The Natural Environment Research Council

Institute of Terrestrial Ecology Report for 1985/86

Contents

Institute of Terrestrial Ecology

Report for the period 1 January 1985-31 March 1986

Director's Introduction

Reductionist and Holistic Aspects of Ecology

Introduction

The rapid development of scientific methodology which we have experienced during the last 40 years actually began in the 1920s. Many of today's concepts of experimental design arose from the work of R A Fisher and his analysis of agricultural experiments. His attempts to analyse historical data directed his attention to the efficient design of experiments and surveys, in order to avoid the difficulties that he encountered in trying to make sense of the unreplicated, unrandomized records of practical trials. The impetus that he had given to scientific methodology was given a further boost during the Second World War, particularly through the multidisciplinary teams that were assembled to tackle operational problems as they arose. Many of the scientists from the more physical disciplines had a strong mathematical background and the solutions that they developed to these operational problems laid the foundations for what has come to be known as Operational Research.

Since that time, perhaps the most significant development has been the rapid evolution of computer hardware and software. The existence of modern computing devices which could carry out calculations that formerly took weeks, or even months, in fractions of a second, has greatly modified our concept of what can be achieved through computation and logical manipulation. The ability to make data machine-readable, and then to store these data for long periods of time so that they can be recalled and used many times over also greatly extends the value of the computer as an operational tool. However, perhaps the most important development to come from the computer is the development of algorithmic languages capable of expressing the most difficult logical relationships in totally unambiguous forms, both for programming the computers and for transferring information from one mind to another. With the help of such algorithmic languages, we have now been able to find computational solutions to analytical problems which previously defied solution through analysis alone. It is through this development that what we now call Information Technology has emerged as a basis for future research and management.

The Reductionist Approach

Traditionally, biology and ecology are reductionist. Simply because the concerns of ecology are essentially multidimensional, multivariate, and multiobjective, ecologists have usually confined their investigations to subsets of the total problem. They have done this by examining the interrelationships of one or a few organisms with their environment, by investigating a limited range of environments, and by manipulating only a small number of the possible variables which are involved in the interactions between organisms and their environment. This reductionist tradition is one that looks back to physics, and it is interesting to note that, where mathematics has been employed in ecology in the past, it has usually been by a direct attempt to use applied mathematics, that is mathematics applied to physics. Such methods assume a deterministic response to changes in the experimental variables, and a response that can be measured without error.

The complicating factor, however, is that ecological systems display an inherent variability. Such variability has its origins in the genetic mechanisms which are an essential part of biological organisms, and which help to ensure that organisms are capable of dealing with a wide variety of changes in their environment. The variability may be expressed in the response of the organisms to their environment, or in their response to each other. It was precisely this variation that Fisher recognized as the source of the difficulties that he encountered in trying to analyse historical data on agricultural experiments.

Faced with such variability, the ecologist has three possible pure strategies, ie survey, experimentation and simulation. He may attempt a survey, which is an exploration of the variation exhibited by the organisms and their environment, but with little or no attempt to control that variability. The end point of the investigation is a measurement and description of the variability that is encountered at different levels in the environment. Alternatively, he may attempt direct experimentation by controlling a limited number of variables so as to explore the effects of the deliberate modification of a small number of the remaining variables. Fisher himself pointed out, quite early in his own work, that it was never sufficient to modify only one variable at a time, because such experiments would never provide information about the interaction between two or more variables. The statistician's development of factorial experiments, with deliberately enforced variation of two or more variables in predetermined combinations, is a device which is still little understood, even by scientists who are supposed to have received adequate training in scientific methodology.

The statistical developments in the design and analysis of experiments have emphasized the importance of randomization and replication, as well as that of the control of treatment structures so as to ensure that the efficiency of the experiment is directed towards the correctly identified objective of the experiment. These treatment structures are related to the hypotheses which are to be tested, or to the estimates to be made by the comparison of the treatment effects. The analysis of experimental results places emphasis upon linear and non-linear models, as well as on the distribution theory which is used in the interpretation of the variability shown by the experimental material in response to the treatments. There remain some further complexities which have yet to be adequately explored by statistical theory, especially with regard to experiments repeated in space and time, and with the analysis of repeated assessments of the same experiment. Nevertheless, both survey and experimentation provide a basis for, and an encouragement to, reductionist approaches to ecological research and management.

The Holistic Approach

The paradigm of the ecosystem, which was formulated by Tansley in 1923, envisages the complex interactions of living organisms with each other and with their environment. Tansley's ecosystem, therefore, is the integration of all living and non-living factors in a system. Ecosystem theory is concerned with the interactions of these organisms in such processes as decomposition and nutrition, in competition between organisms as in host/parasite and predator/prey systems, and in the population dynamics of single organisms or groups of organisms. The boundaries of such ecosystems are set within those of natural systems, or are perhaps related to particular crops or landscapes. The forcing functions for the interactions which are described by ecosystem theory are related to climate or to seasons or to man's actions in his attempts to control and modify his environment. The response of the ecosystem is related to its resilience, to its perturbation through the effects of forcing functions, or, unhappily, in some cases, to its destruction as a result of ill-considered attempts to modify the environment or to harvest the organisms in a crop or natural system.

The recorded history of the world provides plenty of examples of ill-considered use of ecosystems. There are plenty of examples, even today, to illustrate man's inability to think about the environment in an holistic and effective way. The fertile soils of Himalayan valleys are being washed away in such quantities that a new island is forming in the Bay of Bengal, an island of soil which, if the land had been properly managed, would still be growing food. Such erosion is not confined to developing countries, and in the century during which it has been cultivated, southern Iowa of the USA has lost as much as half of its topsoil. The deserts of the world are expanding at a rate of almost 60,000 km^2 a year—an area twice the size of Belgium.

The resource base of major industries is shrinking as tropical forests contract rapidly, and as the coastal support systems of fisheries are polluted or removed altogether. At present rates of clearance, the remaining area of unlogged productive forests will be halved by the end of this century, and it has been estimated that tropical rain forests (genetically the richest land environments on the planet) are being felled and burned at the rate of 11 million hectares a year. All tropical rain forests will have disappeared within 85 years if felling continues at this rate. As a result of the spread of environmental destruction, some 25,000 plant species and more than 1,000 species and subspecies of mammals, birds, amphibians, reptiles and fish are threatened with extinction. These figures do not take account of the inevitable losses of small plant and animal species whose habitats are being eliminated in their entirety, or being modified in such a way that essential life support systems cannot be maintained. All of this mismanagement of the world's ecology comes from current attempts by a quarter of the world's people to continue to consume two-thirds of the world's resources, and by half the people simply to stay alive, attempts which are destroying the very means by which all people can survive and prosper. If ever there was an operational problem, this is it!

Systems Analysis

Faced with the need for holistic solutions to essentially practical problems, ecologists have come to place much reliance upon models, defined as formal expressions of the essential elements of a problem in either physical or mathematical terms, and in Systems Analysis. A precise definition of Systems Analysis is elusive, but, in the sense in which I am using the term in this essay, it is the orderly and logical organization of data and information into models, followed by the rigorous testing and exploration of these models necessary for their validation and improvement. In contrast, therefore, to the methods of survey and experimentation, Systems Analysis is a method of synthesis, ie an attempt to put together various theories and ideas about an ecological system in such a way, that these theories make a coherent whole. Having derived such a synthesis, it will, of course, be necessary to test the model or models against reality by direct experiments, but in such a way that each of these experiments can be related to the behaviour of the model as a whole.

The purpose of Systems Analysis are to provide an adequate description of an ecological system, to make predictions about the changes which might take place as a result of attempts to modify the system, and, ultimately, to provide a mechanism for making decisions, especially in the face of uncertainty.

Criticisms of Ecological Research

One of the frequently voiced criticisms of ecological research, as it has been conducted in the past, is that it emphasizes complexity, whereas those seeking solutions, as in land planning, agriculture, forestry and resource management, are searching for simplicity. Indeed, it has frequently been said by economists and by sociologists that the only kind of ecological model that they can use is a simple one. However, ecologists are acutely aware that the interrelationships between organism and between organisms and their environment, are extremely complex, in the sense that they are non-linear and that they carry considerable degrees of feedback. This complexity is an essential characteristic of the operation of an ecosystem, and it may be unreal to search for, and express, such relationships in a wholly simplistic way that the economists and resource managers would find acceptable. We may have to accept the complexity as the price that has to be paid for an adequate understanding of the way in which the natural environment operates.

A second criticism is that ecological research to date has failed to find an adequate set of principles or guidelines: in other words, ecological research has not resulted in an adequate ecological theory. There is, of course, some truth in this accusation and it is clear that the complexity of the system has resulted in ecologists seeking and exploring many diverse expressions of the variation of these interrelationships without necessarily drawing together the underlying principles. Nevertheless, some generalities can now be expressed, although they are inevitably, at this stage, qualified by exceptions and special cases.

A more pertinent criticism is that transfer of information from ecological research to the management of ecological systems has been inadequate. Like other scientists, ecologists have concentrated on the publication of research results in the scientific journals—such publication is essential for the development of the career of the scientist, and for ensuring that the scientist is a member of the national and international 'club' which will guarantee that he or she is in communication with fellow scientists working in the same or similar fields. However, communication between scientists does not provide for the transfer of information to the administrator, the resource manager, and the general public, who are either directly concerned with the management of ecosystems of various kinds, or have an interest in the ways in which our systems are managed. While there is a wealth of rather generalized and popular information about biology and ecology, very little of this information is sufficiently detailed to act as a guide in the management of a system, or in the conduct of affairs related to a direct effect on ecological systems.

Future Developments

Fortunately, some help can be visualized in the current developments of information theory and of scientific methodology. One of the inhibitions of transferring information about ecological systems is the sheer quantity of information necessary to demonstrate the complexity of the problem.

Extensive data bases already exist for many aspects of ecology. In ITE, for example, we have the Biological Records Centre which contains many millions of records of the presence or absence of plant and animal species in localities in Britain. ITE regularly produces atlases of the distributions of species, but this is a very restricted presentation of data which are constantly changing, and which could be used to illustrate many of the problems occurring in British ecological systems. With the advent of package switched networks and improved Viewdata systems, however, it will soon be possible to provide access to data such as are held by the Biological Records Centre for a modest annual subscription. It will also be possible to provide a great deal of flexibility in the ways in which the data can be presented and reviewed.

An even more exciting development is that of the Expert System. An Expert System is the embodiment within a computer of a knowledge-based component from an expert skill in such a form that the system can offer intelligent advice or take an intelligent decision about a processing function. A desirable additional characteristic, which many would regard as fundamental, is the capability of the system, on demand, to justify its own line of reasoning in a manner directly intelligible to the enquiries. The difference between such a system and the usual 'black box' of the mathematical model is an important one and should go a long way towards providing both for a more integrated science of ecology and for the transfer of information from research scientists to the potential users of the information.

J N R Jeffers

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Research Reports

Forest and Woodland Ecology

Songbird Populations and Woodland Diversity

Foresters and landowners are increasingly concerned with issues of conservation and public amenity. One aspect of this concern is the richness, in both numbers and species, of songbirds, a highly 'visible', and ecologically important group of animals. The aim of the research was therefore to obtain data on songbird populations in a variety of woodland types on Deeside, to examine the relationships between these populations and habitat features (eg tree species, structural heterogeneity, presence and types of shrub) and, from these relationships, to derive recommendations for forest management to maximize the richness of woodland songbird populations. Detailed consideration of individual bird species has been deliberately avoided in favour of concentration, the problem of what sort of wood or forest will contain a rich songbird population (ie many birds, of many different species, in a relatively small area), as a rich population will inevitably contain 'specialist' or 'interesting' species, as well as those with more catholic requirements. The few species not covered by these means require special study, which is beyond the scope of this project. One exception to this general rule is the woodpeckers, which are considered specifically (see below) because of their effect on availability of nest sites for several other species.

Initially, a number of semi-natural woods were surveyed, to assess the ideas that forest structure and tree type (ie conifer/broadleaf) both affected songbird populations (some results of this work were reported in Jenkins *et al.* 1984). The sample was then extended to include plantation forests and to test in more detail the effects of mixtures of tree types and of a tall-shrub layer. In addition to these general surveys, changes in bird populations were monitored following changes in forest management in some woods.

The total sample included 6 conifer stands, 3 birch/aspen, one oak/birch, and 6 mixed conifer/broadleaf, of which one was mainly conifer, 2 mainly broadleaf trees and 3 approaching equal proportions of the 2 tree types.

Two series of observations were made, to relate bird populations to habitat features (French *et al.* 1986). Briefly, bird territories were estimated by a mapping method (BTO Common Bird Census, Marchant 1983) and the species divided into 8 'ecological groups' according to their use of habitat for nesting and foraging. From these data were also calculated the summary (population) parameters 'Number of birds' (actually number of mappable territories per 10ha), 'Number of species', and 'Bird species diversity' (BSD), using the Shannon Index for diversity (Shannon & Weaver 1949). None of these parameters is, by itself, a satisfactory measure of the 'richness' of a population, but together they provide a fairly good index of the consistency of the effects of any combination of habitat features.

Habitat surveys included estimation of vegetation profiles in 100m^2 plots, classification of profile types, and measurement of horizontal heterogeneity and canopy composition by a transect method (van Berkel 1979; Opdam & van Bladeren 1981). From the profile and transect data were calculated 3 measures of the structural diversity of the habitat, *viz* 'Foliage height diversity' (FHD) using 4 or 5 height classes, by the Shannon Index, 'Horizontal heterogeneity' after Opdam and van Bladeren (1981) using 3 or 4 vegetation layers, and 'Number of profile types' (NPT) from the classification of vegetation profiles. Figure 1 gives an example of contrasting profiles and FHD, and an evaluation of profile types for NPT. For further details, see French *et al.* (1986).

Results

Some summary data are presented in Table 1. The Table should be read as 'background' and not as the 'definitive' data set, because the actual analyses of the relationships described often included the use of more detailed data, eg numbers of birds of individual species, or subdivisions of census plots.

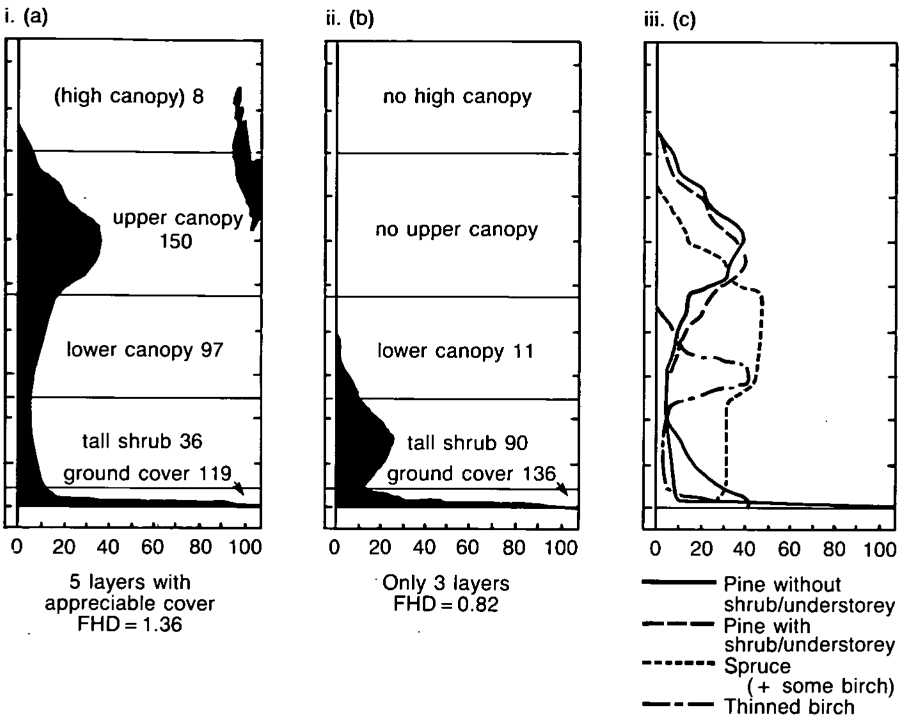
Numbers of birds and species, and the range of species observed, were typical of the variation found generally in woods in northern Scotland. Thirty-three species were present, including all species listed by Newton (1986), except redwing and chiffchaff (both seen but never shown to hold territory), whitethroat and pied flycatcher. These 4 species are generally uncommon in north-east Scotland. The richness of the songbird populations were assessed in relation to age of stand, type of trees (broadleaf/conifer/mixed), structural heterogeneity, and different combinations of shrub and canopy layers.

Age of Stand

Young woods were not good

habitats for most woodland songbirds (the 'canopy' habitat is missing), but there was little difference between subsequent stages.

Figure 1. Example of vegetation profiles, calculation of FHD, and classification of profile types: (i) a diverse profile with a wide height range (average profile of site E), (ii) a simpler profile, lacking some layers (site H), (iii) 4 distinct profile types within site E add to 3-dimensional heterogeneity



surprising, and contradicts the view that broadleaf trees are universally 'better' for songbirds than conifers. It may be that previous studies have (i) confounded tree species with structural characteristics of a wood, (ii) tended to group all broadleaf species in comparisons, and (iii) not distinguished between single-species stands and mixtures of species of the same tree type. Similarly, while coniferous woods generally were not the 'best' for songbirds, it is notable that 2 of the richest sites were mainly conifer (site K) or 100% pine (site F) and that both were plantations rather than 'natural' woods.

Because mixtures were generally ranked higher than single tree types they were examined in more detail to see if we could define an optimum configuration, ie what is the minimum proportion of the secondary tree type required to give a marked increase in the richness of the songbird population, and is there an optimal spatial distribution of the secondary type? Comparing mixed stands with different proportions of tree types, and with even or clumped distributions of the secondary tree type, suggests: (i), if the secondary type is less than 20% of the canopy there may not be any marked

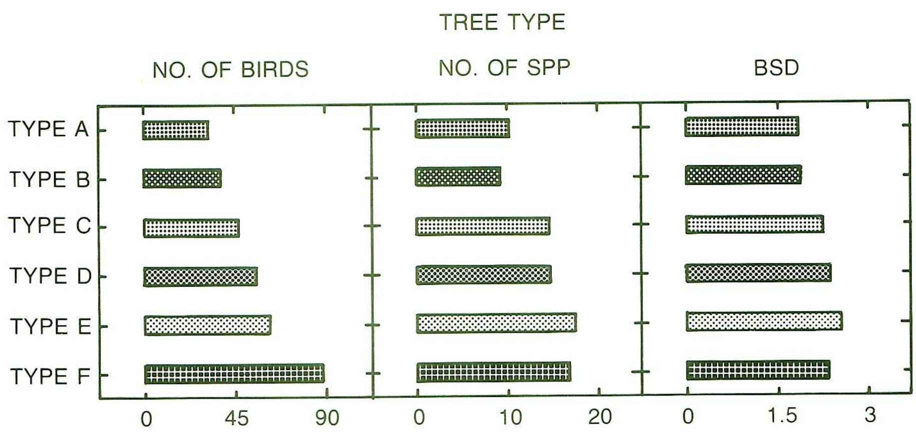
Table 1. Summary data on woodland characteristics and songbird populations in some woods on Deeside.

	Site	Tree type(s)	Age	Tall shrub	Upper canopy	FHD	NPT	Number of Birds	Number of species	BSD
A	Strone	C	Y	+		0.77	3	41.6	6.2	1.66
B	Gairney	C	O		+ +	1.23	1	37.1	8.0	1.73
C	Allachy	C	V		+ +	1.07	4	29.0	11.3	2.07
D	Drum	C	V		+	0.98	3	37.2	8.3	1.83
E	Glassel Road	C	M	+	+ +	1.36	4	42.6	11.0	2.13
F	Glen Dye	C	O	+	+ +	1.29	5	62.9	15.0	2.39
G	Dinnet Roadside	B	Y	+		0.59	3	22.1	8.2	1.62
H	Huntly Road	B	M	+		0.82	2	51.3	11.0	2.01
I	Ord Hill	B	O	+	+	1.20	4	45.6	13.0	2.11
J1	Dinnet Oakwood (+rhododendron)	OH	O	+	+	1.34	5	64.9	16.0	2.43
J2	Dinnet Oakwood (−rhododendron)	OH	O	+	+	1.32	4	52.0	14.3	2.35
K	Potarch	C(B)(H)	M	+	+	1.05	7	62.0	17.5	2.54
L	Braeroddach	B(C)	M		+	1.10	4	30.9	12.0	2.09
M	Craigendarroch	O(B)(C)	O	+	+ +	1.25	4	58.4	16.5	2.36
N1	Cambus o' May (pre-felling)	BC	O		+ +	1.26	7	56.9	16.0	2.43
N2	Cambus o' May (post-felling)	B(C)	O		+ +	1.24	6	46.2	16.0	2.42
O1	Corsedardar (pre-felling)	CB	Y/M	+	+	0.94	4	56.1	13.0	1.91
02	Corsedardar (post-felling)	CB	Y/M	+	+	0.88	4	66.0	14.0	2.01
P	Crathie	BC(H)	V	+	+ +	1.29	7	118.6	19.0	2.53

Tree types: C, conifer (pine, spruce, fir); B, birch/aspen; O, oak; H, other broadleaf spp.; ( ) = <25% of canopy
Age: Y, young (no appreciable canopy); M, medium (lower canopy mixture of Y and O); O, old (mature trees, <100yr old or, if >100, 1st generation); V, very old (trees >100yr, or mixed-age but wood ≫100yr)
Tall shrub: + present over ⩾15% of total area. Upper canopy + canopy 12–20m present; + + canopy 12–20m and canopy >20m present
Sites A-D, G-I, L, N, P were semi-natural woods, the others plantation woods.

Tree Type (Broadleaf/Conifer/Mixed)
The 'worst' tree type for songbirds of those sampled was birch/aspen. Conifers were, on average, slightly better, and oak or mixed broadleaf (other than birch/aspen) had richer populations than either (though our sample did not include any young oak stands). Mixed woods generally supported richer bird populations than single tree types, although those with more than 75% broadleaf trees showed considerable overlap with single-tree type stands. Mixtures that were mainly conifers were better than those that were mainly broadleaf species, and mixed woods with more equal proportions of conifers and broadleaf trees best of all (Figure 2 shows the mean values for the 3 bird summary parameters). The low ranking of birch/aspen is

improvement over a single tree type; (ii) that small clumps of the secondary type are likely to be more effective than an even scatter of single trees (Figure 3). We have no data on the effect of larger agglomerations of the secondary tree type. The sample size, however, was small, so the effects of removing part or all of the secondary type at 2 sites where trees had been selectively felled in



Key: Type A: Birch/aspen; B. Conifer; C. Mixed (mainly broadleaf); D Oak/mixed (broadleaf); E. Mixed (mainly conifer); F. Mixed (equal conifer and broadleaf).

Figure 2. Mean values of bird summary parameters in woods with differing types of trees (birch, conifer, etc)

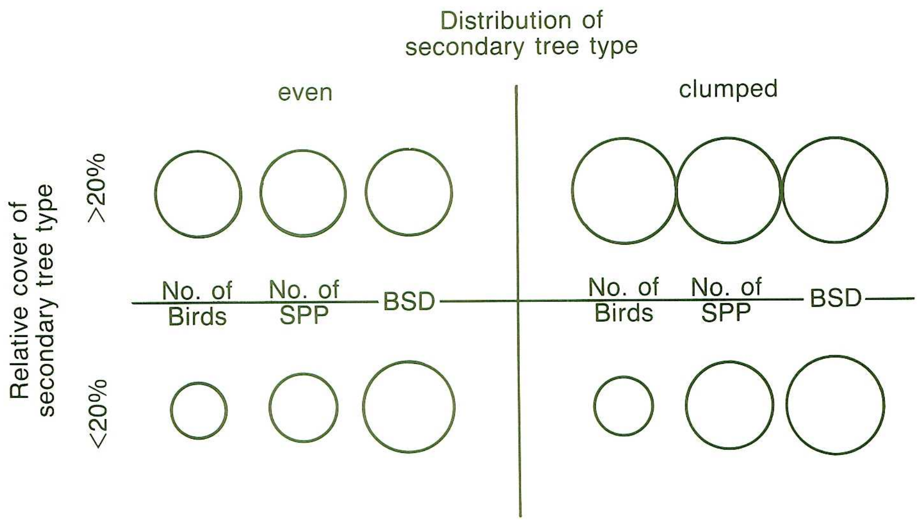


Figure 3. Bird summary parameters in relation to canopy composition of mixed woods: effects of proportion of secondary tree type and of spatial distribution of secondary type (even = no groups of > 2–3 trees of secondary type, clumped = appreciable aggregations, ⩾5 trees or ⩾0.15ha, present. Diameter of circles proportional to bird summary parameter (for bird summary parameters, see Table 1).

parts of formerly homogeneous blocks were examined, providing the possibility of a 'split-plot' or matched-sample comparison. In one of these sites, there was a definite detrimental effect of removing the secondary tree type, but in the other site there was no demonstrable effect of selective felling on the songbird population (for details, see French *et al.* 1986).

Structural Heterogeneity

Structural heterogeneity was found to be more generally important than age or tree type (effects of these 2 factors are often simply due to the associated variation in profile characteristics) in determining the richness of songbird populations. There were positive correlations between the bird summary parameters and all the 3 indices of structural diversity, reaching especially high values with combinations of FHD and NPT or FHD and horizontal heterogeneity (ie measures of 3-dimensional heterogeneity), up to a correlation of 0.93 between BSD and (FHD × NPT). NPT was generally more closely related to bird summary parameters than horizontal heterogeneity, and one potentially useful result for management purposes was that woods with less than 4 distinct profile types in 10ha always had a poor songbird population, but those with more than 4 profile types always had a rich one.

The presence of gaps in the canopy increases structural heterogeneity. How many or what cover

What kind of wood is best for song birds?
(a) "Natural" Brodleaf wood (birch)?—but even aged, no tall-shrub layer, generally simple structure: poor songbird population
(b) Conifer Plantation (pine)?—but old stand, with much natural regeneration functioning like a tall-shrub layer, and generally complex structure: rich songbird population

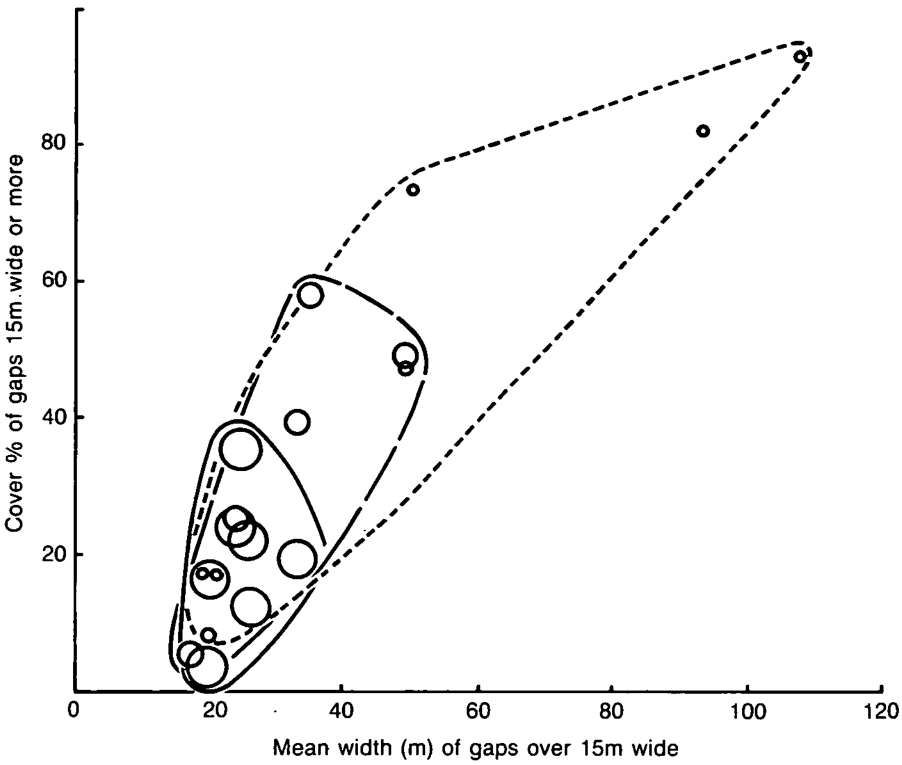


Figure 4. An example of the effects of size and cover of gaps on Bird Species Diversity
O—BSD > 2.3 ('rich' woods), O— — 2.0 ≤ BSD ≤ 2.3 ('intermediate' woods), O - - - - BSD < 2.0 ('poor' woods)

(percentage of total area) of gaps should there be, and what size(s) is (are)best? Taking 15m as the minimum width for gaps in the canopy likely to be created by normal forestry practices, and examining the relationship between cover and size of gaps and the richness of the songbird population, it was found that there was a broad relation between bird populations and cover and size of gaps, insofar as all the richest sites were within a narrow range of both cover and size (Figure 4). Outside this range, songbird populations became progressively poorer. However, there were several woods which were inside the range for the rich woods but which still had poor songbird populations. There is also a lack of data on woods with only a very few large gaps (eg 10% in a single gap about 100m wide) in an otherwise uniformly closed canopy, so the above result may not be as 'definite' as it seems. It is, nevertheless, likely to indicate, at least broadly, a 'true' relationship.

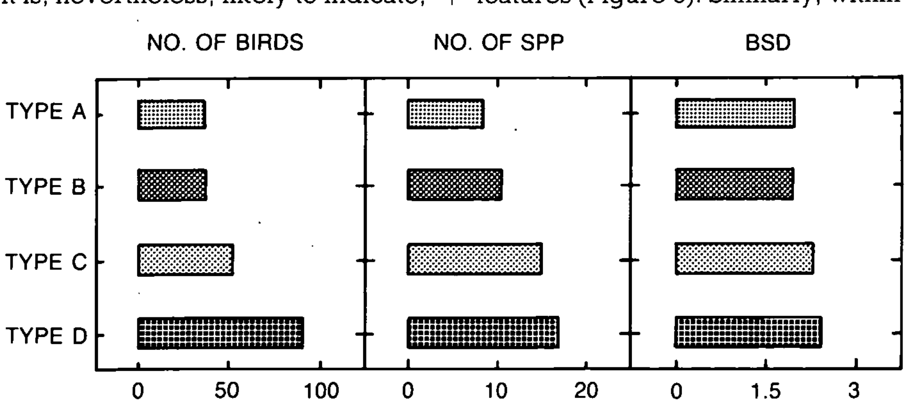
Importance of a Tall-shrub Layer

Structural heterogeneity depends in part on the spatial arrangement of different 'layers' of vegetation. Of the possible combinations, the relative distributions of upper (over 12m high) canopy and 'tall-shrub' (or foliage from 2–6m) seem particularly important. Woods either without a tall-shrub layer or without an upper canopy all had far poorer songbird populations than woods where both layers were present. Within the latter group, woods with tall-shrub and an upper canopy, each over at least one third of the census plot, and with all possible combinations of canopy and shrub, especially if they also had even a small amount of 'high' canopy (over 20m), had richer songbird populations than woods lacking one or more of these features (Figure 5). Similarly, within 3 sites, where there were distinct, coherent, adjacent blocks with canopy and with or without a shrub layer, the songbird populations were always richer, especially in Number of species and BSD, in the areas with a tall-shrub layer.

At one site (Dinnet Oakwood, Site J), there was an opportunity for 'experimental' monitoring when a shrub layer of rhododendron, which formerly covered about one third of the census plot, was removed during 1980 and 1981. There are 3 distinct areas in the census plot, all of approximately equal size, *viz* oak with rhododendron up to 1980–81 but not thereafter, oak without rhododendron, and oak mixed with other broadleaf species. The latter 2 areas provide partial controls for assessing the effects of shrub removal in the rhododendron area.

Comparing successive biennial periods (1980–81, 1982–83, 1984–85) within each of these areas, there was a dramatic decrease in the richness of the songbird population in the former rhododendron area following removal of the shrub layer. The number of recorded territories fell by over 75%, the number of species was halved, and BSD fell from 2.43 to only 1.71, while of the 12 species originally present, only one was not reduced in numbers, and 7 became locally extinct. Only one new species came into the area after rhododendron removal, and that only in small numbers. The other 2 areas, in contrast, showed no significant changes at all.

All the above comparisons indicate the importance of a tall-shrub canopy combination. Is this another purely structural effect, or does it matter what types of tree and shrub are present? The data allowed comparisons between some combinations of tree and shrub



Key: Type A. Shrub present, but no upper canopy (>12m). Type B. Present, but no shrub layer; Type C. U/canopy and shrub present, but not in all combinations, or shrub cover less than ⅓ of area (but >15%); Type D. U/canopy and shrub present, in all combinations, and shrub cover is more than ⅓ of area.

Figure 5. Mean values of bird summary parameters in relation to 4 combinations of 'tall-shrub' and 'upper canopy' layers

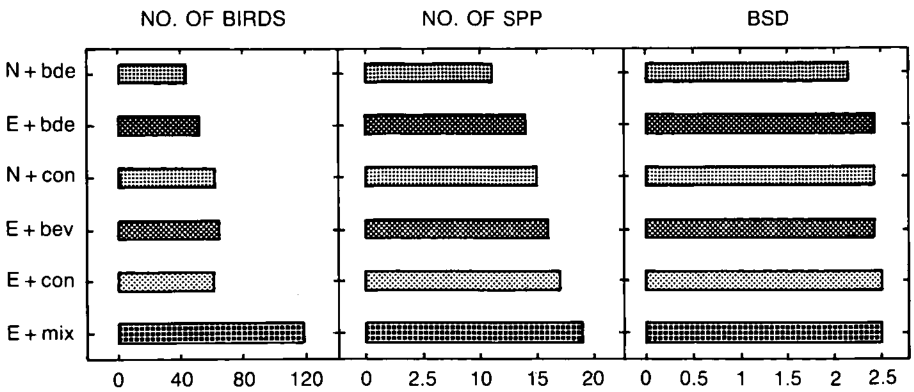


Figure 6. Effects of tree and shrub type on bird population parameters. con, conifer; bde, broadleaf deciduous; bev, broadleaf evergreen; mix, mixed conifer/broadleaf. Capitals indicate canopy tree type, lower case 'shrub' (including young trees in the 2–6m height class).

types (Figure 6). There are, of course, some combinations missing from this series, but the results do indicate that an evergreen shrub layer (conifer or broadleaf), or a mixture of types, is 'better' than a purely deciduous one. The data also suggest that the structural characteristics of a shrub/canopy combination are at least as important as their species composition.

Dead Wood

It is frequently said that some dead wood (stumps, logs, large branches or whole dead trees) is desirable for hole-nesting birds, and also to provide an invertebrate food supply for some species. This statement is likely to be especially true if it enables residence by woodpeckers, which will make holes to be used later by several other birds. Komdeur and Vestjens (1983) show strong positive correlations between numbers of woodpeckers and of other hole-nesting species. They also cite use of a single old woodpecker hole by a succession of 6 other species. The data suggest that, for great spotted woodpeckers, just 2–3 dead trees plus a few stumps or large fallen branches in 10ha is generally sufficient dead wood to enable the species to maintain territory in many kinds of wood, but that, on Deeside, green woodpeckers require additional resources, and were found in the study areas only where there was both a plentiful supply of ants (mainly *Formica rufa*) and either acorns or juniper berries as a winter food supplement. Beyond a small proportion of the stand, however, additional dead wood seems to have little effect on the songbird population, and small branches and twigs effectively none at all (other than some use of brash piles by wrens).

Implications for Forest Management

How can our results be translated into recommendations for forest management? Our studies to date have enabled us to establish a series of '*desiderata*', which give a guide to the sort of woodland structure for which a forester should aim in order to encourage a wide variety of songbirds. While they are not all entirely compatible with maximizing a commercial timber crop, most can be achieved at little cost.

1. The wood must be sufficiently established to contain at least one third mature or old (ie post-thicket) trees. Alternatively, there must be 'upper canopy' (>12m high) over at least one third of the area. A small amount of 'high canopy' (>20m) is especially beneficial.

2. There must be at least 4 distinct profile types in any area bigger than 10ha. Large-scale, even-age planting and felling should be avoided.

3. There should be a tall-shrub layer or equivalent, preferably evergreen of some kind, over about one quarter to one third of the total area. If possible, this layer should overlap with canopy over about one third to half of its area.

These three conditions are probably the most important, and all relate to structural features of the wood. The next three are much more tentative as to details, and we cannot, as yet, judge their relative importance.

4. Gaps in the canopy 15m wide or more should occupy about 20% of the total area. Most of these gaps should be between 0.1 and 0.3ha, but with 0.5ha or more of 1 or 2 in any 10ha area. Any gaps much larger than 1ha should probably include some 'shrubs'. A length: breadth ratio up to 5:1 is probably acceptable for widths up to 50m, especially if the gap contains shrub or understorey.

5. A mixture of broadleaf and coniferous trees should be present, in a ratio between 3:1 and 5:1 (in either direction), with the secondary type mainly in clumps or blocks about 15–20m wide and with some aggregations (of these clumps) totalling 1ha or more.

6. A small amount of dead wood (0.5% ground cover, or 2–3 dead trees plus a few stumps or fallen branches in 10–15ha) is useful to encourage woodpeckers and other hole-nesting birds.

The practicability of these *desiderata*, and suggested strategies for their attainment have been discussed elsewhere (French *et al.* 1986). The work so far has enabled us to refine (and in some cases redefine) current knowledge on the management of woods for songbirds, and to show that it is possible for plantation forests, if suitably managed, to be at least as rich in songbirds as many 'natural' woods. The present need is for more experimental studies, assessing the effects on songbird populations of varying habitat features by forest management under (as far as possible) controlled conditions, and it is hoped to expand ITE's efforts in this direction in future years, in collaboration with local foresters.

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D D French, D Jenkins and J W H Conroy

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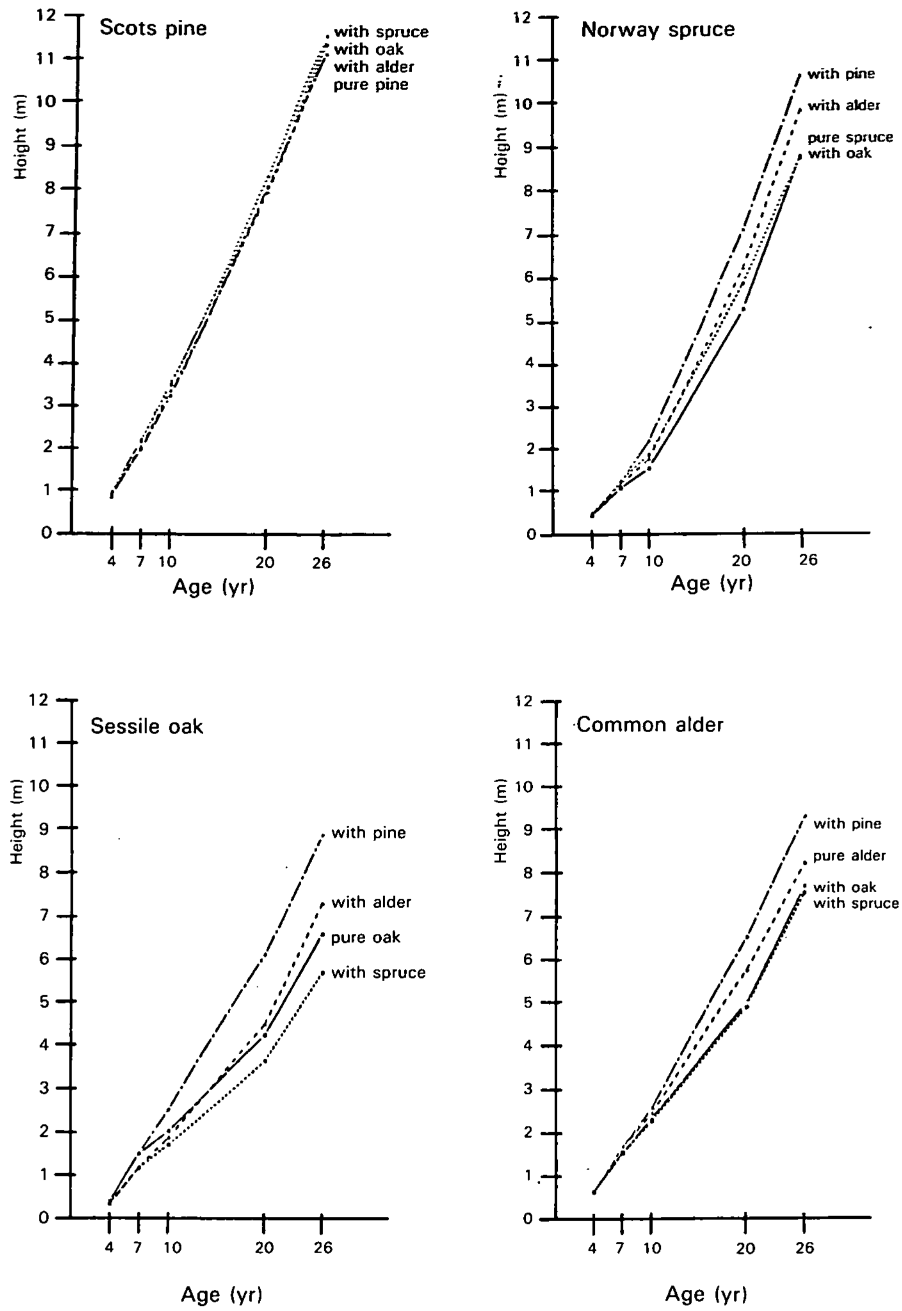

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Effects of Different Tree Species on Each Other: The Gisburn Mixture Experiment

There is currently much interest in the beneficial effects of mixtures in forestry: in particular, the improved growth of spruce when mixed with pine or larch on sites of low fertility (O'Carroll 1978; McIntosh & Tabbush 1981).

The experiment at Gisburn (Bowland Forest, NW England), jointly established in 1955 by the research branches of the Forestry Commission and the former Nature Conservancy (now ITE) (Holmes & Lines 1956), provides comparisons between a variety of single species and mixed stands of trees. The experiment includes Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*), oak (*Quercus petraea*) and alder (*Alnus glutinosa*), planted as 0.2ha plots in pure stands and all possible 2-species mixtures. The 10 treatments are replicated 3 times.

The heights of the trees, measured at intervals since planting, indicate several different types of mixture effects (Figure 7).

1. In mixtures, the pines have invariably improved the growth of the 3 other species (Lines 1982). This effect was apparent at an early stage, becoming statistically significant by age 10 or before. In contrast, the heights of the pines remained virtually unaffected by spruce, oak and alder. Hence, in all pine mixtures, plot average heights were greater than the mean heights of the 2 components when grown separately.

Judging from studies of spruce at Gisburn (Brown & Harrison 1983; Brown 1986), this type of mixture effect appears to reflect the improved availability of nitrogen and phosphorus, attributed to the accelerated 'turnover' of organic matter. As far as improved nitrogen nutrition at least is concerned, this suggestion is supported by observations in parallel studies done elsewhere, in which the growth of Sitka spruce (*Picea sitchensis*) was improved in mixtures with Lodgepole pine (*Pinus contorta*) or larch (*Larix* spp.) (O'Carroll 1978; McIntosh & Tabbush 1981).

2. Alder in mixtures has improved the growth of spruce and oak, although, interestingly, the size of the effect attributable to alder was always less marked than that associated with pine; further, its appearance was delayed until nearly 20 years after planting. In contrast to the effects of pine, the stimulation of height growth of oak and spruce by alder has been at the expense of the alder's own growth. Overall, plot average heights were therefore virtually identical to the means of the heights of the 2 component species when grown in pure stands: the improvements in spruce or oak were largely balanced by decreased growth of alder. These effects may be explained largely on the basis of differences in competitive ability, although, as suggested later, they may also reflect the effects of inhibitory substances produced by oak and spruce.

3. In addition to decreasing the growth of alder, spruce and oak tend to decrease each other's growth. As a result, plot average heights of spruce/oak mixtures were less than the means for the 2 components when grown separately. This negative effect may reflect the production of secondary plant compounds, such as polyphenols, which may inhibit microbial activity, and hence lessen nutrient release. A preliminary *in vitro* investigation of microbial inhibition by water-soluble materials from spruce foliage and fresh oak leaf litter supports this suggestion.

It is evident from the Gisburn replicated experiment that trees can influence each other in several ways. In planning future mixed forest plantations, the possible occurrence of different types of interactions, including negative effects, should be borne in mind.

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Reconciling Conservation and Amenity with Production Forestry

The United Kingdom is the second largest timber importer in the world, meeting only 9% of its current demand from trees grown in the UK. The shortfall is imported at a cost of £4,000 million per annum (Forestry Commission 1985). For the future, UK consumption is forecast to increase 50% above the current level by the year 2000, with similar increases envisaged for the other countries of the Commission of European Communities (CEC), all of which are timber importers (CAS 1980).

With timber demands elsewhere in the world also increasing inexorably (CAS 1980), it is not surprising that there have been repeated calls for increasing the afforested area of Britain (Forestry Commission 1977; CAS 1980). The arguments have been strengthened by recent, and proposed, changes in the CEC Common Agricultural Policy, aimed at reducing surpluses of agricultural products in the Communities. These changes in support for agricultural commodities are likely to lead to the release of land from agriculture, with the possibility that some will be afforested, or converted to agro-forestry.

These developments and the fact that much of the existing forest estate is approaching the end of its first rotation have encouraged policy-makers to reconsider their attitudes, in principle and detail, to conventional forestry practices and policies. Coincidentally, increasing awareness and concern among statutory and non-governmental bodies responsible for (i) water quality (Jack 1980; Stretton 1984) and (ii) wildlife conservation (Ratcliffe 1977; Nature Conservancy Council 1984; Prestt 1985) have found expression in the 1985 amendment to the 1967 Forestry Act. This amendment enhances the Forestry Commission's role in conserving the natural beauty, wildlife value and general amenity of the countryside. Increased planting and promotion of broadleaves is a major feature of the revised legislation.

Clearly, increased afforestation on a large scale will only occur if objectors can be convinced that the environmental effects are fully understood and that damaging influences can, and will, be kept to acceptable levels. Assurances of this sort cannot be given unless sound ecological data, detailing the multiple interactions, are available.

It is the Institute's intention to equip itself, through research and in co-operation with other appropriate bodies, to provide sound advice on the design and management of new and existing plantations, so as to retain or increase specific conservation or amenity interests. It is well understood that actions favouring wildlife conservation may also benefit actual, or potential, pests of (i) trees and (ii) surrounding agricultural enterprises (foxes, pigeons); they are also likely to increase the nuisance value of biting insects, so deterring recreation.

In order to restructure the Institute's woodland research so as to meet the requirements of such a policy, it was thought that a review of conservation and amenity in plantation forests was needed. It would detail the current state of national and international knowledge, highlight deficiencies that need to be rectified, and ascribe priorities for research: opportunities for establishing joint research programmes should be grasped. In undertaking such a review, it was decided to canvass

How can large-scale forests such as this be managed so as to maximize their nature conservation and amenity interest? ITE research on their basic ecology is providing some of the answers.

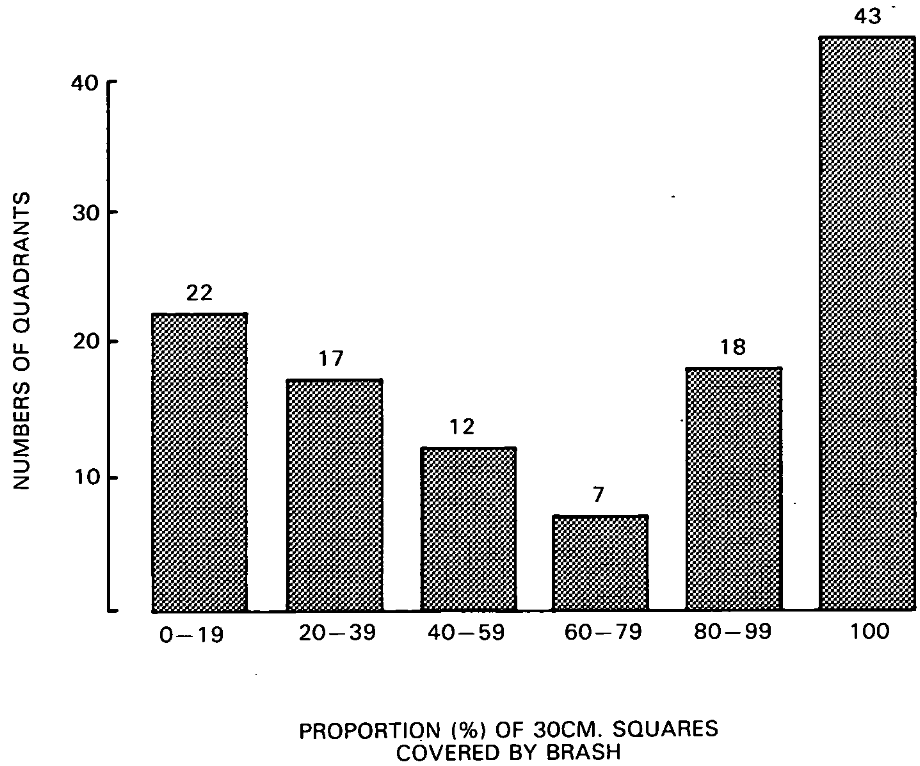

Figure 8. Frequency of brash-cover classes in 30cm squares after traditional harvesting of Sitka spruce.

the views of a range of organizations. Accordingly, discussions have been held with staff of universities, Forestry Commission, the private forestry sector, Ministry of Agriculture, Fisheries and Food, Nature Conservancy Council, Countryside Commission, and the Royal Society for the Protection of Birds. It is intended to publish the review.

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Establishment and Growth of Vegetation in a Newly Cleared Upland Forest

When Sitka spruce is felled, the sources of regenerating ground vegetation are various. A few plants may be present as established individuals, notably mosses and ferns. Grasses are often present along racks remaining after the extraction of thinnings. Many other kinds of plant are present in the soil, but only as viable long-dormant seed, notably heather (*Calluna vulgaris*), sedges (*Carex* spp.), foxglove (*Digitalis purpurea*) and rushes (*Juncus* spp.) (Hill & Stevens 1981). Plants with wind-borne seeds, such as birch (*Betula* spp.), willow herb (*Chamaenerion angustifolium*) and Sitka spruce (*Picea sitchensis*) are often present as seeds on the forest floor before clear-felling, but can also invade bare ground after trees have been felled.

Although the seed sources of plants composing the ground vegetation are now well known, we still have relatively little information on rates of regrowth of plant cover, and the speed at which individual plants can shed seed to recolonize bare areas. In order to obtain more information on these processes, a series of 16 permanent plots was arranged in Beddgelert Forest, north Wales. Eight of the plots were located on ground where trees were harvested traditionally with brash being left on site; the other 8 were located on ground that was whole-tree harvested, ie where trees were felled and then removed, together with their branches and tops. This arrangement enabled comparisons to be made of the development of ground vegetation, following tree removal, on brash-covered and brash-free ground. Each plot of size 10m x 10m encompassed 20 quadrats in each 30cm square.

The ground is not usually completely covered by brash when traditional methods of tree harvesting are used. One of the 16

Table 2. Effects of whole-tree harvesting on emergence and survival of seedlings (numbers m^{-2}) in the first year after clear-felling in Beddgelert Forest.

Species	Traditional harvesting				Whole-tree harvesting			
		Pre-felling	Post-felling			Pre-felling	Post-felling	
	Plants	Seeds	Births	Deaths	Plants	Seeds	Births	Deaths
Agrostis spp.	–	337	1	–	.05	190	2	–
Calluna vulgaris	–	–	–	–	–	–	2	–
Chamaenerion ang.	–	43	–	–	–	80	–	–
Carex binervis	.01	–	–	–	.01	–	7	4
Deschampsia caesp.	.01	16	1	–	.08	3	1	–
D. flexuosa	.03	–	1	–	.03	–	1	1
Digitalis purpurea	1.50	6151	4	2	.03	447	2	1
Galium saxatile	.01	1662	–	–	.01	340	2	1
Juncus bulbosus	–	–	–	–	–	–	2	–
J. effusus	–	13006	3	–	–	9538	16	10
Picea sitchensis	1.11	9	4	1	1.94	–	18	7
Total	2.67	21224	13	3	2.15	10598	53	24

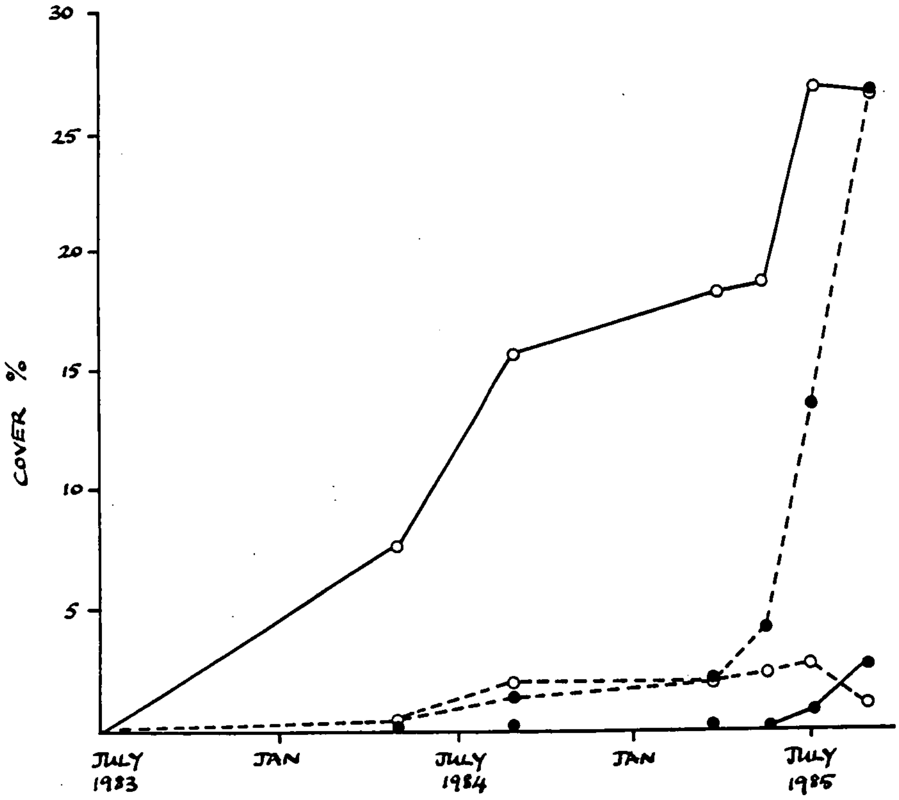

Figure 9. Cover of wavy hair-grass (*Deschampsia flexuosa*) (●) and sedge (*Carex binervis*) (○) on contrasting whole-tree harvested plots (4/11, - - -; 4/16 ——) during the first 2 years after clear-felling in July 1983.

study plots was damaged by wind, which uprooted most of the trees before scheduled clear-felling. This plot was only 31% covered by brash after the windthrown trees had been tidied up and fallen stems removed. On plots that were not windthrown, normal harvesting resulted in about 62% of the ground being covered with brash: of the 30cm square quadrats within the larger plots, 33% were completely covered by brash, 33% were less than 40% covered, while the remainder had 40–95% cover (Figure 8).

In the absence of previous windthrow, and before felling, there was very little ground vegetation. It consisted chiefly of the fern *Dryopteris dilatata*, with 3.5 individuals m^{-2}, feather-mosses of the genera *Hypnum* and *Plagiothecium*, Sitka spruce seedlings and, very locally, foxgloves (Table 2). However, the spruce seedlings and foxgloves rarely persisted for more than a few weeks until the dominant trees were felled. Those found after felling mostly developed from seeds that germinated after clear-felling – they were new recruits.

Initial germination

In the first season after clear-felling, germinating seeds were mostly sedges and rushes, whose seeds have a long dormancy. However, Sitka spruce (a short-lived species) was also well represented. Its seeds, which are shed in winter, must have entered the site after clear-felling, from standing trees nearby. Few seedlings of any species died. Deaths were mainly associated with frost-heave in winter and surface drought in summer. Numbers of seedlings in the traditionally harvested plots were substantially less than in the whole-tree harvested plots, the difference being roughly in proportion to the amount of bare ground covered by brash. Following clear-felling, appreciable amounts of brash were redistributed by wind. In some of the traditionally harvested plots, grazing by voles was severe. However, vole damage was not a significant cause of death in the 320 quadrats being observed.

Although most of the colonizing seedlings were of local origin, some were derived from seeds brought to the site over relatively long distances by wind.

The chief vascular plant invader was sheep's fescue (*Festuca ovina*), which was absent before clear-felling; its seeds do not remain viable in buried seed banks. In the season after clear-felling, plants of fescue established themselves on the whole-tree harvested plots at a density of 0.02 individuals m^{-2}. Likewise, pieces of moss, of non-local origin, were blown on to the plots. Chief among these were *Pleurozium schreberi* and *Rhytidiadelphus squarrosus*, which, along with sheep's fescue, were abundant on the sheepwalk adjoining the forest, but absent under standing trees. On the other hand, colonies of the large moss *Polytrichum formosum*, which began to spread extensively after clear-felling, could invariably be traced to colonies that had existed on the site before clear-felling.

Effects of initial composition

From what is already known of the establishment and growth of plants invading areas of forest that have been cleared, it seems unlikely that those of non-local origin will play more than a minor role in the assemblages of vegetation occurring before the canopies of succeeding crops close. Sheep's fescue is ecologically similar to wavy hair-grass (*Deschampsia flexuosa*), which was present in small quantity on the site before clear-felling, and which regenerated abundantly. In the sort of grassland that would have occupied the site before planting, sheep's fescue and matgrass (*Nardus stricta*) are dominant but, if grazing pressure is removed, as was the case, wavy hair-grass tends to become dominant.

There is a greater degree of uncertainty about the balance that will be maintained between species already present on the site. In the early stages, much depends on initial site condition. For example, two 10 m square plots, which were both whole-tree harvested, on similar soil, and separated by only 40 m, behaved totally differently (Figure 9). Plot 4/11 was close to the forest edge and had a small pre-existing population of wavy hair-grass, about 5 individuals m^{-2}. In the first summer, the grass shed abundant seed, which germinated during the subsequent autumn and winter, to give about 300 seedlings m^{-2} the following April. The seedlings were patchy, and there were some mortalities during the summer. Nevertheless, the cover attributed to wavy hair-grass exceeded 25% at the end of the second summer.

By contrast, the sedge *Carex binervis*, which also had a density of $5m^{-2}$ at the beginning, decreased in density to $1m^{-2}$ by the end of the second season. On the nearby plot 4/16, however, the sedge germinated abundantly from buried viable seed, achieving a density of about $20m^{-2}$ after the first

Table 3 Butterflies recorded on a Butterfly Monitoring Scheme transect at Picket Wood, Wiltshire in 1983 The recording weeks are from 1 April to 29 September The bracketted figures in week 21 are estimates The index values are the sum of the mean weekly counts I, II refer to generations of butterflies, S, A refer to spring and autumn flights of species which overwinter as adults * indicates an annual index value given to species with more than one generation in the year, but with the generations not discrete Picket Wood is a young conifer plantation on an ancient woodland site (Recorder M Fuller)

Butterfly monitoring scheme

Index value by weeks

Year 1984 Site 102 Picket Wood

Number of transects		1	1	2	2	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	0	1	1	1	1	0
			April				May					June				July				August				September			
Week number		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
Species	Annual index																										
119 Essx skipper	362	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	3	1	●	●	●		●	●	●	●	
120 Sml skipper		●	●	●	●	●	●	●	●	●	●	●	●	●	26	59	96	88	33	33	15	(8)	●	●	●	●	
88 Lge skipper	56	●	●	●	●	●	●	●	●	●	●	7	13	22	10	2	1	●	1	●	●		●	●	●	●	
46 Dngy skipper	18	●	●	●	●	●	1	●	4	6	4	3	●	●	●	●	●	●	●	●	●		●	●	●	●	
110 Griz skipper	27	●	●	●	●	5	3	●	3	5	5	5	1	●	●	●	●	●	●	●	●		●	●	●	●	
34 Cloud yellow	1*	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●		●	●	1	●	
54 Brimstone	526 A4	5	10	3	2	2	2	1	1	●	●	●	●	●	●	●	●	1	2	●	●		●	●	1	●	
98 Large white	I4 II7	●	●	●	●	●	●	●	●	●	2	1	●	1	●	1	●	2	●	●	1	(1)	●	1	1	●	
100 Small white	I10 I33	●	●	●	●	2	3	●	●	●	3	1	●	●	1	1	2	4	5	4	5	(4)	2	2	2	2	
99 Grn-vnd whte	I13 I23	●	●	●	1	●	4	1	2	●	1	2	1	●	1	●	2	4	3	2	5	(4)	2	1	●	●	
4 Orange tip	4	●	●	●	1	1	2	●	●	●	●	●	●	●	●	●	●	●	●	●	●		●	●	●	●	
23 Grn hairstrk	1	●	●	●	●	●	●	●	●	●	●	●	1	●	●	●	●	●	●	●	●		●	●	●	●	
116 Purp hairstrk	8	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	1	2	2	●	2	(1)	●	●	●	●	
68 Small copper	I1 II+III41	●	●	●	●	●	●	●	●	1	●	●	●	●	●	●	●	5	4	6	7	(5)	3	3	4	4	
20 Brown argus	I1 II32	●	●	●	●	●	●	●	●	●	●	●	●	1	●	●	●	5	3	8	6	(5)	3	1	1	●	
106 Common blue	I31 II185	●	●	●	●	●	●	●	●	●	1	7	13	8	2	●	●	2	19	41	40	(32)	23	22	6	●	
71 Chlkhill blue	1	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	1	●		●	●	●	●	
27 Holly blue	I1 II1	●	●	●	1	●	●	●	●	●	●	●	●	●	●	●	●	1	●	●	●		●	●	●	●	
56 Du bgdy frit	27	●	●	●	●	●	●	5	7	4	7	4	●	●	●	●	●	●	●	●	●		●	●	●	●	
64 Whte admiral	18	●	●	●	●	●	●	●	●	●	●	●	●	●	5	6	3	1	1	2	●		●	●	●	●	
122 Red admiral	3*	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	1	●	●	●		●	1	1	●	
2 Small tort	240*	●	2	1	●	●	●	●	●	●	●	●	3	58	62	42	9	5	7	18	15	(10)	4	2	●	2	
84 Peacock	530 A126	1	4	7	3	4	4	3	3	●	1	●	●	●	●	●	4	49	46	12	8	(4)	●	1	1	1	
104 Comma	15*	●	1	1	1	●	1	●	●	●	●	●	●	●	●	●	1	●	●	●	●	(1)	1	1	3	4	
18 Sml p b frit	26	●	●	●	●	●	●	●	●	3	4	6	5	6	●	2	●	●	●	●	●		●	●	●	●	
14 Prl brd frit	38	●	●	●	●	1	9	8	10	2	7	2	●	●	●	●	●	●	●	●	●		●	●	●	●	
12 Dk grn frit	2	●	●	●	●	●	●	●	●	●	●	●	●	●	●	2	●	●	●	●	●		●	●	●	●	
17 Slv – wsh fr	37	●	●	●	●	●	●	●	●	●	●	●	●	2	4	5	4	5	7	4	4		●	●	●	●	
50 Marsh frit	2	●	●	●	●	●	●	●	1	●	●	1	●	●	●	●	●	●	●	●	●		●	●	●	●	
93 Spckled wood	94*	●	●	●	1	1	●	●	1	1	1	2	2	5	4	●	●	●	3	4	4		18	15	9	12	
94 Wall	I0 II2	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	1		●	●	●	●	
78 Marbled whte	177	●	●	●	●	●	●	●	●	●	●	●	●	●	25	39	62	42	6	3	●		●	●	●	●	
76 Hedge brown	748	●	●	●	●	●	●	●	●	●	●	●	●	●	●	1	31	79	138	133	186	(118)	50	11	1	●	
75 Meadow brown	186	●	●	●	●	●	●	●	●	●	●	●	3	28	52	22	33	26	14	2	4	(23)	●	●	●	●	
29 Small heath	10*	●	●	●	●	●	●	●	●	●	●	●	2	3	1	●	1	1	●	●	●	(1)	1	●	●	●	
8 Ringlet	168	●	●	●	●	●	●	●	●	●	●	●	●	1	19	27	70	38	7	4	1	(1)	●	●	●	●	

season, which increased to $30 m^{-2}$ at the end of the second season Its cover had reached 25% when that of wavy hair-grass was still only 3%

It is not clear whether this initial difference will persist The sedge seeded abundantly in 1985, and may increase further from seed shed in that season, but it does not have the potential for an explosive increase in numbers, such as that shown by wavy hair-grass on plot 4/11 Furthermore, the sedge is more susceptible to winter dieback and vole damage Thus, initial differences between plots may be much reduced before the canopy of the second crop closes in about the year 2000

M O Hill, D F Evans and Shirley A Bell

Reference

Hill, M O & Stevens, P A 1981 The density of viable seed in soils of forest plantations in upland Britain *J Ecol*, **69**, 693–709

Management of Conifer Plantations for Invertebrates, Especially Butterflies

(This work was supported by Nature Conservance Council funds)

In lowland Britain, many primary woodland sites have been planted with conifers by the Forestry Commission or by private landowners There has been concern that the floras and faunas associated with some of these primary woods may, as a result, be damaged However, it should be understood that many butterfly species, which used to thrive in deciduous woods when coppiced, have disappeared since this form of management was terminated, even when conifers have not been introduced Conditions in such unmanaged woods gradually become too shaded for most butterflies Paradoxically, clearance and replanting with conifers has, for a time at least, provided ideal conditions for species such as the pearl-bordered fritillary, the Duke of Burgundy and the wood white which 'like' cleared areas within woodlands Today, many of the best sites for these butterflies are young conifer plantations, Pichet Wood in Wiltshire is such an example (Table 3) Now, in their turn, some of the older conifer plantations are becoming more shaded and their populations of butterflies are decreasing

The present study aims to provide guidelines for modifying the management of conifer plantations in an attempt to maintain their butterfly faunas Inevitably advice, mainly relying on the management of ride edges, will be based on limited data and experience In the long term, the effects of conifers on ground floras and litter accumulation, in the large majority of woodlands, may be such that the modification of ride edges will not be sufficient to ensure the survival of butterflies It is therefore essential to establish a number of sites which will be managed, following recommended prescriptions, so as to conserve butterflies

The butterflies of a number of conifer plantations have already been monitored for several years, as part of the ITE Butterfly Monitoring Scheme Other sites have been monitored using the same method of transect counts, but independently of the national scheme At the monitored sites data on the distribution and abundance of butterflies, along a transect, are available In the first year of this study, simple records of factors such as width of rides, shade, and abundance of some important plant species were made in the monitored woods These data are being used in an attempt to quantify some of the characteristics which are believed to provide good conditions for the woodland butterflies.

The information obtained in the first year will help to form a basis for management guidelines, and also for recommendations for further monitoring. For some species, there is likely to be a close agreement between the distribution of adults and their breeding areas, and for these, monitoring of adult numbers will be sufficient; for other species, the agreement may be poor, and alternative methods for monitoring breeding areas will be needed. In the second year of the study some of the 1st year study sites will be revisited to examine relationships between the distribution of adult butterflies and their breeding areas.

As an 'antidote' to exclusive reliance on butterflies, as representatives of a second group of invertebrates, the Heteroptera, were sometimes sampled in the first year. Heteroptera were selected because they form a convenient sized group, with a wide range of habitat requirements. In the coming season, insects associated with deciduous scrub, which frequently occurs along the ride edges, will be included. The aim of these additional studies is not to attempt to determine, in detail, the habitat requirements of these species but to provide some indication as to whether recommendations made for butterfly conversation will be beneficial or detrimental to other elements of the fauna.

Marney L Hall, N Greatorex-Davies and E Pollard

Freshwater Ecology

Effects of Low pH on Egg and Tadpole Development in the Common Frog

In the light of accumulating evidence that some fresh waters in the UK have undergone recent acidification similar to that reported from Scandinavia and North America, ongoing research into the life history of the common frog *Rana temporaria* has been expanded to investigate the effects on this species of low pH, and associated conditions such as high levels of dissolved aluminium. Field work began in 1985 in the Cairnsmore of Fleet region of Galloway, in South-west Scotland, where diatom records indicate a substantial and rapid increase in lake acidity since the late-19th century (Flower & Battarbee 1983), and where several lochs are now fishless (Harriman *et al.* 1986). In 1985, frogs in the study area spawned over a period of 5–6 weeks, ranging from late February, on open moorland and in lower-altitude forest pools, to early April higher in the forest and at Loch Fleet. Heavy frost in March caused some mortality in the early spawn in exposed sites, and these sites were excluded from the study. Levels of pH, sodium, potassium, magnesium, calcium and aluminium were measured on 2 occasions at most of the 20 breeding sites in or near the forest. The lowest recorded pH where frogs spawned was pH 4.0 and the highest pH 7.0, although readings as low as pH 3.3 were taken in water draining from the forest after heavy rain. Levels of dissolved inorganic monomeric aluminium at spawning sites varied from $0\mu g\ l^{-1}$ in a peaty pool to $740\mu g\ l^{-1}$ in a clearwater lochan. Egg mortality varied between sites, from less than 5% in a circumneutral pool, to 100% in the lowest-pH pools. Freshly laid clumps of spawn were bisected and transplanted into spawning sites where egg mortality was more or less apparent – patterns of mortality among transplanted eggs corresponded to that among eggs laid at those sites, supporting the idea that some aspect of water quality was responsible for the mortality.

Laboratory experiments tested the effect of pH on *in vitro* fertilization of eggs and egg survival, and the effects of water pH and ionic strength on hatching. Exposing eggs or sperms to low-pH water for short periods, prior to the mixing of eggs and sperm, did not significantly reduce the percentage of eggs fertilized, probably because the buffering capacity of the milt provided a micro-environment in which fertilization could take place. The levels of pH which caused egg mortality in the laboratory were similar to those measured in the field, suggesting that the mortality observed in the field could be accounted for by prevailing levels of pH alone. Moreover, the symptoms accompanying egg mortality at low pH in the laboratory were the same as those observed in the field, ie disruption of the yolk or embryo, and the appearance of a semi-opaque zone in the surrounding jelly. Lowering the pH reduced egg survival and increased the incidence of deformities among hatchlings. Hatching was delayed, or prevented, at low pH and low ionic strength.

Further experiments examined the effects on tadpoles of chronic exposure to low pH and high levels of aluminium (Cummins 1986). Although tadpoles survived at levels of pH similar to those measured at Cairnsmore of Fleet, decreasing pH reduced growth rate and size at metamorphosis, and increased the time taken to reach metamorphosis, right across the range of pH tested. Growth and development rates are recognized components of tadpole fitness, so decreasing pH is certain to be detrimental to individual survival, or reproductive success. Tadpoles exposed to levels of aluminium similar to the highest level recorded at Cairnsmore of Fleet suffered reduced growth and delayed metamorphosis. There was also some mortality at metamorphosis among aluminium-treated tadpoles, but none among control tadpoles. The effects of lower levels of aluminium have yet to be tested.

The responses of common frog eggs to low pH are qualitatively similar to those of other amphibian species (see Pierce 1985; Tome & Pough, 1982), and even though *R. temporaria* is among the less sensitive species, it is clear, even from these preliminary results, that acid conditions can and do restrict its breeding success in the UK. Even in waters which are not sufficiently acid to prevent hatching, tadpole performance can be impaired by acid conditions. Of course, acid conditions occur naturally and may constitute natural barriers to populations in the field, but acidification of areas currently supporting frog populations could result in further restriction of suitable habitat. In some respects, the types of habitat most at risk – typically, upland areas with poor soils, high rainfall and, perhaps, recent afforestation – are those which have provided a refuge for the common frog during the time when many lowland habitats have been lost to intensive agriculture. It is also important to realize that hitherto suitable habitat could become unsuitable without necessarily being permanently acidified. Frogs typically breed in small, temporary pools, which often rely heavily on surface runoff, that has had relatively little contact with buffering agents in the soil. Pulses of low pH lasting a few hours and caused by heavy rain or snow-melt can kill frog eggs, and any increase in the frequency, duration or severity of such acid events could reduce breeding success, and hence population size.

C P Cummins

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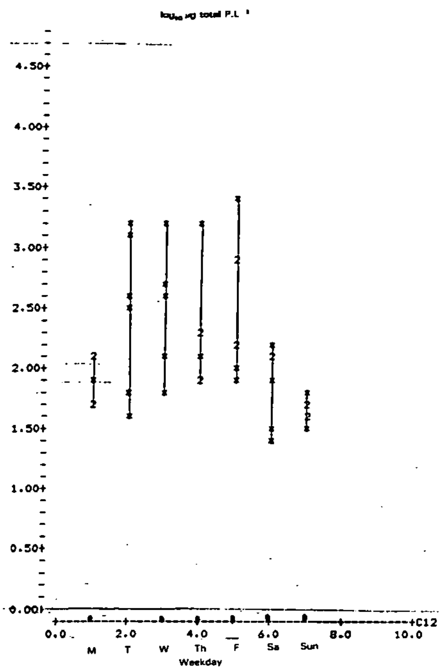

Figure 10. Total P concentrations ($\mu g\ l^{-1}$, plotted on $\log_{10}$ scale) on different days of the week from January to October 1985, in a major inflow to Loch Leven, which receives industrial effluent.

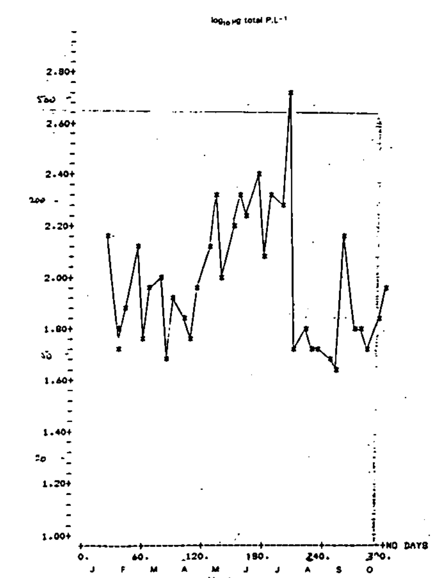

Figure 11. A comparison between total P concentrations ($\mu g\ l^{-1}$ plotted on $\log_{10}$ scale) above (Nc) and below (Na) an outfall of treated sewage on a major feeder stream to Loch Leven, January–October 1985.

Amount of Phosphorus Entering Loch Leven

Intensive ecological surveillance of Loch Leven, since the late 1960s, indicates that phosphorus (P) is of special importance in the eutrophication of the loch and to the growth of its plankton (Bailey-Watts 1979, 1981; Bailey-Watts *et al.* 1983). Recent interest in P levels has arisen because of a continuing deterioration in water quality of some of the inflows and of the loch itself. Concern over this trend has been expressed by official bodies, including the Nature Conservancy Council (NCC), which manages the loch as a National Nature Reserve, and the Forth River Purification Board (FRPB), which is responsible for water quality in the catchment of the loch, and by downstream industrial abstractors of water from the loch.

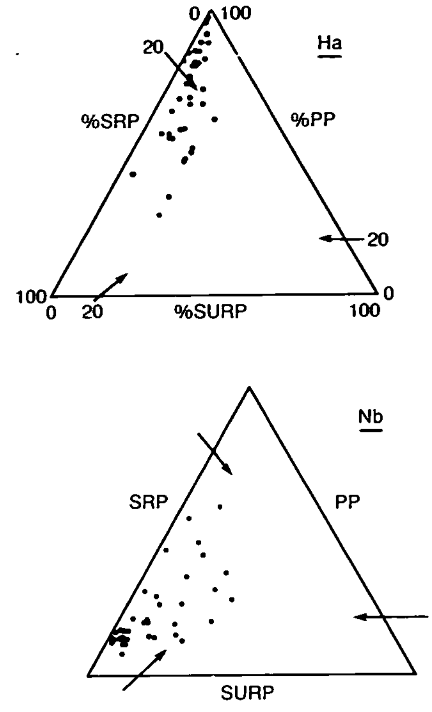

Figure 12. Triangular plots of contrasting proportions of soluble reactive P (SRP), soluble unreactive P (SURP), and particulate P (PP), in a small silty stream (Ha) and a major river affected by sewage effluent (Nb) flowing into Loch Leven.

As summarized by Bailey-Watts and Kirika (1984), the interest led to a desk study commissioned by NCC to assess (i) the likely current (then 1982–83) loading of P to the loch, (ii) the various contributions to the total input, and (iii) implications for their control. The study took account of analytical results from an earlier loading assessment made by the Department of Agriculture and Fisheries for Scotland (DAFS) (Holden 1976; Holden & Caines 1974, unpublished data to 1978), and information on nutrient content, obtained by ITE between 1980 and 1983. The exercise concluded that, whilst point sources continued to contribute the major part of the total loading (as found by the earlier study), new measurements were necessary to establish the actual quantities currently involved. First, the sewer-served population in the loch catchment had increased, giving a higher input from sewage treatment works. Second, recent analyses of a major feeder stream receiving P-rich industrial effluent indicated that the input from this source had increased considerably since the late 1970s. Third, P inputs in rain falling directly on the loch surface were likely to be lower than originally thought. Fourth, more data were needed to estimate the more diffuse sources of P, such as in runoff from agricultural land and in wildfowl faeces. Each of these aspects is now being studied in a new project funded by DAFS, NCC, the Scottish Development Department and the Tayside Regional Council (with a grant from the Commission of European Communities). The major part of the work involves sampling all inflows to the loch, as well as the loch itself, at 8-day intervals throughout a calendar year (Bailey-Watts & Kirika 1987). An 8-day schedule was adopted because it was suspected that some water courses receive effluent whose chemistry varies with day of the week. This suspicion is justified by results from a major inflow receiving industrial P waste (Figure 10); concentrations of P were considerably higher on Tuesdays to Fridays than on other days, especially Sundays. The impact of effluent from sewage treatment works on P levels in another river was also considerable. Figure 11 shows that, despite dilution of effluent by the river, the concentrations downstream of the discharge were very much greater than 'background' levels upstream.

The above examples refer to total P, but our analyses also take account of the particulate and dissolved fractions. The proportions of particulate P, soluble reactive P, and soluble unreactive P vary seasonally within a stream and between different streams. Figure 12 contrasts a small stream (Ha), rich in particulates from road drainage, with a larger river (Nb), which is relatively richer in dissolved P from treated sewage.

Although P is the main focus of the study, water from the mouths of various streams was also analyzed for levels of nitrate and dissolved silica. The programme is integrated with FRPB work defining the height-discharge characteristics of the inflows, so that nutrient concentrations can be converted to loadings (ie the products of flow and concentration) by relating continuous and spot recordings of river heights to chemical concentrations. As well as the seasonal surveillance, a number of intensive 24-hour studies are being made to assess variations between night and day. Other sub-projects focus on external inputs of P in (i) rainwater, (ii) wildfowl faeces, and

(iii) selected agricultural areas, and on internal source P, namely that derived by recycling of the nutrient from the sediments of the loch itself.

A E Bailey-Watts and A Kirika

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Rehabilitation of Disturbed Ecosystems

Creating Attractive Grasslands

(This work is supported by Nature Conservancy Council funds)

Much of the stimulus for research on the creation of plant communities has come from the need to restore or revegetate areas of derelict land left by mining and quarrying industries in the developed countries, notably in Britain, America and Australia. A recent review (Bradshaw & Chadwick 1980) gives an account of progress in this particular area of research, where special problems, such as extremes of temperature, acidity and alkalinity, high salinity and metal toxicities, or shortage of water and nutrients, have been encountered. Much less attention has been given to establishing grasslands which contain a range of colourful forbs on land where extremes of soil and water conditions do not prevail.

It has been estimated by the Nature Conservancy Council (Anon 1984) that 95% of all lowland herb-rich grassland and about 80% of lowland chalk and limestone grasslands have been destroyed since 1949, largely by conversion to arable land. While the defence of the best remaining areas of grassland is clearly a primary objective of nature conservation, it is nonetheless now appreciated that grasslands and meadows created by sowing mixtures of grasses and dicotyledons may have an important role in conserving wildlife in the countryside as a whole.

Opportunities for creating attractive grasslands are widespread. They occur when new verges are made on motorways or trunk roads; in urban areas in new towns, such as Milton Keynes, Peterborough and Warrington; in newly created Country Parks; in the grounds of schools and colleges, where the functional use of grass may be combined with an educative role; on the banks and surrounds of public reservoirs and on newly made farm reservoirs; on farms and estates where the owners or tenants wish to create a more attractive environment and to encourage wildlife.

Methods Available for Establishing Attractive Grasslands

In theory, there are 5 ways in which grasslands can be established incorporating wild flowers and native grasses:

1. by natural colonization of bare soil from local or nearby seed sources;
2. by spreading top soil containing the seed of grassland species;
3. by transplanting turf from species-rich grassland which overlies areas that are to be destroyed by quarrying or road-making;
4. by sowing grass/herb mixtures into prepared seed beds;
5. by diversifying established swards, using either the slot-seeding technique, or inserting pot-grown plants with a bulb planter.

In practice, methods (1), (2) and (3) have a number of undesirable features which ensure that they are rarely used, or considered for use, except in special circumstances. Natural colonization depends on the ability of propagules to reach a site. As semi-natural habitats become increasingly fragmented and dispersed, the probability of seed arriving at a site becomes low, even for those species with an effective means of dispersal, seeds of many grassland species have no dispersal mechanism and are shed within one metre of the mother plants, so the probability of their reaching sites miles away is very small. Natural colonization is a slow process, and the engineer and landscape architect often require a vegetation cover quickly. Spreading top soil in the hope that it contains the seeds of grassland species is not acceptable, as experience has shown that the seed bank consists mostly of weeds of arable land, particularly members of the Polygonaceae, Cruciferae and Compositae. Furthermore, top soil is a variable commodity, and it is extremely difficult to determine or predict the type of vegetation that will result when it is spread and not seeded.

Turf transplants, obtained by stripping the turf from areas before they are quarried, have been used successfully to revegetate restored land after quarrying (Gilbert & Wathern 1980). This method does not increase the area of grassland, but does save a valuable resource and is to be encouraged, although the area of land involved is very small.

The principal means of establishing grass/wild flower mixtures is either by sowing seed mixtures into prepared seed beds, or by diversifying existing grasslands. Some results from experiments to investigate these methods in more detail are discussed below.

Establishment of Grass/Herb Mixtures From Seed

The following are the main requirements for successful establishment from seed.

i) **Careful selection of species suitable for the ecological conditions of the site.** The mixtures suggested by Wells *et al.* (1981) for clay, chalk and alluvial soils provide a guide as to the most suitable species for those soil types. Criteria used in selecting species for inclusion in these mixtures are given in Table 4.

ii) **A weed-free seed bed.** It is essential that perennial weeds such as common couch (*Agropyron repens*), docks (*Rumex*, spp.) and common nettle (*Urtica dioica*) are killed before sowing by using a herbicide, such as glyphosate, according to the manufacturer's instructions.

Table 4. Some criteria used for selecting species for inclusion in wild flower seed mixtures

1. Ecologically suitable for particular soil/water conditions
2. Common grassland species
3. Not rare or locally distributed
4. Preferably perennial and long-lived
5. With colourful and attractive flowers
6. Attractive to insects as nectar or pollen sources
7. Not highly competitive or invasive
8. Seed germinates easily over a range of temperatures

iii) **Good seed bed preparation.** A fine seed bed, with a good tilth, free of stones, is required. It is a fallacy that wild flower seed mixtures can be sown successfully in rough seed beds. Soil compaction, especially on heavy clay soils, is a major problem on sites such as new road verges, and is to be avoided.

iv) **Careful management of the sown area, especially during the first year when annual weeds may be a problem on some sites.** It is difficult to give hard and fast rules regarding management as each site is different, but, generally, the newly sown area may require cutting at least 3 times during the first year, with the cut material being removed each time. The timing of the cuts will depend on the stage of growth of both the weed species and the sown species. The type of management given to the mixtures after the first year will depend on (i) the fertility of the site, (ii) the type of mixture sown, and (iii) the effect required by the manager. In general, the more fertile the site, the greater will be the requirement for management, and for this and other reasons, wild flower mixtures do best when sown on sites where the nutrients are low. As the mixtures currently in use are mostly composed of tall, or medium-tall, herbs and grasses, a hayfield type of management is often appropriate. At Monks Wood, mixtures in experiments are cut in the late July or early August, and again in late October. On both occasions, the cut material is removed and burnt or turned into hay. Using this management regime, attractive grasslands with flowers from late March to early August can be achieved; at Monks Wood, the succession of flowering begins with cowslips and daisies and the year ends with hardheads (*Centaurea* spp.) lady's bedstraw (*Galium verum*), dropwort (*Filipendula vulgaris*) and meadow crane's-bill (*Geranium pratense*). On large areas, a system of rotational management may be devised, whereby the appearance, structure, and floristic composition of the grassland is manipulated for particular objectives, such as wildlife conservation or game preservation.

v) **Using a nurse crop of Westerwolds rye-grass (*Lolium perenne*) to enhance establishment.** This crop is included in the grass/wild flower mixture at 3.0–4.5 g m^2, the higher rate being used on the more infertile sites. A nurse crop has several advantages; it germinates quickly and establishes a cover of green vegetation (the so-called greening effect) which engineers and architects like to see; it tends to suppress excessive annual weed growth; and it provides shelter for the slower germinating forbs. Providing Westerwolds is cut before it sheds seed, it behaves as an annual and disappears from the sward within 2 years, being replaced by the sown perennial grasses and forbs. Even when some seed is shed, it never forms a major part of the vegetation after 2 years, and disappears eventually.

Diversifying Established Swards
Considerable interest has arisen in the past 2–3 years in enriching existing, predominantly grass, swards with wild flowers. Interest has arisen in 2 main areas: (i) among those with large areas of grassland surrounding their residence or house, particularly some stately home-owners, and (ii) from certain local authorities with large areas of species-poor grassland. In both cases, destroying existing grassland with a herbicide and sowing seed into a prepared seed bed have not been options, the owner wishing to keep the existing grassland.

Slot-seeding
Slot-seeding has been developed in Britain by workers at the Weed Research Organization as a method for introducing grass and clover into existing swards (Squires *et al.* Elliot 1979). Essentially, it consists of spraying a band of herbicide (usually paraquat) to kill the sward, and drilling the desired species or mixtures into a slit cut into the ground within the band sprayed. The theory is that, in the absence of competition, the drilled seed will germinate, establish, and grow to a competitive size before the grass sward recovers and fills the sprayed area. As this technique may be used for introducing wild flower seeds into grassland, trials were laid down in October 1984, to test the effectiveness of the method. The preliminary results from one such trial are presented here.

Twelve species of dicotyledons (see Table 5) were drilled into 9 amenity grass species or mixtures (Table 6) sown 6 years previously, arranged in a randomized block design. A Stanhay precision drill, to which a spray unit had been attached, was used for drilling the seed. Drills were 50cm apart, 3 drills being made with one pass of the tractor. Each drill was band-sprayed (*c* 10cm wide) with paraquat (used at 5 litres ha^{-1} in 1361 litres of water) to kill the sward. Weighed quantities of seed were mixed with a 'filler' of barley meal in order to 'dilute' the seed and to enable it to be drilled accurately at low seed rates. The aim was to drill the small-seeded species at about 5 seed cm^{-1} and the large-seed species at 1 seed per cm. The actual amounts drilled varied from 3.2 to 7.7 seeds cm^{-1} for the small-seeded species and from 0.2 to 0.9 seed cm^{-1} for the larger-seeded species. Differences in the texture of the seed coat, in the shape of the seed and the jolting of the machine were the main causes of the various seed rates achieved. Plots were drilled on 17 October 1984. Some species, such as common bird's-foot trefoil (*Lotus corniculatus*), germinated within a week, but were killed off later in the year by a combination of low temperatures and waterlogged soils. Most species germinated in early spring.

Seedlings were counted in May 1985 in the central metre of every 3m row length to assess establishment. There were no differences in establishment related to the different swards into which the seed was sown, but there were significant differences (P = 0.001%) between species in establishment (Table 5). The most important points to note are that: (i) despite large differences in seed size, all 12 sown species established; (ii) establishment varied from 4.4% (bird's-foot trefoil) to 51.7% (meadow buttercup (*Ranunculus acris*)), with 6 species achieving over 20% establishment; (iii) some species, eg yellow rattle (*Rhinanthus minor*) and bird's-foot trefoil, flowered in the first year after sowing; and (iv) the effect of the band spray in reducing competition from the sward lasted for about 6 months, which appears to give species time to establish and to be able to compete with the older grassland. It will be interesting to see how the established plants respond to competition as the rows close in, or whether they prevent the grass from re-establishing.

Pot-grown Plants
Native plants can be raised from seed quite easily in peat or Jiffy pots, using conventional horticultural techniques (Wells 1983). In our experience, 4-month-old plants, with about 4 true leaves, are ideal-sized plants for inserting into existing grasslands using a bulb-planter. In an experiment at Monks Wood, 699 plants were inserted into a short, previously mown turf on 5–6 June 1984. The 14 species (Table 7) were distributed randomly in 70 rows, each row being 5m long × 1m wide. Planting density was 2 plants m^{-2}. The survival and state of the plants were recorded on 25 August 1984, and again in June 1985 (Table 7). Despite low rainfall in the 2 months after planting, all species except bulbous buttercup (*Ranunculus bulbosus*) had a survivorship of more than

Table 5. Seed rates and percentage establishment of 12 dicotyledon species sown 17 October 1984 at Monks Wood using the slot-seeding technique

Species	Seed rate (seeds cm^{-1})	% establishment
Oxeye daisy (*Leucanthemum vulgare*)	6.9	10.0
Common bird's-foot-trefoil (*Lotus corniculatus*) (native)	7.7	4.4
Common bird's-foot-trefoil (*Lotus corniculatus*) ('Leo')	6.8	7.2
Hoary plantain (*Plantago media*)	4.6	26.9
Cowslip (*Primula veris*)	5.1	48.1
Selfheal (*Prunella vulgaris*)	5.4	29.4
Meadow buttercup (*Ranunculus acris*)	3.3	51.7
Common knapweed (*Centaurea nigra*)	0.9	22.3
Greater knapweed (*Centaurea scabiosa*)	0.1	11.5
Field scabious (*Knautia arvenis*)	0.2	17.6
Salad burnet (*Poterium sanguisorba*)	0.5	19.8
Yellow rattle (*Rhinanthus minor*)	0.4	23.5
	SED	3.23

Table 6. The composition of 9 swards sown at Monks Wood on 5 September 1978 into which 12 forbs were drilled, using the slot-seeder, on 17 October 1984

1. Red fescue *Festuca rubra* ssp. *commutata* 'Cascade'
2. Red fescue *Festuca rubra* ssp. *commutata* 'Highlight'
3. Red fescue *Festuca rubra* ssp. *rubra* 'Rapid'
4. Red fescue *Festuca rubra* ssp. *rubra* 'Boreal'
5. Red fescue *Festuca rubra* ssp. *rubra* 'Dawson'
6. Red fescue *Festuca rubra* ssp. *rubra* 'Scaldis', 35%
   Red fescue *Festuca rubra* ssp. *rubra* 'Dawson', 15%
   Red fescue *Festuca rubra* ssp. *rubra* 'Ruby', 25%
   Smooth meadow-grass *Poa pratensis* 'Parade', 5%
   Smooth meadow-grass *Poa pratensis* 'Prato', 10%
   Common bent *Agrostis tenuis* 'Highland', 10%
7. Crested dog's tail *Cynosurus cristatus*
8. Red fescue *Festuca rubra* ssp. *commutata* 'Waldorf'
9. Common bent *Agrostis tenuis*, 40%
   Timothy *Phleum pratense* 'Eskimo', 40%
   Perennial rye-grass *Lolium perenne* 'Stadion'
   'Grandstand' 20%
   'Majestic'

Table 7. The percentage survival of 14 species inserted into permanent grassland as 4½-month-old pot-grown plants. Planted 5–6 June 1984, recorded 25–26 August 1984 and 17–20 June 1985

Species	Number of pots inserted	% survival Aug 1984	% survival June 1985
Kidney vetch (*Anthyllis vulneraria*)	42	95.2	4.6
Betony (*Betonica officinalis*)	41	97.6	92.5
Clustered bellflower (*Campanula glomerata*)	36	91.7	16.6
Common knapweed (*Centaurea nigra*)	51	100.0	82.7
Greater knapweed (*Centaurea scabiosa*)	51	100.0	65.3
Oxeye daisy (*Leucanthemum vulgare*)	45	100.0	80.4
Field scabious (*Knautia arvenis*)	43	97.7	84.1
Rough hawkbit (*Leontodon hispidus*)	50	100.0	52.0
Ragged-robin (*Lychnis flos-cuculi*)	52	96.2	84.6
Spiny restharrow (*Ononis spinosa*)	50	98.0	42.0
Meadow buttercup (*Ranunculus acris*)	51	94.1	58.8
Bulbous buttercup (*Ranunculus bulbosus*)	45	53.3	35.6
Hoary plantain (*Plantago media*)	55	98.2	74.1
Cowslip (*Primula veris*)	52	100.0	96.1
Unidentified species*	35	0	0
Total	699	90.0	60.8

*35 plants were recorded as missing, presumed dead, when recording took place in August, but, because of an error on the original planting plan, could not be identified to the species level

90%. The plots were mown in September, and again in late October.

Kidney vetch (*Anthyllis vulneraria*), a short-lived perennial, flowered in the year of planting, dying thereafter, the few plants that did not flower surviving until 1985. Some deaths occurred during the period September 1984–June 1985 in all species, the least vigorous species, clustered bellflower (*Campanula glomerata*) dying in competition with the taller grasses, and only 16.6% surviving until June 1985. The highest survivorship was shown by cowslip (*Primula veris*) (96.1%), which, like the other species, flowered in 1985.

Observations made on plants inserted into roadside banks at Basildon confirm that plants will flower the year after planting, and survivorship in a range of species appeared good. Although more expensive than other methods of creating diverse swards, pot-grown plants have the advantage of creating 'instant' colour, and this method will probably find a use where quick results are required.

Conclusions

It is now possible to create grassland habitats using native species with a variety of techniques; by direct seeding into arable land; by diversifying existing swards using the slot-seeder; or by inserting pot-grown plants with a bulb-planter. Using native species is not a cheap option – seed and plants are more expensive than conventional seed mixtures, and the same care must be given to seed bed preparation and sowing as is required for producing amenity swards. Best results are obtained when sown on thin, nutrient-impoverished soils, or even on to subsoil, so considerable savings can be made by not importing top soil and by not having to purchase fertilizers.

The use of wild flower mixtures in landscape themes is in its infancy in Britain, and much remains to be learnt concerning the choice of mixtures, the best time to sow, and, particularly, how best to manage the grassland in its early stages of development. Nevertheless, the results from experimental sowings made over the past 12 years, and from the increasing number of larger planting schemes, give rise to guarded optimism, and extend a challenge to researchers and amenity horticulturists in the future.

T C E Wells, A J Frost and Ruth Cox

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Creation of Butterfly Habitats on a Landfill Site

(This work is supported by Essex County Council funds)

Waste disposal poses 3 types of problems for local authorities: the choice of suitable sites, the technical aspects (including minimization of hazards and nuisance), and the restoration of the land for after-use. Essex County Council is investigating a form of intermediate, low-cost restoration for certain landfill sites as an alternative to restoration for agriculture. It involves the creation of attractive grassland areas using native flowers and grasses, with the eventual aim of providing a country park.

At the Martin's Farm site, near St Osyth, the emphasis is on the experimental development of conditions which will attract a wide range of butterflies. Little is known about the natural colonization of new habitats by flora and fauna, or the ability of vegetation to grow on heavily compacted landfill soils. The covering material varies from a clay loam to a sandy loam subsoil, with variable but generally low nutrient status. Filling and covering were nearly finished in 1982 when proposals were submitted to Essex County Council. These proposals involved the sowing of 2 mixtures of grasses and wild flowers based on those recommended by Wells *et al.* (1981), with modifications to suit the local conditions and to provide food plants for the larvae of certain butterflies (Table 8).

Two other treatments were included, a control to monitor natural colonization and succession, and a 'pioneer' treatment which would be cultivated every few years to maintain open ground conditions for early succession species. This last treatment also has mounds of limestone material to support additional nectar and larval food plants and to provide some shelter. The 4 treatments are replicated 4 times in a randomized block design, with plots about 60m x 50m. The rest of the site is used for other experiments on revegetating and managing such sites, and for the planting of tree belts (Figure 13).

A weekly butterfly recording programme was started in April 1983, using the methods of the national monitoring scheme (Hall 1981). The route traverses the whole site and passes through the middle of all the plots. The 'tall' and 'short' grassland mixtures were sown in September 1983, after recording the original condition of all the plots. No fertilizer or nurse crop was used. Establishment of the sown vegetation and natural colonization had been recorded annually, by random quadrats in June, and fixed quadrats in July.

Twenty-nine of the 31 sown grasses and wild flowers were recorded in 1985, of which 14 species flowered (Table 8). In addition, a very rich natural vegetation had also established itself in the experimental plots, with 92 species

Martins Farm: Leucanthemum

including many small, annual species exploiting the open conditions. The vegetation cover has varied considerably, partly because of natural spread from the older southern end of the site to the more recently completed northern end, and partly because of the cultivation in August 1983 on all but the control plots. By June 1984, the overall average cover was 33%, but by June 1985 it had increased to 69%. The dominant species (in frequency and cover) throughout most of the experimental plots was creeping bent (*Agrostis stolonifera*).

Eleven species of butterflies were recorded over the whole route in 1983, 14 in 1984, and 15 in 1985 (Table 9). Most of them have probably not yet bred on the site for lack of suitable food plants or conditions, but 3 species have established strong colonies. The common blue (*Polyommatus icarus*), meadow brown (*Maniola jurtina*) and small heath (*Coenonympha pamphilus*) increased markedly in 1985, in contrast to the national and regional trends, as 1985 was generally a poor year for butterflies. Analysis of the data shows that the site as a whole

Table 8. Mixtures of 'tall' and 'short' grasses and wild flowers for experimental plots with sowing rates in September 1982 (kg ha^{-1}) and recorded frequencies in 32 random quadrats in June 1985. Other records shown by √

	Rate	Frequency		Rate	Frequency
SHORT			TALL		
Grasses			Grasses		
Meadow Foxtail (*Alopecurus pratensis*)	1.5	√	Meadow foxtail (*Alopecurus pratensis*)	3.8	√
Sweet vernal-grass (*Anthoxanthum odoratum*)	1.5	5	Crested dog's-tail (*Cynosurus cristatus*)	3.8	29
Quaking grass (*Briza media*)	0.3		Cock's-foot (*Dactylis glomerata*)	1.2	5
Red fescue (*Festuca rubra*)	14.6	23	Red fescue (*Festuca rubra*)	14.6	26
Yellow oat-grass (*Trisetum flavescens*)	2.9	19	Yorkshire-fog (*Holcus lanatus*)	2.1	24
			Timothy (*Phleum pratense*)	1.2	3
			Smooth meadow-grass (*Poa pratensis*)	2.9	1
Flowers			Flowers		
Kidney vetch (*Anthyllis vulneraria*)	1.5	4	Common knapweed (*Centaurea nigra*)	0.3	8
Cuckooflower (*Cardamine pratensis*)	1.5		Greater knapweed (*Centaurea scabiosa*)	0.3	
Lady's bedstraw (*Galium verum*)	0.3	7	Wild carrot (*Daucus carota*)	0.3	14
Rough Hawkbit (*Leontodon hispidus*)	0.2	5	Cat's-ear (*Hypochaeris radicata*)	0.2	15
Black Medick (*Medicago lupulina*)	1.5	14	Field scabious (*Knautia arvenis*)	0.4	2
Hoary Plantain (*Plantago media*)	0.3	11	Oxeye daisy (*Leucanthemum vulgare*)	0.5	23
Cowslip (*Primula veris*)	0.2	√	Common bird's-foot-trefoil (*Lotus corniculatus*)	0.7	13
Self-heal (*Prunella vulgaris*)	0.3	5	Ribwort plantain (*Plantago lanceolata*)	0.3	15
Yellow Rattle (*Rhinanthus minor*)	0.1	1	Meadow buttercup (*Ranunculus acris*)	0.2	√
			Common sorrel (*Rumex acetosa*)	0.5	1
			Great burnet (*Sanguisorba minor*)	0.4	5
			White campion (*Silene alba*)	0.5	√

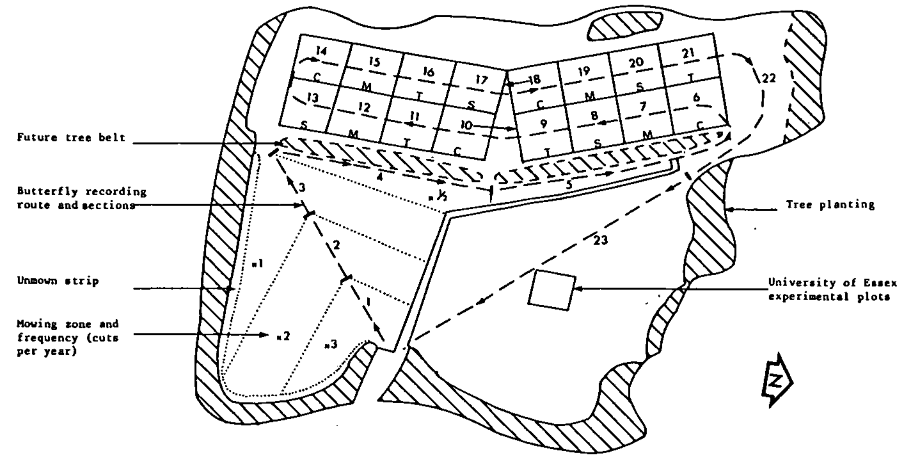

Figure 13.
Martin's Farm, St Osyth
Experimental plots, butterfly recording route and sections (plots 1–16 = Sections 6–21)
C = control, M = mound, S = short, T = tall

Table 9. Seasonal indices for all butterflies recorded in 1984 and 1985. *Minor increase in 1985, **major increase

	1984	1985
Small/Essex skipper (*Thymellicus sylvestris/T. lineola*)	38	32
Large white (*Pieris brassicae*)	15	73*
Small white (*Pieris rapae*)	2	38*
Green-veined white (*Pieris napae*)	0	1
Orange tip (*Anthocaris cardamines*)	4	2
Small copper (*Lycaena phlaeas*)	2	1
Common blue (*Polyommatus icarus*)	49	181**
Holly blue (*Celastrina argiolus*)	2	0
Red admiral (*Vanessa atalanta*)	2	4
Painted lady (*Cynthia cardui*)	0	2
Small tortoiseshell (*Aglais urticae*)	13	47*
Peacock (*Inachis io*)	3	2
Wall (*Lasiommata megera*)	1	1
Hedge brown (*Pyronia tithonus*)	5	13
Meadow brown (*Maniola jurtina*)	98	283**
Small heath (*Coenonympha pamphilus*)	140	514**
Totals	374	1194

has improved for these early-colonizing species, but there is as yet no significant difference between treatments for the numbers of adults, whose distributions are greatly influenced by flowers such as thistles (*Cirsium* spp.).

B N K Davis

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Likely Ecological Effects of Decontaminating Gruinard Island of Anthrax

(This work is supported by Ministry of Defence funds)

During biological warfare trials in 1942–43, Gruinard Island in north-west Scotland was contaminated with long-lived spores of a virulent strain of anthrax (*Bacillus anthracis*), thus preventing subsequent occupation by man or farm livestock. Studies since 1978 by staff of the Chemical Defence Establishment (CDE) (Manchee *et al.* 1981, 1983) have shown that:

i) viable anthrax spores are present in detectable numbers only in the surface soil over 3ha of shallow blanket peat in the southern half of the island;

ii) the application of 5% formaldehyde solution (a protein-denaturing agent) at 50 l m^{-2} effectively disinfects the peat.

The Ministry of Defence now wishes to decontaminate the island, and to return it to civilian use. ITE was commissioned in 1983 to advise CDE on the likely ecological consequences of decontamination by applying 50 l m^{-2} of a 5% solution of formaldehyde in sea-water, and on ways of ameliorating any damage.

The main concerns were about damage to the vegetation, and the possibilities of subsequent peat erosion, and of runoff polluting the seashore. Damage to freshwater organisms was not a concern, as there are no streams or lochs on the island. There is a very low risk that any vertebrates would be harmed; because of the very poor fauna, none should be resident or breeding on the site in summer, the most likely time for decontamination.

Because there is negligible published information relevant to these concerns, several small experiments were done, and have led to the following conclusions about the effects of large-scale decontamination.

The vegetation of the treated area will be almost entirely destroyed by the formaldehyde in sea-water treatment. It is the typical low-altitude blanket bog of north-west Scotland, with heather (*Calluna vulgaris*), cross-leaved heath (*Erica tetralix*), purple moor-grass (*Molinia caerulea*), bog-moss (*Sphagnum* spp.) and the feather moss *Pleurozium shreberi*, predominant. The most resistant species is common cotton grass (*Eriophorum angustifolium*), but fewer than one shoot of this will survive per m^2. For most species, all plants will be killed. However, about 2% of the population of buried viable seeds will survive (400–1000m^{-2}), enough to regenerate the sward.

Regeneration of the vegetation will be slow, but applying NPK fertilizer will accelerate its recovery, so that remedial reseeding should not be necessary. Table 10 gives an example. To investigate whether the vegetation reduced the efficiency of disinfection, CDE staff have examined the effects of burning and of cutting and removing the vegetation before disinfection. Regeneration was fastest on burnt ground (Table 10) because this was the best substrate for seed germination and for moss development. Accordingly, burning the vegetation is recommended, if decontamination proceeds.

Because the contaminated site has an average slope of only 3°, significant erosion of peat is unlikely. In 12 experimental plots on the island, each 3m by 3m, there were no signs of erosion 2 years after treatment with formaldehyde.

Although formaldehyde is toxic to soil micro-organisms, it is biologically degradable (Dickerson *et al.* 1954). The evidence suggests that:

i) the formaldehyde treatment will not significantly reduce the intrinsic decomposability of plant litter,

Table 10. Re-establishment after 2 years of bog vegetation on Gruinard Island treated experimentally with 50 $l\,m^{-2}$ of 5% solution of formaldehyde in seawater

	Intact	With vegetation Cut and removed	Burnt off
Total % cover			
Plots unfertilized	1.5	0.8	18
Plots fertilized	20	18	75
% cover of mosses			
Plots unfertilized	0.2	<0.1	13
Plots fertilized	13	12	70
Seedling density (number $l\,m^{-2}$)			
Plots unfertilized	13	18	55
Plots fertilized	6	17	51

which might have been expected from the protein-denaturing action of formaldehyde;

ii) the native microbial populations, and soil decomposition processes, will recover within a few months;

iii) applying NPK fertilizer will enhance the re-establishment of soil microbial populations, and reduce the effects of formaldehyde on soil processes.

The formaldehyde will not spread in toxic concentrations more than a few metres from the edge of the treated area, except locally along natural lines of drainage, where heather, the most susceptible plant species, may be killed for a few tens of metres. Pollution of the seashore, 400m distant, is thus precluded.

J Miles, Pamela M Latter and IR Smith

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Management of Vegetation, Natural and Manmade

Competition in Turfgrass Mixtures – A Predictive Model

A model is being developed which predicts the effects of competition on plant growth and mortality during the establishment of grass turf from seed. By taking account of competition, the model predicts the final composition of the turf, thus providing a rational basis for the selection of seed mixtures for amenity turf.

A wide range of grass species, cultivars and mixtures is now available for use on areas of amenity grass. In 1983–84, about 7500 tonnes of grass seed, with a market value of over £10 million, were sold for amenity use. Ryegrass (*Lolium perenne*) accounted for about half of the seed, fescues (*Festuca* spp.) 38% meadow grasses (*Poa* spp.) 7%, and bent grasses (*Agrostis* spp.) 5%. Less popular species such as timothy (*Phleum pratense*) were also used. These grasses are rarely sown as monocultures; instead, mixtures are used in which the component species all have individual characteristics likely to be complementary and of value in established turf. For example, ryegrass may be chosen for its rapid rate of establishment and wear resistance, whereas the fescues and bents may be included for their tolerance to close mowing. However, in practice, the relationship between the composition of the seed mixture and the species composition of the established turf is often not very clear (Gore *et al.* 1979), a feature that poses problems when specifying mixtures to be sown. Furthermore, the seed rate at which the mixture is sown may also affect turf structure and performance (Parr 1981). Recommended seed rates may be as large as 50g m^{-2}, at which rate there may be as many as 60 seedlings in each square centimetre. The combination of mixtures of species and large seed rates ensures that inter- and intra-specific competition will influence the development and composition of turf during establishment.

Model development and testing

The influences of species and seed rates have been modelled using data from a field experiment done at Monks Wood Experimental Station. In this experiment, 5 species (Table 11) were sown as monocultures, also in all possible pairs and a mixture of all 5 species. In the monocultures, seeds were sown at 4 rates (2.5, 5.0, 10.0 or 20.0g m^{-2}). The mixtures were sown at a total rate of 20g m^{-2}, with equal proportions (by weight) of each species. Each seed mixture was replicated 3 times with or without 250kg N ha^{-1} yr^{-1}. The plots were sown in September 1982 and mown to a height of 32mm at 2-weekly intervals beginning in April 1983. During the first year of growth, turf biomass and plant densities were measured on 4 occasions.

Data from the monocultures were used to develop single species models of turf growth (Figure 14). These models simulated daily changes in plant density and mean plant weight during the first year of establishment. They incorporated 3 interrelated processes: germination, mortality and plant growth.

Germination rates and initial seedling sizes were independent of initial seed rates and amounts of nitrogen, but they varied between species (Table 11).

Plant density declined exponentially during the first year. Mortality rates (m) were estimated for each experimental plot from the following equation:

$$m = (\log(N_o) - \log(N_t))/t$$

where 'N_o' was the density of plants after germination and 'N_t' was the density after one year, ie 't' days later. Plant mortality was density dependent in all species, except ryegrass (Figure 15). In the model, mortality was described as a linear function of seed rate, although eventually an expression of size dependent mortality may be more realistic.

Daily growth rates of mean plant weight (w) were estimated using Gompertz growth curves:

$$\log w = a(1 - e^{-kt})$$

where 'a' is the maximum plant size after one year, 'k' is a parameter related to the initial growth rate, and 't' is time in days. Maximum plant size was dependent on population densities at time 't' and on final shoot biomass attained after one

Table 11. Germination of 5 grass species used in a predictive model of competition in turfgrass mixtures (from observations made 24 days after sowing)

	Seeds g^{-1}	% germination	Seedling dry weights (mg $plant^{-1}$)
Lolium perenne	640	98	1.88
Phleum pratense	2960	57	0.49
Festuca rubra var. *commutata*	890	75	0.61
Poa pratensis	2620	40	0.28
Agrostis castellana	8830	27	0.21

year of growth (Figure 16). In the absence of applied nitrogen, final shoot biomass was independent of initial seed rate but, with the application of 250kg N ha^{-1} yr^{-1}, shoot biomasses of ryegrass, timothy and bent (*Agrostis castellana*), were inversely proportional to seed rates. This effect possibly occurs because the larger plants produced by these species at the small seed rates made relatively more efficient use of available resources than denser populations of smaller plants derived from larger seed rates.

Competition between species was modelled on the assumption that all species had identical resource requirements. Hence, during establishment, when there was assumed to be no recycling of nutrients, the outcome of competition was determined by the relative rates at which the species occupied the limited available space (or the resources which that space contained). This assumption is consistent with the finding that mixtures of grasses usually have yields intermediate between those of the component species, with relative yield totals of approximately one (Trenbath 1974). The parameter values used in the model for mixtures were derived from observations made on the single species plots. Therefore, comparisons of the field data from the plots of grass mixtures, and model predictions provide an opportunity of assessing the validity of the assumption made when structuring the model.

Does the model work?
Predictions of the proportions of each species in the mixtures were in good agreement with the field data (Table 12). In 14 of 20 mixture combinations, the predictions were within the 95% confidence limits of the field data. The model was also accurate for the more complex 5-species mixture (Figure 17), in which the proportions of all the species were estimated to within 4% of actual field values.

These results indicate that the assumption made in the model about the mechanism of competition was satisfactory and that the model could be used confidently to predict the changes that might occur in novel mixtures. For example, it could predict the proportions of species in seed mixtures needed to produce a turf with a specified composition. Different grass species have different competitive abilities, and 50:50 seed mixtures rarely lead to a 50:50 mixture at establishment (Table 12). Both ryegrass and bent established quickly and dominated mixtures in which they were sown, although each species achieved its dominance in different ways. Both species germinated quickly and had seedlings with rapid relative growth rates, but whereas ryegrass had large seedlings and small plant densities, the seedlings of bent were smaller but occurred in denser stands. In contrast, timothy germinated slowly and produced a small population of slow-growing seedlings, and so its eventual contribution to the biomass of the established turf was small.

The model accurately predicted that the dominance of ryegrass would be greater in the absence, rather than in the presence, of applied nitrogen: without added nitrogen, ryegrass accounted for 70% of total plot biomass when in mixtures with bent and 95% in mixtures with timothy. Hence, although ryegrass is usually associated with 'rich' sites, in the short term its ability to pre-empt space gives it an even greater competitive advantage where only small amounts of nitrogen are available.

The model also demonstrates the extravagance of currently recommended seed rates for many types of amenity turf. Comparisons between seed rates of 5 and 20g m^{-2} of ryegrass indicate that after 25 days there was a 4-fold difference in turf biomass, reflecting the initial differences. After a further 8 weeks, this difference was only 2-fold. Within 20 weeks of sowing, there was no difference at all. These

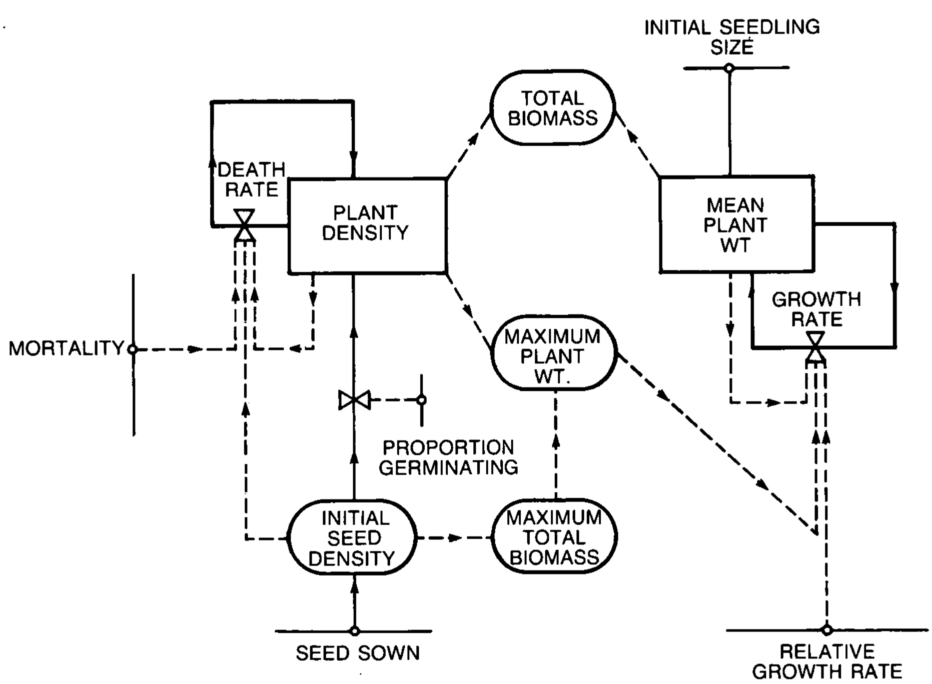

Figure 14. Model of the growth of turf containing a single species of grass.

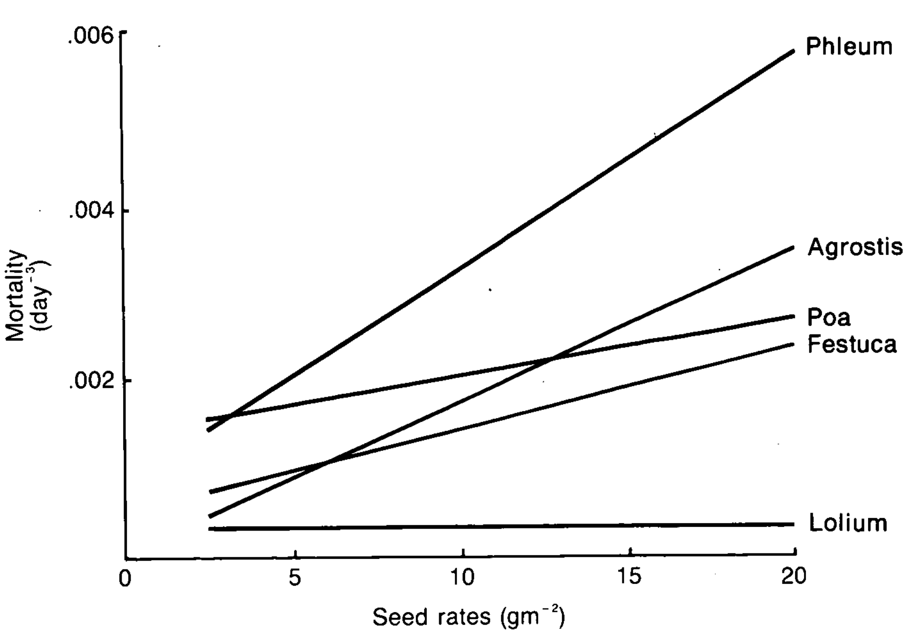

Figure 15. Relationship between seedling mortality during the first year after sowing and the initial seed rates of 5 grass species. The linear regressions (n = 12), except for ryegrass, were significant ($P < 0.05$).

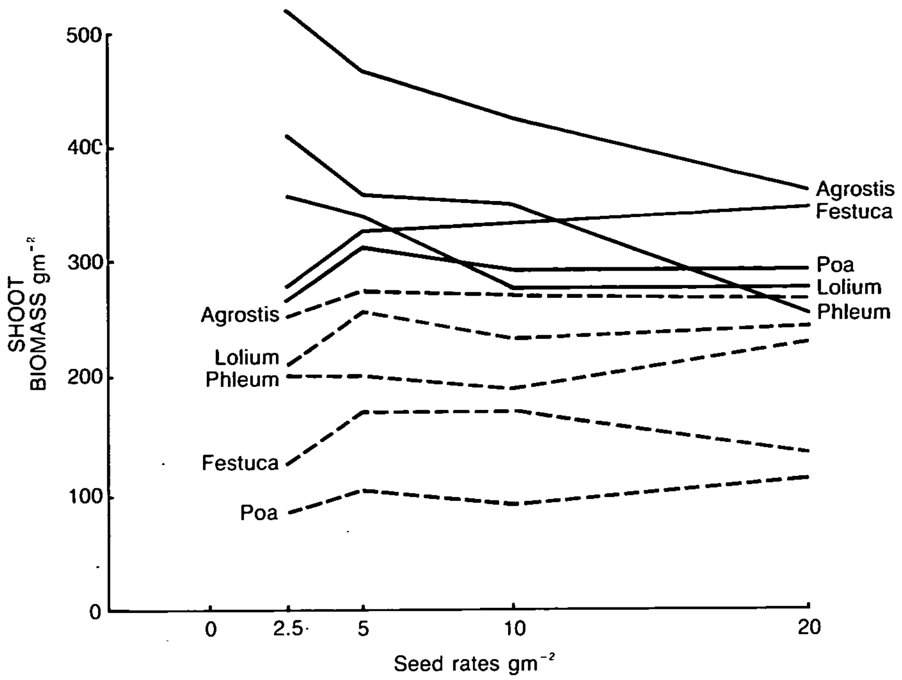

Figure 16. Effects, at the end of the first year, of seed rates on shoot biomass of turves with (—) or without (----) added nitrogen fertilizer.

Table 12. Comparisons of field data and model predictions when 2 grasses were sown in equal mixtures at a total rate of 20g m^{-2}, in plots with or without applied nitrogen fertilizer

Grass species sown in mixtures	250kg N ha^{-1} yr^{-1} Field data (±SE)	250kg N ha^{-1} yr^{-1} Model prediction	No nitrogen Field data (±SE)	No nitrogen Model prediction
i. 2 species mixtures (data refer to % of first species)				
Lolium + Phleum	67 ± 5	79	80 ± 5	89
Lolium + Festuca	75 ± 2	72	77 ± 2	90
Lolium + Poa	87 ± 2	87	97 ± 2	95
Lolium + Agrostis	57 ± 4	53	71 ± 4	70
Phleum + Festuca	44 ± 3	45	47 ± 3	70
Phleum + Poa	87 ± 1	70	94 ± 1	88
Phleum + Agrostis	22 ± 7	26	22 ± 7	26
Festuca + Poa	75 ± 1	74	90 ± 1	76
Festuca + Agrostis	24 ± 10	30	37 ± 10	15
Poa + Agrostis	7 ± 1	13	2 ± 1	5
ii. 5 species mixtures (% each species)				
Lolium	40	43	60	64
Phleum	14	12	11	8
Festuca	10	7	8	4
Poa	2	3	1	1
Agrostis	34	35	20	23

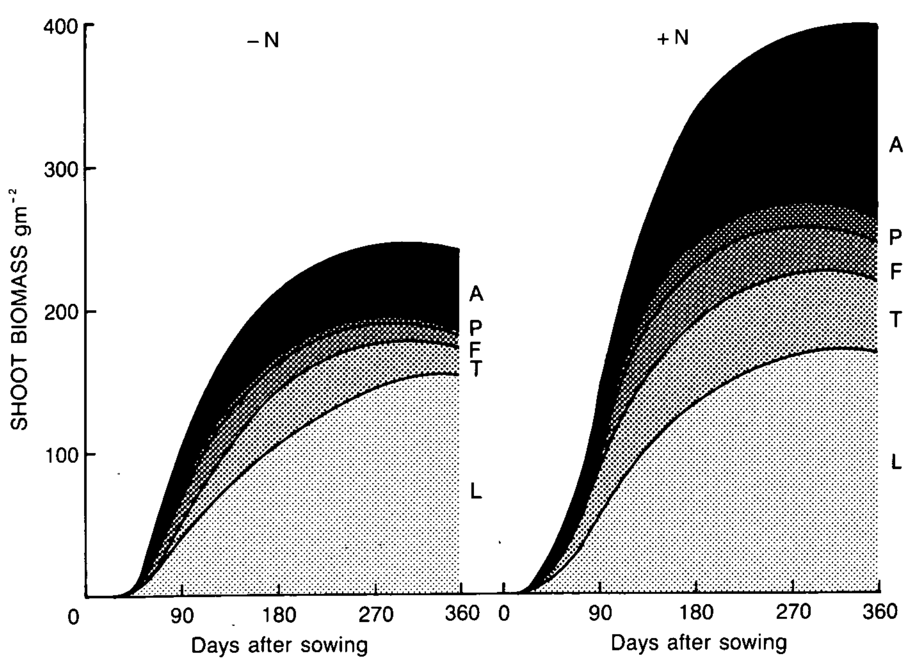

Figure 17. Predicted shoot biomasses, at different intervals after sowing, of 5 grasses in a mixture cultivated with (250kg ha^{-1} yr^{-1}) or without applied nitrogen. (*L. perenne* shown by (L), *P. pratense* (T), *F. rubra* (F), *P. pratensis* (P) and *A. castellana* (A)).

results are based on growth during autumn, winter and early spring when growth rates are slow. During a period of rapid growth, such as late spring, the initial effects of seed rate on turf biomass will probably diminish even more rapidly.

The model is also a general aid to understanding ecological aspects of the establishment of amenity and agricultural swards. It is now being developed to cover a wider range of environmental conditions and management strategies (eg cutting). It will also be used to assess the effects of seed rates and species mixtures on the growth of weed species (Parr 1985), so possibly enabling an assessment of potential yield losses attributable to weeds occurring at an early stage in sward development. In turn, the model should make available information to help in assessing the economics of weed control.

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Dynamics of the succession of Chalk Grassland to Scrub

Unless they are continually managed, many plant communities, eg the grasslands that abound in Britain, would progressively change with the invasion of shrub and tree species, the progression, or succession, reflecting the change from 'plagioclimax' to 'climax' vegetation. Typically, chalk grasslands – plagioclimax communities – are species-rich, and at the same time they are particularly vulnerable to changes in grazing pressure. When grazing pressures are decreased, scrub vegetation begins to take over, thus setting in motion seral changes that would lead, unless checked, to the development of woodland. Changes can also be triggered by other types of management, such as burning, mowing and disturbance.

To improve our understanding of the management of chalk grassland, a long-term experiment was set up in 1969 at Aston Rowant NNR in the Chiltern Hills. By exclusion from some areas, it was intended to examine the effect of continuous grazing and of no grazing by sheep and wild rabbits. The effects of disturbance, caused by rotavation, and by burning, were also tested. These treatments were applied in 1969, and the subsequent successional changes in the chalk grassland were followed. Each treatment was assessed on 4 replicate plots, each measuring 10 × 12m; within each plot, there were 2 randomly positioned permanent quadrats, each 1 × 2m. While trees and shrubs have been studied intensively, this report is concerned with the effects of treatments on non-woody vegetation during the first 14 years of the experiment. Total numbers of species recorded between 1969 and 1983 were 148; numbers ranged from 32–78 per plot. Total numbers have fluctuated, but the fluctuations could not be clearly related to treatments. Grazed plots have shown a rise in total mean species for each plot, coinciding with increased grazing by rabbits as populations of these animals rose to a maximum in the mid-1970s before being controlled. On the untreated 'control', plots there was a slow decrease in species numbers, while plots disturbed by burning or rotavating usually had larger numbers of species than grazed or untreated plots. However, this pattern was reversed when mean numbers of species in the quadrats, rather than mean numbers in the plots, were studied. In the sample quadrats, the highest numbers of species were usually recorded in the grazed plots. This discrepancy between plots and quadrats is explained by differences in the packing (distribution) of species. Grazed plots were usually more uniform, with large numbers of species per unit area. In contrast, ungrazed plots usually had fewer species in the small quadrats but more encompassed within the larger area of the plots. The fluctuations in numbers of species in the plots and quadrats are mainly related to the weather, and under extreme conditions the effects may be apparent on all plots, however treated. Thus, after the severe drought in 1976, numbers of species increased on almost all plots and quadrats, and these increases persisted for several years.

Because the dynamic changes occurring after changes in management were not clearly reflected by changes in total numbers of species, a new descriptive method was devised. Mean numbers of species present in each of the 8 quadrats in the first year were listed, and their rates of loss calculated over 14 years. Mean numbers of species in the grazed grassland quadrats decreased from 20.5 to 11.7, while species in the rotavated quadrats decreased more steeply from 22.0 to 7.0, as happened also in the untreated 'control' quadrats. The burned quadrats were intermediate, with numbers falling from 20.8 to 9.5 species. Burning apparently allowed the deeper-rooted perennials to survive, and these grew well and prevented subsequent invasion by other species. Nutrients were possibly lost during burning, as shown by the slow growth of some woody plants. In the second year and thereafter, numbers of species new to the quadrats, compared with previous years, were recorded, and annual rates of loss were calculated. Recruitment of species to quadrats fluctuated annually but, generally, numbers were highest in the grazed quadrats, ranging from 1.8 to 6.1. Numbers recruited to the rotavated quadrats were next highest, followed by fewer in the burnt plots and ungrazed controls. The greatest recruitment was on the disturbed plots in the first 3 years, but many species were lost quickly, particularly the arable weeds in the rotavated plots. However, a few species persisted throughout the years of the succession, eg wild candytuft (*Iberis amara*), while others have persisted for several years, eg oxeye daisy (*Chrysanthemum leucanthemum*). Loss of species was greatest in the first year, when mostly annuals were lost, and there was then a slow fall-off. Thus, although there is a core of species that turn over very slowly, there are also considerable fluctuations: when grazed and ungrazed grasslands are compared, it is seen that the highest rates of change are in the grazed quadrats. This result emphasizes the dynamic state of plagioclimax grassland. Its vegetation is checked continuously by grazing animals, with some plants being killed. Turnover of species is much slower on ungrazed, than on grazed, grassland, which is often characteristic of secondary successions where factors of growth, ultimate height and life span of individuals are significant in determining the course and outcome of succession (Drury & Nisbet 1973).

The actual details of changes among the numerous species are complex. There are species with generally decreasing populations which may be lost altogether. The shorter-lived annuals and biennials and other low-growing plants tend to be lost first as the taller vegetation grows and amounts of litter increase. Wild thyme (*Thymus drucei*) (Figure 18) commonly occurs in grazed chalk grassland. Its numbers increased to a peak during the mid-1970s, when rabbit grazing was most intensive, but, on the plots without grazing, thyme has slowly declined. Several species show gains in numbers, especially the woody plants and some grasses. An example of a species in the field layer showing an increase in cover is the false oat-grass (*Arrhenatherum elatius*) (Figure 18, Plate 1). On the grazed plots, this species is sparse, but it increased on the ungrazed plots, especially on those that remained untreated or were rotavated. There is some evidence of a fall-off in cover in later years. This reduction is not shown very clearly in the Figure but has been more apparent since the fourteenth year (recording is continuing). Oat-grass will decline as shading increases and woody plants grow. Another category of species includes those that increase rapidly at first and then decline, as, for example, the annual fairy flax (*Linum catharticum*) (Figure 18). This species has covered a small area in most years in the grazed plots, being more abundant in the early, than in the late, years of the experiment. It quickly became less frequent in the untreated plots but was abundant at first on the disturbed plots, especially those which had been rotavated, presumably because buried seeds were activated. Fairy flax is also known to have years of abundance, and it seems likely that 1979 was such a year, as the plant appeared in several quadrats in which it had been absent for several years before. Diagrams like these have been constructed for some 30 species which are reasonably common in chalk grassland, and help to explain the effects of the treatments, replicate positions, successional changes, and, in some cases, species interactions.

Chalk grassland (Wells 1975) and scrub vary in relation to local factors, such as soil variation, abundance of seed parents and history of management. Any grassland site can be regarded as unique because its detailed composition varies in response to differences in climate and grazing pressure. This variation will be shown to be especially important for the populations of woody plants that are invading the grassland and which set the pattern for the years of succession to come. According to

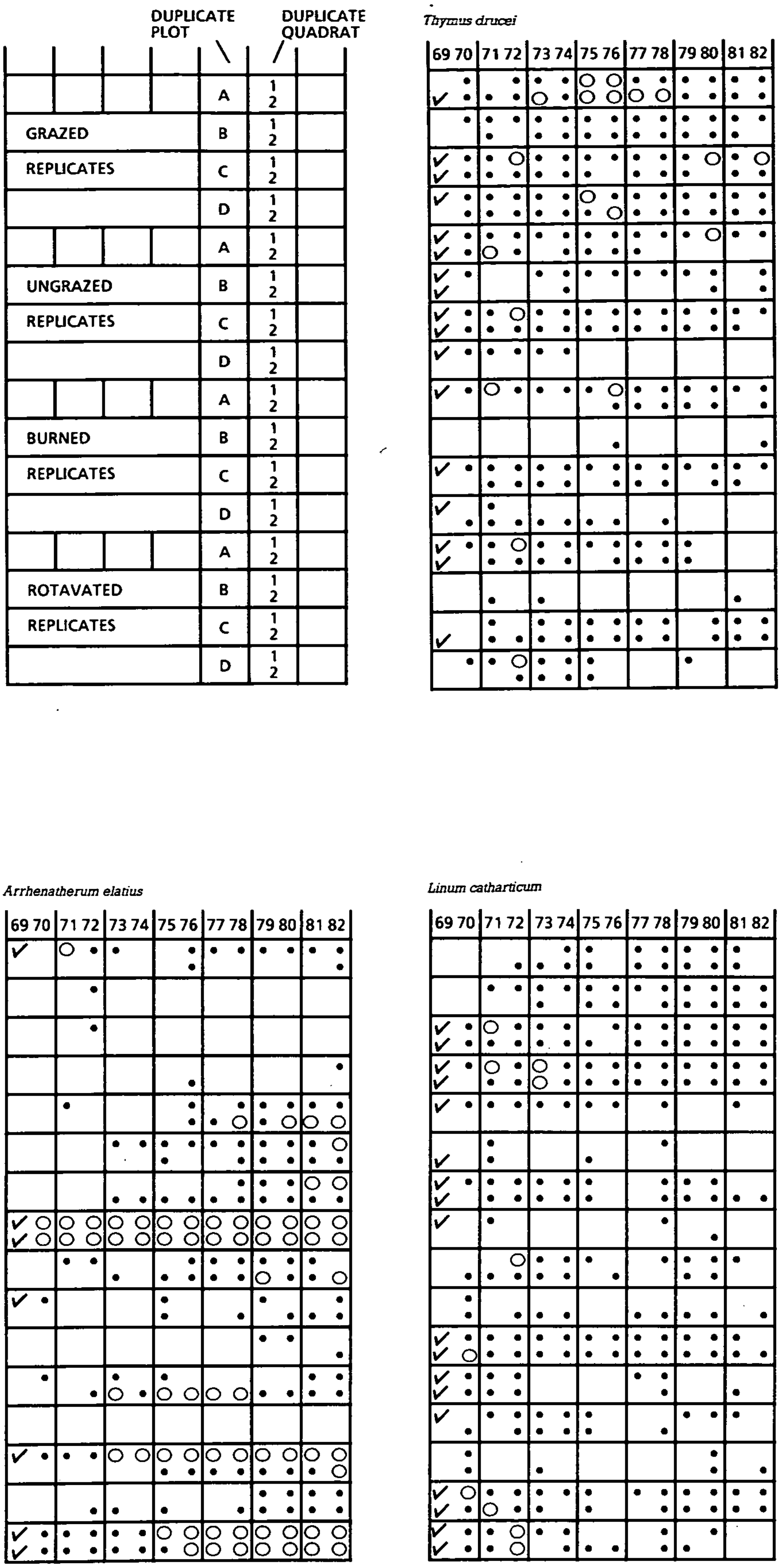

Figure 18. Effects of grazing, burning or rotavating on the amount of groundcover achieved by 3 species of chalk grassland plants at Aston Rowant NNR (1969–1982). The data relate to observations made in duplicate quadrats (1 and 2) in each of 4 replicate plots (A–D). (. <5% cover; O 5–33% cover; ● >33% cover; √ present in 1969).

the success of the different woody species and related soil factors, the speed of succession also varies. The change to closed canopy scrub at Aston Rowant is much faster on some plots than on others, but is generally fairly slow compared to scrub on more fertile soils. Only one plot out of the 12 non-grazed plots had reached 50% cover by woody plants after 14 years.

For nature conservation of species-rich chalk grassland, continuous, frequent grazing is important to prevent scrub invasion. However, where grassland is of lower quality, then it might be desirable to direct the succession to scrub, or even to woodland. For amenity areas, scrub vegetation is also useful in landscaping and in directing or screening the movements of people (Ward 1979). Every area has a potential scrub vegetation, and the experiment at Aston Rowant shows how it may be predicted for other sites by initial investigations of present vegetation, local seed parents, soil seed bank, and soils. For nature reserves, it is important to have straightforward descriptive accounts of likely succession, seral changes induced by various forms of management, so that actions can proceed with the knowledge of likely results. Modification of the initial vegetation has been shown to be carried forward into the subsequent succession, and 'seres' may be manipulated also by the selected removal of undesirable woody plants. In America, trees have been removed from woody assemblages to prevent taller growth which would interfere with power lines. The Aston Rowant experiment is also relevant to the management of grassland on rotational principles, where blocks of land are allowed to pass into the succession, and after a longer or shorter time, are reclaimed to grassland. Even after 14 years, most of the grassland species initially present in the vegetation are still there, although often in very small numbers and in an etiolated state at the base of the deep grasses and litter. Smaller annuals and biennials are lost, but are likely to appear again from the seed bank. Thus, reclamation management is still practical after this period of time. The phase where the initial vegetation is almost, or entirely, lost as the shade cast by the encroaching scrub increases is only just beginning at Aston Rowant. This is a critical time in rotational management schemes, when decisions need to be taken about whether to allow the succession to be restarted with the impoverished remnants of the previous vegetation still present, or whether to allow the sere to pass to closed canopy with the virtual elimination of the herbaceous vegetation.

Lena K Ward and R D Jennings

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Survey and monitoring

Rangeland and Rainfall Mapping in the Sahel

(This work is supported by CEC funds)

Information from earth observation satellites is becoming increasingly important for assessing and managing rangeland in many parts of the world. In the Sahelian zone of Africa, particular interest is being shown in the use of satellite imagery as an operational management tool for monitoring the condition of grassland in order to ameliorate the effects of drought.

The Overseas Development Directorate of the Commission of the European Communities (DGVIII) is funding a programme in a number of African states, entitled 'Programme contre le faim'. Part of this programme is intended to develop methods for the operational use of remotely sensed data. ITE (in collaboration with Silsoe College, the Institute of Hydrology, the Meteorological Department of Reading University, and the Geography Department of Bristol University) is engaged in developing models which can be used, in the first instance, to assess rangeland productivity from multispectral imagery, and, ultimately, to predict rangeland condition using data acquired from meteorological satellites.

There are 2 components to this collaborative project. The first is concerned with methods of mapping rainfall from tropical storms. The method involves tracking the storms by means of meteorological satellites and then correlating characteristics, such as cloud temperature, with measured rainfall on the ground. ITE is contributing to the second part of the project, in developing procedures to map and monitor rangeland vegetation, qualitatively and quantitatively, from satellite imagery. At a later stage, these results will be linked to rainfall mapping to create a system for forecasting rangeland productivity. It will be a relatively simple matter to incorporate estimates of carrying capacity, and thus to provide authorities in the Sahelian countries with the means of taking advance measures to forestall the effects of drought.

The study is based in Niger, West Africa. Data from the Landsat Multispectral Scanner (MSS) are used in the first instance, although eventually Advanced Very-High Resolution Radiometer (AVHRR) imagery from the NOAA-7 satellite will be employed, because the frequency with which these data are available is most appropriate for an operational monitoring system. The basic image-processing methods were developed using NERC image-analysis facilities at ITE, Bangor, and the GEMS image processing system at Silsoe College. The final operational system will make use of microcomputers, which can be distributed to regional agricultural and meteorological services in the countries of the Sahel.

We have made 2 field visits to the Republique du Niger, concentrating our studies in the region of Kao. On the first occasion, towards the end of the dry season in March 1985, we took measurements of soil reflectance, of the distribution of basic soil types, and of shrub and tree vegetation (there was very little herbaceous vegetation at that time). We used these observations to support preliminary interpretation of imagery acquired during the same dry season. Measurements of the reflectance of bare soils of various types were taken from the Landsat imagery and correlated with field radiometric observations detected in the satellite imagery. We plotted the 'soil line' in infra-red/red feature space (Figure 19) and, using this basic relationship, computed soil brightness (SBI) and perpendicular vegetation indices (PVI) by axis rotation. From these indices, it was possible to compute a 'soil brightness' image and a 'PVI' image covering the test site at Kao. Each image was coloured by a simple density-slice approach, using our understanding of soil and vegetation distributions from the field visits to select slice limits interactively.

We took the maps to Niger on a second field visit during the 1985 wet season (August–September), and evaluated the soil and vegetation classes derived from the Landsat imagery by direct field

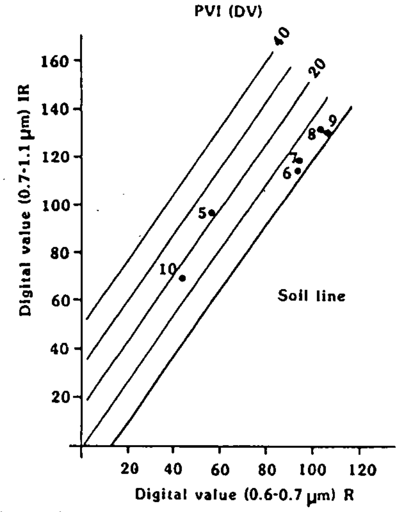


Figure 19. Mean Landsat digital values for training areas of vegetation cover classes.

observation. Quantitative vegetation data were collected along 8 transects, representative of the main soil vegetation types identified in the imagery. The measurements were taken:

- herbaceous biomass, by drying and weighing clipped samples from 50cm × 50cm (0.25m^2) quadrats;
- tree counts;
- measurements of tree circumferences.

We obtained a further Landsat image, contemporary with the second field visit. Once again, we extracted soil reflectance from the image, computed the soil line, and derived soil brightness and PVI images. Mean values of the PVI along each of the transects were estimated from the PVI image, and we constructed a correlation curve, relating dry herbaceous biomass with PVI (Figure 20). We successfully tested this relationship against measures of mean biomass from a second ground survey site

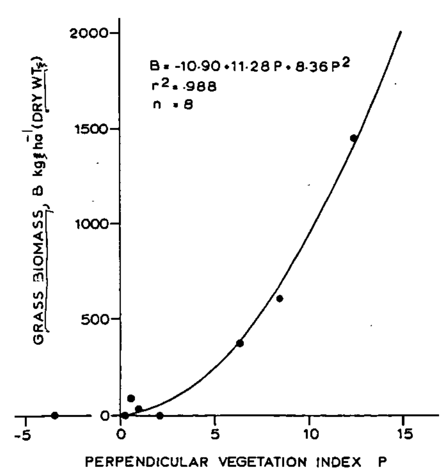


Figure 20. Calibration curve for prediction of dry grass biomass from the perpendicular vegetation index.

(measured biomass 1025kg ha^{-1} estimated biomass 1040 kg ha^{-1}). The soil brightness maps generated from dry season and wet season imagery are remarkably consistent, and suggest that the basic approach is tolerant of changes in extraneous conditions, provided rudimentary corrections are made to the imagery for variation in sun elevation and azimuth.

We plan to test the biomass/PVI relationship (which is crucial to the whole methodology) against further wet-season field data, and to examine the effect of using AVHRR imagery in place of Landsat-MSS data. We have already simulated AVHRR by degrading Landsat data spatially and radiometrically, and the results are promising. We expect AVHRR images of West Africa shortly to become routinely available from the ESA satellite receiving station at Laspalomas in the Canary Islands. At this stage, it will be possible to implement a simplified system on a suitable microcomputer system and, after a period of training local staff, to begin a series of pilot trials.

We gratefully acknowledge the major contributions of Dr J Taylor and Mr A Belward, of Silsoe College to the work described, and the help of Mr G Dugdale, of Reading University, in planning the field programmes.

D G Hewett and B K Wyatt

The 'Biotopes' Project of the European Commission Information Programme 'CORINE'

The Commission of the European Communities is undertaking a major programme to create an information system on the state of the environment in Europe (Council Decision of 27 June 1985). This programme is called CORINE – Co-ordinated Information on the European environment. CORINE is designed as a means of harmonizing environmental data collection in the Member States of the European Economic Communities (EEC), to improve data comparability. It will provide a source of information to guide environmental policy-making in the European Commission (EC) and to improve understanding of the possible environmental effects of activities in other sectors of management.

A 4-year development programme has been approved, in which information on a variety of environmental variables will be collected at various scales across the whole of the EEC territories and will be assembled in computer-readable form, making use of modern Geographic Information System (GIS) technology. These activities are being undertaken by means of a set of independent, but linked, projects, each concerned with one group of variables, one geographical region, or with a particular methodological approach. This phased implementation of the system permits useful information covering particular problems and issues to be assembled relatively quickly and cheaply, without committing the EC irrevocably to a programme beyond its present resources. In most cases, existing data are being assembled, usually from published sources; primary data collection is not envisaged, other than in exceptional circumstances.

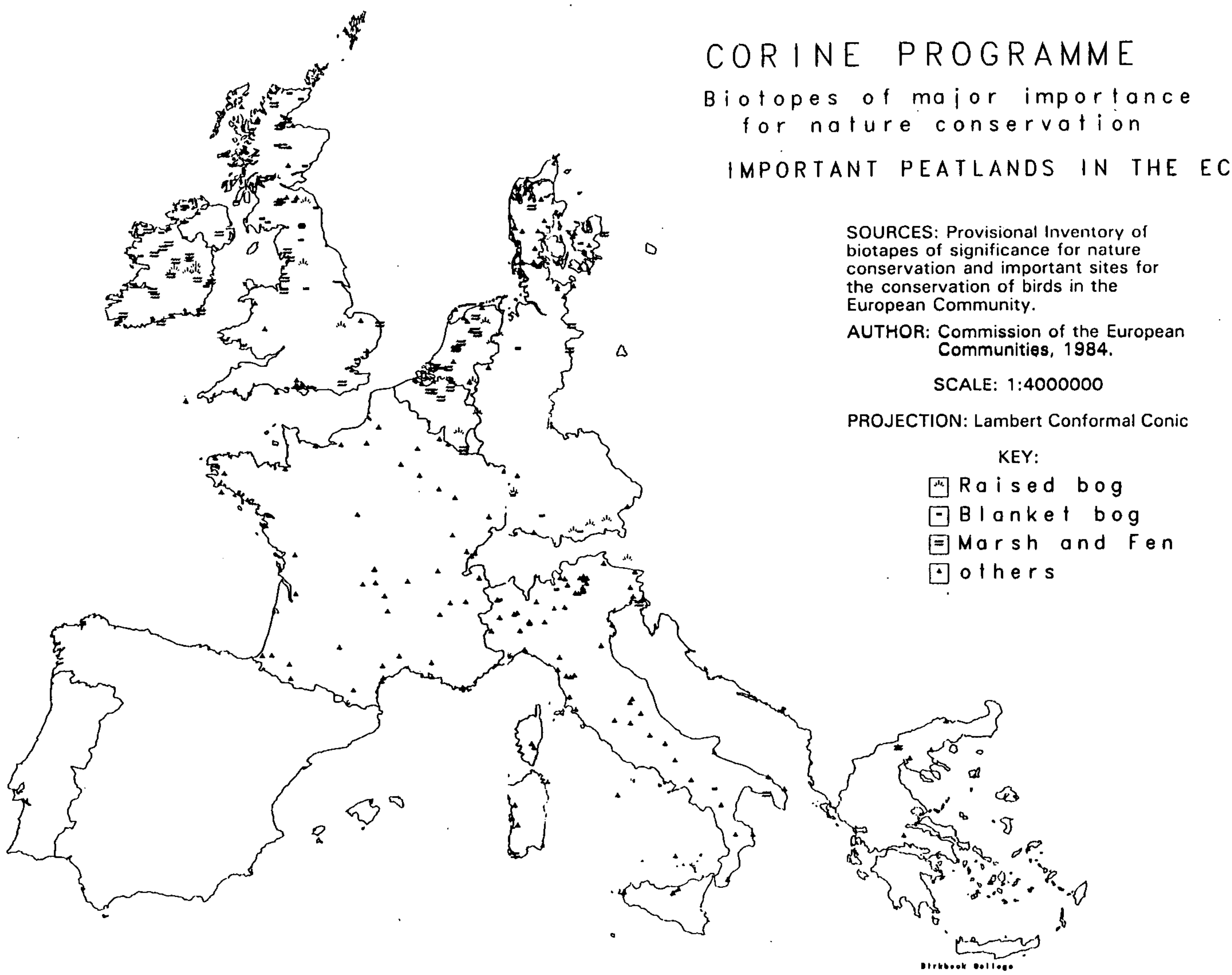
The projects which have been undertaken in the framework of the CORINE programme include:

1. development and planning of the computer system;
2. acquisition of basic digital data (from topographic maps, soil maps, climatic records, etc);
3. compilation of an inventory of environmental data sources across Europe;
4. mapping and modelling of atmospheric emissions, using existing emission inventories and models based on socio-economic data;
5. mapping and modelling of water resources and quality in the Mediterranean region;
6. mapping and modelling soil quality and erosion risk in the Mediterranean region;
7. study of the feasibility of using satellite remotely sensed data to compile a consistent digital map of land cover across all EEC territories;
8. compilation of a computer-readable register of sites of importance for nature conservation ('biotopes') over the whole of the EEC.

Members of ITE have been involved as consultants in planning the CORINE programme for several years. In the course of this work, it has been useful to draw upon existing experience within the Institute in the design and operation of environmental data bases, including land use and land cover information systems (Bunce & Claridge 1985; Ball 1983), systems recording information on the distribution of biological species (Harding *et al.* 1983), and in the integrated use of digital cartographic data and remote sensing as a source of spatially referenced information on the terrestrial environment (Brown *et al.* 1985).

Table 13. CORINE biotope inventory – record specification

Date field	Contents
Country	Standard country code of the EC Statistics Office
Site number	Sequential number assigned to each site by respondent
Site-Id	Key derived from latitude/longitude co-ordinates and unique to each site
Date	Date of notification
Respondent	Name and address of person/organization giving notification
Site name	Name of site in local language
Region	Name of standard EC region (eg county) in local language
Region code	Standard region code of the EC Statistics Office
District	Name of district(s) in which site occurs in local language
Co-ordinates	Geographical co-ordinates (latitude/longitude to nearest second) of site centre
Area	Area of site in ha
Altitude	Maximum, minimum and mean altitudes of site in m
Description	Free-text site description, including: – site character – presence and identity of important species, communities, habitats or ecosystems – assessment of site quality – assessment of its vulnerability – summary of any protection measures (eg legal, planning constraints) which affect the site – information relating to site ownership – summary of the scientific motivation for declaring the site – summary of references to the site in the scientific literature and any other source of additional information on the site
Habitat	Coded information on habitats represented on the site, and estimates of the surface cover of each habitat type
Species	Lists of important biological species found on the site
Protection	Coded description of the protection status of the site and estimates of the proportion of the site in each protection category (see also the free-text description of site protection under 'description')
Motivation	Coded description of the factors which determine the importance of the site for scientific or conservation interests (see also the free-text description of motivation under 'description')
Human activities	Coded description of human activities which may affect the future stability of the site and an estimate of the proportion of the site that is vulnerable to these influences (see also the free-text description of 'vulnerability' under 'description')
Site map	A map of the site boundaries. In the case of larger sites, these boundaries will be digitized and included in the CORINE data base



ITE is now directly concerned in the implementation of 2 of the above projects within the CORINE programme. The Remote Sensing Applications Centre at Bangor is one of the laboratories conducting a controlled evaluation of the role of satellite imagery for land use mapping in each of the 12 Member States of the EEC.

Members of ITE staff are also principal consultants in the 'Biotopes' programme to catalogue and map important nature conservation sites throughout the EEC. A team of experts from each of the Member States and from the Council of Europe in Strasbourg has been established. With the advice of this team, ITE has designed a standard form (see Table 13) for recording the characteristics of such sites. This information will enable the EC to assess, for example, the distribution of different European habitats, the relative value of sites for scientific interest or conservation value, the effectiveness of existing conservation measures and the need for further regulation, the pressure on important sites from human and other influences, and risks from development policies of the Member States and of the EC itself. The map illustrates one of the many forms in which this material can be presented.

Staff at Bangor have developed a computer-based information storage and retrieval system to handle these site records. The team of experts are busy assembling information on important sites in each of the Member States, and ITE is processing site descriptions provided on paper forms, on magnetic tape and on floppy disc into a single integrated data base. The project is being carried out in 2 phases.

In the first phase, completed in June 1986, basic information on the site characteristics and records of the most threatened species of flora and fauna has been recorded. This data base holds information on about 4000 sites at present; it is expected that, when complete, 10 000–15 000 sites from across Europe will be included.

In the second stage, more detailed information on habitats, species present, site protection status and human influences will be sought. Where available, maps of the sites will be acquired and digitized. These digital records will be merged with the spatial data collected by other CORINE projects to enable more sophisticated analysis of the relationship between important sites, their geographical setting and other factors which may influence their future stability.

B K Wyatt

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Furzey Island – saltmarsh monitoring

(This work is supported by BP Development Ltd funds)

In 1985, BP Development Ltd was granted permission for appraisal drilling of an oil well on Furzey Island, in the centre of Poole Harbour, Dorset. This drilling opened up the possibility, however remote, of oil being spilled within the Harbour, and, as part of the planning process, ITE was commissioned to analyse the relative sensitivity to water-borne oil of the different local shoreline types (Gray 1985). Because of the construction of a jetty on Furzey Island, and in view of the possible effects of the drilling operation on the island margins, ITE was also contracted to map the saltmarshes fringing the island and to monitor the changes on these marshes and associated mudflats.

The positions and extent of the major saltmarsh plant communities have been mapped, using a combination of plane tabling and aerial photography, along the south and east shores and in the north-east corner of the island. The south shore marsh is zoned into recognizable plant assemblages, with a community dominated by common cord-grass (*Spartina anglica*) at the lowest level being replaced at higher elevations by a zone dominated by sea purslane (*Halimione portulacoides*), a 'species-rich' sward with sea plantain (*Plantago maritima*), thrift (*Armeria maritima*), common sea-lavender (*Limonium vulgare*) and sea arrowgrass (*Triglochin maritima*) particularly common, and, at the level of the highest spring tides, a narrow fringe of sea couch-grass (*Elymus pycnanthus*) with driftline species such as beet (*Beta maritima*) and spear-leaved orache (*Atriplex hastata*). The thin fringe of eroding saltmarsh on the eastern shore is less clearly zoned, although the same assemblages are present, and is the remnant of an extensive cord-grass sward which projected more than 1 km eastwards from the island less than 30 years ago.

The saltmarsh in the north-east corner is, by contrast, an environment of sedimentary deposition. It has developed behind an eastward-projecting sand bar and is protected to the east by a shingle bar. The tide enters and leaves via a single channel in the north-east corner, flooding the marsh through a dendritic creek system. Both floristically simple areas, dominated by *Spartina*, and species-rich areas at higher elevations are found within this marsh.

The changes in the marshes and mudflats are being measured by 2 methods. First, 20 transect lines, accurately levelled to Ordnance Datum, have been established at right angles to the shoreline. These lines (totalling 1022m in length) provide marsh and beach profiles which can be resurveyed to detect gross changes in the accretion/erosion rates, particularly along the south and east shores. Second, small-scale changes in sediment levels are being measured by a series of Kestner cores sited in selected areas along the transect lines. The cores consist of a small, T-shaped plug of molochite, a calcined china clay which is biologically and chemically inert (kindly made available by English China Clays Ltd), of similar grain size (70μ) to the intertidal sediment. A total of 187 cores was established in July 1985, and evidence of sediment accretion or erosion is being recorded, before their removal to record changes after one year. It is hoped to develop a saltmarsh accretion model from the Kestner core investigations.

A J Gray

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Gray, A J. 1985. *Poole Harbour. Ecological sensitivity analysis of the shoreline.* Abbots Ripton: Institute of Terrestrial Ecology.

A survey of sand dunes in relation to grazing

(This work is supported by Nature Conservancy Council funds)

Many dune systems have a rich and varied flora and fauna. The plant communities of the dune complex are dynamic and are continually the subject of cyclical and successional change. Their present species diversity reflects both their past use and present management. This effect is particularly true of the impact of grazing by both domestic and wild animals. Many areas with a long history of grazing are floristically diverse. However, at the present time, the grazing intensity of both wild and domestic animals is much less than it was formerly and, as a result, there is a wholesale development of coarse vegetation and invasion of scrub, with the loss of species-rich short grass communities. In some other areas, the converse has happened. On acid dune systems, heavy grazing has resulted in the replacement of dune heath with a species-poor acid grassland. A wide range of problems is associated with the selection of the optimum level of grazing for the maintenance of species diversity in different types of dune system.

In the first year of the study, emphasis has been placed on visiting a wide range of British dune sites to ascertain the present intensity of grazing and the degree of species diversity. To date, 41 sites have been recorded, ranging

Aberlady, Midlothian. Spread of the inedible nettle, as a result of heavy rabbit grazing, along the edge of scrub which provides cover for the rabbits.

resources in the Community. *Official Journal of the European Communities no. L176/14*, 6 July 1985.

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A survey of sand dunes in relation to grazing

(This work is supported by Nature Conservancy Council funds)

Many dune systems have a rich and varied flora and fauna. The plant communities of the dune complex are dynamic and are continually the subject of cyclical and successional change. Their present species diversity reflects both their past use and present management. This effect is particularly true of the impact of grazing by both domestic and wild animals. Many areas with a long history of grazing are floristically diverse. However, at the present time, the grazing intensity of both wild and domestic animals is much less than it was formerly and, as a result, there is a wholesale development of coarse vegetation and invasion of scrub, with the loss of species-rich short grass communities. In some other areas, the converse has happened. On acid dune systems, heavy grazing has resulted in the replacement of dune heath with a species-poor acid grassland. A wide range of problems is associated with the selection of the optimum level of grazing for the maintenance of species diversity in different types of dune system.

In the first year of the study, emphasis has been placed on visiting a wide range of British dune sites to ascertain the present intensity of grazing and the degree of species diversity. To date, 41 sites have been recorded, ranging

Aberlady, Midlothian. Spread of the inedible nettle, as a result of heavy rabbit grazing, along the edge of scrub which provides cover for the rabbits.

from Great Bay, St Martins, in the Isles of Scilly, to Breckon, Yell, in Shetland. On these 41 sites, no less than 39 were grazed by rabbits to some extent. Sixteen sites were affected by cattle grazing and 15 by sheep grazing. Grazing by hares was noted on 3 sites, while pony grazing only had a noticeable effect on one site.

The vegetation was recorded within 652 2m × 2m quadrats distributed between the 5 main herbaceous dune plant communities: yellow dune, dune heath, damp slack, wet slack and dune grassland. The data collected are still being analysed, but certain features are already clear. Within the dune grassland category, the mean number of species per quadrat on each site varied between 22 at Aberffraw, Anglesey, and 7 at Winterton, Norfolk. Where it was possible to distinguish between grazed and ungrazed sections within a single site, the impact of grazing became clear. For example, grazed dune grassland at Lindisfarne, Northumberland, had a mean of 17 species per quadrat, while ungrazed dune grassland only had 10. Within the sheep and cattle grazed enclosures at Saltfleetby, Lincolnshire, there were 15 species per quadrat, but only 8 in the grassland outside.

While, generally, the areas with a high species diversity were closely grazed, there were some areas, such as Kenfig, Glamorgan, where there was little or no grazing but nevertheless a high diversity. However, records show that all such areas had been grazed regularly in the past and that this practice had been reduced only recently. Experimental rabbit enclosures at Holkham, north Norfolk, had shown that, for a period of about 3 years after the cessation of grazing, species diversity is maintained or even increased; the loss of species only occurs some 5–10 years later. In contrast to the many species-rich grazed areas, there were more sites like Gibraltar Point, Lincolnshire, with a high intensity of grazing but a rather low species diversity.

The abundance of many ruderal species, such as creeping thistle (*Cirsium arvense*) and common nettle (*Urtica dioica*), indicated that the nutrient status of the soil was abnormally high as a result of the extensive growth of the nitrogen-fixing shrub, sea buckthorn (*Hippophae rhamnoides*). Previous studies (Boorman & Fuller 1982) showed that quite small increases in soil nutrient levels decreased species diversity. Many of the less vigorous dune species at Gibraltar Point were being excluded by the combined effects of competition from the growth of the ruderals and the extreme rabbit grazing pressure, which was accentuated by the dominance of unpalatable ruderal species.

L A Boorman

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Airborne Pollutants, including Radionuclides

Throughfall and Stemflow Under Different Trees

In a study of Scots pine (*Pinus sylvestris*) in Devilla Forest, it was found that large concentrations of sulphate and acidity reached the forest floor in throughfall, and especially in stemflow (Nicholson *et al.* 1980a). These results raised many important questions about the ways in which the canopy of Scots pine influences the chemical properties of precipitation (rain). They drew attention to the deposition of atmospheric pollutants on foliage and branches, and to the effects of these deposits on the chemistry of throughfall and stemflow. These effects are of particular interest as afforestation of moorland catchments is sometimes reflected in increases in stream acidification. For example, studies at Loch Ard Forest, 30km north of Glasgow, showed that chloride and sulphate concentrations in streams increased as stands of Sitka spruce (*Picea sitchensis*) grew older, and as afforested areas increased. It was suggested that closed forest canopies are effective 'filters' for air pollutants (Triennial Review of Research 1979–81).

To help in extending the findings at Devilla Forest from the specific (one tree species at one site) to the general, it was decided to examine the influence of a range of tree species growing at sites exposed to different mixtures of air pollutants (pollution climates).

Design of Study

Forest stands were selected at 3 locations in northern Britain: Devilla Forest, north-west of Edinburgh, where the previous study was made; Crathes Forest, near Banchory in north-east Scotland; and Gisburn Forest, in the Pennine hills of north-west England.

As Scots pine occurs at all 3 locations, it has been possible to make comparisons between sites. Other species available at some of the sites included Norway spruce (*Picea abies*) and Sitka spruce, enabling comparisons to be made of evergreen conifers with a deciduous conifer, European larch (*Larix decidua*), and broadleaved species, alder (*Alnus glutinosa*) and oak (*Quercus petraea*).

Crathes Forest (Scots pine, larch and Sitka spruce) was considered to be an 'unpolluted' site, with estimated mean SO_2 concentrations below 5ppbV. In contrast, at Devilla Forest (Scots pine and larch), annual mean concentrations of SO_2 and NO_2 were 12ppbV and 14ppbV respectively, when measured in 1978 (Nicholson *et al.* 1980b). The pollution climate at Gisburn Forest was thought to be similar to that at Devilla, and this was borne out by measurements of NO_2 concentrations at both sites during the experiments (Figure 21). At Gisburn, 4 tree species (Scots pine, Norway spruce, oak and alder)

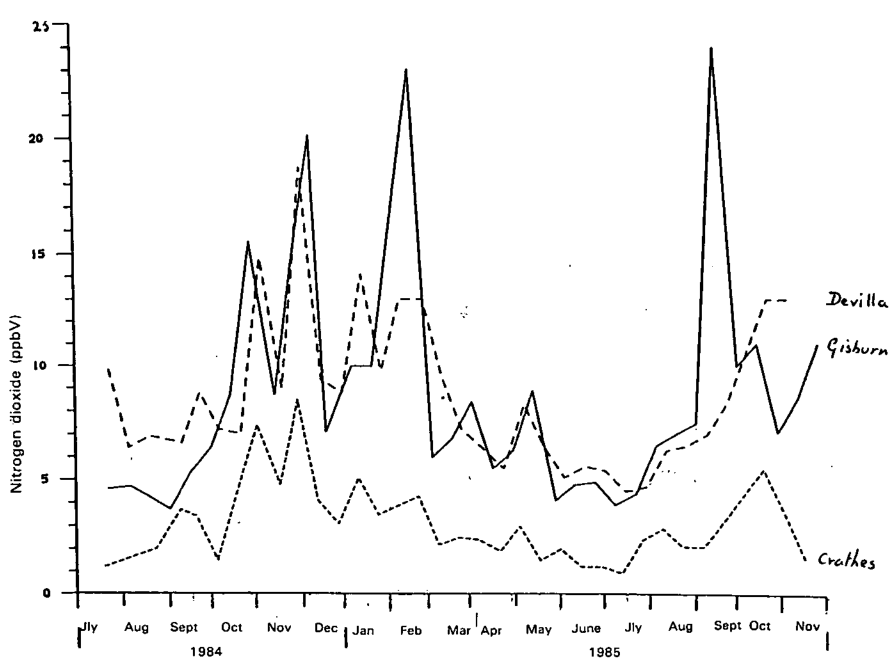
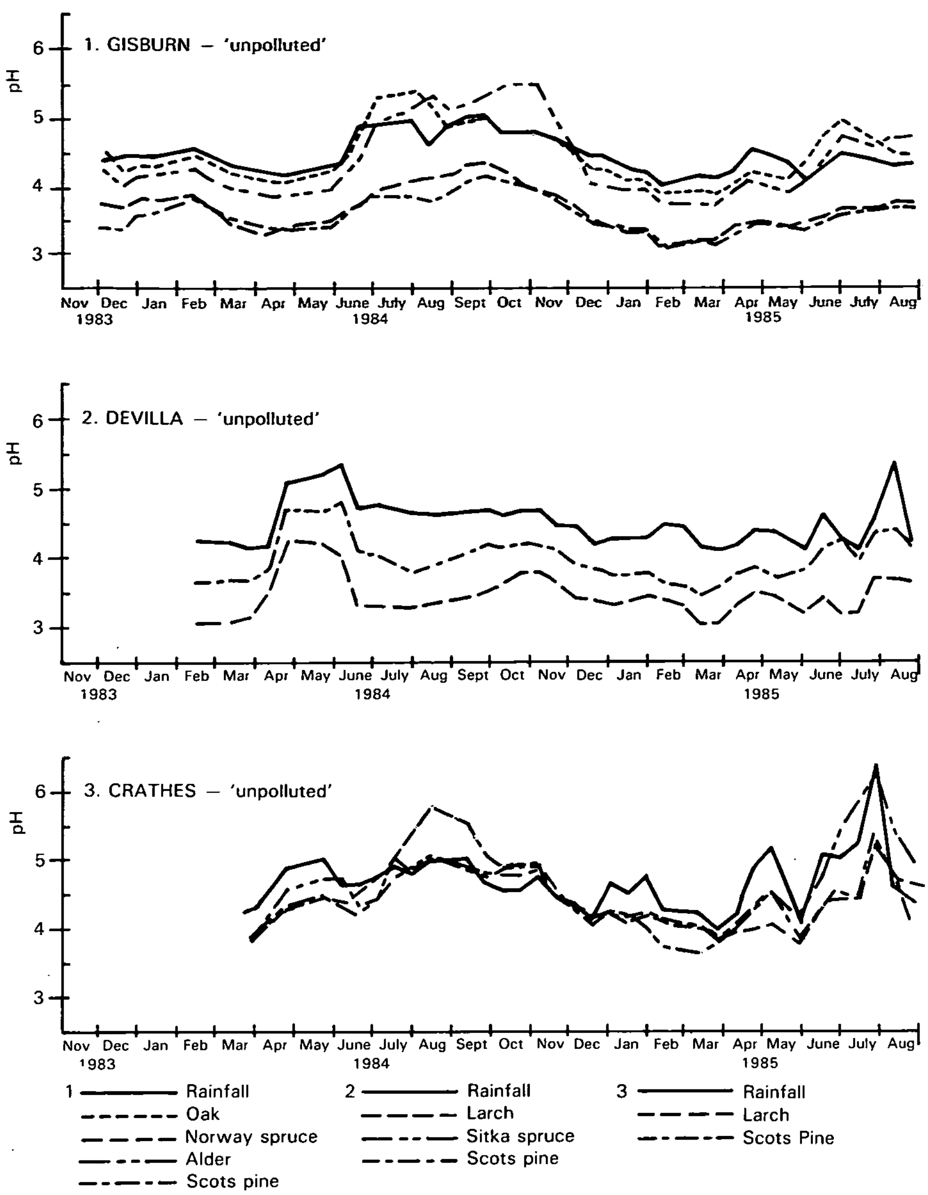


Figure 21. Atmospheric concentrations of NO_2 at Gisburn, Devilla and Crathes.



(a) Seasonal pH changes (running means) in rain and throughfall collected beneath different tree species at three locations.

were planted in replicate plots 30 years ago by the Forestry Commission.

Techniques for collecting incident rain, throughfall and stemflow were the same as in the previous study (Nicholson *et al.* 1980a). On each occasion (fortnightly) at each site, at least 2 samples of incident rain were collected and analysed. Six samples of throughfall were taken from under each tree species, 3 from under dense canopies and 3 from under less dense canopies, but only data from dense canopies are used in this account. Six stemflow samples were also taken for each tree species, 3 from large diameter trees and 3 from small diameter trees. In addition to measuring pH and conductivity of rain, throughfall and stemflow samples, concentrations of calcium, potassium, magnesium, sodium, ammonium and sulphate, nitrate, phosphate and chloride were measured.

Results

1. Atmospheric concentrations of nitrogen dioxide (NO_2) at the 3 sites Measurements were made to confirm the atmospheric concentrations of pollutant gases at Gisburn, Devilla and Crathes. Amounts of nitrogen dioxide (NO_2) were determined using diffusion tubes supplied by the Atomic Energy Research Establishment (AERE), Harwell. Measurements made from July 1984 to November 1985 showed similar annual mean concentrations at Gisburn and Devilla (8.8 and 8.7ppbV respectively). At Crathes, the annual mean concentration of NO_2 was 3.0ppbV. The seasonal changes at all 3 sites were similar (Figure 21). Concentrations from spring to autumn were relatively small. During winter, larger concentrations (> 15ppbV as a 2-week average) were observed at Devilla and Gisburn.

2. Seasonal pH changes in rain, throughfall and stemflow

2.1 Gisburn

Rainfall – as expected, rain was more acidic in winter than in summer (Figure 22).

Throughfall – the most acidic throughfall was collected under Norway spruce and Scots pine. Beneath these species, it was always more acidic than rain, the seasonal variation paralleling that of rain. In contrast, throughfall collected under oak and alder was less acidic than rain during parts of the summer and autumn, and even in winter it was less acidic than under the evergreen conifers (Figure 22).

Stemflow – irrespective of species (coniferous or broadleaved), stemflow was always more acidic than rain and throughfall (Figure 23). It was most acidic for the conifers in late spring, with pH less than 3.

2.2 Devilla

Rainfall – the season variation in acidity was small, with low values (high pH) in spring 1984 (Figure 22).

Throughfall – as at Gisburn, rain was markedly acidified by Scots pine foliage. It was acidified even more by larch, both in winter and summer, suggesting that even bare twigs have a significant acidifying effect (Figure 22).

Stemflow – this was significantly more acidic than throughfall. Stemflow from larch was more acidic than from Scots pine, except during April and May.

2.3 Crathes

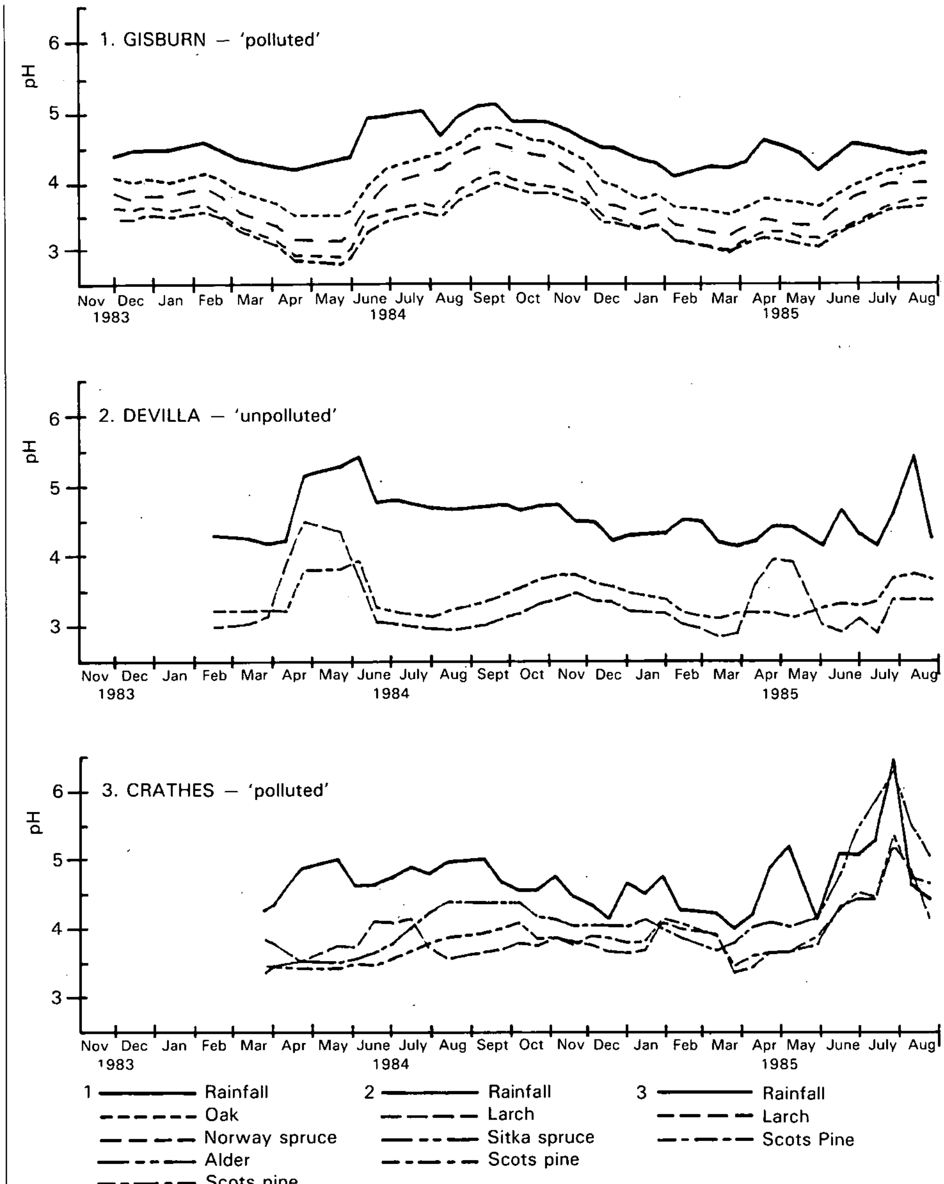
Rainfall – as at Gisburn, there was a seasonal cycle, with lower acidity (larger pH) in summer (Figure 22). Although concentrations of gaseous pollutants were less than at the other 2 sites, the rainfall acidity was not markedly different.

Throughfall – the acidity of throughfall from larch and Scots pine was similar to that of rain during summer and autumn, but was significantly greater during spring 1984 and winter 1984–85. In contrast, throughfall from Sitka spruce was less acid than rain during the summer (Figure 22).

Stemflow – as at the other sites, stemflow was usually more acidic than rain (Figure 23), the exception being stemflow collected from Sitka spruce during summer 1985.

Annual Inputs

Preliminary estimates have been obtained for the period August 1984–July 1985. The amounts of the major ions deposited in precipitation during this 12-month period are shown in Table 14. At all sites, a large proportion of the total ionic deposition was derived from sea salts (Na, Cl, Mg, some SO_4-S). The theoretical Cl:Na ratio for sea-



(*b*) Seasonal pH changes (running means) in rain and stemflow collected from different tree species at three locations.

Table 14. Inputs of major ions in rain at Gisburn, Devilla and Crathes, 1984–85

Experimental site	Na	Ca	Mg	K	Cl	SO_4-S	Rain (mm)
	Inputs (kg ha^{-1})						
Gisburn	29.8	6.1	3.4	1.9	45.9	20.1	1858
Devilla	10.2	4.5	1.8	2.1	28.9	12.5	940
Crathes	27.1	6.6	3.5	4.9	50.4	16.4	1312

derived material is 1.8, so there is evidence at Devilla of non-sea chloride in rain, presumably from the solution of hydrogen chloride gas (HCl) released by local industry. The absolute amounts of deposition were strongly influenced by the rainfall; the average sulphate concentration in rain at Devilla was 40% greater than at Gisburn, but, as there was twice as much rain at Gisburn, the amount of deposited sulphate was much greater.

The only tree specied studied at all 3 sites was Scots pine. The additional amounts of the major ions deposited on the forest floor below Scots pine (ie not attributable to rain) are shown in Table 15. The results are expressed as a percentage of the total deposition on the forest floor. The influence of non-sea chloride is clearly shown in the data from Devilla, suggesting that the additional sodium and chloride deposition was approximately in the ratio to be expected of sea salt. The values for sulphate of 64%, 54% and 40% for Gisburn, Devilla and Crathes respectively are consistent with the assessment of the relative exposure of the 3 sites to air pollution, but may also be related to the observed leaching of cations.

Table 15. Inputs of Na, Ca, Mg, K, Cl and SO_4-S under Scots pine at three sites: per cent attributable to sources other than rain

	Gisburn	Devilla	Crathes
Na	44	41	51
Ca	62	58	64
Mg	58	59	59
K	89	79	67
Cl	55	24	51
SO_4-S	64	53	40

In comparing the different tree species, it was found that, at Gisburn, the deposition of major ions not attributable to rain was greatest under Norway spruce. At Devilla, deposition attributable to non-rainfall sources was substantially greater under larch than under pine, whereas at Crathes the differences between larch and pine were less marked. Such comparisons, however, are confounded by canopy structure and planting density; the larch stand at Crathes was relatively more open (1600 stems ha^{-1}) than the Scots pine stand (2700 stems ha^{-1}).

Discussion

The amounts of mineral nutrients and other chemicals reaching the forest floor are largely determined by the chemical composition of throughfall and stemflow. This, in turn, is dependent upon the tree species and the concentrations of atmospheric pollutants present at different sites, but the mechanisms responsible are ill-defined. The relative importance of dry deposition to the canopy and leaching from foliage, twigs and branches need to be clarified. Current evidence tends to emphasize the rôle of foliar leaching, which we suspect has been underestimated (Cape *et al.* 1986).

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Cloudwater: A Pollutant Deposition Mechanism

Reports that forest decline in Germany and the USA occurred initially at high elevations have led to many theories implicating stresses attributable to air pollution (Schuut & Cowling 1985; Johnson & Siccama 1983, 1984). In these situations, 3 pollution deposition pathways seem likely to be of particular significance: (i) the dry deposition of nitric acid vapour and photochemically generated pollutants such as ozone (Ashmore *et al.* 1985; Smidt 1983); (ii) the heavy and episodic (orographic) rainfall in which concentrations of pollutants are likely to be increased by the seeder-feeder mechanism (Carruthers & Choularton 1984); and (iii) the capture by vegetation of very small wind-driven cloud drops that contain large concentrations of pollutants (Dollard *et al.* 1983).

To examine the properties of wind-driven cloud droplets which are trapped inefficiently by standard rain gauges, collections were made at Castlelaw Hill in the Pentlands, and Dunslair Heights near Peebles, both locations in south-east Scotland. Samples were collected using fine-filament gauges (Figure 24) based on the technique described in May (1961); the filaments were either nylon or PTFE. The efficiency with which cloud droplets impact on strings is directly related to windspeed and the ratio of string diameter: droplet size. Gauges with fine filaments are more efficient than those with coarse filaments; their efficiency also increases with increased windspeed (Chamberlain 1975). After being impacted on the filaments, the fine droplets coalesce into drops large enough to flow by gravity into collecting funnels. To estimate contamination by rain, comparisons were made between collections from gauges which were either open to the atmosphere or sheltered by a covering lid, 1.2m diameter. The constituents of these samples were analysed by ion chromatography and compared with those in rain collected in standard, 200m diameter, open glass funnels. An automatic weather station was also installed at Castlelaw.

Samples show that cloud droplets had consistently larger concentrations of hydrogen ions (they were more acidic) than rain and, as expected, by preventing the diluting effect of contaminating rain, the collections of cloudwater from lidded gauges were more acidic than those from open, unsheltered gauges (Figure 25). Cloudwater droplets typically had 2–5 times larger concentrations of hydrogen ions than rainwater, the most acid events being predominantly associated with air masses from continental Europe.

Unlike rain, the liquid collected by the fine-filament gauges was frequently brownish/black, an effect attributed to increased concentrations of particles (Figure 26).

When examined with a scanning electron microscope, the particles, which were spherical, were found to be 0.5–5μ min diameter, typical of pulverized fuel ash (PFA) produced by the industrial combustion of coal and/or aggregates of carbon commonly associated with domestic use of wood and coal (Figures 27 & 28). Because particles in the range 0.5–5μm diameter are inefficiently trapped by the gauge filaments in dry conditions, it is likely that they were collected during cloudwater

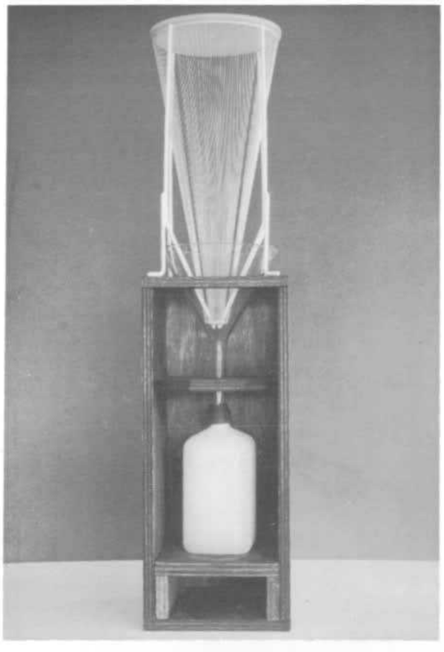


Figure 24. A fine filament gauge for collecting cloudwater droplets (see May, 1961) illustrates the construction of the open cloud gauge, with a polypropylene toothed edge lid, nylon collecting filaments, polyethylene coated frame, glass funnel and polypropylene collecting bottle.

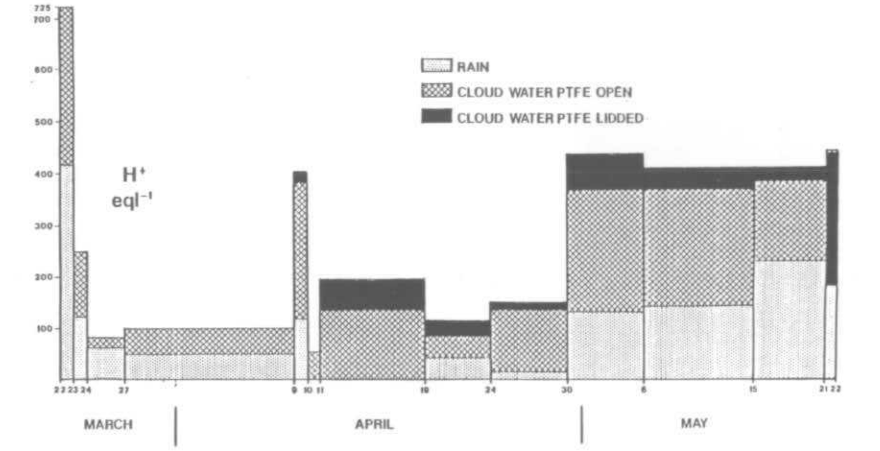


Figure 25. Comparisons of the concentrations of hydrogen ions detected in rain and cloudwater droplets, the latter being collected from gauges which were either open to the atmosphere or sheltering under a lid ('lidded'), (Castlelaw Hill 1985).

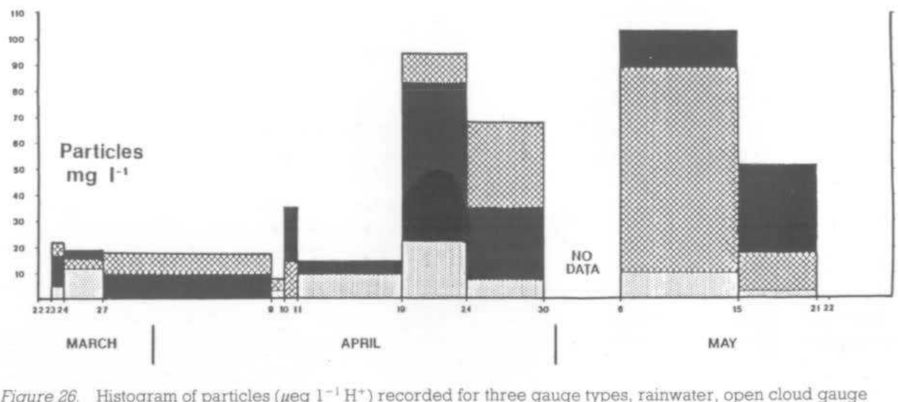
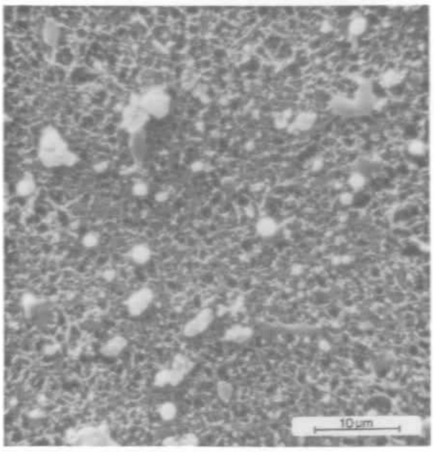


Figure 26. Histogram of particles (μeq l^{-1} H^+) recorded for three gauge types, rainwater, open cloud gauge and lidded cloud gauge at Castlelaw Hill from 22nd March 1985 to 22nd May 1985. Each collection period spans between the sample dates untreated, producing time averaged concentrations.



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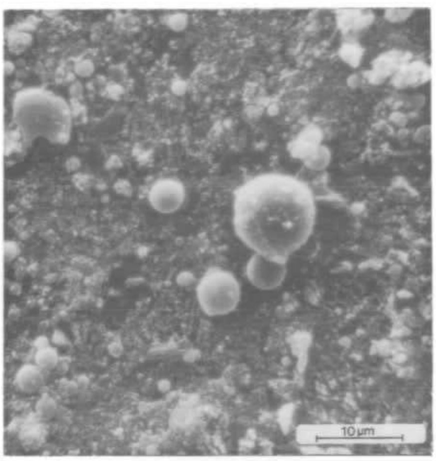

B

Figures 27 and 28. Scanning electron microscope comparisons of the particles separated from rain (A) and cloudwater (B) when samples, collected during the same 'event', were filtered through 0.2μm cellulose nitrate filters. Fine particles assumed to be carbon; large particles are pulverised fuel ash (PFA).

events. Over the course of time, the filaments became heavily contaminated by adhering particles which were removed neither by 5% HCl, as recommended by Falconer and Falconer (1980), nor by ultrasonication when immersed in solvent. Means of alleviating this problem, including gauge design, are being considered.

Theory suggests that tall plants with 'fine' foliage, such as conifers, are likely to be efficient collectors of cloudwater. It is likely, therefore, that trees growing in locations with frequent cloudwater events, as at high altitude, will be subject to a pollution load that occurs less frequently at low altitudes.

Effects of acidity on plant surfaces have seldom been observed, unless the solutions were more acid than pH 3 (Jacobson 1980). When working with rain, events of this sort were thought to occur relatively rarely, but the new work with cloudwater suggests that a re-appraisal is necessary. It will be necessary to determine the frequency of events with different hydrogen ion concentrations (pH, 'x' H^+ eq l^{-1}; pH 4.0, 'y' H^+ eq l^{-1}; pH 3.0, 'z' H^+ eq l^{-1}).

The role of particles in increasing the rates of leaf surface degradation was suggested by a related study of Scots pine (*Pinus sylvestris*) at a polluted site in the Pennines (Crossley & Fowler 1986). At this location, the stomatal antechambers were choked with PFA particles. We now need more evidence of the combined effects of particle accumulations and intensely acid solutions on the foliar exchanges of carbon dioxide and water vapour, and experiments are in progress.

A Crossley

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Towards Deriving a Method for Assessing the Vulnerability of River and Lake Catchments to Acid Deposition

Catchments draining poorly weathered bedrock and soils, such as those found in areas of volcanic origin, are known to be susceptible to acid precipitation. To a large extent, the 'susceptibility' is due to a lack of calcium, which is a major factor in providing, in surface waters, a buffering system to prevent them from becoming acid. Without adequate chemical buffering, surface waters may become increasingly acid, conditions favouring the mobilization of aluminium (Bull & Hall 1986). The resulting concentrations of aluminium, together with high acidity and small concentrations of calcium, create conditions which are harmful to freshwater biota, especially fish.

Several catchments in the UK are being studied so as to identify and measure the physical and chemical processes involved in the acidification of soils and fresh waters. Some of these studies involve members of the British Geological Survey, Freshwater Biological Association, Institute of Hydrology and Institute of Terrestrial Ecology, in addition to water authorities and river purification boards. We are beginning to understand how, and when, acid conditions are also likely to develop the concomitant concentrations of aluminium. Models now exist which can describe changes of stream acidity for individual catchments quite effectively (Cosby *et al.* 1986).

However, most catchments remain unstudied, while many of those being investigated are monitored only occasionally. To make generalizations, applicable to the majority of British fresh waters, we need a method for extrapolating from current detailed knowledge of a few catchments to the remainder. The method should provide the means for quantifying important factors, such as changing land use, which may influence the impact of acid precipitation on fresh waters.

Already, members of the British Geological Survey have mapped the susceptibility of UK groundwaters to acid deposition (BGS 1984), while ITE is classifying soils in relation to acid waters. We have been examining the possibility of classifying catchments, using a modification of the techniques developed for the classification of terrestrial habitats into land classes (Bunce & Heal 1984). The technique is well established and has provided a means for examining land use and the effects of changes in land use in areas in England (Bunce & Smith 1978), Scotland (Bunce & Last 1981) and Great Britain (Bunce & Heal 1984). The classification has provided a base for describing the present environment of Britain and, at the same time, for predicting the effects of potential changes.

In the ITE studies, we have used individual catchment areas as study units. They are attractive to work with as they may be defined easily from contour maps. Each is a convenient modelling unit in its own right, having identifiable sources (rainfall, springs) and sinks (outflow, evaporation, loss to aquifers). We are developing classifications which will group catchments into classes with similar ranges of physical, chemical and biological characteristics; they will then form the basis for assessing the vulnerability of surface waters to acid deposition.

Currently, catchments are being assessed in north-west England which drain into rivers sampled regularly by the North West Water Authority (NWWA). Information concerned with more than 100 different attributes related to geology, soil, rainfall and geographical location are being abstracted from maps for 87 river catchments and 33 lake catchments. With the application of cluster analyses and other discriminating procedures, it should be possible to sort the catchments into different classes, and also to identify key discriminating attributes. The latter should enable catchments, not included in the original classification, to be apportioned to the relevant class.

Initial studies on tributaries of the Rivers Esk and Duddon, rivers with problems of acidity (Crawshaw 1984), have shown differences between upland and lowland catchments which are correlated with chemical and biological measurements made by the NWWA. Streams draining upland catchments are usually more acid, more deficient in calcium, and lacking in acid-sensitive fauna (Figure 29). If the classification is extended to include other streams monitored by NWWA, catchment size becomes an important discriminator. Most Esk and Duddon catchments, however, are classified as 'small' (Figure 30), whilst a majority of the 'larger' class are not Esk or Duddon tributaries. Significantly, the 'small' class is subdivided into upland and lowland catchments, as before. If catchments from the southern Pennines are also included, then geological differences become important in the analysis.

It is planned to extend this classification to catchments being studied intensively by others elsewhere in Britain, so that these detailed studies can be placed into a wider UK perspective, facilitating more assured predictions.

The method of classification has several advantages. It is flexible and the data can be readily re-appraised with the development of new classifications. It enables catchments with similar combinations of characteristics to be identified readily, an advantage that facilitates the search for representative samples. If the field responses to acid inputs are correlated with catchment classes, it is possible to envisage predictive models. The absence of such a relation would indicate the undesirable limitation in the extent of our current knowledge.

Because of costs, detailed studies can only be made in a few catchments. However, the system of catchment classification may allow predictions to be made by extrapolation. For this reason, it was decided to arrange a DoE/NERC-sponsored workshop, in March 1986, to bring together interests in catchment classification and modelling, areas of importance to scientists and government advisers.

K R Bull & Jane R Hall

40 ESK AND DUDDON CATCHMENTS

Indicators:
Low minimum altitude (<100m)
medium low rainfall (1750–2500mm)
fenced fields
small amount of drift soils present
24

Indicators:
medium high rainfall (2500–3250mm)
16

'LOWLAND' STREAMS
13 Esk streams
11 Duddon streams
24 streams Ca > 2mg^{-1}
12 streams Ca > 4mg l^{-1}
18 streams mayfly larvae present

'UPLAND' STREAMS
4 Esk streams
12 Duddon streams
10 streams Ca < 2mg l^{-1}
6 streams Ca > 2mg l^{-1}
2 streams Ca > 4mg l^{-1}
2 streams mayfly larvae present

Figure 29. Classification of Esk and Duddon tributaries showing 'lowland' and 'upland' classes. Chemical and biological data collected by North West Water Authority (Prigg 1983) are shown which illustrate the difference between the classes.

72 CATCHMENTS

fenced fields
low stream gradient
presence of waterfalls in catchment
25

low size (< 3.3km^2)
low rain volume (< 20m^3 yr^{-1})
47

'LARGE STREAMS'
2 Esk streams
5 Duddon streams
18 other streams

medium low rainfall (1750–2500mm)
low minimum altitude (< 100m)
small amount of drift soils present
22

high maximum altitude (> 750m)
medium high rainfall (2500– 3250mm)
25

'SMALL LOWLAND' STREAMS
11 Esk streams
6 Duddon streams
5 other streams

'SMALL UPLAND' STREAMS
4 Esk streams
12 Duddon streams
9 other streams

Figure 30. Classification of 72 catchments from NW England. The classification includes the 40 catchments of the Esk and Duddon tributaries. Most of the Esk and Duddon catchments fall into the same 'lowland' and 'upland' classes in Figure 29.

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How Much Hydrochloric Acid is Emitted into the Atmosphere Over Britain?

Hydrochloric acid gas (HCl) is often disregarded as a contributor to 'acid rain'. However, rain chemistry records suggest that, at some sites, HCl can be a significant source of acidity. An investigation of HCl emissions has recently been completed. It was sponsored by 2 major plastics manufacturers, Imperial Chemical Industries plc (ICI) and Norsk Hydro, who are responding to developments in other European countries, such as Switzerland, where possible damage from refuse incinerator emissions is the subject of public concern. They required estimates of the amounts of HCl produced when polyvinyl chloride (PVC) plastic waste was burnt in domestic refuse incinerators.

HCl is produced when substances containing chlorides are burned. Coal is the major source of HCl in Britain, and British coal has an unusually large chloride content, averaging 0.23%. It is estimated that 94% of this chloride is found as HCl in flue gases (Iapalucci *et al.* 1969). With an annual UK coal consumption of about 12.5 Mt, some 227 kt of HCl is likely to be emitted each year. Other fuels, such as oil, have a very small chloride content and appear to be insignificant sources of HCl.

Estimating HCl emissions from waste incinerators is difficult, as concentrations in the flue gases fluctuate greatly from hour to hour. These fluctuations probably reflect variations in the refuse being burned, particularly chloride-containing wastes such as PVC, salt, bleached paper and batteries, which all produce HCl during incineration. Variations in the wastes themselves inevitably increase the problem of obtaining reliable estimates of their composition. The results of published surveys are variable; for example, reports in the literature over the last 15 years give the percentage of PVC in domestic waste at between 0.1% and 1.5%. From figures supplied by the British Plastics Federation for the consumption of PVC in Britain, it is possible to make some assumptions about (i) the fate of PVC products and (ii) the percentages of the different products that are likely to be found in domestic waste. The figures suggest that British domestic refuse contains a maximum of 0.7% PVC, ie about 230 kt of PVC is disposed of each year as refuse. Of the domestic waste, about 10%, and therefore 10% of the PVC, is burned in Britain. Because 1 t of PVC produces about 0.43 t of HCl (Robertson 1974), it seems that 10 kt HCl will be emitted each year. PVC is not the only substance in domestic waste that produces HCl during incineration. Estimates in the literature suggest that the incineration of non-PVC wastes accounts for between 24% and 75% of all incinerator emissions of HCl. A recent survey of British waste (Warren Spring Laboratory, pers. comm.) supports a median value of about 50%. Thus, PVC and non-PVC wastes contribute equally to the HCl emitted from waste incinerators. Industrial sources of HCl in Britain include the steel and glass industries. However, their emissions are small, and together with other minor sources, such as automobile exhausts and HCl produced by the breakdown of chlorinated hydrocarbons, they account for only 3 kt of HCl each year.

Total annual HCl emissions to the atmosphere in Britain are, therefore, about 250 kt, 91% of which is attributable to coal burning, 8% to waste incineration (including 4% for PVC wastes), and 1% to other sources. In terms of total potential acidity, these emissions are small compared with other acid-forming pollutants, ie sulphur dioxide (SO_2) and nitrogen oxides (NO_x). Of the total acid emissions from the UK, 71% are attributable to SO_2, 25% to NO_x and only 4% to HCl. However, the fate of HCl in the atmosphere differs from that of SO_2 or NO_x. The latter gases remain in the atmosphere for relatively long periods (several days) before being removed by wet or dry deposition.

In contrast, the more reactive HCl is removed very efficiently by natural surfaces, such as water, soil or vegetation. HCl is also highly soluble, and dissolves rapidly in rain and cloudwater. It will thus be removed from the atmosphere quickly, and is unlikely to be transported long distances from sources of emissions, as happens with SO_2 or NO_x.

As a result of its rapid deposition, the environmental effects of HCl are mostly local, rather than 'long range', and include foliar scorching in woodland near a PVC-cable salvage installation (Wood 1968) and damage to garden plants near a hospital incinerator (Bohne 1969). However, these events are rare and HCl emissions are mostly successfully controlled by legislation. HCl has been implicated in neither the acidification of fresh waters and soils nor the etiology of forest dieback. However, it may intensify the acidity of rain near large sources (Pellett *et al.* 1983), which could not only damage vegetation but also corrode metalwork and paintwork.

P J Lightowlers

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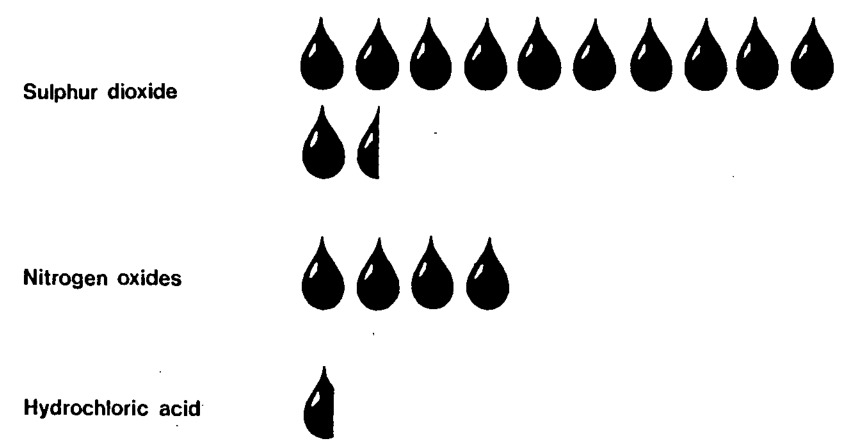

Figure 31. Acidity in the environment: the contribution of acid gases from Britain. 1 symbol = 10 kt acidity (H^+) yr^{-1}

Influences of an Aluminium Reduction Plant on the Accumulation of Fluoride in Invertebrates

For several years, ITE has examined the pathway of fluoride released from an aluminium reduction plant near Holyhead in Anglesey, north Wales. Accumulations in lichens, trees, other vegetation, birds and mammals have been described previously (eg Perkins 1985). This note describes the concentrations of fluoride found in a wide range of invertebrate species from a range of groups. Apart from the report of Dewey (1973) and review of Alstad *et al.* (1982), little was known of the fluoride/invertebrate relationship.

Eight sites in a range of habitats within 1km of the reduction plant were sampled, and 3 control sites in the Lleyn peninsula, 50km to the south. Invertebrates were sampled using a selection of methods: pitfall trapping, sweep netting, beating, searching 'by eye', and heat, flooding and hand extraction from turf and litter samples. Specimens collected were identified, dried at 60°C, and analyzed for fluoride. When necessary, samples from a single site on different occasions were combined to obtain the minimum weight, 0.05g dry tissue, needed for accurate analysis.

The sites were located in 3 distinct exposure zones: (i) 3 sites in a control zone, with no detectable fluoride deposits; (ii) 3 sites in an intermediate exposure zone upwind, with an average of 0.2g m^{-2} yr^{-1} total bulk deposition of fluoride; and (iii) 5 sites in a heavily polluted downwind zone, with 1.2g F m^{-2} yr^{-1} (Perkins, pers. comm.).

The largest concentrations of fluoride, more than 1000μg F g^{-1} dry tissue, were found in (i) woodlice in the heavily polluted zone and (ii) millipedes in the intermediate zone (Figure 32). These figures were followed in descending order by 671μg F g^{-1} in woodlice in the intermediate zone and approximately 400μg F g^{-1} in spiders and mites in the heavily polluted zone. The smallest mean concentrations, $\leqslant$10μg F g^{-1}, were detected in grasshoppers and harvestmen, in the intermediate and control zones, respectively.

Within each systematic group of invertebrates, mean concentrations of fluoride were largest in the heavily polluted zone and least in the control zone. However, the mean concentrations in some groups in the control zone were larger than those in other groups in the heavily polluted zone. For instance, beetles had only 50μg F g^{-1} in the heavily polluted zone, whereas woodlice and millipedes in the control zone had 100μg F g^{-1}. Although partly obscured by these differences in concentrations between the groups and variation in feeding habit within each group, there was a tendency for accumulation to increase in the following sequence: herbivores (eg grasshoppers)→predators (eg harvestmen and spiders)→ scavengers (eg woodlice and millipedes). Dead vegetation, a large part of the food of scavengers, has been shown to have about twice as much fluoride as living vegetation (Davison & Blakemore 1976). Studies at species level (Buse 1986) also demonstrated this tendency: staphylinid beetles, principally scavengers, had a larger mean fluoride concentration (134μg F g^{-1}) in the heavily polluted zone than the mean (38μg F g^{-1}) for beetles in this zone.

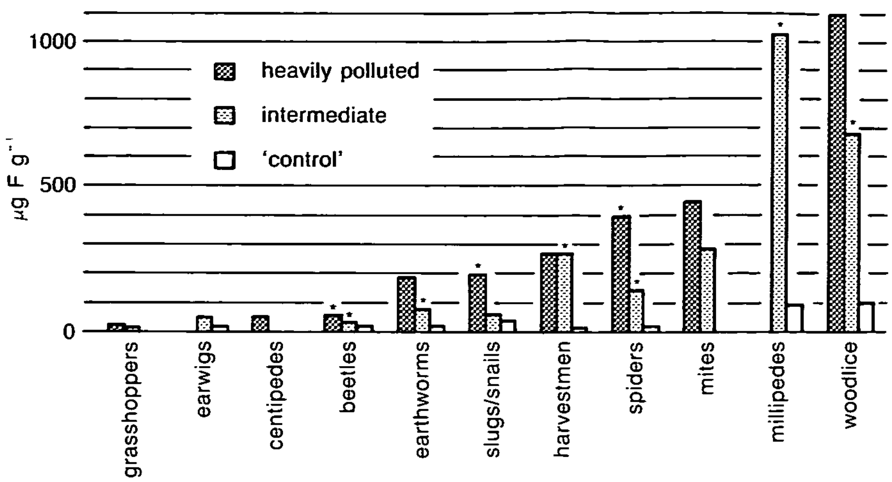

Figure 32. The different accumulations of fluoride (μg F g^{-1} dry tissue) found in invertebrates collected at sites affected to different degrees ('control', intermediate and heavily polluted) by emissions from an aluminium reduction plant.
*, indicates that tissue concentrations in intermediate and heavily polluted sites were significantly larger than in 'controls' or intermediate sites respectively.

Although the actual amounts of fluoride in individual species are important in passing fluoride to predators, they do not necessarily reflect the importance of different invertebrate species in the pathway of fluoride. Their role needs further investigation.

A Buse

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^{137}Cs and $^{239/240}$Pu in Sheep Milk

(This work is funded by the Ministry of Agriculture, Fisheries and Food and was carried out in conjunction with the Hill Farming Research Organisation)

Low-level liquid discharges into the Irish Sea by the British Nuclear Fuels plc reprocessing plant at Sellafield have resulted in enhanced levels of many radionuclides on the tidally inundated saltmarshes of the Esk estuary (Horrill 1983, 1984). Recent field studies into the transfer of ^{137}Cs and $^{239/240}$Pu from saltmarsh vegetation to sheep tissues have shown consistently higher concentrations of ^{137}Cs in lamb tissues compared to the tissues of ewes. In contrast, the concentration of $^{239/240}$Pu was higher in ewe liver than lamb liver, and similar in other tissues of both ewes and lambs (Howard & Lindley 1985). The increased ^{137}Cs activity in lamb tissues could be due to differences in a number of physiological parameters, such as intestinal absorption rates, body tissue turnover rates or dietary intakes. In the latter case, ^{137}Cs ingested by lambs in ewes' milk may be more available for absorption than ^{137}Cs associated with saltmarsh vegetation. During the lactating period of 1985, ewes grazing the saltmarsh were milked at regular intervals and the relative importance of ^{137}Cs and $^{239/240}$Pu intake by lambs via milk was estimated.

The Drigg saltmarsh (National Grid reference SD/065975) lies about 7km south of the Sellafield reprocessing plant. A range of different fission and activation products are deposited on the saltmarsh, in association with silt particles brought in during tidal inundation (Howard 1985). The radioactivity of the saltmarsh vegetation is consequently considerably higher than the heathland and sand dunes beyond, to which the flock of sheep grazing the saltmarsh have free access. The grazing behaviour of the sheep and its effect on intakes of radionuclides have already been described (Howard 1985). The ewes are removed from the saltmarsh site to a pasture close to the farmstead for the lambing period. They are returned to the saltmarsh about 2–3 weeks after giving birth.

The ewes were milked fortnightly from late May until mid-August, covering about week 2 to week 14 of lactation, and the first sample was taken before the sheep were returned to the saltmarsh. The sheep were gathered in from the saltmarsh, and penned separately from their lambs. An intravenous administration of 1ml of oxytocin (10 units ml^{-1}) was used to enable hand milking of the ewes which were restrained on a raised stretcher. Vegetation samples were taken from the area of the saltmarsh where the sheep had been grazing, and also from the pasture where lambing had occurred.

^{137}Cs was determined in milk and dried ground vegetation by gamma spectroscopy. $^{239/240}Pu$ analysis was carried out using chemical separation and alpha spectrometry.

The mean daily production of milk by the ewes gradually declined through the lactating period, from 1.55l in week 2 to 0.3l in week 14. The only gamma-emitting fission product detected in the milk was ^{137}Cs; the mean concentration of ^{137}Cs found in the milk was considerably greater than that of $^{239/240}Pu$ (Figure 33). There was a

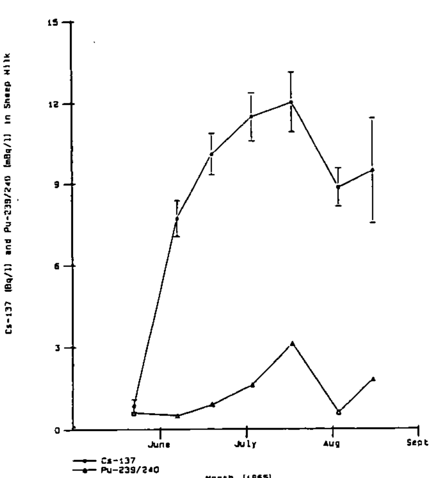

Figure 33. The variation in the concentration of ^{137}Cs and $^{239/240}Pu$ in ewe milk over the lactating period.

gradual rise in the concentration of both radionuclides over the first 6 weeks on the saltmarsh (lactation weeks 4–10), until a drop in activity in lactation week 12 when the ewes were taken off the saltmarsh for dipping, 4 days before the samples were taken. The activities recovered slightly in week 14 after the sheep were returned to the saltmarsh, indicating a fairly rapid response to the differing activities of ingested vegetation. In comparison, activities of ^{137}Cs and $^{239/240}Pu$ in milk from a ewe in east Scotland were 0.11Bq l^{-1} and 0.2mBq l^{-1} respectively.

By combining milk production with radionuclide concentrations, the daily output of ^{137}Cs and $^{239/240}Pu$ in milk available to lambs was found to reach a maximum in lactation in week 8 for ^{137}Cs and in week 10 for $^{230/240}Pu$, and then declined rapidly (Figure 34).

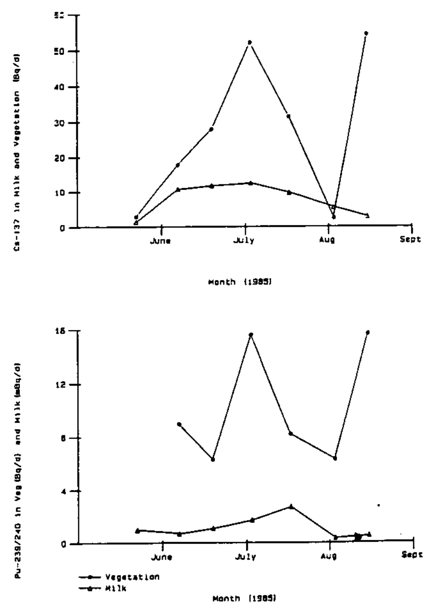

Figure 34. Estimate intake of ^{137}Cs

Estimates of vegetation intake by weaning lambs were used to calculate the gradual increase in lamb ingestion of radionuclides associated with saltmarsh vegetation (Figure 34). ^{137}Cs intake by lambs from milk constitutes a significant proportion (up to 38%) of the total intake in the early lactation weeks. In contrast, milk is a relatively insignificant source of $^{239/240}Pu$, accounting for no more than 0.4% of lamb intake at any point over the study period. ^{137}Cs in the milk may be more available for absorption than that associated with saltmarsh vegetation. Much of the ^{137}Cs is strongly bound to silt particles on the saltmarsh vegetation and passes through the gut so that faecal concentrations of ^{137}Cs are about 2–3 times higher than vegetation (Allen *et al.* 1983). Laboratory experiments are currently being conducted by ITE and the Hill Farming Research Organisation to compare the absorption by lambs of ^{137}Cs from milk and saltmarsh vegetation.

The transfer coefficient from saltmarsh vegetation to ewe milk can be used to compare radionuclide levels in vegetation and milk, using the formula:

$$Fm = \frac{^{137}Cs \text{ concentration in milk } (Bq\ l^{-1})}{\text{daily intake of } ^{137}Cs\ (Bq\ day^{-1})}$$

The daily intake of the ewes was estimated from the radionuclide content of the vegetation, the daily intake of vegetation by lactating ewes (Milne, pers. comm.), and the grazing behaviour of the flock (Howard 1985). Transfer coefficients for both ^{137}Cs and $^{239/240}Pu$ increased over the lactating period to a maximum of 8.3×10^{-2}d l^{-1} and 8.2×10^{-5}d l^{-1} respectively. Those for ^{137}Cs were 3–4 orders of magnitude greater than for $^{239/240}Pu$, reflecting the greater mobility of ^{137}Cs in biological systems.

Ewe milking has been a comparatively minor farming practice in the United Kingdom. Recently, renewed interest has appeared in milking sheep, and several farms in Cumbria and the Scottish Borders now have British milk sheep. Sheep milk is unlikely ever to rival cows milk in the British diet, but we can now predict the expected ^{137}Cs and $^{239/240}Pu$ activity of the milk.

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- **Plant Physiology and Genetics**
- **Cone Induction in Sitka Spruce**

Introduction and Methods
Considerable progress has been made in recent decades in overcoming some of the problems which have beset research on reproduction in forest trees (Longman 1985a, b; Ross & Pharis 1985). Compared with those of annual and biennial crop plants, the long life cycles of trees generally make it necessary to prepare for investigations a long time in advance; the experiments may involve the grafting (on to seedling rootstocks) of 'mature' scions from the crowns of older trees that have passed through the 'juvenile', largely non-flowering, stage. Until recently, most reproductive studies in forest trees have been made on sizeable specimens growing in the field. These studies involve working with awkwardly large material possessing a complex shoot system that is normally mainly or wholly vegetative, in circumstances in which biological variability can easily defeat the whole object of the research. However, with lodgepole pine (*Pinus contorta*), western red cedar (*Thuja plicata*) and birch (*Betula* spp.), methods have been developed which permit the miniaturization of experimental trees so that they can be grown in pots in glasshouses or growth chambers, and it may even become possible to study cone formation in aseptic culture (Coleman & Thorpe 1978).

An experiment was started in 1982 within a 10-year-old plot of clonal, mature grafts of Sitka spruce (*Picea sitchensis*), growing near Edinburgh, Scotland. Based on successful results with cone induction in other genera, 51 of the 94 trees were completely 'ringed' (girdled) in May 1982, just above the origin on the main stem of vigorous 5/6-year-old branches, the rings being treated with wound paint. In June 1983, following an encouraging preliminary trial, the plant hormone gibberellin was injected (20 mg per tree of a mixture of GA_4 and GA_7 in alcohol), using the methods of Dick and Longman (1985). Half the dose was put into each of 2 holes drilled on opposite sides of the main stem in 25 ringed and 21 unringed trees, generally below the 3/4-year-old 'interwhorl' branches of each tree (see Figure 38). Because cones are formed within the buds during the summer, and then emerge the following spring, assessments of the effects of treatments were done in 1983 and 1984, with an additional count in 1985 to determine whether coning was still being influenced.

Cone Induction
Ringing slightly increased male and female cone formation in 1982, which year, judged by flowering records for 6 previous seasons, was unfavourable for cone initiation at this site, as was 1984. By contrast, in the warmer, sunnier and drier weather conditions of 1983, both ringing and GA injection stimulated cone formation to a remarkable extent (Plates 2–4). Mean numbers

Plate 2. Upper crowns of two Sitka spruce grafts of the prolific clone 143 in September 1984, showing ripening female cones that were initiated in 1983; left – untreated control; right – tree injected with GA and ringed

Plate 3. Substantial pollen cloud released in May 1984 from a Sitka spruce graft of clone 684 that had been injected with GA and ringed

Plate 4. Female terminal and male lateral cones on the same shoot of a Sitka spruce graft of clone 804 that had received the GA + ring treatment. Here the cones are on the tip section of a 5-year-old 'whorl' branch. (18/5/84)

(All photographs by K A Longman)

of female cones per tree were increased more than 9-fold above the control value by ringing, and almost 12-fold when injected with $GA_{4/7}$ (Figure 35i). On trees given both treatments, the effects were additive, and an average of 600 female cones was produced. Numbers of male cones were also greatly increased by each treatment when used alone, especially by ringing, with mean values of nearly 900 cones per tree, compared with 120 in the controls (Figure 35ii). When both treatments were

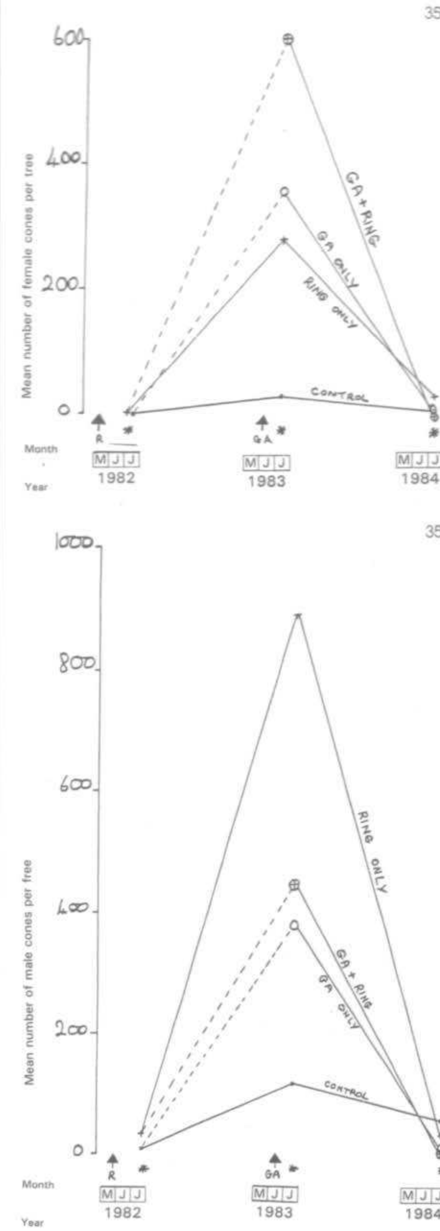

Figure 35. Effects of ringing and/or injection with 20mg of a $GA_{4/7}$ mixture on the numbers of cones formed per tree in 1982–84 by Sitka spruce grafts: i. female cones; ii. male cones. ↑ – indicates time of month and year when ringed (R) and/or injected (GA); * – shows approximate time at which cones begin to differentiate (Owens & Molder 1976)

applied together, however, there was a significant antagonistic effect, in contrast to the effects on female cones; only about 400 male cones per tree were formed in GA-injected trees, whether or not they were ringed. Perhaps there was competition between the sexes for coning sites at such high levels of reproductive activity.

The intensity of coning was also assessed by estimating the proportion of potential sites actually occupied by male and female cones. On average, less than 10% were occupied by cones in the controls: most of the sites contained pre-formed vegetative shoots. In contrast, more than 40% contained cones after treatment with GA, about 60% after ringing, and about 65% after GA injection and ringing. Because the proportion of vegetative buds was correspondingly decreased, the induction of large numbers of cones is likely to have decreased the production of needles substantially. Whether carbon assimilation per tree would be strongly reduced will depend on the ability of trees to compensate for this loss, a topic being investigated using another member of the Pinaceae, lodgepole pine (*Pinus contorta*).

The responses of different clones were often markedly different. Total numbers of buds available for coning ranged from less than 500 in clone 788 to more than 3000 in clone 143 (Figure 36). Clones 1224, 142, 1002 and 455 initiated a small proportion of cones, whereas 30–70% of buds in clones 683, 555, 567, 684 and 143 formed cones. A pronounced female tendency (85–95% of cones were female) was shown in clones 1224, 142 and 683, while a 3:1 male bias was seen in clones 1226 and 684. Judged by absolute numbers of male cones produced, and assuming that they directly reflect the ability to produce pollen, it is clear that more than 60% of the pollen cloud would have originated from just 2 of the 12 clones (see Plate 3). To prevent seed orchards being dominated by a few prolific male parents, future research will investigate if the reproductive tendencies of clones can be altered by changing the doses of applied growth regulators or by adopting other treatments. It should be remembered, however, that the successful fertilization of female cones also depends on synchrony between pollen release and ovule receptivity, and on genetic compatibility between male and female partners.

Seed Production
The results of this experiment were used to predict the likely seed yields obtainable from a seed orchard (Table 16). In September 1984, sample cones were taken from the 5 clones which had produced ripe female cones in the untreated controls. It was found that the cone induction treatments had appreciably decreased numbers of filled seeds per cone, possibly because of competition where heavy crops of cones were produced (Plate 2). Germination percentages were high, presumably related to the formation of an effective pollen cloud (Plate 3).

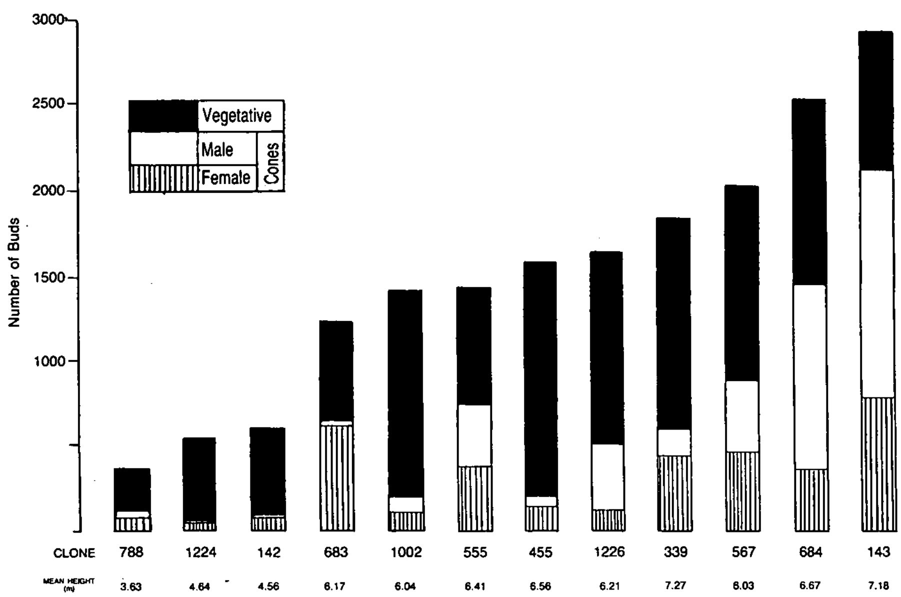

Figure 36. Mean number of reproductive and vegetative buds in different grafted clones of Sitka spruce. Clones ranked in order of increasing total numbers of buds in the majority of the upper crown; mean heights at the end of 1983, 11 years after planting

Table 16. Effects of GA injection and ringing on viable seed production by Sitka spruce grafts following cone initiation in 1983 (after Longman *et al.* 1986)

Treatments	Number of seeds per cone	% germination	Number of viable seeds per tree	Projected viable seed yield (kg ha^{-1})
Control	88	91	4 400	36
GA	67	88	42 800	310
Ringed	56	92	19 400	135
GA + ring	46	79	20 600	136
	NS	*	*	—

* Statistically significant; NS not statistically significant.

A small but significantly lowered germination percentage occurred when trees had received $GA_{4/7}$, but germination and early seedling growth appeared to be normal. Despite these reductions, numbers of viable seeds per tree and projected seed yields per hectare were still greatly increased by treatment. Production was enhanced from 36 kg ha^{-1} in the controls to 135/136 kg ha^{-1} by ringing (with or without GA) to 310 kg ha^{-1} by GA injection alone. While yields of seed orchards depend on the choice of male and female parents, the ages of the trees, seasonal factors and site, it is clear that cone-inducing treatments offer a real opportunity to overcome the sparse and irregular performance typical of spruce species.

Cone Distribution
There is little doubt that lack of flowering, and of reliable methods for stimulating it, are major reasons for the slow progress made with forest tree improvement, compared with that of other crops. In order to be in a position to develop and refine practical cone induction techniques, much more needs to be known about the morphology and physiology of reproduction. For this reason, the successful stimulation of coning in Sitka spruce was used to make a detailed study of cone distribution. Cones are initiated on current year shoots, and can occur either terminally or laterally (Figure 37). Untreated control trees had a predominance of terminal male cones, with fewest terminal female cones. GA injection, on its own, stimulated all categories of cones, but especially those produced laterally. Similarly, ringing increased all types of cones, but in this instance male cones predominated. The combination of GA injection and ringing, in contrast, favoured female cones particularly.

These results indicate that the different treatments did not uniformly stimulate each type of cone. However, they do occur in a precisely defined sequence, with lateral female cones highest in the crowns, followed by terminal female cones, lateral male and terminal male cones in overlapping zones down the tree (Figure 38). This sequence was not appreciably disturbed by treatment (Dick *et al.* 1986), although the overlapping zones may be more or less extensive, or absent altogether. Two cone types may occur on a single shoot (Plate 4).

A systematic horizontal progression of cone types from tip to base was also noticeable on the larger branches. When examined in detail

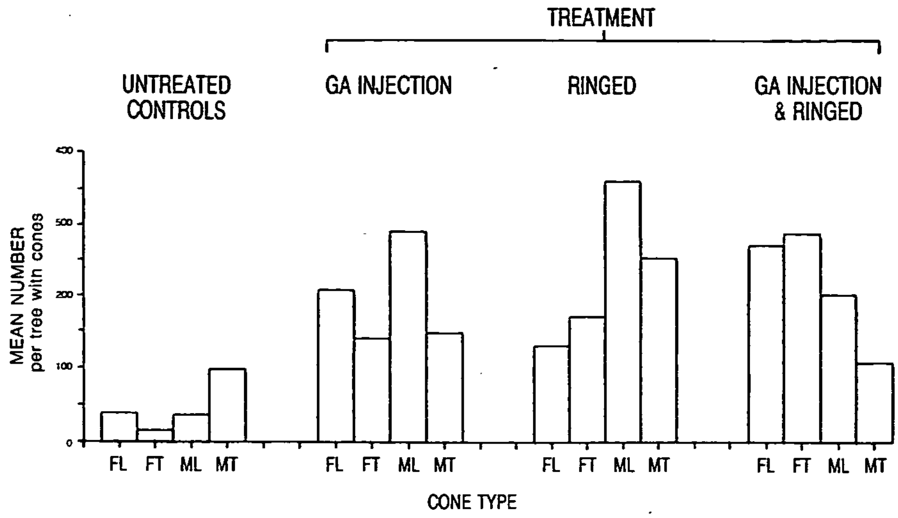

Figure 37. Effects of GA injection and/or ringing on mean numbers of cones per coning tree on Sitka spruce grafts. Types of cones: F – female; M – male; L – lateral; T – terminal

in clone 686, this progression was found to be related to the 'order' of their different side branches. The proportions of lateral female and male cones and terminal females were maximal on second order branches, whereas terminal males were most abundant on third order shoots (Figure 39). Very few cones

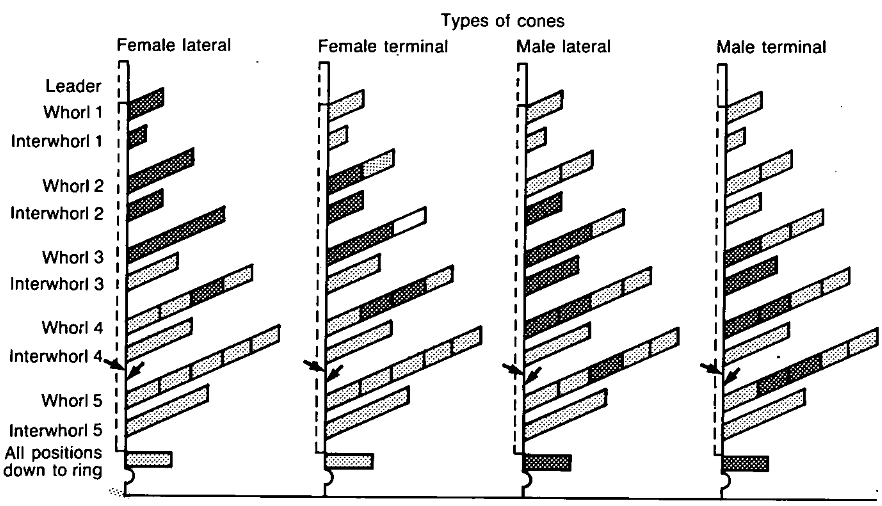

Figure 38. Distribution of the 4 types of cone on Sitka spruce grafts. Areas shaded are those containing 5% or more of the mean number of that type occurring in each section of the crowns of the 48 trees, irrespective of treatment or clone; 'whorl' branches divided into yearly sections. ↓ – usual injection site; ( ) – ringing, usually above the 7/8-year-old 'whorl'

developed on fourth order shoots, the highest branch order produced.

For the future, it is planned to explore further the relationships between the 4 cone types and the vigour and position of shoots and buds; to study the effects of different amounts of growth substances; and to breed clones that might start reproduction, while the plants are still small enough to be grown in controlled environments. These studies need to be paralleled by detailed morphological records of reproductive and vegetative development (Owens & Molder 1976; Couper 1985), so as to understand the precise timing and nature of key physiological 'decisions'. It now seems that the study of tree reproduction, a long-neglected area of plant physiology, is yielding to the kind of thorough study that could have a profound influence upon the genetic improvement of forests in the 21st century.

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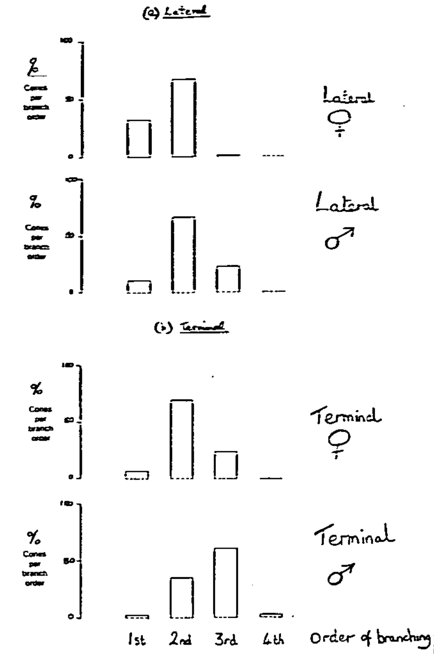

Figure 39. Percentage distribution of the four cone types appearing on 1st, 2nd, 3rd and 4th order branches in one clone of Sitka spruce grafts

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Stem Bending When Trees are Being Windblown

Many measurements have been made in the UK of the mechanics of tree movement (eg Mayhead *et al.* 1975), but few studies have fully described the relationship between overturning and windspeed.

Petty and Swain (1985) described the bending and breakage of stems, taking into account the vertical distribution of forces in conditions in which canopies were subject to 'wind loading'. More recently, staff at the Forestry Commission's Northern Research Station have extensively investigated aeromechanical aspects of the problem in a stand of Sitka spruce (*Picea sitchensis*) at Rivox Forest, near an Institute of Terrestrial Ecology field station.

Results from this aeromechanical research are now becoming available (Scannell 1983; Miller 1986), and ITE has also collected data describing the distribution of canopy biomass. Hence, it is opportune to combine the 2 sets of information into the construction of a mathematical model of wind overturning (Milne 1986).

The stand of Sitka spruce in Rivox Forest was planted in 1962. In autumn 1983, it was decided that one block of the forest should be thinned experimentally and the aeromechanical effects investigated. Before thinning, top heights and diameters at breast height of 168 trees, distributed throughout the block, were measured. At thinning, 9 trees selected as representative of the range of size classes were subject to a series of detailed measurements, and each tree was allocated to one of the 3 height classes, 3–6m, 6–11m and 11–13m, found in the extensive sample. These measurements characterized: (i) mean vertical distributions (fresh weights) of branches + needles; (ii) dead branches by 0.5m sections, each weight being expressed as a fraction of the total for each of the 3 classes; (iii) leaf area index distribution by whorl; (iv) the weights of the 0.5m stem sections which were found to be related through a fourth order polynomial to mean weights per unit stem length; (v) stem diameters at 0.5m intervals, which were likewise related by a fourth order polynomial to diameter at one fifth top height.

From the 9 sample trees, curvilinear relationships were established between top height and (i) total fresh weights of needles + branch wood, (ii) total weight of dead branches, (iii) total stem weight, and (iv) stem diameter at one-fifth top height. From these various relationships, it has been possible to reconstruct the canopies of trees of different heights, or the distribution of trees as described by the 168 height and diameter samples.

Petty and Swain (1985) have described the bending of tree stems, assuming that the stresses in the outer layers of the stem are uniform all the way up the tree. This hypothesis was used, together with canopy and stem biomasses and leaf area estimates, to predict stem bending in trees 12.4m tall, a height representative of dominant trees rising above the main bulk of the canopy. Wind profiles within the tree canopy were assumed to follow that measured when the windspeed at the top of the canopy was 8m sec^{-1}, with proportional adjustments for other canopy top windspeeds.

Momentum absorbed (F) in a canopy layer is given by:

$$F = \rho u^2 C_d L$$

where ρ is air density, u is windspeed, C_d is the drag coefficient at that windspeed, and L is leaf area in the relevant layer of the canopy. Landsberg and Jarvis (1973) have described a relationship between windspeed and drag coefficient (C_d) for Sitka spruce shoots.

Using this estimate of absorbed momentum and a selected canopy top windspeed, the total turning moment at the base of the tree was calculated. Bending of a uniform cantilever beam of 0.5m length and appropriate diameter was also calculated. Assuming that there was no root movement, the position of the opposite end of this section provided a starting point for the bending of the next higher 0.5m section. For each higher section, the stress was assumed constant, but the appropriately narrower diameter was used. As the stem bent, the effect of the stem and canopy weight was added, and, through an iterative procedure, the equilibrium position of the bent stem, where wind plus weight forces were balanced by the restoring moment of the bent stemwood, was identified.

The moments applied to the stem through this 'static' approach to wind bending were calculated for canopy top windspeeds up to 60m sec^{-1} (Figure 40). Coutts (1986) and Deans and Ford (1983) have presented data obtained when trees were pulled over with a winch, and, for Sitka spruce of similar size to those at Rivox, an overturning moment of 10–20 kN m was typical. Using the 'static' wind bending approach, a windspeed of greater than 40m sec^{-1} at canopy top would be required, but it is known that trees blow over at much lower windspeeds.

This discrepancy is probably attributable to the 'dynamic' nature of a bending tree stem. It is well known that the turbulence in wind applies varying, not constant, forces to trees, and that trees have a natural frequency of stem sway at which maximum displacements occur. To estimate how much more effective wind forces are in bending tree stems when applied as gusts varying at the natural sway frequency of the tree, as compared with constant winds, the mechanical theory of a simple cantilever beam proved useful. This theory shows that, at the natural sway frequency, wind forces will be $1/2\zeta$ times more effective, where ζ is the viscous damping ratio of the stem. Mayhead *et al.* (1975) and White *et al.* (1976) have measured this damping ratio for Sitka spruce in forest stands. They noted that the value of ζ may be affected by thinning, but a typical value was 0.1. This value leads to an estimate that wind gusts at the natural sway frequency could be 5 times more effective in generating overturning forces than a constant windspeed. When this scaling factor is applied to drag forces, the stem-bending model indicates that canopy top windspeeds gusting at around 20m sec^{-1} would be sufficient to cause overturning moments in the 10–20kN m range (Figure 40).

The shape of the bent stem was calculated for such applied wind gusts, and some discrepancy was found between tree-top horizontal displacements for a given bending moment compared with those observed by Coutts (1986) when tree pulling. This could indicate the difficulties in choosing the correct Young's Modulus for living material

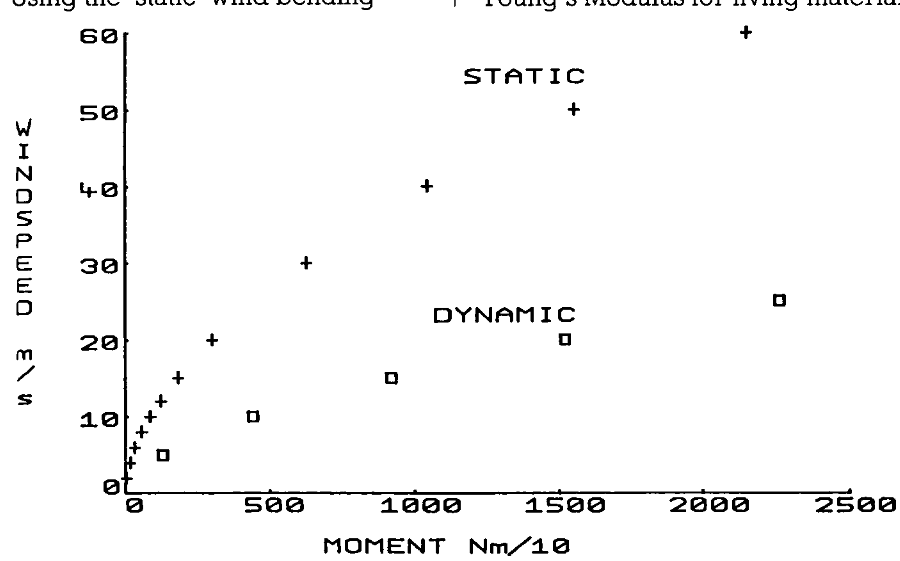

Figure 40. Bending moments under wind-loading measured at the base of a 12.4m tall Sitka spruce tree. The differing effects of wind applied constantly (STATIC) and in gusts at the natural sway frequency of the tree (DYNAMICS) are contrasted.

and in assuming the uniform stress along the length of a stem. In this work, a value of $7 \times 10^9\,N\,m^{-2}$ was used, but values of half or less may be more appropriate, as they would produce horizontal displacements comparable with those observed when tree pulling.

R Milne

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Influence of Sheathing (Ecto-)Mycorrhizas on the Zinc Tolerance of Birch Seedlings

Birch (*Betula* spp.) seedlings with roots having sheathing mycorrhizas have been found to grow larger in substrates with relatively high concentrations of zinc than seedlings without mycorrhizas. In tests done by Brown and Wilkins (1985), the aerial parts of tolerant mycorrhizal seedlings had lower concentrations of zinc than their zinc-sensitive non-mycorrhizal counterparts. In contrast, the roots of mycorrhizal seedlings had higher concentrations of zinc than their non-mycorrhizal controls.

To investigate the mechanisms controlling zinc sensitivity/tolerance, cuttings of birch were grown aseptically in glass boiling tubes containing 1.5g acid washed perlite plus $10cm^3$ modified Ingestad medium restricted to $5g\,m^{-3}$ glucose (Brown & Wilkins 1955); where appropriate, $2.3\,mmol\,dm^{-3}$ zinc were added as zinc sulphate. Mycorrhizas were synthesized by adding a plug of *Paxillus involutus* culture cut from the periphery of agar cultures.

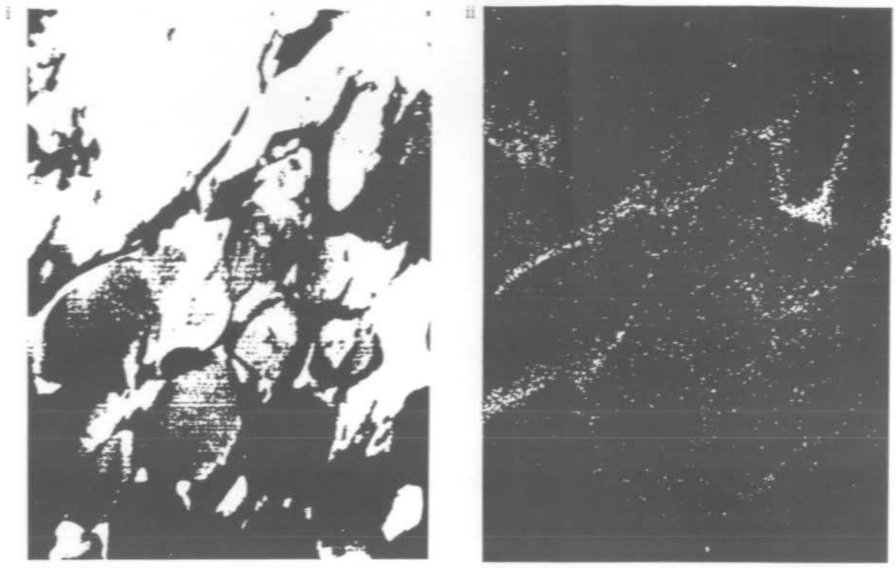

Plate 5. Mycorrhizas on birch seedlings attributable to *Paxillus involutus*
i) Scanning, transmission, electron image of part of cortex cell (top left) and mantle hyphae (the rest). Section was freeze-substituted and is about 1.5um thick, hence lack of definition and contrast.
ii) X-ray map for zinc of the same area. White dots indicate X-rays of wavelength coinciding with a zinc peak (therefore some background too). Note that zinc has accumulated in the extracellular regions of the hyphae (adsorbed to cell wall or slime?) and in the electron dense granules within the cortical cell (other story)

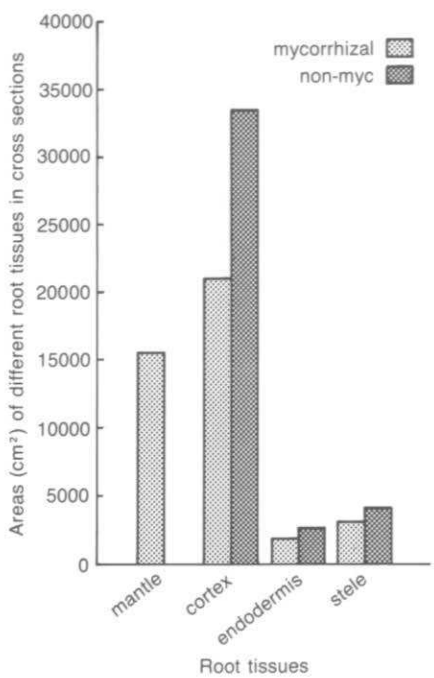

Figure 41. Relative sizes of different types of tissues in root systems of birch seedlings with, and without, sheathing mycorrhizas

Energy dispersive X-ray analysis (EDAX) was used to measure concentrations and distributions of zinc in tissues when harvested after 8 weeks (Chandler 1977). Plant materials were freeze substituted (Harvey *et al.* 1976), embedded im Taab-transmit-EM-resin, sectioned and mounted on formvar-coated aluminium grids. X-rays were used to either calculate tissue concentrations of zinc or produce X-ray maps showing the location of zinc accumulations.

When the first experiment was terminated, root tips from birch seedlings with and without mycorrhizas were examined. Estimates were made of (i) mean concentrations of zinc in different root tissues and (ii) the areas of the different tissues (Figure 41). Concentrations of zinc were highest in the endodermis and lowest in the stele (Figure 42). Concentrations of zinc were significantly lower in the cortical and stele tissues of mycorrhizal plants than in comparable tissues of non-mycorrhizal plants. When the relative areas of the different tissues were taken into account, it seems that the presence of mycorrhizas lowered the concentrations of zinc in roots of birch, an effect

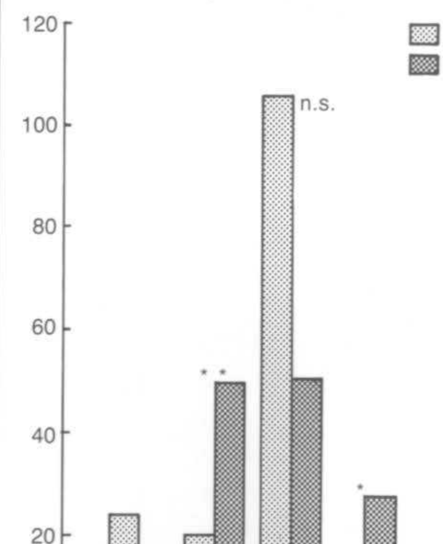

Figure 42. Effects of sheathing mycorrhizas on the concentrations of zinc found in the different types of root tissue of birch seedlings grown in a substrate with a relatively high concentration of zinc

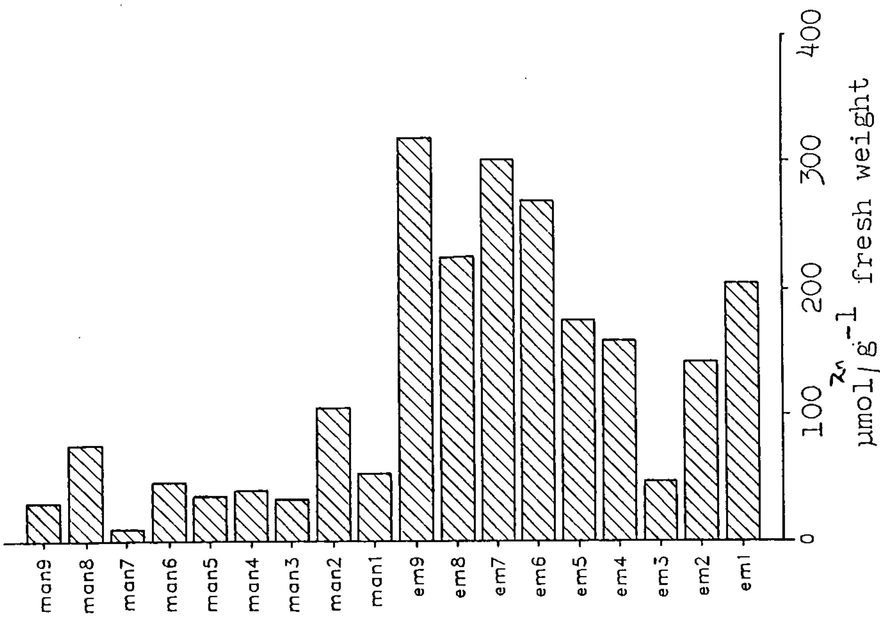

Figure 43. Concentrations of zinc found in the extramatrical and mantle hyphae of birch seedlings with mycorrhizas attributable to *Paxillus involutus*. The seedlings were grown in a substrate with a relatively high concentration of zinc

contrasting with that reported by Brown and Wilkins. However, the latter examined whole root systems, including 'old' as well as young roots, while the present experiment was restricted to the examination of root tips.

In a second experiment, mycorrhizal tips and tufts of mantle and extramatrical mycelium, radiating from mycorrhizas, were analysed (Figure 43). Substantially more zinc accumulated in extra-mycelium than in mantle hyphae. It therefore seems that extramatrical mycelia adsorb zinc and, as a result, effectively decrease the availability of substrate zinc. This would minimize the amounts of zinc that might otherwise have been accumulated in the mycorrhizal root tips, a set of circumstances that may explain the reasons for the discrepancy already noted.

To gain a clearer insight into the spatial distribution of zinc, root tissues were subject to X-ray and electron microscope analyses. It was found that zinc accumulated in the extracellular spaces between hyphae (Plate 5). It is possibly adsorbed to hypal cell walls or extrahyphal slime, its immobilization in this way according well with the idea that zinc adsorbed by extramatrical hyphae is not translocated to mycorrhizal root tips.

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The Taxonomy of Large Amoebae: East and West

An extensive taxonomic study of the family Amoebidae, to which most large gymnamoebae (lobose naked amoebae) belong, has been completed at ITE's Culture Centre of Algae and Protozoa (CCAP), with the help of colleagues in Britain, the USSR, Denmark and the Netherlands. Sixteen strains of amoebae were investigated; they originated in Britain, Hungary, the Netherlands, Poland, USSR, Canada, and the USA. Colleagues at the Leningrad Institute of Cytology contributed to 2 collaborative papers (Page & Kalinina 1984; Kalinina *et al.* 1986) and also supplied several isolates for electron microscope studies at the CCAP. In addition to the cultures, slide preparations of Amoebidae, made 80 years ago by the Swiss protozoologist Eugène Penard, were examined (Page 1981).

The Amoebidae are of special interest for 2 reasons. First, some larger members of the family are widely used in cell biological work and, second, because they have been found to ingest both algae and protozoa, their dependence upon other micro-organisms merits attention. Despite these interests, little attention has been paid to the identities and relationships of different species and genera.

As a result of the present series of investigations, a fixation procedure equally applicable to all strains has been developed (Page 1986). Details of ultrastructural and non-morphological characters have been accumulated. The non-morphological information was obtained by colleagues in Leningrad, including nucleo-cytoplasmic compatibility (tested by nuclear transplantation), nuclear DNA content throughout the cell cycle, effects of physical and chemical stresses, generation times and cloning efficiencies, serological reactions, adhesiveness, and total protein composition as determined by electrophoresis. The most useful ultrastructural characters for distinguishing between species and genera include cell surface coats, nuclear envelopes, Golgi bodies, and mitochondria. While taxonomic distinctions have been firmly established on the basis of electron microscope and non-morphological characters, attempts have been made to correlate them with characters discernible under widely available microscopes.

The 16 strains under investigation proved to be 10 species belonging to 6 genera. Other important taxonomic results were as follows.

1. *Amoeba proteus*-like organisms belong to several species.

2. A new genus has been established to accommodate smaller members of the family which are normally polypodial (having several pseudopodia) but differ in surface coat and other characters from larger members.

3. Multinucleate members (*Chaos*) are closely related to *Amoeba proteus.*

4. *Hydramoeba hydroxena*, an ectoparasite of freshwater coelenterates distributed widely in the northern hemisphere, is not distinguishable (except by its parasitism) from the non-parasitic genus *Trichamoeba* (Page & Siemensma 1986).

Strains of *A. proteus* from the USSR and USA were indistinguishable in their ultrastructure, a result supporting the validity of the characters employed for organisms from widely separated sites.

F C Page

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Limax Amoebae and 'Slime Moulds'

These 2 terms, often misused, designate common organisms which may have considerable ecological importance. A new investigation made with Dr R L Blanton, visiting from the University of Georgia, USA, has advanced our understanding of limax amoebae and 'slime moulds' and demonstrated relationships between them.

Limax amoebae, which occur in freshwater, terrestrial, and marine habitats, move as elongate, tubular cells; many produce resting cysts. In contrast, slime moulds or mycetozoans, a diverse group of amoeboid organisms, produce spore-bearing fruiting bodies (Plate 6). Because the latter superficially resemble the fruiting bodies of fungi, mycetozoans have been studied by mycologists and implicitly or explicitly associated with fungi. Like gymnamoebae (non-fruiting, naked, lobose amoebae), the amoeboid stages of mycetozoans feed by phagocytosis on bacteria and yeasts.

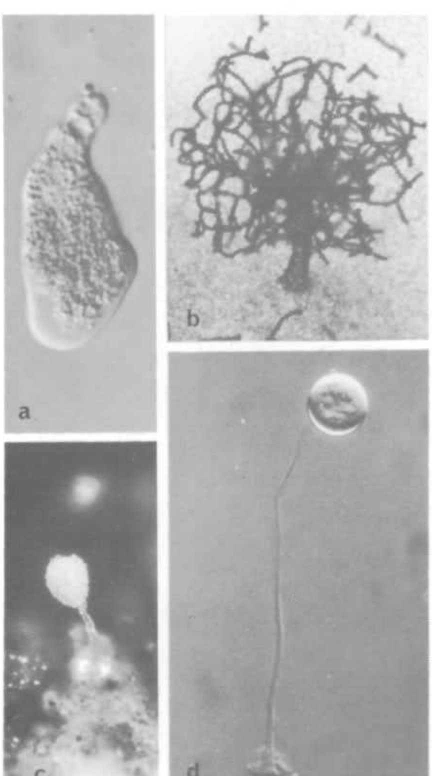

Plate 6. The amoeboid form and fruiting structures of different species of slime moulds.

a. *Acrasis rosea*, amoeba (× 1000)

b. *Acrasis rosea*, fruiting body; isolated from moribund carrot tissues, Higher Bockhampton, Dorset (× 86)

c. *Pocheina rosea*, fruiting body; growing on bark of giant sequoia collected in Cambridge. The amoeboid stage is like that of *Acrasis rosea* (× 86)

d. *Protostelium irregularis*, fruiting body, from moribund carrots. The amoebae of this genus are distinct from those of *Acrasis* and *Pocheina* (× 918)

(Photomicrographs R L Blanton & F C Page).

On the basis of their locomotive activity, occurrence of flagellate stages, and mitotic patterns, most limax amoebae had been allocated to 2 families, Vahlkampfiidae and Hartmannellidae. However, to obtain further indications about the homogeneity of each family, generic distinctions, and wider relationships, an extensive electron microscopic investigation was undertaken.

The following conclusions have been made:

1. The Vahlkampfiidae and the Hartmannellidae can be distinguished by their fine structure, especially of mitochondria and Golgi systems. The Vahlkampfiidae form a homogenous, natural group which is unrelated to the Hartmannellidae.

2. The order Acrasida, as anticipated, is heterogenous; the family Acrasidae is closely related to the Vahlkampfiidae.

3. Because the Vahlkampfiidae and Acrasidae are related, a new class of protozoa, the Heterolobosea, has been created (Page & Blanton 1985). This is the first formal recognition of a close relationship between these gymnamoebae and mycetozoans. It reinforces the idea that mycetozoans are protozoa.

F C Page

Reference

Page, F C & Blanton, R L. 1985. The Heterolobosea (Sarcodina: Rhizopoda), a new class uniting the Schizopyrenida and the Acrasidae (Acrasida). *Protistologica*, **21,** 121–132.

Ecophysiology and Pollution in Animals

Dispersal of Young Sparrowhawks

The population dynamics and ecology of the sparrowhawk (*Accipiter nisus*) have been the subject of extensive research by ITE for many years. One aspect of this raptor's ecology recently investigated was the post-fledging period and dispersal of the young (Wyllie 1985). Eight young birds from 4 different broods were marked with back-mounted radio-transmitters whilst in the nest and their activities monitored for a period of 6 weeks. At the study area, in Rockingham Forest in the east midlands, sparrowhawks had previously been absent for about 20 years, probably owing to organochlorine pesticide use (Newton & Haas 1984). The objectives were to discover precise post-fledging periods of the young, and to learn of their subsequent movements and distances travelled on reaching independence.

The young left the nest some 26–30 days after hatching and remained within the nest vicinity for a further 4 weeks (Table 17). They were thus dependent upon their parents for a total period of about 2 months.

Immediately prior to dispersing, the young were noted to be constantly calling for food, suggesting that their parents had cut their rations and that this action initiated dispersal. One bird (no 8) dispersed at about 65 days after joining an adjacent brood and leaving when they did. Such incidents are not uncommon in sparrowhawks and further support the idea that the parents control the date of dispersal. Stopping the supply of food is the most obvious way.

To test this idea, in 1985, a further 4 broods were experimentally provided with additional food at the nest for some weeks beyond the normal dependence period. Compared with unfed broods, these birds remained in the nest vicinity for a further 2–3 weeks, apparently relying entirely upon the experimentally provided food.

Table 17. Fledging and dispersal times of young sparrowhawks, with distances and directions travelled from nest

Bird number	Age left nest (days)	Age left nest area (days)	Maximum distance travelled (km)	Direction from nest
1	28	54	22	S
2	29	56	4	W
3	28	*	—	—
4	26	54	—	—
5	29	56	16	NW
6	30	55	7	S
7	30	57	—	—
8	—	*c*65†	17	S

*Died 2 days after fledging
†Temporarily joined adjacent brood, dispersing when they did

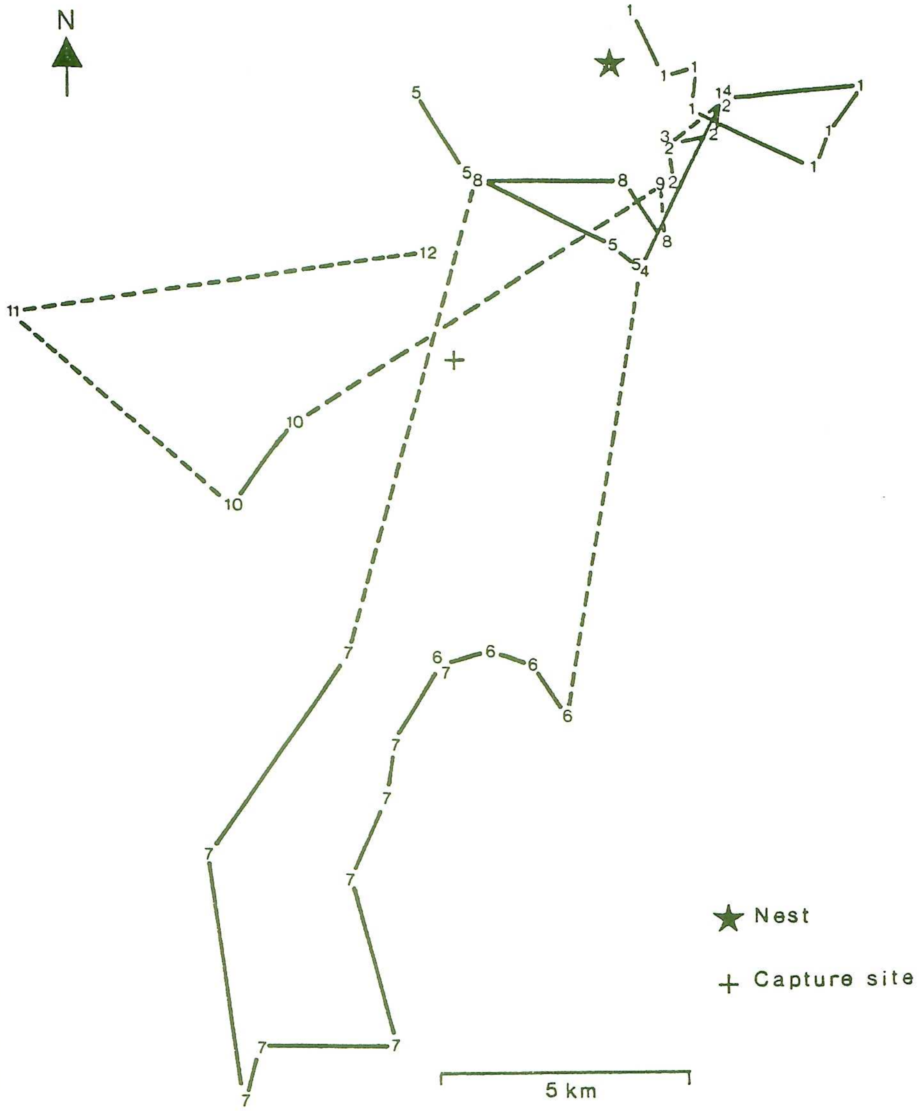

Figure 44. Movements of a young radio-tagged sparrowhawk (no 1) after reaching independence. Numbers 1–12 represent chronological sequence. Solid lines represent known movements on one day

They dispersed when food was no longer given.

The young left, independently of one another, in various directions from the nest. One female (illustrated in Figure 44) was followed for 3 weeks, during which time she travelled up to 22km from the nest. She was recaptured 61 days after leaving the nest area, at a point 6km from her birthplace.

I Wyllie

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Foraging Patterns of Radio-tagged Grey and Red Squirrels

Despite a campaign to label the introduced North American grey squirrel (*Sciurus carolinensis*) as a 'tree rat', both this species and the native Eurasian red squirrel (*Sciurus vulgaris*) belong in the same genus of tree squirrels. Recent ITE research has shown by radio-tagging that there are many similarities in the ecology of the 2 species, but there are also marked differences. These differences may well explain why grey squirrels have replaced their red congener in most British deciduous woodlands. This report summarizes work at Monks Wood and Furzebrook, and by Melody Tonkin, an ITE/Bradford University CASE student at Merlewood. The findings are being confirmed and extended in a study on the Isle of Wight by Jessica Holm, an ITE/Royal Holloway College CASE student.

Grey squirrels have been trapped and radio-tagged at 4 sites in the Midlands, including Monks Wood itself, and at 2 on the south coast. In each case, a grid of 15–26 Legg multiple capture traps was set on the ground at 80–100m spacing. Trapped squirrels were weighed, their sex, age and reproductive status noted, and equipped with 25g radio-tags. These tags have a fixed tuned loop brass collar which fits over the squirrel's head, and a cable tie which is tightened to reduce the internal loop circumference so that it cannot slip off (Kenward 1982a). The tags

A good Acorn crop: an unfortunate source of food for grey squirrels

produce a pulsed radio signal, with an operating life of 6–10 months. Squirrels with these tags had the same recapture rates, weight changes between sessions, and breeding activity as squirrels marked only by toe-clipping (Kenward 1982b). On the tag's exposed lower surface is a thermistor temperature sensor, which increases the signal pulse rate when a squirrel curls up in its drey, and decreases it when the squirrel goes out. The forays of all squirrels with detectable signals can therefore be recorded automatically by a programmable scanning receiver linked to a data logger.

To study foraging and other movements, hand-held receiving equipment was used to record each squirrel's position 3 times a day for 10 days (recording for longer periods produced no marked increase in observed range size). We also recorded whether each fix was in a tree, and of what species, or on the ground. Maximum range sizes were estimated as the areas of convex polygons (polygons with all external angles $>180°$) which enclosed all the fixes. Because the maximum convex polygon shapes and areas sometimes depended mainly on a few outlying fixes, recorded when squirrels made excursions outside their usual range, a BBC BASIC program was developed to estimate convex polygon core ranges. This program calculated the arithmetic mean co-ordinate for all the fixes, then rejected the furthest fix from this 'activity centre', and recalculated the mean co-ordinate. By repeating this process, core ranges were estimated from the densest fixes. To obtain ranges based on the main foraging areas, rather than on the most commonly used dreys, only one fix was used in the analysis from each of a squirrel's 1–3 drey sites.

Female ranges showed a tendency to decline in size during the winter, but otherwise varied much less than male ranges during the course of the year (Kenward 1985). Male ranges tended to increase dramatically in size between April and July, the period of mating for

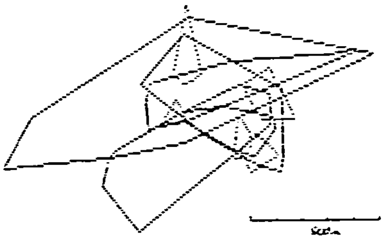


Figure 45. Maximum convex polygon ranges of adult male grey squirrels in Monks Wood in March 1984 (dotted lines) and May 1984 (solid lines) to show the range size increase during courtship.

summer litters (Figure 45). These range expansions were associated with the males attending mating chases well outside their normal ranges. Until 1984–85, there was no evidence of similar range expansion during the December–February period of mating for spring litters, despite artificial feeding in Monks Wood from December 1983 to May 1984 and the presence of some males with scrotal testes. It therefore seemed that exposure to cold or to avian predation might militate against this 'mobile lek' mating system in winter: the goshawk (*Accipiter gentilis*) is an important squirrel predator, and one released in Britain during January 1979 took 7 grey squirrels in 10 days (unpublished data). Nevertheless, some male squirrels had enlarged ranges in Monks Wood in January 1985, so there is more to discover about the control of winter mating activity.

From trapping and observation of visually marked squirrels, it has long been thought that grey squirrels have a dominance hierarchy within a system of extensively overlapping ranges (Flyger 1960; Thomson 1978). Nevertheless, squirrel ranges have generally been smallest in studies where their density was highest (Don 1983). This tendency could have been a correlate of varying food supplies, but winter range size in Monks Wood has correlated inversely with density, and not with winter food (Table 18).

To investigate squirrel social interactions in more detail, winter ranges were recorded for 27 of the 39 squirrels present on the Monks Wood trap grid, from September 1983 to March 1984. Among ranges which touched, there was a tendency for the cores either not to overlap, or to overlap more than expected from randomly overlapping the ranges. Thus, as core size decreased, the extent of overlap increased for the ranges which still touched (Figure 46), and differed significantly ($P < 0.02$) from the random overlap value for the densest 70% of female fixes and 50% for males. A similar tendency, for ranges either to be exclusive or to overlap extensively, could be seen for the densest 90% of female fixes the following winter (Figure 47), at a time when excursions, and thus total range sizes, may have been restricted by the increased squirrel density (see Table 18). As the squirrels which shared core ranges also shared dreys, they were in fact living in small social groups, with a tendency for group ranges to be exclusive. Members of some groups were known, or thought, to be related, but unrelated squirrels were also found sharing ranges and dreys.

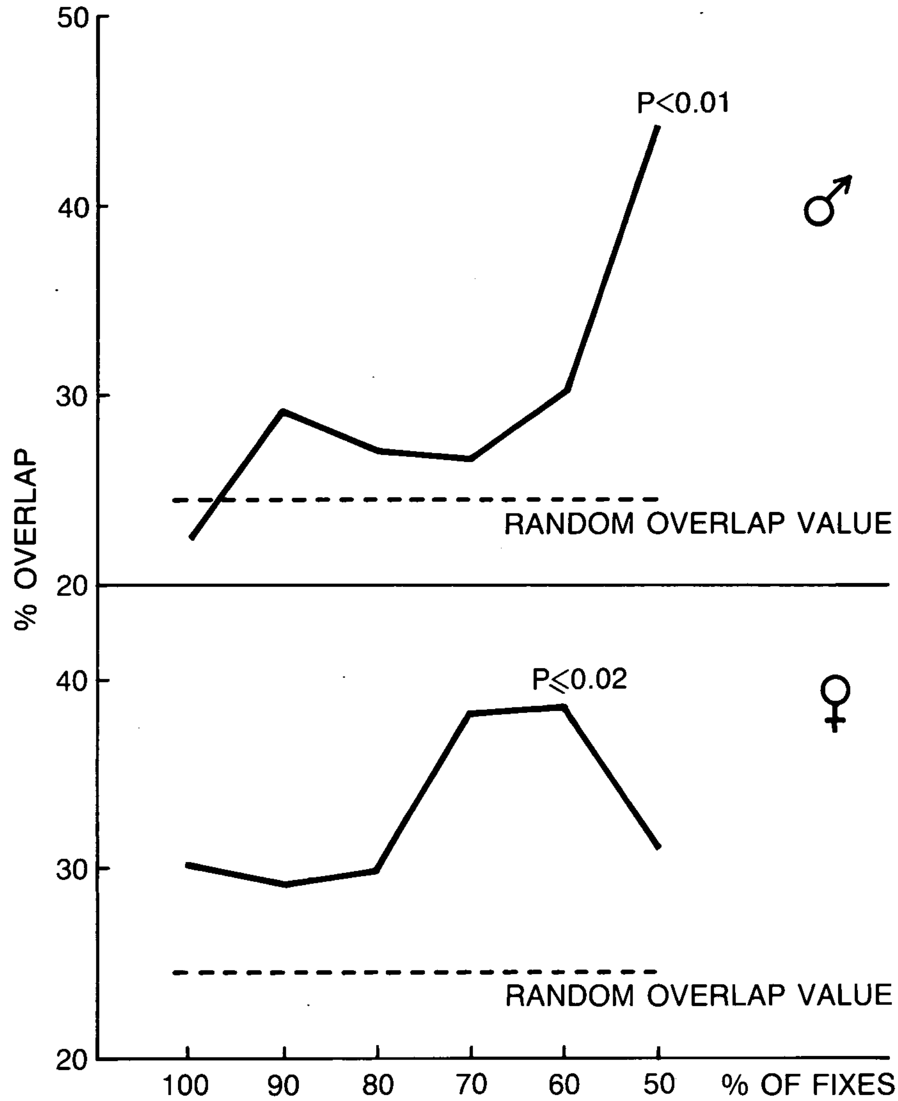


Figure 46. The overlap of male and female Monks Wood squirrel winter ranges in 1982–83 as outlying fixes are progessively excluded. The increasing overlap shows that some squirrels are sharing core ranges

Table 18. Squirrel density, range size (excluding courting males), and winter food index during December–March at 2 sites over 5 years

Site & year	Winter food (acorn index)	Squirrel density	Range size (N)
Monks Wood			
1980–81	Fair (6.4)	0.67 ha^{-1}	5.66 ha (10)
1981–82	Good (10.4)	0.73 ha^{-1}	5.63 ha (14)
1983–84	Poor (3.3)	1.53 ha^{-1}	3.07 ha (12)
1984–85	Poor (3.4)	1.81 ha^{-1}	1.67 ha (12)
Elton			
1979–80	Good*	2.33 ha^{-1}	1.79 ha (16)

*All radio-tagged squirrels at Elton used pheasant feed sites in winter.

Red squirrels were trapped in a grid of single-capture traps mounted at breast height on tree trunks in Lawns Wood, a 29ha block of woodland in south Cumbria. Like Monks Wood, Lawns Wood contains old hazel (*Corylus avellana*) coppice, with oak (*Quercus robur*, *Q, petraea*), ash (*Fraxinus excelsior*) and birch (*Betula pendula*) as the dominant mature trees, but also contains 14% yew (*Taxus baccata*). Field maple (*Acer campestris*) is abundant only in Monks Wood, which lacks yew. Red squirrel ranges were similar in size to those of the grey squirrels

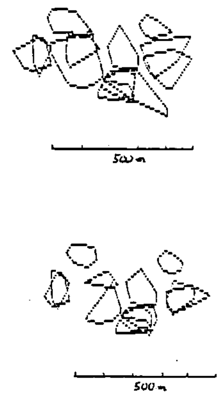


Figure 47. The relationship between maximum convex polygon ranges of female Monks Wood squirrels in 1983–84. Ranges which overlap when all fixes are included tend either (i) to become separate, or (ii) to form 3 sharing groups, when based on the densest 90% of the fixes

(Tonkin 1983a), and male ranges showed similar expansion during the breeding season (J Holm, pers. comm.). The most obvious difference between the 2 species was in their arboreal foraging.

Between September and March, grey squirrels spent most of their time on the ground, cacheing and later recovering the acorn crop, although they also ate any field maple seeds that were available. The acorns were usually cached after they had fallen, although in autumn 1986, when the crop was late to fall, squirrels spent quite a lot of time fetching acorns down from the trees. Arboreal foraging peaked for grey squirrels in spring and summer. In spring, they mainly ate flowers of oak, ash, poplar (*Populus trichocarpa*) and beech (*Fagus sylvatica*), changing from species to species over short periods as flower availability varied (Figure 48). In woods with conifers, they also ate cones of European larch (*Larix decidua*) and Scots pine (*Pinus sylvestris*) at this time (Figure 49), but still spent about 50% of their time on the ground.

In contrast, the red squirrels spent only 39% of their time on the ground in April, and not more than 20% between May and August (Figure 50). They foraged in trees much more often than the grey squirrels in every month of the year, averaging 67% of their time there, compared with only 14% for the grey squirrels in Monks Wood (Kenward & Tonkin 1986).

As well as these differences in habitat use, there were also biometric differences which may have given red squirrels an adaptive advantage for foraging in trees. Grey squirrel body and limb lengths were 11–14% greater than those of the red squirrel, which would give a 35–48% difference in weight (by cubing the length difference) if their bodies were the same shape, but grey squirrel monthly average weights were 79–138% greater than the averages for the red squirrel. The grey squirrels were therefore more heavily built than their congener. Moreover, grey squirrels increased their weight by an average 25% in winter, compared with only 12% for the red squirrels. A large winter weight increase could be a disadvantage for animals foraging on fine branches.

The automatic activity recording and visual observations showed that red and grey squirrels foraged for most of the day in the autumn, but minimized the time spent out of their dreys in mid-winter (Tonkin 1983b), especially when fed artificially (Kenward & Parish, unpublished). Between January and March 1981, when data were available for both species, squirrels in Monks Wood spent an average 3.0 hours per day out of their dreys, a figure significantly lower than the 4.5 hours per day spent by the red squirrels in Lawns Wood. A similar difference in winter activity exists between red squirrels on the Isle of Wight and grey squirrels just across the Solent (Kenward & Holm, unpublished). Whether or not this results from a difference in foraging efficiency between the 2 species, the red squirrels must have a relatively higher winter energy expenditure than the grey squirrels, especially when they feed in exposed deciduous tree tops.

The grey squirrel is in origin an inhabitant of American deciduous woodland, living from early autumn to late spring on fallen mast and nut crops, which it scatter-hoards in competition with birds and other squirrel species. A stocky build could be an advantage when burying and recovering this food, and winter fattening would be useful if hard frost or crusty snow made caches temporarily unavailable. In contrast, the red squirrel lives among conifers through most of its Eurasian range. It presumably evolved in this habitat, where the food cones are available in trees during the winter. Such evolution should favour adaptations for arboreal foraging, including a slender build and perhaps a behavioural preference for seeking food above ground (note also that grey squirrels are trapped easily on the ground, whereas red squirrel traps are best set in trees). It is curious that no deciduous woodland squirrel has evolved in Eurasia, whereas nuts and acorns are exploited by the fox squirrel (*S. niger*) and the chipmunk (*Tamias striatus*), as well as by the grey squirrel in North American woods. A crucial factor may be North America's lack of a native pig in this woodland. The Eurasian wild boar (*Sus scrofa*) would not only compete for fallen tree seeds, but would also probably dig up squirrel caches.

Although the red squirrel occurs in deciduous woodland throughout Europe, recorded densities were only 0.50–0.82 squirrels ha^{-1} in Lawns Wood (Tonkin 1983a), and 0.75–0.94 squirrels ha^{-1} in a Belgian deciduous wood (Wauters & Dhont 1986), compared with 0.67–1.81

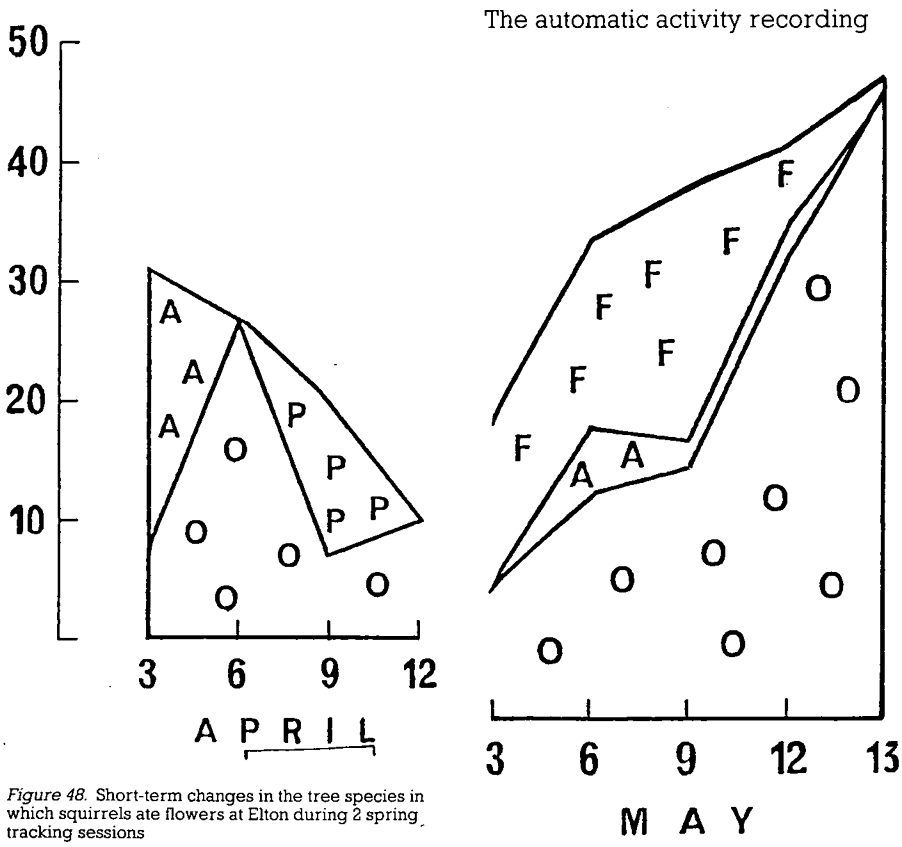


Figure 48. Short-term changes in the tree species in which squirrels ate flowers at Elton during 2 spring tracking sessions

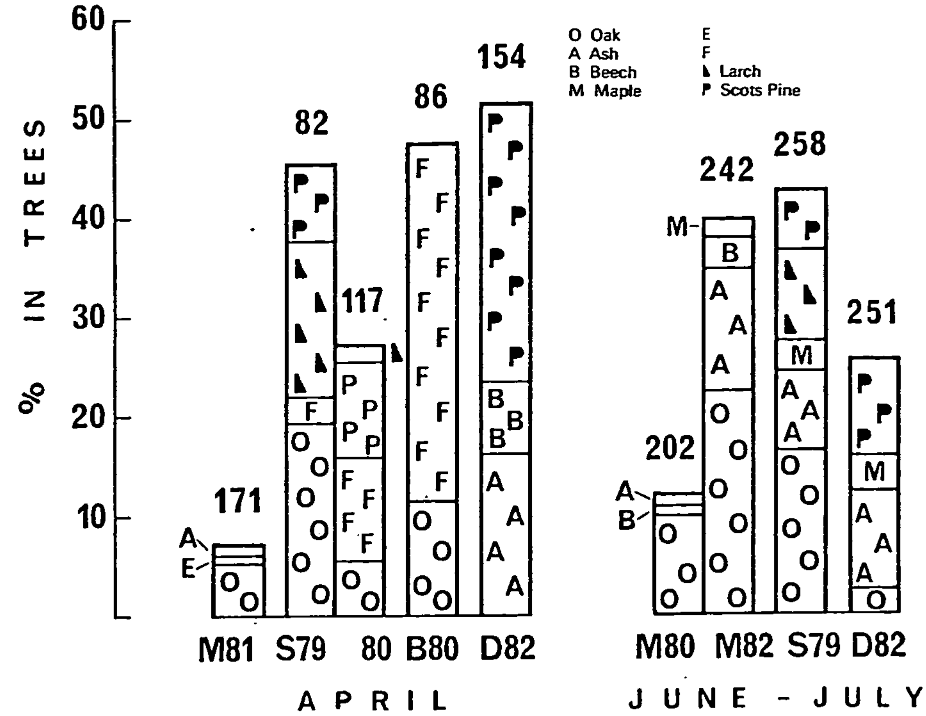
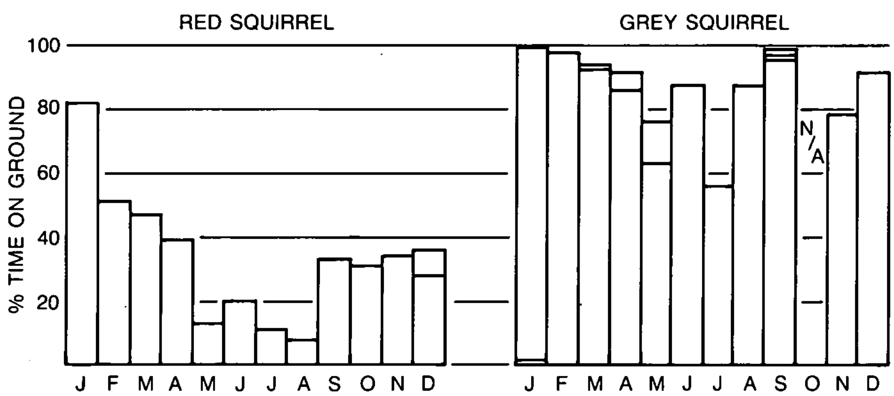


Figure 49. Variation between woods in the trees in which grey squirrels foraged in spring, season when grey and red squirrels feed most in trees



The proportion of time Red and Grey Squirrels spent on the ground or in trees throughout the year. Data from more than one year are recorded separately.

Figure 50. The contrast in the extent of arboreal foraging between grey squirrels in Monks Wood, Cambridgeshire, and red squirrels in Lawns Wood, Cumbria. Grey areas show differences in months when data were available for more than one year. No grey squirrel data were available for October

grey squirrels ha^{-1} in Monks Wood and up to 8 squirrels ha^{-1} in other British woodland (Don 1983; Gurnell 1983). It may well be that specialization for arboreal foraging puts the red squirrel at a competitive disadvantage when the 2 species meet in deciduous woodland, and that this factor has caused its replacement by the grey squirrel through so much of Britain.

R E Kenward and T Parish

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Population Genetics of the Mute Swan

Genetic differences between individuals within populations are fundamental to neo-Darwinian evolutionary theory, as the inherited units on which natural selection operates. Population genetics theory clearly shows that ecological factors (habitat and seasonal differences) could be expected to maintain genetic variation within single populations. Conversely, population ecologists rarely assess likely effects of such genetic variation, and this lack of consideration could impair our understanding of population processes.

The mute swan (*Cygnus olor*) is a convenient species for such work, being long-lived and having large broods; collaboration with existing population studies has greatly increased the information obtained from genetic data collected over only a few years. Initial studies, started at Oxford University (Bacon 1980, 1981), established that there were 2 biochemical polymorphisms in mute swans that had genotypes sufficiently common for field studies to be worthwhile.

The first polymorphism, an esterase enzyme, is inherited as a co-dominant autosomal locus. There are 2 genes, S and F, giving rise to 3 genotypes (SS, SF and FF). The distribution of these genotypes in Britain is shown in Figure 51; all are fairly common throughout the country, at ratios of around 5:4:1. Detailed data on breeding success from the Oxford study area show that SS females lay significantly earlier, and larger clutches, resulting in greater numbers of cygnets fledged per season (see Figure 52) (Birkhead *et al.* 1983). Recent analysis of egg volumes has shown them to be inversely related to clutch size between the genotypes (for volumes FF > SF > SS). In line with recent theoretical arguments by Sibley and Calow (1983), the genes seem

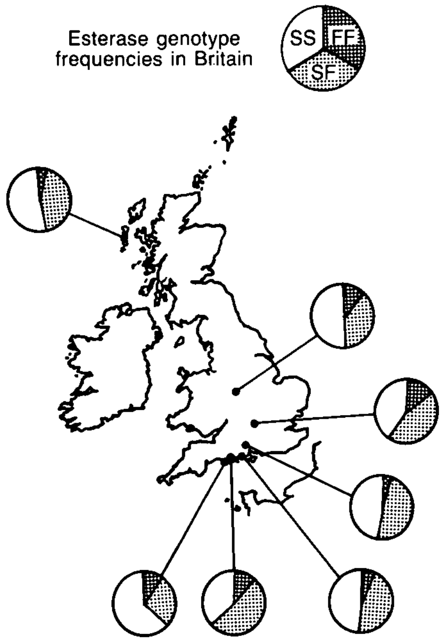

Figure 51. Distribution of esterase genotype frequencies in Britain

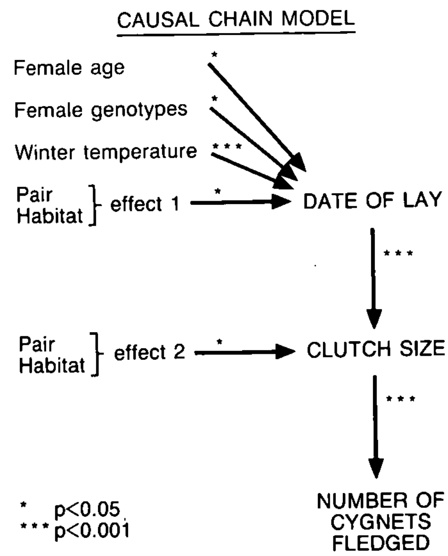

Figure 52. Factors shown to be significant in predicting mute swan breeding success in the Oxford study area

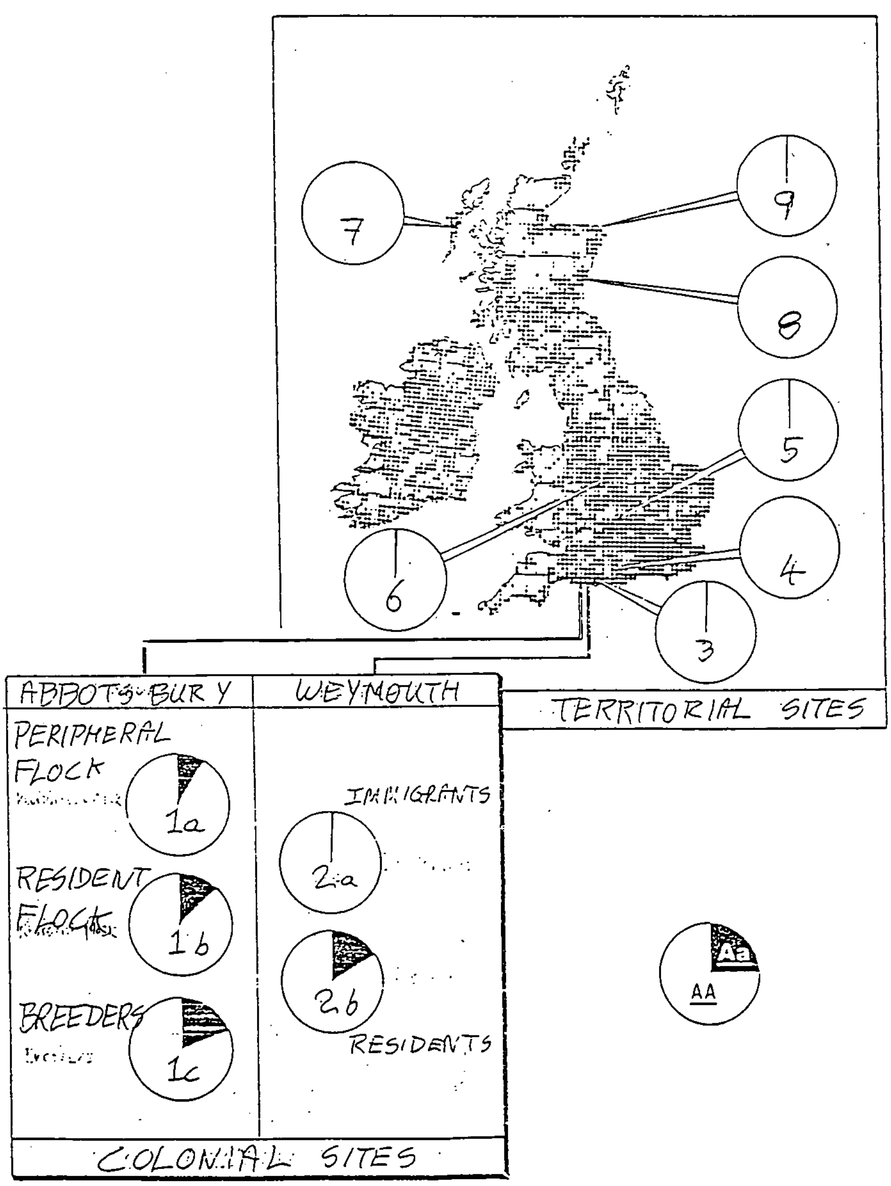

Figure 53. Distribution of lactate dehydrogenase genotypes in Britain

to act as 'genetic markers' for swans that exploit different resource allocation strategies, SS females tending to lay larger clutches of smaller eggs earlier in richer environments, and FF females laying smaller clutches of larger eggs later in poorer habitats. Biometric studies (Bacon & Coleman 1986) are being extended to allow more accurate assessment of cygnet growth, to test this resource allocation hypothesis in detail.

The second polymorphism, the enzyme lactate dehydrogenase (LDH), is also of 2 genes, A and a, at an autosomal locus. The AA genotype comprises over 99% of most British populations, but significantly less, 85–90%, at the only 2 sites in Britain where mute swans, which are normally territorial, nest in colonies (Figure 53). The high proportion of 25% immigrant breeders to the Abbotsbury colony (Perrins & Ogilvie 1981) makes it highly unlikely that such a difference could have arisen by chance $P<0.001$), and initial data on breeding success suggest that LDH-Aa heterozygotes breed significantly more successfully ($P<0.05$). This finding implies a selective advantage of a factor of 2, which could easily produce the observed elevated frequency of the LDH-a gene (Bacon 1980, 1981). Colonial nesting of mute swans is much commoner in Denmark (38% of pairs) than in Britain (5%), and preliminary collaborative work with the Zoological Museum at København has recently shown LDH-Aa heterozygotes to be significantly commoner in 2 Danish colonies than in adjacent territorial populations. As the Danish and English mute swan populations have been effectively isolated for about 1000 generations, this dual finding suggests the LDH-a allele may be closely linked to genes that fundamentally affect mute swan social behaviour or ecology.

P J Bacon

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Factors Influencing the Metal Burden in the Stone Loach

(This work is supported by CEC funds)

Introduction

There is a lack of understanding of the dose-response relationship in animals under field conditions. The objective of this study is to develop a mathematical model to describe the factors that influence the metal burden in stone loach (*Noemacheilus barbatulus*) in the field.

It is a well known fact that aquatic organisms can accumulate cadmium and lead from both ambient water and from their food. However, most studies on uptake of metals from water by fish are restricted to soft water, and studies on accumulation and effects through the food are limited. Usually, explanations of the amounts found in field specimens are derived from laboratory experiments. More information about processes in the field needs to be combined with such experimental data to form a more complete picture of the variables that influence the metal burden in fish.

To study the dose-response relationship in nature, any field survey should include sampling sites with different metal concentrations. Streams in Derbyshire are naturally contaminated with cadmium and lead. The water is reasonably hard (50–70 mg Ca^{2+} l^{-1}), and it is presumed, therefore, that only low concentrations of these metals occur in solution. The metals can also be present in particulate and colloidal forms.

It has been suggested that the sediments play an important role in the uptake of metals from the environment by fish, by releasing the metals into the water. On the other hand, the importance of food as a source of metal is not yet understood.

The River Ecclesbourne in Derbyshire has been the subject of some detailed studies. Reynolds (1981) studied the water and the sediments of the river and found high concentrations of cadmium and lead in the sediments. Moriarty *et al.* (1982, 1984) reported, respectively, studies on the sediments, and on the metal burden in the bullhead or miller's thumb (*Cottus gobio*). They concluded that metal burdens in the bullhead are higher at those sites where sediments contain higher concentrations of metals.

Methods

Ideally, the species chosen for study needs to be abundant in streams, and must also be easy to maintain in the laboratory. Two species of fish, the bullhead and the stone loach, are common in the naturally contaminated streams in Derbyshire. Previous studies have shown that the bullhead eats little or no food, and becomes very thin in the laboratory, while the stone loach can be kept alive with artificial food. Therefore, this study will concentrate on the stone loach, and the model for the effect of variables on the metal burden in this fish will be based on results from field work in different streams in Derbyshire, including the River Ecclesbourne, and from laboratory experiments.

A one-year sampling programme was started on 22 May 1985, samples being taken from fish, sediment and water. Additional measurements in the water are also made for water quality, such as pH and conductivity.

Fish are being analysed for cadmium and lead content in the gills and in the rest of the body. The gills are being treated separately on the assumption that their metal content is a good index of recent exposure: metals in solution are thought to enter the body principally through the gills. During this study, the magnitude of recent exposure to metals in solution is estimated by that which passes through a filter of 0.45μm.

The metals come from the mineral veins at the head of the valley, but it does not seem likely that fish take them up directly from the sediments. However, the amount of metal in the stone loach will be compared with the concentration in the sediments. After completion of the one-year sampling programme, additional samples will be taken if necessary.

Assessment of pollution uptake from the food is technically difficult, in both the field and the laboratory. Experiments will be carried out to determine the effect of different factors on the rates of uptake, and of elimination, of metals in a continuous-flow system. Pollutant sources which are important include contamination of water and food. The factors which will be studied are:

- efficiency of uptake in the gills and in the gut;
- the rate of clearance after exposure at different temperatures for different periods;
- body weight and temperature as important variables which influence the level of metabolism in the fish.

These various field and laboratory studies should provide the data needed to construct a mathematical model that describes the metal burden of the stone loach.

P E T Douben

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Plant Population Ecology

The Performance of Natural Populations of the Marsh Gentian

A population model of the marsh gentian (*Gentiana pneumonanthe*) has been described in a previous annual report (Chapman *et al.* 1982). That model relates population levels of the marsh gentian to flowering, establishment, survival and competition with the associated heathland vegetation. Such models are valuable in the formulation and testing of hypotheses regarding the interrelations between different components of the model and the possible importance and sensitivity of individual features included within the population.

Whilst such models can be used to examine hypotheses, it is important that the data employed within the model relate to values existing within the natural ecosystem. In the case of perennial, and especially

Gentiana Pneumonanthe Longdown

long-lived, species, it is often difficult to obtain reliable estimates for many of the demographic variables.

Nine years of data have now been obtained from 4 populations of marsh gentian (2 in the New Forest, and 2 in south-east Dorset). Preliminary analyses of the data have provided better estimates of variables such as flowering, recruitment, mortality and the age structure of the populations. However, the same results demonstrate some of the difficulties that arise in relating such parameters to climatic variation. Results from the 2 Dorset sites are summarized in Table 19. Site A is an area on the Hartland Moor National Nature Reserve that was burnt during the dry summer of 1976. Site B is an adjacent area that has not been burnt for about 20 years. The results from Site A demonstrate the typical pattern of events that follow upon areas of freshly burnt heathland (Chapman & Rose 1983). There is an initial increase in the percentage of plants that flower, and a subsequent increase in recruitment, after which the levels of flowering and recruitment drop as the associated heathland vegetation regenerates. However, the results obtained from Site B are similar, as the effect of the hot, dry summer of 1976 also produced increased levels of flowering on many unburnt sites. The mean yearly loss of plants from those present when recording began in 1977 has been 9.1%, with the result that about half of the original plants still remain within the observation plots.

Now that sufficient data are available regarding the ages of individuals in the population, part of the area will be burnt, in the hope that the effect of burning can be followed under more normal climatic conditions than occurred in 1977.

SB Chapman and RJ Rose

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Variations in the distribution and ecology of *Sphagnum*

Plants of the moss genus *Sphagnum* have existed since at least the Miocene. Present-day species (150–200) are found from the Arctic to the sub-Antarctic. Although present in tropical parts of Africa, South America and South-East Asia, as well as along the Andes and in Australasia, they are found in greatest abundance in the boreal and temperate zones of the northern hemisphere. *Sphagnum* has a more or less continuous circumpolar distribution across the northern parts of Eurasia and North America, and frequently forms extensive carpets over wide areas of waterlogged terrain. This dominance of vegetation cover is unusual in bryophytes, and seems to have occurred in spite of certain structural and physiological limitations that confine *Sphagnum* species to habitats which are, essentially, semi-aquatic. Nonetheless, within these restrictions, there is a range of habitat conditions under which different species flourish, leading to variation in species distribution on both a broad, geographical scale, and locally, in relations to small-scale differences in environmental conditions.

All the species of *Sphagnum* found in Europe occur in North America, and some are distributed even more widely. In general terms, European species may be placed in 3 distributional groups (Daniels & Eddy 1985):

1. Species which occur throughout Eurasia and North America, and extend from the boreal zone to the tropics or sub-tropics. Two species, *S. fimbriatum* and *S. magellanicum*, are also found in the southern hemisphere (the latter reaching as far as Tierra del Fuego).

2. Species which have an oceanic or sub-oceanic distribution, and are most abundant close to the Atlantic coastal areas. Within this group are species whose main centre of distribution is in eastern North America (*S. angermanicum* and *S. pylaesii*), but which are restricted in Europe. A few, eg *S. imbricatum*, are also found on the Pacific coasts of North America and Asia.

3. Species found in the boreal and sub-arctic areas of the northern hemisphere. In Europe, these are most common in the continental interior, and are rare (eg *S. majus*), or absent (eg *S. wulfianum*) in the more maritime areas, including Britain.

Within each of these broad geographical groups, detailed distribution is dependent upon local conditions, in particular water regime, nutrient status and shade. The species growing under different combinations of these conditions show varying levels of morphological and physiological adaptation. Peatlands (the main habitat of *Sphagnum*) are frequently poor in available plant nutrient ions. Although there is continuous variation between the extreme conditions found, it is convenient to refer to sites as either oligotrophic (where the substrate and its contained water are especially low in nutrients, and are usually distinctly acid), mesotrophic (having an intermediate level of nutrient supply), or eutrophic (containing comparatively high levels of inorganic ions, and being circumneutral in reaction).

Sphagnum plants are adapted physiologically and biochemically to grow in nutrient-poor situations, and a combination of high pH with high calcium concentration is fatal to most species (Clymo & Hayward 1982). Ability to grow successfully in habitats with different nutrient and pH combinations varies from species to species. Only a few occur in the more eutrophic habitats (eg *S. contortum, S. squarrosum*), whilst the majority are found in acid situations, where pH values in the surrounding water are usually lower than 4.5.

Sphagnum species themselves contribute to the acidity of their immediate environment, by ion exchange. The cell walls of the plants contain uronic acids which release hydrogen ions in exchange for mineral cations in the

Table 19. Summary of May/September weather and population statistics for 2 populations (A and B) of marsh gentian from Hartland Moor NNR in Dorset between 1976 and 1985

Year	May–September Mean temperature (°C)	Rainfall (mm)	Daily sunshine (h)	Recruits (%)		Mortality (%)		Plants flowering (%)		Flowers/ flowering plant	
				A	B	A	B	A	B	A	B
1976	15.9	165	8.08	–	–	–	–	–	–	–	–
1977	13.7	317	6.02	–	–	–	–	55	82	2.06	1.28
1978	14.0	220	6.14	21	29	16	26	24	23	1.22	1.14
1979	13.6	240	6.44	11	20	16	23	25	17	1.20	1.30
1980	14.2	313	6.00	12	13	12	10	25	7	1.25	1.19
1981	14.6	370	5.78	7	4	8	2	23	3	1.0	1.46
1982	14.9	361	6.40	3	2	3	3	40	7	1.03	1.14
1983	15.5	280	6.48	1	2	2	<1	33	3	1.0	1.17
1984	14.7	192	6.86	3	3	3	0	23	7	0.88	1.13
1985	14.1	292	6.26	1	1	3	5	38	10	1.06	1.36

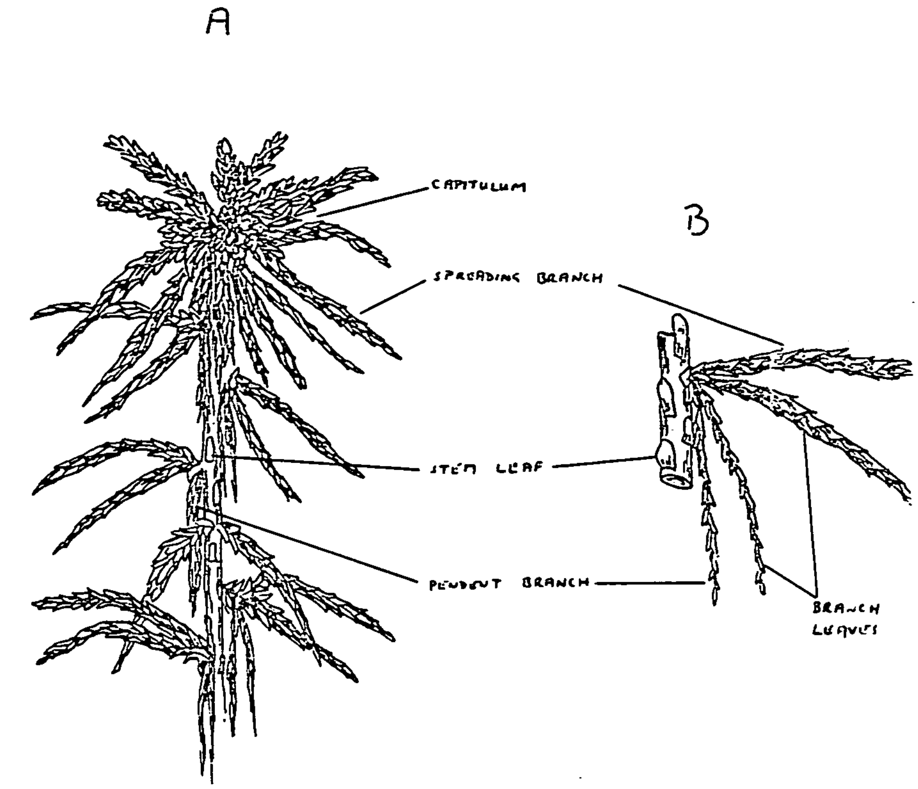

Figure 54. The structure of a *Sphagnum* plant (A), and of a single fascicle (B).

surrounding solution. Different species have different exchange capacities and, hence, tend to produce characteristic pH conditions in their immediate surroundings. Within the range of chemical conditions encountered in *Sphagnum* habitats, each species is restricted to part of the range, though simple measurements of acidity or total cation content may not give a clear picture of the nutrient conditions available to the plant. Where flow of water takes place, there will be a greater actual availability of nutrients than analysis of that water would indicate. In addition, plants may occupy different positions on the nutrient gradient in different parts of their geographical range; for example, *S. papillosum* is a species of oligotrophic situations in Britain, but is found in mesotrophic areas in Fennoscandia, where it is often associated with flushing or influx of water from mineral substrates.

The other major factor affecting local distribution patterns is water level, or the time for which plants are exposed to desiccation. Adaptations to different water regimes are reflected in morphological variation. The basic form of the *Sphagnum* plant is shown in Figure 54. The plant consists of a single upright stem, which carries leaves, and fascicles of branches, each branch being clothed in overlapping leaves. Both types of leaf consist of networks of narrow photosynthetic cells, and associated large, empty cells (hyaline cells) with pores. These hyaline cells hold water. Branches are of 2 types: spreading and pendent. As the plants possess no conducting tissue for the upward transport of water and nutrients, capillaries within and between the pendant branches and stems act as a transport system. In those species which grow in pools or wet hollows, the branches show a tendency to wider spacing, less distinction between spreading and pendent branches, and more widely spreading leaves. This plumose habit may be seen readily in submerged forms of *S. cuspidatum*. At the opposite extreme are species which form hummocks raised above the general water level: these plants possess a number of structural and growth form modifications which increase the efficiency of capillary water movement and reduce water loss. In plants of hummocks, the distance between fascicles is less, and there is a distinct difference between the weak hanging branches (whose leaves do not photosynthesize) and the more tumid spreading branches in which there is a high degree of overlap of the leaves. Species growing in these more exposed situations tend to branch more frequently, as shown in Table 20.

Within pure stands of 5 species, 5 replicate sample were collected from 100 cm^{-2} areas and the numbers of capitula (heads of tightly bunched young branches surrounding an apical cell) within each sample were counted. Each stem was categorized according to the number of capitula it carried. The numbers within each group were then expressed as percentages of the total numbers of stems. All samples were collected at the same site, within 50m of one another. The 2 species found in wet hollows (*S. cuspidatum*) or on wet lawns (*S. recurvum*) had the highest percentage of simple stems. *S. papillosum*, growing on low hummocks, had as many as 6 capitula per stem, whilst the 2 species growing in shaded, wet woodland, with a high humidity (*S. fimbriatum, S. palustre*), showed intermediate rates of branching.

The ability of plants to withstand variations in normal conditions differs from species to species, and may be seen as a major factor in determining overall abundance, though limiting conditions may vary from one locality to another. Among species with a comparatively narrow range of tolerance is *S. obtusum*. This species is confined to moderately eutrophic fens and fen woodlands, where it grows at or just above water level. In contrast, *S. papillosum* is found over a range of oligotrophic to mesotrophic habitats (depending upon geographical location) and may form low hummocks, or lawns close to the water table. Two extreme examples of species able to grow in dissimilar situations are *S. compactum* and *S. imbricatum*. Within the latter species, 2

Table 20. Percentages of stems with different numbers of capitula for *Sphagnum* species growing in different habitats.

	Numbers of capitula per stem					
	1	2	3	4	5	6
Species of wet, open hollows						
S. cuspidatum	90.5	8.5	1.0			
S. recurvum-	91.8	6.9	0.9	0.2	0.2	
Species of shaded woodland						
S. palustre	74.8	19.5	5.6			
S. fimbriatum	64.5	29.3	5.9	0.2		
Species of low hummocks						
S. papillosum	68.4	21.2	5.4	1.8	1.6	1.4

subspecies have been recognized (Flatberg 1984), and plants may either form hummocks in acid peatland (subsp. *austinii*), or grow in wetter, more mesotrophic situations (subsp. *affine*).

In *S. compactum*, 2 separate subspecies have not been recognized, but plants are found mostly in 2 different habitats. They either grow partly submerged in pools (eg in oceanic patterned mires in western Scotland or, more especially, in the patterned 'aapa' mires of Fennoscandia) or on wet heath, where there is only a thin layer of peat (usually less than 5 cm thick). Apart from the general tendency to produce more compact forms in drier situations, there appears to be little difference between plants found in these 2 habitat types. Examination of isoenzyme systems (Daniels 1985) indicates a similarity between the 2 different site types, though some detailed variations in band pattern are found. Overall, there tend to be larger numbers of bands for a given enzyme system than in species of more restricted habitat conditions (eg *S. pulchrum*). This suggests that there may be differently adapted enzyme systems which may be switched on or off, depending upon the habitat conditions prevailing.

It would appear that *Sphagnum* species are able to adapt to varying conditions by virtue of plasticity in growth form and, possibly, in physiology. There are 2 means by which adaptability may have developed: either by production of a number of genotypes within each population, each suited to specific conditions; or by the development of an adaptable genotype, which is capable of responding to different habitat conditions by growth modification or stimulation of specifically adapted variants of enzyme systems. Differential evolution of either type of system would lead to variations in the ecological preferences and ranges of different species. The extent to which observed variation is dependent upon inherent plasticity in morphological development, or physiological and biochemical processes, within single genotypes, is being investigated. The results are being contrasted with the overall level of variability found within individual populations from different parts of the geographical and ecological ranges of particular species. In this way, it is hoped to gain insight into the ways in which adaptation and specialisation have occurred, both of which have contributed to the success of the genus in dominating significant areas of the world.

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Preliminary Results of Electrophoretic Screening of *Spartina* Species

Marchant (1967, 1968) gives detailed support for the theory that the sterile F1 hybrid *Spartina x townsendii* is a hybrid arising from the European species, *S. maritima*, and the accidentally introduced, North American species, *S. alterniflora*. His cytological work substantiates the idea that the fertile amphidiploid – *S. anglica* (the rapid colonizer of mudflats) – is the product of a natural chromosome doubling in *S. x townsendii*.

In order to gain further insight into the interrelations between the species of *Spartina*, use was made of a small collection maintained in a glasshouse at ITE's Furzebrook Research Station. This collection includes specimens of (i) a sample of the remaining *S. maritima* populations on the Essex coast, (ii), *S. alterniflora* from Goldhanger Creek, (iii) *S. anglica* from several estuaries, including Poole Harbour and Morecambe Bay, and (iv) *S. x townsendii* from the classic F1 hybrid site at Hythe in Southampton Water.

To identify the different forms (isozymes) of the enzyme phosphoglucose isomerase (EC no. 5.3.1.9.), leaf and root samples were taken from glasshouse stocks and crushed in a 2-mercaptoethanol solution. The extracts were absorbed on to filter-paper wicks – 1 wick per sample. These were inserted into a slit (the 'origin') cut into a starch gel, through which an electric current was then passed for 4 to 5 hours. During this period of electrophoresis, enzymes in the samples migrate across the gel at rates dependent upon their molecular size and net electric charge. After electrophoresis, the gel was sliced and stained with an enzyme-specific reagent. Recognizable bands were produced at different distances from the 'origin' by the different isozymes.

Results to date indicate that extracts from *S. x townsendii* and some samples of *S. anglica* produce 5 bands (see Figure 55 [c]), including 3 characteristic of *S. maritima* [a] and 3 of *S. alterniflora* [b]. Other samples of *S. anglica* have the distinctive banding patterns [d] and [e], suggesting the existence of at least 3 phenotypes in this species.

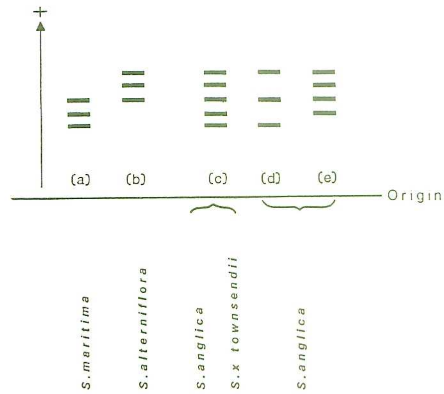

Figure 55. Distribution of isozymes of phosphoglucose isomerase extracted from leaf and root material from different populations of *Spartina maritima*, *S. alterniflora*, *S. x townsendii* and *S. anglica*. Tissue extracts were examined by horizontal gel electrophoresis

Cytological studies are being made concurrently at the University of Birmingham using *Spartina* material from the Furzebrook collection, while electrophoretic screening continues at Furzebrook for a range of enzymes.

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An Improved Data Base for the Antarctic Flora

To enhance the taxonomic value of the herbarium held by the British Antarctic Survey (BAS), members of the Institute have developed a data base of the specimens in the herbarium from Antarctic regions. The herbarium has had a

A species rich community of mosses on the subantarctic island of Isle de la Possession, Isles Crozet.

computerized data base from its inception in 1969 (Greene 1972a, b), enabling information to be retrieved in many ways, eg by species, by collector, or by locality of collection. The system initially used numerical codes for the different items of data; an awkward system which had the disadvantage of being relatively inaccessible. It was stored under contract on a commercial mainframe which could normally be searched only once a month. With the help of NERC computer services, a more convenient system has been designed.

The new data base uses STATUS, a text retrieval system, held on the NERC IBM computer at the Institute of Hydrology, Wallingford STATUS was designed to enable librarians to retrieve 'articles' containing particular words or combinations of words. On being adapted to the needs of the BAS herbarium, each library 'article' became synonymous with a specimen. Different 'sections' in each 'article' contain the name, accession number, name of collector, habitat details, and collection locality of the specimens. As a result of this structure – articles and sections – a very powerful and flexible tool has been developed for the retrieval of specimen information. Apart from its greater flexibility, the STATUS data base has 4 other major benefits.

1. Instant access. The data base can be consulted at short notice, several times a day if necessary.

2. Readability. The information is presented as text and does not need to be decoded.

3. Open to all users. The data base can be consulted by many users, including BAS staff and the academic community, who can extract information and insert new data.

4. Output. The data base can be used to produce a variety of different outputs, including computer-plotted distribution maps and labels for specimens, so avoiding laborious typing.

Because of its completeness, the data base is like an Antarctic equivalent of ITE's Biological Records Centre. It currently contains nearly 50,000 'articles', which mainly refer to specimens held in the BAS herbarium, but also include records of important specimens held in other herbaria. It is probably the most complete record of the Antarctic and sub-Antarctic flora in existence. Recently it has been used to provide data to facilitate the designation of several Sites of Special Scientific Interest in the Antarctic. Lists of bryophytes were provided by the ITE data base while BAS staff produced management plans for each of the sites, now protected under the international Antarctic Treaty.

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Autecology of Animals

Some Effects of the Host Plant on the Pine Beauty Moth

There has been considerable argument among population ecologists for many years about which factors regulate, or limit, the size of insect populations. Although there have been some dissenting opinions (eg Milne 1962; Ehrlich *et al.* 1972), the widespread view until the late 1970s was that insect populations are seldom limited by food, but usually by the action of predators, parasites and pathogens (Denno & McClure 1983). One persuasive argument to support the view that insect populations are regulated by natural enemies is that plants are abundant and rarely show signs of serious damage (Hairston *et al.* 1960). There are 2 counter-arguments to this view. First, serious food resource depletion is not as uncommon as has been argued (Dempster 1983), particularly bearing in mind the length of time an insect population needs to grow to damaging levels. Second, what may appear to be a suitable food plant to the human observer may not be for the insect. Alternatively, a host plant which is palatable now may have been unpalatable when the insect was particularly sensitive to the quality of its host plant.

The aim of this contribution is to describe how variability in host plant quality affects the larvae of the pine beauty moth (*Panolis flammea*).

Plant Water Stress

It has been argued that many insect herbivores feed on host plants which are generally of a very poor nutritive quality, but that this quality dramatically improves if the plants are water-stressed (White 1984). Under drought, or waterlogged conditions, the nitrogen content of plants is thought to increase, and it has also been suggested that water stress results in a decrease in the concentration of toxic chemicals in plant tissues (Rhoades 1983). Consequently, water shortage, or water logging, can increase insect survival and abundance. Plant stress has been implicated in the population dynamics of a number of forest pests, including the pine beauty moth. There are 2 different aspects to the effect of plant stress. First, trees are likely to experience different levels of waterlogging and drought according to the rainfall they receive each year. Second, some sites may be more prone to stress than others, because of soil type and topography. A series of experiments was started in 1983, with the principal aim of investigating the second aspect.

In 1983 and 1984, artificially manipulated populations of the pine beauty moth were monitored on lodgepole pine (*Pinus contorta*) growing in deep unflushed peat and iron pan soils (at Elchies, Speyside Forest) to test the hypothesis that pine beauty moth outbreaks tend to occur in deep peat areas, because the trees growing there are more nutritious to pine beauty larvae. In both years, no significant difference could be found between the population development of pine beauty moth on trees growing in the different soils (Watt 1985). In 1985, natural populations were studied in the same area, because of concern that the high levels of mortality observed in 1983 and 1984 were an artifact of the method used. However, the same result was obtained: populations on trees growing in different soils behaved in the same way. This finding seemed to refute the stress hypothesis, but there was some concern that population monitoring was too crude a technique to detect differences in larval survival, owing to variability in host plant quality.

In 1983, foliage was removed from trees growing in 2 different soils (deep peat and iron pan) at Elchies on 1 June to test larval performance under constant temperature conditions. Shoots were placed in small cylindrical containers (8.5cm x 10cm), 5 cages per treatment, and 20 pine beauty moth eggs were placed in each. After 2 weeks, the number of surviving larvae was recorded, and 10 larvae

Table 21. The survival, weight and growth rate of pine beauty moth larvae reared in the laboratory on foliage taken from trees growing in different soil types. None of the differences between soil types are significant at P = 0.05

	Foliage collection date			
	1 June		15 June	
	Soil type			
	deep peat	iron pan soil	deep peat	iron pan soil
Survival % (from 100 eggs)	59	66	68	76
Weight (mg) (after 2 weeks)	64	55	35	40
Growth rate (between 2 & 3 weeks)	0.1133	0.0646	0.1409	0.1695

Table 22. The survival, weight and development of pine beauty moth larvae reared on trees growing in the field in different soil types. None of the differences were significant at P = 0.05

	Year			
	1984		1985	
	Soil type			
	deep peat	iron pan soil	deep peat	iron pan soil
Survival %	66.9	69.8	72.1	70.9
Weight (mg)	12.2	11.7	15.3	13.7
Development %	64.8	65.0	34.8	31.6

from each cage were weighed. One week later, these 10 larvae were weighed again, and their growth rates were calculated. The experiment was repeated using foliage collected on 15 June. In both experiments, larval survival was found to be high, irrespective of whether the foliage came from trees growing in deep peat or iron pan soils (Table 21). Similarly, there was no significant difference in either the weight of larvae or their growth rate. However, these experiments were perhaps an unsatisfactory test of larval performance, because nested analysis of variance (Sokai & Rohlf 1969) revealed large significant differences in weight and growth rate between the cages within treatments. There may have been differences in the quality of foliage from trees sampled at the same site, or the foliage in the different cages may have deteriorated at different rates during the course of the experiment. It was decided that subsequent experiments would be done on live, rather than excised, foliage.

In 1984 and 1985, experiments on larval performance were done on larvae caged on to the foliage of trees 25–30 years old at Elchies. Organza cages were placed on 35th whorl branches on trees growing in deep peat and in an iron pan soil. Two cages were placed on each tree and 5 (1984) or 10 (1985) trees were used on each soil type. Pine beauty moth eggs were placed inside each cage in early May, and were allowed to hatch naturally. In late June, the caged branches were taken to the laboratory and the number, age (to instar), and weight of the surviving larvae were recorded. In both years, no significant differences were found in the survival, weight or development of larvae reared on trees growing in the 2 different soils (Table 22).

Thus, it was concluded that trees growing in deep unflushed peat do not provide a better food source for pine beauty larvae than trees growing in an iron pan soil. In 1983 and 1985, the pines at Elchies were unlikely to have been water-stressed. However, 1984 was a dry year (Table 23). The chemical composition of lodgepole pine foliage showed marked variability during May–July each year, but did not differ substantially between the 3 study years. The nitrogen concentration in both new and old foliage was no higher in 1984 than 1985, but the soluble tannin content of old foliage, which is generally (but not exclusively) thought to cause unpalatibility to insects, was actually higher in 1984 than in the other 2 years.

In 1984, a laboratory experiment was done to see whether artificially induced water shortage, or waterlogging, would produce plants which were preferred as oviposition sites, or cause an improvement in larval performance. Two-year-old lodgepole pine plants were either watered normally, left unwatered, or overwatered (by preventing drainage). Eight plants in each treatment were left for a week and then placed randomly in 2 constant temperature cabinets at 18°C. Thirty-five adult moths were placed in each cabinet and allowed to lay their full complement of eggs. At the end of the experiment, 24 more plants were treated in the same way and, then 20 pine beauty eggs were caged on to each of them. Two weeks later, the surviving larvae were counted and weighed.

Adult pine beauty moths laid an equal number of eggs on the watered plants, and plants stressed by underwatering or overwatering (Table 24). However, both the survival and weight of larvae were greater on normally watered plants than on either of the stressed plants.

Thus, it appears that the pine beauty moth is insensitive to variations in plant quality in field-grown trees which may result from water shortage, waterlogging, or certain soil types. However, when lodgepole pines are subjected to more extreme levels of stress, they provide a less suitable source of food than healthy plants.

Host Plant Growth Stage

Pine beauty larvae hatch and develop during the part of the year when pine foliage is growing and developing rapidly. From 1983 onwards, a series of laboratory experiments was done to see whether the survival and growth of pine beauty larvae were sensitive to the growth stage of lodgepole pine and Scots pine (*Pinus sylvestris*).

In each experiment, groups of plants at a similar stage of

Table 23. Between year variability in the rainfall at Glenlivet, stress index (proportional deviation from the long-term average rainfall), chemical composition of old and young foliage sampled in May–July from lodgepole pine at Elchies (% dry weight), and the average survival rate of pine beauty moth larvae.

		Year		
		1983	1984	1985
Rainfall (mm) April–June		252	87	309
Stress index		+0.23	−0.58	+0.51
Nitrogen	(old) %	0.87	1.20	1.24
	(young) %	1.50	1.75	1.67
Phosphorus	(old) %	0.08	0.13	0.13
	(young) %	0.22	0.28	0.30
Soluble tannin	(old) %	5.54	8.16	6.49
	(young) %	5.40	5.44	4.54
Larval survival %		67.3	68.4	71.5

Table 24. The number of eggs laid, larval survival and larval weight of the pine beauty moth on normally watered, underwatered and overwatered 2-year-old lodgepole pine

	State of lodgepole pine			
	Normally watered	Underwatered	Overwatered	Significance
Eggs laid per plant	66.3	49.6	84.1	NS
Survival%	85.0	51.9	59.0	*
Weight (mg)	33.7	21.2	23.4	**

development were measured and placed in a constant temperature cabinet at 18°C. Pine beauty eggs, which were near to hatching, were caged on to each plant. Two weeks later, the numbers of surviving larvae were recorded, and in some experiments larvae were weighed after 2 and 3 weeks.

Pine beauty larvae failed to survive if they were confined to the previous year's needles. However, if the larvae were given access to the current year's shoots, they attained a very high level of survival (80–93%), until the needles had grown to 4.6cm (Figure 56).

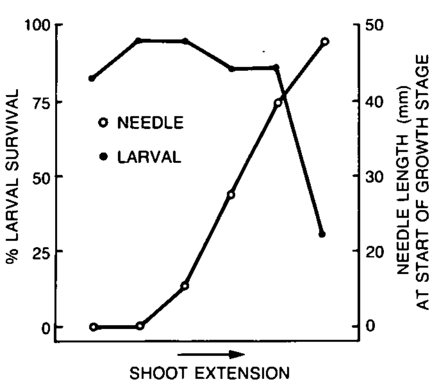

Figure 56. Survival of the pine beauty moth larvae reared on shoots of 2-year-old lodgepole pine at different growth stages, reflected in different needle lengths at each stage

Similar results were obtained when larvae were reared on Scots pine. The growth of the pine beauty moth was studied on lodgepole pine at 3 stages of development and Scots pine at 4 stages of development. On both plant species, early larval growth was lowest on plants at an early stage of development, rose to a maximum when the needles were nearly full elongated, and then, at least on Scots pine, decreased (Figure 57). On lodgepole pine, the subsequent growth rate of older larvae was unaffected by host plant growth stage, but on Scots pine the growth rate actually showed a significant decline (Figure 57).

These rather contradictory results can be explained by looking at the degree to which the plants grew during the experiment: plants which were at the most suitable stage for the growth of young larvae became less suitable by the time the larvae were older.

Larvae which were fed on the previous year's needles, of both pines, died before becoming established. However, older larvae in the field, and in the laboratory, have been observed feeding on old needles. An experiment was therefore done to establish the age at which pine beauty larvae can survive on old needles of lodgepole pine. Pine beauty eggs

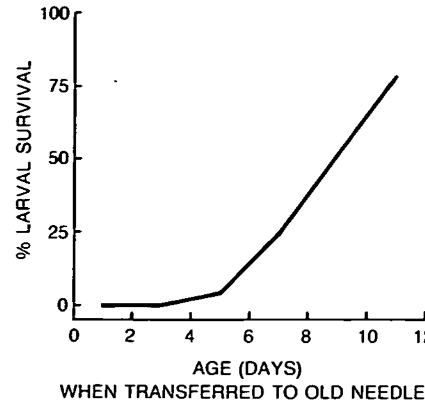

Figure 58. The survival of the pine beauty moth on one-year-old needles of lodgepole pine after being reared for different lengths of time on young foliage

were allowed to hatch in plastic containers without food. After hatching, they were placed on young shoots of lodgepole pine. Larvae one, 3, 5, 7 and 11 days old were then transferred to old needles, and the number surviving 2 weeks later was recorded. Survival remained at a very low level until the larvae were 7 days old when transferred to old needles, but, by the time they were 11 days old when transferred, their survival was as high as if they had been reared on young growth throughout (Figure 58). Thus, the effect of plant growth stage on survival can be considerably different for larvae of different ages.

Conclusions

White (1976) expanded his hypothesis on the effect of plant stress on insect population dynamics to propose that stress mainly affects insects which feed on mature foliage, but the plant stress is not an important factor in the population ecology of insects whose young larvae feed on new plant growth. White (1974) provided evidence to show that the abundance of 2 looper species (including *Bupalus piniarius*, an occasional pest of Scots pine in the UK), which feed on mature pine needles, is affected by plant water stress. In contrast, the pine beauty moth, whose larvae feed on young foliage, is not affected by host plant stress (unless the stress is severe, when they are detrimentally, not beneficially, affected).

Pine beauty larvae are very sensitive to the growth stage of their host plants, which particularly affects larval growth. In the experiments reported here, the survival of pine beauty larvae appears to be less severely affected than larval growth. Moreover, experiments in progress, on plants at an earlier stage of development than previously tested, suggest that lodgepole pine becomes suitable for the establishment of pine beauty

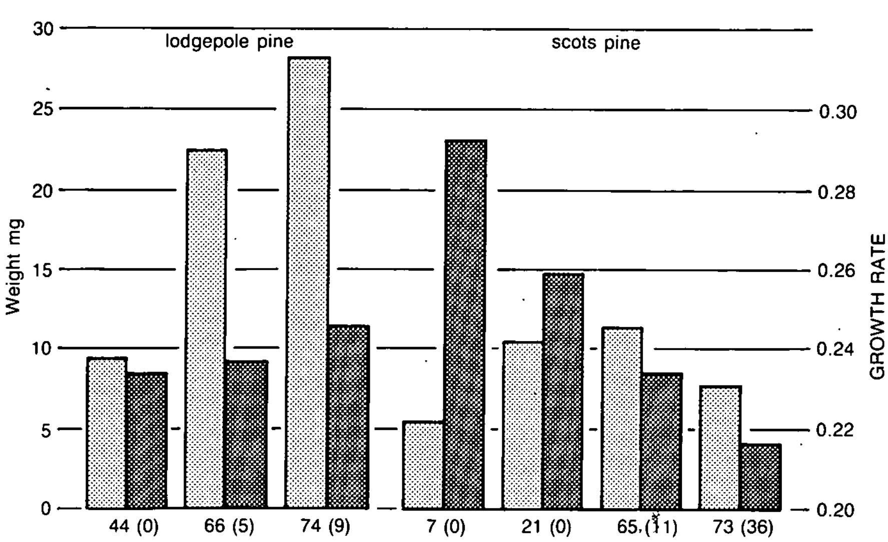

Figure 57. The weight of the pine beauty moth after 2 weeks (□) and their growth rate between 2 and 3 weeks (■) when reared on lodgepole and Scots pine shoots at different growth stages as indicated by needle lengths

larvae as early as mid-April. Growing pines present a source of food whose quality is ever-changing. Mature pine foliage may appear to the human observer to be an adequate food source – which it may be for older larvae. However, young pine beauty larvae need young pine shoots for their successful establishment. Indeed, the pine beauty moth may be a pest on lodgepole pine because that host provides suitable conditions for larval growth and survival at just the time of year when pine beauty larvae hatch.

Laboratory assistance was provided by C Beetham, J Clarke and R Evans.

A D Watt

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Population Dynamics of 2 Tephritid Flies Exploiting Burdock Flowerheads

Populations of lesser burdock (*Arctium minus*) have been studied in Monks Wood NNR, Cambridgeshire, over the period 1983–85, with the objective of determining the role of food supply in the population dynamics of its seed-feeding insects. Dempster and Pollard (1981) and Dempster (1983) indicated that changes in levels of basic resources are often a major cause of fluctuation in insect population numbers, but too few studies, which include an adequate measure of resources, have been completed to determine the relative importance of this process compared to the regulation of herbivore populations by natural enemies.

Burdock is a facultative biennial (*sensu* Kelly 1985) producing rosette plants from seed. The plants grow vegetatively for one to several years before producing a single flower stem, which may support several hundreds of flowerheads. After flowering, the plant dies. Seeds are eaten by larvae of 2 fly species, *Tephritis bardanae* and *Orellia tussilaginis* (Diptera; Tephritidae), and by caterpillars of *Aethes Rubigana* (Lepidoptera; Cochylidae) and *Metzneria lappella* (Lepidoptera; Gelechiidae). All 4 species are specific to burdock.

During April–May each year, all burdock plants in Monks Wood were located, and in June all flower stems were labelled. Information was collected on plant morphology and flowerhead production in different habitat types. During 1985, relative rates of bud growth and development on stems growing under different levels of shade were established in relation to the timing of fly attack.

The main life table data for the tephritids, their parasitoids and the 2 moths were obtained from 250 heads collected each September when larval development was complete. Heads were dissected and their contents analysed to determine events occurring over the previous months. In addition, 100 green heads were collected in August to estimate *Tephritis* egg numbers. Over-winter loss of seeds and *Orellia* larvae on the ground was estimated by exposing marked seeds between November and the following spring. Birds and beetles had little effect, but mice destroyed 60–70% of deposited seed.

Burdock flower stems were widely scattered, yet highly clumped within Monks Wood, with large changes in numbers between years (Figure 59). This spatial and temporal variability was due to the following facts: (i) seed germination and seedling survival were highest on bare ground of disturbed areas, compared with areas of dense vegetation and deep shade; hence burdock was confined to 'edge' habitats; (ii) the proportion of the total plant population which flowered in any one year was variable and probably weather-dependent.

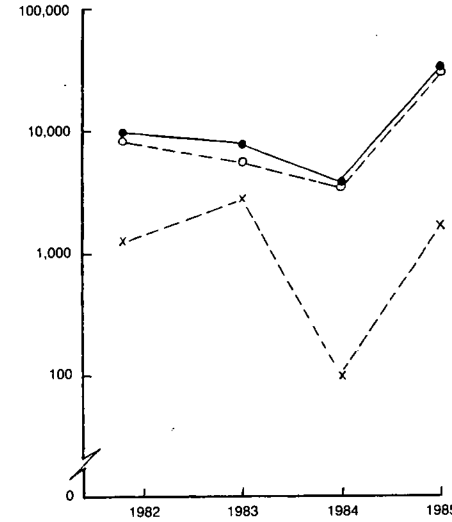

Figure 59. Changes in the population numbers of burdock plants in Monks Wood NNR, Cambridgeshire, 1982–85.

Population numbers of *Tephritis* closely followed changes in total seed numbers (Figure 60), even though only 12–13% of total flowerheads were attacked each year. Similarly, *Orellia* numbers crashed between 1983 and 1984, when 54% and 58% of heads were attacked, but failed to increase in 1985 (0.02% heads attacked). Each year, the greatest 'mortality' of tephritids resulted from the failure to lay eggs (ie the difference between potential eggs and actual numbers of eggs laid), suggesting flowerhead numbers were limiting Some heads were of unsuitable size for oviposition during the tephritid flight periods, but it is likely that a larger number simply could not be found in the search time available. Flowerheads matured sequentially from open to shaded habitats over a period of several weeks, but individual heads were only of suitable size for egg-laying for about 8 days in the case of *Tephritis* and 14 days for *Orellia*. This factor accentuated the difficulty of locating the scattered resource. In 1985, wet weather prevented *Orellia* from flying and fewer eggs were laid than expected.

Intraspecific competition occurred each year due to the clumped distribution of larvae in heads, and accounted for 6–24% of deaths, but interspecific competition was negligible. *Tephritis* suffered 44% and 67% parasitism in 1983 and 1984, but the rate of parasitism was not related directly to *Tephritis* numbers. The tephritids shared parasitoid species, but, because *Orellia* was more abundant, it supported 80% of parasitoid individuals, although they caused only 12–16% loss of *Orellia* larvae.

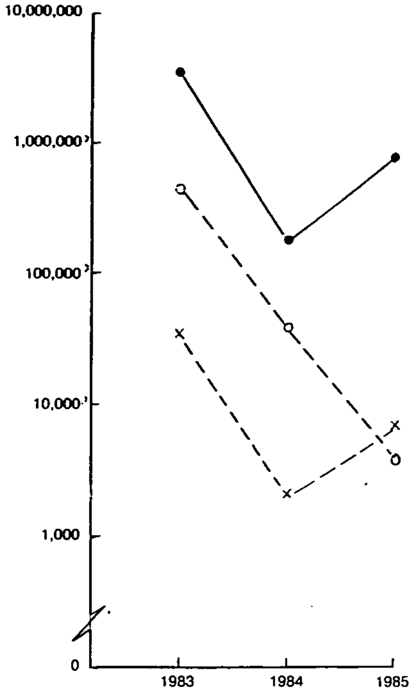

Figure 60. Changes in food supply and population numbers of tephritid flies attacking burdock in Monks Wood NNR, 1983–85

Raising or lowering tephritid infestation rates inside heads, by relaxation of intensifying parasitism, would have been insufficient to modify the fluctuations in fly numbers imposed by the dramatic changes in number of flowerheads between years.

N A Straw

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Are Guillemots Still Increasing in Numbers?

The British population of guillemots (*Uria aalge*) increased from 580 000 birds in 1969–70 to 1.1 M in 1982 (Stowe & Harris 1984). The population on the Isle of May, Firth of Forth, Scotland, showed a similar large increase 1956–83 (Figure 61). Guillemots feed their young mainly on sandeels (*Ammodytes* spp.), herring (*Clupea harengus*) and sprat (*Sprattus sprattus*), and there is an expanding human fishery for these fish for conversion into fish-meal (Bailey 1983). If both the fishery and the seabird populations continue to grow, there must inevitably be competition. ITE has been collecting population and biological data on guillemots and puffins (*Fratercula arctica*) which can be used as a base-line against which to monitor future changes in

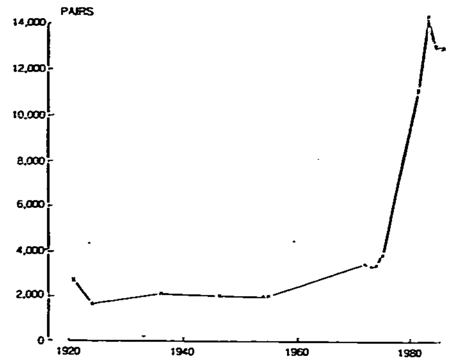

Figure 61. Number of pairs of guillemots counted on the Isle of May, 1921–85

numbers, food given to the young, and breeding performance of these seabirds.

The population changes of guillemots are monitored in 3 ways.

1. All birds present at the colony are counted each June. This task takes about 2 days and the counts are converted into pairs using correction factors obtained from study plots where a known number of pairs breed.
2. Individual birds present in 11 clearly defined plots distributed at random throughout the colony are counted on 8–10 days between 1 June and 20 June each year.
3. The number of pairs which actually lay in the study plots is recorded each year by daily checks of breeding sites.

Results from all methods suggest that the period of rapid population increase has come to an end (Figure 62).

The annual survival of breeding adults has remained high, varying between 92% and 93% in 1982–85. Breeding success has also been high (Table 25). The slightly lower figure for 1984 was due to some young dying. Disease was suspected, and the young were certainly not starving.

Young are fed on fish which the adult carries back singly in its bill. The fish are easily visible and can be counted, identified and their length (and so weight) estimated, so that the daily food intake of a young bird can be assessed (Harris & Wanless 1985). There was a progressive decline in the mean

Figure 62. Changes in numbers of guillemots on the Isle of May, 1981–85

weight of fish brought to young each year in 1981–1985 but little change in the feeding rate (Table 26), with the result that 1985 young received only 50% of the food received by young in 1981. Large fish have a higher calorific value per unit weight than small fish, and sprats have higher values than sandeels. Although there was no overall trend during the period, sprats made up a higher proportion of the diet in 1981 (40%) than in 1985 (20%) and the sandeels brought to young were much larger in 1981. From this evidence, it was calculated that young in 1985 received only 40% of the calorie intake of the young in 1981.

The effect of this reduced food intake is difficult to assess, as young birds leave the colony when only a quarter grown and are fed at sea. Any deficit in food might be made up then. Several hundred young have been aged, weighed and ringed each year, and it is hoped to monitor the survival of these different year classes when they return to the colony in order to determine whether the recruitment rate of immatures into the population has been reduced.

M P Harris

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Table 25. Nesting success of guillemots on the Isle of May, 1981–85

Year	Number of pairs laying	Number of young leaving	Proportion of pairs rearing a young bird
1981	276	219	0.79
1982	532	422	0.79
1983	552	427	0.77
1984	654	462	0.71
1985	662	544	0.82

Table 26. Daily food intake of young guillemots on the Isle of May, 1981–85

Year	Days	Number of feeds day^{-1} Mean ± SE	Number	Fish brought to young: Mean wt (g)	Fish brought to young: Calorific value KJ g^{-1} wet weight	Daily intake of young: g	Daily intake of young: KJ
1981	1	5.20	90	11.7	9.7	61	590
1982	3	3.40±0.5	529	13.3	7.8	45	354
1983	8	4.12±0.6	1071	10.7	8.8	44	386
1984	5	3.60±0.2	761	10.0	8.2	36	295
1985	3	3.77±0.3	720	7.9	7.9	30	235

Harris, M P & Wanless, S. 1985. Fish fed to young guillemots *Uria aalge*, and used in display on the Isle of May, Scotland. *J. Zool., Lond.* (A), **207**, 441–458.

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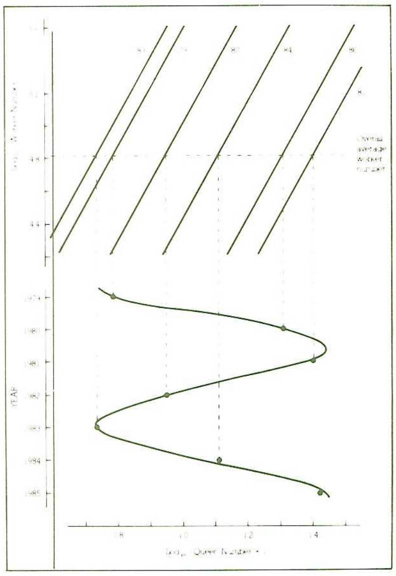
The Adaptive Speciation of Red Ants

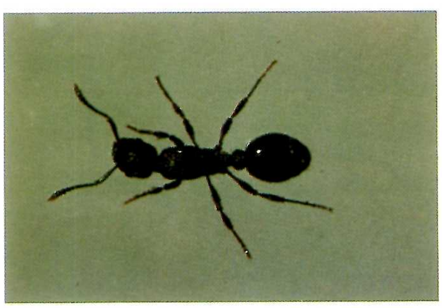
The ants, bees and wasps (Hymenoptera) are haplodiploid; that is, males develop from unfertilized eggs and females from fertilized eggs. Workers are simply females that fail to achieve their full sexuality. Under this sex system, sisters are related by a factor of $\frac{3}{4}$, rather than the normal $\frac{1}{2}$; thus, in a colony with a single mother queen, the average relatedness of all individuals (including the workers) is $\frac{3}{4}$. This fraction has been used to explain why so many species of the Hymenoptera are social.

If a colony has more than one fertile mother queen, it is called polygynous. This situation is particularly common among the ants, all of which live in highly organized societies (Elmes 1985). The average relatedness between individuals of a polygynous society is likely to be low; even if all the queens are full sisters, the average relatedness of all individuals is only $\frac{3}{8}$. Genetic studies have shown that in most natural polygynous colonies the average relatedness is little higher than the relatedness between all the individuals in the entire local population (Pearson 1982). Thus, polygyny, and its widespread occurrence among the ants, is a vexed question for students of the theory of the evolution of insect sociality. At the moment, polygyny is best explained as a secondary adaptation, by established societies, for the exploitation of new or difficult habitats (Elmes 1985).

Myrmica sulcinodis is a striking and robust red ant that is common on the mountains and moorlands of Europe. Habitat which is roughly central to the range of habitats used by *M. sulcinodis*, occurs on Tulloch Moor, in Scotland. Here, the ant mostly has large, monogynous colonies (Elmes 1974). In southern England, *M. sulcinodis* lives on damp, sandy heathlands, where its colonies appear to be smaller and more polygynous. In 1979, a sample of colonies was excavated from 2 Dorset heaths (Stoborough and Winfrith) to test this impression. It was hoped that data from these and other sites would enable any variation in the level of polygyny observed to be interpreted in terms of the species' success in the different habitats (ie a comparison of the size and abundance of colonies, breeding success, etc). However, before starting the general sampling programme, the Dorset sites were resampled in 1980, in order to check the consistency of the estimate of the mean numbers of queens per colony. Between 1979 and 1980, there was a dramatic increase in average queen numbers per nest at both sites, and, although the data are naturally very variable, the increase seemed larger than would be expected from sampling error. Consequently, the wider programme was suspended, and the Dorset sites have been sampled each year until the present.



The regression of queens against worker numbers in colonies of *Myrmica sulcinodis* was plotted for the years 1979–84 (Figure 63). The 2 sites, analysed separately, gave results which were very similar to each other; therefore, they have been combined here into a single data set. The predicted queen number at the overall average for worker number for each year is projected downwards on to a timescale. A sine wave accounts for about 90% of the variation between these predicted means. If the annual means are merely estimates of a single true mean, then the chance of obtaining 6 sequential estimates that give some sort of wave is about 5%. The chance that waves of the same form will be obtained independently at 2 sites is about 0.3%. The wave, calculated from the 1979–84 data, is extrapolated to 1985, and the weighted estimate of queen number from the field in 1985 is added; this expression fits the prediction well. The probability of obtaining a value in 1985 that more-or-less fits the extrapolated wave is about 30% at each site, or $<10\%$ at both sites. The likelihood of obtaining a wave from a 7-point series at 2 sites independently is $<0.1\%$. Therefore, it is likely that the average number of queens in *M. sulcinodis* colonies, in Dorset, varies in a cyclic manner with time. Initially, both sites seemed to follow the same trend, although the data for Stoborough are now best described by a wave with a period of 5 years, and those for Winfrith by a 4-year cycle. Queen number is naturally very variable (Elmes 1973); the size of a colony, measured by worker number, is the only factor that accounts for a significant proportion of this individual colony variation. Analysis of the data for *M. sulcinodis* showed that, for each year, there is a separate regression of queen number against worker number; the slopes of these regressions are the same, but their intercepts are significantly different. When the annual data sets are standardized for worker number (taking the overall mean), the wave accounts for nearly all the variation between the predicted annual means (Figure 63).



Red Ant Queen

At the level of the individual colony, a cycle for queen numbers can be generated in several different ways, the most likely one being by a periodic recruitment of new queens with a short life span. The wave length represents the maximum longevity of a queen. At the site level, it is much harder to see why most colonies should be sufficiently in phase for the existence of the wave to be detected. Phasing could be caused by some past environmental catastrophe; alternatively, the queen cycle could be a response to an ongoing environmental pressure that itself happened to be cyclic over the period 1979–85. The habitats of both sites were destroyed by fire in 1976, and this could be a sufficient catastrophe to put the *M. sulcinodis* colonies in phase. On the other hand, no short-term fluctuating environmental variables have been identified yet which support the alternative hypothesis. If the first explanation is correct, then it is important to know whether an apparent stability of average queen numbers results from the breakdown of the phasing of individual colonies, which continue to have their own queen cycle, or whether a real stability is achieved within individual colonies. I believe that the former hypothesis will prove to be the case.

This work shows that it is now doubtful whether the actual level of polygyny of a species, living in any site, can be accurately assessed from a single sample of nests. This conclusion questions the value of much of the data used as the basis of theoretical debate on the role of polygyny, because most are for single species, from single sites, taken in a single year.

G W Elmes

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Animal Species Interactions and Communities

Wading Birds and Reclamation on the Wash

(This work is supported by Department of the Environment funds)

Introduction

The marsh which fringes the Wash in east England has been reclaimed for agriculture for hundreds of years. The normal sequence of events is that the mudflats at the top of the beach are gradually invaded by colonizing marsh plants which, as the level of the mud builds up, are replaced by plants characteristic of more mature marshes, which are then grazed by cattle. Eventually, a sea wall is built across the bottom of the marsh and, after a suitable period to allow salt to be washed out of the soil, the old marsh is ploughed and crops planted. Over the last 700 years, many hectares of agricultural land have been obtained in this way.

The economic pressures persist for farms that border the Wash to continue this process of reclamation. In recent years, however, there has been growing concern amongst conservationists that the continuous down-shore progression of agricultural development will, in time, be detrimental to the large numbers of wading birds and wildfowl which feed on the mud and sand flats below the marsh edge. Unless the low water mark migrates seawards at the same rate at which the marsh edge moves down the shore, the area of feeding grounds available for these birds must inevitably decrease.

In 1981, Lincolnshire County Council proposed a moratorium on further reclamation of the Wash so that the effects of further reclamation on the ecology of the area could be examined. A working party, with representatives from the Nature Conservancy Council (NCC), the Department of the Environment, and the Ministry of Agriculture, Fisheries and Food, was set up to identify research priorities. Studies of (i) the saltmarsh flora and breeding birds, (ii) the intertidal sediments, and (iii) the wading birds and wildfowl that feed on the intertidal flats were recommended. ITE was commissioned by the DoE to undertake the third project.

A study by the NCC suggests that, despite continuous reclamation, the low water mark has hardly shifted over the last 100 years. It cannot therefore be assumed that, as reclamation continues, there will be a compensatory seawards movement in the position of the bottom of the beach. The ITE project was designed to predict the cumulative effect on the birds, and the invertebrates on which they feed, of a continuing contraction in the width of the beach.

Project Design

The project is in 2 parts. In the descriptive phase, we are simply measuring how much of the birds' feeding occurs at different levels of the shore, in different regions of the Wash. This information will enable the customer to project what effect the removal of, say, the top 2km of beach, in a particular part of the Wash, would have on the birds' current feeding activities. Birds which feed up-shore throughout most of the low water period would clearly lose more than those which feed at the bottom. Many of the measurements we make are therefore related to distance down-shore.

However, simply measuring the proportion of the existing feeding activities that would be lost might be rather unrealistic and represent a worst-case prediction, because reclamations proceed gradually, and, at any one time, only the marsh itself is removed. Though some birds do feed there, the majority do not. A new marsh will gradually build up seawards of the new sea walls, and the remaining intertidal substrates will gradually change. Those invertebrates, for example, which live in the upper reaches of the beach would gradually move seawards as the top of the beach itself moves towards the sea. The beach might become narrower, but the invertebrates available to the birds at different points down the shore might remain the same.

The second phase of the project is designed to enable predictions to be made as to the likely distribution and densities of the main invertebrate prey species down a contracted width of beach. We expect that the densities of the invertebrates living at any point down the beach will depend on the nature of the substrate, and the length of time for which the place is covered by the tide. The existing pattern of surface sediments around the Wash should provide a means for predicting how a gradual narrowing of the beach, and consequent increasing of its slope, would change the substrate, and therefore the densities of invertebrates available for the birds as food. The effect of reducing the width of the beach by different amounts can then be explored, and these predictions used to investigate the extent to which changes in the substrate would offset the gross loss of feeding areas for birds, due to reclamation.

It is unlikely that the changes in the substrate would be so benign that there would not be some loss of feeding opportunities for the birds. If the low water mark does, indeed, move rather little, the feeding area would be reduced. The birds would then have to pack into a reduced space, thus increasing any competition for food that might occur. An important part of phase 2 of the project is, therefore, to estimate the extent to which the birds' feeding would be deleteriously affected by an increase in their own density. Studies on other estuarine systems have shown two different effects. First, wading birds eat a significant proportion of their food supply during the winter. Second, birds often interfere with each other's feeding, if they are forced to feed together at high densities.

By reducing shore width, and thus the feeding space available, any difficulty the birds have in finding enough food could be made worse through these 2 mechanisms. Observations on the birds themselves and measurements on the depletion of the prey will be done to quantify the importance of increased competition between birds.

Most effort on both phases of the project is being made during the winter and spring – the most critical time for the birds. In spring, they are laying down fat to migrate to their breeding grounds to the north, west and east. In winter, feeding conditions are already sometimes so severe that many birds die. Increasing any difficulty the birds have now could decrease the size of their populations, by reducing either overwinter survival or breeding success during the summer.

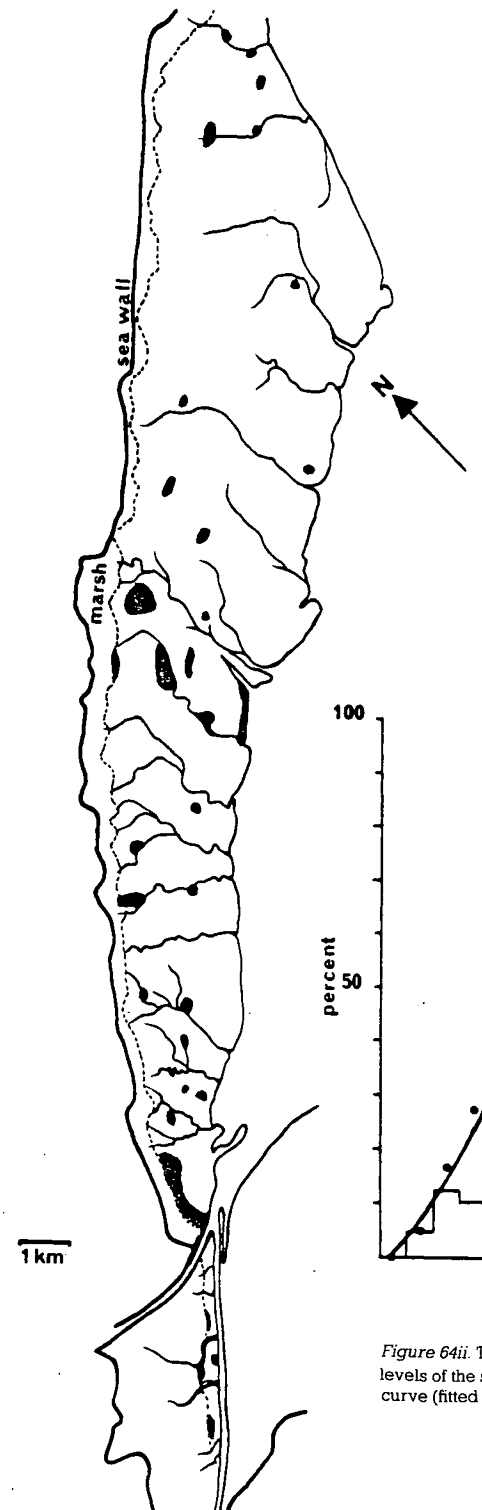
Field work on the birds
We began in July 1985 by deciding to survey the west side of the Wash during the first year of the 3-year project, ie from Gibraltar Point to Kirton at the mouth of the River Welland. The remaining areas, from the Welland to the River Ouse and then along the east side up to Heacham, will be surveyed in the 1986–87 season. Spot-checks will be made around the Wash during the final year to detect any annual variations in distribution.

For the purpose of surveying the birds' feeding areas, we defined the low water period as spanning 2 hours before to 2 hours after low water. The birds' feeding areas are exposed then and the birds' distribution is more-or-less stable. An area is covered on foot and, by regularly scanning through a telescope, it is possible to devise a route which minimizes disturbance. When located, the birds are counted, the proportion feeding recorded, and their position determined relative to that of the observer. The observer's position is then recorded, using cross-bearings on 2 or more reference points. So far, the whole west side has been surveyed twice, once during the autumn when many migrant waders are on the Wash, and once in the winter when the overwintering birds are present. The species and numbers recorded during the autumn count are given in Table 27. Another winter survey and a spring survey are planned.

Table 27. Autumn numbers of the main species of waders on low water feeding areas on the west side of the Wash

Species	Numbers
Dunlin (*Calidris alpina*)	5824
Sanderling (*Calidris alba*)	115
Ringed plover (*Charadrius hiaticula*)	118
Redshank (*Tringa totanus*)	1286
Knot (*Calidris canutus*)	7433
Bar-tailed godwit (*Limosa lapponica*)	4752
Grey plover (*Pluvialis squatarola*)	541
Oystercatcher (*Haematopus ostralegus*)	10525
Curlew (*Numenius arquata*)	368

The birds were patchily distributed during the autumn survey. The low water distribution of grey plovers (*Pluvialis squatarola*) (Figure 64i) and bar-tailed godwit (*Limosa lapponica*) (Figure 65i) are good examples. However, the distribution of the birds down-shore



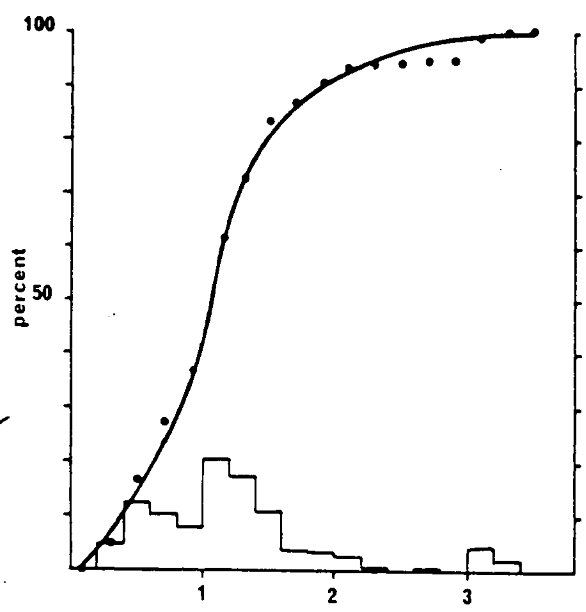


Figure 64ii. The proportion of grey plover feeding at different levels of the shore, expressed as a histogram and a cumulative curve (fitted by eye).

Figure 64i. The distribution of grey plover (shaded areas) along the west side of the Wash in the autumn of 1985.

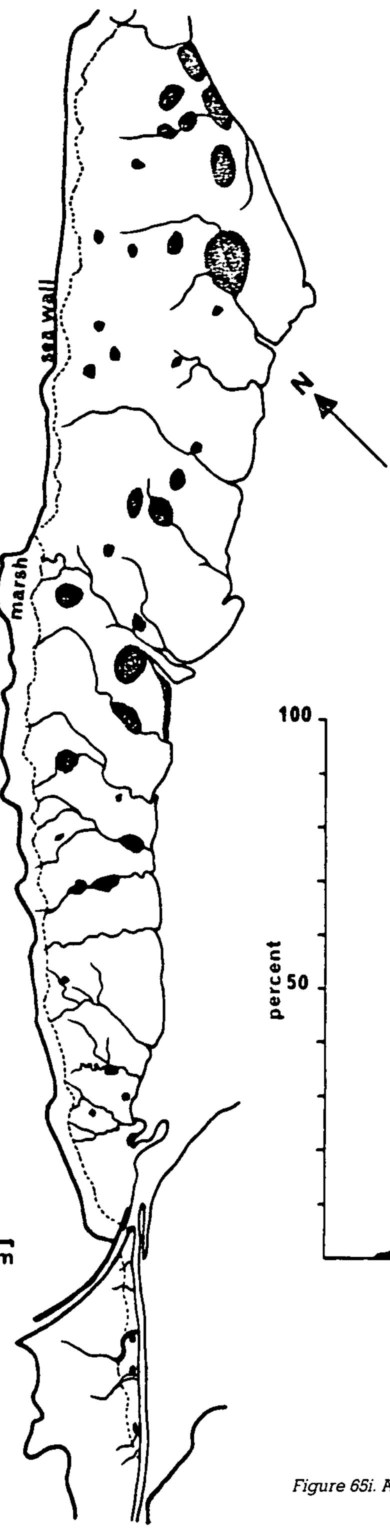


Figure 65i. As Figure 64i, but for bar-tailed godwits.

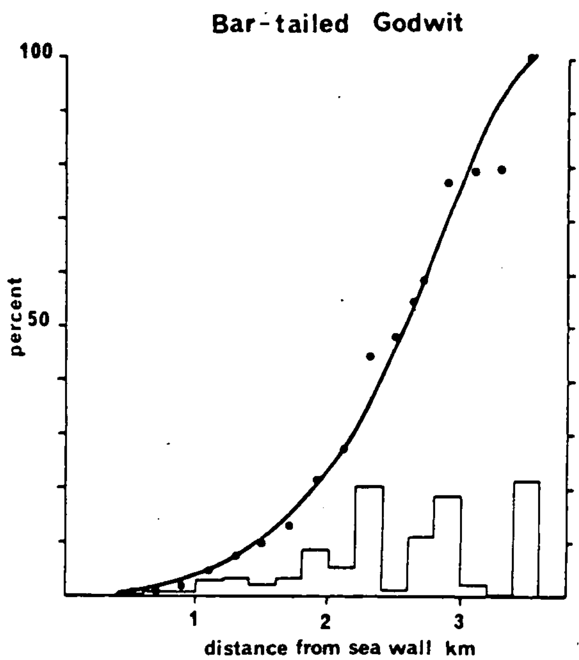


Figure 65ii. As Figure 64ii, but for bar-tailed godwits.

was very different in the 2 species, with plovers occurring at the top of the beach and the godwits at the bottom. This contrast is revealed clearly when the number of each species occurring at different distances from the sea wall is converted to a percentage of the total numbers present, and then expressed as cumulative percentages in relation to distance down the shore (Figures 64ii & 65ii). Fifty per cent of the 575 grey plovers occurred within 1km of the sea wall, while the majority of the 4843 bar-tailed godwits occurred between 2 and 3km down the beach.

These cumulative curves give a measure of the use made of different levels of the shore at low water, but they underestimate the use made of the upshore areas, particularly by species like the bar-tailed godwit. These birds feed far down the beach at low water, but on the upshore areas as the tide ebbs and flows, particularly during the winter when they are more pressed. So, to adjust the cumulative curves based on the low water distributions, observations are being made from a hide placed on a tower, 5m high, at the marsh edge. The numbers of birds feeding in the top km of beach are recorded throughout the tidal cycle to measure how much use is made of the top of the beach. When all observations are combined, it will be possible to convert the cumulative curves of low water distribution to curves depicting the proportion of the feeding done at each level of the shore throughout the tidal cycle.

The food eaten by the waders can often be determined simply by watching them, although it is often useful to examine pellets and droppings to confirm the identity of prey. It is already clear that most oystercatchers (*Haematopus ostralegus*) eat cockles, *Cerastoderma edule*, that most knot (*Calidris canutus*) eat the small clam, *Macoma balthica*, and that godwits and grey plover eat many worms, either the lugworm *Arenicola marina* or the ribbon-like, tube-dwelling worm, *Lanice conchilega*.

Field work on the Invertebrates

We expect that much of the variation in the distribution of the birds will be related to that of their invertebrate prey. The invertebrate sampling programme has been designed to produce distribution maps on which the feeding areas of the birds can be superimposed. It has also been designed to detect changes in invertebrate density and size down the shore, and to relate both to variations in substrate and exposure time. This survey should enable us both to account for the birds' distributions and to predict how changes in the profile of the shore and in the substrate might affect the abundance of their main prey.

The west side of the Wash was surveyed in October after the birds' distribution had been established. The survey consists of 9 transects of 9 sites each, with 5 samples being taken at each site. Sediment was also collected at each site for analysis of grain size and organic content. The transects were not distributed evenly down the west side, but were placed so as to cover the major variations in beach width and sediment type, and to include areas with and without major concentrations of birds. The 9 sites along each transect were distributed evenly down the beach, so equivalent sites on all the transects were at roughly the same level in relation to tidal exposure. Each site was one hectare, from which 5 samples were taken at random co-ordinates. Each sample covered $1/64\,m^{-2}$, and was taken to a depth of 30cm. The animals were sieved out and bottled. Estimates of the abundance of the lugworm, for which this sampling technique is inadequate, were made by counting the number of their casts in a one metre square adjacent to each core sample. Samples were collected down one transect by digging up areas at several points down the shore.

At the time of writing, the samples of invertebrates are still being processed. However, the results for the lugworm exemplify some of the uses to which they will be put. As Figure 66 shows, there are marked variations in the density of the worm, both down-shore and along-shore; but to the birds, prey size is as important in determining the quality of a feeding area as is prey density. Figure 67 shows that the worms at the top of the beach are small, compared with those lower

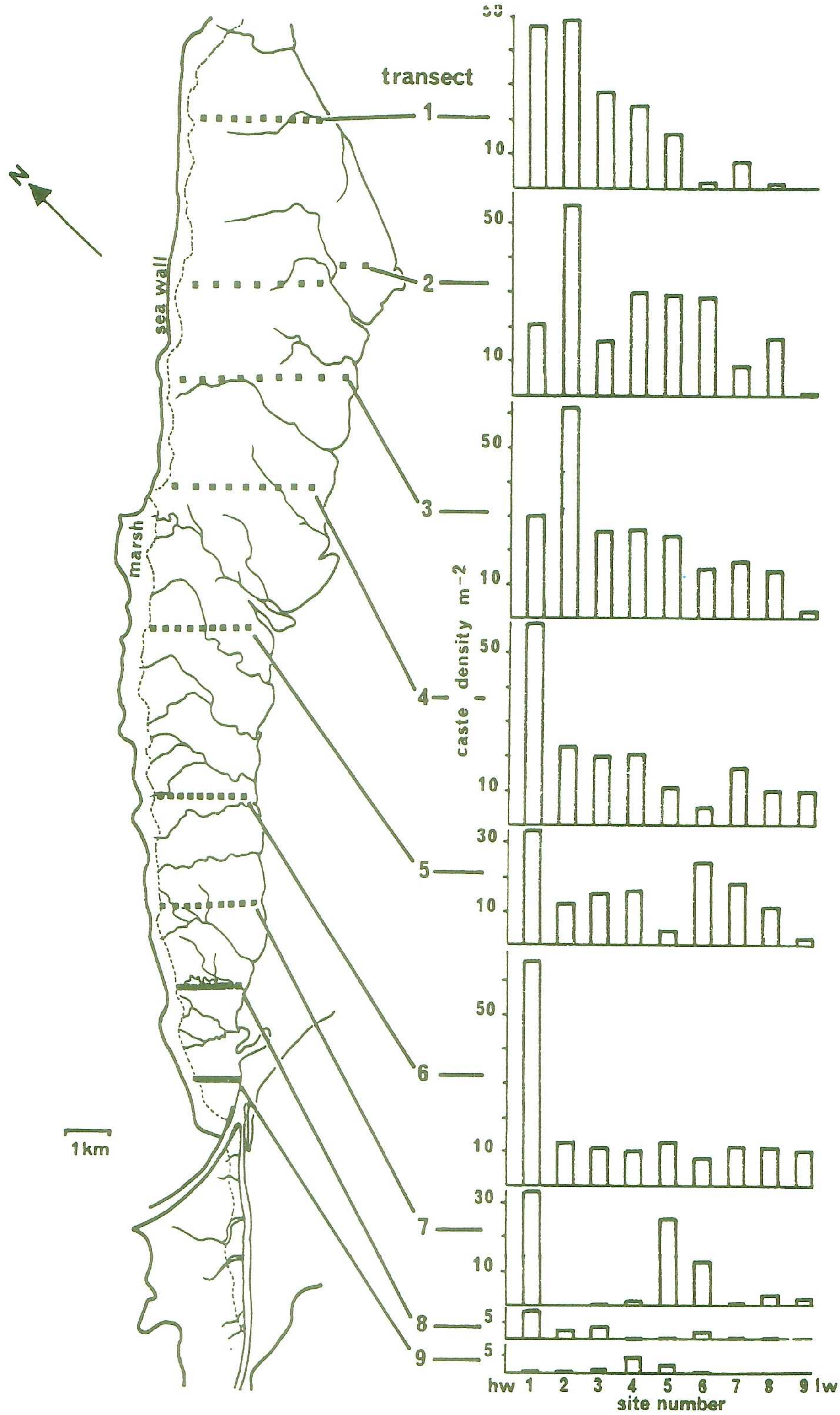


Figure 66. The position of the sampling sites along the 9 transects, and the density of lugworm casts at each site.

down. They also weigh less: an animal of constant length weighs almost twice as much at the bottom of the beach as it does at the top, so that for a bird eating lugworms feeding conditions are likely to be much better down the shore. Such changes in the quality of the prey down the shore will have to be combined with the cumulative curves to describe properly the importance of different levels of the beach to each wader species, and therefore how reclamations to different distances down the shore would, in the worst case, affect the

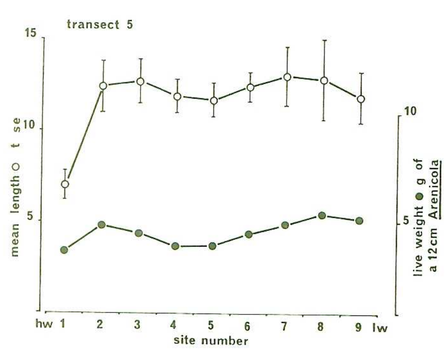


Figure 67. The mean length (○) of lugworms along transect 5, and the net weight (●) of a typical lugworm 12cm long.

birds. The extent to which this effect is offset by subsequent changes in the substrates, and therefore the density and size of the prey, will be investigated when more work has been done on the factors affecting the abundance of the invertebrates.

JD Goss-Custard, MG Yates, SMcGrorty, SEA le V dit Durell and IL Moy

Butterfly Farming in Irian Jaya, Indonesia

(This work was supported by World Wildlife Fund (International))

The concept of 'conservation for development', as formulated in the World Conservation Strategy (Anon 1980), is now being widely applied to the utilization and conservation of wildlife resources in the Third World. The combination of utilization with conservation is important because it provides an argument for wildlife conservation which otherwise would depend on inappropriate, 'developed world' attitudes, and because it has potential for improving the welfare of the rural poor in areas where wildlife resources are abundant, but other forms of development are problematical.

A consultancy was agreed between ITE, World Wildlife Fund (International) and the United States Agency for International Development for a 4-month study of the potential for utilization of butterfly resources by farming in Irian Jaya, the western half of the island of New Guinea and the poorest and most sparsely-inhabited province of Indonesia. The butterfly fauna of SE Asia is exceptionally rich; Collins and Morris (1985), in an analysis of 'critical faunas', conclude that Indonesia is the single most important political unit for the conservation of the world's swallowtail butterflies (Papilionidae), while most of the highly-prized species of birdwings (*Ornithoptera*) are endemic to New Guinea.

Considerable success has been achieved by Papua New Guinea (PNG) in farming and utilizing

A Common Birdwing being examined.

butterflies for the world specialist trade. Specimens are produced for sale to enthusiasts, both professional and amateur, through a network of dealers. The trade provides important additional income for Papua New Guineans in many parts of the country. The establishment of an Insect Farming and Trading Agency (IFTA) in 1976 has provided a service for individual butterfly farmers and ensured that, through responsible marketing, no damage has been caused to wild faunas. By diversifying to include part of the decorative market (display boxes of butterflies) as well as the specialist trade (specimens of butterflies for study and research), IFTA achieved self-sufficiency in 1984.

From January to April 1985, 4 field trips were made from a base in Jayapura to undeveloped areas of Irian Jaya in order to assess their potential for butterfly farming similar to that being done in PNG. The Arfak Mountains, Biak, central Highlands, Paniai Lakes region, and Star Mountains (Figure 68) were the main areas visited. In the Arfak Mountains, some trade in butterfly specimens already occurs, but little farming is done. In the other areas, there is considerable interest in the idea of butterfly farming, but little or no trade, or farming activity.

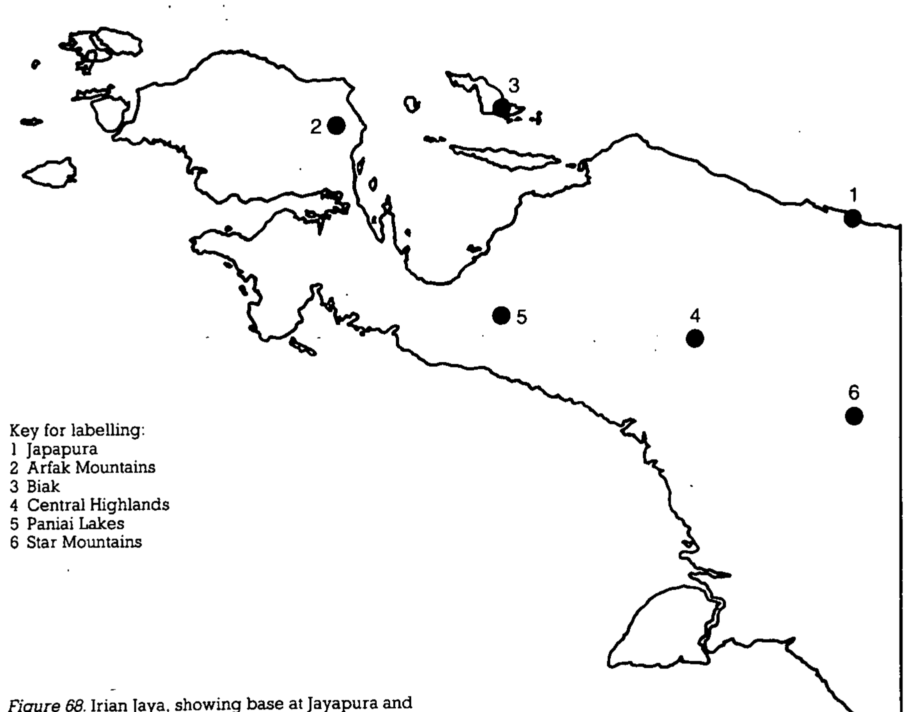


Figure 68. Irian Jaya, showing base at Jayapura and areas visited during butterfly farming consultancy

Most interest was shown in the potential of butterfly farming by mission organizations (Catholic and Protestant), by individual missionaries, and by other bodies interested in improving the welfare of the indigenous Papuans. Discussions with these organizations, with expatriate funding bodies, and with official government bodies such as the Directorate-General of Forest Protection and Nature Conservation, indicated that an agency similar to PNG's IFTA, but even more supportive, was essential for butterfly farming to become viable, and a source of income for the rural poor. A report has been prepared, and, at the time of writing, it is known that USAID has committed funds to establish an agency, provided that the necessary 25% matching funds can be produced within Irian Jaya. It seems likely that this requirement will be met by the Catholic Church, perhaps in the form of premises, or land for the agency.

The important resource of *Ornithoptera* birdwing butterflies merits detailed consideration, both for utilization and conservation. All *Ornithoptera* are currently protected under Indonesian law, as well as being Schedule II species under the Convention on International Trade in Endangered Species of Fauna and Flora (CITES). Proposals have been made for the planned agency to have an exclusive licence to trade in these species. Alternatively, some might be removed from the protected list. The conservation of birdwings in Irian Jaya is fortunately ensured through the establishment of a series of large and well-designed Cagar Alam (strict nature reserves) (Petocz 1984). Not all these reserves have been gazetted, but when they are, and if they are satisfactorily monitored, managed and wardened, they will conserve all the birdwing species, leaving good populations outside the reserves for utilization in the farming programme.

Other important insect resources, such as longhorn beetles, stick- and leaf-insects, and other butterflies, including the colourful and popular *Delias* spp., will be carefully utilized as wild-caught specimens. Eighty per cent of Irian Jaya remains covered with primary forest and the human population is low, though increases through 'transmigration' are government policy. Utilization and conservation of butterfly resources in such an area are not only compatible but complementary.

M G Morris

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Rotifer resting eggs in lake sediments

Rotifers are small invertebrate animals which are common in every type of freshwater habitat. Although their distribution as a group is widespread, at the species level rotifers are very discriminating in their response to environment; thus, many species are now considered to be indicators of certain environmental conditions. For example, recent work has shown a close correlation between the level of acidity of freshwater habitats and the species composition of the associated rotifer community (Ruttner-Kolisko 1974; Raddum *et al.* 1980; McConathy & Stahl 1982; Chengalath *et al.* 1984; Siegfried *et al.* 1984; Pejler (Sweden) pers. comm.). In consequence, several species are now thought to be indicators of acid environments.

The use of rotifers as environmental indicators is complicated by the practical problems of obtaining representative samples for any given site. Many species occur seasonally and, using the standard method of collecting open-water samples, a complete species list for each location can be obtained only by taking several samples during the year. Table 28 shows a species list of planktonic rotifers collected in open-water samples from Loch Leven between 1977 and 1982. The monthly occurrence of each species over this 6-year period is indicated. The table shows that some species,

Table 28. A species list of planktonic rotifers from Loch Leven, compiled from a 6-year series of weekly and fortnightly sampling visits (1977-82). The figures 1–6 show the relative frequency with which a given species was found in each month. For comparison, those species found in sediment samples collected on a single sampling occasion in February 1984 are indicated by a cross (+)

Species	In open-water samples												Species in sediment
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	
Keratella cochlearis	6	6	6	6	6	6	6	6	6	6	6	6	+
Synchaeta kitina	5	6	6	6	5	5	6	6	6	4	4	4	+
Notholca squamula	6	6	6	6	1	–	–	–	–	–	1	2	+
Polyarthra dolichoptera	6	6	6	6	6	6	1	–	1	1	1	2	+
Keratella quadrata	4	4	5	5	5	5	5	4	4	2	3	3	+
Asplanchna priodonta	–	–	–	–	4	4	1	1	–	–	–	–	+
Conochilus unicornis	–	–	–	1	5	5	3	–	–	–	1	1	+
Polyarthra major	–	–	–	–	1	4	4	–	–	–	–	–	+
Pompholyx sulcata	–	–	–	–	2	4	5	6	6	5	1	–	+
Trichocerca pusilla	–	–	–	–	–	1	6	6	6	3	–	–	+
Lecane lunaris	–	–	–	1	–	2	3	1	2	1	–	–	+
Colurella adriatica	1	–	–	2	1	2	3	1	2	1	1	–	+
Synchaeta grandis	–	1	1	1	–	2	3	1	1	2	1	1	+
Filinia longiseta	–	–	–	–	1	1	1	2	4	1	1	–	+
Brachionus angularis	–	–	–	–	–	–	2	–	–	–	–	–	+

in particular *Keratella cochlearis* and *Synchaeta kitina*, were generally present throughout the year, and would be found in almost every sample collected. In contrast, the winter species, *Notholca squamula* and *Polyarthra dolichoptera* were usually present from December to April and November to June, respectively. These rotifers would occur only in samples collected during the winter and early spring. Similarly, warm stenotherms, such as *Pompholyx sulcata* and *Trichocerca pusilla*, would be recorded only from summer samples. Table 28 shows that there is no time of year when a single open-water sample would yield a complete species list for the loch.

As part of their natural life cycle, rotifers produce resting eggs which are very resistant to decomposition. These resting eggs fall to the bottom of the lake where they may remain in the sediments for very long periods. Recent work suggests that, in early spring, most rotifer species are 'overwintering' as resting eggs in the surface mud. Samples of sediment collected in early spring can provide a full species list from a single site visit (Table 28).

In addition to providing information on present-day rotifer communities, resting eggs in sediment also have the potential for providing information on the past histories of lake environments. Rotifer resting eggs, being resistant to decomposition, are preserved in lake sediments for many years (Gilbert & Wurdak 1978). The resting eggs of *Filinia* sp., for example, have been described in Quaternary remains from Lake Balaton, Hungary (Sebestyen 1974), and those of other species have been recorded in sediments up to 5000 years old (Müller 1970). However, rotifer eggs have rarely been used for palaeolimnological purposes, even though the strict ecological limitation of many species is of potential interest in this field of limnological research (Ruttner-Kolisko 1974). Deeper sediments from freshwater sites in Scotland are now being examined to find resting eggs of indicator species which could provide information on past environmental conditions.

Linda May

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Guidelines for the safe and humane handling of live deer in Great Britain

These guidelines have been prepared by the Deer Liaison Committee (DLC) (1983), a body comprising members from many scientific, government and private organizations concerned with deer in Great Britain.

Immobilised red deer, fitted with radio collar for ITE studies on deer in woodlands.

The DLC was set up in 1981 to provide a forum where these organizations could meet and discuss matters of mutual concern, to provide a platform where conflicting views may be reconciled, and also to initiate action on matters of common interest. The guidelines are the result of such joint action.

The need to capture deer in Great Britain has risen over the last 20 years due to a considerable increase in the amount of field research, and also due to the advent of intensive deer farming. Much was known about the various capture techniques, but this information was widely scattered throughout the international scientific literature and amongst people with practical experience; it was not readily available to everyone. The guidelines attempt to fill this gap by bringing together what is known about the capture and handling of the various deer species found in Great Britain, emphasizing the animals' welfare and the safety of the people involved.

The publication has 10 sections covering methods of capture, restraint, methods of marking, drugs, transportation, safety precautions and first aid. There is also a separate chapter on the law, which highlights significant parts of the various Deer Acts and wildlife legislation, and includes sections on the law relating to animal welfare, veterinary controls, health and safety, drugs, firearms, etc.

The guidelines are intended to help both beginners and the more experienced deer handlers, and to establish voluntary standards for the humane treatment of these animals. The guidelines are published by the Nature Conservancy Council (NCC), as part III of a comprehensive handbook on the capture and handling of deer (Rudge 1983). They are also available as a separate document, free of charge, from the NCC, Peterborough, or the Institute of Biology, London.

B W Staines

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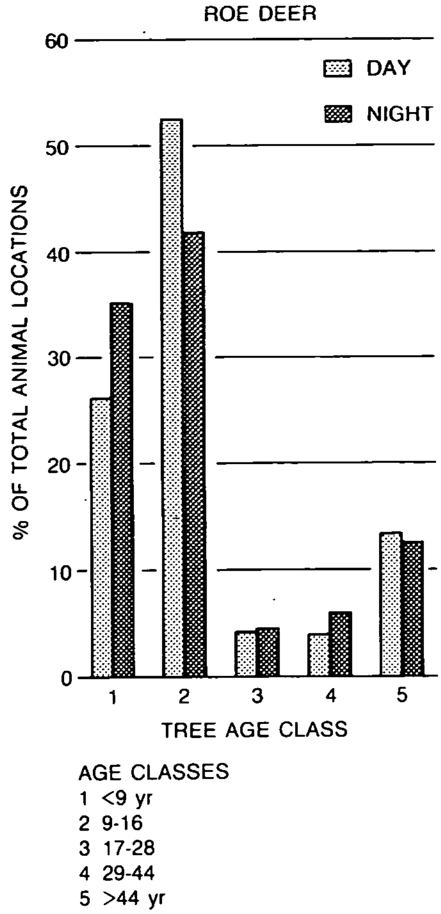
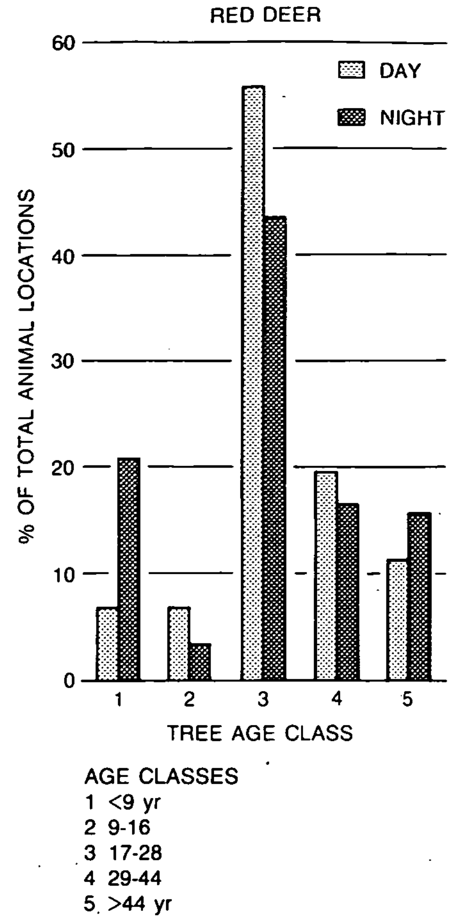
Ecology of Sympatric Red and Roe Deer

(This work was supported by the Natural Environment Research Council with additional funds from the Forestry Commission)





Colonization by red (*Cervus elaphus*) and roe deer (*Capreolus capreolus*) of newly afforested land has led to the need for efficient methods of deer control to protect the tree crop. With this need, a greater knowledge of the ecology of these woodlands was vital. This study is part of a collaborative research programme by the Institute of Terrestrial Ecology, Banchory, and the Forestry Commission to investigate the behaviour of woodland deer, their population dynamics and their impact on the trees (Staines & Welch 1984; Ratcliffe 1985). The specific aims of this study were to:

1. investigate the range use of red deer and roe deer in a conifer plantation;

2. identify the factors that may influence an animal's distribution within its range; and,

3. assess the importance of each factor identified to red and roe deer with reference to potential competition.

The study area was Glenbranter Forest, south Argyll. Glenbranter Forest is composed mainly of Sitka spruce (*Picea sitchensis*) and is in the second rotation, thus providing a mosaic of different-aged stands of trees. This mosaic gives each deer species the opportunity to select its own niche.

Radio-triangulation was used to locate radio-collared deer to study habitat selection and range use. A system to monitor transmitter signals automatically was designed to study the activity patterns of both deer species.

Red deer selected areas of young conifers approximately 20 years old where canopy closure had just occurred (Figure 69). As these areas contained little food, heavy use of adjacent open areas occurred. Roe deer made relatively more use of younger conifer stages up to 15 years. These younger stages provided abundant food and cover intimately mixed, but possibly not enough cover for the larger red deer. Roe were found in open habitat types both by day and night, whereas red deer used open areas predominantly at night.

The mean home range size, calculated from data collected over 6 successive days each month, was 16.9ha for red deer, with core areas (Kaufmann 1962) occupying approximately 25% of the range in both species. The centres of activity of individual deer shifted between months. Red deer generally had smaller daily ranges in winter than in summer. Roe deer, however, showed the reverse, and this could be attributed to the Jarman-Bell principle (Jarman 1968; Bell 1971) where energy requirements are a function of body weight$^{0.75}$. Thus, small herbivores, such as roe deer, have to be more selective, as they require a relatively high energy diet with low fibre content, which can only be attained in winter by increased searching for higher-quality foods, which have a patchy distribution. The time spent active during the 24 hours, approximately 60%, was similar for both deer species, but the number of activity bouts and their duration differed (Staines *et al.* 1985). Dietary overlap between red and roe deer was low in summer and high in winter, where both species ate more heather (*Calluna vulgaris*) (Staines *et al.* 1985).

The preliminary findings of this study suggest that there is little competition between red and roe deer in this mixed-aged conifer forest. Spatial overlap was low by day and dietary overlap minimal, at least in summer. However, in large conifer plantations of more uniform age and structure, where open spaces and food supplies may be at a premium, the numbers of one species may well be suppressed by the presence of the other. This aspect would be an interesting point for further study.

M D C Hinge

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South American Southern Beech (*Nothofagus*) and its Insect Fauna

(This work was supported by a Sir Winston Churchill Memorial Trust Travelling Fellowship)

Southern beech, of the genus *Nothofagus* (Fagaceae), is predominantly an evergreen tree with a natural distribution confined to South America and Australasia. Of the 7 deciduous species, *N. gunnii* is an alpine shrub in Tasmania, and *N. glauca* and *N. alessandri* are very local and rare species in the Talca and Maule Provinces of central Chile (Donoso & Landaeta 1983). *N. obliqua* and *N. procera* are characteristic trees of the Valdivian temperate rainforest in Chile and the drier forests of the Andean foothills in the Nequen Province of Argentina. *N. antarctica*, besides growing at high altitudes in the Andes, flourishes in frost pockets, while *N. pumilio* is more typically the treeline species. Both occur as far south as Tierra del Fuego, where *N. pumilio* and the evergreen *N. betuloides* are the slow-growing emergents of these cold southern rainforests. In the northern part of its range in Chile, the evergreen *N. dombeyi* grows with *N. obliqua* in the central valley, and with *N. procera* in the coastal cordillera. The closely related evergreen *N. nitida* has a limited distribution centred on the island of Chiloe.

Although all these species have now been introduced into Britain, only the deciduous *N. obliqua* and *N. procera* have shown potential as fast-growing hardwood trees (Tuley 1980). Since 1978, our studies have shown that an unexpectedly large number of British insects have colonized these 2 species since their introduction early this century (Welch 1981). A special study has been made of the defoliating Lepidoptera larvae, which are most numerous in the spring. Of the 78 species recorded feeding on *Nothofagus*, approximately 75% were 'looper' caterpillars of the family Geometridae. Phytophagous beetles were not particularly numerous, but the weevils *Strophosomus melanogrammus* and 4 species of *Phyllobius* were regularly recorded. Later in the summer, typhlocybine leaf-hoppers and Psocoptera were locally abundant (Claridge & Wilson 1981). Having built up an inventory of insect species associated with *Nothofagus* in Britain, this was compared with that of other British Fagaceae, but it was thought that it would be of greater interest to be able to compare them with their native fauna in South America.

Much of the limited published literature on insects of *Nothofagus* forests is either of a taxonomic nature, or is concerned with the evidence such taxa provide to support theories of continental drift (Schlinger 1974). Studies on the biology and life history of *Nothofagus* insects are restricted to a few species of economic importance, such as the cerambycid *Cheloderus childreni*, which bores into live *N. dombeyi* and *N. obliqua* (Cameron & Real 1974), and the cambium-feeding moth larva of a species of *Opostega* (Carey *et al.* 1978). Lanfranco (1977) studied insect communities in Patagonian *N. pumilio* forests, but fungus gnats (Diptera, Mycetophilidae) comprised 95% of all terrestrial and flying insects collected. Identification of the remainder was only possible to family level. Etchegaray and Fuentes (1980) sampled defoliating insects on 7 species of Chilean mattoral shrub. Four of the 'morphospecies' recognized were Chrysomelidae (Halticinae), whilst the fifth included all Lepidoptera larvae. Defoliators of *Nothofagus* appear to have been largely ignored. However, Donoso (1981) mentioned a scarabaeid beetle, *Hylamorpha elegans*, and caterpillars of saturnid moths of the genus *Ormiscodes* defoliating *N. obliqua*, whilst larvae of *Cerospastus volupis* (Hymenoptera, Pergidae) fed more commonly on *N. procera* than *N. obliqua*. South American *Nothofagus* are known to be hosts to a large insect fauna, many of which are still undescribed, or their ecology is unknown.

Nothofagus in Chile

In the southern Hemisphere, facilities were provided by the Austral Universidad de Chile at Valdivia for a study of the insect fauna of *Nothofagus* in Chile's Region X. It was soon learned that *N. obliqua* suffered periodic severe defoliation in the central valley in 1984 and had done so locally in 1983. As in England, these trees showed some recovery by the production of lammas growth later in the summer. Sampling the foliage by beating and insecticidal fogging revealed the presence of at least a dozen species of larval Lepidoptera. With the exception of one species of Lycaenidae and one unidentified species of gregarious larva (? Lymantriidae), most were Geometridae. A few larvae were successfully reared to adult in the laboratory, and one of the common species was identified as *Eugerona valdiviana*. Another major *Nothofagus* herbivore at Valdivia was the larva of a leaf beetle, *Hornius grandis* (Chrysomelidae). Adult beetles of this family were frequently the most abundant insects in the samples. Many Scarabaeidae have root-feeding larvae, but the adults of species, such as the golden *Lagris mutabilis*, and species of *Sericoides* and *Brachysternus* are foliage feeders.

Nothofagus has a particularly rich weevil fauna, including several species of *Aegorhinus* with wood-boring larvae. Feeding by the ungainly *Rhyephenes maillei* can cause the death of branch tips, whilst *Polydrosus nothofagi* eats small holes in the leaves, much as members of this genus do in Britain. A little understood group of *Apion* species either gall *Nothofagus* stems or inhabit galls vacated by Hymenoptera. The best known insects associated with *Nothofagus* are to be found among the Cerambycidae. Not only are many large, and strikingly coloured, but their larvae greatly reduce timber values by their borings, which are often into the live trees. Fallen trees and dead wood attract many species of Buprestidae, Tenebrionidae and Lucanidae. *Uleiota chilensis* is common under *Nothofagus* bark, paralleling the occurrence of *U. planata* in *Fagus* (& *Pinus*) in Britain.

It appears probable that most of the above insects are not specific to one species of *Nothofagus*, but may be known from a mixture of deciduous and evergreen species, and occasionally from other, unrelated, forest trees and shrubs.

In mid-November, a visit was made to the Lanin National Park at San Martin de los Andes, Argentina. The colder, drier, climate in the rain shadow of the Andes results in insects emerging much later than the same species in the milder, wet, Chilean rainforest. This factor facilitated sampling *Nothofagus* insects a month later, at the same latitude (40°S), and yet at the same stage in their development as those collected at Valdivia. Similarly, even by early December, the severity of the climate near Punta Arenas in the Magallanes Region (53°S) is such that many lepidopterous larvae were still in their first or second instars. However, their numbers indicated that both *N. pumilio* and *N. antarctica* would suffer severe defoliation later that month.

Already, some interesting comparisons can be made between the insect fauna which *N. obliqua* and *N. procera* have acquired in Britain with that which is associated with these species in their native environments. It is hoped that a better understanding will be obtained as the numerous samples collected in Chile and Argentina are sorted and identified.

R C Welch

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Cycling of Nutrients

Land use and Vegetation changes: Their effects on soils in the Scottish Highlands

Vegetation patterns in the Scottish highlands have, as elsewhere in Britain, been changing since the end of the last ice age, at first because of changing climate, and later because of interference by man. Below the mountain tops, most vegetation is now quite unnatural in composition. The mosaics of different vegetation types owe more to past management for sheepwalk, deer forest and grouse moor, than to intrinsic differences in the underlying soils. These vegetation and management changes are now widely appreciated, but it is less well known that they can profoundly alter many soil properties that critically affect plant growth, eg pH and nutrient cycling rates (Miles 1985). However, it is inevitable that at least some soil properties change whenever vegetation changes. For example, the chemical composition of different plant species, and the rates at which their litters decompose, can vary markedly. Further, different plants alter the chemical composition of throughfall and stemflow to different extents. These plant influences can have major effects on the poorly buffered, relatively freely drained, sandy soils prevalent in the Scottish highlands, whereas on well-buffered soils, typical of much of the lowlands, their effects are minimal.

Broadly, 2 contrasting trends of soil change occur under the main types of vegetation found on well-drained soils in the highlands. Stands of birch (*Betula pendula* and *B. pubescens*), aspen (*Populus tremula*), bracken (*Pteridium aquilinum*), bent-fescue (*Agrostis-Festuca*) grassland, and probably juniper (*Juniperus communis*) tend to (i) make soils less acid, with relatively high rates of nutrient cycling, and (ii) obliterate the bleached Ea horizon of podzol profiles by biological mixing.

In contrast, stands of Scots pine (*Pinus sylvestris*), most exotic conifers, heather (*Calluna vulgaris*) and other ericaceous species, gorse (*Ulex europaeus*), broom (*Sarothamnus scoparius*), mat-grass (*Nardus stricta*) and wavy hair-grass (*Deschampsia flexuosa*) acidify the surface soil, and are often associated with accelerated podzolization.

Because land use and management practices are continually varying, the resultant vegetation mosaics are also constantly changing. Broadly, 3 patterns of change seem to occur. With low grazing pressures and little or no burning, birch and pine woodlands eventually re-establish. Stands of these 2 species appear naturally to alternate over much of the highlands, and thus to have alternating influences on the soil. With high grazing pressures and/or frequent burning, the predominant trend is towards the development of bent-fescue grassland, and thus the maintenance or development of unpodzolized profiles. However, at intermediate intensities of grazing and frequencies of burning, the successional trends are much more varied. Many different vegetation types can co-exist in complex and dynamic mosaics, in which the contrasting soil trends may often tend to cancel out each other.

Little could be included about the rates of vegetation and soil change, and even less about the relative frequency at which different successional transitions occur regionally or locally. To correct these deficiencies, successional data are being extracted from air photographs of the Scottish highlands taken at intervals since 1946 (ITE project 934 – *Vegetation dynamics and soils*). A large core area of 40km^2 in mid-Deeside is being studied in collaboration with Aberdeen University, plus initially a stratified random sample of 50 sites of 0.25–1.0km^2 in the north-east highlands, supplemented by a few selected sites to give more information on less common but ecologically important vegetation types. Information on soil changes is being obtained concurrently from these sites.

With a better understanding of the vegetation changes resulting from different management practices, it is hoped eventually to model successional change on the scale of a landscape, catchment or estate. Additionally, it is planned to combine this model with others to predict, for example, soil changes and changes in populations of various species of bird and mammal.

J Miles

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The Use of Reeds in Sewage Treatment

Sewage has been treated for centuries by applying it to land, or by passing it through marshes and lakes. These methods were acceptable in times of greater land availability, and less public sensitivity to environmental pollution, but modern sewage treatment tends to conserve land at the expense of higher inputs of energy and capital.

Notwithstanding this change, an 'old-fashioned' approach to the treatment of sewage is now being tested at a commercial scale by several of the Water Authorities in England and Wales. It is known as the 'root zone method', and has several distinguishing features (Figure 71), the most important of which is a potentially large saving in cost.

Members of ITE have been collaborating with the Water Research Centre in assessing some of the biological aspects of this form of sewage treatment. Reeds can be established by rhizome transplants, seeding, stem cuttings or layering, and these options are being examined experimentally. A 3-year establishment period is likely to be necessary before the bed is able to treat sewage at the design optimum of 2–3m^2 per person equivalent.

The Water Authorities plan to install 30 commercial scale root zone beds during 1986. These beds will variously be used for whole sewage treatment, sludge treatment, or for the final polishing of partially treated effluents. The surface of most beds will be unflooded, remarkably free from odours, and should provide a suitable habitat for many invertebrates. Reed beds and wetlands are a threatened habitat in Britain, and it is encouraging that sewage treatment should provide an opportunity to resist this decline.

G J Lawson

Figure 71. The Root-Zone Method of sewage treatment. (not to scale)

a) Reeds are planted in carefully selected soil on a sloping bed, whose dimensions are calculated to match the characteristics of the sewage.
b) Solids remain on the surface where they mix with dead reed leaves and undergo aerobic composting. Periodic storm-water flows distribute this layer.
c) Liquids filter through to the rooting zone of the reeds, where the horizontal rhizomes create an area of high hydraulic conductivity.
d) Sorption of phosphate takes place in the soil, particularly those with a high content of iron and aluminium. The anion exchange capacity of the reedbed will be exhausted after 15–30 years, and the soil, which might provide a useful horticultural compost, must be replaced.
e) The liquors are purified by a variety of micro-organisms which are associated with a zone surrounding the roots and rhizomes. Some microbes function in anaerobic conditions (eg. denitrifiers), while others (eg. nitrifiers) need a supply of oxygen, which leaks from the cortex of growing roots. This diffusion rate may approach 5–50g $O_2 m^{-2} day^{-1}$.

Land Resources and Land Use

Rural Land Resources and Landscape Change

Field surveys in 1984 of a wide range of land use, habitat and landscape characteristics have obtained quantitative comprehensive data for 384 Ordnance Survey 1km × 1km grid squares. These squares, distributed throughout Great Britain, are 12 replicate samples in each of the 32 land classes resulting from a multivariate land classification (Bunce *et al.* 1983); 256 of these squares (8 in each land class) had been surveyed previously in 1977–78 in a similar, though not identical, way.

The 1984 survey (Barr *et al.* 1985) recorded in 'Field assessment booklets' (one per square) a total of 225 land cover, landscape and land use feature items per grid square, giving a data set with some 87 000 records. Land class averages can be determined for the recorded features from data for the 12 squares per land class. By extrapolation from the known proportions in which these land classes occur, estimates of the status of these features in 1984 can be given nationally and for large regions. Comparison of estimates for appropriate single or grouped features between 1977–78 and 1984 enables rural landscape changes to be assessed and similarly extrapolated.

The detailed mapped and other information from the 1984 survey is being digitized and computer-stored for comprehensive analysis. An interim report (Barr *et al.* 1986), covering selected categories, shows the general range of data available, and, by relating results from the 2 surveys, outlines some aspects of recent changes in rural landscapes. Twenty-four land use and other landscape features are considered nationally and for 12 regions of Great Britain, highlighting directions and extent of overall changes and the balance of compensating losses and gains. Examples of the data presented in this interim report are given in Table 29.

In this Table, as in the interim report, statistical error terms are not included, but these will be considered in a later, full report, in relation to the sampling framework and to the extent and distribution characteristics of individual features. A comprehensive statistical study is planned as soon as compilation of the digitized data for 1984 and comparable material from the 1977–78 survey has been completed.

Comparisons of ITE estimates with MAFF statistics available for some land use categories show that ITE figures, based on a quite small stratified sample of the country, are in good agreement with the MAFF statistics from farm returns. This agreement supports confidence in the applicability of other figures from the ITE study in national and regional contexts. Considering a few points from Table 29, it can be seen, for example, that there were increases of 66% and 1000% in the areas under wheat and oilseed rape crops respectively between the 2 dates, and decreases of 13% and 3% respectively in the areas of barley and rough grazing. Broadleaved woodland removals and plantings appear in general balance, although, of course, the ecological and landscape value of what has been lost and what has been gained can be very different. For hedgerows, only 12.5% of the lost length was balanced by new

Table 29. Preliminary estimates of rural landscape changes in Great Britain between 1978 and 1984

Land use or landscape feature		Change estimated between 1978 and 1984 (or status. in 1984)	
Agricultural land			
Cereals	– wheat	+0.7 million ha	(increase 66%)
	– barley	–0.3 " "	(decrease 13%)
Oilseed rape		+165 000 "	(tenfold increase)
Rough grazing improvement		–146 000 "	(decrease 7%)
Woodland and trees			
Woodland removal	– broadleaf	–25 000 ha	
	– conifer	–46 000 "	
New planting	– broadleaf	+26 000 "	
	– conifer	+177 000"	
Hedgerow and other young (<5yr) solitry trees		+220 000 individuals	
Boundaries			
Total removal	– hedge	–28 000 km	
	– wire fence	–12 000 km	
	– wall	–1 400 km	
Completely new	– hedge	+3 500 km	
	– wire fence	+48 000 km	
	– wall	no new walls	
	– wooden fence	+13 700 km	
Neglected boundaries	– hedge	(104 600 km estimated in 1984)	
Built environment			
New housing estates		+39 000 ha	
New agricultural buildings		+105 500 buildings	
New roads and tracks	– tarmac	+4 300 km tarmac road	
	– constructed	+5 000 km constructed tracks	
Recreation			
Golf courses		+14 000 ha	
Caravan sites		+4 000 ha	
Horses		(560 000 estimated in 1984)	

plantings. The figure of 104 600km of 'neglected' hedges suggests the level of hedgerow loss that is potentially highly possible, as neglect implies no effective contribution of a hedge to farm management. Other figures included are for categories on which little or no information is available, eg the total length of new roads and tracks over the period, and an estimate of the number of horses in 1984.

In conjunction with the field survey, but independent of it, 1:10 000 colour air photography was flown for 28 1km × 1km squares in 1984 and a further 18 in 1985, to give 3 or 4 replicate squares of 12 out of the 32 land classes. As many as possible of the land use and landscape features recorded in the field survey have been identified and mapped on air photo overlays. A table has been prepared listing these features and commenting on problems relating to their identification on air photographs. The intention of this study is to compare area and length measurements from the photo-interpretation with figures from the field survey. The results of this comparison will be used as part of an analysis of the cost-effectiveness and strengths of the 2 methods of data collection, separately or in combination, in determining landscape features and their changes.

D F Ball, C J Barr and J Dale

References

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Barr, C J, Benefield C, Bunce R G H, Ridsdale H A & Whittaker M. 1986. *Landscape Changes in Britain.* Abbots Ripton: Institute of Terrestrial Ecology.

Bunce, R G H, Barr, C J & Whittaker, H A. 1983. A stratification system for ecological sampling. In: *Ecological mapping from ground, air and space*, edited by R M Fuller, 39–46. (ITE Symposium no. 10). Cambridge: Institute of Terrestrial Ecology.

The BBC Domesday Project

(This work was largely supported by funds from BBC Enterprises)

1986 is the 900th anniversary of the remarkable compilation of the earliest English public record, *The Domesday book*, on the orders of William the Conqueror. This book recorded, for most English counties, details of all land ownerships, tenancies, values and productivity, and thus supplied the king with an account of the agricultural, human and economic resources of the country, as the means for more efficient taxation and administration. It became known as the *Domesday book*, because it is said that, in the scale of information it gave the king, people considered it to be comparable to the anticipated comprehensive record with which the dead would be assessed at the 'Day of Judgement'.

As a major commemoration of this anniversary, the British Broadcasting Corporation, through BBC Enterprises, arranged in autumn 1984 to carry out its own Domesday project, using a staff team supported by outside consultants. This project is creating a data base that will give a wide-ranging 'snapshot' of life and resources in the United Kingdom in the 1980s, using new videodisc technology linked to microcomputers for the storage and retrieval of the material being collected. The task is complex requiring the successful commercial production of appropriate disc hardware; the production of input and output software capable of dealing with text, pictures, graphs and mapped spatial data, while allowing interactive interrogation of the content by the user; and the provision of as much information as possible within tight time and resource constraints.

The Videodisc Project

Two linked videodiscs, '*community*' and '*national*', are being prepared. The '*community*' *disc* will contain text, photo and spatial data on land cover and amenities supplied by local groups (mainly schools) in standard format for areas of 4km × 3km, based on Ordnance Survey (OS) 1km × 1km grid squares. The mosaic of these contributions, covering as much of the country as proved possible, is related to broad regional frameworks of maps, images and text, while some of the local spatial data are also being integrated into the content of the '*national*' *disc.* The latter will include, along with overview text, pictures, and contemporary press and journal cuttings describing life in the UK in the mid-80s, spatial data at scales between 1km × 1km OS grid squares, and administrative counties and regions.

The BBC has contracted 4 groups to supply spatial and statistical data for the national disc. These groups are located at the Departments of Geography of Birkbeck College, London, and of the University of Newcastle; at the Economic and Social Research Council's Data Archive at the University of Essex; and at ITE's Bangor Research Station. Project leaders from these contractors, with BBC staff and other specialists in different fields of British life and history, are members of the Project Editorial Board, whose responsibilities include recommendations on disc content; the balancing of an ideal content against the constraints of availability, resources and time; and the maintenance of project schedules in conjunction with the work of hardware and software development groups.

Community Disc Spatial Data
At an early stage it was necessary to decide on realistic sets of land cover and 'amenity' or 'function' categories to be recorded by the community groups, and on appropriate recording methods suitable for non-specialists. The community groups followed instructions contained in a Domesday project 'Survey guide', a 'Teachers' handbook' and an 'Acorn disc users' guide' prepared from the contributions of the BBC in-house team and their contractors. A 20-category land cover classification was developed by ITE for the Domesday survey from a consideration of existing schemes, and confirmed after discussion by the Editorial Board. this classification has been used to define the dominant land cover type, or co-dominant types, in 1km x 1km OS squares of the 4km x 3km area for which a group was responsible. About 50% of the country will have been covered by such groups or, in less detail, by individuals.

National Disc Spatial Data
The ITE contribution to the BBC Domesday project then concentrated on the content of the national disc. The different types of data to be held on the disc are indexed initially in 4 primary categories; culture, economy, environment and society. ITE has been particularly concerned with spatial environmental data, drawn from data bases at the 10km x 10km OS grid square scale; the National Land Characteristics and Classification (Natlac) data set for land and land use attributes (ITE Project 534), and, for plant and animal species distribution, data bases organized by ITE's Biological Records Centre (BRC) (eg ITE project 529). Additional material has been provided by ITE colleagues at Edinburgh (spatial data relevant to the nature of 'acid rain'), and through liaison with other NERC Institutes, notably the British Geological Survey, and organizations such as the British Trust for Ornithology.

Although BRC and Natlac 10km x 10km spatial data already existed as computer-held material, the special format demands of the Domesday project, including the need for supporting text files, have involved substantial data handling effort. Spatial data items have been supplied as separate files for 10km x 10km grid squares in the 3 geographic reference systems involved: for Great Britain the standard OS grid; for Northern Ireland the Irish national grid; and for the Channel Islands the UTM grid. Each data file has 3 components: a *header block*, containing data definition records, cross-references to supporting text files, and keywords for indexing; a *label block*, containing annotations to appear on the final display image; and a sequence of *data blocks*, containing grid references and data values for individual grid cells. Each data file was cross-referenced to 3 text files: a *descriptive file* carrying details of data sources and appropriate acknowledgements; a *technical file* describing the methods of data compilation; and a *private file* giving sufficient definition of the data item for the user to appreciate the displays capable of being generated from the data. In addition to data files, boundary definitions at the 10km x 10km scale have been provided for subjectively delineated natural geographic regions and for statutorily designated landscape areas, so that a user of the disc can frame queries on environmental and other factors in relation to specified areas, such as the Weald, the southern uplands or the Snowdonia National Park, as well as to the administrative and other regions that are also held as boundary files.

Data and accompanying text files were prepared for 555 data items. Table 30 outlines the material provided by ITE and the number of items in each data category for Great Britain, Northern Ireland and the Channel Islands.

The technological potential for data supply and use contained in this videodisc approach is almost equalled by the problems that have been involved, for BBC staff and contractors, in bringing this pioneer project to fruition, because hardware, software, data availability and data input have all had to be advanced, more or less in step in a very tight timetable, and on a scale not previously attempted. The degree of success achieved will become clear after the launch of the BBC Domesday project videodiscs at the end of 1986.

D F Ball and G L Radford

Pesticides and Nature Conservation: A History
With the publication of the report on *Agriculture and pollution* by the Royal Commission on Environmental Pollution in 1979, the time seemed ripe for an historical review of the circumstances in which the threat of pesticides to wildlife populations was first recognized, and how administrators and scientists responded to that perceived threat, given the resources and constraints of the period. As the Institute of Terrestrial Ecology absorbed the research stations and staff of the former Nature Conservancy, including the Monks Wood

Table 30. Types of attribute and numbers of data items prepared by ITE for the BBC Domesday Project

Types of attribute	Number of data items: Great Britain	Northern Ireland	Channel Islands
LAND AND LAND USE			
Altitude	15	15	15
Other physiography	7	7	7
Geology: stratigraphy	9	9	9
lithology	16	16	16
drift	8	8	0
mines and quarries	29	0	0
map units	1	0	0
Annual rainfall	9	9	9
Seasonal climate	19	0	0
Soils	8	8	0
Topography	3	3	3
Land Use	19	2	2
Agricultural land classes	7	0	0
Landscape designations	2	0	0
Pollution	4	0	0
	156	77	61
SPECIES			
Mammals	8	6	0
Breeding birds	23	18	13
Wintering birds	19	19	17
Other vertebrates	3	2	2
Butterflies	14	6	7
Other invertebrates	16	5	6
Flowering plants and ferns	27	20	20
Lower plants	6	3	1
	116	79	66
TOTAL	272	156	127

Experimental Station where most of the Conservancy's pioneer pesticide/wildlife research was done, it was well placed to make an historical reconstruction.

The outcome of this historical reconstruction has been the publication of a book, based not only on published material and the recollections of those who played a key role in the events described, but also on the files and papers that survived at Monks Wood and in the registry of the former Nature Conservancy (Sheail 1985).

The book illustrates how a chemical revolution took place on Britain's farms during the 1950s and 1960s. Most of the damage inflicted on wildlife was caused by a small number of relatively persistent compounds used in insecticides, notably aldrin, dieldrin and heptachlor. Research programmes were set up to investigate how different forms of wildlife were being affected. The voluntary controls already imposed on the use of pesticides were continually re-appraised against a background of mounting public concern. Experience gained in this field of applied ecology was to have important repercussions for the regulation of environmental pollution generally. Because of the range of material available to the author, the book is necessarily written from a conservation viewpoint. Many years will elapse before the full documentation of the pesticide and farming industries becomes available. In the meantime, the book should provide some insight into how research and executive action over the effects of pesticides on wildlife populations came about.

J Sheail

Reference
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Chemical and Technical Sciences

Most of the Institute's technical staff are assigned to Programme 14, and it is their job to provide the specialist support which is so often needed in the research projects. The work of this Programme rarely hits the headlines, but the range of skills, knowledge and experience of its staff is probably wider than that in any other Programme.

The largest single group in the Programme, with half of its total staff, is the analytical chemistry services at Merlewood. This section services the requirements for the entire Institute, but there are other analytical chemists associated with particular research projects. At Monks Wood there is a small team concerned with organic pesticides and heavy metals under Programme 8. In addition, there are chemists at Edinburgh and Bangor dedicated to acid rain, fluoride pollution and geochemical studies. There is a good liaison, indeed, to a certain extent, a professional fraternity, between all the chemists in the Institute. At Merlewood perhaps the major and continuing problem is to reconcile quantity and quality. There is a continuous pressure for more samples to be processed, yet the 'customer' is always ready to complain if standards drop, generating doubts about accuracy and precision. The way these and other problems are resolved is described in subsequent contributions to this report.

The radiochemistry and mass spectrometry service units specialize in the measurement of radioisotopes and stable isotopes (^{15}N only at present) respectively. Developing rigorous chemical techniques and keeping the complex instruments working at their optimum efficiency feature strongly in the work of both these units.

In contrast, the role of the engineers is very extensive – involving at one extreme the development and construction of sophisticated instruments, often microprocessor-controlled, and at the other extreme basic service work and station repairs. Too often, unfortunately, we have to depend on the inventor to rewire the electric plug. This need for a multipurpose engineer arises mainly because of the scattered nature of the Institute, with each station needing its own technician. As a result, the Institute lacks many of the facilities of a large central engineering laboratory, although Bangor, the only station with more than one engineer on site, tries to meet this need. The problem of providing the engineers with the latest precision equipment in competition with other research needs is bad enough, without having to disperse engineering allocations between stations.

Geographical considerations are much less important for the nursery staff, because most of the botanists and foresters depending on plant culture support are based at the same station (Edinburgh). Always to the forefront for the nursery staff is the need to maintain healthy plant stock, with the perpetual nightmare of having to be called out on a cold night because of failure of glasshouse control equipment. The only significant plant culture done in ITE apart from that at Edinburgh is at Monks Wood, and this work is described under the appropriate Programmes. Monks Wood is also the location of the Institute's photographic service. This is another service that unfortunately is often involved in a losing battle for new equipment, yet still manages, albeit with difficulty, to meet a steady request for photographic processing of prints and slides.

Progress Reports of the Service Sections

Analytical chemistry (H M Grimshaw, J A Parkinson, J D Roberts and A P Rowland)

Demands for chemical analyses during 1985 continued to be high. More than 10 000 samples were processed in the laboratories for a total of some 70 000 parameters. As in the previous year, the majority of samples analysed were waters from long-term experimental sites. Clear-felling (ITE 594 and 625) and acid rain studies (ITE 841) were the major contributors. They generated a wide range of water sample types, including lysimeter waters, soil solutions, throughfall solutions and stemflow solutions, as well as the more usual rain, stream and lake waters. Such a wide variety of water samples has necessitated the continued assessment and refinement of analytical techniques to accommodate the range of nutrient levels and considerable variation in sample matrices.

Ion chromatography was introduced for the determination of anions in these waters. Problems associated with matrix interference and poor calcium performance were eventually resolved or greatly reduced. Wash water quality was found to be particularly critical, and resulted in the introduction of a rigorous water purification system. Additional filtration techniques also had to be introduced for stemflow, throughfall and other coloured waters to improve the efficiency in determinations of nitrate, chloride and sulphate ions.

The introduction of a synthetic water reference sample for running alongside all batches of waters has strengthened laboratory quality control and provided a useful early warning of analytical problems. Twice during the year the laboratory participated in inter-laboratory trials set up by the Warren Spring Laboratory. The results were reassuring, demonstrating that the laboratory methods were adequate, even for the very low levels of some of the elements present in the synthetic standards.

Many ITE projects generated vegetation samples during the year. The main requests were for determinations of the principal nutrient elements, work which generally presented few problems. Alternative reference materials for vegetation were examined, with a view to increasing the effectiveness of the quality control procedures. Large numbers of plant and animal materials were also processed for fluoride.

One of the non-routine tasks was the development of a method for titanium levels in vegetation and faecal droppings. An X-ray fluorescence technique was found to be the most appropriate for this purpose, and the method is now in routine use. A standard fusion technique was used in the calibration method.

Two outside contracts looking at possible sources of pollution led to the development of new digest techniques for vegetation and lichen material requiring analysis for trace levels of lead and cadmium. The standard digest procedure was unsuitable because of the insolubility of lead and barium sulphates. A method using nitric acid and hydrogen peroxide was evaluated and finally used.

Renewed interest in the determination of bioenergies led to the resurrection of bomb calorimetric techniques to measure calorific values in vegetation, fuel pellets and fish samples. The bomb calorimeter was also tried as an adjunct to ion chromatography for determining sulphur levels in vegetation. Initial results have been most encouraging.

Less time was spent on soil analyses in 1985 than in previous years. However, work started towards the end of the year on the analysis of a large batch of soils originating from the tree mixtures study at Gisburn (ITE 367). A more unusual soil type to be examined was some vermiculite-peat material (ITE 808). This material proved particularly difficult to analyse because of its light weight and non-homogenous nature. Satisfactory analytical results could only be achieved by taking larger sample weights than usual, and increasing the number of replicate samples. Another of the non-routine studies needing an analytical chemistry contribution was the use of resin-bag techniques as an alternative method for determining mineralizable nitrogen in soils.

A highlight in the year was the conference entitled 'Chemical analysis in environmental research', hosted by the section at a local hotel in mid-November 1985. Ninety delegates attended, from a range of scientific institutes and universities as well as ITE. Sixteen papers and 12 poster papers were presented covering topics which included soil and vegetation analysis, quality control, use of chemical sensors, ion chromatography, ICP and pH measurement. The conference proceedings will be published in 1986, as part of the ITE symposium series.

Radiochemistry (F R Livens)
In the past year, 2 aspects of the laboratory's work have received particular attention. Development studies have been carried out to optimize the techniques in use and to extend the range of sample types analysed, while considerable emphasis has also been placed on accelerating laboratory throughput to keep up with the sampling programmes.

Several quality control exercises have been undertaken. Reference materials for both soil and vegetation have been prepared in large quantities and validated by independent analyses elsewhere and repeated analysis at Merlewood. Animal tissue and a bone reference are also being prepared and standardized. The precision of the analytical methods was found to be 7.8% for actinides in soil and vegetation.

Participation in 2 inter-laboratory comparisons has been used to test the accuracy of the existing methodology, which was found to be satisfactory. One set of samples was circulated by AERE Harwell and the other set was prepared at and distributed from Merlewood.

Developments in the determination of alpha-emitters have largely been directed towards increasing sample throughput. The lengthy total dissolution of animal tissue samples has been shortened by incorporating a hydrofluoric acid digestion step into the procedure, and it has proved possible to eliminate some co-precipitation steps from the analytical method, reducing sample processing time by 50%.

A different approach has been adopted for the determination of americium in all sample types. A highly selective extractant, diethyl-N,N-dibutyl carbamoyl phosphonate (DDCP), has recently become available and is very useful for extracting americium from strong acid solutions. It can tolerate large amounts of potentially interfering matrix components, notably iron and phosphate, which makes it ideally suited for americium analysis in environmental materials. Whilst its adoption does not increase sample throughput, the processing of a batch of samples now requires significantly less operator time, resulting in greater efficiency in the laboratory.

The existing laboratory techniques have been extended to process a variety of new sample types. Provided that sample pre-treatment is adequate, the tissue methods have been used in the analysis of large (1–2 litre) samples of sheep urine, sheep milk, natterjack toads, annelid worms and birds' eggs.

Recently, considerable interest has been expressed in the behaviour of low levels of plutonium/americium, sometimes in very small samples. These analyses require methods which consistently give high yields in order to keep the alpha counting time reasonable (less than 3 days). The modified laboratory techniques have been successful in this respect, although counting time limits the number of analyses which can be done to 500 per year. In the very low-level work, the evaluation of detection limits is of great importance and a simple computer program has been written to calculate these limits in terms of counting time, sample weight, detection efficiency and chemical yield. Instrumental developments during 1985 included the purchase of an ultra-pure germanium gamma-ray detector and an updated computer software package for the interpretation of gamma spectra.

Stable isotope unit (C Quarmby)
The operating difficulties with the VG SIRA 9 mass spectrometer which were touched on in last year's report kept the instrument out of commission early in the year, and it was not until July that all the problems were solved. Since that time, however, the machine has performed very well and the backlog of analyses has been cleared; at the time of writing, about 75% of the projected sample capacity for the coming year has been booked by workers within NERC.

In a recent study (Marshall & Whiteway 1985), an automatic analyser operating on the Dumas principle was coupled to a stable isotope mass spectrometer. Apart from the benefit of unattended operation, this procedure markedly reduces the size of sample required for the determination of ^{15}N, a vital consideration in some biological work. To achieve the same end, we are altering the inlet of the mass spectrometer to enable sample sizes to be handled with a lower limit of about 50μg-N. At the same time, the automatic manifold will be modified, to reduce deadspace and improve sensitivity. Preliminary experiments have shown that transfer of the gaseous sample, generated in the Rittenburg reaction, can be carried out efficiently, and without fractionation, using adsorption on to charcoal at liquid nitrogen temperatures. If this initial work is successful, the capacity of the automated system can be increased to 40 samples without further alteration to the mass spectrometer.

Reference

Marshall, R B & Whiteway, J N. 1985. Automation of an interface between a nitrogen analyser and an isotope ratio mass spectrometer. *Analyst*, 110, 867–871.

Engineering (G H Owen)
The engineering service has continued to be involved in general and technical support work such as maintenance, repair, design and development of mechanical, electro-mechanical and electronic equipment.

This year the engineering support required by research projects has shown a pronounced bias towards equipment for studying airborne pollution and its effects on groundwater. For instance, for a Welsh NO_x survey, a large number of tubes designed to absorb NO_x by diffusion had to be assembled. Acid rain monitoring required the construction of many tipping bucket gauges for measuring vegetation throughfall, stem flow and soil water flow. Other equipment for pollution studies, still under construction at the end of the year, includes a device for acid rain simulation trials (Bangor) and field chambers for examining the effects of gaseous pollutants on plants (Edinburgh). Also, for an Edinburgh project (ITE 924), a mist and snow collecting apparatus is being modified so that tree injury due to acid mist can be examined.

Stream water sampling equipment is still being developed for use in the assessment of aluminium in waters (ITE 1016 and 797), involving mechanical development at Monks Wood and electronic design of the control system at Bangor.

Engineering at Merlewood was biased towards improvements to working facilities and equipment modification and maintenance. Mechanical modifications to the SIRA 9 mass spectrometer are helping to improve the automatic manifold for sample handling. New deionized water supplies have been installed and the fitting of a new air compressor has meant that air supplies to various analytical instruments in the chemistry and soil laboratories are now more dependable. A new form of 'wet only' rain collector is being developed, primarily for the investigation of acid waters in Wales (ITE 923). This device excludes dry atmospheric deposition and should give a measure of dry pollution settling out from the atmosphere at a variety of field locations.

Plant Culture (R F Ottley)
i) Glasshouse accommodation
Glasshouse facilities were not over-stretched in 1985. One of the principal tasks has been the management of stock birch (*Betula* spp.) plants to produce epicormic shoots which tend to root more readily as cuttings. Two thousand cuttings were inserted, from which 850 plants were selected to form the stock for further propagation in 1986. In the case of lodgepole pine (*Pinus contorta*), it was found that cuttings could root fairly well in October which relieves the normal rooting pressure in March. This aspect is being investigated further. Accommodation was also provided for 900 red alder (*Alnus rubra*) plants undergoing mycorrhizal screening, and 3 glasshouses were still in use for tropical plants. Indications are that the glasshouses will be heavily used in 1986 for bud-burst experiments, work on protection of emerged buds, induction of shoot growth for early birch propagation, and for more extensive birch production.

There has been a significant development in mist propagation, moving from misting by demand using an electronic 'leaf', to a timed system which can be adjusted for frequency and duration of mist burst to suit varying requirements of different species. The system now being developed will be able to differentiate between the presence or absence of sunshine.

The environmental control equipment which is so essential in glasshouse culture is slowly becoming more troublesome. The original electric fan heaters have deteriorated beyond safe and effective use and will have to be stripped out. Ideally, the low-pressure hot water system now in part-use should be extended to all the glasshouses. This system has the advantage that it can be operated by standby generators in the event of a power failure.

ii) Field plots
The field plots, totalling 9.58ha, are now almost fully planted, with space only for odd-shaped plantings such as clone banks or plantings not requiring a statistical design. All areas are now under a low-maintenance rye-grass sward which provides ease of access in all weathers at all times of the year. The shortage of new land for further planting is now limiting the scale of experimental work. Plant protection is also a problem, and is necessary because of damage to the perimeter fence by vandalism, especially at Roslin which is near a housing estate.

iii) Landscaping
Landscaping around the new Bush laboratory extension has been seriously affected because of the site condition after completion of the building and because of the wet weather. A stock of 3600 plants propagated last year is now ready for planting, but the landscaping is not likely to be completed until autumn 1986.

Photography (P G Ainsworth)
The unit continues to produce large numbers of both black and white, and colour prints for publication, as well as for displays at seminars, exhibitions, open days and records. There is also a steady demand for colour slides for use in lectures. Special tasks have involved the production of black and white enlargements used for counting birds on the Isle of May, producing photomicrographs to an accurate scale size for CCAP, and studio photographs of various items from potted plant seedlings to butterflies.

A continuous review of new materials, equipment and techniques is maintained, and new materials are evaluated before routine use. A technique for the production of coloured lecture slides direct from black and white artwork was recently developed. Other tests are being carried out on new colour material to produce large colour transparencies for display work.

The general financial situation, coupled with price rises in photographic materials, has resulted in the need to husband resources, which has decreased the stock levels. The need to replace major equipment, notably an enlarger, is particularly pressing.

Research and Development

Computer developments in analytical chemistry (A P Rowland)
Since the late 1970s, an on-line laboratory data processor has been used to collect balance weights and monitor analogue signals from continuous flow and atomic absorption instruments (see Annual Report 1979). Commercial software was provided to determine peak heights and to correct for drift in base-line and instrumental gain. This package was specially adapted for use with a high level language (BASIC), simultaneously with data collection. The application proved broadly successful. However, the additional development of other applications overloaded the single

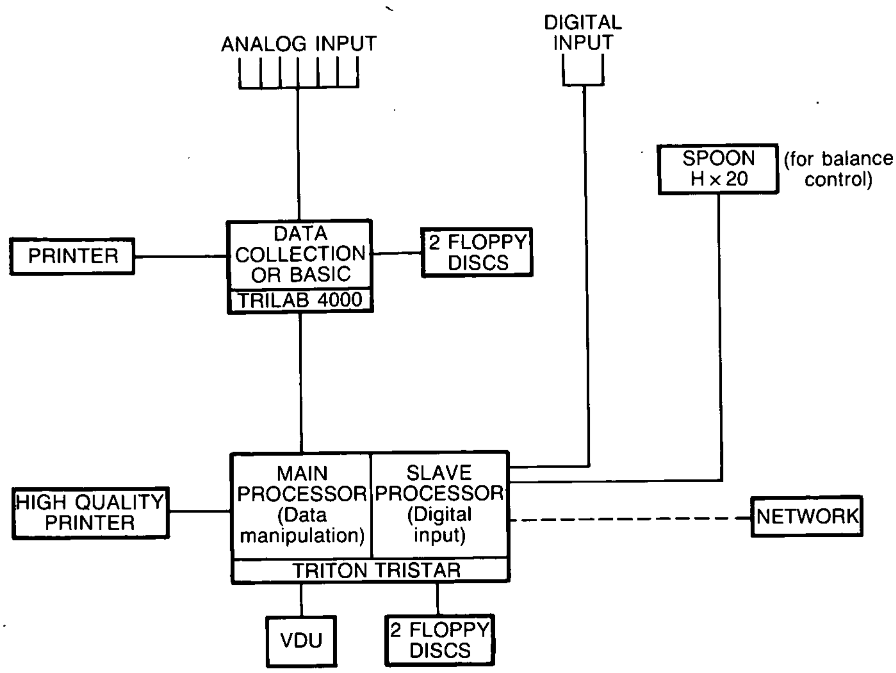

Figure 72. Plan of computerized laboratory system for analytical chemistry data

processor system, and so it was recently replaced when the hardware became expensive to maintain and when the commercial software was no longer supported.

The Trivector replacement system was a development from the previous laboratory data processor using standard laboratory computers based on 3 microprocessors (Figure 72). The main data collection processor has many additional features, including the ability to compare calibration signals with sample signals for predicting solution concentration levels automatically. The menu-driven system can be programmed to quantify samples close to the detection limit of each method, without the loss of peak synchronization which had previously been a problem. A special algorithm was needed to collect data from the atomic absorption instruments. There were minor software faults which delayed the full implementation of the system for almost 2 years after installation.

The remaining 2 microprocessors are used for data manipulation. A suite of programs has been developed for calibration, calculation, customer report compilation and simple statistical tests. The manufacturers have had problems with the communication between the 2 microprocessors which has delayed the development of an automated data collection system from the electronic balances. Plans to link into the NERC network have been deferred until the laboratory system is fully operational, but it is hoped that this will shortly be possible.

Birds' egg measurement (F Moriarty, V W Snapes)
A mechanical engineering assignment called for a measuring device to determine the shell profile, area and thickness of birds' eggs. Egg thickness is often estimated, crudely, by Ratcliffe's Index (I), where $I = W/B \times L$ (W is shell weight in mg, L and B are maximum length and breadth respectively in mm). For current work on the effects of egg size and shape on shell thickness (ITE 289), a more accurate measure is needed, where $J = W/A$ (J is the revised index, and A is the surface area section). An equation to describe the longitudinal profile can be derived from measurements of known shell diameters at known distances from the centre of the major axis. Areas and shell thickness can then be readily calculated. The machine developed for these measurements uses a series of plates with circular holes of known diameter (correct to 0.01mm). Eggs are placed in these holes and distances to the centre of the egg are measured by a dial gauge reading to 0.01mm. The principal error is lack of circularity in birds' eggs, although there are reliefs in the holes to accommodate any major excrescences on the shells.

Electronic developments (C R Rafarel)
A dual heat Milton radiometer is being used as part of the remote sensing project (ITE 951) to help gather ground truth data. An interface unit was designed to scan the 8 analogue output channels of the radiometer and send the data via a serial link to an Epson portable computer. The computer displays the data and can record it on tape together with date, time and any user notes. A terminal emulation and file transfer program on the Epson then allows transfer of the data to a VAX computer for subsequent processing. The project required the writing of an assembler language program for the microprocessor which was used in the interface unit, as well as the generation of software in BASIC for the Epson and VAX computers. Although originally designed for use with a radiometer, this unit has wider applications for monitoring analogue signals via a computer serial port.

The design of a rainfall trigger unit (Annual Report 1984) has been followed by its successful trial by the Welsh Water Authority. The trigger, using the signal from a commercial tipping bucket rain gauge, monitors rainfall, and models, in a simple way, the build-up and decay of groundwater in a system. When the current level is exceeded, the sampler is triggered so that the water chemistry is monitored from just before the start of the stream flushing. So far, 12 units have been built for the Welsh Water Authority and 5 more are under construction.

S E Allen

Agriculture and the Environment

Changes in the Plant Life of Grazing Marsh Systems

(This work is supported by Nature Conservancy Council funds)

The need for more precise data on change and stability in ecosystems, based on well-planned and long-continued quantitative observations, has long been recognized. In a keynote address to a symposium on 'Ecology and the industrial society', convened by the British Ecological Society in 1964, Professor Roy Clapham spoke of how, lacking such information, ecologists were at a serious disadvantage when asked to 'substantiate statements about declining numbers of this or that species in relation to some form of environmental modification' (Goodman *et al.* 1965). Over the last 20 years, there has been a marked increase of concern as to the effects of modern farming techniques on wildlife.

As part of this concern, the Nature Conservancy Council has commissioned a study of the impact of agricultural land drainage on the wild plant life of those types of grazing marsh encountered in the Romney Marsh, Somerset Moors and Levels, and the Idle/Misson Levels of Nottinghamshire, Humberside and South Yorkshire.

The study carried out by ITE is providing opportunities to establish baselines from which future changes in the chronology and extent of changes in plant life, the pattern of agricultural land use and management, and drainage regime might be measured, and for assessing how far baseline data might be available for points in time in the past. An ultimate goal is to identify the influence of one type of change on another, and the consequent scope for preserving and enhancing the biological interest of these 'wetland' areas in the future.

The stratified random sampling programme, adopted in the 3 areas, was described in the Annual Report for 1983, and in reports now published by the Nature Conservancy Council (Mountford & Sheail 1982, 1984a, b).

Changes in Agricultural Land Use
During the course of the surveys, it became clear that the grasslands of the study areas were limited in extent and poor in species numbers and diversity. From quadrat analyses, the vegetation was found to consist mainly of species widespread and common to agriculturally improved grasslands generally. Regional or nationally rare species were absent.

Published and manuscript land use data suggest that this is a comparatively new situation. The Ordnance Survey recorded about 80% of the Romney Marsh as pasture in the 1870s; over 90% of the area was described as grassland in the first Land Use Survey of the early 1930s. The most striking changes came in the Second World War, when the proportion of farmland under permanent grass, in those parishes wholly within the Marsh, fell from 81% to 55%. According to the annual census of the Ministry of Agriculture, a further marked decline occurred in the late 1960s, when the area under permanent grass declined from 43% to 31% between 1965 and 1969. Although the area under tillage was not maintained, only about 35% of farmland was classified as permanent grassland in the early 1980s (Sheail & Mountford 1984).

Large-scale changes in the land use of the Idle/Misson Levels did not occur until the late 1970s, when a pump drainage scheme was installed, designed to improve both the productivity and character of over 5480 hectares of land. The intention was to convert much of the washlands, previously left to grass, to cereals, roots and vegetables. A comparison between the land use information, collected during the survey of 1983, with the manuscript maps of the Second Land Use Survey, compiled in the early 1960s, indicates that about 80% of the grassland recorded in the earlier survey had been ploughed up by 1983. The area of grassland converted to arable was 7 times greater than that recorded as arable in the early 1960s and as grassland in 1983.

Changes in Plant Species
By comparing the species lists of the present day with those compiled from old Floras and the manuscript records of earlier botanists, it is possible to follow trends in species populations and distribution. Comparisons over time, even within limited areas, are inhibited by differences in the thoroughness and competence shown by those compiling the information. The records for West Sedgemoor, for example, are far fewer than those for parts of the Somerset Moors closer to railway stations and main roads. Despite the inherent limitations of the historical information, a distinct difference can be seen between those species which have increased and those which have declined over the last 100 years (Table 31). In all 3 study areas, most of the species which increased are aliens and recent arrivals. The largest group of species to have declined is made up of those plants associated with damp pastures, or those dependent on shallow, open water, subject to grazing.

Table 31. Numbers of species showing a change in abundance

	Romney Marsh				Somerset Levels				Misson, Idle Carrs			
	Increase in abundance and/or distribution		Decrease in abundance and/or distribution		Increase in abundance and/or distribution		Decrease in abundance and/or distribution		Increase in abundance and/or distribution		Decrease in abundance and/or distribution	
	Marked	Slight	Marked	Slight	Marked	Slight	Marked	Slight	Marked	Slight	Marked	Slight
	5	20	55	42	11	21	43	58	3	5	75	47
Totals	25		97		32		101		8		122	

Table 32. Species change in the Misson Fenny Fields

Species tending to decline or disappear since 1950	Species evidently as widespread in 1983 as in 1950	Species more widespread or abundant in 1983 than in 1950
Lesser water-plantain (*Baldellia ranunculoides*)	Sneezewort (*Achillea ptarmica*)	Hastate orache (*Atriplex prostrata*)
Slender tufted-sedge (*Carex acuta*)	Purple small-reed (*Calamagrostis canescens*)	Creeping thistle (*Cirsium arvense*)
Carnation-sedge (*Carex panicea*)	Brown sedge (*Carex disticha*)	Couch-grass (*Elymus repens*)
Bladder-sedge (*Carex vesicaria*)	Ragged-robin (*Lychnis flos-cuculi*)	Common hemp-nettle (*Galeopsis tetrahit* s.l.)
Meadow thistle (*Cirsium dissectum*)	Yellow loosestrife (*Lysimachia vulgaris*)	Cleavers (*Galium aparine*)
Irish marsh-orchid (*Dactylorhiza majalis*)	Tubular water-dropwort (*Oenanthe fistulosa*)	Common reed (*Phragmites australis*)
Fen orchid (*Dactylorhiza praetermissa*)	Great yellow-cress (*Rorippa amphibia*)	Knotgrass (*Polygonum aviculare* s.l.)
Mare's-tail (*Hippuris vulgaris*)	Great burnet (*Sanguisorba officinalis*)	Common nettle (*Urtica dioica*)
Marsh pea (*Lathyrus palustris*)	Marsh ragwort (*Senecio aquaticus*)	
Adder's-tongue (*Ophioglossum vulgatum*)	Marsh stitchwort (*Stellaria palustris*)	
Marsh cinquefoil (*Potentilla palustris*)	Common meadow-rue (*Thalictrum flavum*)	
Yellow rattle (*Rhinanthus minor*)		
Brookweed (*Samolus valerandi*)		
Floating club-rush (*Scirpus fluitans*)		
Devil's-bit scabious (*Succisa pratensis*)		
Marsh valerian (*Valeriana dioica*)		
Fen violet (*Viola palustris*)		

When plant lists are available from the past for sites which can be accurately located, there is the opportunity to carry out case studies of wider trends in plant life. In the Idle/Misson Levels, surveys of the Misson Fenny Fields, a low-lying peaty area, often with standing water on parts of the meadows in winter, and the ditches permanently wet, were made in 1952, 1954, 1955 and 1969. The grasslands, which were formerly mown for hay and then grazed only in late summer, were improved by ploughing and reseeding in 1954. The installation of the pump drainage scheme in the late 1970s resulted in most of the land being used for arable crops. The changes in flora between the early 1950s and the survey of 1983 are summarized in Table 32. The very rich fen flora, characteristic of short, damp turf and wet hay meadows (containing such national rarities as fen violet (*Viola persicifolia*) and marsh pea (*Lathyrus palustris*)) has been largely destroyed. Arable weeds have greatly increased.

Characteristics of the Farm Ditch

The loss of species-rich grasslands has had the effect of enhancing the importance of another artifact of earlier systems of farming, the ditches and cuttings which now act as the principal refuge for many of the rarer species.

In order to discover the effects which the ditch characteristics and environmental factors exert on the bank and aquatic vegetation, the data derived from the field sampling programmes of 1981–83 were submitted to 2 related types of multivariate statistical analyses, namely Indicator Species Analysis (ISA) (Hill *et al.* 1975), and TWINSPAN (Hill 1979). In practice, it is often difficult to distinguish the effects of one type of ditch characteristics from another, because each in turn is affected by wider environmental factors. The impact of distinctive soil types on the incidence of plant species is often modified to the movement of ditch water from one type to another, either as a result of natural flow or pumping operations.

In the Somerset Moors and Levels, 35 species displayed a tendency towards sites with deeper ditches, and 39 to shallow ditches, with 20 of the latter group particularly associated with those that were generally dry (Table 33). The list for the shallow and/or dry ditches reflected 3 types of situation. First, there was a small number of rich sites, where the ditch is a shallow depression in the waterlogged turf. Second, a large number of sites were mainly occupied by terrestrial species, or densely shaded by woody plants. Third, 39 species were more closely associated with sites with a comparatively wide ditch, where the water was generally deeper, and, in some cases, flowing. In this third category, there was a significant cover of floating and submerged vegetation. The 28 species that had a preference for narrow ditches tended to be emergent swamp species. Forty-four species were common at sites with low banks, compared with only 14 species where high banks existed. Five times as many species occurred more frequently on sites with gently sloping banks than in ditches with steeper banks.

Improvements in arterial and field drainage have led to the elimination, or redesign, of many ditches. In the Idle/Misson Levels, 52 of 200 ditches, selected randomly

Table 33. Ditch characteristics: ditch depth

Preferential for shallow ditches (0.25m)	Preferential for deep ditches (0.75m)
Couch-grass (*Elymus repens*)	Filamentous algae
Bog pimpernel (*Anagallis tenella*)	Marsh foxtail (*Alopecurus geniculatus*)
Sweet vernal-grass (*Anthoxanthum odoratum*)	Water fern (*Azolla filiculoides*)
Hastate orache (*Atriplex prostrata*)	Flowering-rush (*Butomus umbellatus*)
Lesser water-plantain (*Baldellia ranunculoides*)*	Rigid hornwort (*Ceratophyllum demersum*)
Common water-starwort (*Callitriche stagnalis*)*	Canadian waterweed (*Elodea canadensis*)*
Hedge bindweed (*Calystegia sepium*)	Tall fescue (*Festuca arundinacea*)*
Common yellow-sedge (*Carex demissa*)	*Galium elongatum**
Glaucous sedge (*Carex flacca*)	Floating sweet-grass (*Glyceria fluitans*)*
Carnation sedge (*Carex panicea*)	Reed sweet-grass (*Glyceria maxima*)*
Greater tussock-sedge (*Carex paniculata*)	*Elodea nuttallii*
Marsh thistle (*Cirsium palustre*)	Frogbit (*Hydrocharis morsus-ranae*)*
Great willowherb (*Epilobium hirsutum*)	Yellow iris (*Iris pseudacorus*)*
Field horsetail (*Equisetum arvense*)*	Fat duckweed (*Lemna gibba*)*
Meadowsweet (*Filipendula ulmaria*)	*Lemna polyrhiza*
Cleavers (*Galium aparine*)	Gipsywort (*Lycopus europaeus*)*
Square-stalked St John's-wort (*Hypericum tetrapterum*)*	Water forget-me-not (*Myosotis scorpioides*)
Sharp-flowered rush (*Juncus acutiflorus*)	Spiked water-milfoil (*Myriophyllum spicatum*)
Blunt-flowered rush (*Juncus subnodulosus*)	Yellow water-lily (*Nuphar lutea*)
Greater bird's-foot-trefoil (*Lotus uliginosus*)	Tasteless water-pepper (*Polygonum mite*)*
Ragged-robin (*Lychnis flos-cuculi*)	Small pondweed (*Potamogeton berchtoldii*)
Creeping-Jenny (*Lysimachia nummularia*)	Curled pondweed (*Potamogeton crispus*)
Purple loosestrife (*Lythrum salicaria*)	Shining pondweed (*Potamogeton lucens*)
Greater plantain (*Plantago major*)	Fennel pondweed (*Potamogeton pectinatus*)
Pale persicaria (*Polygonum lapathifolium*)	Lesser pondweed (*Potamogeton pusillus*)
Fen pondweed (*Potamogeton coloratus*)	Water crow-foot (*Ranunculus penicillatus*)
Silverweed (*Potentilla anserina*)	Curled dock (*Rumex crispus*)*
Common fleabane (*Pulicaria dysenterica*)	Wood dock (*Rumex sanguineus*)*
Meadow buttercup (*Ranunculus acris*)	Arrowhead (*Sagittaria sagittifolia*)
Lesser spearwort (*Rannuculus flammula*)	Common willow (*Salix cinerea* spp. *atrocinerea*)*
Clustered dock (*Rumex conglomeratus*)	Common bulrush (*Schoenoplectus l. lacustris*)
Procumbent pearlwort (*Sagina procumbens*)	Skullcap (*Scutellaria galericulata*)
Glaucous bulrush (*Schoenoplectus l. tabernaemontani*)	Unbranched bur-reed (*Sparganium emersum*)
Marsh ragwort (*Senecio aquaticus*)	Pink water-speedwell (*Veronica catenata*)*
Bittersweet (*Solanum dulcamara*)	Rootless duckweed (*Wolffia arrhiza*)
Common nettle (*Urtica dioica*)	
Common valerian (*Valeriana officinalis*)	
Brooklime (*Veronica beccabunga*)	
Heath dog-violet (*Viola canina*)	

* indicates the species shows only a slight preference

and plotted on Ordnance Survey 1:25 000 maps for sampling, were subsequently found to have been destroyed since the last revision of those maps in 1948–51, suggesting that about a quarter of the ditches of the area had been eliminated over that period. During the course of field work, many of the surviving ditches were found to be dry in summer, or made redundant as a result of the deepening of main drains, leaving the field ditches as 'dry hanging valley'.

Data kindly made available by the Ministry of Agriculture suggest that about 60% of the Romney Marsh, 30% of the Idle/Misson Levels, and 10% of the Somerset Moors and Levels experienced the direct effects of field drainage schemes between 1940 and 1980. In the survey of the Somerset Moors and Levels in 1982, it was found that only 45 of the 480 fields adjacent to the sampled ditches had been affected by a grant-aided field drainage scheme. A survey was made of a further 35 ditches in 1983, known to be adjacent to land that had undergone subsurface drainage. A comparison of the species complement of sites next to a field affected by a scheme with the remaining sites sampled in the 2 years suggested that subsurface drainage led, not so much to a distinctive ditch community, as to an impoverished variant of the associations found on the sites prior to drainage. Of the 150 fields adjacent to ditches with 8 or fewer aquatic species in a 20m length, 46 had been underdrained. Only 16 of the 116 fields adjacent to ditches with 15 or more aquatic species had experienced underdrainage.

Impact of Management Practices

Some types of change in the management of habitats can be just as important as site destruction in bringing about species losses. In the Somerset Moors and Levels, about 3 times as many species were confined to, or showed a preference for, ditch banks which were regularly grazed and subject to trampling, as for those where no grazing occurred. The several open-water species and many low-growing plants comprising the major category require relatively high light levels, and are eliminated wherever reed growth is permitted. The cessation of grazing, either by the conversion of adjacent land to arable, or the erection of a fence between the ditch and pasture, means that ditch cleaning may become even more important as a form of vegetation management. The lists of species found growing most often in ditches managed annually, or at less frequent intervals, represent in effect different stages in a hydrosere. The most recently cleaned ditches correspond with the open-water stage of greater water depths and a more diverse submerged vegetation. Where the frequency of management varies between parts of the water courses, the local catchment may be characterized by a particularly wide diversity of vegetation.

In order to help gauge the representativeness of records made on a site as a result of a single visit, bearing in mind the scope for changes in plant life during the course of a year or series of years, a quarter of the sites visited in the Somerset Moors and Levels was resurveyed a year later, in 1983, and the subset, together with the merged data set of the 240 sites recorded in 1982, was analysed by means of TWINSPAN and ISA. Of the 60 sites examined in both years, 36 fell in the same group, and 16 in a very similar group. In only 8 cases did the 1983 sample appear very different. Five of these sites had been dredged in the intervening period.

The long-term effect of regular maintenance may be to keep the ditch at the same stage in seral development. Although a large proportion of the annual production of the ditch is removed, there survive viable propagules (usually in the form of vegetative fragments) of most species, causing an almost identical vegetation to develop over the course of the ensuing months. Much more catastrophic changes are likely to come about, either where ditch cleaning is accompanied by the considerable enlargement of the ditch, and the consequent removal of the substrate and steepening of the banks, or where management ceases altogether, and succession is allowed to occur. In the latter case, the depth of water decreases as a result of the accumulation of plant remains and the establishment of low emergents, and ultimately of reed. Both types of situation are characterized by low plant species diversity, and have become increasingly common where grazing marshes have been converted to arable.

Future Research

When the analyses of the surveys of the 3 study areas have been completed, and correlated with information derived from a survey of 5 lengths of valley in the western part of the county of Dyfed, a comprehensive, yet detailed, insight may have been gained into the diversity of conditions likely to be encountered in the management of freshwater 'wetland' areas for conservation purposes. The relative importance of the ditch bank, as opposed to the adjacent fields, for the conservation of plant life is already clear. The categorization of ditch types is likely to highlight not only the constraints now imposed on sustaining a diverse and distinctive flora within modern farming systems, but the challenge presented to plant ecologists of creating *de novo* such a flora explicitly for conservation purposes, based on a fuller knowledge of the autecology of the species involved and of plant dynamics in a grazing marsh system.

J O Mountford and J Sheail

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Modern Agriculture and Wildlife

In recent years there has been increasing interest both from farmers and conservationists in the ecology and management of field margins. From the number and content of recent symposia and meetings, the management of field boundaries appears to be a topic urgently requiring ecological research to produce sound advice on future management for specific objectives.

Very little is known about the way changes in hedge, ditch and crop margin management affect the fauna and flora. The existence of some particularly species-rich boundaries, even on intensive arable farms, is an indication of the wildlife potential of this ecosystem. Hedges, ditches and any uncropped strips of land at the edges of fields are currently subjected to a wide variety of treatment for livestock shelter, game production, pest control, weed control, ease of management, landscape and amenity value, conservation, tradition, or the farmer's personal preference.

As a preliminary investigation into the effects of these different agricultural practices, a survey was undertaken of the capacity of a range of types of farmland to support birds in winter. Three types of farmland were selected: small pasture fields, small arable fields, and large intensively managed arable fields. Bird numbers and species were recorded monthly in 5 transects in each of 5 replicates of each type of farmland. Each transect consisted of a 200m length of field boundary and a 10m wide strip of crop on each side. Birds seen elsewhere in adjacent fields were recorded separately. As a second stage, the study is now being extended to compare winter and summer populations.

A preliminary analysis of the data according to farm type shows that, in winter, the majority of species occur, and are more abundant, in and around small pasture fields. There is very little difference in species present between small and large arable fields, but bird numbers are often lower in the latter. With larger fields there is not only less boundary per hectare, but generally there is less hedgerow left on these boundaries. In summer, birds seem to spread into many areas which appear less favourable during the winter.

When all the data have been collected for the 75 transects, it should be possible to look at the effects of certain habitat features, such as height of hedge, presence of a ditch, adjacent crop type, use of herbicides on the crop edge, etc. For at least some of the sites, information is also being collected on the flora and the distribution of invertebrate animals. This will provide additional data upon which to base future studies.

The ultimate objective is to produce a simple standardized, broad spectrum, survey method for the fauna and the flora of field margins. This method could produce a data base for comparison of habitats and management effects in both the short and long term. It would be particularly useful for the evaluation of conservation measures and for monitoring the effects of changing agricultural policy across the whole country.

T Parish

Joint Research Fellowship in Common Agricultural Policy

This timely award, based at ITE Merlewood, represents the first collaborative Fellowship between the Natural Environment Research Council (NERC) and the Economic and Social Research Council (ESRC). The appointee, Dr Malcolm Bell, began a 2-year secondment from the Land Use Department of the National Farmers' Union in April 1985.

The intentions of the Fellowship are 3-fold. First, it provides a researcher with a background in social science, law and economics within ITE but also actively contributing to the ESRC's Environmental Issues Programme. Second, co-ordinating the work with Merlewood's land classification and survey team allows the possibility of building social and planning criteria into that data base. Their inclusion enhances the utility of the data for interpreting and explaining countryside change. Third, the enhancement of the data base provides further opportunities for predictive modelling. The specific brief for the Fellow is to focus on

Table 34. Land uses which occur predominantly within Rural Development Areas (1978 survey data, in hectares)

Land use	Inside RDA	(% of RDA)	Outside RDA	(% of rest of England)	% of that use within RDA
Hay/silage	54391	(1.2)	81532	(1.0)	40
Rye-grass-(*Lolium*) dominated permanent pasture	162995	(3.6)	195579	(2.3)	45.5
Dog's-tail (*Cynosurus*)/neglected permanent pasture	136157	(3.0)	194861	(2.3)	41.1
Mixed rough pasture	60378	(1.4)	65530	(0.8)	48
Rush- (*Juncus*) infested pasture	30055	(0.7)	33374	(0.4)	47.4
Bracken- (*Pteridium aquilinum*) infested pasture	11018	(0.2)	10272	(0.1)	51.8
Mat-grass- (*Nardus*) dominated pasture	5965	(0.1)	4549	(0.1)	56.7
Heather- (*Calluna vulgaris*) pasture	123410	(2.8)	31609	(0.4)	79.6
Cranberry (*Vaccinium*) dominated pasture	2794	(0.1)	218	(0.0)	92.8
Rush- (*Juncus*) dominated marsh	33978	(0.8)	15630	(0.2)	68.5
Moor-grass- (*Molinia*) dominated	41444	(0.9)	47057	(0.6)	46.8
Cottongrass- (*Eriophorum*) dominated	6170	(0.1)	1081	(0.0)	85.1
Herb-rich grass	965	(0.0)	169	(0.0)	85.1
Turnips/roots	29780	(0.7)	39401	(0.5)	43
Lake		(1.4)	82302	(1.0)	44
Quarry/pit	64557	(0.2)	11215	(0.1)	44.1
Rock	8857	(0.2)	3697	(0.0)	70.9
Conifer shelterbelt	9005	(0.0)	1681	(0.0)	44.8
Gillside wood	1364	(0.2)	7002	(0.1)	49.6
Conifer woodland	6880	(6.6)	262961	(3.1)	52.9
Mat-grass (*Nardus stricta*)	295935	(1.2)	14762	(0.2)	78.8
Moor-grass (*Molinia*)/deergrass (*Scirpus*)/	54818	(0.7)	5734	(0.1)	83.8
cottongrass (*Eriophorum*)	29759				
Sub-arctic vegetation	3591	(0.1)	31	(0.0)	99.1
Bilberry (*Vaccinium myrtillus*)	4948	(0.1)	1384	(0.0)	78.1
Mixed mountain/grassland	27000	(0.6)	7469	(0.1)	78.3
Mixed mountain/moorland	56079	(1.3)	30832	(0.4)	64.5
Deergrass (*Trichophorum*)/heather (*Calluna*)	10792	(0.2)	1976	(0.0)	84.5
Heath rush (*Juncus squarrosus*) dominant	2622	(0.1)	447	(0.0)	86.7
Heather (*Calluna*)/cottongrass (*Eriophorum*)	34875	(0.8)	8729	(0.1)	80.0
Heather (*Calluna*)/Cranberry (*Vaccinium*)	31671	(0.7)	2708	(0.0)	92.1
Burnt	5123	(0.1)	74	(0.0)	98.6
Parkland	4496	(0.1)	3468	(0.0)	56.5
Mixed grain	13654	(0.3)	7600	(0.1)	64.2

Designated Rural Development Areas cover some 34.3% of England using a consistent methodology and excluding London and the Isle of Man. The 40% level of occurrence within RDA has been selected as cut-off for this tabulation possible alterations to the Common Agricultural Policy (CAP) regimes of market and structural support, in order to consider the likely environmental and social effects of such change.

In the rapidly developing academic and popular debate over the future of the CAP, the Fellow has contributed a number of position papers drawing together agricultural, environmental and rural development aspects. Evidence was submitted in response to a request from the European Parliament's Environmental, Public Health and Consumer Affairs Committee, and the Fellow attended a subsequent 3-day Public Audition of experts on Agriculture and Environment in Brussels. Invited contributions have also been made to the proceedings of the annual conference of Rural Community Councils and similar wider public bodies, as well as a range of academic working groups and conferences.

Initial work in extending the range of interfaces with the land use data collected by Bunce *et al.* has concentrated on a purely socio-economically derived designation, and one with a mixture of environmental and social characteristics. Table 34 illustrates one interesting output of this linkage. It permits us to determine the land uses which have been found by survey using the environmentally derived land classification strata, compared with the boundaries of Rural Development Areas designated by the Development Commission as parts of the English countryside in need of special assistance due to social and economic deprivation. To place planning constraints on the improvement of such land may thus inherently contradict development policy. Table 35 illustrates the remarkable correspondence with the areas of England and Wales recognized as agriculturally Less Favoured due to moderate or severe handicaps, and thus in receipt of special aid under EEC Directive 797/85 on Socio-Structural Policy.

This extension of the ability to present land use data in increasingly relevant areas for agricultural and rural policy has contributed to a joint study with the Centre for Agricultural Strategy at the University of Reading. This 6-month study is commissioned by the Department of Environment and Development Commission, and is seeking to make an early initial assessment of the countryside effects of 5 different scenarios for the future of the CAP, ranging from a continuation of present levels of support to a removal of mechanisms leaving prices to fall to free market levels. The work involves a combination of modelling, and assessment of the ecological and planning impact of the changes predicted by the modelling exercise.

M Bell

Table 35. Relationship between Land classes and designation of Less Favoured Areas (squares surveyed in 1984 in England and Wales only)*

	Land class	No of squares in LFA†	No of squares not in LFA
1	Undulating country	2	10
2	Open, gentle sloping lowland	—	12
3	Flat arable land	—	12
4	Flat intensive agriculture	—	12
5	Enclosed, mixed farmers	4	8
6	Fertile pasture	4	8
7	Coastal	2	10
8	Coastal, estuarine pasture	1	7
9	Flat, often built-up	—	12
10	Flat arable/grass plains	3	9
11	Rich alluvial plains	—	12
12	Fertile coastal plains	—	12
13	Variable land form	1	8
14	Level coasts with arable	—	9
15	Valley bottoms – pastoral	1	11
16	Undulating lowland	6	4
17	Improvable permanent pasture	12	—
18	Rounded hills & moorlands	6	—
19	Heather moors	6	—
20	Mid-valley slopes	4	—
21	High mountains & moorlands	4	—
23	Mountain summits	2	—
24	Northern fertile lowlands	2	—
27	Northern mixed farming	1	2
28	Northern lowland margins	1	—

* In each class, 12 squares were sampled, but some examples are in Scotland or the Isle of Man
† Includes those squares which are partially in A

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