merlewood and Monks Wood) automatic scintillation counters have been installed. These were primarily associated with specific projects, but the increasing desire to use radiochemicals for other experiments, has resulted in a limited service requirement. The Subdivision of Chemistry and Instrumentation is responsible for organisation and liaison on these matters in conjunction with the other groups concerned.

Most research institutes have one or more full time photographers on their staff, but, for a number of reasons, this has not been possible yet within ITE. The individual stations have the usual darkroom and photographic equipment. These are administered through a local officer linked with an officer at Merlewood who has an overall responsibility on coordination, ordering and advice (C. Quarmby). It is hoped to provide a few specialised photographic services by making use of equipment at Colney (P. G. Ainsworth).

RESEARCH AND DEVELOPMENT PROJECTS

A few of the special projects undertaken by the Subdivision's staff are reviewed below. Some are classed as research projects, but most are subsidiary studies concerned with technical problems or construction jobs.

Plant nutrient survey and data banking

All the outstanding chemical analyses from the national survey on plant nutrients were completed and some of the data was processed during the year. Initial attention was given to the inter-relations of various nutrient elements in the leaves of the different species. Soil values were also examined. Interpretable and stable relationships between plant nutrients and environmental variables have been detected, and work on these data is continuing.

With the assistance of Mr D. D. French, a series of computer programs was devised which made it possible to use the small Merlewood Research Station computer for a relatively complex data bank. A start was made in selecting and transferring data for this bank, making use initially of the plant nutrient survey data.

H. M. Grimshaw S. E. Allen

Sulphur pollution studies

The Merlewood Analytical Section has been heavily involved in the group of sulphur pollution projects reviewed elsewhere in this report. A great deal of development work has been required to produce satisfactory methods for extracting and fractionating sulphur compounds in plant materials. Analytical methods for their subsequent determination have also had to be examined in detail because none of the existing sulphur methods have been universally accepted and they are not readily applicable to automation. For the surface and inorganic sulphur fractions, it was necessary to examine different extractants and extracting conditions. Samples for these and other investigations were obtained from a number of pollution zones, the main sites being in the Sheffield area. The samples were also examined in relation to weather conditions, and it was established that a very heavy build up of surface sulphur occurred during long dry spells and this concentration was washed off very rapidly as a result of heavy rain.

In the laboratory, attempts were made to adapt most of the published sulphur analytical techniques to automation. The most satisfactory of the methods was found to be one in which a lead salt was used to precipitate the sulphate ion before measuring the excess lead by atomic absorption. This method was adopted for the determination of sulphate in the surface washings. A simplified turbidity method was used for other norganic fractions and X-ray fluorescence was used for the organic fraction. The schematic outline summarises this section of the work. (See Figure 21.)

S. E. Allen J. A. Parkinson A. P. Rowland



Figure 21 Sulphur pollution studies; analytical sequence.

Comparisons with past records of chemical data

Two service projects have involved the analyses of soil samples collected from sites which had previously been examined over twenty years earlier. The projects included one from the Forestry Commission who were looking at changes on some woodland sites studied in the past by Dr Ovington and which at the same time attracted a great deal of interest. The other samples came from the Gisburn site, where the effects of tree growth on an upland site are being examined over a long period (Project 367). Since both investigations involved comparisons with past data, it was necessary to see how far it was possible to reproduce the analytical conditions used by previous workers. In view of the large numbers of samples involved, it was not practicable to stick entirely to the relatively tedious procedures formerly used and special correlation tests were then needed. In the course of the work, some soils which had been stored for fifteen years or more were examined, and some unexpected changes were detected, particularly in the levels of extractable phosphorus.

J. A. Parkinson H. M. Grimshaw

Nature Conservancy Council contract analyses

Some of the contract work coming from the staff of the Nature Conservancy Council has had unusual features. Examples include:

(1) Weekly monitoring of water from the Ainsdale Nature Reserve in connection with an unexpected mortality of Natterjack toads.

(2) Analysis of soils and plants, from the Lizard Nature Reserve following seepage from a nearby abattoir.

(3) Examination of mud samples from the Arne peninsula in Dorset in relation to proposals to extract china clay.

(4) Examination of estuarine muds to determine the effects of pollution on the feeding grounds of waders.

(5) Tests on samples to check the effects of farm and sewage seepage on an adjacent peat moss.

(6) Analysis of waters flowing from abandoned mine workings and waste tips for heavy metals.

J. A. Parkinson J. D. Roberts

The use of monoterpenes for taxonomic purposes

Over the year, much more work has been done on this subject. Early studies were done in the Merlewood

Laboratories on Scots pine. In this period, the basic methods for extracting the samples and gas chromatographic separation were worked out. Towards the end of the year, the Monks Wood Analytical Section took over responsibility for the terpene work. The major innovation then possible was the coupling of the GC output to an integrator. The results obtained with this device are far more precise than those obtained by the earlier triangulation methods and a higher rate of production has been possible. In addition, by using the mass spectrometer it has been possible to identify some of the less common constituents. The taxonomic studies have now been extended to include Lodgepole pine.

M. C. French C. Quarmby

Examination of samples treated with asulam

Asulam is a selective herbicide now widely used for the control of bracken. It is a sulphonamide derivative and its effectiveness as a herbicide is probably due to its interference in the folic acid metabolism. The effects of sub-lethal doses of asulam are being studied in Dryopteris dilatata and Blechnum spicant (Project 48). Samples from these experiments had to be analysed immediately for total asulam. The method used had been developed in the laboratories of May and Baker Ltd., but a number of modifications were required. In particular, the sequence of solvents for the liquid-liquid extractions were changed and it was finally possible to achieve a consistent recovery of 78% over a range of 10-1000 µg/g asulam. The results are expressed by relating the weight of asulam found in a given plant to the surface area of the fronds.

C. Quarmby

Examination of birds and eggs for organic pesticides

The year saw the completion of a long-term survey in which guillemot and razorbill eggs were examined for organochlorine compounds. The samples had been obtained from sites around the coast of Great Britain. Other analyses were carried out in connection with suspected poisoning incidents. Poisoning was established in the case of Greylag geese (due to carbophenothion) and sparrows (aldrin), but the many other incidents were all shown to be negative. There was an unusual case involving some grebes, killed it was thought by pesticide poisoning, although it was later shown that an algal bloom had been responsible.

M. C. French R. J. Mellor

Special activities of the Nursery Unit

The most demanding of the projects which have involved the Glasshouse and Nursery staff has been the

one concerned with vegetative propagation studies on threatened tropical tree species. The three species being studied are *Troplochiton sceroxylon*, *Gmelina* spp. and *Cedrela odorata*. The watering and feeding regime for these plants is particularly demanding and the ambient conditions have to be controlled by the use of an inner chamber within the main glasshouse.

Another major project which has involved the Unit's staff in 1975 has been a study on the wear resistance and recovery of sports turf mixtures. Plots have been established at three separate sites and a particular problem has been the difficulty of standardising treatments at those different sites, especially in view of variable weather conditions. The plots are subject to a wear programme designed to stimulate the damage they will receive during sporting activities. This programme is being carried out in conjunction with staff at Monks Wood and at the Sports Turf Research Institute's trial grounds at Bingley.

The Unit is also contributing to studies on the recolonisation of industrial spoil heaps. In this work, the main requirement is for the creation of a clone bank of tolerant strains and species.

R. F. Ottley

Growth cabinet studies

The year was particularly successful and trouble-free for the use of the growth cabinets at Colney Research Station. Experiments on germination and growth from tillers under different light conditions were carried out using genotypes of *Puccinellia maritima*. Other growth rate studies involved sand dune annuals, and culture experiments were carried out on salt marsh algae.

In September, a conference on the use of growth cabinets for ecological purposes was sponsored at Sheffield University in cooperation with Dr I. Rorison of the Unit of Comparative Plant Ecology. It was a good opportunity for everyone present to exchange know-ledge about the use and technical problems of growth cabinets. Recommendations were made for their future development in ITE.

R. J. Parsell

Single digestion technique

Before analysing plant and soil samples for their total nutrient contents, using wet chemical techniques, it is necessary to decompose the sample by acid oxidation or dry combustion methods. A real difficulty is always caused through having to carry out at least two separate operations to include all the mineral nutrients, phosphorus and nitrogen. A single digestion method was developed, based on the use of hydrogen peroxide and sulphuric acid in the presence of lithium sulphate and selenium, by which it was possible to produce a single solution in which all the above elements could be estimated. Three reports have been published describing this work.

S. E. Allen J. A. Parkinson

Engineering construction

A few examples of jobs carried out by the Engineering Section are given here to illustrate the range of work carried out.

(1) Instruments were constructed for recording bat movements. These incorporate two photoelectric detector heads to detect whether a bat enters or leaves a hole. These detectors are used in conjunction with a pre-set printing counter. Entry or departure can be determined by the order of passing the detector heads. (Plate 59.)

(2) Some relatively simple, but ingenious, time-lapse cameras have been constructed by coupling a pre-set magnetic device to close the shutters of some inexpensive cine cameras. The assembly works from a dry battery and is robust enough for field use.

(3) A rather more massive piece of equipment has been assembled for seed germination experiments. In this instrument, a bank of thermogradient bars has been constructed to operate across any temperature range between 0 and 50°C. The low temperatures are achieved by using a thermoelectric cooling system backed up by a refrigeration unit. The hot end is connected to constant voltage heaters. Allowance has been made for monitoring the temperature of each bar with precision thermistors. Apart from its use for seed germination studies, the equipment can be adapted for experiments with seedlings. (Plate 60.)

(4) A salinity meter has been constructed for the measurement of salinity in dune slacks, although it can also be adapted for use in estuarine waters and muds. The head of the meter contains two toroidal cores and a signal fed into one, when compared with the output from the other, can be related to the ambient salinity.

(5) A considerable effort went into the development and construction of small radio transmitters which could be attached to birds and small animals to enable their movements to be followed. Progress was most encouraging, but the work has had to be temporarily suspended.

G. H. Owen C. R. Rafarel V. W. Snapes

Section IV

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N. Picozzi

H. Kruuk

R. Moss

Projects listed by subdivisions as at January 1976

KEY

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ANIMAL ECOLOGY: VERTEBRATE ECOLOGY

Static	n code

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

Project status

- Proposal not yet approved by management group
- t Paid for by external contract
- ŧ Supported by Nature **Conservancy Council funds**
- ð Supported by Department of Environment funds

V. P. W. Lowe Red deer ecology on Rhum V. P. W. Lowe Red deer/Sika taxonomy V. P. W. Lowe Bark stripping by Grey squirrels V. P. W. Lowe Taxonomy of the Red squirrel J. D. Goss-Custard Prev selection in redshank J. D. Goss-Custard **Dispersion** in waders B. W. Staines Distribution and segregation of Red deer B. W. Staines Movements of marked Red deer B. W. Staines Red deer food studies B. Mitchell Annual cycles in Scottish Red deer B. Mitchell Population dynamics of Red deer P. S. Maitland Freshwater survey of Shetland 117[‡] P. S. Maitland Freshwater synoptic survey P. S. Maitland Zoobenthos at Loch Leven P. S. Maitland Fish distribution and conservation D. Jenkins Shelducks at Aberlady Bay N. Picozzi Research on buzzards Hen harrier ecology 137‡ I. Newton Sparrowhawk research 138‡ M. P. Harris Puffin research 159 D. C. Seel Upland bird project 291 # R. E. Stebbings Population ecology of bats 292 R. E. Stebbings Specialist advice on bats 322 D. Jenkins Aquatic mustelids 325† I. Newton Carrion-feeding birds in Wales J. D. Goss-Custard Prey selection in wading birds N. Charles Dispersion of Field voles, Scotland Behaviour and dispersion of badgers V. P. W. Lowe British mammals (Red fox) J. D. Goss-Custard Burry inlet cockle/oystercatcher data V. P. W. Lowe Intraspecific variation in Polar bears J. D. Goss-Custard Weight loss in waders D. Jenkins Dynamics of Mute swan population B. Mitchell Red deer population on Isle of Scarba Ecology of capercaillie

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ANIMAL ECOLOGY: INVERTEBRATE ECOLOGY

64	S. McGrorty	Intertidal invertebrate surveys
64	S. McGrorty	Invertebrate population studies
66	S. McGrorty	Variation in strandlines
161	A. Buse	Littoral fauna of Llyn Peris
162‡	A. Buse	Freshwater gastropods in North Wales
185	B. N. K. Davis	Effect of urbanisation
188	R. C. Welch	Woodland invertebrates
201	E. Pollard	The White admiral butterfly
202	E. Pollard	The Roman snail
203	J. P. Dempster	The Cinnabar moth
204‡	E. Pollard	Assessing butterfly abundance
205	E. Pollard	Invertebrates in hawthorn hedges
229	M. G. Morris	Ecology/taxonomy – Spanish hemiptera
230	M. G. Morris	Cutting experiment (Coleoptera)
231	M. G. Morris	Barton Hills grazing experiment
232	M. G. Morris	Butterfly studies (Porton Range)

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233‡ 234 236 241 243‡	M. G. Morris E. Duffey E. Duffey L. K. Ward L. K. Ward
255	G. W. Elmes
256	B. Pearson
261	B. Pearson
262	A. Abbott
270	P. Merrett
271	P. Merrett
272	N. R. Webb
273	N. R. Webb
274	N. R. Webb
277	N. R. Webb
278	P. Merrett
293	L. K. Ward
295	L. K. Ward
296‡	L. K. Ward
309‡	L. K. Ward
338	A. Buse
381	D. G. George
393	J. P. Dempster
399	B. N. K. Davis
400‡	J. A. Thomas
403	J. A. Thomas
404	J. A. Thomas
405‡	R. C. Welch
406	P. T. Harding
407	R. C. Welch
414	P. Merrett
423	A. M. Nicholson
450	P. E. Jones

Cutting experiment (Hemintera)
Grassland management by fire
Invertebrate populations in grass sward
The fauna of Box
Scrub succession at Aston Bowant NNR
Ecology of <i>Myrmica</i> species
Protein electrophoresis
Caste bias in <i>Myrmica</i> engs
Distributional studies on spiders
Spider populations on gorse
Decomposition of <i>Calluna</i> litter
Decomposition of Canana Inter
Soil microbos and soil fauna
Soli filiciones and soli faura
Spider populations on heather
Study of found in juniper
Survey of juniper in N. England
Sorvey of juliper in N. England
Scrub management at Castor Hanglands
Phytophayous insect data bank
Role of bilds in spread of Mr V (Nuclear
Polyneural virus)
The Swellow toil butterfly
The Swallowian buttering
Isolated phytophagous insects
Ecology of Large blue bullerity
Black hairstreak butterily
Brown hairstreak butterily
Fauna of mature timber habitat
Non-marine Isopoda
British Staphylinidae (Coleoptera)
Hartland Moor spider survey
Predator/prey relations on neathland
Ecology of pseudo scorpions

ANIMAL ECOLOGY: ANIMAL FUNCTION

178‡

179‡

181‡

182‡

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F. Moriarty	Toxicology of pollutants	1
J. Parslow	Pollutants in seabirds	1
J. Parslow	Pollutants in estuarine waders	1
A. A. Bell	Birds of prey and pollution	1
H. R. A. Scorgie	Aquatic herbicides	1
A. S. Cooke	Frogs and pollution	1
N. J. Westwood	Stone curlew and lapwing	1
R. K. Murton	Laboratory studies of the feral pigeon	1
R. K. Murton	Waterfowl reproduction control	1
R. K. Murton	Avian breeding regulation	1
R. K. Murton	The Eared dove in South America	1
F. Moriarty	Pollutants in aquatic animals	1
R. K. Murton	Goshawk predation and toxic residues	1
A Tve	Social behaviour of thrushes	1
S. Dobson	Endocrine lesions in birds	1

ANIMAL ECOLOGY: GROUSE AND MOORLAND ECOLOGY

129	A. Watson	Red grouse and ptarmigan populations	8
130	A. Watson	Management of grouse and moorlands	8
131	A. Watson	Golden plover populations	· 8
132	A. Watson	Effect of human impact on wildlife	8

ANIMAL ECOLOGY: HEATHLAND SOCIAL INSECTS

252 253 258 259 260 264 370 371	M. V. Brian M. V. Brian	Hartland Moor NNR survey <i>Tetramorium caespitum</i> populations Queen effect of larvae growth Larvae and worker communication Queen recognition by workers IBP ant and termite synthesis volume Reduction of inter-species competition Male production in <i>Myrmica</i>	4 4 4 4 4 4 4
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PLANT ECOLOGY: PLANT BIOLOGY

2	E. J. White	Meteorological factors in classification
19	E. J. White	Nutrient input in rainfall
53	A. S. Gardiner	Variation in British woodland trees
58	A. S. Gardiner	Hazel and birch on Shetland
69	R. Scott	Study of <i>Cakile</i>
73	A. J. Gray	Puccinellia maritima
79	G. R. Miller	Glen Feshie vegetation
80	G. R. Miller	Red deer grazing of saplings
81	G. R. Miller	Creag Fhiaclach vegetation
82	G. R. Miller	Seed produced by montane plants
99	N. G. Bayfield	Trial of nature trail questionnaire
100	N. G. Bayfield	Reseed vegetation on Cairngorm
101	N. G. Bayfield	Vegetation trampling on Cairngorm
102	N. G. Bayfield	Mountain vegetation populations
121	M. E. Bindloss	Phytoplankton productivity
125	R. E. Daniels	Peatland monograph
126	R. E. Daniels	Peatland bibliography
127	R. E. Daniels	Mineral utilisation
128	R. E. Daniels	Blood moss
157	D. F. Perkins	Snowdonia IBP study
158	D. F. Perkins	Community processes (physiology)
160§	D. F. Perkins	Fluorein pollution studies
166	R. O. Millar	Hippophae rhamnoides study
245	J. Pelham	Genetics of Betula nutrition
246	E. D. Ford	Physical environment, forest structure
247	K. A. Longman	Physiology of flowering
248†	K. A. Longman	Physiology of root initiation
249	M. G. Cannell	Morpho-physiological differences
250	R. C. Warren	Microbial populations in trees
265	S. B. Chapman	Aerial production of lowland heaths
266	S. B. Chapman	Root production and soil organic matter
267	S. B. Chapman	Organic matter accumulation
268	S. B. Chapman	Ecology of <i>Erica ciliaris</i>
269	S. B. Chapman	Autecology of Gentiana pneumonanthe
329	E. J. White	Response of Scots pine
346	A. J. Gray	Genecology of grass species

359 410 411 412 419 427	M. G. Cannell N. J. Collins S. W. Greene B. G. Bell N. G. Bayfield	Fibre yield of poplar coppice Tundra plants (Bryophytes) Taxonomy of Bryophytes Genecology of <i>Racomitrium</i> Vehicular tracks in Scotland Eurther acological studies on Wash	5 5 5 7 3
437	A. J. Gray	Further ecological studies on Wash	3

PLANT ECOLOGY: PLANT COMMUNITY ECOLOGY

1	R. G. H. Bunce	Semi-natural woodland classification	2
6‡	R. G. H. Bunce	Scottish native pinewood survey	2
9	J. M. Sykes	Monitoring at Stone Chest	2
10±	J. M. Sykes	Monitoring at Kirkconnel Flow	2
11±	I M Sykes	Post-fire vegetation at Shieldag SSSI	2
12 ± 12	A D Horrill	Monitoring in North West Scotland	2
12 -	M W Shaw	NW (E) England commercial forest survey	2
1/		Tree girth changes in 5 NNRs	2
15+	A. D. Horrill	Vegetation changes with grazing	2
10+	A. D. Horrill	Bryophyte monitoring in Borrowdale	2
10+	A. L. P. Goro	Primary production – Moor House bog	1
41	A. J. P. Gore	Plant growth of <i>Molinia caerulea</i>	1
42	A. J. F. Gore		2
40	D. R. Helliveli	Landscape perception	2
48+	A. D. HOMII	Defaliation of oak appdlings	2
50		Defonation of oak seedings	2
55	A. H. F. Brown	Establishment of trees at Moor House	2
60	D. R. Helliwell	Experimental transplants of <i>Printula Vulgans</i>	2
70‡	L. A. Boorman	Management of sand dunes (E. Anglia)	ა ი
/1	D. S. Ranwell	Zostera/Spartina muditat studies	ა ი
72	D. S. Ranwell	Salt marsh management	3
74	D. S. Ranwell	Sand dune stabilization	3
75	D. G. Hewett	Control of Spartina	9
76	D. G. Hewett	Mature shingle beach vegetation, Sussex	9
77	D. G. Hewett	Cliff vegetation methods.	9
78	D. G. Hewett	Management of sand dunes (Wales)	9
83‡	J. W. Kinnaird	Management of birch regeneration	7
84‡	J. W. Kinnaird	Tree age and woodland history, Scotland	7
85‡	J. W. Kinnaird	Growth and survival of birch in shade	7
86‡	J. W. Kinnaird	Seed production of <i>Betula pubescens</i>	7
91	I. A. Nicholson	Vegetational succession: a review	7
92§	D. Welch	Grazing intensities causing change	7
93§	D. Welch	Assessing animal usage, N.E. Scotland	7
94	I. A. Nicholson	Grazing effect on 30 sites, Scotland	7
95	D. Welch	Importance of dung for botany change	7
96	D. Welch	Narthecium ossifragum and burning	7
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226	T. C. E. Wells
227‡	T. C. E. Wells
228‡	T. C. E. Wells
237‡	T. C. E. Wells
242‡	T. C. E. Wells
251	J. E. G. Good
287‡	J. Sheail
288	J. Sheail
318	A. J. P. Gore
319‡	M. J. Liddle
340‡	D. S. Ranwell
348‡	T. C. E. Wells
349†	L. A. Boorman
360	J. E. G. Good
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367	A. H. F. Brown
369§	J. W. Kinnaird
373‡	J. M. Sykes
374	L. A. Boorman
377	J. Sheail
379‡	J. M. Sykes
380§	I. A. Nicholson
383	D. R. Helliwell
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388	J. M. Sykes
389‡	A. H. F. Brown
392†	A. J. P. Gore
413	I. Wyllie
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426§	I. A. Nicholson
427†	T. C. E. Wells
435	C. J. Barr
454‡	J. M. Sykes

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22	J. C. Frankland	Fungal decomposition of leaf litter
23	K. L. Bocock	Soil temperature in Meathop wood
27	J. C. Frankland	Fungal biomass – Meathop litter and soil
29	A. F. Harrison	Phosphorus circulation
30	J. C. Frankland	Biomass and decay of Mycena in Meathop
32	O. W. Heal	Moor House IBP study
.33	O. W. Heal	Vegetation decomposition, Moor House
34	O. W. Heal	Radiation and temperature, Moor House
39	A. F. Harrison	Phosphorus turnover in soils
40	P. J. A. Howard	Woodland organic matter decomposition
45	O. W. Heal	Tundra biome IBP
51	P. M. Latter	Food consumption of Enchytraeidae

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61	A. F. Harrison	Variation in growth of birch and sycamore	2
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90	J. Miles	Birch on moorland soil and vegetation	7
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140	M. Hornung	Weathering and soil formation, Whin Sill	9
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368‡	M. O. Hill	Afforestation effect on uplands	9
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431	P. J. A. Howard	Soil change through afforestation	2
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438	J. C. Frankland	Ecology of Mycena galopus	2
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170	R. E. Hughes	Arctic/alpine vegetation survey	9
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207‡	F. H. Perring	Atlas of British flora	1
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209‡	H. Arnold	Amphibians and reptiles survey	1
210‡	H. Arnold	Mammal distribution survey	1
211‡	J. Heath	Lepidoptera distribution maps scheme	1
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213‡	J. Heath	Orthoptera distribution maps scheme	1
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215	F. H. Perring	Biological information network	1

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2	23	J. Heath	European invertebrate survey	1
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2	98	D. Brown	Detecting regular pattern in plane	10
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3	02	M. D. Mountford	Population growth and regulation	10
3	03	M. D. Mountford	Method of cluster analysis	10
3	04	M. D. Mountford	Estimation of quantiles	10
3	06	P. Rothery	Spatial processes and application	10
3	07	P. H. Cryer	Index of egg shell thickness	10
3	08	P. H. Cryer	Data from multi-compartment systems	10
3	10	D. F. Spalding	Polluted watercourses survey	10
3	11	D. F. Spalding	Data definition and validation	10
3	12	K. H. Lakhani	Population dynamics of the shrimp	10
3	13	M. D. Mountford	Seals research	10
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441*	J. D. Goss-Custard	Oystercatcher and shellfish interaction	3
443*	D. K. Lindley	Woodland enumeration	2
445*	J. H. Belcher	Marine flaggellates taxonomy	12
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448*	E. M. F. Swale	Colourless flagellates taxonomy	12
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456*	D. Osborn	Heavy metals in avian species	1
457*	C. Milner	Grazing models	9
458*	C. Milner	Shetland publication	9

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Publications

(ADAMS. R.) and HOOPER, M. D. (1975). Nature through the seasons. Kestrel.

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