Natural Environment Research Council

# Institute of Terrestrial Ecology

1979

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# Annual Report 1979

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COVER PHOTOGRAPHS

A tagged rabbit free-living at Monks Wood Experimental Station.
Photograph: D T Davies

Sporocarp (toadstool) of fly agaric.
Photograph: J Pelham

*Populus trichocarpa* growing at a range of spacings (0·3-1·0m) in fertile agricultural soil at Bush, near Edinburgh.
Photographed 5 years after planting cuttings.
Photograph: M G R Cannell

Concrete mixer modified by ITE engineers for the bulk mixing and sieving of soils.
Photograph: S E Allen

Male cuckoo—head and throat in moult.
Photograph: I Wyllie

Toad. Photograph by the late J E Lousley from his collection presented to ITE by Mrs J E Lousley.

*Ramalina siliquosa* lichen.
Photograph: R O Millar

*Gentiana pneumonanthe* L. in flower.
Photograph: S B Chapman

Male wood white butterfly.
Photograph: M S Warren

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

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

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

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

# Contents

# Research on Terrestrial Ecology : Summary Report

During the last 3 years, in particular, the research programme of the Institute of Terrestrial Ecology has been gradually modified. ITE's research strategy was presented in detail in last year's Annual Report, and, in the pursuit of that strategy, some important changes have been introduced, with the approval of the Natural Environment Research Council, to meet and to anticipate the requirements of existing and potential customers for commissioned research, while maintaining a healthy balance of fundamental ecological research. The effects of these changes may be summarised as follows :

1. There has been an increased concentration of research on the ecological consequences of changes, actual or proposed, in land use.

2. There has been a reduced emphasis on research concerned with species and habitats of purely conservation interest, except where conservation agencies like the Nature Conservancy Council have been willing to commission the research. Because the Nature Conservancy Council's support for commissioned research in ITE has declined sharply, the reduction in research on wildlife conservation has also been marked.

3. Many overseas countries are showing considerable interest in ecological research, and ITE has therefore given increased emphasis to aspects of ecology likely to be of interest to overseas customers. Some useful and interesting contracts have already been obtained.

Financial constraints during the next 3-5 years may necessitate further changes, but it is the wish of the Council that ITE should be able to maintain and develop the following general programme of research :

1. Theoretical and applied studies of land classification and land use. Such studies have already shown the significance of ecology to structure plans in local government and to national and regional policies for the rural environment. Locational strategies for major industries are also likely to have important environmental impacts which will need to be assessed ecologically.

2. Effects of radionuclides on terrestrial and freshwater ecosystems. Although a relatively new field of research for ITE, there are indications that there are detectable effects, and public interest in this highly emotive topic makes it essential that decisions are based on facts not conjecture.

3. Effects of sulphur, fluorine and other airborne pollutants. Again, sufficient progress has been made with research in this field to indicate the need for a better evaluation of the interacting effects of various airborne pollutants. In the past, monitoring of such pollutants has largely been concentrated in urban areas, and the effects on crop and semi-natural ecosystems require clarification.

4. Toxicology of organic pollutants and heavy metals in terrestrial and freshwater systems. Although much work has already been done on these pollutants, monitoring of the effects of existing and new pollutants remains an essential task. More exact understanding of the effects of pollutants also needs to be related to dynamic changes in the physiology of organisms.

5. Synoptic limnology—freshwater ecosystems. Water is an essential resource for man, but it is also one of the controlling influences of terrestrial ecology. As yet, we have insufficient knowledge of the ecology of Britain's extensive freshwater systems, and ITE has chosen to work on the synoptic aspects of these systems in collaboration with the Freshwater Biological Association and the Institute of Hydrology.

6. Cycling of plant nutrients, with particular emphasis on woodland and grassland ecosystems. While much of this research is necessarily fundamental in character, the understanding of nutrient and pollutant pathways in ecological systems represents ITE's principal contribution to a wide range of practical applications in ecology.

7. Plant demography and the dynamics of plant communities, with special reference to the management of woodland and grassland. These studies are again fundamental to the understanding of change in ecological systems, and to the management of rural areas.

8. Physiology and population dynamics of invertebrate and vertebrate animals. As for the plants, the inter-relationships between animals and their environment provide the basis for control of pest species, conservation of wildlife, and the prediction of change.

9. Genecology and the implications of variation in natural and man-made ecosystems. Reproductive strategies of plant and animal organisms play an

important role in the management of crop and semi-natural systems, but, as yet, our knowledge of the genetics and variation of many plants and animals is incomplete. ITE therefore places considerable emphasis on this programme of research.

Although, for ease of description, these research topics have been listed separately, they actually form part of a much larger integrated programme of research. Indeed, one of the major advantages of ITE is that it contains, within a single Institute, expertise that covers a wide field of terrestrial and freshwater ecology, so that comprehensive research projects can be initiated and maintained. This Annual Report contains examples of these projects.

In addition to the programmes listed above, there are some important new topics which are in need of fundamental research supported from the Department of Education and Science budget, and of applied research funded by the appropriate customers. At present, however, there are no funds available for these additional programmes, which include:

1. Study of the ecological consequences of an expanded forestry programme in Britain. Both the Forestry Commission and the Centre for Agricultural Strategy, Reading University, have recently indicated the desirability of a larger area of productive forest in Britain. Any substantial increase in the forest area of Britain would have to be carefully integrated with other land uses, including agriculture, water resources, recreation, wildlife conservation and visual amenity. The current classification and land use studies of ITE would provide an ideal base for detailed studies of the ways in which an increased forest estate could be established and maintained, but this research could only be extended if more staff and resources were available.

2. Study of the ecological consequences of the various energy strategies for Britain. It is clear that Britain is on the threshold of major changes in industrial and domestic use of energy as oil becomes more expensive and less readily available on world markets. Strategies for obtaining energy from alternative sources include exploration of coal reserves, nuclear energy and tidal barrages, and combinations of these other sources. The ecological consequences of the various options need to be examined well in advance of any final decision if we are to avoid attempts to remedy major environmental problems after they have been created. Again, however, resources are not available for this important line of research.

3. Development of long-term strategies for the control of pests and pathogens, particularly in forestry. Many of the pests and pathogens of forest and agricultural crops have their origins in semi-natural habitats, and short-term tactical treatment of disease organisms by spraying, trapping and shooting is relatively ineffective and is expensive. ITE's studies of plant demography and dynamics, and of physiology and populations of invertebrate and vertebrate animals provide a basis for long-term control, and, possibly, for the avoidance of outbreaks of potentially harmful organisms. The pine beauty moth (currently causing severe damage in forest crops), the roe deer and several genera of bark beetles are included in a list of organisms for which research is currently restricted by lack of available resources.

Council places considerable priority on items 1 and 3 above, but, as before, what can be achieved by research in terrestrial ecology depends upon the support for such research from the DES Science Budget and from customers.

J.N.R. JEFFERS
Director, I.T.E.

# Longer research reports

*Introduction*

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

The first 2 reports are concerned with vertebrate animals. ITE's revised programme of research on red deer in collaboration with the Forestry Commission and the Red Deer Commission has necessitated the development of methods for estimating and comparing populations of red deer in the concealing habitats of forests and woodlands. Current progress with these methods is described in the first of the reports. The second report describes the progress that has been made in the study of the ecology and physiology of the rabbit through the use of enclosures.

Not all ecological research is successful, and the next report gives a contrast between failure and success in the conservation of 2 butterflies. Although we now know a great deal about the ecology of the large blue butterfly, we were unable to prevent it from becoming extinct in Britain. In contrast, knowledge of the ecology of the black hairstreak butterfly has enabled it to be conserved. The lesson that research needs to be started long before extinction is threatened cannot be overemphasised.

ITE has been closely involved in a study of the potential contribution of energy gained from plants to British national energy requirements. This report summarises an assessment of the productivity of natural vegetation as a renewable energy resource, and concludes that the potential of British vegetation for fixing solar energy is under-employed and could provide a significant contribution to our increasing demands for fuel.

Two contrasting reports follow, although both are concerned with research methods. The first reviews some of the statistical problems of land classification, and describes methods which have become an integral part of ITE's approach to this important topic. The second report reviews the development of methods for interpreting records of species occurrence and density as descriptions of variation in the environment. The fact that some of the views of the authors of these 2 reports are in conflict gives a fair indication of the closeness of these questions to the limits of our knowledge.

Finally, some aspects of the nutrient status of a range of native British plants are described in a report summarising progress in ITE's national vegetation survey. This is the kind of long-term, geographically-dispersed project that can only be initiated by an Institute like ITE, and provides some much needed information on the variability in the chemical composition of common plants.

## ESTIMATING AND COMPARING POPULATION DENSITIES OF RED DEER *CERVUS ELAPHUS* L. IN CONCEALING HABITATS

*The problem*

The vast majority of Britain's red deer occur in Scotland, mainly on exposed hill range, having been excluded by habitat destruction and land use pressures from their preferred woodland and woodland edge habitats. In this rough hill range, with only remnants of natural woodland, the animals are not too difficult to detect, count and classify, given experienced manpower (professional deer stalkers) and favourable weather. They are best counted in late winter to early spring, when they occupy the lowest parts of their home ranges (the lower hill slopes and valley floors), and where they can be counted without disturbance by men traversing the hillsides. Extra men are often necessary to flush any deer from concealment in rough ground or patches of woodland cover, and effective team-work depends on good communication, eg use of 2-way radios. Error due to double-counting can be prevented by good team-work, the main problem being the few deer which escape detection; in most cases, such losses are only a few per cent of the total, and the counts have a high degree of reliability. The importance of deer counting as a prerequisite to the efficient cropping and control of red deer on this kind of ground has been recognised for over 20 years. In consequence, deer are now cropped much more adequately than hitherto.

Red and other deer species, principally roe, fallow and Sika, are widely distributed in Britain, and are of some ecological significance or concern to man in habitats where they are much more difficult to detect and quantify. These concealing habitats include natural and man-made woodlands, thickets of willows, gorse and broom, and even tall stands of bracken where deer can hide themselves in late summer. Information on the abundance of the deer can be important to those people involved in the management of these kinds of habitat, or of the deer contained therein. The management problem may be one of reducing animal impact (eg damage to commercially valuable trees) through animal control. Alternatively, a deer population may be considered as a potentially important secondary resource, but only when its density is below the level at which habitat damage becomes appreciable. Finally, research on the habitat requirements of deer living largely in concealment needs methods for finding where the deer occur and for what proportions of their time.

Red deer are now of special concern to those managing commercial forests in Scotland. Many of the tree species most suited to Scottish conditions are exceptionally vulnerable to damage by red deer, and the abundance of deer on neighbouring land means that plantations require the protection of deer fences (which do not always remain deer-proof!). Sudden break-ins by large groups of deer, mainly in winter, are one of the problems facing foresters. However, the deer which are most difficult to detect and eliminate are those which have become residents; these 'woodland deer' behave quite differently from any 'hill deer' which have newly broken in. The newcomers to a forest tend to remain in large groups, making for high open ground when disturbed, but established residents are more widely dispersed, making good use of available cover when necessary. Therefore, extra expenditure is required for checking the presence and numbers of deer, as well as for actually controlling them. It is generally considered that keeping all planted land completely free of deer is an impractical ideal; in most cases, the attainable objective is in keeping deer numbers low enough to minimise damage. However, this needs reliable methods for detecting and quantifying the presence of deer; foresters would find it more useful to be able to predict when and where their control efforts should be placed next, than simply to respond to sudden outbreaks of damage.

*Alternative methods*

A good deal of research has been done, elsewhere in the world, on the problem of estimating the abundance of large mammals in woodland habitats, and of finding indices of population density which are sensitive enough to reliably detect differences between areas or changes with time. There can be few, if any, potentially useful methods which have yet to be considered in principle. However, up to now, little has been done in Britain to test, compare and apply any of the most promising approaches. Existing literature provides guidance on those methods which might be applicable to Scottish conditions, as well as those which can be discounted. Amongst the latter, it seems that new technical developments in aerial survey (eg thermal imagery) do not give reliable results with animals under heavy forest cover, and they are expensive to apply. Indeed, cost is a crucial question in both the application of a method of population assessment, and in its testing. The most attractive procedures are those requiring only existing manpower and equipment.

Our second introductory paragraph outlines some of the main purposes in management and research for which population density assessments are needed. It is clear that, for some purposes, estimates of the actual size or density of a population are required, whilst, for other purposes, relative indices will suffice; the latter are likely to be less demanding of manpower than the former.

Methods of population assessment may be classed as 'direct' if they depend on animal sightings, and as 'indirect' when based on animal tracks, signs or products. 'Drive counting' and 'index counting' are the 2 most commonly used direct methods. Drive counting is very simple in concept; the idea is to flush all the deer from cover so that they can be tallied by carefully positioned observers. Although it requires many people, it may be the only effective way of getting information on the size and composition of a woodland deer population. How a count is organised depends on local conditions. For a block of unfenced woodland, the best procedure is to have several men beating their way in line through the woodland, with others as observers at suitable vantage points outside the woodland; the deer are counted as they emerge on to the open land. In enclosed woodlands, all the men are used as beaters, and they count any deer breaking back between them or any moving back along the fencelines. The main requirement is for sufficient men to disturb and detect all the deer; clearly, the beaters should not be spaced too widely.

Various kinds of index counting methods have been developed for comparative purposes; here the assumption is that standardised observations tend to detect a consistent fraction of the population. The problem with these kinds of observations is that they are much more difficult to standardise for between-area than for within-area comparisons. Nonetheless, one advantage of this approach is that it requires fewer people; a forest ranger, for example, could gather useful data (animals seen along given routes, or map records of animal sightings over defined periods) for population monitoring in the course of other work.

The tracks, signs and products (ie faeces) of animals have been used in various ways as estimators, or indicators, of their population density, each approach having its own advantages and limitations. One difficulty is that quantitative measures of animal tracks and signs usually reflect the combined effects of population density *and* animal activity, leading to questions of interpretation. Nonetheless, if such methods could be shown to work reliably in practice, then they would have value as working tools, their logical bases being of secondary interest. However, there has been a good deal of work, mainly in North America and New Zealand, suggesting that animal faeces offer a wider variety of potentially reliable methods, the premise being that there must be a reasonable relationship between the occurrence of the animals and that of their faeces.

Whereas faecal material can be quantified in several ways (eg by volume or dry weight, or, more simply, by the numbers of apparent defaecations), there have been 2 quite different approaches to the use of these measurements in population assessment. These are: (i) relating the population density of the animals to the *density* per unit area of their faeces, and (ii) relating population density to the *rate of accumulation* of faeces. Largely because of the need for rapid survey methods, the main work in New Zealand has been centred on density; in essence, a density measurement requires one visit per site, whilst a rate measurement requires 2. Moreover, marked plots are not necessary for density measurements, the 'nearest neighbour' procedure being relevant here. By contrast, most of the North American work has been concerned with rates of accumulation, possibly giving more reliable results at the cost of more effort. In fact, the 2 approaches may differ less in labour requirements than the 'visits per site' argument suggests (see below).

The measurement of faecal density derives from the assumption that, when the population of deer and habitat are in balance, there will be a steady relationship between the population density of the animals and that of their faecal depositions. This is a reasonable assumption for a steady situation, but, in reality, the decomposition rate of faecal material is likely to be the most variable factor. In consequence, deriving correction factors to remove the effects of decomposition must necessitate much extra research effort, ie getting information on how the decomposition rate varies with site and season.

As the defaecation rate (for a given species) is likely to vary less than the faecal decomposition rate, measuring the rate of accumulation of faecal material in an area seems a more reasonable way of assessing the number of animals. By themselves, therefore, faecal accumulation rates provide indices of population density for comparative purposes. However, with additional information on the defaecation rate of the species and how it varies between habitats, these indices become estimators of abundance, and hence more meaningful. One application could be in estimating the size or density of a local population, that is to say numbers of animals (per area) from faecal depositions/unit area/unit time. Alternatively, the problem may be to estimate the occupancy by animals (in, say, animal days/ha) of comparatively small areas within a larger home range.

A key problem in measuring faecal accumulation rates is in deciding the interval to allow between the initial clearance of faecal material from sample plots and their subsequent examination. The time should be short enough to minimise the effects of faecal decomposition, but long enough to economise on effort. As mammalian herbivores mostly produce a group of faecal pellets at each defaecation, the simplest (and most widely used) procedure is to count the numbers of pellet groups.

*Research in ITE*

i. *Planning*

Research on methods for assessing red deer populations in woodland habitats in Scotland began just over 2 years ago. The plan was for a 4-year project concentrating on the 2 most promising methods, ie the direct approach of drive counting, and the indirect one of using measurements of faecal accumulation rates. The main aim was to evaluate and compare these methods in fenced areas of woodland where the actual numbers of deer could be either known in advance or determined subsequently, ie either by introducing known numbers of deer into deer-free woodland enclosures, or by using enclosures with resident deer which could be shot-out later. The best test of a population estimate is by comparison with the real population value. It was anticipated that most of the research effort would be devoted to the faecal accumulation studies; drive counting is much simpler in concept, and its main problems are those of manpower organisation. It was evident also that much of the work would depend on using the facilities and co-operation of other bodies, because leasing land to set up study situations for short-term research would be unnecessarily expensive. Whilst enclosed woodlands would not be required for much of the preliminary work on the faecal accumulation method, they would be essential for comparative tests of methods. With these considerations in mind, 2 stages of research were planned:

1. A period concentrating on the principles and practicalities of the faecal accumulation method, together with making enquiries about study situations for stage 2.
2. Comparative tests of the 2 methods in a number of fenced woodland areas with known populations of red deer.

ii. *Stage 1*

The applicability of the faecal accumulation method depends on having the following kinds of information:

1. Rates of faecal decomposition in relation to habitat and climatic differences.
2. Rates of faecal output by the animals in different habitats, ie in relation to the main kinds of forage available.
3. Rates of search, and of success in finding faeces in different kinds of vegetation.
4. Ease and efficiency in identifying faeces when 2 or more herbivore species occupy the same area.
5. Whether or not defaecations are spread reasonably evenly in time; are the numbers of defaecations proportionate to the time spent by the animals in different parts of their home range?
6. As a subsidiary interest in this context, whether or not faeces can give any other useful information on the behaviour of the animals.

To this list should be added the practical considerations of sampling, eg stratification of areas, size and shape of plots, and sampling intensity.

Following captive red deer for several hours at a time, and making periodic observations on ground occupied by red deer both showed that counting separate defaecations was relatively simple. However, there were seasonal changes in some habitats, presumably due to changes in forage digestibility, in the kind of faecal material voided. In grassy habitats during summer, most depositions were rather amorphous 'dung pats' (fresh moisture content = over 80%), but, elsewhere and at other times, most depositions consisted of groups of faecal pellets (moisture content = 65-70%). Most pellet groups were compact, but a few were more strung out (due to animal movements). In practice, neighbouring groups and 'stringers' were all easy to distinguish and separate by differences in pellet size, colour and state. On average, there were 60-80 pellets/group, the smallest undisturbed groups having rarely less than 30 pellets, and the largest (usually at resting sites) 300 or more. Fresh pellets (and summer dung pats) were characterised by their slimy coating, and, in warm weather, by their attractiveness to dung flies. In dry conditions, the depositions became crusted over and very resistant to decay, but continued moist conditions allowed faster decomposition. The relative age of a deposition could be assessed from whether it was glossy and slimy (=fresh), glossy, crusted, powdering or powdered (= old). Losses of faecal material were brought about by the direct effects of rain, site moisture, invertebrates (adults and larvae of dung flies and dung beetles, and earthworms), and by fungi in dry conditions. Equally, however, faecal material could be obscured by deciduous leaves and plant litter, or be redistributed by rain, wind and snow melt. Trampling was rarely a problem, even in enclosures with large numbers of deer.

There were 2 main aims in finding rates of faecal decomposition/loss. First, there was the need to find how long plots could be left on various kinds of ground before decomposition seriously affected the rate of accumulation of faeces. Second, it was necessary to find whether there was a simple pattern in time, eg linear, negative exponential, or rate increasing with time. The mathematical form of decomposition is clearly relevant to calculating either a 'half life' for comparative purposes, or the average rate during a period from the total over that period. For decomposition tests, fresh faeces were collected at 4–6 week intervals over one year in 2 areas with captive red deer (Anancaun and Glen Saugh, described further below). These faeces were set out, within a few hours of collection, on marked plots at sites representing a variety of soil conditions, and vegetation types, ie 11 sites, 3–6 replicate plots/site, and 10–30 depositions/plot. The visible (surviving) faeces were counted and described every 2 weeks afterwards until all had disappeared. In these preliminary tests, the rates of disappearance varied greatly, with extreme irregularity in pattern. There were distinct seasonal differences, with higher rates of loss in summer and lower rates of loss in winter. The higher rates were at sites with fertile soils (eg well-grazed, herb-rich grasslands) which were rich in invertebrates, and the lowest were on acidic soils poor in invertebrates (eg heathland, bog and Scots pine sites). On rich grasslands, faeces put out in late autumn and winter mostly persisted for several months, but few of those put out in summer persisted for more than 3 months; a few of the latter disappeared within 2 weeks. By contrast, many of the faeces put out on heathland sites were still visible after a year, even from those put out in summer. The irregular patterns of disappearance, especially on good grasslands, were largely due to rainfall; persistent rainfall acting on fresh faeces led to more rapid attack by invertebrates, faeces previously dried by sunshine being much more resistant. On poorer (acidic) sites, rainfall and surface moisture led to a more gradual erosion and scattering of faecal material, such that depositions were still visible long after they had lost their original form.

Although we now know a good deal about the nutritional requirements of red deer, and much more about the energetics and nutrition of domestic ruminants (eg sheep), there is less information about the digestibilities of many of the natural forages available to red deer; and there is no information on the energy costs of movement and temperature maintenance for red deer in natural habitats. Therefore, any attempt to estimate the rate of faecal output by wild red deer, even in terms of dry matter, would be little more than guess-work; and there is no information relating the frequency of defaecation to dry matter output. We can reasonably expect the defaecation rate in individual deer to vary considerably according to sex, age, breeding status, activity, degree of thermal stress, amount and digestibility of available forage, etc. However, in population estimation, population means may be more appropriate, and these will be less variable.

For empirical information on the differences in faecal output (in terms of pellet groups/deer/day) between populations of red deer, studies were made in 2 enclosed areas which differed in vegetation type, ie one (Anancaun, Wester Ross) of grassland representing high digestibility forage, and the other (Glen Saugh Experimental Deer Farm, Kincardineshire) with a predominance of heather and a generally more fibrous type of forage. The work at Anancaun was spread over a full year to give some indication of the seasonal pattern of faecal output, and that at Glen Saugh over the late summer for a within-season comparison. At Anancaun, there were 21 red deer (rising to 29 with a new generation of calves) on 14 ha. Two separate enclosures were used at Glen Saugh: West Greenshiels with 21 deer (mostly hinds) on 8·4 ha, and Slochd with 26 deer (mostly stags) on 17·7 ha. Each enclosure was divided (by topography/vegetation) into a small number of sampling strata, and plots were distributed randomly in each stratum, using a higher sampling intensity in the most variable strata. The plots were 15 × 15 m (0·0225 ha), with a total of 41 plots (= 6% total ground) at Anancaun, and 48 (= 4·2% total ground) at Glen Saugh. All plots were first cleared of existing faecal material, and then revisited to count and clear the new depositions at 4-5 week intervals afterwards when possible; prolonged snow at Anancaun extended one period to 77 days.

*Table 1. Defaecation-rates (numbers of depositions/animal/day) of red deer in three different study situations (see text).*

| Study areas | Periods | | | Deer Stock | | | | Defaecation rates Nos/deer/day ± S.E. | Losses (%) by decomposition | Corrected defaecation rates Nos/deer/day |
|---|---|---|---|---|---|---|---|---|---|---|
| | From | To | Days | Stags | Hinds | Calves | Total | | | |
| Anancaun deer enclosure | March | April | 35 | 4 | 11 | 6 | 21 | 20·6±1·7 | 5·4 | 21·7±1·8 |
| | April | May | 27 | 4 | 11 | 6 | 21 | 24·5±1·8 | 4·0 | 25·5±1·9 |
| | May | June | 35 | 4+3 | 11+3 | (+6 new) | 21(+6) | 30·1±2·1 | 8·4 | 32·6±2·3 |
| | June | July | 28 | 7 | 14 | 7 | 28 | 26·3±1·5 | 16·9 | 30·8±1·8 |
| | July | August | 35 | 7 | 14 | 8 | 29 | 19·0±1·5 | 23·1 | 23·4±1·9 |
| | August | Sept | 35 | 7 | 14 | 8 | 29 | 15·4±1·0 | 13·3 | 17·5±1·1 |
| | Sept | Oct | 28 | 7 | 14 | 8 | 29 | 23·9±1·8 | 34·7 | 32·2±2·4 |
| | Oct | Dec | 49 | 7 | 14 | 8 | 29 | 18·2±1·7 | 3·9 | 18·9±1·8 |
| | Dec | Feb | 77 | 7 | 14 | 8 | 29 | 13·3±1·2 | 1·2 | 13·5±1·2 |
| | Feb | Mar | 24 | 7 | 14 | 8 | 29 | 18·8±2·3 | 0 | 18·8±2·3 |
| | March | April | 29 | 7 | 14 | 8 | 29 | 19·1±2·1 | 6·8 | 20·4±2·2 |
| Glen Saugh enclosures | | | | | | | | | | |
| (a) West Greenshiels | Aug | Sept | 32 | 1 | 16 | 4 | 21 | 26·6±2·2 | 4·1 | 27·7±2·3 |
| (b) Slochd | ,, | ,, | ,, | 16 | 9 | 1 | 26 | 19·1±2·7 | 3·5 | 19·8±2·8 |
| Both | ,, | ,, | ,, | 17 | 25 | 5 | 47 | 22·9±2·4 | 3·8 | 23·8±2·5 |
| Beinn Eighe woodland enclosure | May | June | 48 | 3 | 3 | 0 | 6 | 14·5±1·8 | ? | 14·5±1·8 |
| | June | Aug | 70 | 3 | 3 | (+1) | 6(+1) | 13·6±2·3 | 7·0 | 14·6±2·5 |
| | Aug | Oct | 63 | 3 | 3 | 1 | 7 | 20·0±2·1 | 9·4 | 21·9±2·3 |

Notes :— 1. Young calves (in parenthesis) discounted.
2. Losses by decomposition during periods calculated from measured losses over periods, assuming exponential rates.

The searching was done by a 2-man team, using marker strings to subdivide each plot into strips (1 · 5 m wide) for efficient coverage. Decomposition tests were done during each period in each stratum, but usually with extra visits to check the rates of loss.

Work currently in progress (in Stage 2, described below) includes further measurements of faecal output (= faecal accumulation) by a known number of red deer recently introduced into a woodland enclosure at Beinn Eighe, Wester Ross. Here, the population density is much lower (7 deer/18 ha), but perhaps more typical of some other woodland areas. Some 60 plots of 10 × 10 m (= 3 · 5% total area) are being used, once again in a stratified random layout, and they are being checked at 2-monthly intervals. Tests on decomposition are also in progress in each of the main kinds of vegetation.

The results (Table 1) show several features of interest. Those from Anancaun suggest a trend in faecal output over the year, with higher rates in summer and lower rates in winter. This kind of pattern would be expected in forage intake, with a maximum between calving (June) and when lactation begins to decline (mid-autumn), as it is well known that lactation has a much bigger effect than pregnancy on nutritional requirements. Furthermore, it could be that seasonal changes in forage digestibility (eg higher digestibility and therefore lower dry matter residue in summer) are masked by those in forage intake, thus giving the observed pattern in faecal output. Irregularities in the pattern of these results were undoubtedly caused by short-term fluctuations in the rate of faecal decomposition due to periods of rainfall; measuring the total losses *over* a period may often have given a rather poor guide to the losses from depositions made *during* that period, depending on the weather sequence.

As on other grassland sites (mentioned above) faecal decomposition was more rapid in summer than in winter, a distinct cycle of relatively high amplitude. Losses of faecal material were less at Glen Saugh and in the Beinn Eighe woodland enclosure, and therefore relatively unimportant in their effects on the apparent rates of faecal output. At Glen Saugh, the stags and hinds clearly differed in faecal output, and much larger differences would have occurred with a greater segregation of stock and with a higher (and more typical) proportion of lactating hinds; most of these hinds were still sexually immature. Nonetheless, the average for these 2 lots of deer was very similar to that at Anancaun at the same time of year. Transference of the deer into the Beinn Eighe woodland enclosure may have had a temporary effect on their food intake; they would have taken time to settle in their new environment and to adapt to a new diet. Indeed, the faecal output results show an upward trend, the last one approaching the same level as Anancaun and Glen Saugh; new results will be of considerable interest.

Taken together, these data indicate that defaecation rates (ie population mean values) are rather less variable than might have been expected, thus giving some confidence in the use of faecal accumulation measurements in population density assessment. Nonetheless, these results (ca 20 defaecations/animal/day, from autumn to spring) are appreciably higher than those published for various species of deer mainly in North America (ca 12–15/deer/day), and it is not clear whether this is for biological or technical reasons.

Faecal depositions are more difficult to detect in some kinds of vegetation than in others, and the rate of search must affect the proportion found. One problem in devising realistic tests of the effects of these 2 factors is in avoiding the extra care associated with being under test. In practice, however, we found that people achieved fairly consistent rates of search in given kinds of vegetation, so these became the standards in our tests. Vegetation was classified simply as: (i) 'Easy' (up to 30 cm deep, eg grazed grassland and well-browsed heather); (ii) 'Moderate' (around 60 cm deep, eg tussocky grassland and deep heather); and (iii) 'Difficult' (over 90 cm deep, eg bracken with deep litter or grasses). Thirty plots of 10 × 10 m were marked out on each type of ground, and 1–10 fresh pellet groups were distributed on each plot (using random pairs of co-ordinates for positions and random numbers for the amounts), taking care to give each group a realistic spread (over 150–250 cm²). The results, using a 2-man searching team and one other to put out the groups, were encouraging. 'Easy' plots took an average of 10 minutes to search (excluding time taken to count and collect the groups, ie 0·7 minutes/group), with almost 100% recovery of groups and individual pellets. 'Moderate' plots took around 13 minutes, with 86% of groups and 85% of total pellets found. On 'difficult' plots, the average time was 18 minutes, with a recovery rate of 76% for groups and 71% for total pellets. Generally, some 97% of pellets were found in those groups which were detected; it was relatively easy to recover individual pellets once a group was found. A good deal of the vetetation in woodlands and on hill land in Scotland would fall between our first 2 classes, but more towards 'easy' during the non-growing season when faecal depositions tend to lie on top of the vegetation.

Little has been done up to now on the remaining aspects of Stage 1 research. Clearly, there is some similarity in appearance between the faecal pellets of those ruminants most likely to occur together in various habitats in Scotland. Faecal pellets of red deer and sheep resemble each other to a greater extent than do those of red and roe deer. Discrimination requires studies on authentic pellets from these species in similar habitats; it is already evident that pellets of a given species can vary in form, colour and texture depending on diet. The loss of form in pellets during decomposition, and indeed the production of 'summer dung pats' in some situations are extra problems of identification to contend with in areas where 2 or more ruminants occur.

Whilst the behaviour and patterns of defaecation are related to territoriality in carnivorous mammals, this relationship does not seem to hold with large mammalian herbivores; their defaecations are much more evenly spread over the ground. Even so, our observations suggest that larger faecal depositions occur at sites of rest/rumination, and that smaller accumulations occur on feeding areas. It remains to be shown whether the numbers of faeces, or the total numbers of individual pellets (or, say, total dry weight) at given sites provide the best measure of the time spent by the animals there.

iii. *Stage* 2

This part of the project began in early May 1979, when 6 adult red deer (3 stags and 3 hinds) were transferred from the Anancaun enclosure into a woodland enclosure of 18 ha on the Beinn Eighe National Nature Reserve; a calf born in June brought the total up to 7 red deer. The 6 adults were marked with coloured ear tags so that they were easily recognisable as individuals with binoculars as a means of checking the numbers present thereafter, the calf being easily identified. Apart from being ideal for testing the faecal accumulation method in realistic woodland conditions (results discussed earlier) it is also well suited to preliminary work on drive counting. The site is on rough hill land and offers plenty of concealment for the deer, with over 60% coverage of closely-planted woodland (mainly Scots pine up to 5 m in height), and irregular patches of deciduous species, eg rowan and alder) and large patches of bracken. Much of the ground vegetation is a mixture of *Molinia* and deep heather, both providing good cover for resting deer. The enclosure is approximately rectangular in shape, 330 × 600 m in flat projection, but appreciably more in surface measurements (ca 450 × 650 m). The deer fence is in good condition.

The key problems in drive counting are those of manpower economy and control. Economy of manpower becomes more important with increasing size of area to be counted, and we need to know (for each kind of woodland) the maximum spacing of men that still allows for efficient detection and counting of deer. Spacing must also depend on the kinds of deer being considered; roe deer are more difficult to flush from cover than red deer. The other practical problem is that of maintaining the pace, direction and spacing of the line-up, a question of communication.

The difficulties of detecting red deer in this enclosure were well shown by casual observations made during other work. During visits of several hours a day, there were rarely more than 3 deer seen at a time, although up to 5 individuals might be seen in a day. It often took several days before all 7 deer had been seen; some individuals were obviously more secretive than others.

Several test counts were done in August to October, using from 5 men (spaced 75 m apart) to a maximum of 11 men (35 m apart). The widest spacings meant that neighbouring men were only visible to each other for part of the time, and, even at the closest spacing, there were times when they were out of sight. Each man was asked to note down the details (sex, age, time, and direction of deer movement) of any deer which passed between him and his right-side neighbour, and to also note down the identity of any deer seen. From these records, we could compile a tally for all deer which had been seen, and an inventory check on the individuals actually present. As expected, counts with small numbers of men tended to reveal fewer deer than those done with larger numbers, the critical point being 8 men; with 8 or more men, we usually tallied all 7 deer, but even with 5 men 5-6 deer were usually counted. In almost all counts, all the marked deer were detected, the calf being the animal most frequently missed. More counts are planned for this area, but it is hoped to repeat this kind of study in other woodland areas.

*Acknowledgements*
We thank the Nature Conservancy Council (North-West Scotland Region) for permission to work in the Anancaun deer enclosure and in Enclosure No. 9 on the Beinn Eighe National Nature Reserve, and for kindly agreeing to the introduction of red deer into the latter. We are also grateful to the Hill Farming Research Organisation and the Rowett Research Institute for approval to work at the Experimental Deer Farm at Glen Saugh.

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## RABBIT ENCLOSURES: A VIABLE SCIENTIFIC APPROACH?

*Introduction*
The density of rabbit populations depends primarily on the influence of environmental factors, both physical and biotic, acting on the reproductive potential and survival of individuals. In a free-living population, the relative importance of variables such as density, social status, individual food availability and weather is often difficult, if not impossible, to assess accurately. Furthermore, it is not sufficient merely to describe seasonal events: what is needed is a fundamental understanding of the underlying mechanisms which control these events. In order to understand the influence of each environmental variable on reproductive output, growth and puberty in young animals, captive wild rabbits (Cover photograph) are being studied in an enclosure erected on a 0·81 ha site at Monks Wood and subdivided into 46 separate pens (see ITE Annual Report 1978, Plates 10 and 11 for pictures of enclosure). Within the enclosure, animals can be kept (i) in isolation from social contact, (ii) in single family units, and (iii) in colonies of different densities: a methodical investigation of the effects of individual variables can then be undertaken. Only in the final analysis will the relative importance of each environmental factor be realised, but this approach will provide the information necessary for understanding how breeding success of a rabbit population is regulated. In addition, a free-living rabbit population is monitored and its population dynamics determined so as to allow direct comparison with the enclosure studies.

In any enclosure study, it is important to ensure that (i) the animal reacts 'normally' to its environment, and (ii) food availability is similar inside and outside the enclosure. To determine 'normality' in our enclosed rabbits, several parameters of body function were compared with those from shot samples, or from tagged rabbits in an adjacent free-living population. Breeding success and growth of young rabbits were also determined for animals maintained at 3 different levels of nutrition.

*Experimental approach*
Wild rabbits, captured in November or December 1978 at Monks Wood Experimental Station, were paired and subjected to one of the following feeding regimes, (i) Treatment 1: where rabbits had access to 150 $m^2$/rabbit of naturally occurring pasture (7 replicates); (ii) Treatment 2: where rabbits had access to either 42 or 50 $m^2$/rabbit of naturally occurring pasture (12 replicates); and (iii) Treatment 3: where rabbits, in addition to having access to 50 $m^2$/rabbit of pasture, were also freely provided with commercially available rabbit pellets (11 replicates). Treatment 3 was not started until March 1979. Adults were examined monthly to determine body weight, pregnancy and lactation in the female, and the length and width of the testis in the male. Litter size, data of littering and survival were determined for each pen, all young rabbits being removed at 4–5 weeks of age. Post-mortem data on rabbits shot within 30 km of Monks Wood provided information on seasonal changes in ovulation and testicular size, while information on the duration of the breeding season, growth and survival of the young and changes in adult body weight were obtained from studies of the free-living rabbit population. These free-living warren rabbits numbered 74 adults (49 females, 25 males) in January, reducing to 46 adults (29 females, 17 males) by the start of the breeding season in April. A peak population of 39 adults and 79 weaned young was observed in June.

*Results*

Seasonal change in body function:

(a) Body weight

The body weights of female rabbits during the breeding season are greatly influenced by the reproductive state of the individual. At term, each embryo can weigh as much as 40 g, while hypertrophy of mammary tissue in lactating females can mask any real change in body weight. Weight changes of females were therefore difficult to interpret in the absence of other information on reproductive state. Seasonal fluctuation in body weights of male rabbits was studied both within the enclosure and in the free-living population. Both groups lost weight between late autumn and spring, but thereafter gained steadily. The 3 treatment groups within the enclosure each showed a similar pattern of body weight change and the provision of supplementary commercial rabbit pellets did not significantly improve body condition at any time.

(b) Male fertility

At the height of the breeding season, in May, the testes reached their largest size of about 4 g. They then regressed steadily to reach a minimum weight of 2 g in October. Both in 1978 and 1979, the testes grew significantly between October and November. This growth occurred at a time when a significant increase in the incidence of vaginal sperm, indicative of copulation, was observed in another wild population (Brambell 1944). Since it was impracticable to kill the rabbits in the enclosure, the volume of the testes was determined at regular intervals. More subtle changes in testicular size could be identified by this method when the same individual was examined on several occasions (Figure 1). In these rabbits, testicular regression occurred in 2 phases between May and mid-October. As described for the shot samples, growth of the testes occurred from mid-October onwards. Changes in the circulating levels of the steroid and gonadotrophic hormones are not described in this report.

(c) Breeding system

In the free-living population, only a few animals had conceived by March, and it was not until April that 50% or more of the does were pregnant (Figure 2a). The peak in pregnancies was in May and thereafter the proportion of females that were pregnant fell steadily so that only 2 of 22 does were pregnant in August. A similar breeding pattern was observed for the enclosure rabbits. Breeding was again delayed until April, but, unlike the free-living population, breeding was virtually over by June and only 5 of 52 does were pregnant in

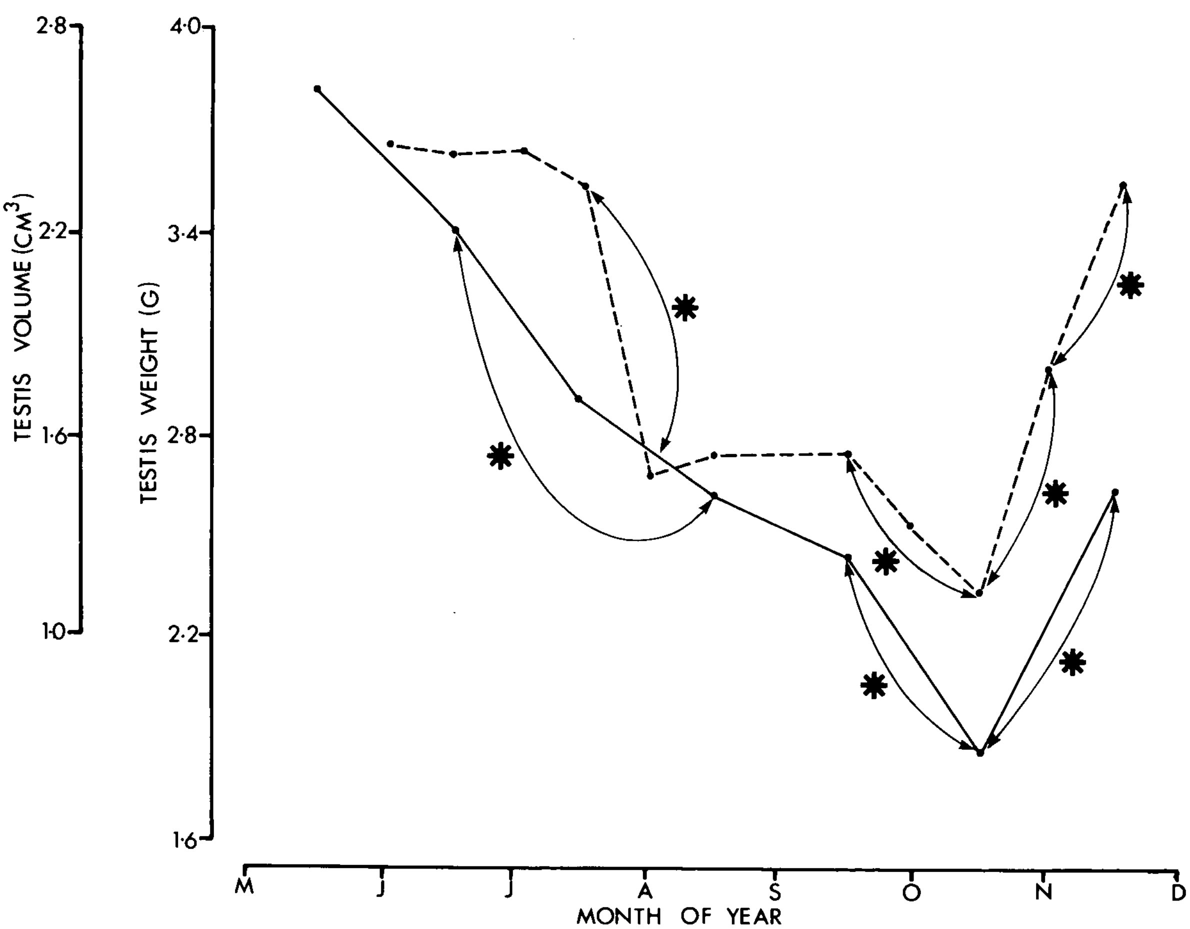


*Figure 1 Seasonal change in the main testicular weight (solid line) for rabbits shot during 1979 in the vicinity of Monks Wood is compared with the change in the mean testicular volume (broken line) for 15 bucks kept in the enclosure for the period May—November.*

*(* denotes significant differences between the connected points)*

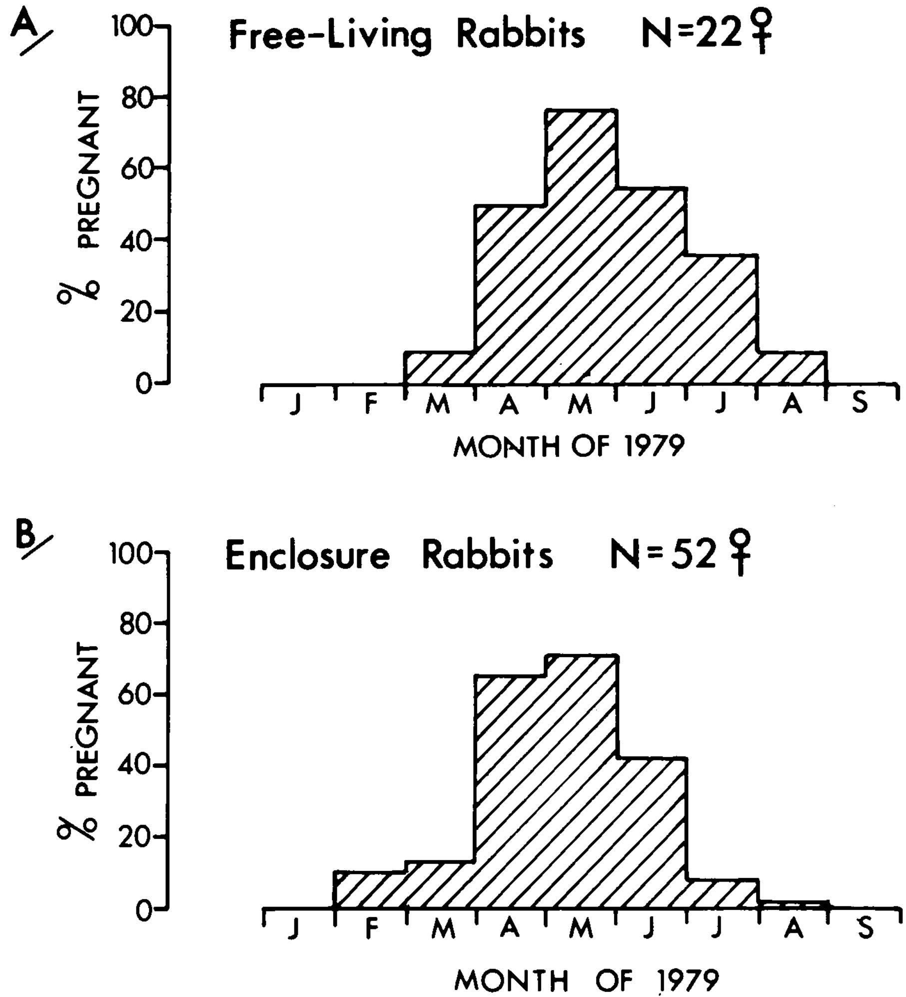


*Figure 2 Histogram showing the percentage (A) of 22 females regularly trapped from the free-living population and (B) of 52 females kept in the enclosure for the period January—September.*

July (Figure 2b). A closer examination of these results revealed that the breeding season differed in the 3 treatment groups. In Treatment 1, where the animals had access to 150 $m^2$/rabbit of pasture, breeding started significantly earlier that in the other 2 treatments with access to only 42 or 50 $m^2$/rabbit of pasture. Breeding in Treatments 1 and 2 stopped abruptly in June, which may have reflected a deterioration in the pasture at this time, whereas those in Treatment 3, now provided with additional pellets, continued breeding until July.

*Breeding success within the enclosure*

During the 1970 breeding season, more than 500 rabbits were born to 52 females. The mean interval in weeks between the first and last conception was significantly shorter in rabbits that had access to only 42 or 50 $m^2$/rabbit of pasture (Treatment 2, Table 2). No difference in the duration of this breeding period was observed between Treatments 1 and 3, perhaps because of the delay in introducing pellets to the rabbits in Treatment 3. The shorter breeding season observed in the Treatment 2 group did not result in reduced fecundity, as, when compared with the other pasture only group (Treatment 1), the total number of births and the number of litters per enclosure were similar. Among the animals that were supplementarily fed with commercial rabbit pellets (Treatment 3), both the young/female/enclosure and the number of litters/female/enclosure were significantly greater than in animals that were not provided with extra food. The size of the litters did not differ between any of the 3 treatments. Hence, the breeding success of an individual appeared to be related to its level of nutrition such that, when food was plentiful, more litters were born per unit time.

Figure 3 compares the number of ova released per ovulation determined from shot rabbits with the number of births in the enclosure. Post-mortem examination of 48 shot pregnant does between March and August 1979 revealed that 5·24 ova were released per pregnancy compared with a mean litter size at birth of only 4·03 for 118 litters observed in the enclosure. Differences in the size of litters between ovulation and birth could result from (i) failure of ova to be fertilised or to implant, (ii) pre-natal mortality of implanted embryos, and (iii) poly-embryony or polyovular follicles resulting in more than one embryo developing from one ovum or from one follicle, ie twins. Pre-natal mortality has been extensively studied by Brambell (1942) who demonstrated that about 60% of all litters were entirely lost under conditions of high population density. In low density populations examined by Lloyd (1963),

*Table 2* Effect of different treatments on the duration of the breeding season, frequency of littering, litter size and total young for the 1979 breeding season

| | Mean Duration of breeding season (weeks) | | Mean No. Young/♀/ enclosure | | Mean Litter size | | Mean No. Litters/♀/ enclosure | | Litters/♀/ enclosure / Duration breeding | |
|---|---|---|---|---|---|---|---|---|---|---|
| Treatment 1: (Pasture only 150 m²/rabbit) | 17·4 | (7)[a] | 9·8 | (7)[a] | 4·2 | (49)[b] | 2·3 | (7)[a] | 0·14 | (7)[a] |
| Treatment 2: (Pasture only 42–50 m²/rabbit) | 11·6 | (12)††† | 7·9 | (12) | 4·0 | (36) | 2·0 | (12) | 0·17 | (12) |
| Treatment 3: (Pasture and pellets 50 m²/rabbit) | 15·1 | (11)** | 11·8 | (11)* | 3·8 | (33) | 3·0 | (11)* | 0·21 | (11)† |

[a], (number of replicates) ; [b], (number of litters)
†, $P<0·05$ ; †††, $P<0·001$ ; significantly different (Student's t-test) from Treatment 1
*, $P<0·05$ ; **, $P<0·01$ ; significantly different (Student's t-test) from Treatment 2

*Table 3.* Differences in litter size and pre-weaning mortality between the first and subsequent litters for 2 groups of rabbits, one having access to 50 sq m/rabbit of pasture only and the other having access to 50 sq m/rabbit of pasture plus commercial rabbit pellets.

| | 1st litter | 2nd litter | 3rd litter | 4th litter |
|---|---|---|---|---|
| Pasture only : | | | | |
| Mean litter size | 2·6(5)[a] | 5·0(5)* | 4·0(2) | |
| Number of young | 12 | 25 | 8 | |
| Number dead prior to weaning | 10 | 3 | 5 | |
| Percentage pre-weaning mortality | 83 | 12 | 63 | |
| Pasture + pellets : | | | | |
| Mean litter size | 3·6(7) | 3·6(7) | 4·8(6) | 5·0(2) |
| Number of young | 26 | 25 | 29 | 10 |
| Number dead prior to weaning | 14 | 8 | 6 | 5 |
| Percentage pre-weaning mortality | 54 | 32 | 21 | 50 |

[a] mean ± S.E. (number of litters)
* $P < 0·05$ significantly different (Student's t-test) compared to the size of the first litter.

no loss of entire litters was detected, although a high proportion of litters did show some loss, which amounted to about 15% of all ovulated ova.

The post-mortem data for the period April-August suggest that the number of ova released per ovulation was constant (Figure 3a). Differences in the size of litters born in the enclosure over the same period may, therefore, represent monthly changes in the incidence of pre-natal mortality, this being high in April/May, but significantly lower in June/July (Figure 3b). In this respect, it was noted that animals with restricted access to only 42 or 50 m²/rabbit of pasture had significantly smaller litters early in the breeding season than animals with access to 150 m²/rabbit.

In addition to providing information on monthly changes in litter size, the enclosure study provided a unique opportunity to compare differences in litter size and pre-weaning mortality between the first and subsequent litters for individual does (Table 3). Twelve pairs of rabbits were each penned in 100 m² enclosures, and 7 of these enclosures were provided with additional commercial rabbit pellets. Only 2 of the 5 does in the 'pasture only' treatment littered 3 times, while 6 of the 7 does provided with additional pellets littered 3 times and 2 littered 4 times. Generally, litter size increased with successive litters, and pre-weaning mortality was greatest in the first and last litters.

*Survival of young rabbits*

The enclosure provided an opportunity to study the survival of young animals in a predator-free environment and to compare their survival with that of young in the free-living population. Young animals were penned at 4 or 5 weeks of age, 3 or 4 to a 100 m² enclosure, and some were also provided with additional rabbit pellets. As can be seen in Figure 4, over the 100-day period between June and September, 84 young rabbits in the free-living population declined to 8. Over the same period, 25 of an original group of 34 rabbits survived in the enclosure. Both predation and dispersal could adversely affect the free-living population, but, as

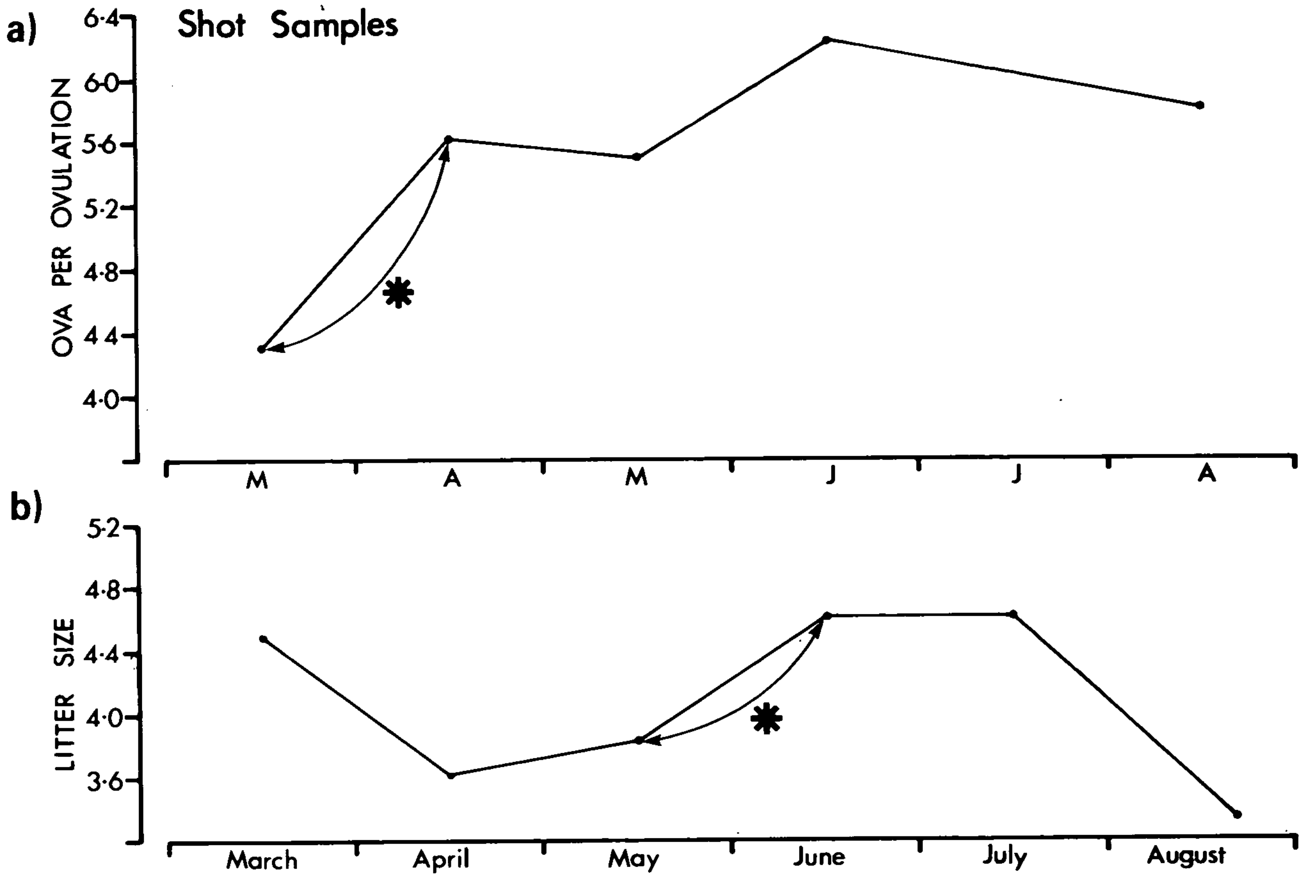


*Figure 3. The mean number of ova released per ovulation (a) for rabbits shot in the vicinity of Monks Wood is compared with the mean litter size at birth (b) for the does in the enclosure for the breeding period March—August. Results for the enclosure study are expressed as the mean litter size for all births examined.*
*(* denotes significant differences between the connected points)*

dispersal does not appear to be of any great significance in the rabbit (Southern 1940), the most likely cause of difference between the 2 study groups was predation. These observations support the conclusion of Gibb *et al.* (1978) that predation has a considerable effect on free-living rabbit populations.

Studies on pre-weaning mortality were feasible only within the enclosure, where every birth was accurately recorded (± 3 days) and the fate of each individual determined. Apart from an unexpected drop in May, survival improved steadily from a low of 25% in March to a high of about 80% in June-August. Comparison of the 3 treatment groups suggested that pre-weaning mortality was not related to the level of nutrition, but was more likely to be influenced by the prevailing weather, especially rainfall. During May, survival of young in Treatment 3 was very poor, at about 6%, despite the addition of supplementary pellets to the parents of these animals. This high mortality in May coincided with a period of heavy rain resulting in wet nesting material and death from exposure.

*Growth of young animals*

Young animals of known age (± 3 days) born in the enclosure were penned in groups of 3 or 4 in 100 m² pens, some of which were freely provided with rabbit pellets. Body weights and tibia lengths were recorded every 14 days. Growth of young rabbits in the free-living population was recorded regularly for comparison. As it was not possible to age accurately the free-living rabbits, a group of 4 individuals which were all of the same weight (240–280 g) and which were caught for the first time on the same day—6 June—were assumed to be of the same age (± 3 days).

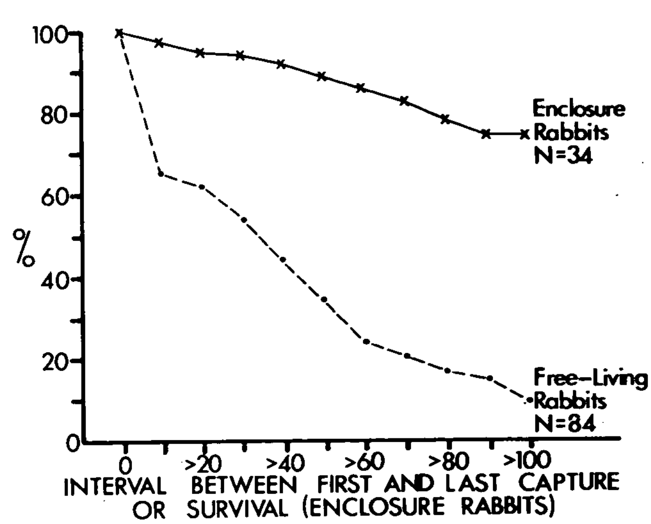


*Figure 4 The survival of 84 young free-living rabbits (broken line) is compared with the survival of 34 young rabbits kept in the enclosure (solid line). The results are expressed as a percentage of the original group size (ie 84 and 34) known to be present for each 10-day period.*

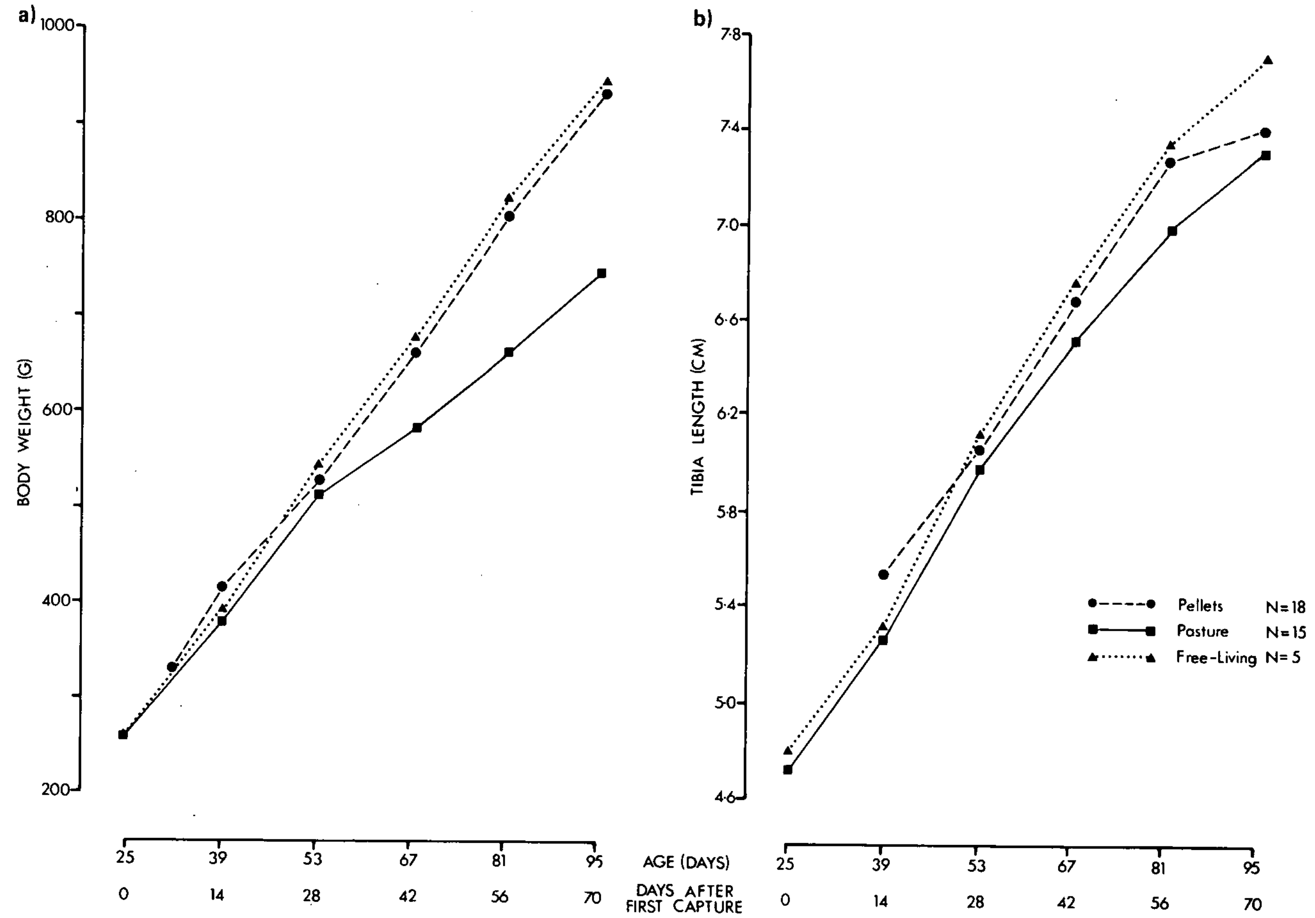


*Figure 5. Changes in (a) mean body weight and (b) mean tibia length are compared for 18 young rabbits provided with commercial pellets (●, broken line) 15 young rabbits with access to pasture only (■, solid line) and 5 rabbits from a free-living population (▲, dotted line). The abscissa show age in days for the enclosed rabbits and days after first capture for the free-living rabbits.*

Southern (1940) states that young rabbits emerge at 21 days, so it was also assumed that these rabbits, first caught on 6 June, had emerged then for the first time. Growth, as indicated by body weight and tibia length, was similar in the free-living rabbits and the enclosure rabbits that were provided with unlimited food (Figures 5a and b). In the group of animals with access only to pasture, body weight gain was reduced after 53 days of age and by 67 days the difference between the 'pasture only' and the pellet-fed rabbits was statistically significant. Difference in tibial growth between the 2 enclosure groups was significant only after 81 days of age, and only at 95 days did the pasture only group differ significantly from the free-living population. In line with many other studies on mammalian body growth, a structural parameter, such as bone length, appeared to be a better indicator of growth than body weight.

## *Conclusions*

To have control of some of the environmental variables is a great asset in any study on population dynamics. An enclosure, such as the one we have at Monks Wood, provides just such an opportunity, because density, social structure and food availability can easily be regulated. For all the parameters studied, eg breeding season, growth of young, seasonal cycles of fertility, etc, rabbits within the enclosure responded in an identical manner to free-living rabbits at Monks Wood and in nearby areas. The ability to handle rabbits at will, to manipulate food availability, so as to alter fecundity, growth and puberty, to collect regular blood samples for hormone assays and accurately monitor breeding and survival has great potential, which will be exploited in the coming years.

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## THE EXTINCTION OF THE LARGE BLUE AND THE CONSERVATION OF THE BLACK HAIRSTREAK BUTTERFLIES (A CONTRAST OF FAILURE AND SUCCESS)

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

The autecology of 7 species of British butterfly has been studied by staff of the Institute. All are rare or local insects, and one aim of the research has been to understand the requirements of each well enough for us to advise conservationists of which measures, if any, should be taken to conserve viable populations.

The contributions that 2 of these studies have made to the conservation of their subject are summarised in this report. One, involving the large blue butterfly *Maculinea arion* L. must be classed as a failure because this species became extinct on its last known British site in 1979. The other, involving the black hairstreak butterfly *Strymonidia pruni* L., has produced results that are sufficiently encouraging that this species is to be classified as 'out of danger' in the forthcoming Red Data Book for British Insects.

*The Large Blue Butterfly*

The large blue is an unusual butterfly that possesses a specialised life cycle. Eggs are laid on thyme *Thymus drucei* flowers which the young larvae eat, but older larvae are carried by red ants *Myrmica* spp. into their underground nests, where the butterfly lives for 9 months and feeds on ant grubs. The large blue has always been a great rarity in Britain and has been in decline for at least 100 years. By the early 1950's, it was still known from 30–40 sites, but only 4 of these colonies survived the next 10 years. These then became extinct in 1969, 1970, 1973 and 1979.

Many attempts have been made to save the large blue over the last 50 years. Unfortunately, these attempts were unsuccessful, and populations declined as rapidly on nature reserves as they did elsewhere. By 1972, it was clear that the particular requirements of this species had not been guessed correctly, and a research programme was started by the then Nature Conservancy to investigate its ecology. This research continued as an ITE project which was funded in some years by the Nature Conservancy Council (NCC).

The main research was an analysis over 5 years of the factors causing annual changes in numbers in the colony on the last site. The survival of individuals in different parts of the site, which had different habitat conditions, was also studied. In addition, the extinction of the penultimate British colony was observed, and research was made into the distribution, status, local races, life cycles, and behaviour of the butterfly. Finally, an analysis was made of the habitat of all former and existing sites.

This research revealed that the large blue had more particular and slightly different requirements than had been thought. These are summarised in the ITE Annual Report for 1976. Briefly, a population of this butterfly can only be supported on a site that contains high densities of *Myrmica sabuleti* nests, distributed over at least one ha of grassland. A large number of nests is needed because few can support more than one butterfly each. Thyme need not grow abundantly on the site, but must be sufficiently well distributed for most ants' nests to contain at least one flowering plant within their foraging ranges.

Experiments were made to discover how these conditions might be created and maintained. It transpired that heavy grazing of the site to produce a sward of about one cm high resulted in the required density of *M. sabuleti*, and that another species of *Myrmica*, *M. scabrinodis*, predominated under a regime of lighter cropping. Ant numbers may change very rapidly, as exemplified by a trial in which dense scrub was burned and the ground was then grazed heavily, except for one 6-month period (Figure 6). The thyme flourishes under both regimes, and the large blue will lay eggs on flowers in either ant species' territory. However, the mortality of larvae in *M. scabrinodis* nests is about 5 times higher than with *M. sabuleti*, and it is most unlikely that a colony of the large blue could survive on sites where *M. scabrinodis* predominates. If sites are left ungrazed for long, both species of *Myrmica* decline rapidly. Thyme is also lost, but at a much slower rate.

The analysis of the habitat of extinct colonies revealed that about half had been destroyed by fundamental changes in their management, such as by ploughing, and that all others were grazed so lightly and spasmodically, if at all, that none had enough nests of *M. sabuleti* to support a colony of the butterfly. The last wave of extinctions of the large blue occurred after myxomatosis reduced rabbit populations in the 1950's, when the changing economics of agriculture also gave an increasingly poor return from grazing 'unimproved' sites to the required intensity. Thus, the specialised conditions needed by this butterfly were unlikely to be produced as a by-product of agriculture after the mid-1950's, and its survival as a British species was only likely to occur on nature reserves. This combination of circumstances was suspected at the time and management agreements were obtained on the 4 last sites, of which 3 were obtained as nature reserves. Unfortunately, the need for high densities of *M. sabuleti* and its dependence on close cropping were not appreciated until after the research programme, and large resources were spent on different conservation measures that are now known to have been largely irrelevant to this insect's needs.

By 1975, the large blue existed as one small population, but enough was known of its requirements for conservation proposals to be made. The last site was still being well grazed, and the habitat was such that a small increase in numbers was predicted for most years from a knowledge of the population dynamics of this

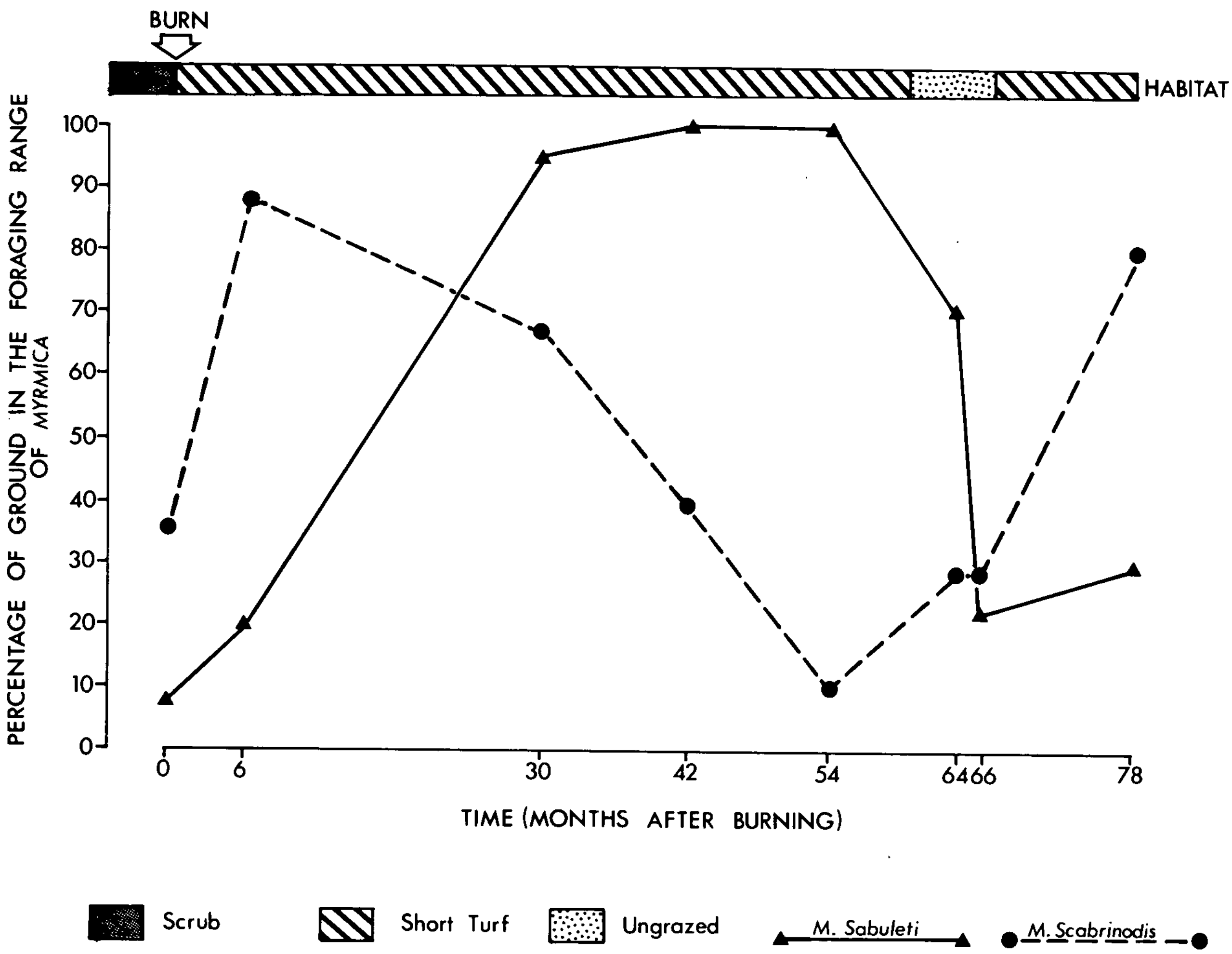


*Figure 6. Changes in status of* Myrmica *following management on a large blue site.*

species. Such an increase did indeed occur on this site in each year from 1964 to 1973. However, it was also clear that the carrying capacity of this site was low and that the largest population it could support might still be too small to withstand any occasional series of adverse effects.

Conservation measures were started with the aim of decreasing the numbers of *M. scabrinodis* and of increasing *M. sabuleti*. It was hoped that this would increase both the survival of larvae and raise the upper limit of the butterfly that could be supported on the site. The main operations were:

1. To burn encroaching scrub on the original breeding areas more regularly than hitherto, which results in an increase of *M. sabuleti* at the expense of *M. scabrinodis*.

2. To introduce thyme to areas where it was missing, but where high densities of *M. sabuleti* occurred. Such areas were already being colonised naturally, but a significant cover would have taken several decades to develop.

3. To create additional breeding areas on nearby land that was dominated by scrub by (i) burning or cutting the scrub, (ii) heavily grazing the clearings, (iii) introducing thyme so that there was one plant per *M. sabuleti* nest, once this ant had colonised these areas naturally.

These operations were producing successful results by 1977, summarised in Table 4. The ratio of *M. sabuleti* to *M. scabrinodis* nests increased from 1·2:1 in 1974 to 7·3:1 in 1978 on the original breeding areas, and similar densities developed in the nearby areas at the rate shown in Figure 6. Thyme has been established in the territory of about 1 000 of these nests, although there is scope for at least another 5 000 plants. Overall, the carrying capacity of this site has already been more than doubled, assuming that these new areas are equally suitable for the butterfly. There is evidence that this is so, although some of the figures on which this assumption is based are rather small (Table 4). Thus, in 1977, egg numbers were slightly higher in new areas than in the old, and the survival of eggs and of larvae on thyme was about the same in both areas. Survival in *M. sabuleti* nests was estimated to be nearly twice as high in new areas in 1978, although the difference between the areas is not statistically significant.

If this analysis of the large blue's requirements is correct, why then was it not saved by these measures? To answer this question, it is necessary to consider the population dynamics of this last colony since 1973.

*Table 4.* A comparison between the original breeding areas of the large blue butterfly and new habitat, created by conservation measures.

| | | ORIGINAL BREEDING AREAS | NEW BREEDING AREAS |
|---|---|---|---|
| 1. | Approximate number of flowering thyme plants in 1978. | 1500 | 1000 |
| 2a. | Status of *Myrmica* in 1978. a. Percentage of thyme plants in the territory of any *Myrmica* spp. | 100 | 100 |
| 2b. | Ratio of *M. sabuleti* to *M. scabrinodis* nests. | 7·3:1 | 6·1:1 |
| 3. | Approximate carrying capacity of each area in a typical year (number of adult large blues). | 300 | 400 |
| 4. | Mean number of large blue eggs laid per plant in 1977. | 0·078<br>0·347 SD | 0·177<br>0·654 SD |
| 5. | Percentage survival of eggs in 1977 (initial number in brackets). | 92 (26) | 93 (28) |
| 6. | Percentage survival of larvae on thyme in 1977 (initial number in brackets). | 59 (22) | 61 (26) |
| 7. | Percentage survival of large blues in *M. sabuleti* nests in 1978 (initial number in brackets). | 27 (33) | 52 (25) |

Numbers had been increasing for some years before this, but in that year they exceeded the carrying capacity of the site. Severe overcrowding occurred when larvae entered ants' nests, which caused unusually heavy mortalities; in one extreme example, about 40 larvae entered one nest and all died, almost certainly from starvation. As a result, the population was reduced from about 300 adults in 1973 to about 100 in 1974. If only the capacity of the site had been enlarged before then, these mortalities would have been much reduced because the larvae would have been spread more thinly through the additional areas. If this had been so, estimates suggest that the population would probably have increased slightly in 1974 instead of being reduced to one third of its previous size.

This decline would not normally have been serious because the population would be expected to recover in most years. Unfortunately, before this could occur, severe droughts in 1975 and 1976 had a further catastrophic effect on the colony and the population fell to about 16 adults by 1977. Extreme summer drought may greatly reduce egg-laying and the ability of an ant's nest to support the butterfly's larvae, but similar harmful droughts have occurred only about once every 25 years in the present century up to 1975. It was unfortunate, therefore, that droughts should occur in 2 consecutive years when the population of the large blue was already low. A similar decline would still have occurred if conservation measures had been taken prior to 1973, but the initial population would possibly have been more than 3 times greater, and a population of over 50 adults might have survived these unusual weather conditions.

By 1977, the site had been improved for the butterfly, but the population was so low by then that it was also subject to chance factors. For example, by ill chance, probably only 5 (possibly 6 or 7) of the estimated population of 16 adults in 1977 were females, though there are usually equal numbers of both sexes. Furthermore, at least one, and probably 2 females failed to pair because all the earlier-emerging and short-lived males had already died. Thus, only about 25% of the 1977 population started the adult period as fertilised females, instead of the usual proportion of about 50% when numbers are higher. At this point, the colony was only likely to survive if 1977 had been a particularly 'good' year. In fact, both egg-laying and the survival of larvae were slightly, though unexceptionally, lower than usual.

It was predicted that even fewer adults would emerge in 1978 and that these would be so liable to chance effects that any natural recovery of the population was rather unlikely. The NCC therefore commissioned ITE to rear the adult, egg, and early larval stages of the 1978 population in captivity in a once-for-all attempt to raise numbers to a viable level. This was an unpredicted operation, but it proved fairly successful. Only 2 females emerged that year, of which one was mated. From her, 59 larvae were introduced to *M. sabuleti* nests on the site. This was 2 · 5 times the average number expected in the wild if both females had paired: longevity figures for this species and the extended emergence of the 5 adults of 1978 suggest that there was a less than 50% chance of one female mating, through no male being alive at the critical time, and only a 7% chance that both would have paired.

It was predicted that adult numbers in 1979 would be greater than in 1978 but would probably still be below the level where the population would be viable. The breeding programme was therefore repeated in a second attempt to achieve this level. Unfortunately, although 22 adults emerged, these failed to pair and the population became extinct. The reason for this failure is not understood, although it is not thought to have been caused by inbreeding. The pairing of butterflies in captivity is always unpredictable and, sadly, was unsuccessful on this occasion. This risk was recognised, but it was considered to be less likely than the high probability of extinction in the wild.

In retrospect, it is clear that the large blue could have been conserved as a British insect had the reasons for its decline been identified and rectified at an earlier date. Sufficient resources to save several colonies were available in time, but the wrong measures were taken through ignorance of its full requirements. The last colony was lost for different reasons, because the site, though well maintained, was too small to support a large enough population to withstand a very unusual sequence of adverse events. It is likely that, if the measures that were taken after 1975 had been made 4 years earlier, the population would have been large enough to survive the abnormal drought.

*The black hairstreak butterfly*

The black hairstreak is a rare butterfly that is confined to a few forest remnants in the east Midlands, although its larval foodplant, blackthorn *Prunus spinosa* L., is a common shrub throughout lowland Britain. Only a small research effort has been made of its requirements, yet enough has been learnt to discover that this, too, was a declining species that was unlikely to survive without specific conservation measures. Unlike the large blue, it is believed that enough is now being done to save this species.

The project began with a survey of sites in 1969. At that time, only 12 colonies were known to the Biological Records Centre, and BRC's files provided a list of amateur entomologists who proved willing to search for this inconspicuous butterfly. Several new colonies were discovered, and, by 1973, a list of 59 former sites had been compiled, of which about 30 still supported colonies.

Surviving populations were crudely classified into 'large', 'medium', or 'small' colonies and the breeding areas and management of most were analysed and compared with the situation found on sites where the butterfly was now extinct. As a result of this analysis, and of research into the behaviour of the species, it was possible to define the conditions in which colonies could survive. Colonies may live in a wide range of situations, but large populations are invariably associated with high densities of *P. spinosa* growing in sheltered, unshaded woodland. Most colonies were restricted to small discrete breeding areas which occupied a small fraction of the woods in which they occurred. These were vulnerable to destruction by forestry operations, which accounts for all known extinctions of the butterfly. However, if the breeding areas remain intact, a colony can tolerate drastic changes, such as clearfelling, to the rest of its wood.

The black hairstreak was found to be a sedentary species that breeds in the same small areas for many years, and is extremely slow to colonise new habitats if these develop elsewhere. It was clear that colonies were being destroyed by modern forestry at a greater rate than that at which they were spreading to new areas, although suitable habitat was still being produced on some sites. Fortunately, the low powers of dispersal and the ability to survive in small isolated populations make this species relatively easy to conserve. In the medium term, it has been sufficient to identify existing breeding areas and to ensure that they are not destroyed. This may enable the colony to survive for up to perhaps 50 years before the breeding area becomes unsuitable, during which time there is a reasonable chance that suitable habitat will have developed nearby and have been colonised. These measures had already been taken before the research programme was started.

More positive measures have been proposed for colonies on nature reserves. On some sites, an attempt is being made to generate new breeding areas near existing colonies, in order to produce ideal conditions for large populations and continuity of habitat. The initial results are encouraging, although it is too early to know whether the butterfly will occupy and increase in these new areas. However, there are grounds for optimism. In 1973, no known colony occupied habitat that matched the synthesis of its ideal requirements, but an example of these conditions was found about 100 km away from the east Midlands. The site was used as a model for management in Monks Wood in 1973. By chance, this site was only 2·5 km from a wood in which the black hairstreak had been successfully introduced about 20 years previously, but which had been clearfelled in 1961. Evidently, the population had spread to an intermediary wood, for it was found on the model site in 1975. Once there, the population increased rapidly, and by 1978 this site supported the largest colony that has been known in Britain for many years. Similar increases will not necessarily occur on nature reserves, but the outlook is promising.

The survival of the black hairstreak as a British insect seems to be fairly safe, although many unprotected colonies will probably be destroyed. Recommendations based on this research programme have been made to the NCC and other conservation organisations, and, by 1979, 12 of Britain's 30 colonies occurred on nature reserves or in woods for which conservation agreements have been made, and positive management to encourage this species is occurring on a few of these reserves.

*Conclusions*

Research into the ecology of the large blue and the black hairstreak butterflies has shown that the habitat conditions needed to support a population of either species are rather specialised and were unlikely to be guessed from our previous knowledge of each insect's biology. Nowadays, suitable conditions for both butterflies are rarely produced as a by-product of commercial land management and, as a result, both species have declined.

Considerable efforts had been made to conserve these insects before the research programmes were started, and both have been well represented on nature reserves. This action has almost certainly saved some colonies of the black hairstreak, although their long-term survival was in doubt because new breeding habitat was not being generated on reserves. This situation is now being remedied on a few sites. Research has also shown that the needs of a colony are not necessarily incompatible with modern forestry provided a few precautions are taken. As a result, it is believed that the population on nature reserves will be supported by several colonies in private woods. The large blue occupies a more ephemoral habitat and the mere acquisition of nature reserves was insufficient to protect colonies, even in the short term. This fact was recognised long ago, but guesses as to how sites should be managed proved to be incorrect. Suitable measures were revealed as a result of research, but this research was only started when the butterfly had declined to 2 colonies, which had a total population of under 300 adults. It is probable that the large blue could have been saved with the resources that were available for its conservation, but, by the time its needs had been discovered, recommendations had been implemented, and these had produced satisfactory results, the butterfly had already declined to an irretrievable level.

It is believed that similar research could contribute to the conservation of other declining British insects. So far, the record of conserving butterflies on nature reserves is rather poor and there are several examples of unusual species being lost. Other butterflies have flourished on reserves, but the reasons are usually unknown. It is generally recognised that sites need particular forms of management if colonies of many of the more interesting species are to be conserved, and studies of the large blue and the black hairstreak suggest that research is needed to identify the best methods. These studies also show how much more successful conservation is likely to be if a species is studied before it has declined to a critical level. Timely research is likely to be easier, quicker to produce results, and consequently cheaper.

*J. A. Thomas*

## A CONCEPTUAL APPROACH TO PLANTS AS A RENEWABLE SOURCE OF ENERGY, WITH PARTICULAR REFERENCE TO GREAT BRITAIN

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*Introduction*

The world's energy balance is a matter of grave concern. Whereas total energy requirements are increasing, fossil energy resources, derived from plants which existed millions of years ago, are being depleted. Furthermore, the land area available for plant growth (primary production) has decreased dramatically during the present century. Recently, North Sea oil has bridged the gap between energy use and production in Great Britain, but this is a limited and non-renewable resource. For the future, nuclear energy sources may fill the gap, but their development is potentially hazardous, and the exploitation of nuclear fuel is also energy-intensive. In contrast, by using plants, which are primary producers and renewable sources of energy, we would be utilising a versatile and harmless energy-capturing system, making use of a constant and inexhaustible energy source—the sun.

In order to evaluate the potential contribution of energy gained from plants to British national energy requirements, the Department of Energy initiated a 'Fuels from biological materials' research programme administered by its Energy Technology Support Unit (ETSU) at Harwell. Initially, the programme consisted of 11 one-year desk studies commissioned from a variety of institutions on the energy potential of different arrays of plants (agricultural crops, single stem trees, coppice, natural vegetation, aquatic species, and species of derelict land), on different chemical conversion processes (anaerobic digestion, fermentation to alcohol and thermal processes), together with (i) a desk study of potential primary production in Great Britain, and (ii) a study of the linking of plant production with chemical conversion via transport systems and other infrastructures. ITE was given responsibility for 'Carbon as a renewable energy resource in the UK—conceptual approach' (Callaghan *et al.* 1978) and 'An assessment of natural vegetation as a renewable energy resource' (Lawson & Callaghan in prep). To assess the possibilities of using freshly-grown plants as renewable sources of energy within Great Britain, estimates were made of actual, as well as potential, primary production by a variety of species and plant assemblages.

*Rates of primary production within Great Britain*

The theoretical maximal rates of dry matter production in Great Britain vary from 89 t $ha^{-1}$ $yr^{-1}$ in the north of Scotland to 134 t $ha^{-1}$ $yr^{-1}$ in Cornwall, assuming a maximum photosynthetic efficiency of 5·5% (Hall 1979). However, these rates are never achieved in practice because of limitations imposed by environmental factors and the innate inefficiencies of many plant species. It was, therefore, appropriate to consider actual rates of primary production (ie dry matter yield), and then to investigate ways of improving efficiency in

*Table 5.* A summary of plant biomass production measured in the United Kingdom.

| *Vegetation Type* | *Species* | *Locality* | *Annual Production* ($t\ ha^{-1}\ yr^{-1}$) | *Number of values reviewed* |
|---|---|---|---|---|
| *Grasslands* | | | | |
| Max: | Italian rye grass | Aberystwyth | 24·0 | 39 |
| Min: | Fescue grassland | Westmorland | 0·56 | |
| Mean: | — | — | 5·94 | |
| *Heath, moor, bog* | | | | |
| Max: | Gorse | New Zealand | 16·86 | 69 |
| Min: | Eroded upland moor | Cairngorms | 0·45 | |
| Mean: | — | — | 3·85 | |
| *Salt marsh* | | | | |
| Max: | Sea lavender | Norfolk | 10·50* | 5 |
| Min: | Glass wort | Norfolk | 8·67* | |
| Mean: | — | — | 9·97* | |
| *Swamp* | | | | |
| Max: | Reedmace | Norfolk | 14·80 | 7 |
| Min: | Reed-grass | Dorset | 2·93 | |
| Mean: | — | — | 8·20 | |
| *Waste ground* | | | | |
| Max: | Japanese knotwood | Manchester | 25·30 | 6 |
| Min: | Meadow-sweet | Derbyshire | 7·10 | |
| Mean: | — | — | 10·80 | |
| *Agricultural crops* | | | | |
| Max: | Forage beet | U.K. | 13·3* | 45 |
| Min: | Hops | U.K. | 2·8* | |
| Mean: | — | — | 9·83 | |
| *Horticultural crops* | | | | |
| Max: | Carrots (roots) | U.K. | 4·9 | 18 |
| Min: | Lettuce | U.K. | 0·87 | |
| Mean: | — | — | 3·75 | |
| *Natural and coppiced woodland* | | | | |
| Max: | Coppiced poplar | U.K. | 20 | 12 |
| Min: | Coppiced hazel | U.K. | 1 | |
| Mean: | — | — | 9·45 | |
| *Managed forests* | | | | |
| Max: | Douglas fir | U.K. | 33·5 | 13 |
| Min: | Lodgepole pine | U.K. | 5·8 | |
| Mean: | — | — | 12·72 | |

*Notes* (a) Production rates are based on above ground parts only unless followed by * which indicates that below ground parts have been included.

(b) No productivity data are available for gorse in the UK and a figure is included for gorse in temperate grassland in New Zealand.

(c) Mean values must be treated with caution particularly where only a few productivity values have been reviewed.

an attempt to approach the theoretically attainable values. In the British Isles, actual production ranges between 4 and 13 $t\ ha^{-1}\ yr^{-1}$, the productivity varying greatly between different types of vegetation with 36 $t\ ha^{-1}\ yr^{-1}$ being produced in exceptional conditions. These yields contrast with 96 $t\ ha^{-1}\ yr^{-1}$ obtained in the most productive regions of the world, the tropics.

The productivity of grasslands (Table 5), from sea level to 840 m, is reported to vary from 0·56-24 $t\ ha^{-1}\ yr^{-1}$, the highest rates being obtained when fertilizers and moisture were optimal. Grass species can provide considerable yields in upland areas, but require continuous inputs of fertilizer and frequent reseeding. Upland areas of heather, cotton grass, etc. are relatively unproductive, but little information is available for lowland heaths and mires. Two common species of heath and moorland, bracken and gorse, appear to have potential as energy crops yielding between 14 and 16·9 $t\ ha^{-1}\ yr^{-1}$. Salt marshes produce about 10 $t\ ha^{-1}\ yr^{-1}$, and energy cropping here would have little competition from other land uses. Swamps can be similarly productive.

Some of the weed species growing on waste ground appear to be exceptionally productive, eg Japanese knotweed *Polygonum cuspidatum*. These yields on harsh disturbed ground would be expected to be increased when subject to favourable management. The biomass yields of agricultural crops differ appreciably. Some agricultural crops can grow almost anywhere in Britain, but it is doubtful if their cultivation would be energy efficient in the high upland areas. Unlike other types of vegetation, agricultural and horticultural crops usually receive considerable fertilizer inputs; they have also been subjected to intensive breeding.

Yield data from natural woodland are scarce, but exceed the minimum values quoted for coppice. However, with selection, the application of fertilizers, and attention to planting densities, much larger yields of coppiced willow are anticipated. Managed forests are generally more productive than natural woodlands, but the estimates take account neither of the potential of particularly high-yielding genetic strains nor of the impact of the intensive use of fertilizers. Estimates for fast-growing indigenous species, single stem trees and woodland are surprisingly scarce, and there is little information on the effects of novel management methods.

*Energy contents (calorific value) of plant matter*

Productivity, in terms of dry weight alone, is an inadequate measure of energy fixation; it is necessary to combine amounts of dry matter produced with the energy content per unit of dry matter. From a survey of 500 plant species, the mean energy content of plant dry matter was found to be $18 \cdot 27 \pm 0 \cdot 112$ kJ $g^{-1}$, the degree of variation being small compared with that associated with amounts of dry matter.

*Current land use in the United Kingdom*

Land availability is central to the discussion of fuels from biomass. The potential for plant production in any region of Britain is determined by (i) the areas of available land and (ii) the quality of that land, assessed by its current rate of primary production. Of the total land area in the United Kingdom, 93% is rural, and 59% of the rural area is cultivated (forestry 11%, arable crops and grassland 89%). The remaining 41% ($9 \cdot 1 \times 10^6$ ha) of rural land is covered by natural or semi-natural vegetation (Table 6).

Areas of semi-natural (rough grazing) and natural communities are particularly important when considering energy cropping because of their great extent and low value for agriculture and forestry. There are several other categories of land amounting to $7 \cdot 97 \times 10^5$ ha, which could be of interest, including $2 \cdot 34 \times 10^5$ ha of street verges, motorway verges and railway embankments—possibly under-utilised resources of fertile land.

*Basic patterns of net primary production in the United Kingdom*

The productivity of the whole of the UK can be estimated by assigning estimates for each vegetation type

*Table 6.* Current land use and provisionally estimated productivity in the United Kingdom

| | Area ha | Primary productivity $t\ ha^{-1}yr^{-1}$ | $t\ yr^{-1}$ |
|---|---|---|---|
| Total UK | 24,402,000 | 11·3 | 274,721,500 |
| Rural | 22,557,000 | 11·9 | 267,451,500 |
| Cultivated | 13,419,000 | 16·3 | 218,941,500 |
| Grassland | 7,211,000 | 19·6 | 141,154,800 |
| Leys | 2,137,000 | 19·6 | 41,831,800 |
| Permanent pasture | 5,074,000 | 19·6 | 99,323,000 |
| Arable | 4,739,000 | 13·2 | 62,577,000 |
| Cereals | 3,651,000 | 15·7 | 57,441,500 |
| Root crops and vegetation | 654,000 | 7·9 | 5,135,500 |
| Fallow | 434,000 | — | — |
| Forest | 1,416,000 | 10·5 | 14,828,100 |
| Coniferous | 1,382,800 | 10·6 | 14,602,400 |
| Coppice, etc. | 33,200 | 6·8 | 225,700 |
| Orchards | 53,000 | 7·2 | 381,600 |
| Natural and semi-natural | 9,138,000 | 5·3 | 48,510,000 |
| Rough grazing | 6,564,000 | 4·1 | 26,649,800 |
| Woodland | 643,500 | 10·0 | 6,412,600 |
| Broadleaved | 339,600 | 12·8 | 4,346,900 |
| Scrub, etc. | 303,900 | 6·8 | 2,065,700 |
| Water | 308,000 | — | — |
| Other | 1,622,500 | 9·5 | 15,447,600 |
| Urban | 1,845,000 | 3·9 | 7,270,000 |
| Amenity | 522,700 | 8·8 | 4,597,000 |
| Other | 1,322,300 | 2·0 | 2,673,000 |

to the land area which it covers. This calculation estimates total annual production of dry matter throughout the UK at $2 \cdot 7 \times 10^8$ t $yr^{-1}$, which is equivalent to an annual gross energy production at $5 \times 10^{18}$ J (Table 6). In England, Scotland and Wales, the total annual production of dry matter is estimated to be $2 \cdot 57 \times 10^8$ t or $4 \cdot 78 \times 10^{18}$ J. The figure for Great Britain represents 59% of the total energy consumption for 1976 ($8 \cdot 6 \times 10^{18}$ J) and 142% of the $3 \cdot 6 \times 10^{18}$ J derived from oil (Department of Energy 1977). It must be stressed, however, that the production estimates are likely to be subject to appreciable errors.

Cultivated land contributes 79 ·5% of the annual dry matter production in the UK, whereas areas of natural and semi-natural vegetation contribute 17 · 8%. Surprisingly, predominantly urban areas may make a contribution of 2 · 7%. Grass leys, pastures (51 · 8%) and arable crops (21 · 1%) are particularly important components of the total annual primary production in the UK, whereas total woodland (7 · 8%) is a relatively minor component. Large amounts of biomass are produced by several natural species, either through their extent (eg heather) or fast growth (eg bracken, gorse). These species and communities could provide biomass for fuel without significantly altering the landscape. In the past, bracken used to be regularly harvested and heather moor is periodically burned to enhance grazing. Could annual yields of $3 \cdot 4 \times 10^6$, $1 \cdot 7 \times 10^6$, and $4 \cdot 5 \times 10^5$ tonnes be obtained if bracken throughout Great Britain, and heather and gorse in England and Wales were harvested, bearing in mind that the growth of bracken is sometimes minimized by repeated cutting?

Urban areas also represent areas of considerable importance for energy cropping. Lawns, for example, annually produce an estimated $2 \cdot 2 \times 10^6$ tonnes of cuttings, most of which are probably discarded. Street verges and motorway embankments also represent areas where considerable energy is already expended in cultivation, but the resulting vegetation is wasted. With little extra effort, street verges could be managed so that prunings and mature trees could be harvested for fuel. It has been estimated that $3 \cdot 3 \times 10^6$ t $yr^{-1}$ could be available from this source without destroying the aesthetic quality of the trees. Similarly, grass from motorway embankments could be harvested, or a more productive energy crop, eg gorse (which is already extensive along many motorways), could be planted and exploited. Railway embankments also offer an unused area capable of supporting highly productive species, and the present estimated total productivity of $2 \cdot 3 \times 10^5$ t $yr^{-1}$ could be increased to $5 \cdot 1 \times 10^5$ t $yr^{-1}$. Finally, hedges occupying $1 \cdot 81 \times 10^5$ ha are another possibly significant source of energy biomass. It appears that, while still acting as wind breaks and boundary markers, they have an estimated production of $1 \cdot 3 \times 10^6$ t $yr^{-1}$.

*Energy inputs required to manage vegetation*

When considering energy crops, it is desirable to consider net gains, ie allowances should be made for the inputs of energy needed for making and applying fertilizers for site preparation including drainage, sowing and harvesting.

Harvesting the aerial biomass of natural vegetation need involve no energy cost other than that required to cut and collect the crop. However, repeated cropping would probably necessitate applications of fertilizers to replace soil nutrients. Forestry operations are periodic and, therefore, annual energy inputs are small, the main energy cost being that of harvesting and collecting (Table 7). Grass crops, which may persist for several years without reseeding, are likely to require, unlike forests, repeated annual applications of fertilizers (accounting for 70% of the total energy input); substantial amounts of energy will also be needed for successional harvesting. The management of agricultural field crops necessitates very large energy inputs via planting, culture and fertilizers.

*The production of fuels from biomass in Cumbria and Great Britain*

1. Cumbria

Using the principles already enumerated, the potential for biomass production in Cumbria has been examined.

1.1 Land classification

Statistically based sampling methods overcome many of the problems associated with the assessment of land use from traditional surveys. Using a method developed by Bunce and Smith (1978), a grid sample of 781 one km squares (ie 11% of the total) was obtained; for each grid square, details of topography, geology and human artefacts were 'read' from existing maps. These data were then analysed to define 16 land classes which were used to allocate the remaining 6 200 one km grid squares of Cumbria to one of the 16 land classes.

Three one km grid squares from each of the 16 land classes were visited and details of the vegetation were recorded. In this way, each land class could be characterised in terms of the nature and frequency of different vegetation types, enabling the total extent and distribution of the vegetation types to be assessed.

Managed grassland was found to be the most extensive form of land use in the region, representing 46% of the total area; natural vegetation was also extensive, occupying 45 · 6% of Cumbria, but arable and forestry usages were limited to small areas (8% and 0 · 4%, respectively).

1.2 Distribution of rates of primary production and total primary production in Cumbria

Literature estimates of net annual primary pro-

*Table 7.* Estimated energy inputs required to manage vegetation (J × $10^9$ $ha^{-1}$ $yr^{-1}$)

| Vegetation Type | Planting and Cultivation | Fertilizers | Harvesting and Collecting | Total Energy Input | Energy Output | Output/Input |
|---|---|---|---|---|---|---|
| *Natural vegetation* | | | | | | |
| Heather (15 year rotation) | 0 | 0 | 0·20 | 0·20 | 42·9 | 214·5 |
| Bracken | 0 | 0 | 3·00 | 3·00 | 265·9 | 88·6 |
| *Forestry* | | | | | | |
| Sweden (Total forest area) | 0·05 | 0·05 | 0·24 | 0·34 | 44·0 | 129·4 |
| U.S.A. (Intensive Sylviculture) | 0·32 | 0·81 | 7·0 | 8·1 | 260 | 32·1 |
| *Agriculture* | | | | | | |
| Grass | | | | | | |
| Grass — all graze | 0·25–0·8 | 9·1–37·4 | 0 | 9·3–38·2 | 147–245 | 15·8– 6·4 |
| — graze + 1 cut hay | 0·31 | 7·5–10·7 | 1·7 | 9·5–12·7 | 132–153 | 13·9–13·2 |
| Field beans | — | 4·5 | — | 10·3 | 125 | 12·2 |
| Peas | — | 1·2 | — | 10·9 | 72 | 6·6 |
| Maize | — | 5·5 | — | 12·6 | 150 | 11·9 |
| Barley | 3·4 | 8·9 | 1·5 | 14·0 | 88 | 6·4 |
| Oats | 3·4 | 8·9 | 1·5 | 13·8 | 96 | 7·0 |
| Wheat | 3·8 | 10·1 | 1·7 | 15·5 | 111 | 7·2 |
| Carrots | — | 9·8 | — | 25·5 | 91 | 3·6 |
| Sugar beet | 6·7 | 15·4 | 5·3 | 27·4 | 208 | 7·6 |
| Grass — 3 cuts hay | 0·9 | 21·6 | 5·2 | 27·7 | 189·5 | 6·8 |
| — silage | — | 21·6 | — | 32·2 | 189·5 | 5·9 |
| Potatoes | 5·2 | 18·7 | 10·1 | 34·0 | 129 | 3·8 |
| Brussel sprouts | — | 27·4 | — | 47·0 | — | — |
| Winter lettuce (heated greenhouse) | 4550–6048 | 0–12 | 0* | 4550–6060 | 10·6+ | ·0023–·0017 |

* Labour = 2870 hours  + Without roots

duction were 'fitted' to the different types of vegetation found in Cumbria, and the total annual primary production for the region was calculated at 6·54 × $10^6$ tonnes. From this calculation, primary production was estimated to range from 11·3 t $ha^{-1}$ $yr^{-1}$ on good agricultural land to 5·8 t $ha^{-1}$ $yr^{-1}$ in the uplands. Patterns of productivity (Figure 7) are, understandably, inversely related to altitude (Figure 8), the more productive Eden Valley, for example, contrasting with the less productive uplands.

1.3 Potential production in Cumbria

The potential biomass production in Cumbria for energy feedstocks obviously depends upon the availability of different types of land. It is possible that present allocations to different land use categories may alter, or be altered, and it is not difficult to construct an extensive series of scenarios to reflect these changes. At one extreme, minimum production of energy feedstock could be achieved, without significantly altering present land use, by harvesting residues from agricultural land and forest plantations (straw and woodchips respectively) with, in addition, the associated natural ground vegetation. Grasslands, however, would be an 'energy desert' because the whole of the production is utilised for grazing. In these circumstances, the total production of feedstock in Cumbria would be 1·72 × $10^6$ t $yr^{-1}$, equivalent to a net energy yield of 32 × $10^{15}$ J $yr^{-1}$.

If, on the other hand, an attempt was made to maximise harvestable yields, it is estimated that 12 × $10^6$ t $yr^{-1}$, equivalent to 232 × $10^{15}$ J gross energy yield, could be obtained. Total maximised productivity (harvestable plus non-harvestable fractions) would be 17·6 × $10^6$ t $yr^{-1}$, which is approximately a 3-fold increase over the estimated present productivity. In making these calculations, each unit of land was assigned a productivity value for the harvestable fraction of each of several crops capable of being sustained (Table 8), the final selection of the most productive crop only being made after allowing for the energy cost of planting, applying fertilizers and harvesting (Table 7).

1·4 Chemical conversion processes and catchment areas

It must be stressed that the above calculations relate to theoretical estimates of production. In practice, only a part of Cumbria's land area could be used for energy cropping. It is necessary, therefore, to investigate the available areas of vegetation (catchment areas) in relation to the requirements of chemical conversion units. Anaerobic digestion is suited to using green biomass as a feedstock, and a unit with an intake of 2 000 t $yr^{-1}$ would require a catchment area of 3·13 $km^2$ in the fertile lowlands. In the uplands a catchment area of 6·3 $km^2$ would be necessary. By growing 'dedicated' energy crops, the areas needed in the uplands and lowlands could be

KEY

| ENERGY IN GJ/HA/YR | 100-120 | 120-140 | 140-150 | 150-190 | 190-194 | 194-200 | 200-205 | SPECIAL |
|---|---|---|---|---|---|---|---|---|
| SYMBOL: | ----- | ===== | [illegible] | [illegible] | MMMMM | [illegible] | [illegible] | SSSSS |
| LAND CLASS: | 14 16 | 9 13 | 8 15 | 10 12 | 3 5 | 4 6 | 1 2 | 7 0 |
| LAND CLASS: | 0 0 | 0 0 | 0 0 | 0 0 | 0 0 | 11 0 | 0 0 | 0 0 |

*Figure 7 Estimated present gross energy production in Cumbria (highest density is equivalent to greatest productivity. (From Callaghan et al. 1978).*

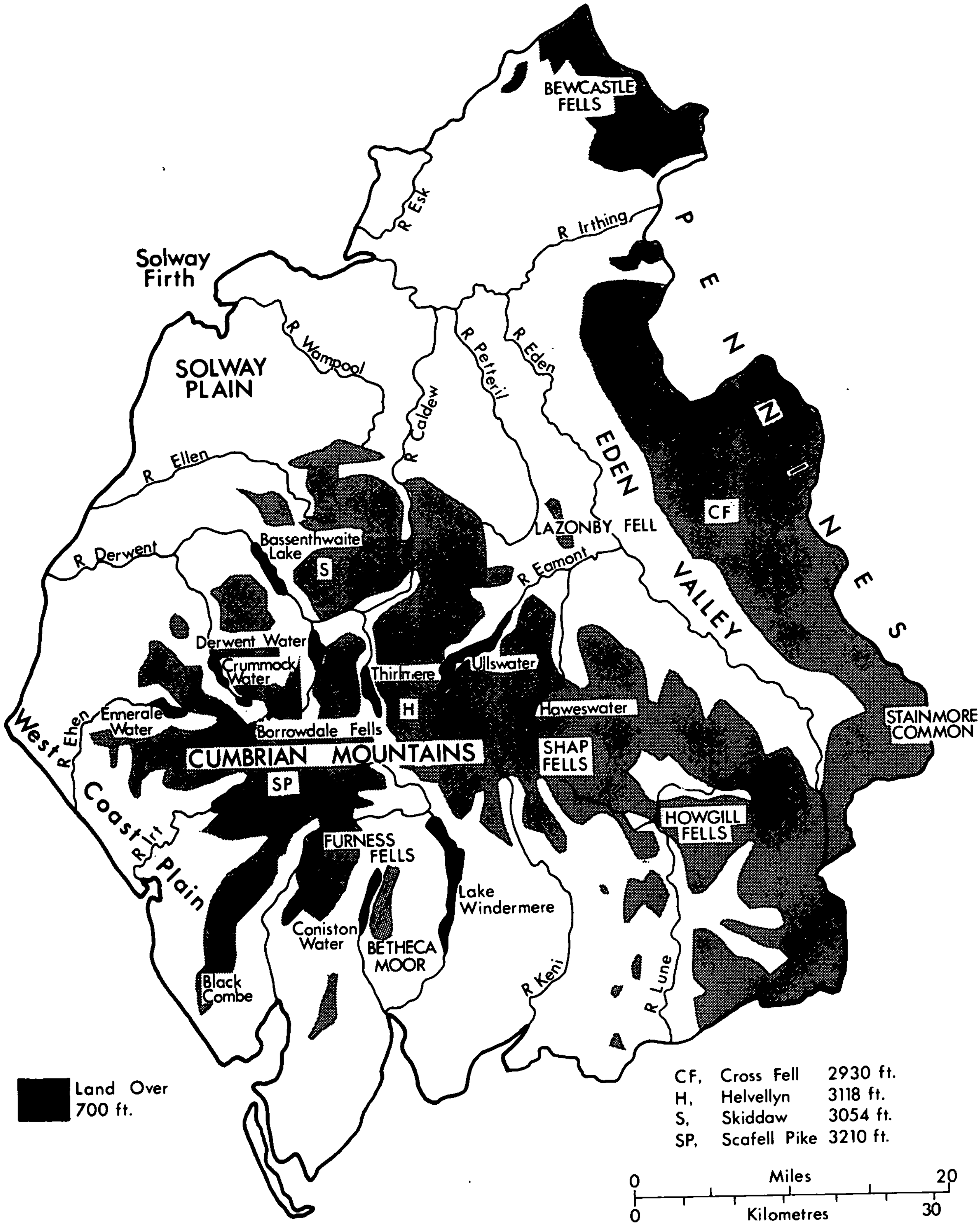



*Figure 8 Topographical map of Cumbria. (From Callaghan* et al. *1978).*

decreased by 33% and 70% respectively. To supply a large alcoholic fermentation unit with an intake of $1 \cdot 25 \times 10^6$ t $yr^{-1}$, almost 4 000 $km^2$ of upland green vegetation would be required (more than half the area of Cumbria). In the lowlands, assuming harvests of cereals and grass, this converter would require vegetation from one quarter of the area of Cumbria. Planting dedicated green energy crops like *Polygonum cuspidatum* (if this species is suitable for fermentation) would reduce the catchment area by 66%, but the required area of fertile lowland is still extensive.

*Table 8.* Estimated energy crop options in Cumbria. (Assuming only above-ground biomass is harvested)

| Present Vegetation | | | Alternative Crops | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | Trees | | | Grass | | | Natural Vegetation | | |
| Vegetation Type | Gross Yield (t ha$^{-1}$ yr$^{-1}$) | Net Yield (GJ ha$^{-1}$ yr$^{-1}$) | Replacement Vegetation Type | Gross Yield (t ha$^{-1}$ yr$^{-1}$) | Net Yield (GJ ha$^{-1}$ yr$^{-1}$) | Replacement Vegetation Type | Gross Yield (t ha$^{-1}$ yr$^{-1}$) | Net Yield (GJ ha$^{-1}$ yr$^{-1}$) | Replacement Vegetation Type | Gross Yield (t ha$^{-1}$ yr$^{-1}$) | Net Yield (GJ ha$^{-1}$ yr$^{-1}$) |
| Arable fields | 10·31 | 80·38 | Sitka spruce (YC 16) | 11·78 | 231·03 | Leys | 8·6 | 146·79 | *Polygonum* cuspidatum* | 25·3 | 484 |
| Leys | 8·6 | 146·79 | Sitka spruce (YC 16) | 11·78 | 231·03 | Leys | 8·6 | 146·79 | *Polygonum* cuspidatum* | 25·3 | 484 |
| Pasture and marginal land | 6·43 | 82·77 | Sitka spruce | 10·3 | 200·99 | — | — | — | *Polygonum* cuspidatum* | 25·3 | 484 |
| *Nardus* moorland | 1·9 | 31·65 | Sitka spruce* (YC 10) | 7·36 | 141·31 | — | — | — | — | — | — |
| Bracken* moorland | 9·82 | 183·38 | Sitka spruce (YC 10) | 7·36 | 141·31 | — | — | — | — | — | — |
| Peat land | 2·43 | 45·12 | Sitka spruce* (YC 9) | 6·62 | 126·29 | — | — | — | — | — | — |
| Basic woodland | 10·04 | 198·55 | Sitka spruce* (YC 14) | 10·3 | 200·99 | Leys | 8·6 | 146·79 | Bracken | 9·82 | 183·38 |
| Acid woodland and hedgerows | 4·05 | 84·54 | Sitka spruce (YC 11) | 8·01 | 154·50 | Leys | 8·6 | 146·79 | Gorse* | 16·86 | 322·2 |
| Sitka spruce* forest | 8·01 | 164·4 | — | — | — | — | — | — | Calluna | 2·43 | 45·12 |

*Vegetation type giving maximum net energy yield
YC = yield class

If dry woody material were to be supplied to a pyrolysis unit with an intake of $73 \times 10^5$ t $yr^{-1}$, virtually the whole area of Cumbria would have to be dedicated to this purpose. If woody species were restricted to the marginal upland areas, the 'catchment' area would be 1 000 $km^2$, but, because of the dispersed distribution of this type of land, transport costs would be prohibitive.

It would seem that the most feasible options, taking note of the requirements of the different conversion processes and the potential availability of biomass, include:

(i) Several small alcoholic fermentation units with catchment areas of bracken in the uplands.
(ii) Several small alcoholic fermentation units with catchment areas of *Polygonum cuspidatum* in the lowlands.
(iii) Possibly one large alcoholic fermentation unit with a catchment area of *Polygonum cuspidatum* in the lowlands.
(iv) Possibly one pyrolysis unit with a catchment area of Sitka spruce *Picea sitchensis* and gorse in the lowlands.
(v) Numerous anaerobic digestion units with catchment areas of either bracken in the uplands or *Polygonum cuspidatum* in the lowlands (Figure 9).

2. Great Britain

A land classification method similar to that described for Cumbria has been developed for Great Britain—identifying 32 land classes (Bunce in press). Potential production in Great Britain was assessed by assigning productivity estimates to 256 one km squares including a representative of each of the 32 different land classes. Separate Department of Energy assessors took responsibility for predicting rates of productivity for their particular crops (natural vegetation, agricultural crops, single stem trees and coppice) in the different land classes, the crop with the highest predicted yield being selected for the present study. Mean primary production estimates for agricultural crops ranged from 18 ·7 t $ha^{-1} yr^{-1}$ for fodder beet on a lowland land class to 7 · 9 t $ha^{-1} yr^{-1}$ for grasses on an upland land class. Single stem trees ranged from 22 ·1 t $ha^{-1} yr^{-1}$ in the lowlands to 4 ·48 t $ha^{-1} yr^{-1}$ in the uplands. Generally lower mean productivity values were predicted for coppice (14 ·9 t $ha^{-1} yr^{-1}$ to 1 ·3 t $ha^{-1} yr^{-1}$) : natural vegetation, unsuspectedly productive, ranged from 25 · 3 t $ha^{-1} yr^{-1}$ to 3 · 7 t $ha^{-1} yr^{-1}$.

In looking at the national estimate of potential production, the effects of topography are immediately apparent, with the upland areas of Dartmoor, Exmoor, the Welsh mountains, the Pennines, southern uplands and Scottish highlands seen to be least productive (Figure 10.) Natural vegetation makes the most significant contribution to maximising the production of each land class, followed by single stem trees: agricultural crops maximise production in 12 · 9% of the one km squares.

The total potential productivity of Great Britain is estimated at 3 ·85 × $10^8$ t $yr^{-1}$ (69 × $10^{18}$ J $yr^{-1}$), an estimate twice the actual production of dry matter (1 ·8 × $10^8$ t $yr^{-1}$). The predicted potential gross energy production is equivalent to twice the energy content of oil used in the UK in 1976 and is 80% of the total energy content of oil used in the UK in 1976 Catchment 'areas' for alcoholic fermentation units, with intakes of 1 · 25 × $10^6$ t $yr^{-1}$, would amount to 942 $km^2$ of lowland Britain and 1 196 $km^2$ of the uplands (Figure 10).

*Constraints on primary production*

The predictions outlined above have been based upon data extracted from the literature. Production is limited by land availability, interception of solar radiation, temperature, water supply, nutrient availability and genetic make-up.

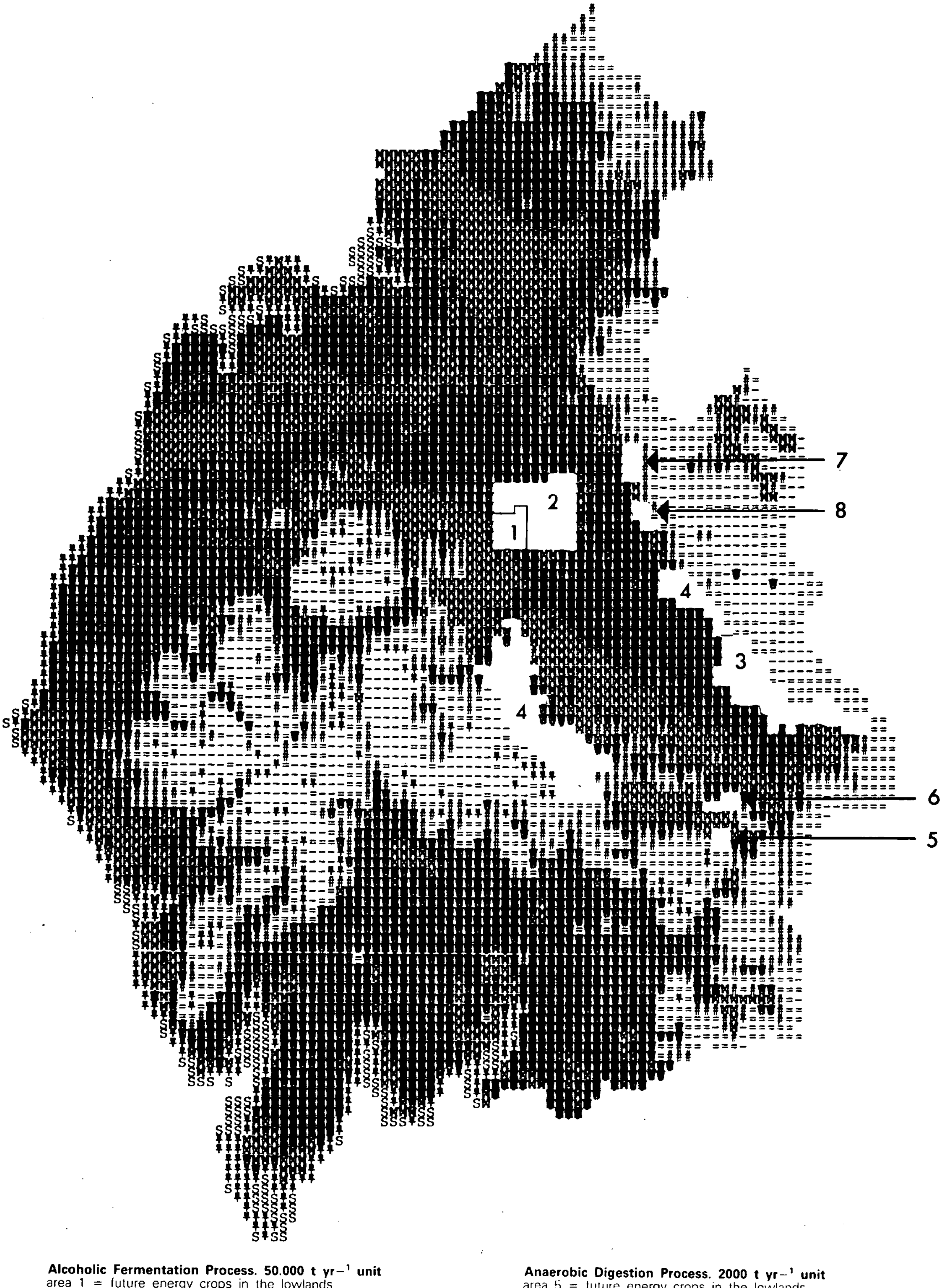
1. Land availability

The value of bio-fuels compared with (i) other fuels and (ii) the crop/recreation/conservation value of land will determine the availability of land which is, therefore, constrained by socio-economic factors. Without doubt, land with a low 'value', however defined, will be the first to be made available. Indeed, large areas of land such as railway and motorway embankments, if used for energy crops, could provide 5 ·1 × $10^5$ tonnes of harvestable dry matter each year. In assessing the present and potential productivity of all land within Great Britain, the constraints of land availability have been ignored.

2. The interception of solar radiation

The amount of radiation intercepted by vegetation is extremely variable. It could be increased by developing 2-crop systems analogous to the cultivation of cereals under poplar (Plate 1), where trees and ground vegetation could both be harvested for energy, or one of the 2 could retain its traditional role. Also, a nitrogen-fixing species could be grown in one of the layers to increase soil fertility and decrease energy inputs. Similarly, the productivity of coppice may be increased by trimming to a height of 2 m (ie pollarding) so allowing the development of ground layer vegetation which could be grazed or harvested as an energy crop. Coniferous forests are already highly efficient in intercepting solar radiation and there is, perhaps, less scope for increasing their efficiency. However, ground vegetation developed before canopies close could be replaced by a suitable nitrogen-fixing species which might enhance the early growth of forest trees and, itself, provide an energy crop.

There appears to be a conflict of strategies within plants aimed at intercepting the maximum amount of solar radiation. An extensive canopy is necessary to capture solar energy, but the support of such a canopy




**Alcoholic Fermentation Process. 50.000 t yr$^{-1}$ unit**
area 1 = future energy crops in the lowlands
area 1+2 = present vegetation in the lowlands
area 3 = future energy crops in the uplands
area 4 = present vegetation in the uplands

**Anaerobic Digestion Process. 2000 t yr$^{-1}$ unit**
area 5 = future energy crops in the lowlands
area 6 = present vegetation in the lowlands
area 7 = future energy crops in the uplands
area 8 = present vegetation in the uplands

*Figure 9 Catchment areas of biomass for different chemical conversion units in Cumbria. (From Callaghan* et al. *1978).*

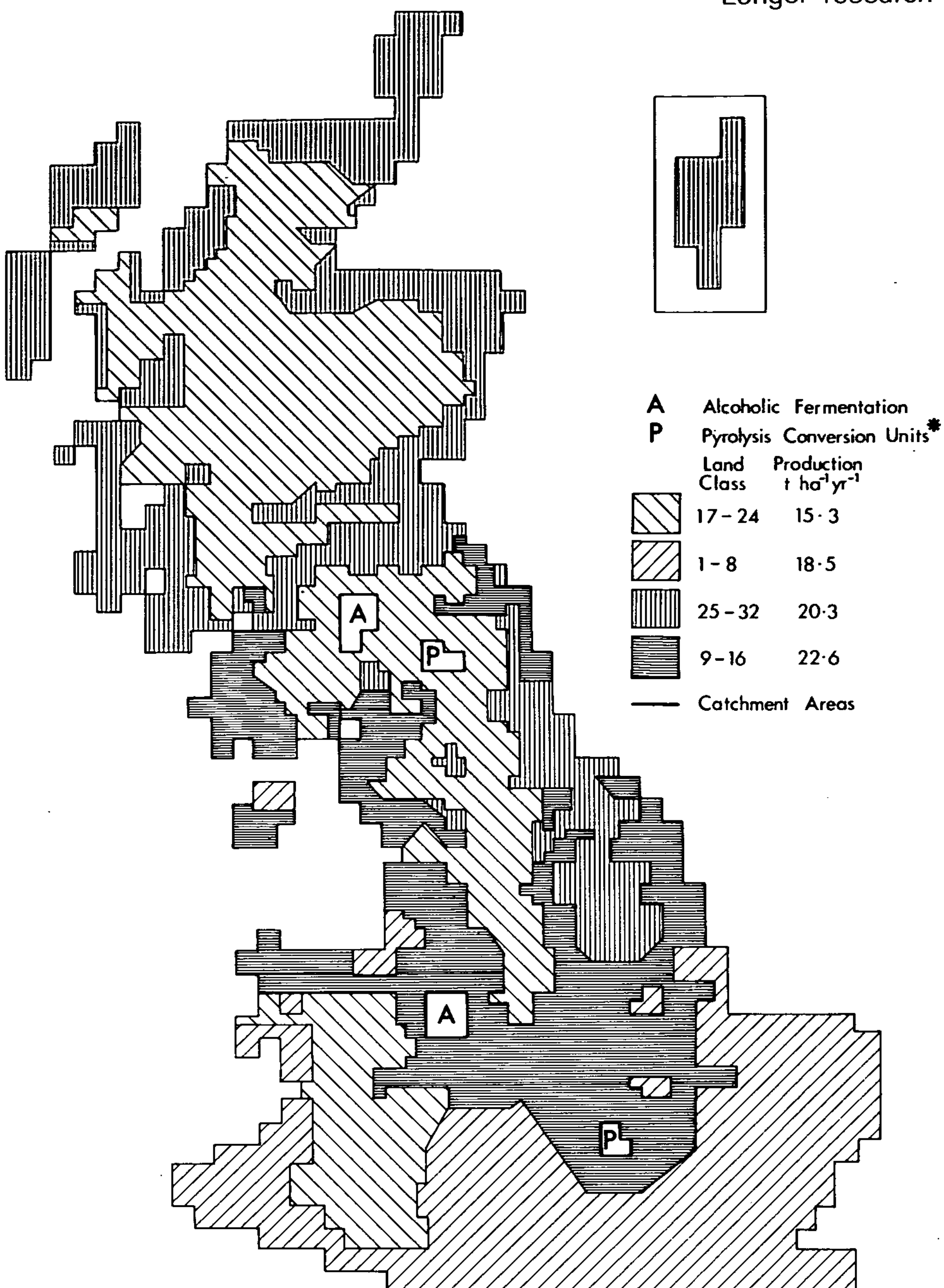



*Figure 10 Potential harvestable production and catchment areas for A, alcoholic fermentation and P, pyrolysis conversion units. (From Callaghan* et al. *1978).*

requires strong tissues which are a drain on energy sources through respiration. Climbing species display vast canopies while possessing a reduced support system (eg *Polygonum baldschuanicum*, one of the fastest growing species in this country). Such species merit further investigation.

3. Temperature

Temperature controls the growth and development of leaves, roots, etc, but is a constraint which is difficult to influence in the context of outdoor energy crops. However, locating crops on south-facing slopes and growing shelter belts (which may themselves be managed as energy crops) around sensitive crops might modify temperature regimes and increase productivity.

Indirectly, temperature constraints may be lessened by plant selection and breeding: additionally, a nursery system may be used for germination and seedling establishment, with, in the instance of kale, yields of $23 \cdot 6$ t $ha^{-1}$ $yr^{-1}$ instead of $6 \cdot 5$ t $ha^{-1}$ $yr^{-1}$. However, future energy crops should be robust in their response to temperature: a crop is of little use if it is devastated by cold spells, despite growing well in average conditions.

4. Water availability
Productivity can be limited by water deficiencies and excesses. The presence of too much water can be remedied by drainage, but waterlogged land in the lowlands could, given suitable techniques, support very productive species. Where water is scarce, irrigation is necessary. Unlike drainage, crops respond to irrigation every year in areas such as East Anglia, where large soil-water deficits build up: however, irrigation is an energy-intensive measure which may not be feasible for energy crops.

5. Mineral nutrients
The availability of mineral nutrients, ie soil fertility, is a major constraint which man is constantly trying to ameliorate. In general, large inputs of fertilizers are already used in agriculture, with less in forestry, and none in the management of natural vegetation. Effects of regular small amounts of fertilizers on tree yields are unknown, but the growth of some conifers on small areas of fertile lowland suggests that tree yields elsewhere might be improved significantly.

The growth of natural plant communities is likely to be increased significantly by small applications of fertilizer. Following harvesting, however, it would be necessary to replace minerals taken from the site in biomass. There would be additional problems associated with soil fertility if both above-ground and below-ground biomasses were removed, possibly damaging soil structure. Two indirect measures which might increase soil fertility would be to plant nitrogen-fixing species or, alternatively, species which tolerate infertile locations, eg bracken.

6. Genetic, inherent, characteristics of plants
Conceptually, the inherent nature of a plant may be regarded as a constraint to production, and this constraint may be lessened by breeding and selection. Agricultural and, to a lesser extent, horticultural tree crops have a history of selection and breeding to increase economic yields (eg cereal grain or top fruit). Breeding programmes have not, however, been extended to maximise the production of the whole crop. Indigenous species have often been naturally selected to tolerate low soil fertility, and a 25% increase in productivity could be expected from the initial selection of wild species, with another 25% increase from cultivation and fertilizer treatments. Some indigenous species grow rapidly and are of potential interest as energy crops.

*Resume*
Many of the interpretations must be considered as being tentative, being insecurely based on fragmentary data. A period of data collection and experimentation is, therefore, essential before firmer conclusions can be made about (i) the merits of different species and assemblages as potential energy crops, and (ii) the success of novel management practices. Provisionally, it has been estimated that the amount of energy captured each year by British vegetation is significantly greater than our annual consumption of energy derived from oil. There is great scope for improving plant capture of solar energy, and, for example, it is predicted that primary production could be increased 3-fold in Cumbria. There seems little doubt that the potential of British vegetation for fixing solar energy is underemployed; it could provide a significant contribution to our increasing demands for fuel, not forgetting the need to produce food.

In recognising this potential, and to make good the lack of information, the programme sponsored by the Department of Energy is now progressing from a desk study to an experimental programme. Note is being taken of the productivity of fast-growing plants, indigenous and naturalised, while the effects of 'management' (eg frequency and time of harvesting, fertilizer applications, etc) on yields are being investigated in controlled field experiments (Callaghan *et al.* in prep).

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## METHODS FOR CLASSIFYING MAP DATA, WITH PARTICULAR REFERENCE TO INDICATOR SPECIES ANALYSIS AND K-MEANS CLUSTERING

Although various land classifications exist in this country (eg the MAFF Agricultural Land Classification and the Soil Survey of England and Wales Land Use Capability Classification), there have been few attempts to produce general land classifications which could be used for a variety of planning purposes, and even fewer attempts to use numerical methods. In recent years

ITE staff have become increasingly involved in the numerical analysis of data obtained from maps and in attempts to produce numerical classifications of map grid squares (see ITE Annual Report 1976, pp 10–15, and 1977, pp 29–30; also ITE 1978). However, numerical classification is still developing, and it presents many problems, both theoretical and practical, which have not so far been discussed in this context. Here, we shall mention some of the general theoretical problems and techniques which have been used in numerical classification in a range of applications, and the new techniques which have been used in recent ITE approaches to the classification of map data. Although the discussion focuses on map data, the general principles are applicable to many types of data.

*Classification and dissection*

Kendall and Stuart (1968, p 314) defined *classification* as the process of dividing a sample of objects, or an entire population, into groups which should be as distinct as possible. The groups should be 'natural' in the sense that members of any group should closely resemble each other and should differ considerably from those of another group. In practice, these criteria are usually interpreted by searching for discontinuities in the distribution, in multivariate space, of points representing the objects, or at least for regions of that space which are occupied by fewer points representing the tails of overlapping distributions and/or 'noise' data (see, eg, Marriott 1974). By contrast, *dissection* implies the division of a sample or population into groups regardless of whether the boundaries are natural or not, and the aim is to find the most convenient way of dividing the individuals into groups. Nonetheless, the groups formed by the dissection should have some definable logical structure.

*Cluster analysis*

This term is applied to a wide range of techniques which seek to separate a collection of objects into groups or categories, there being little or no prior knowledge about the category structure of the data used in the analysis. To a greater or lesser extent, the different techniques involve the imposition of a structure on the data, as well as revealing any structure that may actually pre-exist. As a result, the groups that are identified reflect the degree to which the data conform to the structural forms inherent in the clustering algorithm (Anderberg 1973). Cluster analysis methods which have only a weak tendency to impose structure on the data, eg single-linkage cluster analysis, are particularly useful in exploratory data analysis.

Clustering strategies have several important characteristics; they may be hierarchic or non-hierarchic, agglomerative or divisive, polythetic or monothetic. *Hierarchical* strategies find an optimum pathway between the objects of which a sample is composed, to a single group consisting of the entire sample, via intermediate groupings. This pathway is found by a series of fusions (*agglomerative*) or, in the reverse direction, by a series of fissions (*divisive*), the groups produced being non-overlapping. The groups through which the process passes are not necessarily optimal in themselves, and the best pathway may be obtained at the expense of some slight reduction in homogeneity of the individual groups.

In *non-hierarchical* strategies, the structure of individual groups is optimized, and no pathway is defined between groups and their constituent individuals, or between groups and the complete sample. Marriott (1974) pointed out that a hierarchical strategy can have disadvantages if there is no special reason for requiring the nested structure of such a strategy. For example, if the aim is to decide whether a division into 2 groups gives a better representation of the data than a division into 3 groups, it is necessary to compare the best division into 2 groups with the best division into 3 groups, and a hierarchical strategy will not necessarily give both.

Many of the most widely-used clustering algorithms employ agglomerative hierarchic strategies based on some sort of inter-object distance measure. Because the distance measure is based on several properties, such methods are *polythetic*. Agglomerative hierarchic strategies are inherently prone to a small amount of misclassification at the lowest, inter-object, level, where the possibility of error is greatest. On the other hand, with divisive techniques, there is a greater danger of inappropriate allocation of some objects that cannot later be corrected unless some special terminal re-allocation procedure is used. Inappropriate allocation is particularly likely with *monothetic* techniques, because each division is based on 2 states of a single character, and any object which is aberrant in that character will be misclassified. Another problem with divisive techniques is that each group is made to divide into 2 at each level, an arbitrary restriction that may not reflect the inherent properties of the objects.

In searching for inter-object relationships which may be reflected in the data, the different possible patterns should be borne in mind. With most types of clustering algorithm, it is easy to identify the pattern in which distinct groups are separated by discontinuities in multivariate space, but this type of structure is by no means common. If the group centres are distinct, but the tails of the frequency distributions overlap, single-linkage cluster analysis will be unable to effect a clear division into clusters, although it can serve to indicate where the cluster centres might lie. Subsequently, other methods could be used to dissect the objects into groups, but, because the tails of the distribution overlap, a criterion is needed for the allocation of points in regions of overlap.

Where points representing the objects are more or less uniformly distributed in multivariate space and form a continuum, so that there is no clear structure in the data, classification in the strict sense is impossible;

instead, the problem is overcome by dissection using criteria defined by the objectives of the analyst. Many ecologists, when considering plant assemblages, visualize very complex types of pattern, with numbers of overlapping species whose combined distributions appear to be unimodal (see Hill, pp 41). This concept of a continuum is not unique to ecology (Clifford & Stephenson 1975); it has led to the development of a variety of methods for dividing the continuum into groups of hypothesized homogeneous areas.

The shapes of clusters produced by cluster analysis algorithms may also pose problems. In many clustering methods, some form of constraint is imposed on the spread of the clusters. Wishart (1969) discussed the properties of 13 such methods, and included them in the general category of 'minimum variance' methods. Some of the methods used by plant ecologists impose 'minimum variance' constraints. The minimum variance constraint makes these methods unhelpful, and even misleading, if the aim is to find the structure which actually exists in the data, unless it is known in advance that the structure is of a type for which the constraint is appropriate. However, methods which have this characteristic can be useful in dissection. On the other hand, single-linkage cluster analysis can identify clusters which are not only elongated, but also of complex shapes, if they are distinct.

*Ordination*

Ordination procedures aim to arrange points, representing objects, along new axes so as to preserve as much of the original information as possible, ie to preserve the relationships between the objects as closely as possible. There are, ideally, fewer new axes than original variables. Ordination makes the data easier to handle mathematically in that: (i) it makes graphical representation easier; (ii) it removes difficulties which might arise from variables which are linearly related, or nearly so; (iii) the new axes may lend themselves to reification, ie the interpretation of the mathematics in terms of the original problem, and so may give a useful insight into the structure of the data. If there are 'natural' groups, ie groups which are separated by discontinuities in multivariate space or by regions of the space containing few points which represent the tails of overlapping distributions and/or 'noise' data, this fact should be apparent in the results of the ordination. If there are no such groups, ordination may still help to clarify the relationships between objects. Ordination may also be used to show if a clustering method has been applied to data for which it is not suited.

Ordination is particularly useful if the objects under investigation are distributed along gradients. However, problems occur in studying the distribution of plant species. For example, principal component analysis is a widely-used ordination procedure. It is quite robust, but, as far as plant ecologists are concerned, it has a major deficiency because, if a variable has a non-linear response to an environmental gradient, the resulting component plot shows that gradient to be curved. The complex patterns of plant species distribution described by Hill (pp 42) give complex gradients on component plots. As plant ecologists often attempt to find ordination axes which represent environmental gradients, the lack of correspondence between ordination axes and environmental gradients has caused principal component analysis to fall out of favour in this field. The method of reciprocal averaging (see Hill, pp 44) attempts to overcome this problem.

*Recent approaches to the classification of map data*

Interest in ITE in the numerical classification of map grid squares originates from the concern of Bunce *et al.* (1975) to derive a numerical land classification, eg for use in regional land planning. They also identified this objective with the development of an adequate system of stratification to categorize the range of variation in areas under study. However, stratification and classification are not necessarily the same thing. Bunce *et al.* (1975) reported 2 studies. In one, 150 map squares (0·5 km × 0·5 km based on the National Grid), in the Grizedale area of the English Lake District, were sampled. Twelve variables were recorded and subjected to ordination by principal component analysis. This procedure was followed by a centroid clustering technique based on nearest-neighbour distances (Jeffers & Richens 1970). Centroid clustering methods have now been largely set aside because they are known to have undesirable properties.

In their second study, of the area encompassed by the one-inch (1 : 63 360) Ordnance Survey Tourist Map of the Lake District, Bunce *et al.* changed from the use of continuous variables (such as maximum altitude in the square, distance between highest and lowest points) to presence-absence attributes (eg presence or absence of land in a given altitudinal range, of a road, river, and other features recorded on the map). One hundred and fifty two map-based attributes were noted, and the data were subjected to reciprocal averaging ordination and indicator species analysis (see Hill, pp 42).

Reciprocal averaging and indicator species analysis have been used subsequently by Dr. D. F. Ball and Mr. M. Williams at ITE Bangor Research Station. They obtained data from maps of England and Wales, recording 41 variables covering physiography, 14; climate, 20; soils, 7, for each 10 km × 10 km National Grid square. These variables, except for 8, were expressed in terms of percentage 'occupancy' of each square; 436 squares were considered to be 'upland' in character. To enable indicator species analysis (ISA) to be carried out, Ball and Williams divided the range of some of the variables into 2 or 3 sections, each section being regarded as present or absent. Thus, if an attribute had a percentage occupancy of 60% and the range was divided 0-33%, 34-67%, 68-100%, it would be present in 34–67% and absent from 0-33% and 68–100%. In other instances, variables such as those concerned with surface roughness were pooled before being divided. In all, 51 presence-absence attributes were recorded, and the 8-class level of the subsequent ISA was selected for further examination (ITE 1978).

This approach to the classification of map data, using a method which was developed to deal with problems of plant species distribution, poses some interesting questions. In particular, how well does the scaling method used represent data whose distributional properties are unlike those of plant species? Gauch and Wentworth (1976) found that reciprocal averaging of vegetation data gave clearly interpretable results, but those obtained with environmental data were uninterpretable. Although Hill (1974) stated that continuous data can be analysed in the same way as can discrete data if the ranges of the different variables are divided into discrete sections, it remains to be seen how well this procedure succeeds in practice. In general, the conversion of continuous variables to binary attributes is not particularly desirable. If all non-zero values were simply scored as present, most of the information about the inter-relationships among variables would be lost. Of course, less information would be lost as the number of sections into which a variable is divided is increased, but to handle a large number of sections may prove impracticable. Another important point is that more methods are available for examining continuous variables than for presence-absence attributes. In any classification study, choice of variables, and the way in which they are recorded, is important. Plant ecologists tend to use presence-absence attributes for 2 main reasons; first, because it is less time-consuming (and hence less costly) to gather such data, especially from a large number of quadrats, and, second, because it avoids the problem of choosing and applying a quantitative measure.

ISA is subject to at least 2 criticisms: (i) in common with other divisive methods such as association analysis, the division of each group into 2 at each stage of the analysis is an arbitrary procedure, and (ii) the separation of the objects into 2 groups about the centre of gravity of the ordination strongly influences the initial dichotomy, although this may not be the optimal division. Furthermore, the number of divisions at which the analysis is stopped is entirely arbitrary. On the other hand, Hill *et al.* (1975) noted that ISA has at least 2 important practical advantages. First, it provides a diagnostic key which enables new data to be assigned to a classification produced by ISA without further computation. Second, the computer programs are capable of dealing with the classification of large numbers of objects. However, as Jardine and Sibson (1971) indicated, the production of diagnostic keys is not the primary purpose of classification.

*Re-analysis of the original Ball and Williams' data*

Full details of the re-analysis will be published elsewhere, and only the main findings are reported here. The variables recorded by Ball and Williams were chosen because it was thought that they were germane to problems of land use and could be read largely from published maps, although the climatic data included material from unpublished draft maps kindly made available by the Soil Survey of England and Wales. Some of the variables have very large coefficients of variation (CV), notably the percentage of the land within each square having altitude greater than 3 000 ft (914 m, CV 1203%), or receiving high rainfall (CV 1122%), and variables such as these are more likely to be useful as discriminators than those with narrow ranges of variation, such as sunshine hours (CV 11%).

Few of the variables had even approximately normal frequency distributions; instead, J- or U-shaped distributions were common. These frequency distributions pose problems when correlations are calculated, since the usual Pearson product-moment correlation coefficient assumes that the variables are normally distributed, or approximately so. If, as with J- or U-shaped distributions, it is impossible to resort to a transformation to achieve a normal distribution, it is necessary to use a non-parametric measure such as Spearman's rank correlation coefficient. We therefore calculated correlation matrices using both Pearson's and Spearman's measures for comparison. The product-moment correlation matrix showed many strong correlations; many of the physiographic variables were highly intercorrelated, as were many of the climatic variables. As might be expected, there were also some strong correlations between variables in the 2 groups. In general, the rank correlation coefficients differed only slightly from the product-moment correlation coefficients; fewer of the rank correlation coefficients had very low values and more had large values. Interestingly, the percentage of each square mapped as brown podzolic soil was not strongly correlated with other variables, although this may be a feature of the way in which the map was prepared. River density on a N-S transect of each square was also not strongly correlated with other variables.

A principal component analysis (PCA) of the product-moment correlation matrix showed that the first eigenvalue accounted for only 21% of the total variance, that 16 eigenvalues were necessary to account for 91% of the variance. Therefore, there is no single major axis of variation, and many components (ie dimensions) were needed before an adequate percentage of the variation was explained. As the results of an ordination assist in the interpretation of the results of a subsequent cluster analysis, it is useful to consider the PCA results in a little more detail. The first component axis (Figure 11) is dominated by altitude, and particularly by the percentage of land between 800 ft (244 m) and 2 000 ft (610 m), with accumulated day °C in the range 825–1 099. Map squares represented by points at the lower end of this axis are in areas which have only about 4% of land over 244 m and about 90% of the land in the highest accumulated temperature

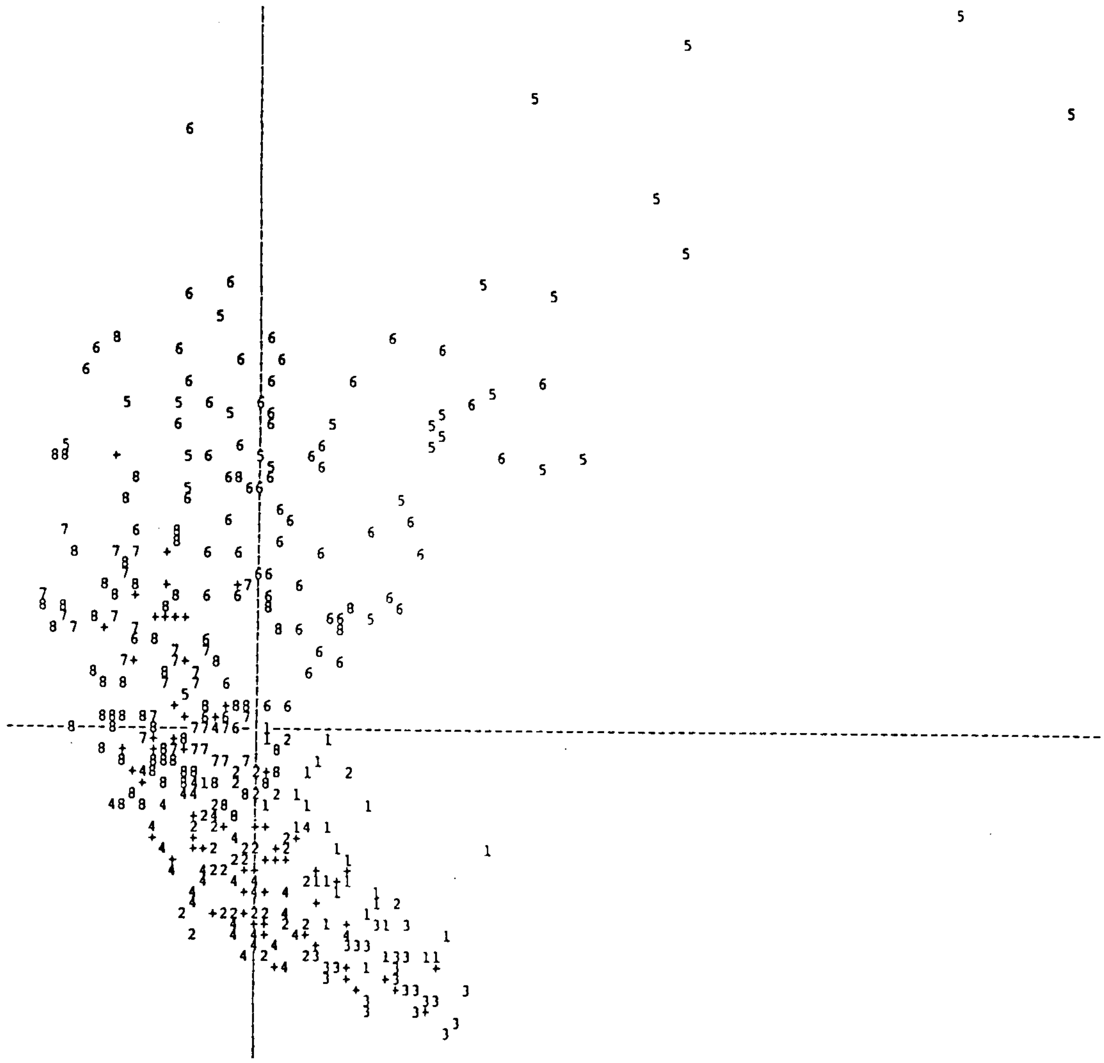

*Figure 11 Plot of components 1 and 2 of the product-moment correlation matrix from 41 variables obtained from 436 10 x 10 National Grid squares with 'upland' characteristics. Except for coincident points (represented by crosses) each point is represented by its ISA class number at the 8-class level.*

class (1 650–2 000 day °C). Conversely, at the top end of the axis are squares with up to 96% of land higher than 244 m and about 80% in the second lowest accumulated temperature class (825-1 099 day °C). Altitude is also important in the second axis, in which the percentage of land over 3 000 ft (914 m), with high rainfall (2 285–5 079 mm), extremely wet soils (soil moisture deficit ⩽0 mm) and slopes greater than 22°, at the right hand end of the axis, contrasts with areas having gentler slopes, lower rainfall (1015-1524 mm), and a slightly greater soil moisture deficit (50–74 mm) at the left-hand end.

In the third axis (Figure 12), the extreme right-hand square has 40% of the area mapped as brown earths and 100% having slopes of 12°–22°. The extreme left-hand square has 100% of the area mapped as podzols, with 60% having slopes greater than 22°. The plots in Figures 1 and 2 show very clearly the markedly curvilinear spatial distribution of the points representing the map squares.

A PCA of the Spearman rank correlation matrix showed that the first eigenvalue accounted for 24% of the total variance. Sixteen eigenvalues were required to account for 80% of the variance, and 23 were required to account for 90% of the variance. The use of a different correlation coefficient resulted in different relative weightings of the variables on the components, although this was less obvious in the first component. The plots of the components obtained from the rank correlation matrix were similar to those in Figures 11 and 12.

For a greater understanding of the component space, and remembering that the components with the largest eigenvalues contribute most to the interpoint distances, the first 16 components, accounting for some 80% of the total variance, of each PCA were analysed in greater detail. Examination of the 2 sets of eigenvectors suggested that, although the sizes of the individual eigenvector elements in the 2 analyses differed, the space defined by the first 16 components was essentially the same in each analysis. This suggests that a cluster analysis using the first 16 components of each PCA would have essentially the same result.

In Figures 11 and 12, except where points (representing map squares) are coincident (and are represented by a

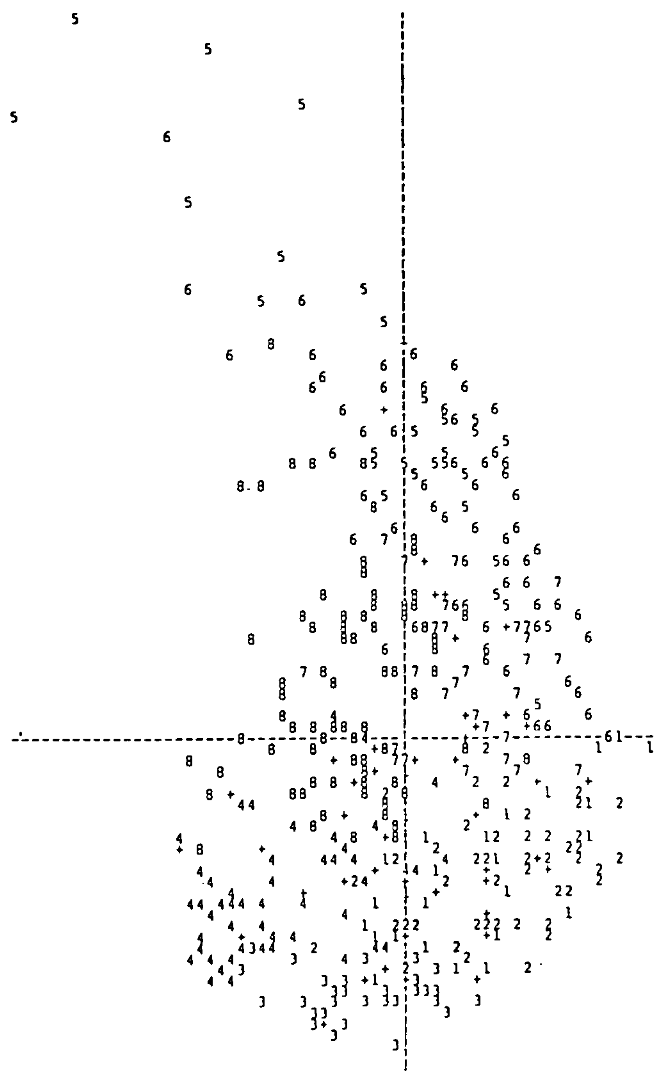

*Figure 12 Plot of components 1 and 3 of the correlation matrix from 41 variables obtained from 436 10 x 10 National Grid squares with 'upland' characteristics. Except for coincident points (represented by crosses) each point is represented by its ISA class number at the 8-class level.*

cross), each square is represented by its ISA class number at the 8-class level, and there are no clear discontinuities in the space defined by the first 3 components. Computation of a single-linkage cluster analysis using the first 16 components from both the product-moment and rank correlation matrices highlighted the lack of discontinuities. Indeed, it showed that the distribution of points is essentially a continuum, containing very little structure, and is therefore not amenable to classification in the strict sense. However, the object of the study is to produce a stratification which can have practical use, so some form of dissection is required.

From Figures 11 and 12, it seems that the squares with extreme values for the first component belong to ISA classes 3 and 5, but that the spatial distributions of ISA classes 1, 2, 4, 6, 7, and 8, nearer the centre of the distribution, are indistinct and overlapping. No improvement was achieved by using 16 component axes. In attempting a dissection which is to be used as a basis of stratification, it is reasonable to expect that points belonging to one class should not be interspersed spatially with those of other classes. This can be achieved using k-means clustering, a non-hierarchic method for producing a specified number of non-overlapping clusters whose within-cluster sums of squares are minimized, producing tight, non-overlapping groups. This method has the advantage that the overall sum of squares, ie the sum of the within-cluster sums of squares, can be used to decide what number of clusters is most acceptable.

Ball and Williams were concerned with 8 classes derived by ISA, therefore the results of k-means clustering with k = 8 are given here for comparison. The results of using different sets of components in k-means clustering can be examined in 2 ways:

1. Between the overall sum of squares (OSS) of the k-means 8 groups derived from the first 16 components of the product-moment correlation matrix (7333·94) with the OSS, calculated using the same component values, of the k-means 8 groups derived from the rank correlation matrix (7350·82), ie comparing (b) with (c) in Table 9.

2. Between the OSS of the k-means 8 groups derived from the first 16 components of the rank correlation matrix (6974·87) with the OSS, calculated using the same component values, of the k-means 8 groups derived from the product-moment correlation matrix (6977·42), ie comparing (e) with (f) in Table 9.

In both comparisons, there is virtually no difference between the OSS. We can compare the results of k-means clustering and ISA in 2 ways:

1. Between the OSS of the k-means 8 groups derived from the first 16 components of the product-moment correlation matrix (7333·94) and the OSS, calculated using the same component values, of the ISA 8-class partition (9135·43) ie comparing (a) with (b) in Table 9.

2. Between the OSS of the k-means 8 groups derived from the first 16 components of the rank correlation matrix (6974·87) and the OSS, calculated using the same component values, of the ISA 8-class partition (8727·47), ie comparing (d) with (f) in Table 9.

These 2 comparisons show that, using both types of correlation matrix, the overall sum of squares for the ISA 8-class partition is considerably greater than that of the k-means 8-group partition, so confirming that the ISA classes tend to be diffuse.

Comparison of the allocation of the National Grid squares to ISA classes and k-means groups showed that individual k-means groups included squares spread over a range of ISA classes. Thus, k-means group F

*Table 9.* Comparison of the overall sums of squares of the ISA 8 classes and k-means 8 groups based on 16 component values from 41 variables obtained from 436 10 km × 10 km National Grid Squares with 'upland' characteristics.

| Partition | Overall sum of squares calculated from 16 components of: Product moment correlation matrix | Rank correlation matrix |
|---|---|---|
| ISA 8-class | 9135·43 (a) | 8727·47 (d) |
| k-means 8 groups from components of product-moment correlation matrix | 7333·94 (b) | 6977·42 (e) |
| k-means 8 groups from components of rank correlation matrix | 7350·82 (c) | 6974·87 (f) |

*Table 10.* Contingency table showing numbers of National Grid 10 km × 10 km 'upland' squares common to ISA classes and k-means groups derived from the first 16 components of the product-moment correlation matrix of 41 variables

| k-means groups derived from components of the product-moment correlation matrix | ISA Class 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | Total |
|---|---|---|---|---|---|---|---|---|---|
| A | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 |
| B | 0 | 0 | 0 | 0 | 3 | 9 | 0 | 6 | 18 |
| C | 0 | 0 | 0 | 0 | 15 | 34 | 0 | 4 | 53 |
| D | 0 | 0 | 0 | 2 | 11 | 18 | 39 | 36 | 106 |
| E | 0 | 5 | 0 | 10 | 0 | 0 | 3 | 25 | 43 |
| F | 16 | 53 | 5 | 0 | 0 | 8 | 3 | 4 | 89 |
| G | 16 | 0 | 7 | 55 | 0 | 0 | 0 | 15 | 93 |
| H | 5 | 0 | 26 | 0 | 0 | 0 | 0 | 0 | 31 |
| Total | 37 | 58 | 38 | 67 | 32 | 69 | 45 | 90 | 436 |

includes squares allocated to ISA classes 1, 2, 3, 6, 7, and 8, but with 1 and 2 predominating (Table 10). k-means group A contains only 3 of the 436 squares, and these 3 squares contain land with extreme properties (Table 11). They therefore form a distinct group, but in ISA they are placed with 29 more squares, having less extreme properties, into class 5. Presumably this is a result of applying methods developed for analysing plant species distribution to another type of data having different properties. In the present instance, reciprocal averaging and indicator species analysis appear to have produced some unrealistic groupings.

In conclusion, it appears that k-means clustering is a useful technique for the dissection of quantitative data obtained from maps. It has the advantage that the overall sum of squares can be used in comparing different allocations of individuals to groups, but, like all numerical methods, it should be used with caution and careful thought.

*P.J.A. Howard and Doreen Howard*

*Table 11.* Properties of the k-means 8 groups based on 16 component values from the analysis of the product-moment correlation matrix of 41 variables obtained from 436 10 km × 10 km National Grid Squares with 'upland' characteristics. The values given for the variables are group means. The type square is the one nearest to the cluster centre, and the co-ordinates of the centre of the type square are given.

| Group | No. in group | Properties |
|---|---|---|
| A | 3 | Contain the only land over 3000 ft (4%), 84% is over 800 ft, 56% is over 1400 ft, and 28% is over 2000 ft. Lowest point 267 ft, highest 3418 ft. Steep slopes (60% is greater than 22°, 93% is greater than 12°). High rainfall (77% has more than 2285 mm). Very wet soils (76% has 24 mm deficit or less). Moderate accumulated temperature (77% has 825 to 1374 day°C). Mainly Podzols (67%). These squares also have the greatest number of freshwater bodies and greatest surface roughness.<br><br>These squares contain the highest Lake District and Snowdonia mountains.<br>Type square: 325 505. |
| B | 18 | Generally high land, 95% is over 800 ft, 61% is over 1400 ft. Lowest point 844 ft, highest point 2334 ft. Gentle to moderate slopes (47% is 0° to 11°, 52% is 12° to 22°). Moderate rainfall (96% has 1015 to 2284 mm). Wet soils (88% has SMD 25 to 74 mm). Low accumulated temperature (64% has 825 to 1099 day°C). Mainly peats (46%) and Stagnohumic gleys (44%).<br><br>These squares are chiefly in the north central Pennines.<br>Type square: 385 535. |
| C | 53 | This group also contains a large proportion of high land, 72% is over 800 ft, 25% is over 1400 ft, but it reaches to a lower altitude than land in group B. Lowest point is 451 ft, highest point is 2253 ft. It has a greater range of slope angles than does group B (20% is 0° to 11°, 55% is 12° to 22°, 25% is greater than 22°). Moderate rainfall (95% has 1525 to 3174 mm). Wet soils (80% has SMD 1 to 49 mm). Moderate accumulated temperature (71% has 1100 to 1649 day°C). 48% is mapped as podzols.<br><br>Central Lake District mountains, western sides of the N. Wales mountains, and the Brecon Beacons.<br>Type square: 275 315. |
| D | 106 | Land generally of intermediate altitude, 76% is over 800 ft, 16% is over 1400 ft. Lowest point 573 ft, highest point 1784 ft. Gentle to moderate slopes (41% is 0° to 11°, 54% is 12° to 22°). Moderate rainfall (87% has 1015 to 2284 mm). Moderately wet soils (99% has SMD 25 to 99 mm). Moderate accumulated temperature (85% has 1100 to 1649 day°C). 41% is mapped as Brown Earths.<br><br>Mainly central southern Pennines, eastern sides of the N. Wales mountains, central Wales, western slopes of Cheviots.<br>Type square: 295 335. |
| E | 43 | Generally fairly low land, 31% is over 800 ft, only 3% is over 1400 ft. Lowest point is 361 ft, highest point is 1496 ft. Gentle slopes (76% is 0° to 11°). Moderate rainfall (79% has 1015 to 1524 mm). Moderately wet soils (89% has SMD 50 to 99 mm). Fairly high accumulated temperature (87% has 1100 to 1649 day°C). 63% is mapped as Gleys.<br><br>Chiefly NW Lake District, western side of the central and southern Pennines.<br>Type square: 395 455. |
| F | 89 | Generally similar to group E in altitude, 23% is over 800 ft., only 2% is over 1400 ft. Lowest point 220 ft, highest point 1301 ft. Gentle to moderate slopes (53% is 0° to 11°, 44% is 12° to 22°). Moderate rainfall (87% has 1015 to 2284 mm). Moderately wet soils (72% has SMD 50 to 99 mm). Fairly high accumulated temperature (93% has 1375 to 2000 day°C). Mainly Brown Earths (81%).<br><br>Southern Lake District, coastal Wales, Exmoor and Brendon Hills, Dartmoor, Bodmin Moor, Mendips.<br>Type square: 245 235. |
| G | 93 | Generally low hills, 24% is over 800 ft, less than 1% is over 1400 ft. Lowest point 345 ft, highest point point 1241 ft. Gentle slopes (73% is 0° to 11°, 27% is 11° to 22°). Low rainfall (94% has 1014 mm or 1241 ft.). Gentle slopes (73% is 0° to 11°, 27% is 11° to 22°). Low rainfall (94% has 1014 mm or less). Fairly dry soils (95% has SMD 75 to 124 mm). Moderate temperature (88% has 1100 to 1649 day°C. Mainly Gleys (42%) and Brown Earths (38%).<br><br>N. York Moors, Eastern Cheviots, Eastern Pennines, Eastern Wales.<br>Type square: 415 485. |
| H | 31 | The lowest hills, only 10% is over 800 ft, no land over 1400 ft. Lowest point 308 ft, highest point 1021 ft. Gentle slopes (72% is 0° to 11°, 26% is 12° to 22°). Low rainfall (96% has 1014 mm or less). Fairly dry soils (98% has SMD of 100 mm or more). High accumulated temperature (99% has 1375 day°C or more). Mainly Brown Earths (47%) and Rendzinas (40%).<br><br>Shropshire Hills, Forest of Dean, Malvern and Clent hills, Radnor-Clun Forest, Brecon Mountains (east side), Cotswold Scarp, Wiltshire Downs, Quantock hills, N. Dorset scarp, Blackdown hills.<br>Type square: 335 245. |

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## ANALYSIS OF MULTIVARIATE VEGETATION DATA

Over the past few years, ITE has made numerous ecological surveys. It has acquired data on the occurrence and abundance of plant species that can be used either for censuses or for the exploration of the relation between vegetation and the environment. Considered as a census, survey data can be analysed by standard statistical methods. There is, however, no standard way of investigating vegetation-environment relations. In principle, each species could be considered separately, but except with very simple communities this is a daunting task, which would, in any event, fail to reveal the resemblance between patterns of distribution of ecologically similar species. Ecologists need to summarise and compare the species composition of differing community types.

### *Classification and ordination*

How can community data be summarised? There are two main approaches—classification and ordination. *Classification* is the simpler concept to understand, as it is an almost automatic function of the human mind. An experienced botanist has only to look at a species list, and he will recognise it as characteristic of a community type such as heathland, woodland or marsh. Mentally, he puts it in a category.

For plant communities, the categories are usually somewhat arbitrary. Plant communities, unlike organisms, have no phylogeny, and are assembled from component species with widely differing Pleistocene histories. But arbitrariness does not necessarily imply irrelevance; division of the spectrum into colours is based on arbitrary boundaries, but is nevertheless very useful. We wish to speak of blue and green, even though there are all shades of blue-green. Likewise for plant communities, the different types of vegetation are often imperceptibly merged to form a 'sliding scale'; but we shall still wish to speak of heaths and bogs, even after recognising that there are numerous communities intermediate between the two.

Given that the classification of plant communities is arbitrary, the question arises of how variation can be summarised in a more natural way. With classifications, the main artificiality lies in the use of discrete classes to describe the continuous variation in nature. *Ordination* (Figure 13) avoids the artificiality by locating communities on continuous scales of variation.

An important logical point should be noted. When ordinating plant assemblages, the available data are normally lists of species together with their abundance. Environmental data are deliberately excluded, though they are used when interpreting the ordination after it has been made. It is, of course, quite permissible to ordinate and classify other types of multivariate data (see Howard & Howard pp 00 of this Report), but plant ecologists normally restrict themselves to species lists. The purpose of this restriction is that ordination and classification then serve to establish trends in species composition, ie to identify and summarise consistent patterns of occurrence in differing species. Environmental data are subsequently used to interpret the observed trends in species composition. In this way, the basic ecological question concerned with the factors controlling species occurrence is retained in a logically central position in the enquiry.

As a strategy for describing vegetational variation, ordination is newer than classification, but has seen rapid development with the increasing availability of electronic computers. Within ITE, both ordination and classification have been used extensively for the interpretation of survey data, and there has been a steady effort to develop better methods. Of the older methods of ordination, principal component analysis and reciprocal averaging have been the most widely used. A new ordination method called 'detrended correspondence analysis' (see below) has recently been developed in collaboration with Dr. R. H. Whittaker and his colleagues at Cornell University in the USA. Of the older classification methods, association analysis and complete-link, single-link and minimum-variance clustering have been widely used in ITE. A newer method called 'indicator species analysis' (Hill, Bunce & Shaw 1975) has been developed within ITE, and is now widely used both within the Institute and outside it.

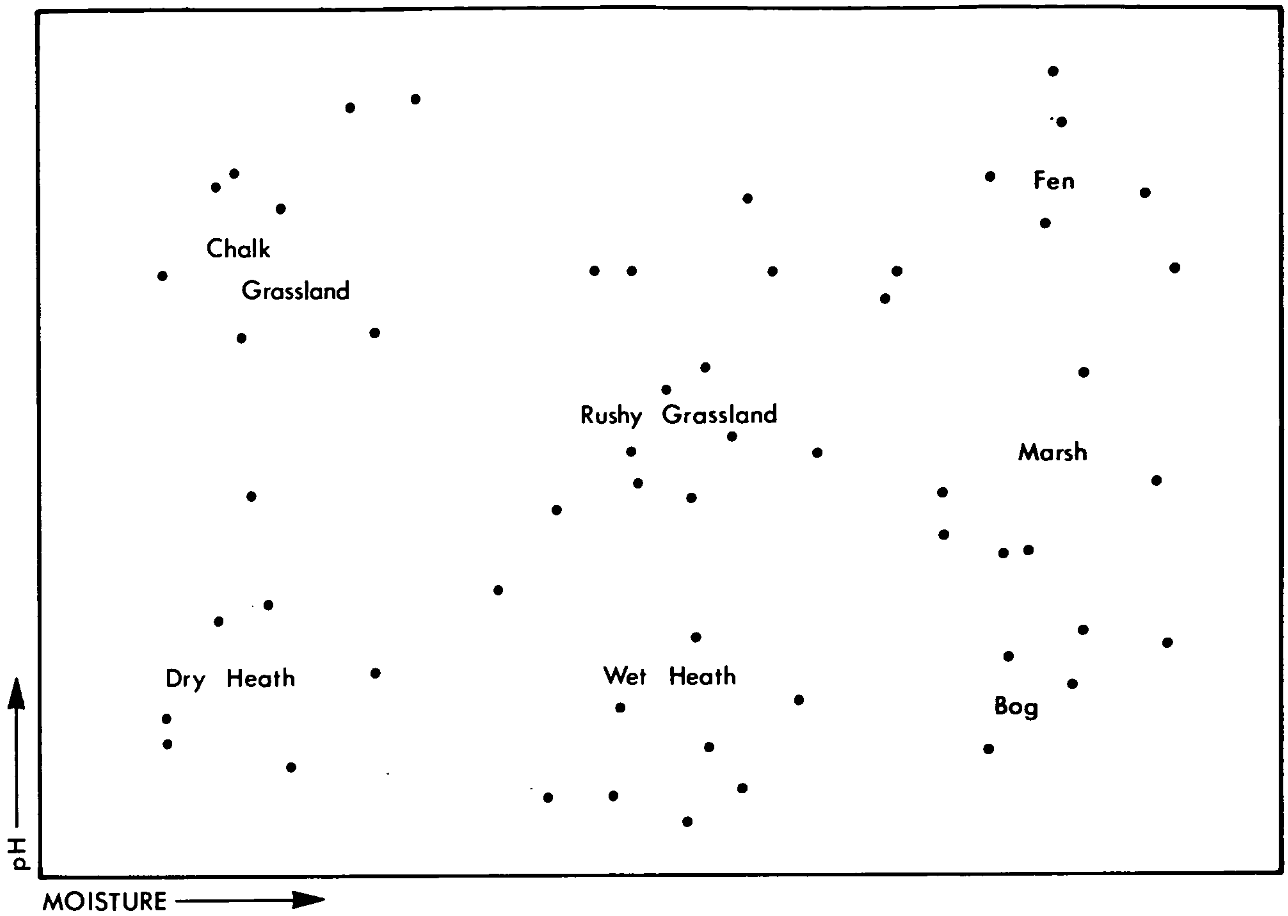


*Figure 13 An ordination diagram (hypothetical data); samples are arranged according to their species composition so that as far as possible similar samples appear close to one another.*

*A model of species abundance*

It is common knowledge that species at the centre of their distributional range are generally more abundant than they are at the edge of their range. The reason for this is that there is a gradual reduction in numbers of suitable habitats towards the periphery. For example, the moss *Pottia starkeana* is a winter annual of open habitats on dry, calcareous soil subject to moderate, but not excessive, disturbance. It is common in the Mediterranean region, but becomes rarer northwards, and is largely confined to the coast in northern Britain. The right combination of environmental conditions can still be found there, but rarely.

Generalising from geographical distributions to other environmental factors, it is reasonable to propose a

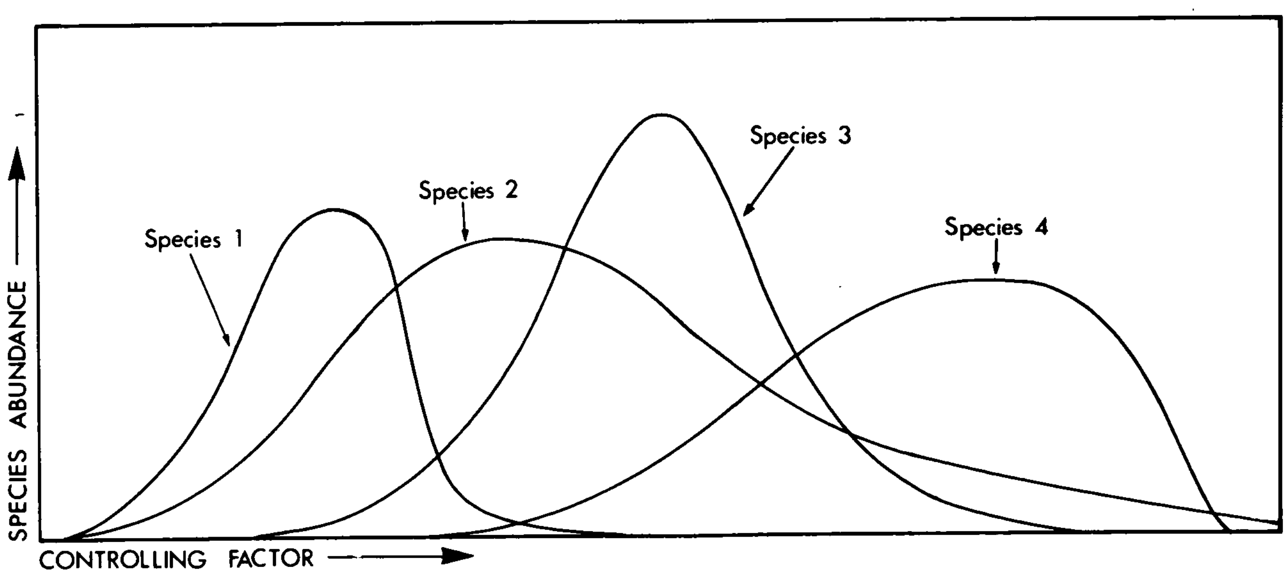


*Figure 14 Principle of unimodal abundance. When the abundance of a species is plotted against a controlling factor (other factors being held equal), then a unimodal curve results.*

principle of unimodal abundance (Figure 14). The principle may be rephrased by saying that, for any controlling factor, each species has a unique optimum for that factor, and its abundance decreases away from that optimum (the optimum may vary if other factors are changed). In contrast, if a species shows a bimodal pattern of abundance with respect to a particular factor, then that factor is not a controlling one. Exceptions to the principle of unimodal abundance are known to occur, but are rare enough not to affect the argument.

What are the implications of this principle for ordination? When ordination is used as an exploratory technique for analysing vegetation data, the aim is to determine hypothetical controlling factors that would best explain the observed multivariate distribution of species. In this application, the principle becomes the model. In other words, starting with the species composition of vegetation samples, the aim is to locate the samples in an abstract space where the species abundances vary in accordance with the model.

*Reciprocal averaging and indicator species analysis*
Reciprocal averaging was first used to ordinate ecological data by W.H. Hatheway (1971). He called it 'contingency table analysis' because the technique was originally developed by R.A. Fisher for the analysis of contingency tables. Another name for the same technique is 'correspondence analysis'. The method simultaneously ordinates both the species and the samples. It is called reciprocal averaging because the samples are scaled so that the position of each sample in the ordination is the average of the positions of the species that it contains, and reciprocally the position of each species in the ordination is the average of the positions of the samples in which it occurs.

There is a vague relation between reciprocal averaging and the unimodal abundance model, in that, if the model holds good, then the score of each species is likely to be close to its mode in the sample ordination. This can be seen by reference to Figure 14, where the ordination is meant to represent a hypothetical controlling factor. Furthermore, if each species is given a score equal to the co-ordinate of its mode, then the average score of the species in a sample will be close to the correct score of the sample.

Reciprocal averaging is especially good at detecting the major trend of variation in sets of vegetation data, the trend appearing as the principal axis of the ordination. Furthermore, the calculations involved are very rapid. The technique is therefore a good basis for classification methods such as indicator species analysis which has already been mentioned. Indicator species analysis is based on the idea that a one-dimensional ordination can be divided into 2 to yield a dichotomy of the data in which those samples with higher values on the axis of the ordination are distinguished from the samples with lower values. The halves can then be split again by ordinating each half separately and applying the same procedure. Repeated dichotomies produce a classificatory hierarchy. With indicator species analysis, there is a complication in that the original dichotomy is modified by a tidying-up process but this need not concern us here. Indicator species analysis has recently been developed further so as to classify the species as well as the samples. When both species and samples have been classified, the data can be presented as an ordered 2-way table.

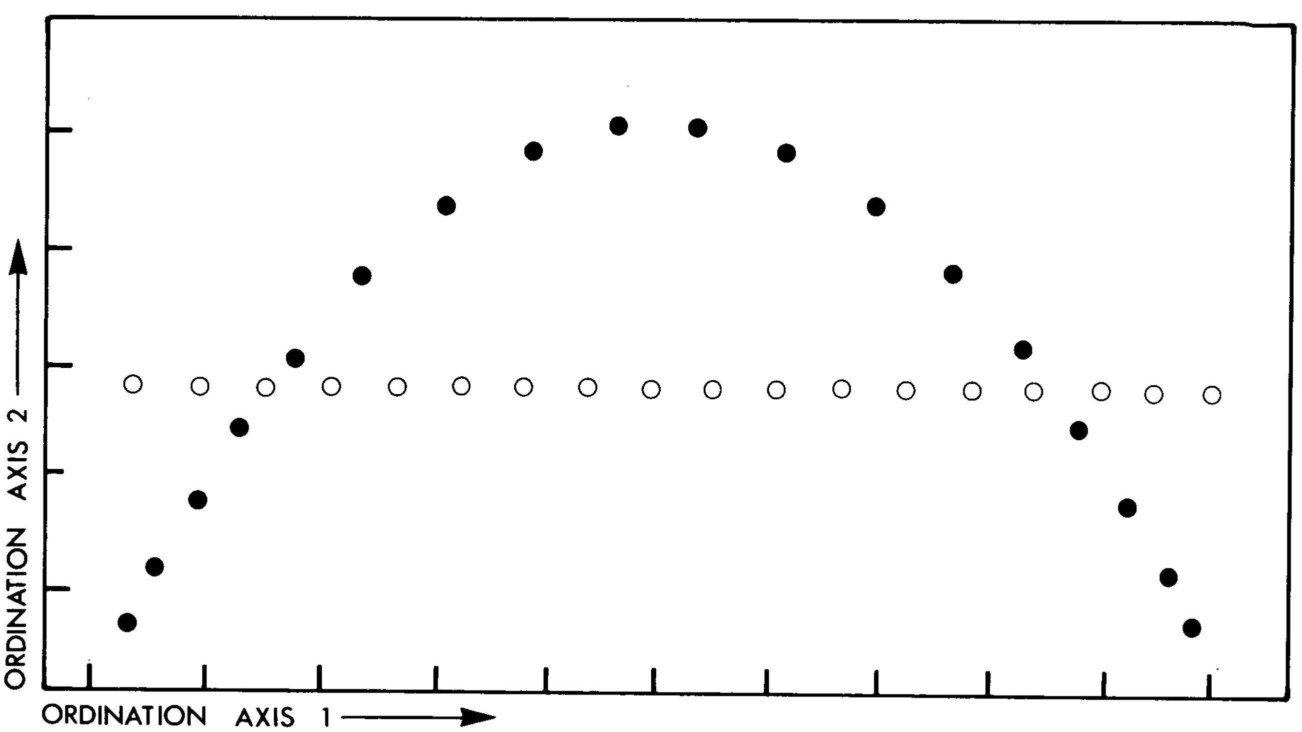


*Figure 15 Distortion of an ordination; with many ordination methods the variation in species composition is displayed in 2 dimensions (closed circles), whereas the true structure should be in one dimension (open circles).*

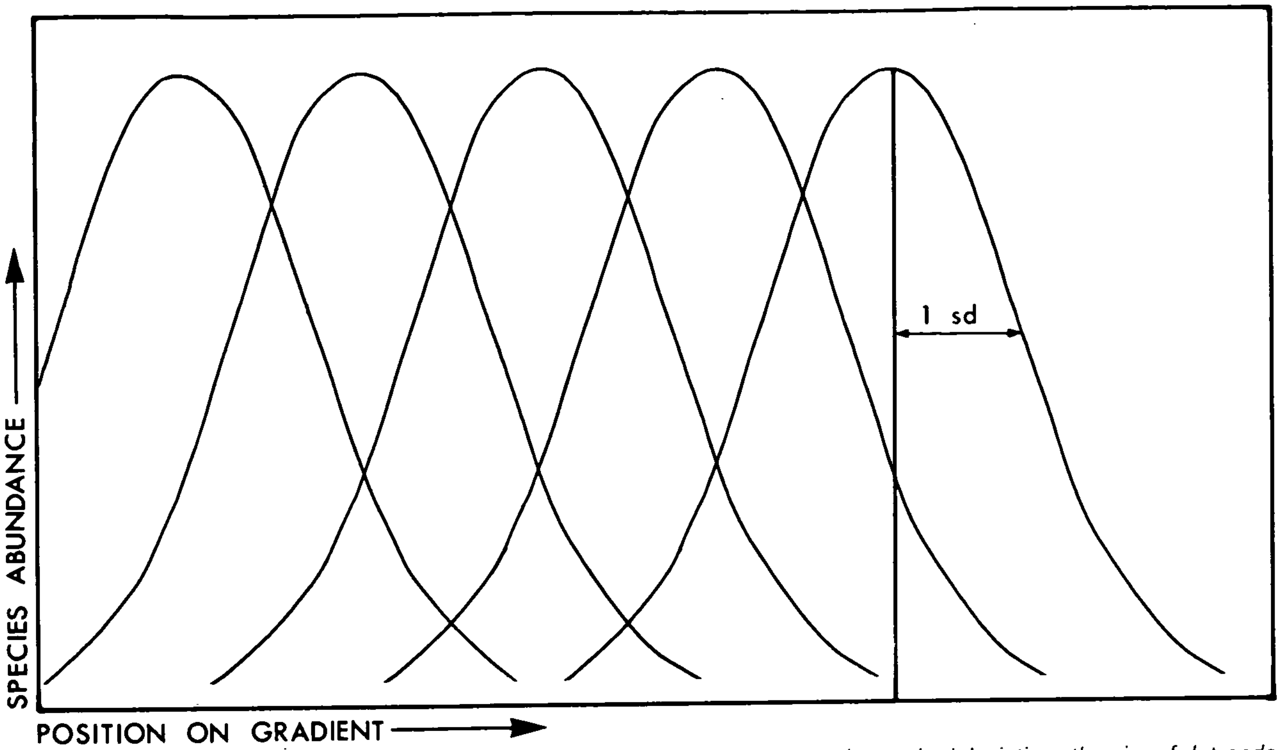


*Figure 16 Ideal scaling of species abundance curves, with each curve having unit standard deviation; the aim of detrended correspondence analysis is to approximate this scaling. In practice, species differ both in their abundance and in the range of habitats that they can tolerate. Scaling is therefore designed so that the average (mean square) dispersion of the species abundance curves is unity.*

*Detrended correspondence analysis*

Most ordination methods used by ecologists were originally developed for other applications—they have been pirated. Principal component analysis, first applied to an ecological problem by D.W. Goodall in 1954, was originally developed by Karl Pearson for morphometric studies: reciprocal averaging was developed for the analysis of contingency tables: non-metric multidimensional scaling originated with the psychometric work of J.B. Kruskall and has recently been applied to ecological problems by M.J.R. Fasham and I.C. Prentice. Unfortunately, these methods have yielded disquieting results in empirical trials on simulated data. Although they correctly detect controlling factors in some instances, they produce distortions in others (Figure 15). None of them has proved entirely reliable in practice, in the main because they have been drawn from various sources with little regard to any realistic model of floristic variation. Detrended correspondence analysis (Hill & Gauch 1980) is a new method, developed from reciprocal averaging and designed with the unimodal abundance model in mind. It does not use the model explicitly, but derives hypothetical controlling factors on which each species is assigned an optimum and each vegetation sample is assigned a position. The scaling is designed to be realistic in terms of the model, in that the species abundance curves (Figure 16) are scaled to have approximately unit standard deviation.

Detrended correspondence analysis has been tested on both simulated data and on field data, with encouraging results. Not only are distortions of the kind shown in Figure 3 avoided, but a reasonable estimate of the length of the gradient is obtained. The calculations are relatively simple, rising only in direct proportion to the amount of data supplied. Most other ordination methods generate diagrams in which the unit of length is arbitrary, or bears little relation to differences in species composition. Furthermore, many of them become computationally intractable when applied to large sets of data.

Detrended correspondence analysis appears to be as good as or better than existing techniques; it points the way ahead by focusing on a model of the vegetation-environment relation but nonetheless has its faults. Ideally, ordination methods should attempt to fit the model explicitly, but there are severe technical difficulties in attempting to do this directly. Detrended correspondence analysis may provide a platform from which explicit model-fitting can be accomplished as the next stage of a successive approximation.

*M.O. Hill*

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## SOME ASPECTS OF THE NUTRIENT STATUS OF NATIVE BRITISH PLANTS

The UK vegetation survey was designed to provide information about the nutrient status of some common native plants. The value of plant nutrient data for this purpose has been assessed critically in the past and the choice of species, sites and sampling procedure had to allow for, though it could not eliminate, a variety of internal and environmental factors which operate in time and space. Ten elements were studied (Table 12) and both plant (photosynthetic component) and soil samples were taken. In the data assessment, particular attention was paid to 15 tree and herbaceous species samples at 25 or more sites (Table 13). This report summarises some conclusions drawn from the plant tissue data.

*Mean concentrations, variation and distribution*

The arithmetic mean concentrations confirmed the published data for these plants. Nitrogen and phosphorus levels varied least overall. The trees and herbs were richer in 4 of the macro-nutrients, and notably in calcium. Unusual values were rare and confined to 5 plants at the most. *Betula* (birch) was outstanding for zinc at 235 ug $g^{-1}$ compared with a mean of 49 ug $g^{-1}$ for the remaining species. The non-marine *Juncus effusus* (common rush) contained 0·29% sodium compared with a mean of 0·034% for the remainder. *Mercurialis* (dog's mercury) had 4·39% potassium compared with 1·52% for the others, which included *Pteridium* (bracken) whose value of 2·34% barely justified its traditional standing as a potash-rich plant.

The between-site variations for individual species were summarised by coefficients of variation (standard deviation as a percentage of the mean). In general, these were surprisingly low for a nation-wide survey. Values for the macro-nutrients were nearly all within 10–40% whilst coefficients above 100% were almost confined entirely to sodium whose levels were the most prone to external (atmospheric) effects. The plants differed relatively little, with the average coefficients for all species falling between 25 and 45% when sodium was excluded. These relatively low coefficients demonstrate a degree of metabolic control over uptake in the field and are also of potential value in planning nutrient surveys and experiments, particularly with regard to numbers of samples required to obtain means of a given precision.

The distributions of concentrations of individual elements were summarised as coefficients of skewness and kurtosis. These values were all significantly different from zero at $P<0·05$ and showed that all the distributions were somewhat skewed and peaked compared with the normal curve. The skewness was positive in all cases as was reflected in the fairly long positive tails made up of outlying values which were subsequently highlighted. Kurtosis values varied more than the skewness coefficients. There were some differences between elements and between species, although a greater range of species or sites would be required to substantiate these trends.

The data have, however, established that nutrient distributions in the species examined are skewed, and this result has implications for elementary significance testing which always assumes the samples are drawn from a normal population. The less robust tests such as the comparison of variances by the F test are most at risk and were not applied to the original data in the current work. On the other hand, the differences between the mode, median and arithmetic mean (2·2, 2·29 and 2·39% respectively for nitrogen in *Pteridium* over 109 sites) did not warrant discarding the almost universally used arithmetic mean at this stage. An approximate normality can sometimes be imposed upon skewed data by a logarithmic transformation, although undue dependence on this practice has been criticised in other spheres of work (Zar 1968; Connor & McCoy 1979). The current work suggests that blocks of plant nutrient data are best assessed on their merits before statistical data processing is begun.

*Inter-element relationships*

Correlation and regression procedures have both been used in this study. Limitations of correlation techniques are well known and the conclusions quoted above suggested that their basic assumptions (linearity of relationship and normality of data), and particularly the latter, should not be overlooked. However, it was shown that the skewness of the data was not sufficient to markedly distort the sample correlation coefficients (r), except when both the correlating elements contained an extreme value at the *same* site. Only 2 instances of this concurrence were noted. (In this work 'extreme' denoted a value greater than the mean plus 4 times the standard deviation.)

A more serious limitation of correlation analysis arises from the skewed nature of the r distribution itself. This is very noticeable in small random sub-samples of a population where a given r value is not consistent. Larger samples are more satisfactory, and a theoretical study suggested the size required to reduce the instability of r to acceptable levels.

The data for *Pteridium* showed the unreliability of the significance of r values in small, random sub-samples taken from a 'population' of 109 sites and suggested that the correlation matrix for this plant began to stabilise only beyond $n = 40$. In a 'real' sample or population, the r values would be influenced by many factors of variation as well as by the skewness of the r distribution itself. However, it appeared that sufficient sites had been sampled to allow a pattern of 'significant' ($P<0·05$) nutrient relationships to emerge that may be characteristic of this species (Table 13). Such a pattern will be strictly valid only for the time of sampling (late July-early August) and will be a consequence of various correlated processes active in the growing

*Plate 5. Female woodwhite butterfly.*

*Plate 6. Typical habitat of the woodwhite butterfly.*

*Plate 7. Woodwhite butterfly 4th instar larva.*

*Plate 8. Woodwhite butterfly pupa.*

*Photographs: M S Warren*

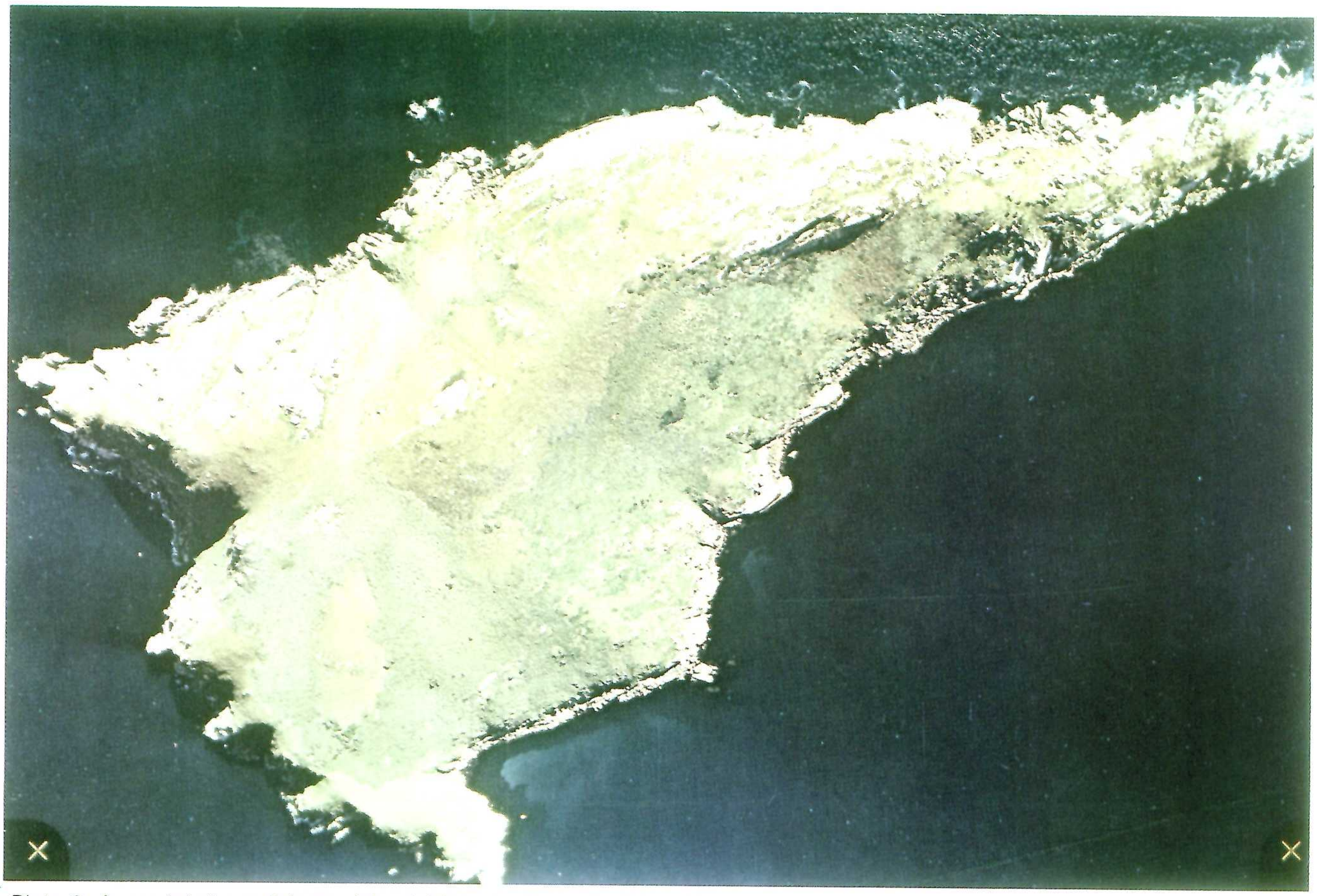

*Plate 9. An aerial view of Anser Island, Victoria, Australia. The different vegetation zones are clearly visible and correspond with differences in the density of short-tailed shearwater* Puffinus tenuirostris *burrows.*
*Photograph: M P Harris.*

*Plate 10. Small cushion-forming species of* Grimmia *and* Andreaea *on a rock surface on South Georgia.*
*Photograph: B Graham Bell.*

*Table 12.* Half correlation matrix for 10 elements within ultimate pinnules of *Pteridium aquilinum* (109 sites). Significant values 0·189 (P < 0·05), 0·246 (P < 0·01).

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Na | −0·354 | 0·050 | 0·308 | 0·023 | −0·126 | −0·157 | −0·102 | 0·025 | −0·133 |
| | K | 0·034 | −0·134 | 0·374 | 0·350 | 0·360 | 0·289 | 0·399 | 0·518 |
| | | Ca | 0·145 | 0·359 | 0·310 | 0·056 | 0·311 | −0·115 | 0·044 |
| | | | Mg | 0·030 | 0·041 | −0·080 | 0·167 | 0·030 | 0·095 |
| | | | | Fe | 0·258 | 0·254 | 0·279 | 0·285 | 0·459 |
| | | | | | Mn | 0·167 | 0·310 | −0·045 | 0·164 |
| | | | | | | Cu | 0·371 | 0·374 | 0·467 |
| | | | | | | | Zn | 0·102 | 0·313 |
| | | | | | | | | P | 0·672 |
| | | | | | | | | | N |

*Table 13.* Numbers of correlations between 10 elements significant at P < 0·05 within 15 species (total correlations per species = 45).

| Species | Sites | Component | Correlations |
|---|---|---|---|
| Quercus spp | 56 | leaves | 6 |
| Betula spp | 50 | leaves | 7 |
| Corylus avellana | 47 | leaves | 8 |
| Fraxinus excelsior | 38 | whole leaves | 15 |
| Alnus glutinosa | 25 | leaves | 6 |
| Calluna vulgaris | 69 | current year's growth | 12 |
| Mercurialis perennis | 47 | leaves | 3 |
| Filipendula ulmaria | 51 | leaflets | 8 |
| Chamaenerion angustifolium | 56 | leaves | 11 |
| Juncus effusus | 64 | aerial growth | 13 |
| Phragmites communis | 37 | leaves | 9 |
| Molinia caerulea | 37 | aerial growth | 8 |
| Deschampsia flexuosa | 44 | aerial growth | 10 |
| Deschampsia caespitosa | 42 | aerial growth | 32 |
| Pteridium aquilinum | 109 | ultimate pinnules | 22 |

*Table 14.* Ranking of elements based on percentage of significant correlations together with the percentage variation of an element explained by 9 other elements. Total correlations per element within 15 species = 135.

| | K | N | P | Ca | Cu | Fe | Zn | Mg | Mn | Na |
|---|---|---|---|---|---|---|---|---|---|---|
| % significant (p < 0·05) | 37 | 36 | 30 | 27 | 27 | 24 | 22 | 21 | 18 | 11 |
| % variation explained | 51 | 48 | 48 | 43 | 41 | 40 | 36 | 37 | 34 | 25 |

season up to this point. These will include nutrient absorption by the root, translocation through and from the rhizome and through the rachis, and utilisation in the pinnae. In this sequence, metabolic activity will be prominent and might be expected to influence the pattern that is revealed.

The other 14 species also had networks of 'significant' r values and were extensive in some, notably in *Deschampsia caespitosa* which exceeded *Pteridium*, and to a lesser extent in *Fraxinus*, *Juncus* and *Calluna*. Others, such as *Mercurialis* and *Filipendula*, showed by contrast very few significant values (Table 12). Although it seemed that this divergence might be genuine, the site coverages for many of the plants were not sufficient for the individual patterns to be accepted as truly characteristic of the species. Although neither the divergence nor the tentative networks could be explained directly, further evidence was sought from the data regarding the relative influence of internal and environmental factors.

Amongst the relationships in general, it was noted that 6 elements (nitrogen, phosphorus, potassium, iron, copper and zinc) were much involved in the strongest correlations (significant at P< 0·01). At P<0·05, the nitrogen-phosphorus correlation was significant in 11 species. These results are borne out by ranking the elements according to the percentage of the total correlations which are significant at P < 0·05 (Table14). In view of the importance of these nutrients in active plant metabolism, it appeared that their functions might have had some influence upon the patterns.

Further evidence was sought from the contributions individual elements made to the total variation within each species, as assessed by principal component analyses. On average, over the 15 species, the first 2 components together accounted for a little under half the total variation of the 10 elements. Whilst this proportion was not high, the components were nevertheless distinct regarding the relative contributions of the elements. In the first component, nitrogen had the highest loading in 6 species, whilst potassium, copper and phosphorus were often prominent. With the possible exception of potassium, these loadings tentatively suggest that the first component of variation in plant nutrient data reflects mainly the protein, enzymic and nucleic aspects of plant metabolism. This evidence bears out a suggestion first made by Garten (1978) in a study of plants in a semi-aquatic community.

Leading elements in the second component were, by contrast, calcium followed by sodium, m anganese and magnesium. This combination did not lend itself to any simple interpretation and it seemed that, whilst calcium and magnesium pointed to the more 'structural' aspects of plant nutrient functions, the presence of sodium hinted at an environmental (atmospheric) contribution. No interpretation was attempted for the third component which generally accounted for little over one tenth of the variation. The evidence from the first 2 was, however, sufficient to suggest there was a marked internal contribution to natural variation of nutrient levels, but not to indicate that this contribution was greater than that from the environment.

Multiple regression analyses were carried out on each species. No element was a clear candidate for the role of 'dependent' variable although initial interest was focused upon the nutrients prominent in the earlier work. These studies showed how far the variation of any one element can be explained by the remaining 9. Table 14 gives the size of the proportion explained and further ranks the elements in an order very similar to that drawn up from the correlation analyses. The regression studies showed that, on average, 40% of the variation of any one element could be explained by the other 9. It was assumed that the inclusion of sulphur (the only prominent nutrient omitted from the study) would not have raised this proportion to one half. Hence, a little more than half the variation remained unexplained and, although some other internal (though non-nutrient) parameters might contribute, it was assumed that the bulk of the unexplained variation would be environmental in origin. Soil nutrient levels will play a part and the relevant data exist to enable an assessment to be made.

In general, this work suggests that, whilst metabolic processes influence nutrient relationships within a plant and are reflected in the main components of variation, the effect of external factors may on average be a little greater. In some common and flourishing plants such as *Mercurialis*, environmental influences appear to have greatly obscured any basic internal control of nutrient levels. Hence, an assessment of the status of such plants in Britain requires consideration of many factors and not just nutrient levels. The results of the survey further strengthen the basic concept of modern plant nutrition which accepts that any plant nutrient level integrates the effects of many internal and external factors (Munson & Nelson 1973).

*H.M. Grimshaw*

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# Research of the Institute in 1979

*Introduction*

This, the main section of the report, gives relatively short accounts of research projects in ITE during 1979. It should be emphasised, however, that the research reported here represents only about one third of ITE's total programme. A full list of ITE projects will be found in Section IV of the report.

As last year, the reports have been grouped according to the main Subdivisions of ITE concerned, beginning with the 3 Subdivisions of Animal Ecology, namely Invertebrate Ecology, Vertebrate Ecology, and Animal Function. These reports are followed by reports of work by the Plant Biology, Plant Community Ecology, and Soil Science Subdivisions of Plant Ecology. Finally, the work of the Subdivisions and centres of the Scientific Services Division is described. The contribution of these service Subdivisions is particularly important to ITE, and enables many of the research contracts and the fundamental research to be undertaken effectively and economically.

## Invertebrate Ecology

### THE INSECT FAUNA OF *HELIANTHEMUM CHAMAECISTUS* IN THE STAMFORD AREA

*Helianthemum chamaecistus* Mill., common rock-rose, is a widely distributed plant of shallow chalk and limestone soils in England and Wales. Large grassland populations occur in some districts, but in the intensely cultivated area around Stamford, Lincolnshire, many populations are small and restricted to road verges, quarries and the steeper slopes of unimproved pastures on the oolitic limestone. Although small, isolated populations of such plants can persist for long periods, little is known about the phytophagous insects that feed on them. Taxonomically, *H. chamaecistus* has few close relatives in Britain and no other members of the Cistaceae occur in the eastern half of Britain. Its insect fauna can therefore be divided into a small group of host-specific species, a range of polyphagous species and, finally, flower visitors whose larvae occur elsewhere. A brief account of those occurring in the Stamford area is given here. The analysis of the effects of habitat size and isolation is still in progress.

The first 2 groups can be divided according to their methods of feeding. Thus, there are several small Lepidoptera that feed during May and June within a tent of leaves spun together. These include the oligophagous gelechiid moth *Teleiodes sequax* (Haw.) and the polyphagous tortricids *Cnephasia interjectana* (Haw.), *C. longana* (Haw.), *Acleris aspersana* (Hubner), and *Olethreutes lacunana* (D. & S.), later instars of which often move into flower heads where they spin the petals together in a similar way. Variation in colour makes it difficult to distinguish these species reliably in the larval stages. The brown argus butterfly *Aricia agestis* (D. & S.) has been seen flying at Barnack Hills and Holes National Nature Reserve in most years, but the larvae, which feed openly on the leaves, have not been found.

There are 2 host-specific leaf mining species, the momphid moth, *Mompha miscella* (D. & S.) and the chrysomelid beetle *Mantura matthewsi* (Curt.). The former has at least 2 generations a year in this district and is very widespread. It has also been reared from seed capsules collected in late July. *M. matthewsi* is less widespread, but locally abundant. Another locally common small chrysomelid is *Aphthona herbigrada* (Curt.). The adults make conspicuous pale blotches on the leaves of rock-rose, whilst the larvae are probably root feeders. Terminal leaf galls are caused by cecidomyid flies. Adults have not been reared but larvae have been tentatively assigned to the genus *Dasineura*.

Two flower beetles *Meligethes solidus* (Kug.) and *M. aeneus* (F.) occur frequently in the flowers of *H. chamaecistus* and probably breed there. *M. solidus* is considered to be host-specific and has a much briefer adult phase than its widely polyphagous relative which occurred in 32 out of 33 sites sampled in 1978 and 1979.

The sap-sucking fauna consists of 3 host-specific Hemiptera, a mirid *Tinicephalus hortulanus* (Meyer-Dur), a cicadellid *Batracomorphus irroratus* Lewis and a stem aphid *Aphis helianthemi* Ferr., and a more polyphagous leaf hopper *Erythroneura parvula* (Boh.). *T. hortulanus* was the second most widespread insect on rock-rose in the sample area, whilst the aphid was only found at 4 sites.

About a dozen non-breeding phytophagous species were found on *H. chamaecistus*. Two of the most common were the polyphagous weevils *Phyllobius roberetanus* (Gred.) and *P. viridiaeris* (Laich.) which fed on petals. Pollen feeders included the beetle *Bruchidius cisti* (F.), whose larvae are known to live in the pods of *Lotus corniculatus*, and the primitive, mandibulate moth *Micropterix aruncella* (Scop.). The weevil *Miarus campanulae* (L.) also occurred regularly in flowers at 3 of the sites where its larval food-plant *Campanula rotundifolia* L. grew.

Preliminary results indicate a strong relationship between the size of rock-rose colony and the numbers of associated species. Barnack Hills and Holes is the largest site and has yielded 19 species, whilst the smallest site produced only 2 host-specific and one polyphagous species.

*B.N.K. Davis and P.E. Jones*

## THE ECOLOGY OF THE WOOD WHITE BUTTERFLY

The wood white butterfly *Leptidea sinapis* (Cover photograph and Plate 5) is an extremely locally distributed butterfly in Britain, where it usually inhabits rides and open areas within woodlands (Plate 6). Over the last 200 years, its range has become greatly restricted and it had become extinct in many areas by the beginning of this century. It is now confined to certain parts of southern and western Britain where it occurs in discrete and often isolated populations.

The larvae (Plates 7 and 8) of the wood white feed on a variety of different vetches, the most important being *Lathyrus pratensis, Lathyrus montanus, Vicia cracca* and *Lotus corniculatus*. However, these plants thrive only in the more open woodland rides and soon die out if they become too shaded. The butterfly's decline, therefore, was probably caused by changing woodland management as well as the clearance of its former habitats. In addition, the species seems to be very slow at colonising new areas, even if they are highly suitable. At present, over half of the existing colonies are in Forestry Commission woods where some open rides are still maintained, allowing the food-plants to thrive.

The present study was started in 1977 and includes a detailed examination of 2 populations in the Yardley Chase woodlands near Northampton. Life-table analysis over the last 3 years has shown that there are 2 main periods of high mortality, the first during the egg and early larval stages and the second during the pupal stage. It is likely that invertebrate predators are responsible for the former, and birds and small mammals for the latter. Parasites were also found in eggs and third instar larvae, but only accounted for a small percentage of the total loss.

Adult numbers were studied by using butterfly monitoring transects (Pollard 1977) and mark-recapture techniques. Adult numbers in the larger of the 2 populations were estimated to be around 2 000 in 1977 and 1978, but fell to just below 1 000 in 1979. This decline was probably caused by reduced egg-laying during the poor summer of 1978, combined with higher mortality in the egg and early larval stages.

Hemispherical photography was used to assess the degree of shade in different woodland rides. Preliminary calculations indicate that the species is most abundant in rides with about 30% shade. Rides with more than 50% shade contain few butterflies and few food-plants. Open rides with less than 30% shade also contain fewer butterflies, although food-plants may be abundant.

Rides were experimentally managed to try to separate the effects of flowers, as nectar sources, and plants, as larval food, on the distribution of wood whites within the colony.

*M.S. Warren*

*References*

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## THE BUTTERFLY MONITORING SCHEME

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

A method of assessing changes in butterfly numbers was described in the 1975 Annual Report. In 1976, a national monitoring scheme was initiated, using this method, and this scheme has expanded steadily since then so that there are now some 80 recorders. Many of the recorders are wardens of National Nature Reserves, but there is a variety of other types of site, including farmland and commercial forestry plantations.

The recording method can be briefly summarised as follows. Walks are made along a fixed route through the site, at a frequency of one per week from April to September inclusive, when weather conditions meet prescribed criteria. The routes are divided into sections to provide information on the local distribution of butterflies. All butterflies encountered within fixed limits are recorded. The weekly counts are used to calculate an index of abundance for each species, which is used for annual comparisons.

The main aims of the scheme are (i) to show annual fluctuations in butterfly numbers and to relate these to weather conditions, or other factors: (ii) to examine trends in numbers at individual sites, and, by relating these trends to regional fluctuations, to assess the importance of local factors, such as habitat change. In addition to these main aims, a considerable body of information has been acquired on the phenology of butterflies and on habitat preferences.

Four years' data from the national scheme are now available and 6 years' data from a limited number of sites in eastern England. Some indications of local trends due to habitat changes are apparent, but, in general, the period of recording is still too short for detailed interpretation.

To calculate regional and national trends, ratio estimates have been calculated using all available data for pairs of years or broods. These ratios are used to build up the average trends over the years. The number of sites in the different (Nature Conservancy Council) regions varies and only in some are there sufficient sites to present regional data. In future years, it should be possible to present data for northern areas in addition to those from southern Britain.

The dominant influence on butterfly numbers in the recording period appears to have been the 1976 drought. This drought caused desiccation of food-plants and perhaps even had direct effects on some

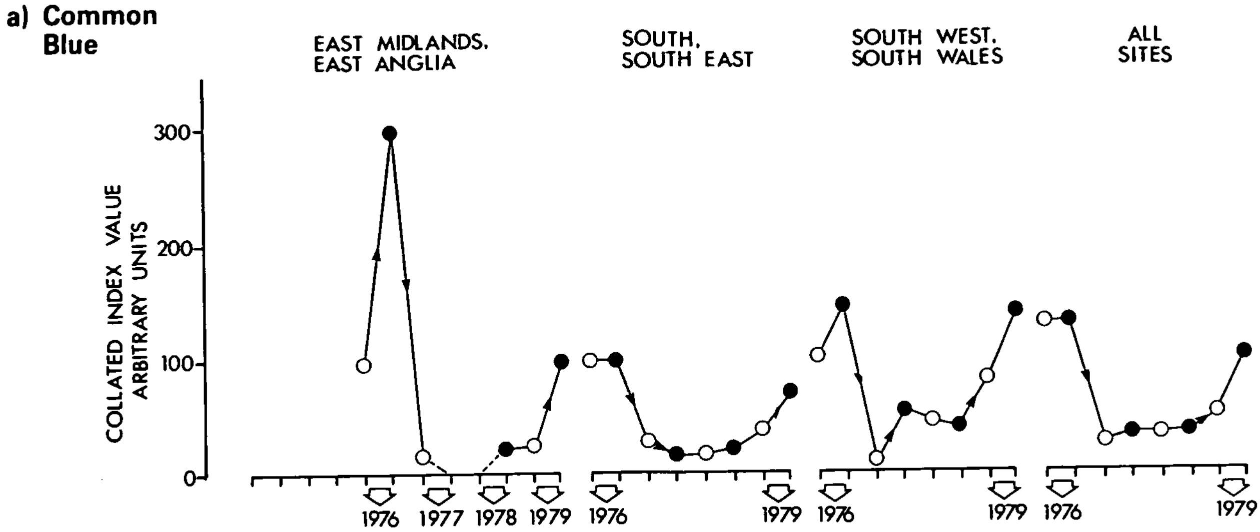
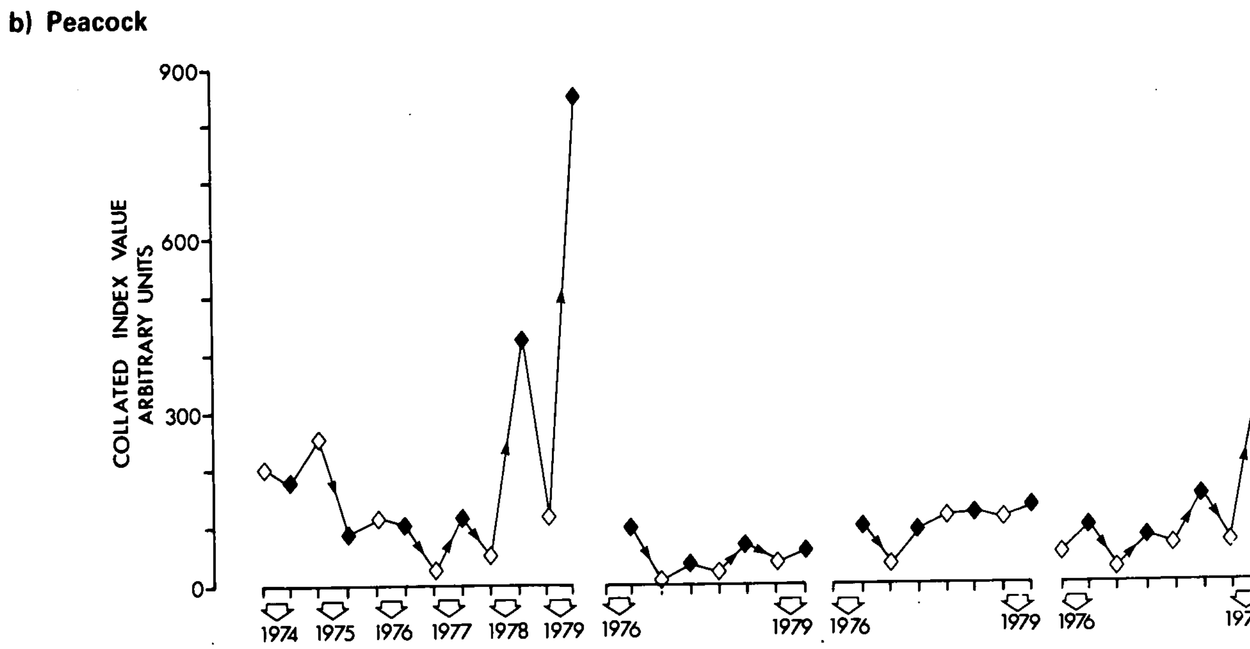



*Figure 17 (a) Collated index values for the common blue butterfly in 3 areas of Britain, and in all sites combined. Units are arbitrary, with a value of 100 for the first 1976 brood. In the east Midlands, East Anglia regions, numbers fell so low in 1977 that the continuity was broken. A new level of 100 was therefore adopted for 1979. Open circles, first brood; closed circles, second brood.*




*(b) Collated index values for the peacock butterfly as above. Open diamond, spring flight; closed diamond, autumn flight. The species has one brood and overwinters as an adult; the same individuals fly in autumn and spring.*

*The arrows indicate where the ratio estimate for a pair of brood indices differs by more than 2 standard errors from 1: that is there is evidence for a real change in index values.*

butterfly species by reducing fecundity. Data on 2 species have been selected to illustrate results from the scheme. The common blue *Polyommatus icarus* showed a steep decline in numbers at the end of 1976 and has been increasing again since then (Figure 17a). The peacock butterfly *Inachis io* showed a similar decline over the whole country after the drought year (Figure 17b), but the numbers have changed very markedly in the different regions since. In the east, it showed big increases in 1977 and 1978, taking it well above the 1976 levels. In other parts of southern Britain, it has recovered from the drought year, but did not show major increases in 1977 and 1978.

*E. Pollard*

THE COMPARATIVE MORPHOLOGY OF *MYRMICA*

Variations between the population ecology of red ant species (genus *Myrmica*) are being examined in this research. Species of *Myrmica* are morphologically similar, but show a wide range of social adaptation to different habitats. It is hoped that this work will eventually highlight those aspects of the social biology of these ants that are critical when a species is adapting to its environment. The work falls into 3 categories, (i) surveying and analysing the field populations in a range of habitats to provide the background population data (Elmes 1976), (ii) laboratory investigation into the comparative social biology of the different species (eg feeding, growth, sexual development), and (iii) investigation into the comparative morphology of the different species. It is this last aspect of the project that is reported here.

*Myrmica* has a bewildering number of described species and forms that show remarkably little morphological variation. As many forms are poorly described, it is likely that many names are synonyms. Nevertheless, in western Europe alone, there are 9 good species and several closely related parasitic species. In central Asia, Mongolia and North America, similar groups of species, some identical with the European forms, have been reported.

Therefore, a taxonomic investigation of the species studied for their population ecology was essential (i) to ensure that we are really dealing with the same species when we study different habitats, and (ii) to try to establish a hierarchy of taxonomic similarity of the species, to compare with a similar ecological hierarchy.

Queens can be considered as representing the full expression of phenotypic variability in ants, males being haploid and workers being incompletely developed females. Therefore, an initial study has been made on samples of about 40 queens from each of 9 European species of *Myrmica*. Two of these, *M. ruginodis* and *M. rubra*, have a microgyne form related in morphology to social parasites, such as *M. hirsuta* (Elmes 1978; Pearson 1977). Twelve body measurements were made on each queen.

These measurements were subjected to canonical variate analysis, which describes the variation by new variables (canonical variates) as linear orthogonal combinations of the original variables. The canonical variates (CVs) maximise the variation between groups (species) and minimise the variation within groups. The 9 species can be plotted in a space described by the first 3 canonical variates which respectively account for 63%, 14% and 11% of the total variation (Figure 18). CV1 is mostly explained by relative variation of the frons width (the minimum distance between the frontal ridges of the head); CV2 is a measure of the shape of the waist region (the petiole and post-petiole); CV3 is a relative measure of the length of the thoracic spines. The 90% confidence limit for each species is represented

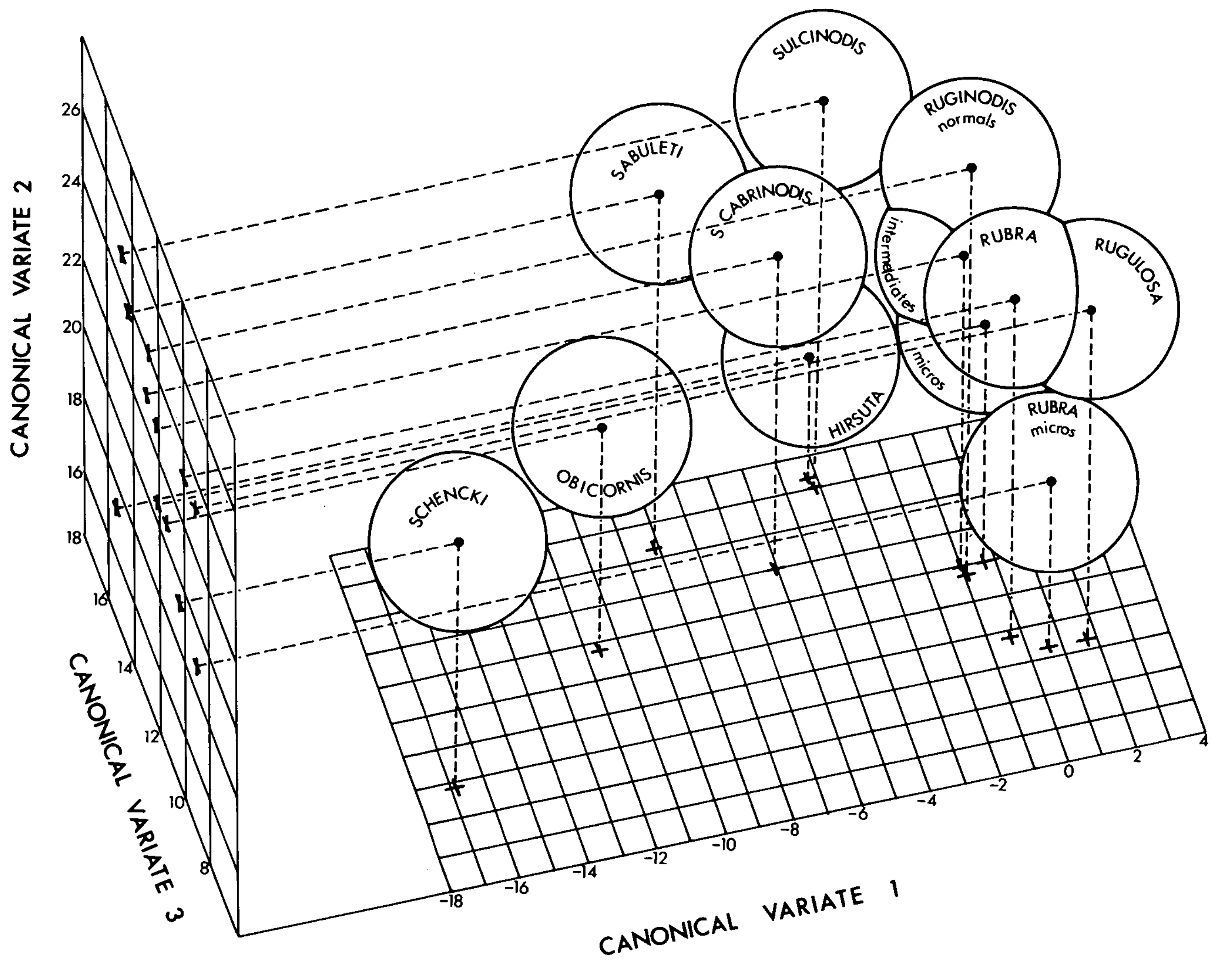



*Figure 18 The mean (spot) and 90% probability space for* Myrmica *species plotted in 3 dimensions, being the first 3 canonical variates that maximise the variation between groups. The groups are the 9 good European species, plus the parasitic* M. hirsuta *and the microgynes of* M. rubra *and* M. ruginodis.

by a sphere in 3 dimensional space (Figure 18); most species are quite distinctly separated by these particular combinations of morphological characters comprising the CVs. However, *M. rubra*, *M. ruginodis* and *M. rugulosa* are not so easily separated from each other, and *M. ruginodis* shows no clear distinction between the microgyne and normal forms, the 90% probability spaces mostly overlapping.

Figure 18 can also be used to illustrate the degree of relatedness of the species in terms of the original variables measured. *M. scabrinodis* seems to lie towards the centre of variation, with *M. schencki* and *M. ruginodis* at opposite extremes. This pattern reflects both a grouping based on the shape of the antennal scape (not measured here) and one based upon ecological similarities.

Recently, the variation within a species has been examined by similar measurements made on individuals of *M. ruginodis*. Workers were used because insufficient queens were available. Ten workers were measured from each of 69 colonies from 19 different sites in 6 countries. A nested analysis of variance was made on each variable separately, and, in every case, this analysis showed highly significant differences between colonies within sites, but no significant variation between sites within countries. Frons width, leg length and thoracic spine length showed significant variation between countries ($P<0\cdot05$). This analysis can be neatly summarised by a similar analysis of variance on each of the first 3 principal components that maximise variation between all individuals (Table 15).

*Table 15.* Effects of the source of variation, expressed as a percentage of the total variation, within the first 3 principal components that maximise the variation between all individuals of *M. ruginodis*. The percentage of the overall variation accounted for by each component is given in parenthesis. Each level of the sources of variation can be compared statistically with the sum of the variation at the lower levels to see whether a significant extra variation can be attributed to that source.
( * $P<0\cdot05$, ** $P<0\cdot01$, *** $P<0\cdot001$).

| Hierarchical Sources of Variation | Percentage of the Variation within Component 1 (73) | Component 2 (6) | Component 3 (5) |
|---|---|---|---|
| between: | | | |
| Individuals | 36 | 56 | 70 |
| Colonies | 61 *** | 23 *** | 10 *** |
| Sites | 0 | 4 | 4 * |
| Countries | 3 | 17 ** | 16 ** |

These components account for a total of 84% of the variation between individuals; component 1 seems to be some overall measure of size, component 2 is mostly a combination of petiole width and distance between the thoracic spines, and component 3 is mostly a combination of negative petiole width and spine length. More than half the variability in component 1 is due to variation between colonies within sites. Neither site nor country differences seem to be a significant source of variation in the size of individual workers of *M. ruginodis* (component 1). In fact, there are no highly significant variations between sites, but, once size differences are eliminated, countries differ significantly on some aspects of morphology (components 2 and 3).

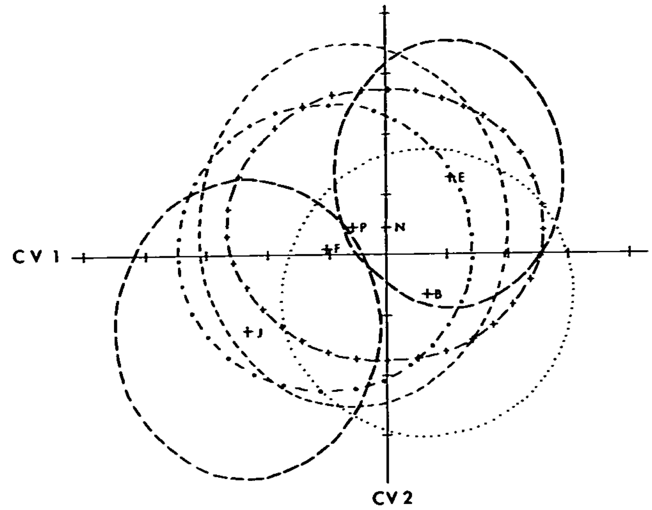



*Figure 19* The mean and 95% probability space for M. ruginodis from 6 countries plotted in the 2 dimensions represented by the first 2 principal components maximising variation between individuals. E + solid line = Spanish Pyrenees; N + dashed/crosses = Norway; P + dashed line = Poland; F + dashed/dots = Finland; B + dotted line = Britain and J + solid line = Japan.

This is illustrated by Figure 19 where the first 2 canonical variates for each country have been plotted; these jointly account for 78% of the variation between individuals from these countries. As a result of non-homogenous variances, the 95% probability limits in these 2 dimensions are represented by elipses. It can be seen that Japan differs significantly from Spain on the aspects of variation measured by these variates, but no other significant differences between countries can be detected.

Finally, the problem of the effect of the microgyne queen was examined by using the data from Britain and Norway, where information on queen size within colonies was available. These data showed that between colony variation accounts for between 47 and 72% of the total variation in any measurement. Of this variation, queen size accounted for between 30 and 50%, so that between 20 and 35% of the total variation is due to differences between colonies regardless of the queen size.

Detailed analyses of these data are still in hand, but it can be concluded that, for the characters measured, there are some differences between countries, but no significant differences between sites. Huge differences between countries are not expected, because, if each country was significantly different from each other with very little overlap, the chances are that the ants from each would have been described as separate species. For example, although all the Japanese *M. ruginodis* were identified as such by Japanese myrmecologists, there is a suspicion that at least one colony belongs to species *M. yoshiokai*, a species that is very similar to *M. rubra*. This observation could explain some of the differences shown in Figure 18. It is surprising that ecological sites within a country do not differ significantly, all the variation being accounted for at the lower level of between colony differences. As sites within a country were generally within 200 miles of each other, but countries are separated by at least 1 000 miles, one interpretation could be that there is good mixing within areas of 200 miles diameter, but some isolation over great distances. The implications of this result upon the field populations studied are being considered.

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## THE DISTRIBUTION OF BEETLES IN SOME UPLAND HABITAT TYPES

Invertebrate survey is difficult because of the vast variety of species and immense number of individuals involved. To make survey manageable, characterisation of the environment into units based on land and vegetation survey often has to be used as the basis for recording. The most commonly used unit is 'habitat' or 'habitat type', as used in the sense of the 'kind of locality, as the sea-shore, chalk hills, or the like .... in which a plant or animal naturally grows or lives' (Onions 1973); 'an area with a certain uniformity in physiography, vegetation or some other quality considered important (or easily recognised) by ecologists' (Andrewartha 1961); or, more specifically, the environment in which a community exists, ie biotope (Whittaker *et al.* 1973). Other environmental units can be more objectively determined. The aim of this study was to examine the validity of the use of environmental characterisations as a basis for invertebrate survey in an upland area, by examining the relationship between the invertebrate species and associations, ie communities, and, in particular, habitat type.

The study area (Plate 1), near Aber in North Wales, was at an altitude of 305 m and was grazed by sheep and mountain ponies. It contained 7 identifiable habitat types, which can be described by their dominant plant species: herb-rich *Agrostis tenuis/Festuca ovina* grassland, *Nardus stricta* grassland, bracken *Pteridium aquilinum*, gorse *Ulex gallii*, *Calluna vulgaris* heath, *Vaccinium myrtillus* heath, and wet flush *Juncus effusus*. There was some gradation from grassland to the shrub habitat types, but any habitat type could occur adjacent to any other. Invertebrates were collected over a 2-year period by pitfall trapping (10 permanent traps in each of 2 examples of each habitat type) and, subsequently, by heat extraction of turves. Only the beetles are being identified at present.

The data are being examined from several viewpoints. The first approach is to examine the relationship of each beetle species with each habitat type in order to determine whether or not any 'preference' is shown. The results of a preliminary analysis of the data for some common carabid and staphylinid species are shown in Figure20. The habitat fidelity value has been derived for each species by calculating the frequency of the species in each habitat. These values are compared in such a way as to result in a range of values from +1 to −1; +1 indicating total 'preference' for a habitat, 0 showing neither 'preference' nor 'rejection', and −1 demonstrating total 'rejection' of that habitat: the intermediate values have intermediate meanings. Although large, mobile carabids might appear to have similar requirements, marked differences in habitat 'preference' are apparent. *Pterostichus madidus* shows a marked and significant 'preference' for bracken, whereas *Nebria salina* 'prefers' *Agrostis* grassland and *Pterostichus nigrita* is found solely in the *Juncus* habitat type. *Carabus problematicus*, however, shows 'preference' for the dwarf shrub habitats: gorse, *Calluna* and *Vaccinium*. The staphylinid species, *Staphylinus aeneocephalus* and *Xantholinus linearis*, both show 'preferences' for the grassland habitat types. The mechanics of such differences in distribution will be examined at a later stage of the research, but it is likely that behavioural differences will provide the immediate selection of habitat type, although differences in food, shelter or physical requirements of either adult or larva might be the basic reason for such separation. Competition between the species might also be involved where the requirements overlap.

The second approach is to use more objective environmental characterisations than habitat type. These will be achieved by using ordination techniques (Hill 1973) to group the pitfall trap sites according to the ground cover (plant species, stones or bare soil) surrounding them. The relationship between the beetle species and these groups can then be examined in a similar manner to that with habitat type.

The third approach is to examine the associations between beetle species independently from their relationships with environmental characterisations. This examination will be achieved by treating the total beetle species found at one pitfall trap location as the basic unit and grouping these by ordination methods.

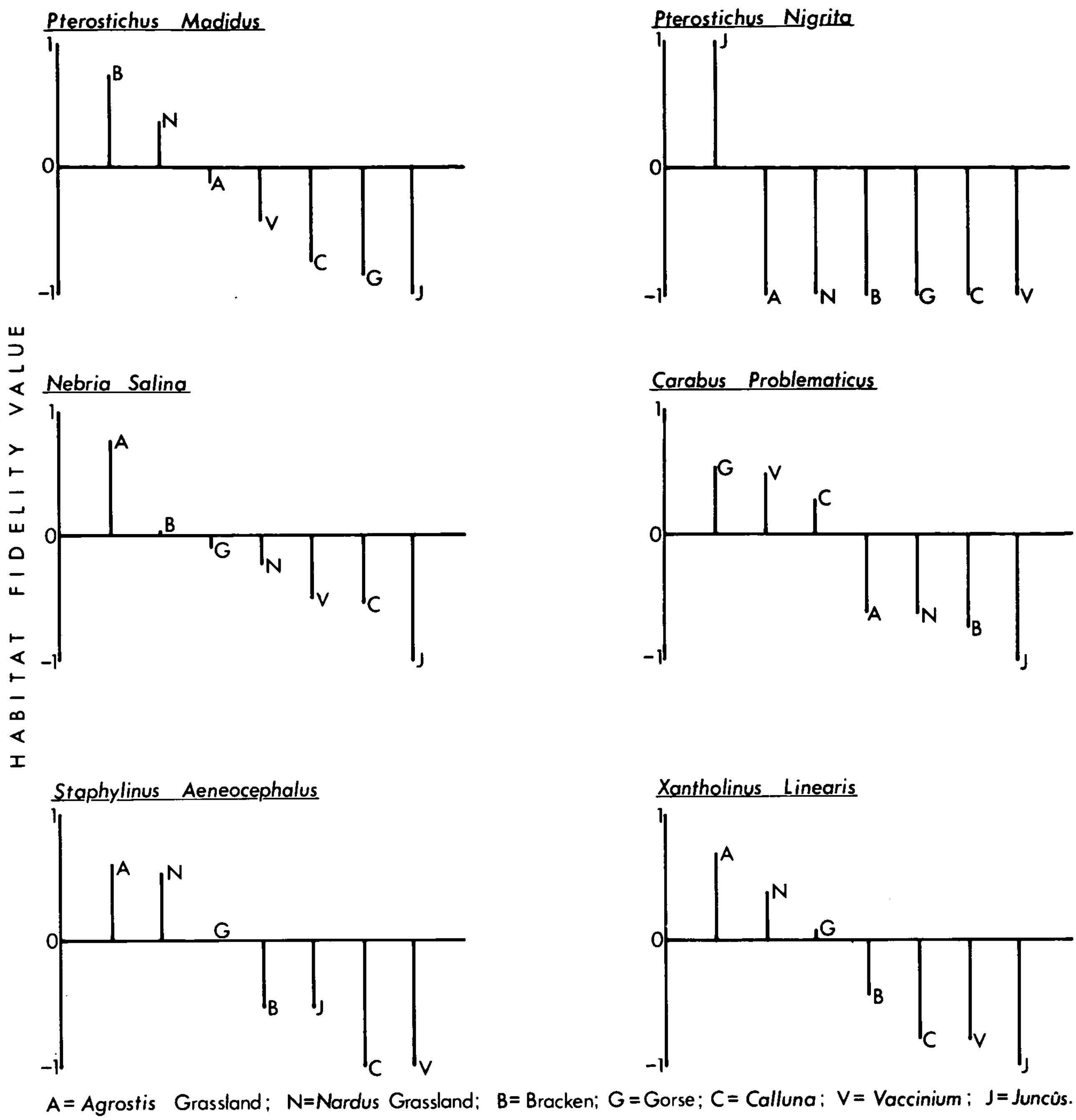


*Figure 20 The relationship between some carabid and staphylinid beetle species and habitat type, as demonstrated by habitat fidelity values.*

The relationship between the resultant species (communities) and habitat type or plant species will be examined.

*A. Buse*

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DORSET HEATHLAND SURVEY

The heathlands of Dorset were formed about 3,600 years ago when Bronze Age men cleared the forests. The open spaces which they made were colonised by heathers (mainly *Calluna vulgaris*) and hazel *Corylus.* Further forest clearances in the late Bronze Age (2950 BC) ensured that open heathlands were created. From the Iron Age until the mid-eighteenth century, few changes either in the extent or the use of these heathlands took place, and, for the most part, they were used as rough grazing by cattle. Sporadic fires, used in an attempt to improve the grazing, and some grazing by deer and rabbits prevented the return to woodland conditions.

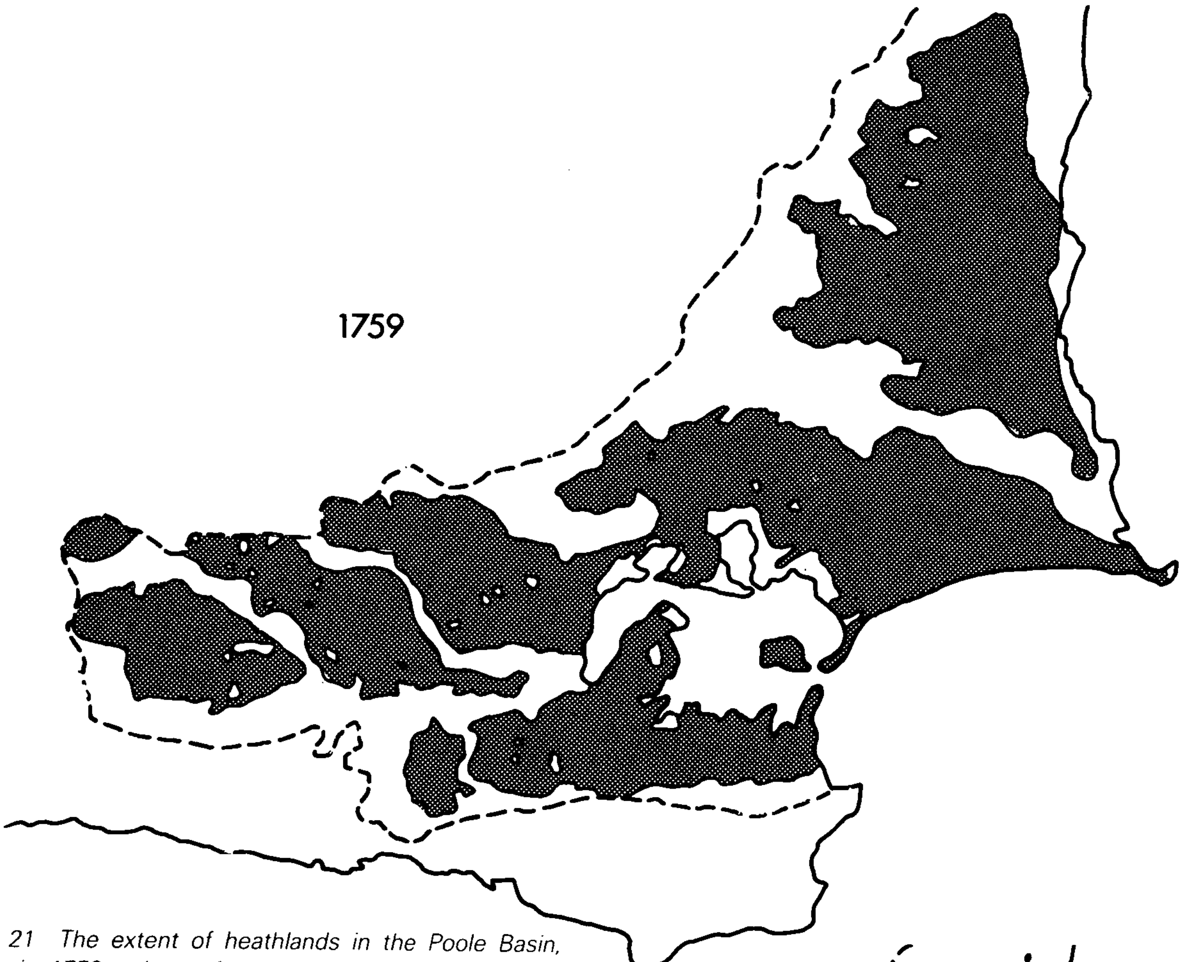
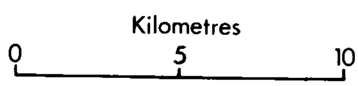



Figure 21 The extent of heathlands in the Poole Basin, Dorset, in 1759 redrawn from the maps of Isaac Taylor.



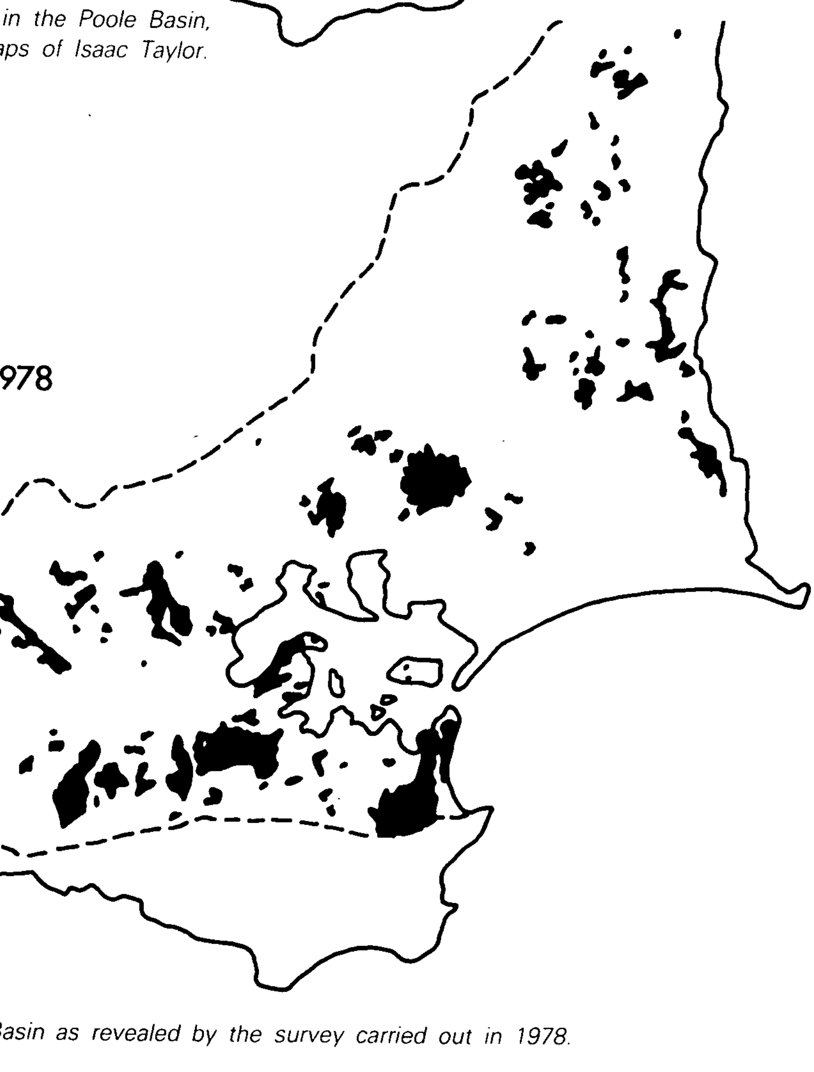




Figure 22 The extent in the Poole Basin as revealed by the survey carried out in 1978.

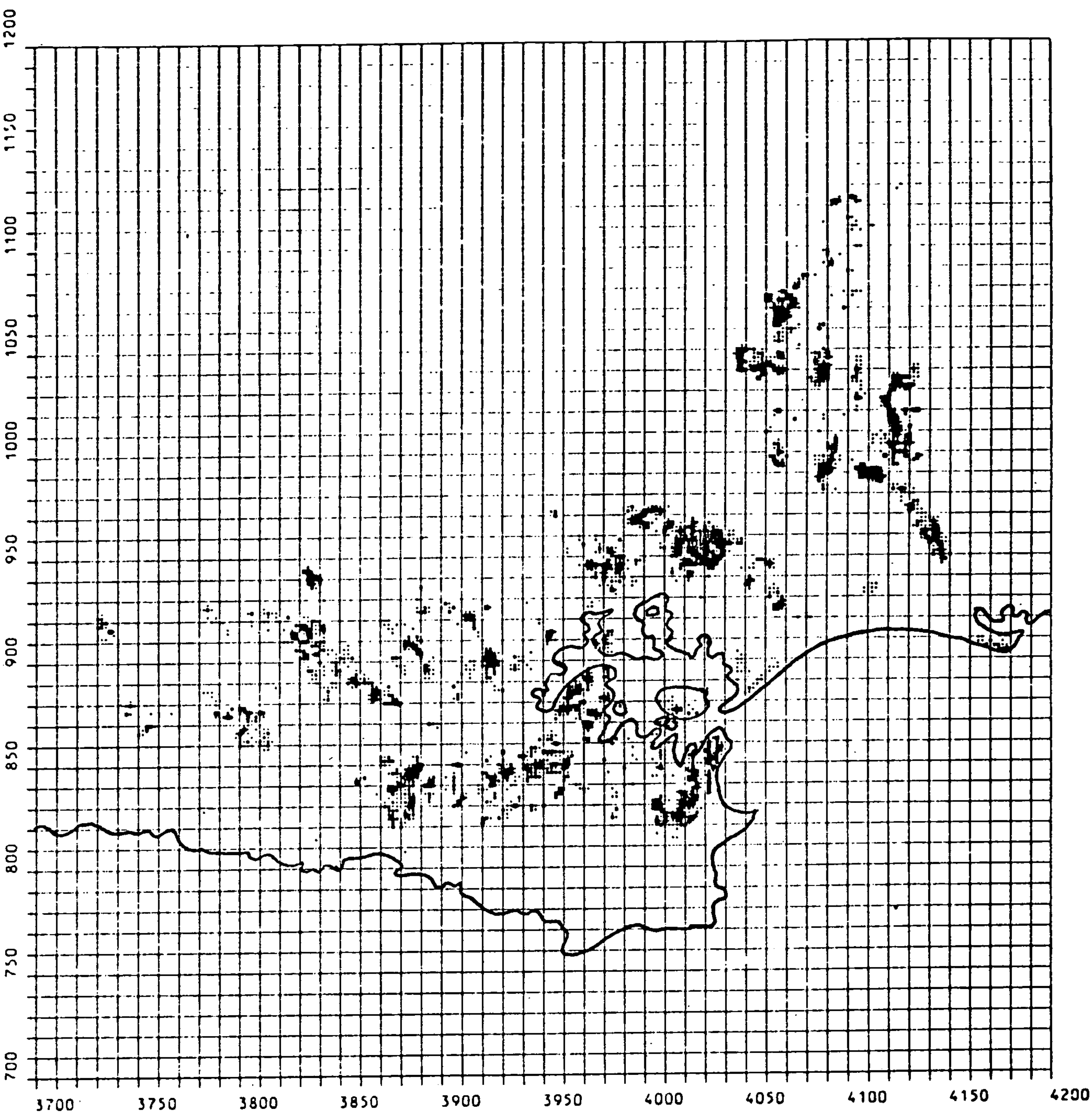



*Figure 23 A computer drawn map for the 1978 survey data showing the distribution of dry heath in the Poole Basin.*

The maps of Isaac Taylor in 1759 (Figure 21) show almost 40 000 ha of heathland in south-east Dorset (Poole Basin). This heathland was in several large patches separated by the river system. Since that time there has been a steady decline in the area of heathland, due to reclamation for agricultural, afforestation, urban development and mineral extraction. From various documentary sources, it has been possible to detail the changes which have taken place.

| | | |
|---|---|---|
| 1759 | 39 960 ha | Isaac Taylor (Haskins 1978) |
| 1811 | 30 400 ha | 1st Edition Ordnance Survey (Haskins 1978) |
| 1896 | 55 000 ha | 2nd Edition Ordnance Survey (Haskins 1978) |
| 1934 | 44 945 ha | Land Utilisation Survey (Haskins 1978) |
| 1960 | 10 000 ha | Moore (1962) |
| 1978 | 5 832 ha | Webb and Haskins (1980) |

Associated with the decline in total area, there has also been considerable fragmentation of the heathlands. Moore (1962) recorded just over 100 pieces with an area greater than 4 ha. Webb and Haskins (1980) showed that there were 768 pieces of heathland, of which 14 were over 100 ha and 169 over 4 ha. Of the remaining 608 pieces, 476 were less than one ha (Figure 22).

Previous surveys of these heathlands had been of a

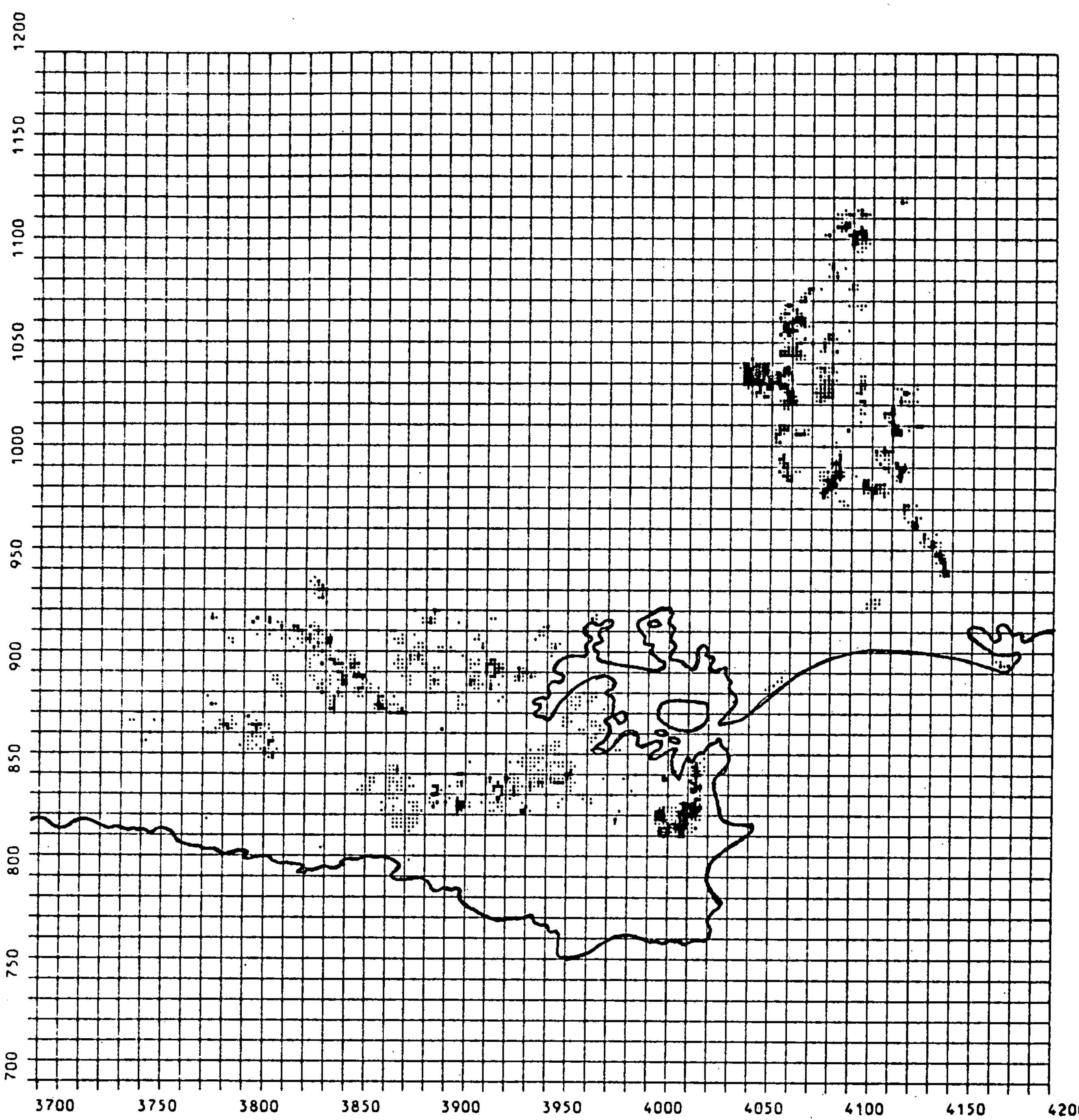



*Figure 24 The distribution of* Ulex minor *in the Poole Basin heathlands.*

general nature and identified the broad patterns and large-scale trends. Because of the continuing pressures on these heathlands, a detailed ecological survey was required which would not only revise previous surveys, but would contain sufficient detail to assess future trends and to present a more precise description of the vegetation types and their extent.

The recording unit for the 1978 survey was a 200 metre grid square derived from the National Grid. A survey team located every square which contained some type of heathland; this survey involved visiting just over 3 000 such squares. For each square, the main heathland types (dry heath, humid heath, wet heath and peatland) were recorded on a 3-point scale expressing a combination of frequency and cover. Then, within each type, the main vegetation associations were recorded in the same way. The various possible plant associations were derived from experience of the Dorset heathlands accumulated over many years rather than from 'objective' methods of vegetation analysis. In addition to the 4 heathland types, a further 8 associated vegetation types and the age of the heathland were recorded. There were 3 other categories which were recorded for each heathland square, namely the presence of species of interest, physiography and land use and management. In all, 184 attributes were recognised, although normally no more than about 30 were recorded from any one site.

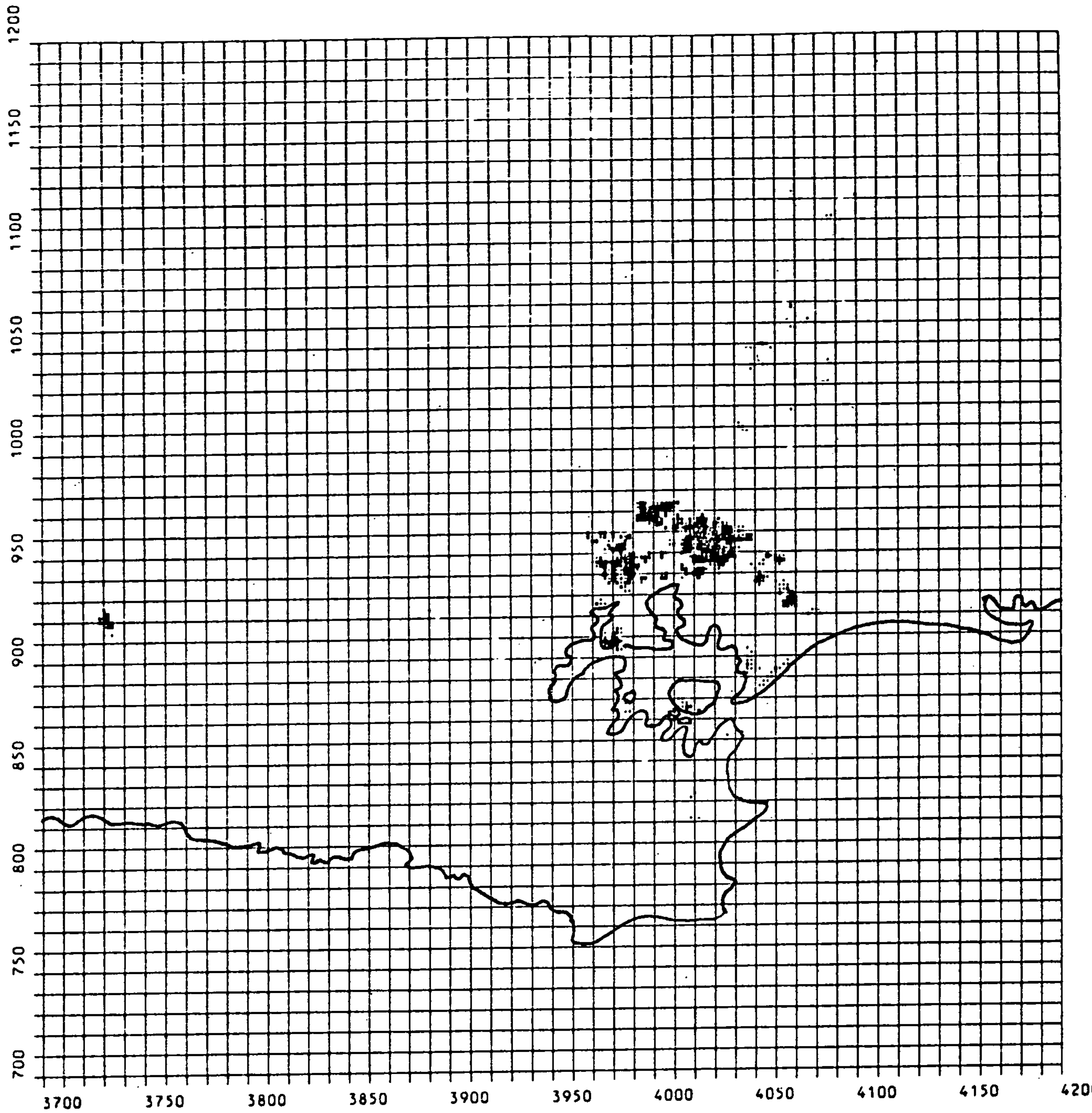



*Figure 25 The distribution of* Ulex gallii *in the Poole Basin.*

The data have been stored on the twin IBM 360/195 computers at the Rutherford Laboratory of the Science Research Council at Harwell. Computer programs have been developed using the NERC G-EXEC data base system which enable the data to be sorted for any combination of attributes. The information recovered by the computer is available in the form of a listing of appropriate squares and their grid references, together with their attribute values. Alternatively, the computer will prepare scaled maps (on which is superimposed an outline of the Dorset coast) of the requested attributes and, if required, with symbols varying with the attribute value.

The information accumulated by this survey makes it possible to map the distribution of the main types of vegetation, or of particular plant distributions. Figure 23 combines these 2 features and shows a map of dry heathland in which the vegetation consists only of associations containing *Calluna vulgaris*. It is also possible to prepare maps of the distributions of single species, or physical features. Figures 24-25 show the distributions of species of dwarf gorse *Ulex*. In the Poole Basin, the distributions of *Ulex minor* and *U. gallii* overlap; the maps show *U. gallii* occupying the centre of the Poole Basin, while *U. minor* occurs to the east and west. There are few places where both species occur (Figure 26). A further use of the survey is where appraisals of individual squares are made, and similar squares located either as sites for single species, or as

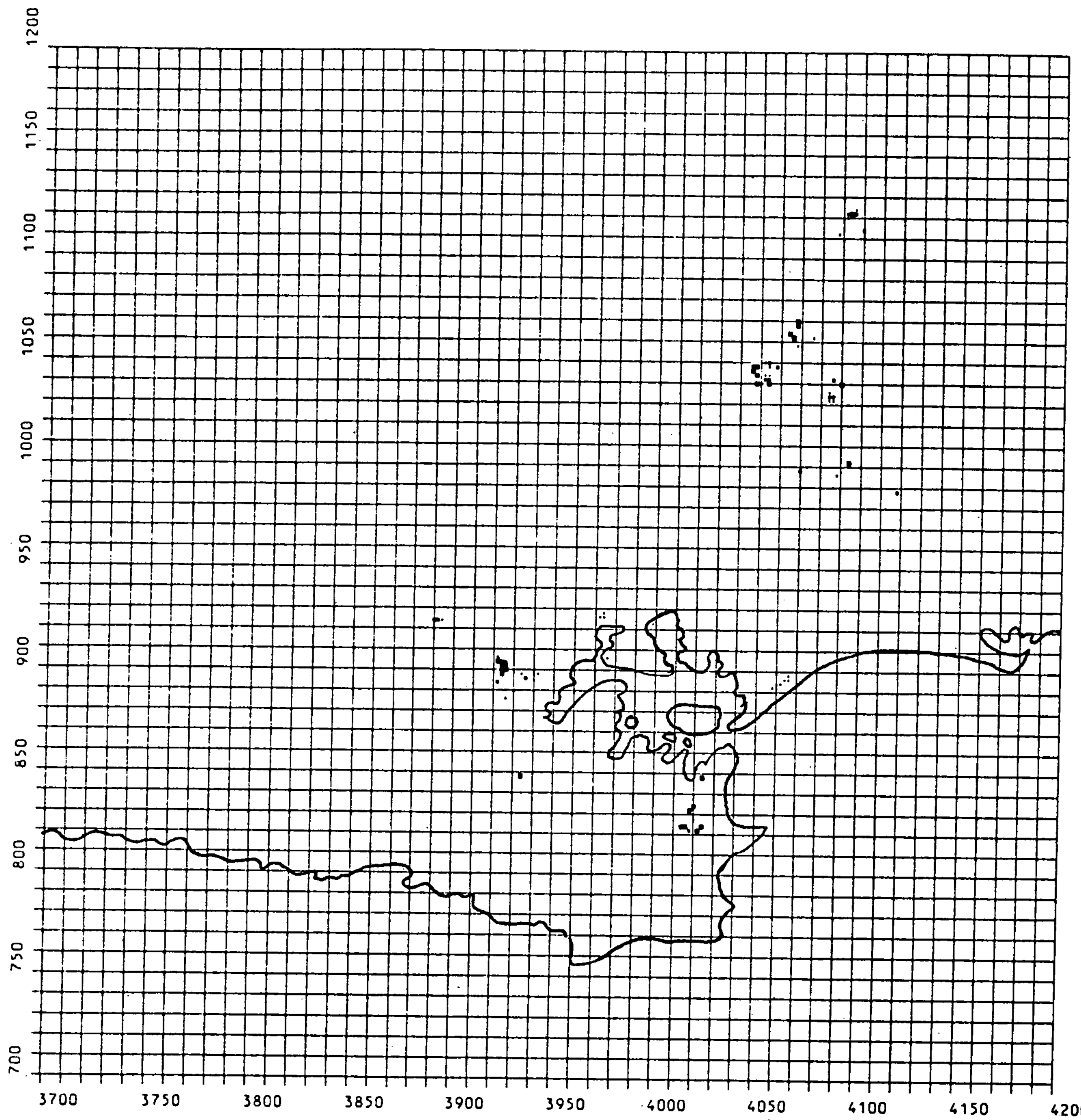



*Figure 26 The 200 x 200 m grid squares in which both* U. minor *and* U. gallii *occurred.*

a means of making an ecological assessment of a particular site in relation to the whole heathland in the Poole Basin. These data also provide a population of sites which can be used for planning sampling programmes.

Considerable use has already been made of the survey data especially for planning research programmes and formulating conservation strategies for the heathlands in the Poole Basin.

We are grateful to the Manpower Services Commission who provided financial support for the field survey team through their Job Creation Scheme.

*N.R. Webb and R.T. Clarke*

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PASTURE WOODLANDS

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

The term 'pasture woodland' is possibly unfamiliar. It can be applied to areas characterised by the presence of broadleaved woodland in an open canopy structure over grassland or heath. Pasture woodlands were managed with the dual objectives of providing grazing land and trees. The trees afforded shelter to domestic stock and deer in winter and could be used to provide winter browse for the animals, or timber, in both cases usually by pollarding. Management of woodland in this way has been known in Britain since at least the 11th century in some royal forests, chases, parks, wooded commons and winter grazed woods. The surviving pasture woodlands contain many over-mature trees and probably always have done so, mainly because pollarding has the effect of prolonging the life of most broadleaved trees. These surviving areas in lowland Britain are thought to contain elements of the flora and fauna of the primaeval Flandrian forest cover, particularly those associated with over-mature trees and dying and dead wood, which are poorly represented in, or absent from, other types of woodland where over-mature trees are usually very uncommon. It is only recently that the importance for wildlife conservation of pasture woodlands (as a distinct woodland type) has become fully realised.

At least 100 species of Coleoptera, such as *Abraeus granulum, Ampedus cardinalis, Phloiotrya vaudoueri* and *Ptenidium gressneri*, appear to occur almost only at sites known to have been managed as pasture woodland for many centuries. The same seems to be true of some species of Diptera and possible species from other taxonomic groups of invertebrates. Similarly, some assemblages of lichens and bryophytes, such as the *Lobarion pulmonariae* community, can be regarded as characteristic of pasture woodlands and to be indicative of ecological continuity (Rose 1976; James *et al.* 1977).

In 1975, the Nature Conservancy Council commissioned work leading to an up-to-date assessment of the extent and condition of the resource of pasture woodland habitats in lowland Britain. The main emphasis of this work was towards the invertebrate fauna, but knowledge of the importance of sites for epiphytic lichens and bryophytes was also taken into account. Information on the epiphyte flora of sites came from work done independently by Dr. F. Rose of King's College, London, and other members of the British Lichen Society. An inventory of 400 sites of known or potential value for wildlife conservation was compiled. Most of the sites were, at least historically, classifiable as pasture woodlands, but all were believed to have large numbers of old trees. Between 1975 and 1978, approximately 100 sites were visited and described. Detailed surveys have been made at 6 parkland sites at which complete inventories of the tree cover were made, the histories of the sites investigated and knowledge of natural history records reviewed. For 3 sites, Moccas Deer Park and Brampton Bryan Park in Hereford/Worcester, and Dynevor Deer Park in Dyfed, the management was examined and proposals made for programmes of replanting and regeneration, and other management aimed at perpetuating the value of the sites for wildlife conservation.

The inventory of sites and results of the various surveys have been reported to the Nature Conservancy Council and are available for use in developing its policies for conserving this hitherto rather neglected type of British woodland.

*P.T. Harding*

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## Vertebrate Ecology

SHEARWATERS IN VICTORIA, AUSTRALIA

(This work was commissioned by the Ministry for Conservation of the Victorian State Government, Australia)

Recently ITE has developed techniques for monitoring the numbers of puffins *Fratercula arctica*. In 1978, these same techniques were used to estimate the numbers of burrow-nesting seabirds breeding in the State of Victoria. This report covers the results obtained for the short-tailed shearwater *Puffinus tenuirostris*, a species endemic to the Bass Strait where it breeds in such large numbers that no previous attempt has been made to count the population.

Most of the coastal islands and the few mainland colonies were visited in November and December 1978, and limits of shearwater colonies were marked on the best available aerial photograph. This demarcation was usually easy as the colony boundaries normally coincided with changes in the vegetation (Plate 9). Large colonies were subdivided where vegetation, or other physical features, made discrimination possible. The area of the colonies was calculated from these photographs by using a planimeter. The areas of small colonies were measured by using ropes or by pacing out.

In small colonies, the numbers of burrows showing signs of current use were counted directly (Plate 3). Otherwise, burrow density was sampled by counting

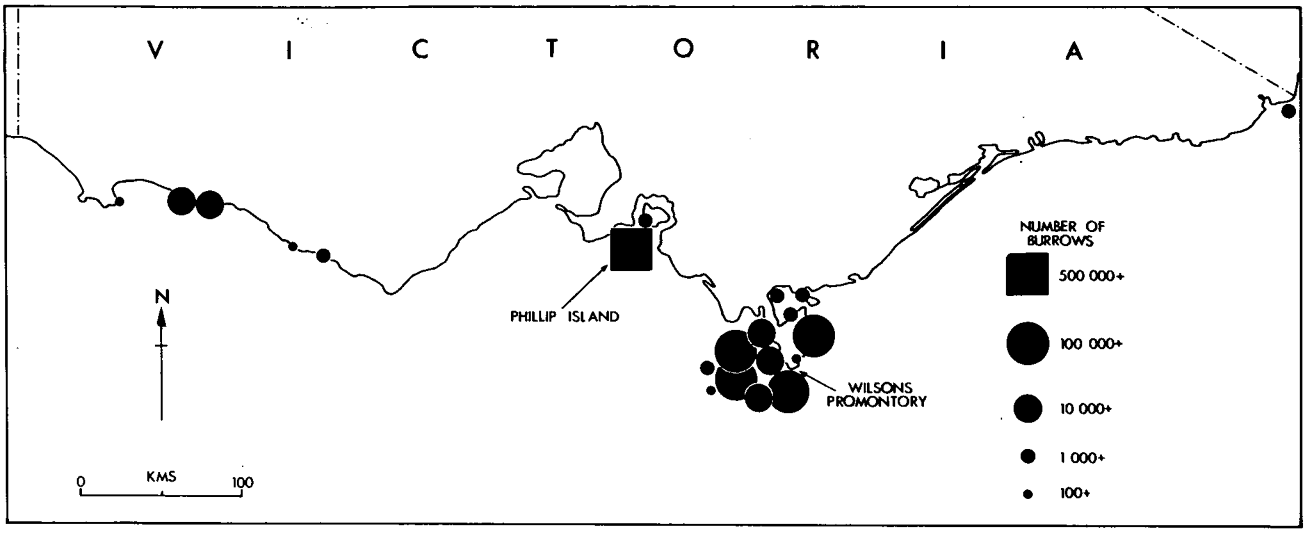


*Figure 27 The distribution of colonies of short-tailed shearwater* Puffinus tenuirostris *colonies in the State of Victoria.*

the number of burrows in circular quadrats of 20 $m^2$ area. In the larger colonies, and those with good landmarks, these quadrats were placed at random, using a grid superimposed on a map or aerial photograph and a table of random numbers. Where uniform terrain, shortage of time, or adverse weather made random sampling impracticable, a semi-systematic method was adopted which involved placing quadrats in a fairly regular arrangement over the area. Sample selection was done by zig-zagging from one side of the colony to the other, so that most of the area was covered, and placing quadrats every 5–10 m, depending on the size of the colony. The exact location of each quadrat was chosen by throwing a metal rod about 5 m ahead. Quadrats were counted even if they fell on exposed rock. Colony size was expressed as the area times the mean burrow density.

All totals refer to burrows. Checks made on the contents of burrows showed that 60–82% of burrows had eggs present. However, it is unwise to convert the burrow figures to pairs. Some birds may have laid eggs and lost them before these checks were made, and others had laid their eggs on the surface, where they were soon taken by predators. This last observation suggested that the nesting habitat was fully utilised. In neither case would these pairs have been counted. Comparisons of counts in different years are best made by comparing totals of burrows counted at approximately the same date each year.

Most of the estimates of burrow density were of known accuracy. Except in a few instances where there were adverse conditions, sample sizes were adequate to give precise estimates. It was doubtful if these estimates could have been substantially improved, as a proportion of quadrats always contained no burrows, because they fell on solid rock or other unsuitable terrain.

The main source of error in the population estimates lies in the measurement of the colony area. There was insufficient time to make more than one map of any colony. The only indication of the magnitude of the variation to be expected comes from Griffith Island, where 2 independent estimates of the area of the shearwater colony by different people were 13·2 and 17·6 ha. The difference appeared to be due to the difficulty in deciding where the colony ended, because of scattered outlying burrows. This difficulty was less acute on small islands where the birds occupied all the available habitat. No allowance was made for the slope of the ground when calculating colony area from maps or photographs. In most cases, the terrain was fairly flat, but the estimates of some colonies were likely to be slightly too small.

There were about 1–8 million shearwater burrows in Victoria in 1978, with the main concentrations on Phillip Island and the islands off Wilsons Promontory (Figure 27). Victoria had about 11% of the colonies listed by Serventy *et al.* (1971). Most of the others are in Tasmania, where a total of 549 352 young were killed for food in 1976 (Warham 1977), but few colony counts and no population estimates are available. Serventy *et al.* (1971) gave 250 000 occupied burrows on Cat Island (Tasmania) as an example of a large colony. Several Victorian colonies were larger than this, and Victoria has a special responsibility to conserve the colonies of this endemic bird.

Destruction of habitat was occurring in several places during this survey, noticeably at Phillip Island, but, while the damage to the immediate populations was severe, the effect on the total population was trivial (Plate 4). Most disturbance was inadvertent, but houses were being built on some colonies. Dogs and foxes killed large numbers of shearwaters at some colonies and young were taken (illegally) for food at others, but the total impact was again trivial. About 60% and 30% of the shearwaters nested in National Parks and in Fisheries and Wildlife State Faunal Wildlife Reserves respectively. Most of the remainder were on Foreshore, Shire or Council Reserves where pro-

*Plate 11. Isolated Scots pine at Coille Coire, Chuilc.*
*Photograph: J M Sykes.*

*Plate 12. Marginal land in Cumbria.*
*Photograph: C B Benefield.*

*Plate 13.* Ramalina polymorpha *— a rare lichen of the Welsh coast.*
*Photograph: R O Millar.*

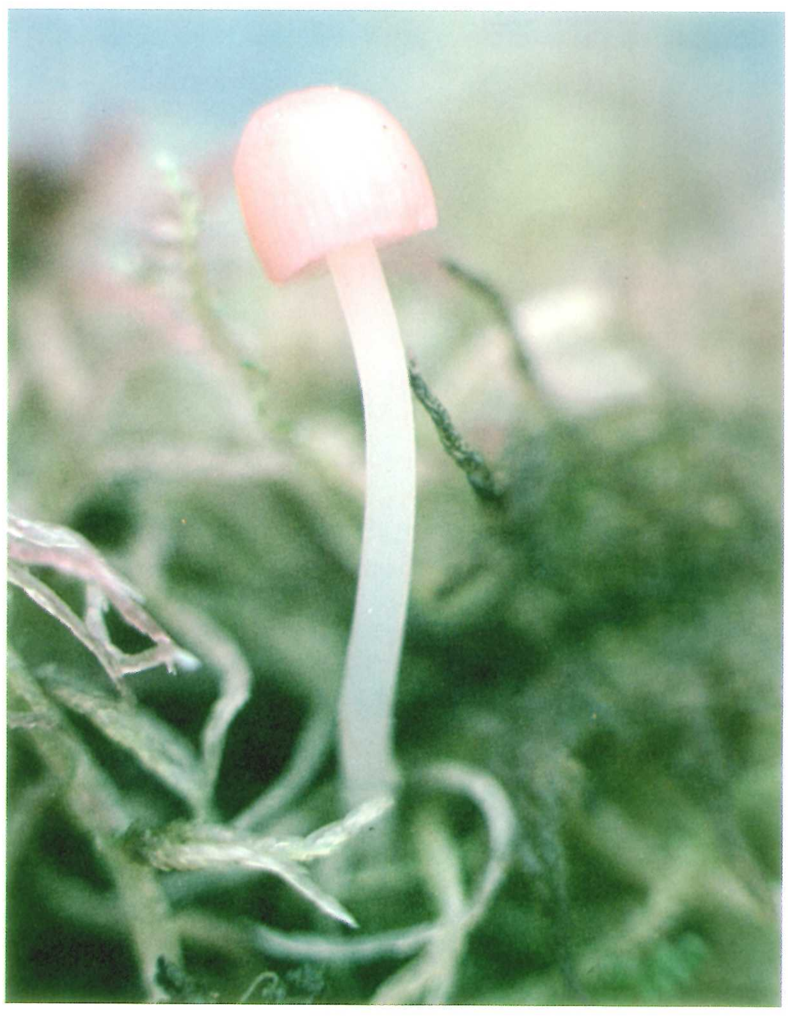

*Plate 14.* Mycena adonis *— this beautiful and rare gil fungus was found growing on a bog hummock of* Hupnum cupressiforme *and* Sphagnum rubellum *in Scotland. The coral red cap is about 5mm in diameter.*
*Photograph: R O Millar.*

*Table 16.* Estimates of the numbers of short-tailed shearwater burrows in Victoria in 1978. Counts in brackets are for colonies which were not visited but viewed from afar.

| Colony | No. of quadrats | Number of burrows (thousands) Total | Standard deviation |
|---|---|---|---|
| Lady Julia Percy | 179 | 15 | 14 |
| Griffith Island | 59 | 45 | 21 |
| Port Fairy | 40 | 9 | 4 |
| Phillip Island | 667 | 542 | 1 330 |
| French Island | 17 | 3 | 3 |
| Great Glennie Island | 518 | 400 | 693 |
| McHugh Island | 50 | 13 | 13 |
| Citadel Island | Count | 0·1 | – |
| Dannevig Island | (not visited) | (3) | – |
| Anser Island | 122 | 252 | 196 |
| Kanowna Island | 59 | 52 | 52 |
| Norman Island | (not visited) | (100) | – |
| Shellback Island | 51 | 110 | 79 |
| Wattle Island | (not visited) | (30) | – |
| Seal Island | 30 | 54 | 19 |
| Notch Island | 45 | 6 | 7 |
| Cliffy Island | 20 | 6 | 3 |
| Rag Island | 31 | 18 | 6 |
| Rabbit Island | 136 | 131 | 92 |
| Rabbit Rocks | 25 | 4 | 1 |
| Granite Island | 50 | 2 | 1 |
| Benison Island | 60 | 7 | 5 |
| Doughboy Island | 22 | 2 | 1 |
| Other small colonies | (not visited) | (10) | – |
| State total | 1·8 million | | |

tection was minimal.

The colonies of short-tailed shearwaters were large. The few older estimates of these populations were all of unknown accuracy and in many cases there was no indication of how the estimates were made, or even if they referred to birds or pairs. However, most colonies appeared to be flourishing. The 1978 survey was extensively documented and made in such a way that it is possible to repeat it in a directly comparable manner whenever required. Thus, future changes in numbers can be accurately measured. (Table 16).

It is unrealistic to expect that all colonies can be given adequate protection, but some of the present reserves need greater protection and better management. The main threats to these seabirds are marine pollution and industrial fishing. The same threats probably apply to shearwaters in most parts of the world, and more research is urgently needed.

*M.P. Harris*

*References*

**Serventy, D. L., Serventy, V. & Warham, J.** 1971. *The handbook of Australian seabirds.* Sydney: Reed.

**Warham, J.** 1977. The incidence, functions and ecological significance of petrel stomach oils. *Proc. N.Z. ecol. Soc.*, **24**, 84–93.

WINTER MOULT IN CUCKOOS

This study used museum skins to investigate the migration of cuckoos from the Western Palaearctic into the Afrotropical Region and to extend our knowledge of the birds' moult and annual cycle. This work supplements knowledge gained from recoveries of ringed birds (Seel 1977).

The new work shows that the cuckoo 'winters' in Africa south of the equator and mostly south of latitude 10°S. The moult of primary feathers takes place in this area, but is begun while the birds are still migrating southward. In some birds, moult is still in progress when the northward migration begins. The birds are not able to complete their primary moult in the time they can stay in the 'wintering' area, but moult on the body as a whole may be at its peak at this time (Cover photograph). Old birds perform the sequence of 'southward migration—primary moult—northward migration' earlier than young birds; the latter achieve the timing shown by the old birds by remaining for a shorter period in the breeding area on the occasion of their return visit.

*D.C. Seel*

*Reference*

**Seel, D.S.** 1977. Migration of the northwestern European population of the cuckoo *Cuculus canorus*, as shown by ringing. *Ibis*, **119**, 309–322.

FLUORIDE IN PREDATORY MAMMALS AND THEIR PREY

Near Holyhead, on Anglesey, there is an aluminium smelter which emits fluoride as an unwanted by-product of aluminium reduction. Most of the fluoride is removed from the gases which are expelled from the smoke stack, but sufficient remains to find its way into the ecosystem.

Work was started in 1977 to find out how much fluoride was present in foxes and their prey, field voles, and in moles and their prey, earthworms. Both earthworms and field voles were assumed to acquire any fluoride which they might contain from the vegetation which they eat. Early results showed that almost all the fluoride in the vertebrates was deposited in the skeleton.

Preliminary results, for field voles and moles, showed a clear pattern of fluoride values which varied inversely with distance from the smelter. There were, however, some puzzling exceptions and later results showed that, even for the field vole, which is almost an annual species, age structure of samples could strongly affect mean fluoride values. Recent work has been directed towards relating fluoride content to age (determined from eye-lens dry weight) in a monthly sample of voles from a site near the smelter.

Preliminary results for foxes from Anglesey showed that, although they contained high levels of fluoride, these levels were not significantly different from those in foxes from central Wales. This finding, together with some inexplicably high values in moles from Shropshire, has drawn attention to the problem of what are 'normal' background levels in these species. Attempts are now being made to obtain material from much wider areas of the country.

Work has also been done to ascertain the ways in which fluoride might reach one of the prey species, namely the field vole. The fluoride content of various parts of its possible food-plants is being studied at regular intervals throughout the year. Also, regular faecal samples have been collected for analysis of food items to find out what voles are actually eating.

*K.C. Walton*

RELATIONSHIPS BETWEEN THE FEEDING ECOLOGY AND SOCIAL ORGANISATION OF CATS

This study has described and compared the feeding ecology and social organisation of the Scottish wildcat *Felix sylvestris* and the domestic cat, with the aim of understanding the adaptive significance of inter- and intra-specific differences in social behaviour. The field work lasted 3 years from November 1975. Wildcats were studied at Glen Tanar Estate, Aberdeenshire. Domestic cats were studied in 2 areas; they were either 'free-ranging' when living unrestrained in farmland in the Outer Hebrides, or 'feral' on the uninhabited Monach Islands.

The main food of wildcats and domestic cats was rabbits, especially young rabbits and rabbits with myxomatosis, which were taken in proportion to their availability. Young rabbits showed different anti-predator behaviour from adult rabbits. Rabbits occurred in patches in particular habitats and fewer were present in winter than in summer. Cats hunted by themselves and they were more successful in finding and catching rabbits by moving around and stalking (mobile strategy) than by lying in wait at rabbit holes (stationary strategy). Differences in hunting success between cats were related to differences in social status; by excluding subordinate cats from good hunting areas, dominant cats had more opportunities to catch rabbits.

Radio tracking revealed that wildcats were solitary and territorial; they also used faeces as scent marks within their territories. Adults had larger ranges than young wildcats, but all were centred on forest-scrub habitats which provided most food, most cover for stalking, and refuge from bad weather in winter. Ranges of males sometimes partly overlapped the ranges of females, but the ranges of females never overlapped. Young males were highly nomadic.

Free-ranging domestic cats had overlapping hunting ranges, but each cat hunted alone. Most litters were born in the fields and breeding pairs were more aggressive, urine-sprayed more frequently and excluded other cats from an area surrounding their dens. In winter, these cats relied on food hand-outs and scavenging from the farms and lived more communally to exploit these highly aggregated food sources.

The feral cats on the island were solitary, and dominant cats defended territories centred on rabbit stronghold areas. Faeces were used as scent posts, as in wildcats, but unlike subordinate and free-ranging domestic cats, which usually buried faeces. Litters were born at any time of year, but, during the study, all kittens died of starvation in winter.

These results were compared with other studies of felids. Most felids are solitary, but lions and domestic cats may live in groups, or alone, or in a mixture of these life styles, and this intraspecific variation is at least as large as the interspecific variation shown between felids. The overall conclusion was that the availability, dispersion and acquisition of food is an important selective force acting on social organisation. The basic hunting technique of all felids is solitary stalking, but, where prey is abundant, relatively large sized or easy to acquire, and patchily distributed, cats may live in groups. In contrast, where prey is less abundant, smaller and more dispersed cats live and hunt solitarily in larger, defined territories.

*L.K. Corbett*

GREY SQUIRREL FORAGING

The aim of this research is to understand why grey squirrels peel bark from hardwood trees, as a first step in the reduction of the damage done by squirrels to trees. When grey squirrels strip bark, they first peel off and drop the hard outer layers before scraping off and eating the sap-containing vascular tissues which remain exposed on the stem or branches. Severe damage typically occurs in young plantations of oak, beech or sycamore, close to mature woodland, usually in June or July when the sap is rich in sugars and the bark is most easily removed. However, bark-stripping does not occur in all vulnerable areas, and it does not occur every year in any one area. To understand why the damage occurs, it is important to know how grey squirrels forage in spring and summer when not stripping bark.

Squirrels are shy and difficult to observe, but their movements can be monitored by using radio transmitters. A radio collar was developed which does not significantly affect weight, movement or mortality compared with controls marked by toe-clipping. These radio collars operate for about 5 months and have been detected at 7 km, although the normal range is between 400 m (ground-ground) and 2 km (ground-tree). Radios were put on 30 squirrels between March and May 1979. The tree containing each squirrel, or the animal's position within 10 m on the ground, was determined 3 times a day for up to 18 squirrels, during 10-day periods between April and October. Automatic radio monitoring at dreys containing young showed that squirrels have 2 foraging periods during long days, and return to a drey from about 0900 and 1300. In summer, therefore, checks were made at 0700–0900, 1300–1500 and 1700–1900. As day length decreased the squirrels shortened their midday rest until they were foraging all day in October. More than 3 500 squirrel positions have been recorded, each taking about 5 minutes, in a 36 ha wood containing a section of mature oak-ash-beech woodland adjacent to a young oak-beech-conifer plantation.

In the spring, squirrels foraged mainly in deciduous trees, and were observed browsing on terminal twigs as leaves started to emerge on beech, oak and ash. As the leaves emerged fully, the squirrels foraged increasingly on the ground and in the young plantation (Figure 28).

While browsing, squirrels probably obtain nourishment from the sap used in leaf growth, and they obtain a similar food in bark-stripping. Stripping normally starts about the time when the browsing ceases and squirrels both increase their use of the young plantation and change their feeding habits. It is quite likely that the availability on stems and branches of the already familiar sap is discovered by exploratory feeding at that time.

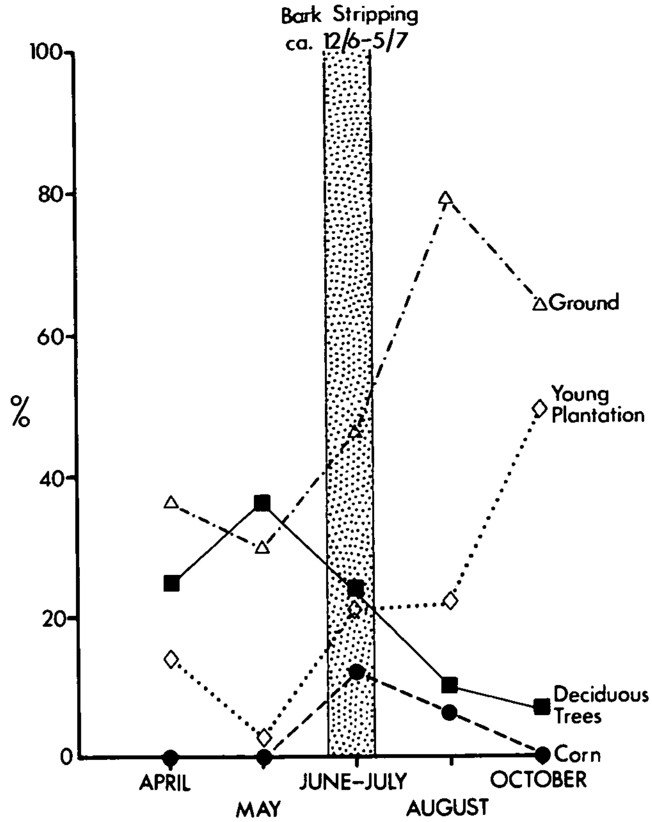


*Figure 28 Time spent by grey squirrels in different foraging locations.*

Even if food is discovered under bark, there may be no extensive bark-stripping. In the study plantation, bark-stripping was very slight in 1979, for the first time in 3 years, coinciding with the first planting of wheat in all the fields round the damage area. All the squirrels studied fed at the edge of this wheat, splitting the stems to extract the green ears within. This food was almost certainly more important than is indicated in Figure 28, since squirrels were recorded as 'on the ground' if they were at the edge of the field, but not definitely in it. The importance of alternative food availability during the bark-stripping period will receive further attention.

*R.E. Kenward*

THE STATUS OF DEER IN ENGLAND AND WALES

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

As a result of general dissatisfaction with the 1963 Deer Act, the Home Office requested the Nature Conservancy Council for a factual report on various aspects of deer biology, including descriptions of the wild as well as feral and potential feral species; purity of stock and hybridisation; changes in distribution and density; estimating deer numbers; habitat requirements; ecological impact on their environment and its assessment; deer as a resource both in direct yields, sporting values, by-products, deer parks and deer farms, and indirectly in terms of tourism. The effects of land management on deer were also to be assessed, including changes in land use, poaching, and control measures. Information was requested on close seasons and the techniques of taking deer, both alive and dead, using deer as a management tool and assessing the effectiveness of management.

ITE was commissioned to undertake the necessary desk study, and this paper describes briefly the findings as they relate to the management of wild and feral deer in Britain.

In Scotland, red deer have been plentiful and distributed over most of the highland region since the turn of the century. Most areas inhabited by deer, and large estates or deer forests have always been managed in accordance with the requirements of the landowner and of sportsmen. In England, on the other hand, there has been no similar tradition of deer management because, until recently, the only large herds of deer leading a wild or feral existence were restricted to a very few localities, such as those in the north-west (Martindale), the south (New Forest) and south-west of England (Exmoor). Since the 1939–45 war, however, land under productive woodland has been increased through afforestation from $7\frac{1}{4}$ to 9%; these young plantations provide optimum habitat for deer.

Information obtained from the Forestry Commission, Government departments, commercial forestry, Deer Control Societies and venison dealers, amongst other sources, showed that, of the 6 species of deer wild or feral in England, only fallow deer, roe deer and muntjac were sufficiently numerous, or expanding their range, to be of some consequence ecologically or economically. Fallow deer did not appear to be increasing in number, but roe deer, which in 1978 were absent only from the midlands and Wales, had apparently increased in number by about 32% during the preceding 5 years. In Scotland, roe deer numbers may have increased much more (61%).

There are no good data for muntjac, which are rarely treated as game animals or pests. However, since becoming feral in Bedfordshire in the 1940s, this species has become established throughout East Anglia, the midlands and the south of England. It continues to spread westwards and northwards more rapidly than roe deer, probably because it is more elusive, less persecuted and its habitat (bramble thickets or dense scrub) is more widespread.

Whereas deer were formerly regarded as rarities, deer of one species or another are now commonplace in almost every county in England and Wales. Moreover, because some species, like roe deer, can double their numbers annually, areas of suitable habitat have mostly become fully stocked and deer are attempting to settle more and more frequently in less suitable habitats.

In England and Wales, where no effective management system is available from the past, and where there is no equivalent to the Red Deer Commission from which advice might be obtained, each landowner or manager with responsibility for deer has evolved his own methods of management. These range from strict protection to complete clearances of deer, with light culls, mainly of males, the rule. As a result, no species of deer can be said to be being adequately cropped in any region of the country at the present time. Estimates of the numbers culled in 1978 in England amounted to 9 500 roe deer and rather less than 4 000 fallow deer. Taken together with the other species of deer, the total was little more than 14 000. Compared with these figures, totals culled in Scotland and Germany amounted to 57 000 and 757 186 respectively.

The conclusions to be drawn appear to be that, while deer in England are unimportant commercially at the moment (£$\frac{1}{2}$ million per annum), they nevertheless require much heavier annual culls in order to prevent increasing conflict with human interests.

*V.P.W. Lowe*

### THE DISPERSION OF RED DEER WITHIN A MIXED-AGED SITKA SPRUCE PLANTATION AND THE INCIDENCE OF BROWSING AND BARK-STRIPPING

The aims of this research, which started in 1978, are to study the distribution and behaviour of red deer in a mixed-aged Sitka spruce forest, and to estimate the amounts of browsing and bark-stripping and their effects on tree form and growth.

Deer in plantations are difficult to control because of their secretive habits and the amount of cover available. There are now resident red deer in many conifer plantations in Scotland, and deer are likely to thrive in many newly-established forests, once the second rotation of planting is reached. At this stage, open ground, young trees and older stands are often intimately mixed, frequently because of windblow, and, as a result, conditions are ideal for the deer. Protection of the young trees by internal fencing is, however, very costly. Unacceptable amounts of damage could well occur through browsing and bark-stripping, but there is as yet little information on the way deer utilise different parts of a forest, or on their longer term effects on the tree crop.

*Sites and methods*

Glenbranter Forest, Argyll, has been chosen as a study area because it already has a mosaic of habitats, young trees being mixed with thicket and high forest stands, and because it offers better opportunities of observing deer than in most similar forests. We have classified the forest into the following structural types: open ground (including rides, etc), pre-thicket, thicket, pole, high forest and deciduous scrub, with some subdivisions depending on the nature of the ground vegetation. Sites were selected within each of these types by stratified random sampling, using basic sampling units of 1–2 ha conforming to the boundaries of the forest sub-compartments. At each site, 6 permanent plots have been established within which faecal pellet accumulation and damage by deer on any trees are recorded. The measurements take place 4 times a year, corresponding to stages in the growth of vegetation and the life cycle of the deer. These data should show the deer's habitat preferences and which trees are most vulnerable to damage, besides seasonal variation and long-term trends in numbers of deer and impact. We also hope to determine how consistent is the relationship between impact and numbers of deer, and whether this relationship is modified by factors such as the ground vegetation and the nature of adjacent habitats.

*Deer studies*
The distribution and abundance of faecal pellets provide an estimate of how the deer herd uses the different parts of the forest, but do not indicate how many different animals occupy a particular site and whether the occupants change over a period of time. To interpret the data from faeces, therefore, we are also studying the movement of individual deer and the main factors affecting their distribution, namely food, shelter (from weather and disturbance) and social behaviour. Information on the extent and structure of home ranges, including the frequency of movements between forest types and the daily and seasonal activity of individuals, is being obtained by means of motion-sensing radio telemetry. Food preferences are estimated from analysis of rumens and faeces, and from direct observations of which plant communities are grazed. The sheltering characteristics of different stand types will be estimated and related to the use made of these places under different weather conditions.

*Tree studies*
The height of small trees on the sampling plots is measured annually and the girth of older trees is measured periodically. All trees below 1·5 m in height, and all other trees receiving damage are individually marked so that their performance can be followed. We record the number of new shoots produced after browsing of leading shoots, and are observing the fate of multiple leading shoots to estimate how many trees are likely to be permanently multi-stemmed. Bark-stripping wounds are examined yearly to find out how many heal and how many become colonised by rot-producing fungi. Part of this study is necessarily long term, since compensatory growth may occur after several years have elapsed, both in individual trees and in the whole population of trees.

The whole study is being done in close liaison with the Wildlife Research Branch of the Forestry Commission, and the information obtained will be used in a general model of deer populations and their economic significance in plantations.

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

## Animal Function

### ECOLOGICAL EFFECTS OF AQUATIC HERBICIDES ON FRESHWATER ECOSYSTEMS

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

An earlier report on this project (ITE Annual Report 1976) considered some of the problems associated with the use of aquatic herbicides, and outlined the results of field experiments with cyanatryn. In these experiments, many invertebrate species suffered a decline in numbers following treatment. Laboratory experiments were set up to examine whether prolonged exposure to the herbicide may have caused the observed declines. Tests were carried out on the mollusc *Lymnaea peregra*, the most abundant species initially, on the crustacean *Daphnia pulex* and on tadpoles of the frog *Rana temporaria*. The last 2 species were already known to be sensitive to chemical pollution and have frequently been used in laboratory toxicity experiments. Individuals were exposed for several days to a range of herbicide concentrations, the lowest being the normal recommended treatment level.

All species were seriously affected by exposure to high concentration of cyanatryn (Scorgie & Cooke 1979). However, *Daphnia pulex* and tadpoles of the frog *Rana temporaria* were also affected by short-term exposure to levels of cyanatryn as low as those recommended for use in the field. At these levels, the effects observed were sublethal resulting in changes in behaviour or reductions in growth. *Lymnaea peregra* showed no adverse effects at these levels, except that egg production appeared to be reduced. As *Lymnaea peregra* survived at field concentrations, it seems unlikely that the population declines observed in field experiments with cyanatryn were due to a direct toxic effect of the herbicide. More likely, they were due to the decline in habitat and food that followed cyanatryn use, and the same was probably true of the various other species as well.

*H.R.A. Scorgie*

*Reference*

**Scorgie, H.R.A. & Cooke, A.S.** 1979. Effects of the triazine herbicide cyanatryn on aquatic animals. *Bull. environ. Contam. & Toxicol.*, **22**, 135–142.

### ACTIVITY AND FEEDING RHYTHMS IN THE STARLING *STURNUS VULGARIS*

Many features of the lives of animals are timed by endogenous rhythms. The different facets of a bird's day, such as feeding, courtship and nest building, do not occur randomly but are carefully sequenced. Interactions between these internal rhythms and external, environmental variables—light, food availability, satiation, suitable nest sites, etc—enable the bird to use its time most effectively and determine the seasonality of its physiology. In normal circumstances, several different endogenous rhythms may be synchronised by the same environmental stimulus; they are said to be entrained. The entraining agent or "Zeitgeber" will usually be the light/dark cycle. Such entrainment of several rhythms obscures their independence and perhaps overemphasises the direct role of light in controlling various aspects of bird physiology.

We have been manipulating food and light periods separately in an attempt to isolate rhythms or groups of rhythms associated with different physiological functions. Individually-caged starlings were initially entrained to a day in which they received 8 hours of food and light at the same time. The remainder of the 24-hour day was spent under very dim green light in which the birds could see sufficiently well to negotiate the perches and feeders in the cage. Use of the perch and feeder was monitored by microswitches and recorded automatically. Twenty-four hour sections of the record were then pasted sequentially on to a board to give a visual impression of changes in the bird's behaviour. In the initial entraining period, all feeding and perch hopping activity was confined to the 8-hour light period and the remaining 16 hours each day were spent inactively.

When the light period was moved relative to the period when food was provided, it was possible to see the separate entrainment of general perch hopping and feeding to the 2 periods of stimulus. In some individuals this complete separation still occurred with the onset of food and light up to 8 hours apart, though, in others, the feeding period was extended to 16 hours on this treatment (Figure 29).

Further separation of the onset of the 2 stimuli (8 hours food and 8 hours light) to 12 hours clearly presented the birds with problems of entrainment. An initial attempt to shift activity onset to the beginning of the light period was aborted when there was no longer any overlap between the beginning of general activity and the end of the period of food availability. At this point, perch hopping activity began at the end of the light period and extended until the dawn 16 hours later.

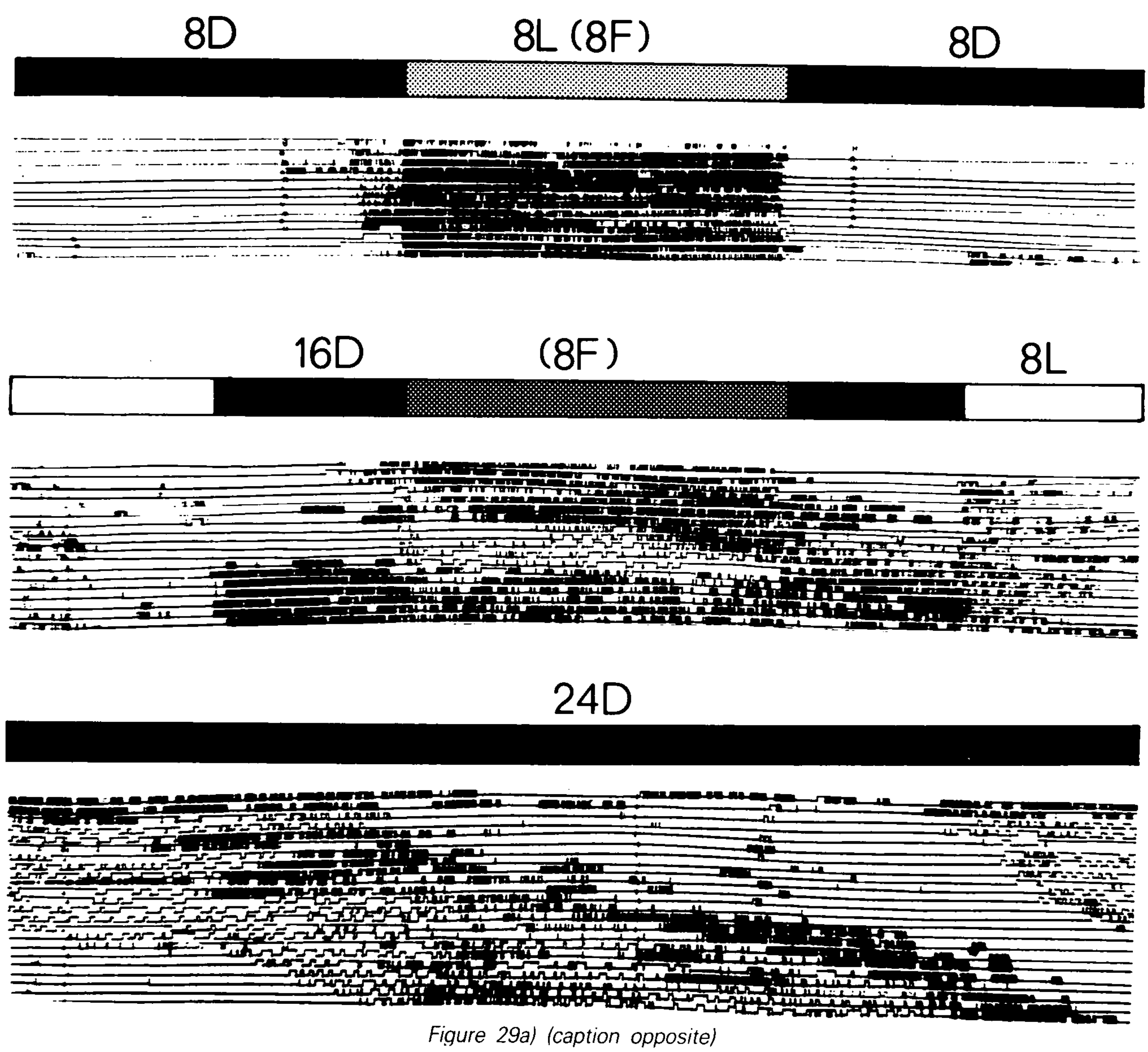


*Figure 29a) (caption opposite)*

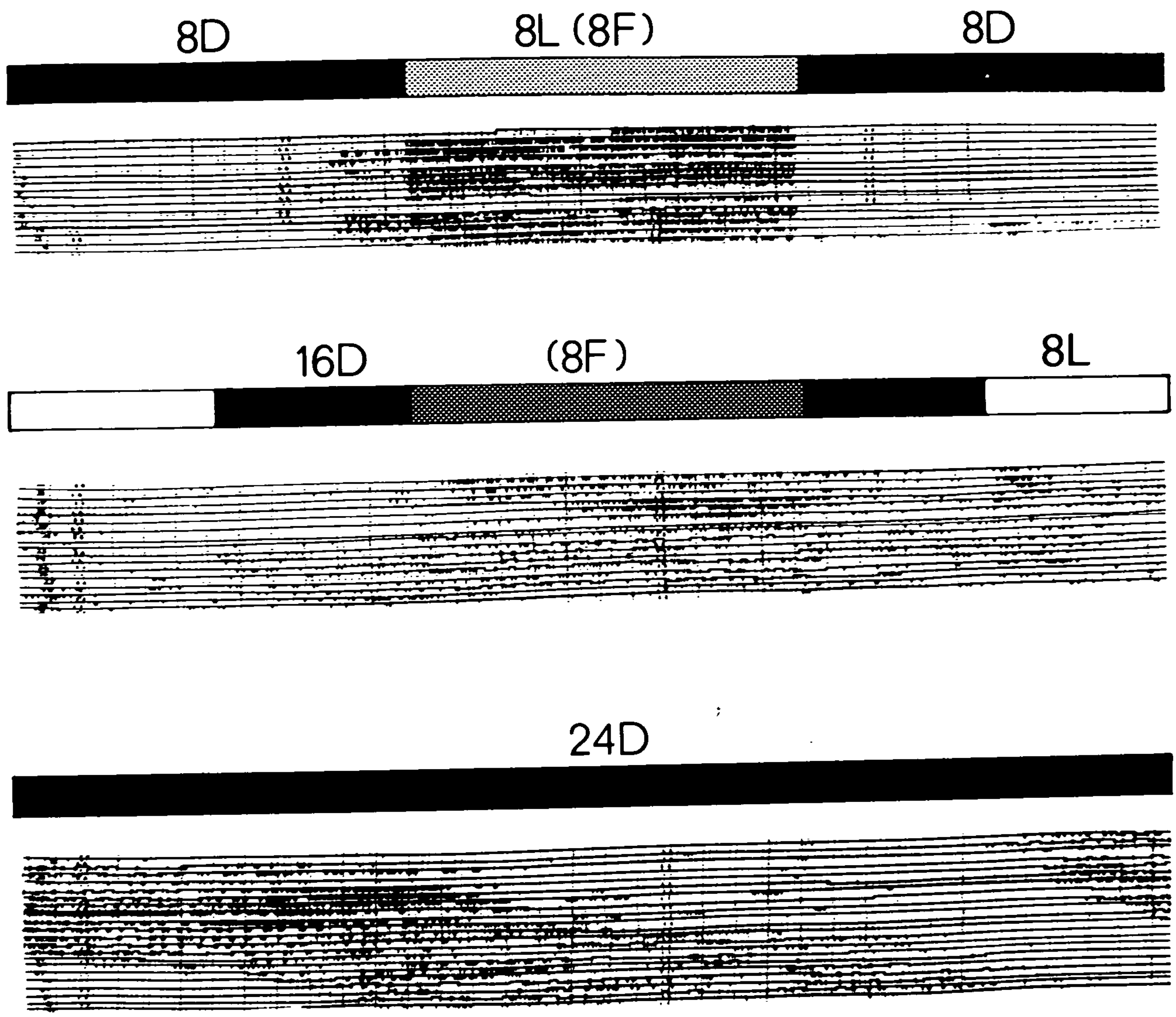


*Figure 29b) Activity patterns a) perch hopping and b) feeding in a starling with the onset of 8 hours of food and 8 hours of light set 12 hours apart. The horizontal scale is 24 hours and each horizontal strip represents one day's activity.*

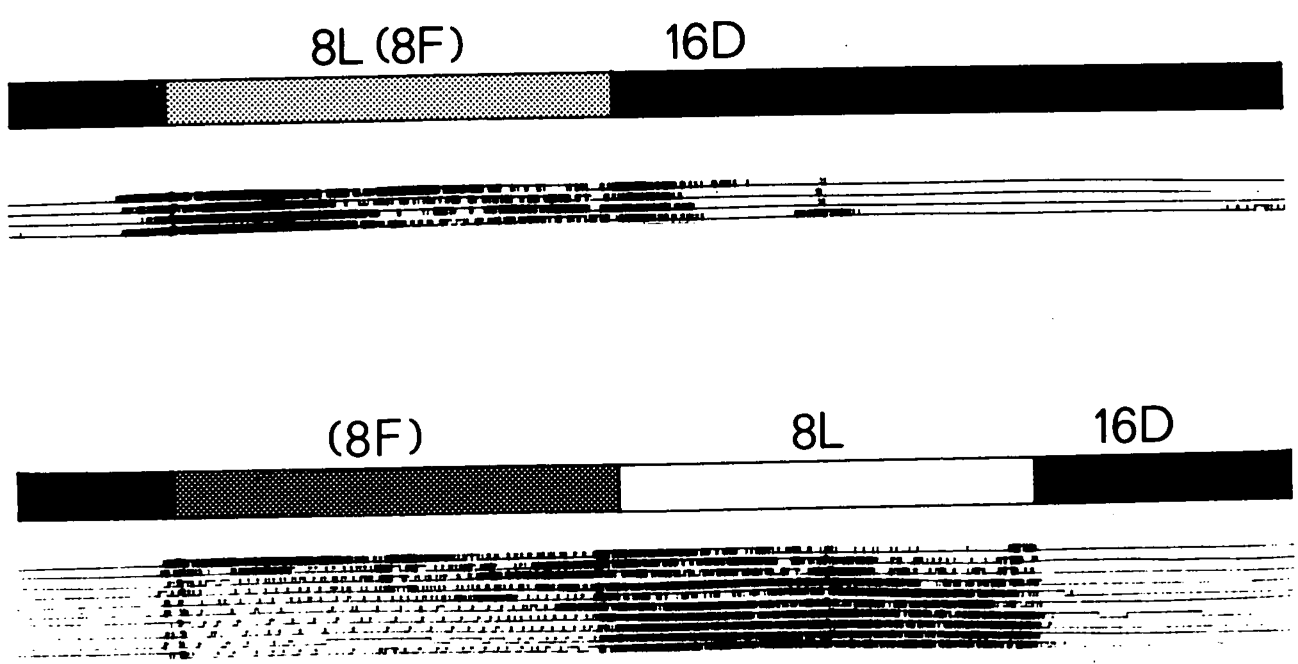


*Figure 30a) (caption overleaf).*

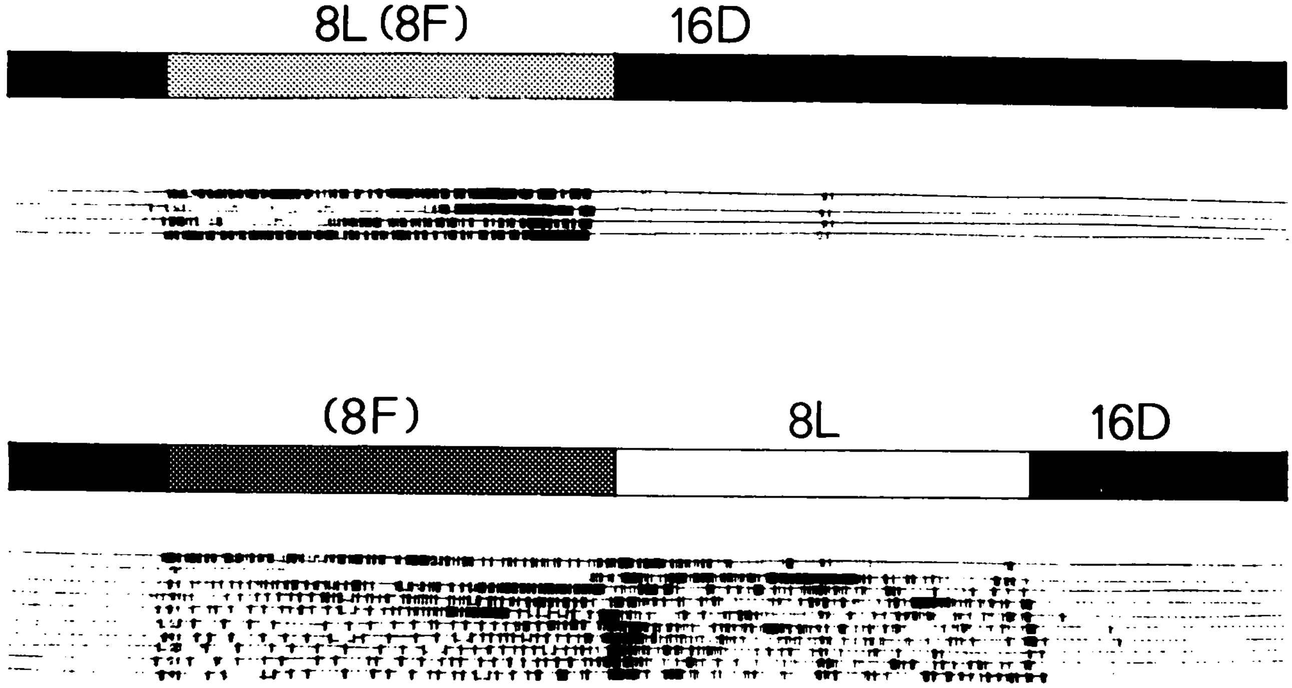


*Figure 30b)* Activity patterns a) perch hopping and b) feeding in a starling with onset of 8 hours of food and 8 hours of light set 8 hours apart.

It was as though the birds "read" the day the wrong way round (Figure 30). The implication is that, although the 2 rhythms are entrainable by different environmental agents, they are nevertheless linked to each other. There are, however, limitations on the configuration of their linkage.

This conclusion might be considered remarkable, except that birds which showed lengthened activity period associated with a 16-hour night also showed the gonadal growth normally seen on a 16-hour day. A similar reverse reading of photoperiods involving gonad growth occurred with very short days (less than 5 hours of light in the starling). Long-term treatment on short photoperiods caused gonad growth without the expected gonadal collapse and moult which normally characterise the end of the breeding season. The work is continuing with the measurement of hormones during periods of unusual entrainment, and it is hoped that fundamental information on the initiation and termination of breeding can be obtained in this way.

*M. Gill and S. Dobson*

BREEDING IN RELATION TO AGE IN SPARROWHAWKS

For several years, we have studied a population of sparrowhawks *Accipiter nisus* in south Scotland, mainly to find what limits numbers and breeding success. Each year, we have ringed as many adults and young as possible, so that, in recent years, the bulk of the population has consisted of known-age birds, which has enabled us to examine the breeding performance of individuals in relation to their age.

Sparrowhawks are relatively short-lived. We could have trapped individuals up to 10 years old (from when large-scale ringing started in the area), but we caught no females older than 8 years and no males older than 5 years (Table 17). This finding was reasonably consistent with the much larger sample of ring recoveries available in the National Ringing Scheme (started in 1908), in which the oldest female died in its 9th year, and the oldest male in its 6th year. In our sample, and in the national ring recoveries, the difference in age composition between the sexes was statistically significant, so it seems that female sparrowhawks are longer-lived than males. As the sex ratio at fledging is equal, there is presumably a surplus of females in the adult population.

*Table 17.* Age composition of samples of known-age sparrowhawks trapped while breeding.

| | Age (years) | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
| Females | 110 | 74 | 26 | 26 | 12 | 9 | 6 | 1 |
| Males | 37 | 29 | 16 | 8 | 3 | 0 | 0 | 0 |

Difference in age composition between sexes, $P<0{\cdot}001$.

For 179 pairs over the years, we knew whether male and female were yearlings or older birds. (These 2 age classes look different, as the yearlings have brown backs, and the older birds have bluish backs.) As shown in Table 18, mating was selective with respect to age, with fewer yearling-older bird matings, and more yearling-yearling and more older bird-older bird matings than expected if mating were random with respect to age. So, at least between brown yearlings and bluish older birds, individuals tended to pair with partners of the same age (plumage class) as themselves. Among older birds, there was no apparent trait for

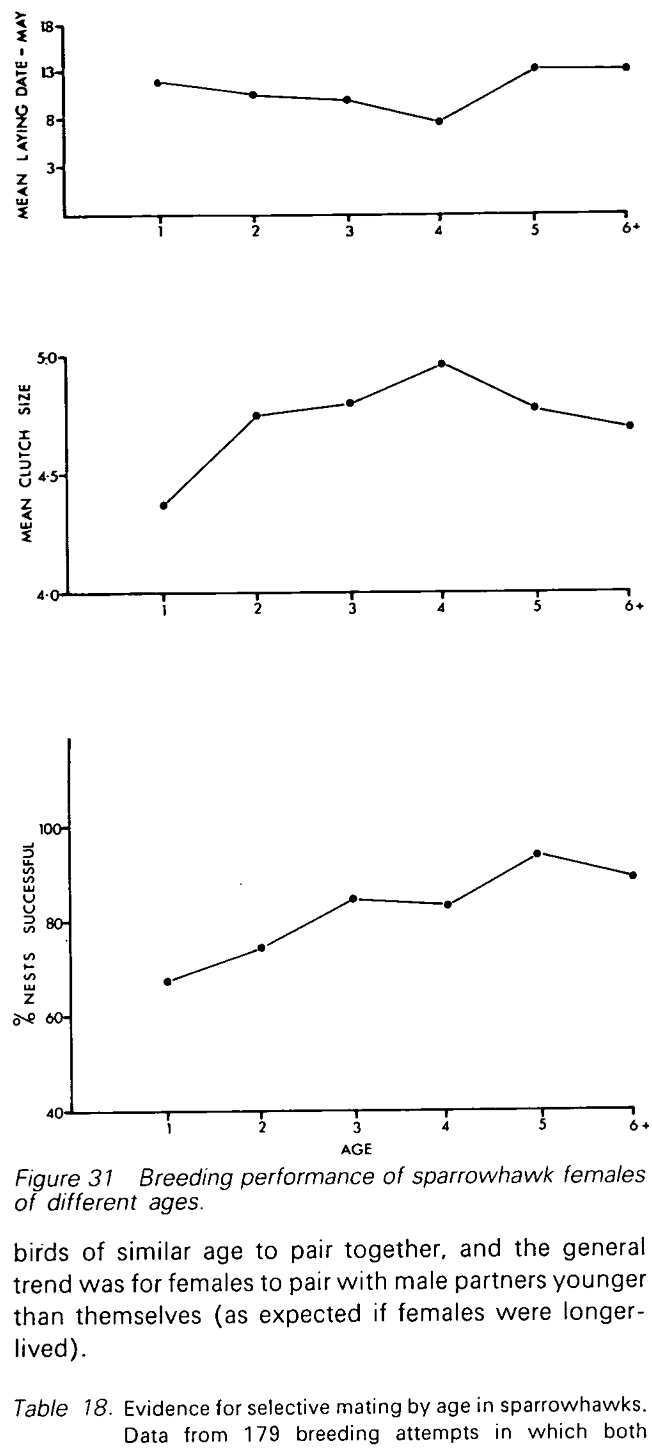


*Figure 31 Breeding performance of sparrowhawk females of different ages.*

birds of similar age to pair together, and the general trend was for females to pair with male partners younger than themselves (as expected if females were longer-lived).

*Table 18.* Evidence for selective mating by age in sparrowhawks. Data from 179 breeding attempts in which both partners were of known age.

| | | Females | |
|---|---|---|---|
| | | Yearling | Older |
| Males | Yearling | 13 | 22 |
| | Older | 14 | 130 |

Probability of a result at least as extreme, by Fisher's Exact Test = 0·0002.

Because we caught and identified more females than males, we could examine female breeding in considerable detail (Figure 31). Females tended to lay their eggs progressively earlier in the year up to age 4, and then later again. Clutch sizes and brood sizes at hatch showed a similar trend, being largest among 4 year olds. On the other hand, brood sizes at fledging and nest success (whether the nest succeeded or failed) improved at least up to age 5–6. After this age, there were so few individuals left alive that we could not be certain of any apparent trends. It seemed, therefore, that several aspects of breeding in female sparrowhawks peaked at age 4 years, while other aspects continued to improve beyond this age. All these trends were statistically significant.

Although we had less information for males, we could show that they, too, had some effect on nest success. Table 19 shows the nests that were successful from each of 4 pair combinations: yearling male-yearling female, yearling male-older female, older male-yearling female, and older male-older female. On average, pairs consisting of 2 older partners were the most successful; pairs consisting of 2 yearling partners were least successful; while mixed pairs were intermediate. The contribution that age of male made to nest success can be seen by comparing the yearling male-yearling female and older male-yearling female matings (on average, 18% more nests were successful with an old male), and by comparing the yearling male-older female and older male-older female matings (on average, 12% more nests were successful with an older male). Similarly, the contribution that age of female made to nest success can be seen by comparing the yearling male-yearling female matings with the yearling male-older female matings (on average, 25% more nests were successful with an older female) and by comparing the older male-yearling female with the older male-older female matings (on average, 19% more nests were successful with an older male). It seems, therefore, that both sexes breed more productively at certain times in their lives, and that both partners contribute to nest success. In several other bird species, evidence has been obtained for an improvement in performance for the first few years of breeding life, but in very few others has evidence been produced for senescence—for a deterioration in performance beyond middle age.

*Table 19.* Percentage of nests that were successful from different pair-combinations in sparrowhawks.
The data were from 179 pairs in which both partners were of known age.

| | First-year male | Older male | Difference attributable to age of female |
|---|---|---|---|
| First-year female | 36% | 54% | 18% |
| Older female | 61% | 73% | 12% |
| Difference attributable to age of female | 25% | 19% | |

*I. Newton and M. Marquiss*

## TOXIC METALS IN PUFFINS *FRATERCULA ARCTICA* FROM THE ISLE OF MAY AND ST KILDA

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

Evidence is accumulating which shows that the marine environment of north-west Scotland may be an area where the fauna accumulate high concentrations of cadmium and mercury in their tissues. It is thought that there may be natural sources for most of the metal accumulated, although care must be taken to allow for a mercury source originating from industries discharging waste into the Irish Sea. Recent work on puffins *Fratercula arctica* supports the view that north-west Scotland is a high metal area, because puffins from St Kilda, an island group west of the Outer Hebrides, have much higher concentrations of toxic metals than do puffins from the Isle of May, an east coast colony in the Firth of Forth (Table 20).

*Table 20.* Regional differences in mean cadmium and mercury concentrations (mg kg$^{-1}$ dry wt) in puffins *Fratercula arctica* collected from the Isle of May and St Kilda, just after egg-lay.

| Tissue | Cd I.o. May n = 11 | Cd St Kilda n = 10 | Hg I.o. May n = 11 | Hg St Kilda n = 10 |
|---|---|---|---|---|
| Liver | $\lesssim$2 | 20 | $\lesssim$1 | 5 |
| Kidney | $\lesssim$10 | 114 | 1 | 5 |
| Pancreas | ND | 22 | $\lesssim$1 | $\lesssim$2 |
| Gonda | $\lesssim$3 | 17 | $\lesssim$3 | 2 |

*Note*: ND = none detected

Whilst it is known that all of the birds sampled on St Kilda were breeding, it is possible that the high metal concentrations there may be imposing some 'stress' from which the Isle of May population is free. It has yet to be determined what influence (if any) the metals have on individual survival, breeding success, or the body size differences which exist between St Kilda and the Isle of May puffins. Possibly, however, the high metal concentrations may exacerbate the problems caused by food shortage that the St Kilda puffins are known to be experiencing.

The data in Table 20 were all collected at the same time of year (although collections were made in different years, this is not thought to influence the results). Comparison between samples must be made with due regard to the time of year, for the puffin, like other birds such as starling *Sturnus vulgaris* and dunlin *Calidris alpina*, seems to undergo seasonal variations in the levels of cadmium and mercury in its tissues (Table 21). In starlings and dunlin, this seasonal change was associated with moult, for the highest concentrations occurred in mid-moult and declined thereafter. Because the puffin moults in winter, the recorded decline in metal concentrations could also be associated with a moult-related peak in these concentrations, as the post-moult period of the puffin coincides with the breeding season.

*Table 21.* Seasonal differences in mean metal concentrations (mg kg$^{-1}$ dry wt) in Isle of May puffins

| Metal | Tissue | Period in reproductive cycle: Pre-lay n = 6 | Rearing n = 6 |
|---|---|---|---|
| Cadmium | Liver | 2 | < < 1 |
| | Kidney | 16 | 5 |
| | Pancreas | 3 | ND |
| | Gonad | < 3 | ND |
| Mercury | Liver | 2 | 0·5 |

*Note*: ND = none detected.

These findings reinforce our current view that seasonal changes, and regional differences, in toxic chemical concentrations should be a central consideration in the design of any environmental monitoring programme. This, and the possible importance of these seasonal variations in the environmental toxicity of the metals, is discussed more fully elsewhere (see references).

*D. Osborn*

*References*

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## POLLUTANTS IN GANNET EGGS

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

Concern over pollution of the seas has persisted ever since it was realised that many toxic chemicals (eg DDT and its metabolites) appear in many forms of marine life, even those living far from industrial or agricultural sources. Consequently, monitoring of pollutants in, and determining the effects of pollution on, seabird populations is an important part of ITE's work, as there are many large internationally important seabird breeding colonies around the British coast.

As part of a monitoring programme, the concentrations of pollutants in eggs of gannets *Sula bassana* collected from the colonies of the Bass Rock (North Sea) and Ailsa Craig (Irish Sea) are being determined each year.

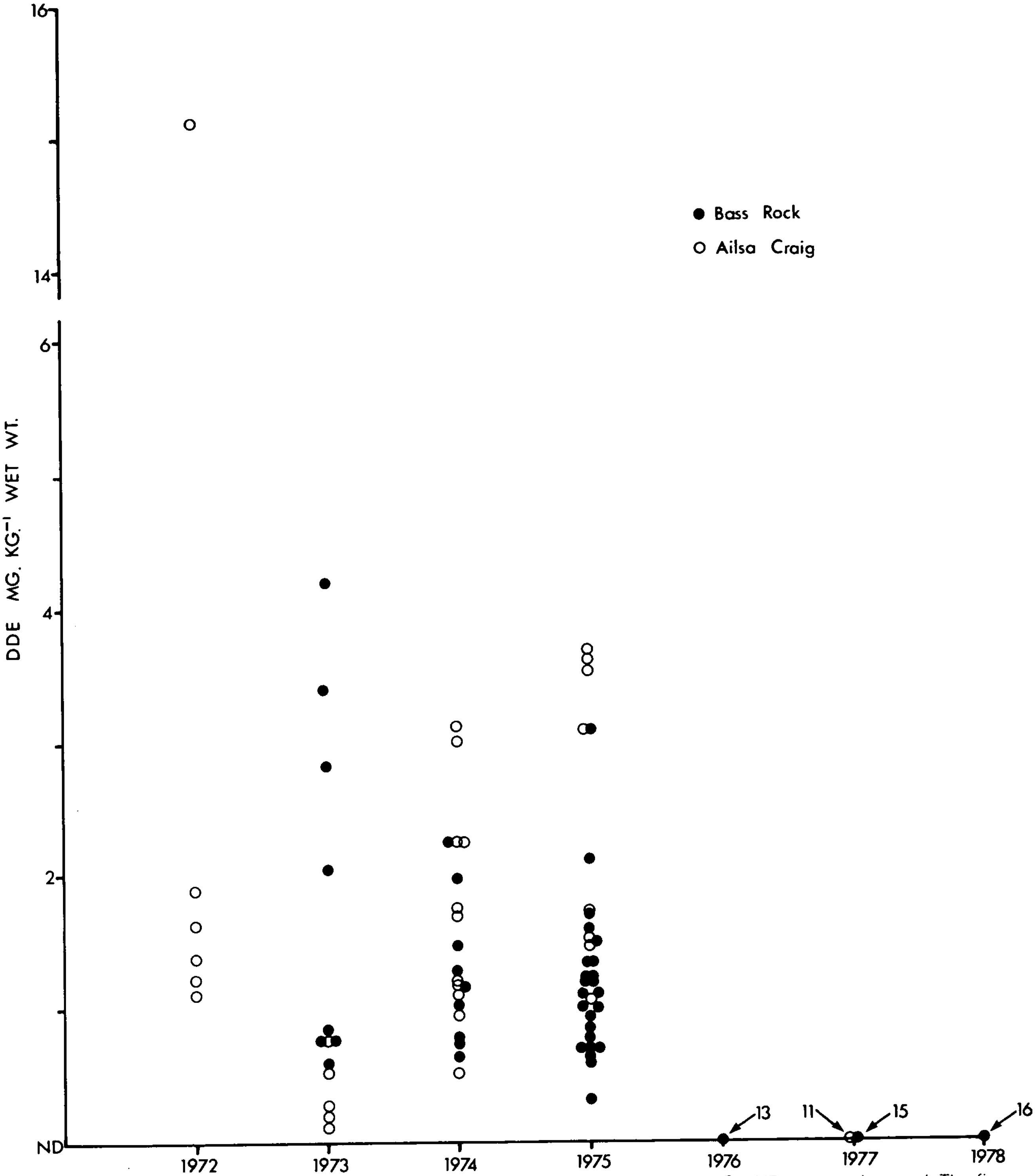


*Figure 32 DDE concentrations in gannet eggs from Bass Rock (●), and Ailsa Craig (O). ND = none detected. The figures on the graphs represent the number of samples in which the chemical was not detected.*

During the period covered so far, a number of important changes have occurred in the pattern of chemical use in Britain, Europe and North America, Notably, the uses of DDT and dieldrin have been much reduced in agriculture and industry, and some of the uses of polychlorinated biphenyls (PCBs) have also been restricted. In addition, the quantity of mercury in the Irish Sea has decreased following reductions in the mercury content of the effluent issuing from industries bordering the Irish Sea. These reductions in the use of toxic chemicals should be reflected in the amounts of DDE (the main metabolite of DDT), HEOD (from aldrin and dieldrin), PCBs, and mercury in gannet eggs.

Figures 32 and 33 show that concentrations of DDE and HEOD have, in fact, declined sharply in recent years, although the decline in DDE occured rather later than did the decline in dieldrin levels.

Figures 34 and 35 show that, despite the restrictions on PCB use and effluent mercury content, neither PCB nor mercury concentrations declined significantly in gannet eggs over the period of the collections, although some decline in the mercury in Bass Rock eggs might have occurred. PCB levels were lowest in 1975, and then increased again.

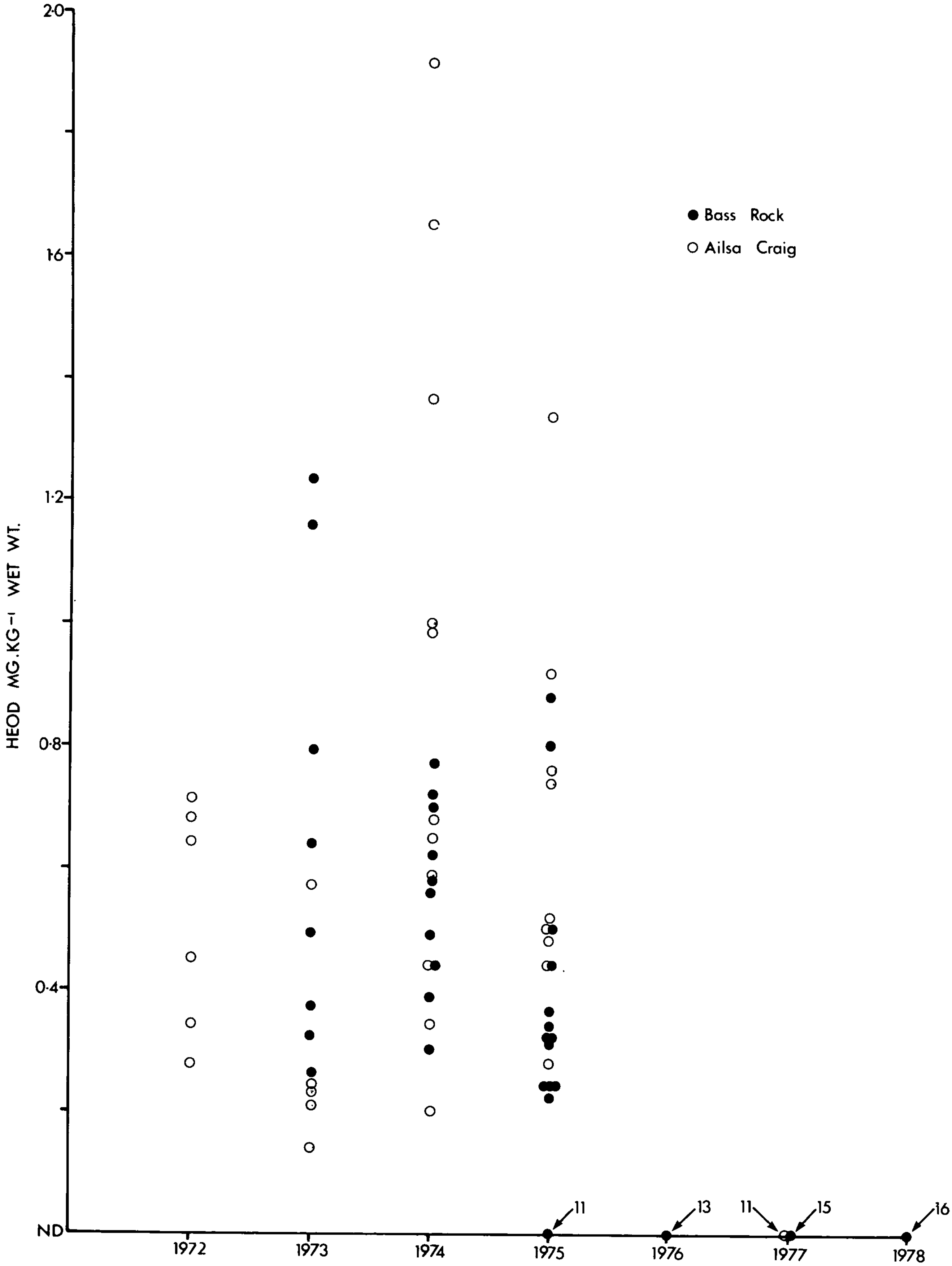


*Figure 33* *HEOD concentrations in gannet eggs from Bass Rock (●), and Ailsa Craig (○). ND = none detected. The figures on the graphs represent the number of samples in which the chemical was not detected.*

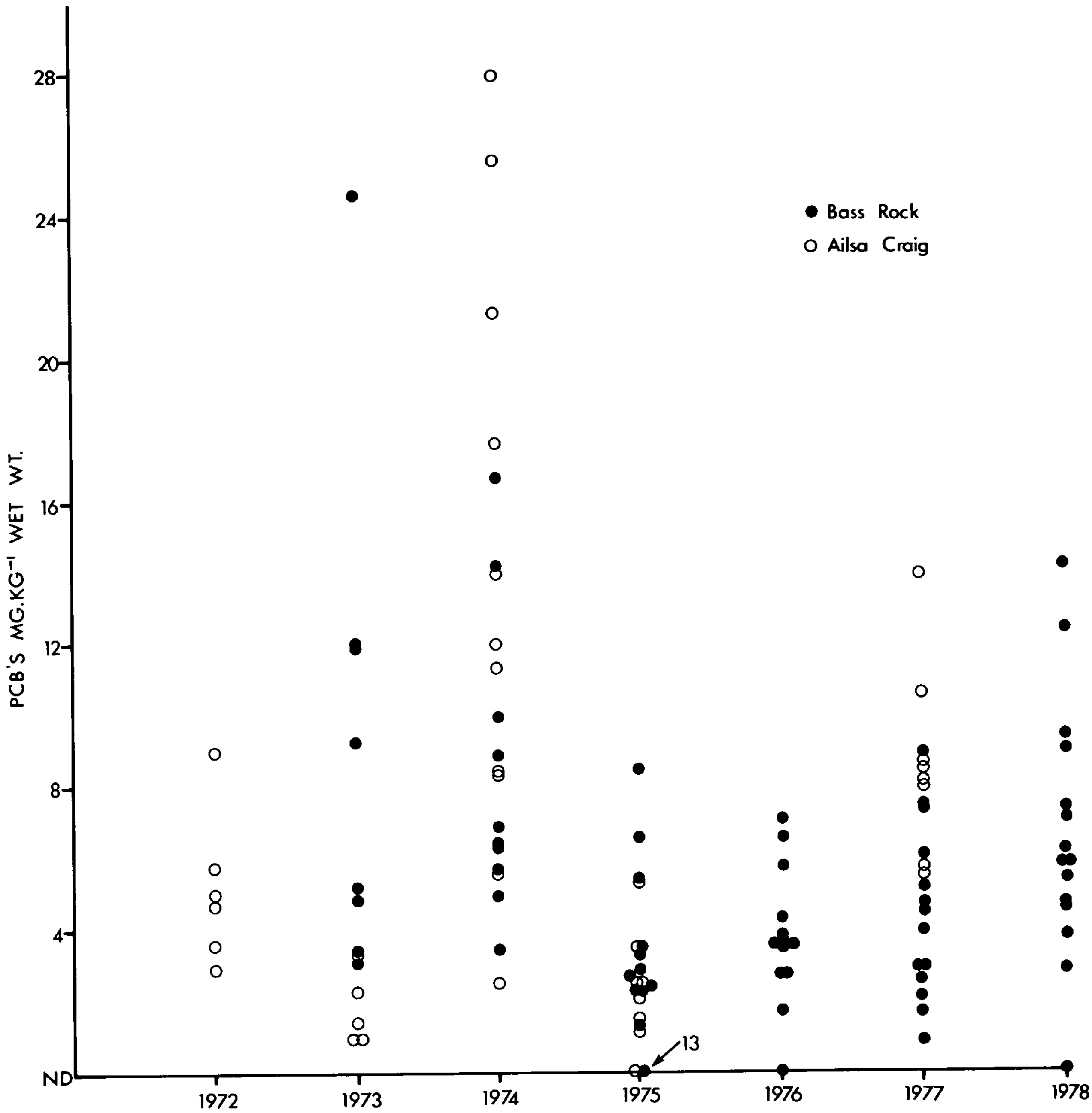


*Figure 34 PCB concentrations in gannet eggs from Bass Rock (●), and Ailsa Craig (O). ND = none detected.*

Cadmium was also measured (Figure 36). The results to date suggest that cadmium is found in the eggs in some years, but it is absent in other years, and no consistent pattern has yet emerged. One factor contributing to the difficulties of interpreting the cadmium figures is that some of the cadmium (and some mercury) may originate from natural sources, and another is that cadmium may not enter eggs readily.

In determining what effects these chemicals might be having on the developing chick, it may well be important to know whether the toxic chemical is present in the yolk or the white of the egg. Accordingly, analysis of the 1977 eggs from Bass Rock was conducted separately on each component of the egg. Virtually all the DDE, PCB and HEOD was found in the yolk, as expected, while almost all the mercury was in the white, a somewhat surprising result as the mercury could well have been mostly methylmercury, which is soluble in fat and therefore expected in yolk.

At present, insufficient research has been conducted to determine the toxic significance of the residues in the adults which the egg values are presumed to reflect.

*D. Osborn*

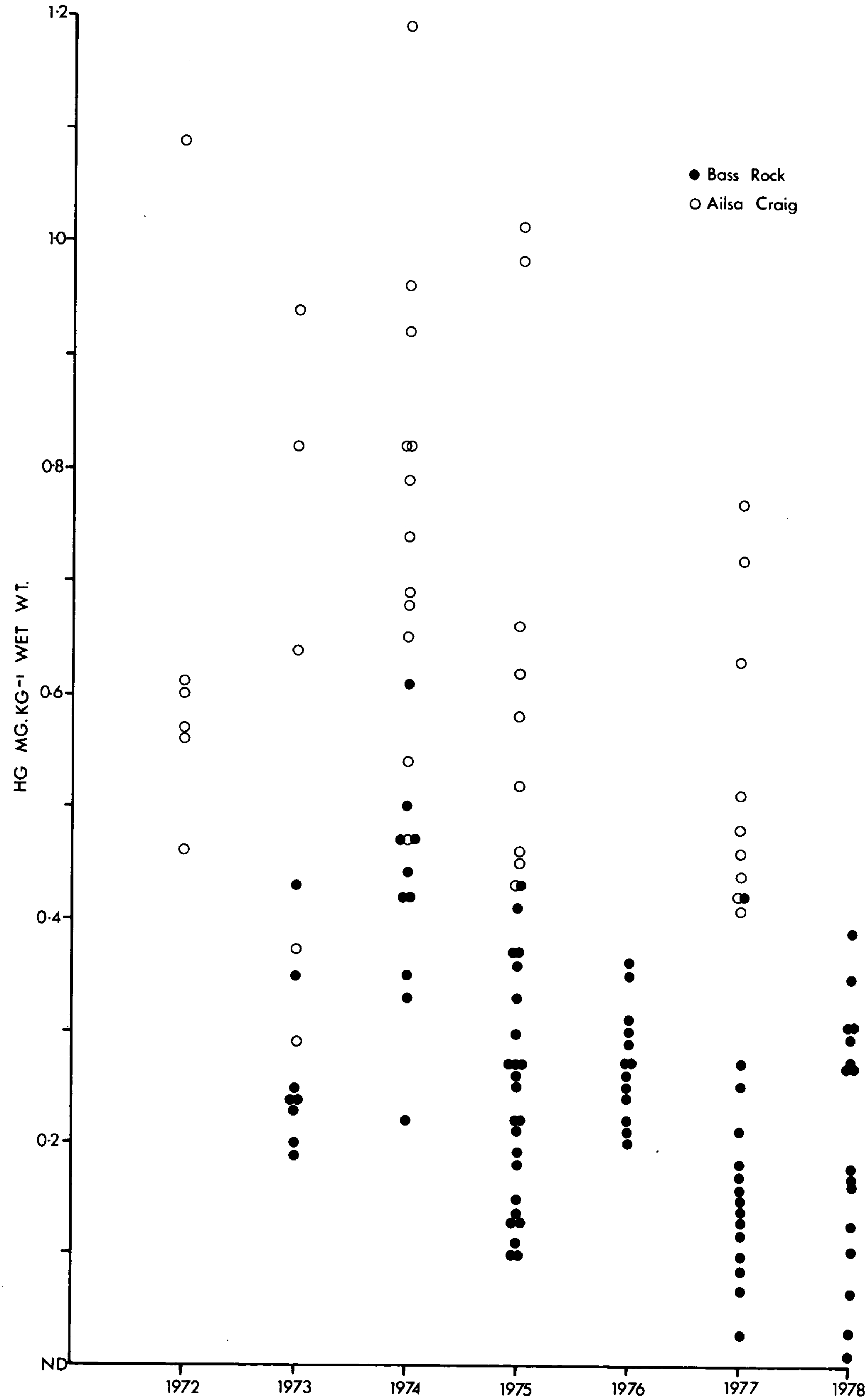


*Figure 35* *Mercury concentrations in gannet eggs from Bass Rock (●), and Ailsa Craig (○). ND = none detected.*

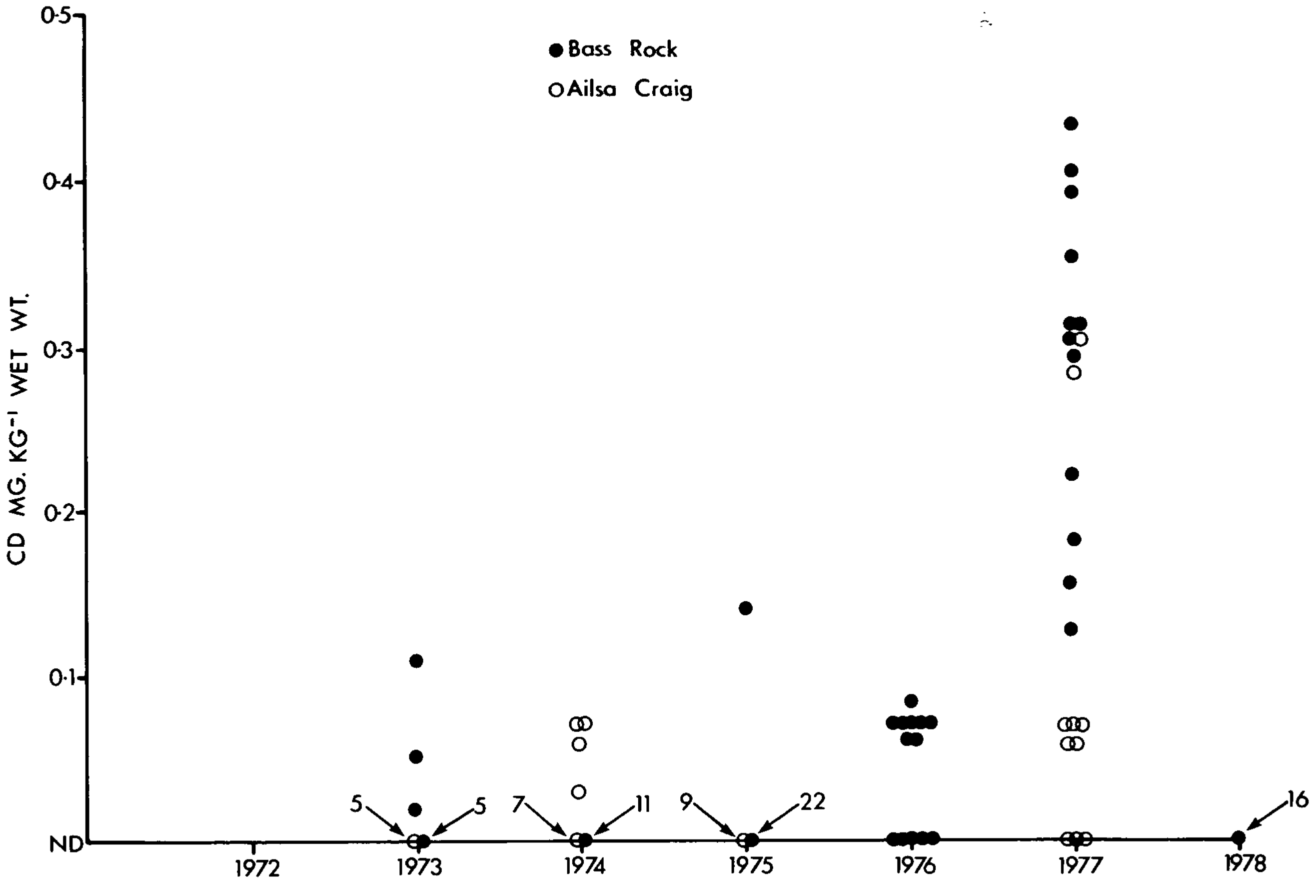


*Figure 36 Cadmium concentrations in gannet eggs from Bass Rock (●), and Ailsa Craig (O). The figures on the graphs represent the number of samples in which the chemical was not detected. ND = none detected.*

POSSIBLE EFFECTS OF WEATHER AND ORGANOCHLORINE RESIDUES ON THE BEHAVIOUR OF THE GREY HERON *ARDEA CINEREA*

The early survey of organochlorine residues in the eggs of wild birds showed that the grey heron contained the highest levels among the species examined (Moore & Walker 1964). This survey resulted in the heron being included in the research programme on predatory birds being initiated at Monks Wood Experimental Station, and a detailed study on the ecology of the species was undertaken at colonies in Lincolnshire (Milstein *et al.* 1970; Prestt 1970).

As in other predatory birds, the egg shell of the heron has become significantly thinner since the introduction of DDT and other organochlorines. Considerable evidence now exists to link shell thinning with the levels of DDT (and its metabolites) in the contents of the egg (see Cooke 1973, 1975; Cooke *et al.* 1976, for details). During their study on heron behaviour, Milstein *et al.* (1970) observed adult herons actively destroying their eggs. Cooke *et al.* (1976) also linked the incidence of egg shell breakage with the levels of DDT in the egg contents.

Examining 71 intact eggs and shells collected in 1973, Cooke *et al.* (1976) showed that eggs which had been broken by the adults had significantly thinner shells than the intact eggs, and that the broken shells contained a higher proportion of shells with a mean thickness of less than 240 μm. They suggested that the chance of an egg surviving incubation was greatly reduced if the shell thickness was less than 240 μm. Such thin shells were weak, could become cracked or broken, and be removed from the nest by the adults. Shells more than 240 μm thick were also occasionally broken by parents. Milstein *et al.* (1970) observed adult herons stabbing what appeared to be uncracked shells. This aberrant behaviour is thought to have been induced by high residue levels in the herons.

Since the early 1960's, regular visits have been made each year to the Lincolnshire colonies in order to determine the numbers of birds and to obtain information on the proportion of egg shells destroyed by the birds (Figure 37). During the early 1960's, when egg shell breakage tended to be high, the population was low. From the beginning of the present decade until the 1978 breeding season, the trends were of an increase in the population and a reduction in the proportion of birds breaking their eggs. In 1979, however, there was a marked increase (from 8% to 46%) in the proportion of eggs being destroyed in the colony at Troy, while the population decreased from 78–64 breeding pairs. The decline in the population was expected because the winter of 1979 was very severe and heron numbers have always declined in the past after hard winters (Reynolds 1979).

Thirty-eight shells identified as having been destroyed during the 1979 breeding season had intact waists and

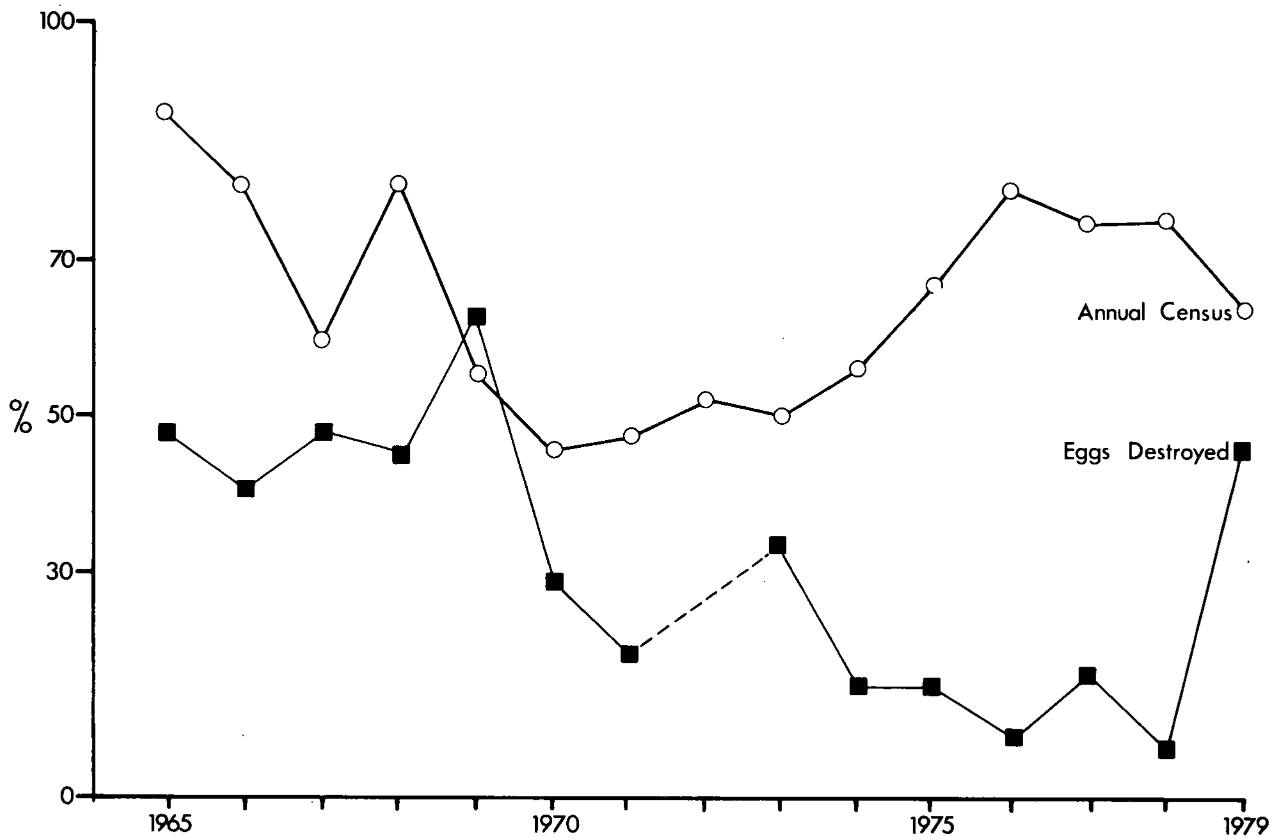


*Figure 37 The proportion of eggs (■) found destroyed and the annual census (O) of occupied nests in the heron colony at Troy.*

their thicknesses were measured. (The method used to measure the shell thickness was the same as that described by Cooke *et al.* 1976.). When the broken shells from 1973 and 1979 were compared, those from 1979 were slightly thicker (265 μm in 1979 and 251 μm in 1973), and the range of values was less (211–310 μm and 160–360 μm). The relative proportions of shells with measurements greater than 240 μm which were broken by the parents in the 2 years were significantly different, with more breakage in 1979 (1973 — 56%, 1979 — 74%). Hence, during the 1979 breeding season, herons destroyed a significantly higher proportion of thick-shelled eggs (ie > 240 μm thick) than in recent years. This behaviour could have been caused by an increase in the DDT levels within the population, which is not evident from current trends in residue levels in eggs, or it could have been due to some quite different factor. Obviously, much remains to be learnt about herons and their response to pesticides.

*J.W.H. Conroy and A. Stephenson*

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## THE EFFECT OF EULAN WA NEW ON FROG TADPOLES

The insecticide dieldrin is now recognised to be a major environmental hazard, having toxic effects on many non-target organisms. Consequently, it is being progressively replaced by alternative substances. One of these is Eulan WA New, which is now used instead of dieldrin to moth-proof textiles, mainly carpets. Unfortunately, it has not proved possible to contain Eulan WA New to the textiles and the manufacturing plant, and thus some assessment of its environmental toxicity is needed, particularly because, like dieldrin, it is appearing in inland waters and their associated wildlife.

A static bioassay system, using frog tadpoles *Rana temporaria* as test animals, has been developed at Monks Wood Experimental Station. This system makes it possible to test the effects of toxic chemicals conveniently and inexpensively in a way which allows comparisons to be made between the toxicity of chemicals to tadpoles. Eulan WA New's toxicity was examined in this way, particular attention being paid to its effect on tadpole weight, development rate, abnormalities, feeding and survival. At the end of the

*Plate 1. Wheat grown as an understorey in a poplar plantation (from Callaghan et al 1978). Photograph: T V Callaghan.*

*Plate 2. Counting burrows of short-tailed shearwater* Puffinus tenuirostris *in circular quadrats at Cape Woolamai, Philip Island, Victoria. This colony covered about 132 ha and contained about a third of a million burrows.*
*Photograph: M P Harris*

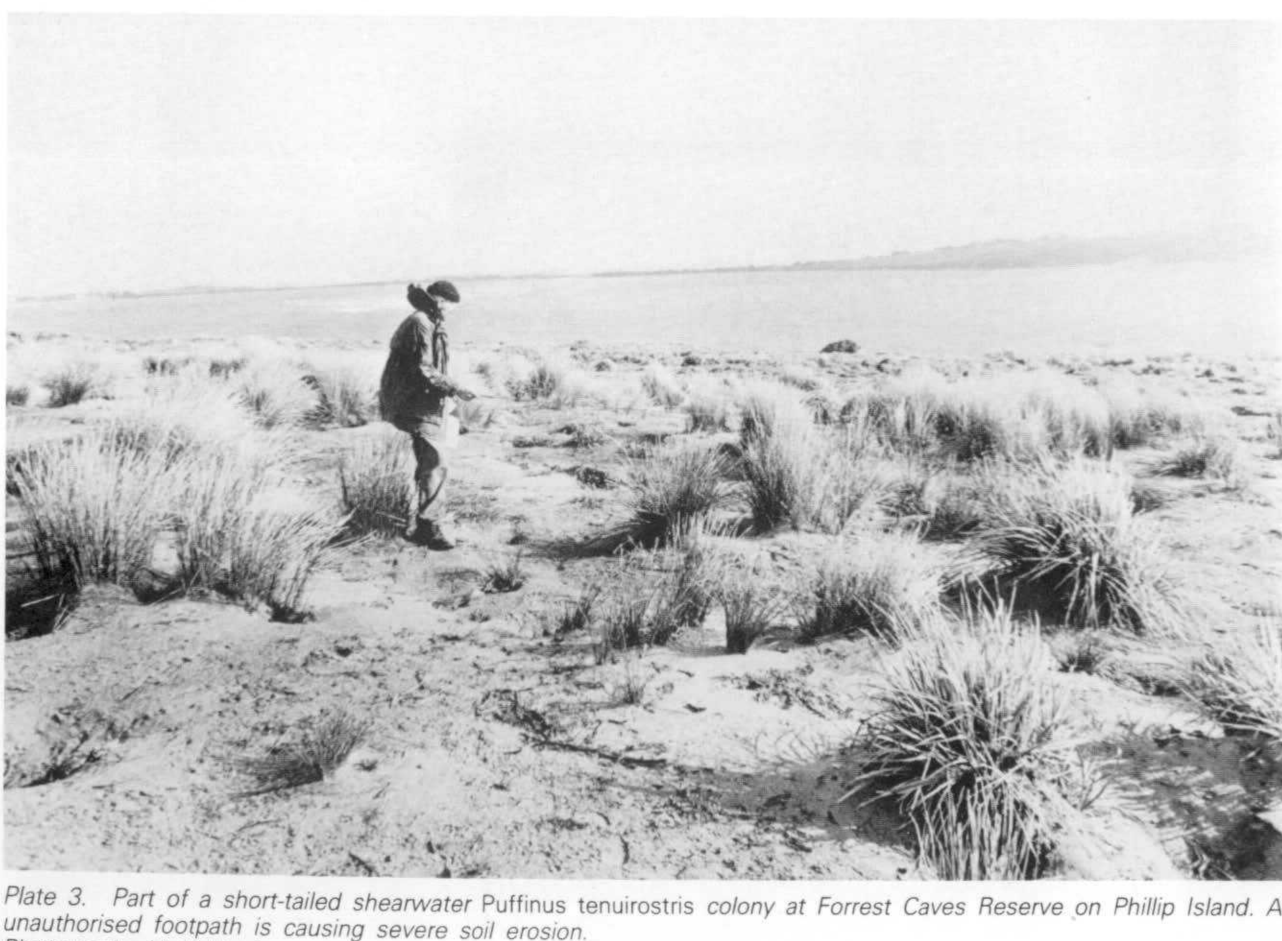

*Plate 3. Part of a short-tailed shearwater* Puffinus tenuirostris *colony at Forrest Caves Reserve on Phillip Island. An unauthorised footpath is causing severe soil erosion.*
*Photograph: M P Harris.*

# ERRATA

opposite page 79

The captions for plates 2 and 3 should be transposed.

experiment, Eulan concentrations in the whole animal were determined. Knowing the effects on the animals, the concentration present and the dose given, some initial attempt could then be made at estimating what levels of Eulan in water bodies and wildlife might constitute a danger.

Survival: Of the 3 concentrations tested (approximately 1·0 mg/l, 0·1 mg/l, and 0·01 mg/l active ingredient in a technical preparation of Eulan WA New), only the highest, 1·0 mg/l, had a significant effect on survival. Of the 80 tadpoles exposed, only 6 survived the month-long experiment. Only 2 animals died in the control dishes.

Development and abnormalities: Development of the tadpoles exposed to 1·0 mg/l appeared to be completely arrested just as hind limbs were developing, while the development of the front limbs and the final stages of metamorphosis into froglets in those treated with 0·1 mg/l Eulan were delayed by a few days. Unlike DDT and dieldrin, Eulan WA New did not appear to induce abnormalities, other than one involving a kink of the tail. This kink appeared spontaneously in the untreated groups of tadpoles, but was 3 times as frequent and was more severe in the groups dosed with Eulan 1·0 mg/l.

Weight: Tadpole weight was reduced at all 3 levels of exposure, although the effect at the lowest concentrations (0·01 mg/l) was not statistically significant (Table 22).

*Table 22*. Weights of tadpoles exposed to Eulan WA New for 36 days.

| Treatment | n | Weight ± mg | S.E. | Stage of development |
|---|---|---|---|---|
| Control | 8 | 541 ± | 12 | 31 |
| Eulan 1·0 mg/l* | 1 | 382 | | 26–29 |
| Eulan 0·1 mg/l | 8 | 493 ± | 8 | 31 |
| Eulan 0·01 mg/l | 8 | 523 ± | 9 | 31 |

* Because of mortality only one weight could be determined.

*Table 23.* Feeding of tadpoles exposed to Eulan WA New during a 48-hour period, when groups of tadpoles were observed on 11 occasions.

| Treatment | No. tadpoles feeding/ Total tadpoles observed |
|---|---|
| Control | 93/880 (11% feeding) |
| Eulan 1·0 mg/l | 27/692 (4% ,, ) |
| Eulan 0·1 mg/l | 74/880 (8% ,, ) |
| Eulan 0·01 mg/l | 80/880 (9% ,, ) |

Feeding: Reduced weight of tadpoles could be caused by reduced feeding activity, as the 1·0 mg/l tadpoles fed much less often than the controls; as did the tadpoles in the other 2 groups, although these effects were not statistically significant (Table 23).

These results suggest that, in the field, Eulan could affect the feeding and development of aquatic animals. Measurement of the concentration of Eulan in the tadpoles (Table 24), determined close to the time when development was affected, but much later than the time when effects on feeding were first observed, indicates that these effects on development and feeding could begin when animals accumulate 1·10 mg/kg Eulan (wet weight). Further research is required to assess the environmental toxicity of Eulan, and it is envisaged that particular attention will be paid to detecting effects at the biochemical level.

*Table 24*. Eulan WA New residues in tadpoles exposed for 36 days.

| Treatment | n | Eulan concentration in whole tadpole ± S.E. (mg $kg^{-1}$. wet wt) |
|---|---|---|
| Control | 4 | ND |
| Eulan 1·0 mg/l* | 1 | 24 |
| Eulan 0·1 mg/l | 4 | 8 ± 2 |
| Eulan 0·01 mg/l | 4 | 0·5 ± 0·1 |

* Because of mortality only one value could be determined. ND = none detected.

*D. Osborn*

GROWTH AND DEVELOPMENT OF TADPOLES OF THE COMMON TOAD *BUFO BUFO* L.

Savage (1961) considered that all tadpoles are not born equal, and that, in the tadpole world, it is the thruster that gets ahead. Competition for food, he believed, could account for the widely different growth rates observed in the field. Relatively little is known of the precise food requirements of tadpoles, and the aim of this work was to examine the effects of different foods, both natural and artificial, on the growth and development of tadpoles of the common toad *Bufo bufo* L. (Cover photograph). The work arose as part of a long-standing study of the ecology and conservation problems of frogs and toads in Britain.

Groups of tadpoles were raised to metamorphosis in the laboratory, and were weighed individually at regular intervals. The foods used were: (i) filamentous algae (*Spirogyra*), washed in distilled water to remove associated debris; (ii) a suspension of fresh baker's yeast; (iii) lightly boiled lettuce leaves; and (iv) a mixture of these foods. A further group was not fed initially, so that the effects of early food deprivation could be observed. Growth rates and development were compared with tadpoles collected regularly from the natural breeding site. These tadpoles were preserved and their gut contents examined microscopically to determine the nature of ingested food.

Tadpoles fed on lettuce and a mixture of foods developed more rapidly, and grew heavier than those fed on *Spirogyra* and yeast. Average rates of weight gain were 9·3 and 10·7 mg $day^{-1}$ compared with 4·2 and 4·3 mg $day^{-1}$. The time taken to complete metamorphosis was broadly related to rate of growth, but tadpoles fed on yeast suffered a protracted final phase and the resulting toadlets were small, though perfectly formed. Tadpoles starved initially developed normally once food (lettuce) was given. Average growth rate in this case was 6·3 mg $day^{-1}$. Growth rates of tadpoles in the field (10·6 mg $day^{-1}$) were similar to those obtained in the mixed foods experiment. However, maximum weights of field tadpoles were greater, at $311 \pm 19$ mg compared with $234 \pm 7$ mg. Guts of tadpoles collected from the field contained organic detritus predominantly, with varying proportions of inorganic particles, diatoms and other unicellular algae, and, particularly in the smaller individuals, filamentous algae.

Metamorphosis was reached in all the trials, which suggests that food, particularly when in short supply or of poor quality, is used primarily for development (differentiation), at the expense of increase in size. *Spirogyra* was the only food tested that was readily available to natural populations of toad tadpoles. It is interesting that growth rates of tadpoles fed on *Spirogyra* were lower than in any other treatment. By washing off the associated debris, the algae had perhaps lost much of its nutritive value. Normal development is probably dependent on the presence of bacteria and other micro-organisms, which may be more readily assimilated than macroscopic algae. Recent studies have shown that many freshwater invertebrates utilise micro-organisms attached to detritus (the major food source of field tadpoles in this study) rather than the detritus itself (see Berrie 1976). Presumably, lightly boiled lettuce is readily digestible and growth on this (unnatural) food is not so dependent on the presence of micro-organisms. In the mixed foods trial, the lettuce was eaten in preference to the other foods available. This kind of selection has also been observed in the field (Savage 1961). Apparently, if the favoured food is limited, small tadpoles prefer to seek alternative foods rather than compete against larger and more vigorous individuals.

*H.R.A. Scorgie*

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## Plant Biology

### TAXONOMY OF SUB-ANTARCTIC MOSSES: *GRIMMIA* AND *SCHISTIDIUM*

The position of the sub-Antarctic island of South Georgia on the Scotia Ridge, which links southern South America with the Antarctic continent, makes a knowledge of its mosses essential to any consideration of the geographical origins or phylogenetic relationships of the bryophytes of Antarctic regions. Moreover, many of its species are well developed and fruit freely, in contrast to the morphological modification or sterility so prevalent in many taxa farther south. To date, there is not a convenient manual to enable identification of the commoner, or ecologically more important, of the island's taxa. Instead, reliance has to be placed on older works with outdated nomenclature and narrow species concepts, the latter mostly showing little or no appreciation of species variability.

Using the rich collections of bryophytes in the herbarium of the British Antarctic Survey, presently on loan to ITE, generic revisions are being prepared of the ecologically more important groups to satisfy the requirements of terrestrial biologists who have a need to identify their material.

Species of the genera *Grimmia* and *Schistidium* are important constituents of the South Georgian bryophyte flora and they occupy a wide range of habitats, including submerged rocks in streams and exposed rock surfaces at high altitudes (Plate 1). A revision of both genera has recently been completed and there is now available a key to species, short descriptions and notes on identification, as well as a detailed consideration of the nomenclature for each species. Some confusion existed in the past regarding the distinctness of the 2 genera, various combinations of gametophytic and sporophytic characters having been used by different authors. As all South Georgian taxa have produced capsules, it is possible to use a single character to give a satisfactory distinction between the 2 genera: ie the columella remains within the capsule (*Grimmia*) or is attached to the operculum (*Schistidium*) when the latter falls away.

Problems at the specific level were, however, not so readily resolved because of the variable anatomy of vegetative leaves, the totally inadequate descriptions and the poor condition of the available material. Indeed, the inadequacy of existing descriptions was such that following the initial stages of study, when taxa were separated by their anatomical and morphological features, it was only in 2 instances, *Schistidium syntrichiaceum* and *S. urnulaceum*, that material could be readily assigned to species previously described from South Georgia. Of the remaining taxa, 2 could be referred to well-known cosmopolitan species, *S. apocarpum* and *S. rivulare*. Four taxa, *Grimmia grisea, G. immerso-leucophaea, Schistidium celatum, S. hyalino-cuspidatum*, were ultimately assigned to species previously described from South Georgia, but only after studying their ranges of variation which indicated the need for modified definitions because the type specimens represent an extreme position in the range of variation and bear little relation to the author's published descriptions. Of the remaining 2 taxa, *G. incrassicapsulis* from New Zealand was found to be a *hominum illegitimum*, while the other proved to be *S. falcatum*, a well-defined species from elsewhere in the sub-Antarctic zone.

Accepting that further detailed studies of the bryophyte flora of adjacent continental landmasses and other sub-Antarctic islands are necessary before a satisfactory thesis dealing with the origins of the South Georgian flora can be proposed, a pattern seems to be emerging. This is shown by the 3 main genera of the family Grimmiaceae, *Grimmia, Racomitrium* and *Schistidium* whose representatives in South Georgia have undergone taxonomic revision. Of the 19 taxa known from the island, 3 are cosmopolitan in distribution, 6 have been reported from southern South America, 3 are from elsewhere in the sub-Antarctic, 3 are from New Zealand, while 3 are from the Antarctic continent, and one is apparently endemic. Because insufficient collections have been made in austral regions, it is probable that the species said to be endemic exists elsewhere but has so far been overlooked.

The 3 cosmopolitan species, *Racomitrium lanuginosum, Schistidium apocarpum* and *S. rivulare*, are extremely widespread and all occur abundantly in southern South America. It seems not unreasonable to suggest that they have arrived since the last glaciation, their propagules being either wind or animal dispersed. They are robust species which, however, do not grow in the most extreme environments. The Antarctic-endemic taxa, on the other hand, grow as tightly compacted short cushions on exposed rock surfaces, and, given the extreme climate of these regions, it is not surprising to find this type of growth form. But, whereas it is easy to conjecture how the cosmopolitan group arrived at these latitudes, what is the origin of this cushion-forming group, apparently absent from southern South America? During the geological past, the Antarctic and the sub-Antarctic islands have emerged during phases of major continental drift and several glaciations. It seems reasonable to suggest that, if bryophytes remained viable throughout successive glaciations, they would be those most capable of surviving on exposed nunataks, namely the compact cushion-forming types characteristic of the Antarctic-endemic category (Plate 10).

The systematic revision of other morphologically similar genera, notably *Andreaea, Ceratodon* and *Dicramoweisia*, has yet to be completed, but could provide more evidence about the geographic origins and phylogenetic relationships of bryophytes of the far south.

*B.G. Bell*

ACCUMULATION AND EFFECTS OF AIRBORNE FLUORIDE ON THE SAXICOLOUS LICHEN *RAMALINA SILIQUOSA*

(This work is supported in part by the Welsh Office)

Although sulphur dioxide is the main cause of their absence from major industrial and urban areas, lichens are sensitive to many other types of air pollutants. When an aluminium reduction plant was established near Holyhead in 1970, the opportunity was taken to study the effect of its fluoride emissions on the ecology of lichen communities.

Lichens have 2 components, fungal and algal, living in close inter-relationship, the different combinations producing thalli with distinctive and identifiable forms. They depend on atmospheric moisture and efficiently accumulate nutrients essential for growth from weak solutions. Lichens growing on trees, corticolous lichens, absorb nutrients from stemflow enriched by leachates from leaves and branches. Those growing on rock surfaces, saxicolous lichens, are more dependent on waters seeping from surrounding areas unless they are closely adpressed to their substrates or are colonizing rapidly weathering rock. Airborne pollutants reach lichens by wet and dry deposition; they are, like other ions, readily absorbed in moist conditions.

Assessments of pollutant concentrations in lichens can be regarded as indicators of aerial contamination, lichens integrating deposition over a period of time between sampling dates. This approach has not been used as widely as that of observing the presence or absence of species to indicate severity of pollution—little work has been done on the changes taking place in established lichen communities following the new introduction of a pollutant. Research currently being done seeks to follow ecological changes taking place following the accumulation of pollutant fluoride in a range of lichen species. However, for the present, results are restricted to the effects on *Ramalina siliquosa*, one of the more frequently occurring saxicolous lichens in the vicinity of the aluminium reduction plant near Holyhead (Cover photograph).

*Material, sites and methods*

*Ramalina siliquosa* is a shrubby fruticose lichen abundant in maritime areas, but is not totally confined to the coast. On Anglesey, it is found all over the island growing on stone walls and outcrops of metamorphic rocks, mainly green-mica-schists. Fluoride concentrations have been determined in samples of the lichen which have been taken annually from sites in all directions from the reduction plant. The analyses were made with an ion-selective electrode following alkali fusion of previously dried and ground lichen.

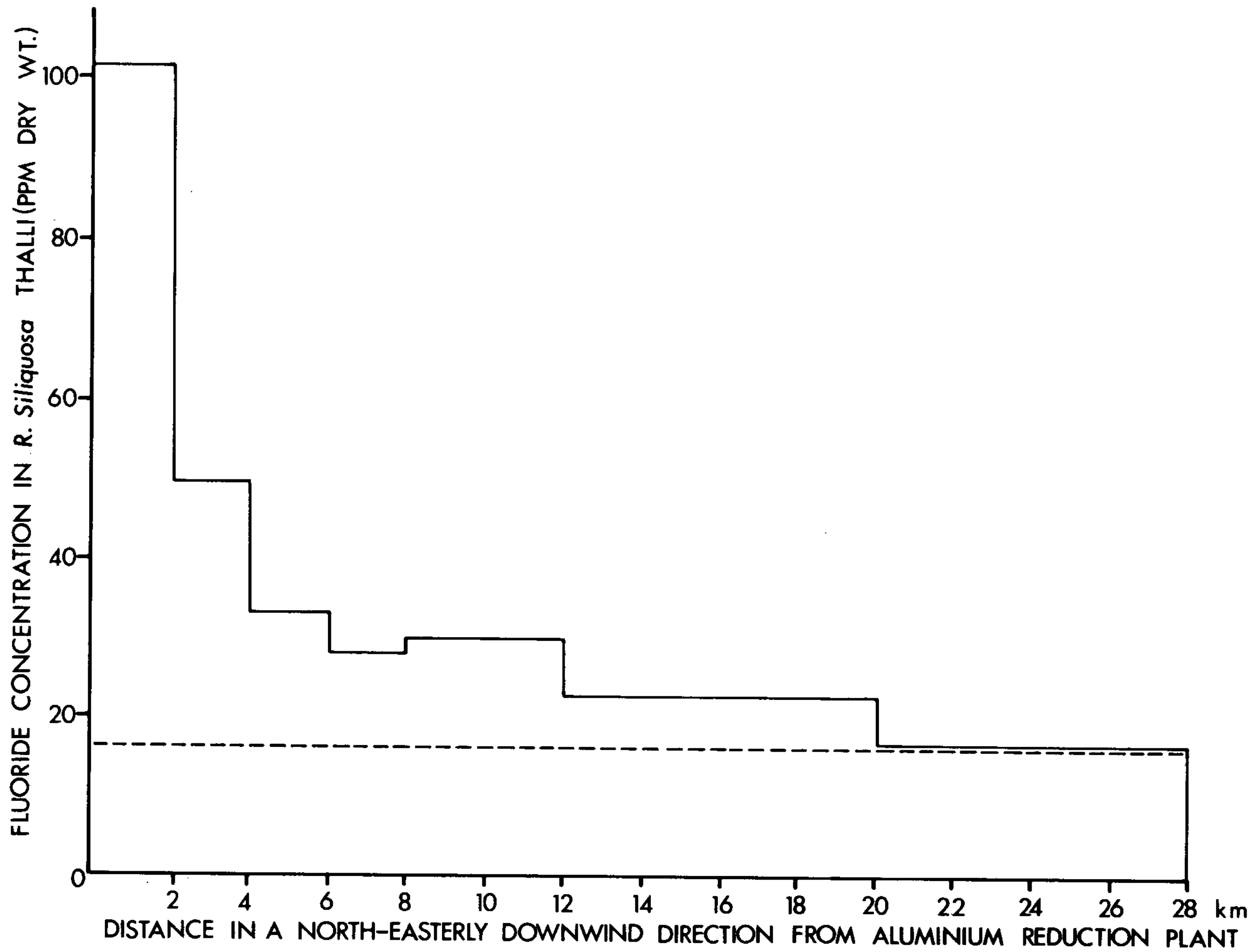


*Figure 38 Concentrations of fluoride in thalli of* Ramalina siliquosa *sampled in April 1979 at increasing distances from an aluminium reduction plant.*

In order to observe changes in lichen communities, permanently marked quadrats (20 cm × 14 cm) were established and photographed annually on colour transparency film. In the laboratory, the series of photographs, some taken before emissions commenced, have been examined for species composition and performance using a set of diagnostic criteria. Percentage cover on the permanent quadrats was assessed quantitatively by determining the presence of individual species at the intersection of a grid comprising 1 288 points superimposed on the projected transparency.

*Accumulations of fluoride*

Concentrations of fluoride in *R. siliquosa* before emissions commenced in 1970 averaged 16± 2 ppm. Although decreasing in a north-easterly, downwind, direction from the reduction plant, accumulations nevertheless increased from 1971-1978 (Perkins, Millar & Neep 1980). In April 1979, 8 years after the first emission, concentrations averaged 102 ppm within 2 km and 50 ppm between 2-4 km distant (Figure 38). With increasing distance, concentrations rapidly decreased so that only small amounts of additional fluoride were detectable in the range 12-20 km, while concentrations at greater distance were indistinguishable from those found in lichens in unpolluted areas.

Wind direction and force affect the dispersion patterns of pollutants. On Anglesey, prevailing winds blow from the south to west quadrant. The pattern of isofluors (lines of approximately equal fluoride concentrations) in 1979 largely reflects the pattern of wind frequency (Figure 39). Isofluors tend to be elongated in a downwind direction as a result of the strong prevailing winds.

*Table 25.* The pattern of damage to thalli of *Ramalina siliquosa* at different distances from an aluminium reduction plant which started to emit fluoride pollutants 4 years earlier.

| Distance from emission source (km) | % number of quadrats with specified amounts of damage | | | |
|---|---|---|---|---|
| | None | Slight | Moderate | Severe |
| 0–2 | 8 | 21 | 33 | 38 |
| 2–4 | 63 | 16 | 11 | 11 |
| 4–8 | 67 | 17 | 17 | 0 |
| 8–20 | 57 | 43 | 0 | 0 |

*Effect of fluoride on the lichen*

At first, fluoride induces a colour change in thalli of *R.*

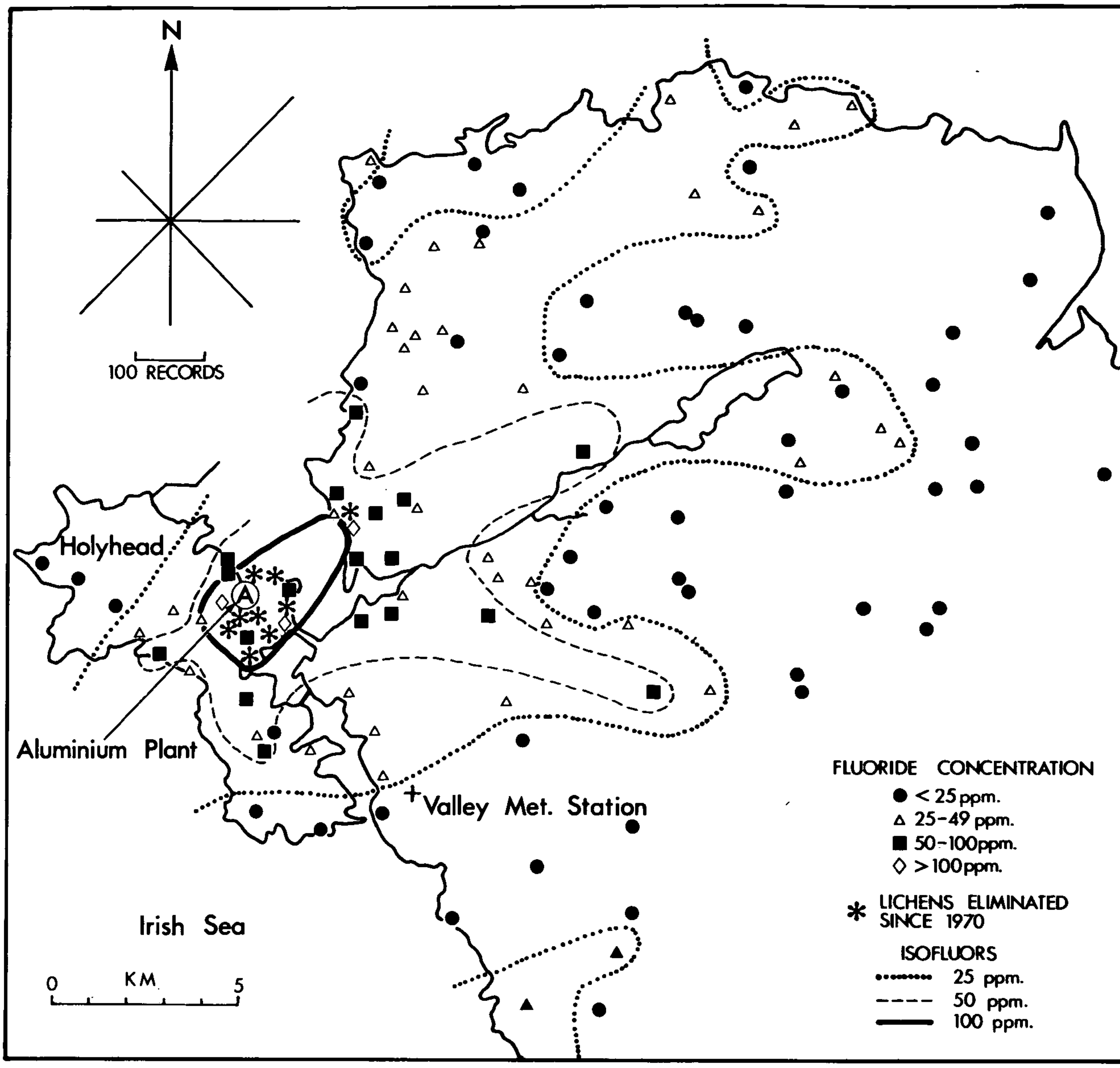


*Figure 39 Relation in April 1979 between wind frequency and isofluors showing the distribution of fluoride accummulations in lichens (mainly* Ramalina *spp.) on part of the Isle of Anglesey influenced by emissions from an aluminium reduction plant (A). The wind frequency diagram (rotated 180° in relation to conventional wind roses) is based on observations made 4 times a day at Valley (Meterological Office, 1978-1979) in the period March 1978 — April 1979.*

*siliquosa*, which are normally pale greenish-grey. They become paler and chlorotic, subsequently developing dark necrotic patches which gradually extend. The algal component of *R. siliquosa* seems to be affected before the fungal component, its cells becoming distorted and damaged. Although the fungal hyphae may become abnormally thickened, they appear to survive for a longer period. The thallus can quickly disintegrate, leaving a basal holdfast which may remain intact and viable for a few years. If amounts of pollutant are maintained, the holdfast attachment eventually weakens and becomes detached from its rock substrate. A basal holdfast may, however, recover if pollution decreases in an area, or if it is experimentally removed to an unpolluted area.

In the 56 quadrats within 2 km of the reduction plant having *R. siliquosa* in 1975, damage was severe, moderate and slight in 38, 33 and 21% respectively. Thalli colonising exposed sites were more affected than those in sheltered locations where damage was slight. At distances greater than 2 km, damage was much less severe, but continued in a small number of quadrats to 9 km particularly downwind in a north-north-east direction (Table 25). The shrubby, fruticose *R. siliquosa* sustained greater damage and more quickly than foliose and crustose species, its growth habit perhaps increasing its vulnerability to atmospheric pollutants.

Inevitably, the abundance of *R. siliquosa* was affected, and the lichen disappeared totally in some quadrats within a few years of exposure. Lichen cover (as percentage of the cover in 1970 before the reduction plant was commissioned) and associated fluoride concentrations are shown in Figure 40 for quadrats at 4 locations. At a distance of 10·6 km (quadrat A), *R. siliquosa* increased its cover (by 66%) from 1973, when first recorded, to 1979. Tissue concentrations of

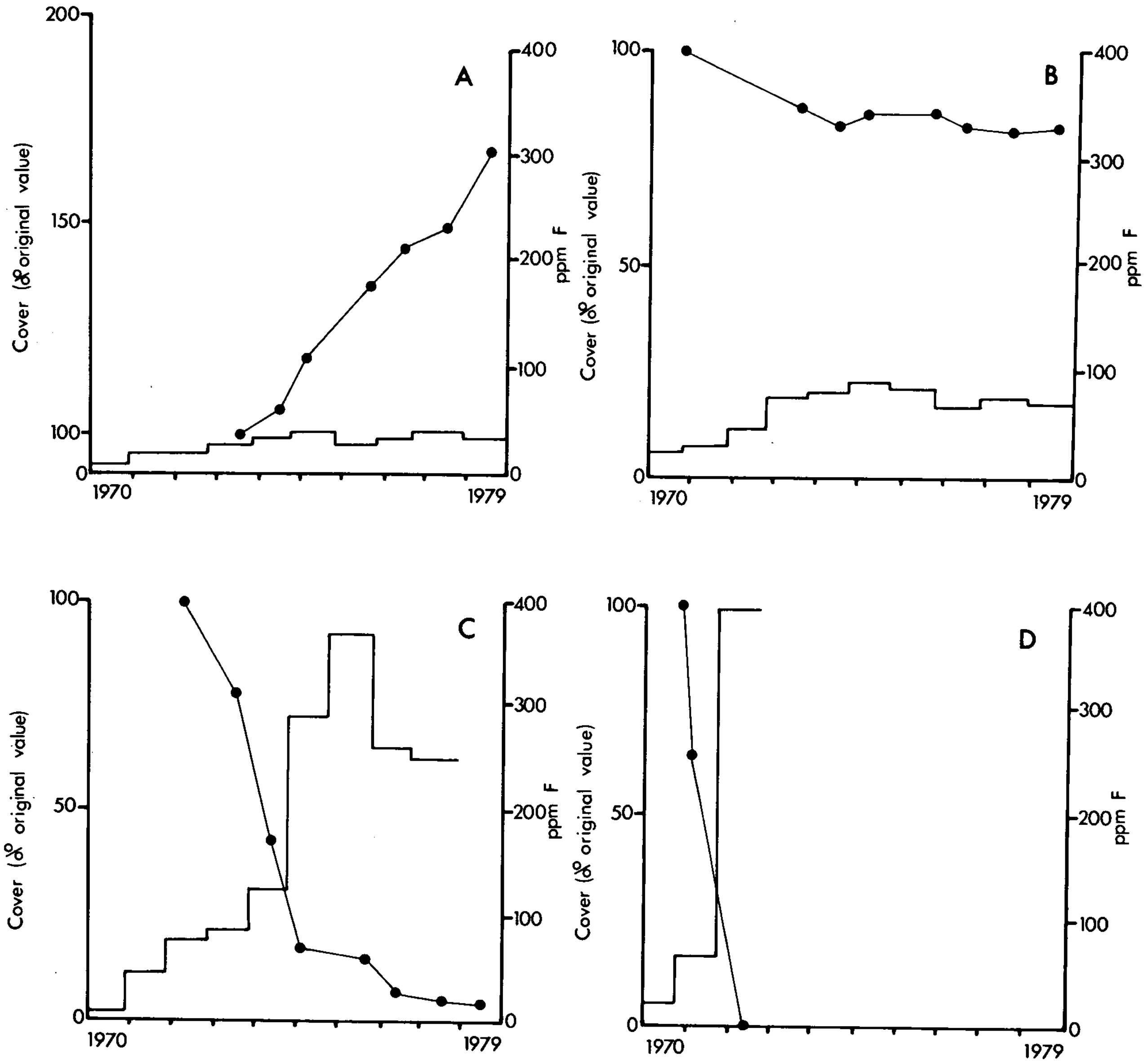


*Figure 40 Relationship between (a) 'cover values' of the saxicolous* R. siliquosa *(as % of value when permanent quadrats were first recorded●——●) and (b) tissue accumulations of fluoride (histogram). A, permanent quadrat 10.6 km from source of emissions; quadrats B, C and D within 1 km of the source which was commissioned in 1970.*

fluoride increased from 11 ppm in 1970 to 41 ppm in 1975 and 1978. In quadrats B-D, all within 1 km of the aluminium reduction plant but subject to different degrees of exposure to emissions, the areas of colonising *R. siliquosa* decreased. In quadrat B, where the fluoride concentration increased to only 88 ppm, the loss in cover amounted to only –19%, whereas the decreases were large, averaging – 98%, in quadrats C and D, where fluoride concentrations increased to 370 ppm or more. In quadrat D, where fluoride concentrations increased particularly rapidly, *R. siliquosa* had totally disappeared by 1974, whereas, in C, where the concentration increased more slowly, fragments, mainly basal holdfasts, were still to be found in 1979.

Although the tissue concentrations of fluoride that *R. siliquosa* thalli closest to the emissions source can tolerate have yet to be established, present indications suggest that they are less than 50 ppm. Thus, many lichens at sites within the 50 ppm isofluor, and now in a moribund condition, will probably disappear.

This research is now being extended to other species of lichens found on the series of quadrats, also to establish the effects of relatively small concentrations of atmospheric fluoride on lichen growth. Laboratory experiments have shown that both photosynthesis and respiration rates are inhibited by small concentrations (eg $10^{-6}$mol) of applied fluoride. However, growth rates of the same lichen in the field differ appreciably at different unpolluted sites. It, therefore, seems likely that the effects of small concentrations of pollutants on lichen growth will only be understood when the interplay between pollutants and environmental factors has been evaluated.

*D.F. Perkins, R.O. Millar and Phyllis Neep*

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THE BREEDING SYSTEM OF *AGROSTIS SETACEA*

The extent to which a species of flowering plant can respond to, or will be affected by, temporal and spatial variation in its environment is to a large measure controlled by its breeding system. For example, a sudden reduction in population size will have very different consequences for outbreeding and inbreeding species. The obligate outbreeder, in whose populations genetic variability is being constantly resorted by gene segregation and recombination, faces 2 immediate risks. First, it may experience a disproportionate and drastic reduction in its individual fecundity, depending on its pollination system (the last surviving individual in the population is doomed to extinction at that site!). Second, its open recombination system, which represents an investment in the variability of future generations (most outbreeders tend towards the flexibility end of the fitness/flexibility compromise distinguished by Mather 1943), exposes it to the vagaries of random effects in small breeding populations. This enables alleles to be fixed and high frequencies of recessive alleles, possibly with deleterious effects, to be unmasked. By contrast, the average individual fecundity of self-compatible species is not decreased by a reduction in population size and the variability, often distributed among homozygous pure lines, may not be significantly reduced in a way which affects immediate fitness (providing only the size and not the nature of the habitat is changed).

The perennial grass *Agrostis setacea* is confined to dry heathland and other well drained acid soils in southern Britain and consequently has a discontinuous distribution. In addition, its habitat, particularly in Dorset, has become increasingly fragmented (by agricultural use, afforestation and urban development) into smaller and more isolated units (Webb & Haskins in press). The species' breeding system has been studied as a first step in an investigation of the effects of population size on genetic structure.

Outcrossing rates were investigated during 1979 in 72 plants which had been collected in the vegetative state from 15 widely-scattered populations in the autumn of 1978. The technique used was mutual bagging without emasculation, the plants being divided into pairs and flowering heads enclosed in pairs in pollen-proof glassine bags prior to panicle emergence in May and June. In most pairs of plants, 3 pairs of heads from the same plant were separately bagged, giving 3 separate selfing tests on all 72 plants, and 3 single heads from each plant were bagged in pairs to give 3 crossing operations for 36 pair crosses. The heads were collected in late July and stored individually before scoring. The hard, ripe caryopses, although small, could be separated from the panicles by teasing with a mounted needle in a large enamel tray. Open-pollinated heads, up to 5 from each plant, were scored for the 72 plants to measure the effect of bagging heads on seed set.

The results clearly demonstrate the outbreeding nature of *A. setacea* (Table 26). If the outcrossing rate in open pollinations is regarded as 100%, there is a less than 1% selfing.

*Table 26.*

| | Selfs | Crosses | Open Pollinations |
|---|---|---|---|
| $\bar{x}$ seed set per panicle | 0·36 | 20·20 | 42·35 |
| range | 0–54 | 0–152 | 0–177 |
| number of panicles setting at least one seed | 23/432 | 124/215 | 132/136 |
| % of plants producing at least one seed | 13·6 | 79·2 | 95·8 |

The average values disguise considerable variation in the numbers of seed set, even in different bags of the same cross. A number of flowering tillers appeared to have died during the experiment, and, if these are excluded, the average seed set per panicle was 27·7 in crosses and 44·2 in open pollinations. Of the total of 157 seeds found in the selfing tests, 126 were from only 3 panicles, containing 54, 50 and 22 seeds respectively. It is possible that, in these cases, heads from 2 different individuals had been unknowingly included in the same bag. Observations of post-fire seedling establishment in permanent quadrats on Hartland Moor have indicated that what appear to be discreet individuals in the field (and were collected as such for these experiments) may, in fact, consist of a tightly packed cohort, usually of even-aged plants.

Analyses of variance have revealed no evidence of significant between-population differences in outcrossing (or selfing) rates, and no evidence of differences in crossing rates attributable to the distances apart of the populations (in fact the bagged head with the highest number of seed was from Carrine, Cornwall, crossed with a plant from Hartland, Dorset). Most of the variation in crossing rates was attributable to factors affecting the supply of pollen to receptive stigmas such as the coincidence of anthesis times, the amount of physical contact between the panicles and the general vigour of the plant. For example, in a number of crosses, a panicle which had extended to the top of the bag set few seed and the one below it many seed. Crosses made in the second week of the experiment (nearer to their anthesis date) had significantly higher seed set rates than those made in the first week. In addition to the effect of bagging, as revealed by the open pollinations, the enclosure of the plants in a glasshouse may have reduced seed set. Ivimey-Cook (1959) suggests that between 250–300 seeds are produced in each panicle in the field.

The basis of the self-incompatibility mechanism in *A. setacea* cannot, of course, be deduced from the results of these experiments. In all the cases of predominantly outbreeding grasses which have been investigated, self-incompatibility has been shown to be determined by 2 multi-allelic genes, generally designated S and Z, the control of the pollen phenotype being gametophytic (see e.g. Cornish, Hayward and Lawrence 1979). It is interesting, therefore, to note that 4 out of the 6 crosses which failed to produce a single seed were between plants taken from the same field population.

Although, as noted earlier, outbreeding carries attendant risks, it is often accompanied by balancing factors which regulate the recombination system (Grant 1958). For example, *A. setacea*, like many self-incompatible plants, is a perennial. Calculations of the effects of population size reductions on gene and genotype frequencies therefore need to take account of the plants' generation time and the population age structure. Conversely, apparently large populations may, in fact, have a small effective population size. For example, the effective size of populations is considerably reduced by cyclic fluctuations (to the harmonic mean of the population numbers over time—Wright 1938) and populations of *A. setacea* frequently have a history of 'bottlenecking' caused by heathland fires. The effect on genetic structure of a permanent reduction in population size is likely to depend on the interaction of the species' genetic system, its population demography and its ecological amplitude. The discovery that it is predominantly outcrossing is a small but important first step towards an understanding of this interaction.

*A.J. Gray and Helen E. Bates*

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## ECOLOGY OF THE MARSH GENTIAN

The marsh gentian *Gentiana pneumonanthe* is a perennial species of wet heathlands (Cover photograph). It was once much more widely distributed in Britain than at present, the decrease in the main resulting from losses of habitats. However, even in the remaining sites of its occurrence, *G. pneumonanthe* shows considerable variation in performance, as does the vegetation type in which it occurs.

Experiments and field observations have shown the importance of soil temperatures on numbers of flowers and seed production which increased with increasing temperatures (Figure 41). Flowering periods, which differ noticeably in natural populations, were also lengthened by high soil temperatures. While numbers of *G. pneumonanthe* remained similar from year to year, despite an annual turnover of between 20 and 30% of individuals, the production of spikes and flowers differed appreciably (Table 27). In 1977, following a fire during the dry summer of 1976, flowering at Hartland Moor was prolific, but decreased in 1978 and 1979. The 2 sites in the New Forest are grazed by ponies and cattle and have not been burnt for several years. Undoubtedly, flowering is site-dependent; it also differs with plant age and climate, 2 of the many factors determining the occurrence of *G. pneumonanthe* (Figure 42).

Although shading has little effect on the growth of *G. pneumonanthe*, the proximity of plants of *Calluna vulgaris* causes marked suppression of flowering and performance. Direct tests are being made to see if *G. pneumonanthe* is directly affected by heather, and also to check for possible allelopathic effects.

*S.B. Chapman and R.J. Rose*

## THE ESTABLISHMENT OF SEEDLINGS ON LOWLAND HEATHS

The maintenance of heathland vegetation in lowland Britain is largely the result of vegetative regeneration from the rootstocks of heather *Calluna vulgaris* that remain after heathland fires (Chapman & Webb 1976), a situation contrasting with that in moorlands where seedlings play an increasingly important role in regeneration after muirburn (controlled burning) (Miller & Miles 1970). The establishment of new plants and the possible imposition of a mixed age structure are features of considerable interest to heathland ecologists. These features are also of importance to conservation. Old heathland in southern England is important for reptiles such as the sand lizard *Lacerta agilis* and the smooth snake *Coronella austriaca*, and better knowledge of the dynamic processes involved in the maintenance of old heathland ecosystems is required to assess management proposals for these and other animal species.

On regrowing, heathland passes through the post-burn, building and mature phases of development to reach the degenerate phase after about 30 years (Chapman *et al.* 1975) when stands of *C. vulgaris* become open and patchy. Because few *C. vulgaris* seedlings establish themselves in the 'gaps', several factors likely to be of relevance to the establishment of

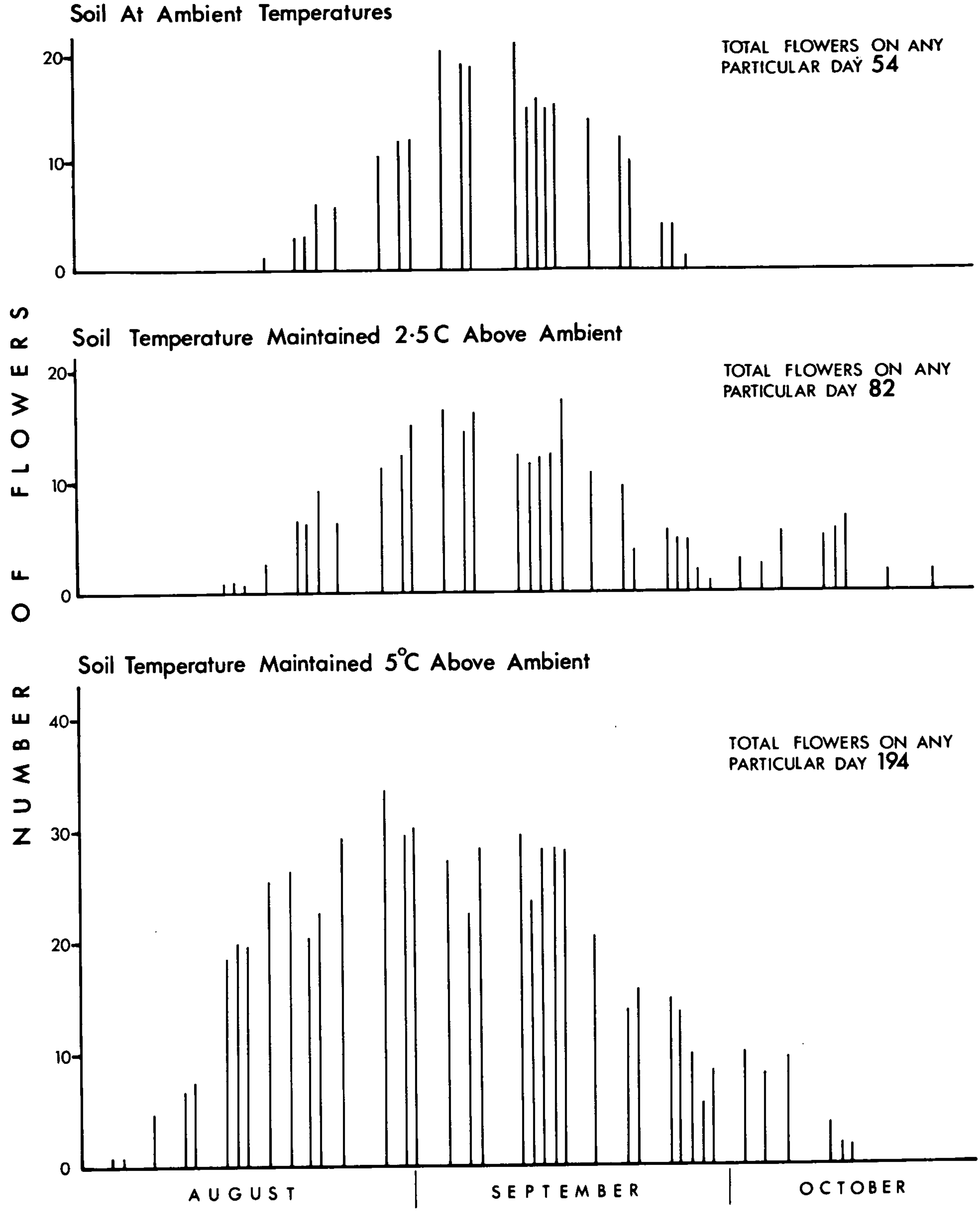


*Figure 41 Effects of soil temperatures on the flowering of* Gentiana pneumonanthe *using replicate sets of 10 plants.*

seedlings of *C. vulgaris* under stands of 'mature' *Calluna* have been examined. Because considerable quantities of viable seeds were found in soil and plant litter from under different aged stands of heather, and because seeds and seedlings of *C. vulgaris*, *Erica cinerea* or *Ulex minor* grew readily when planted in soil cores kept adequately moist in glasshouse experiments, it seems that the lack of germination and/or establishment in the field is likely to be due to moisture deficiencies in the litter layer attributable to the physical characteristics of the components of the litter.

Results so far obtained from series of field experiments investigating the effects of litter removal, soil disturbance and the exclusion of roots of established plants on the establishment of *C. vulgaris* show that 'natural'

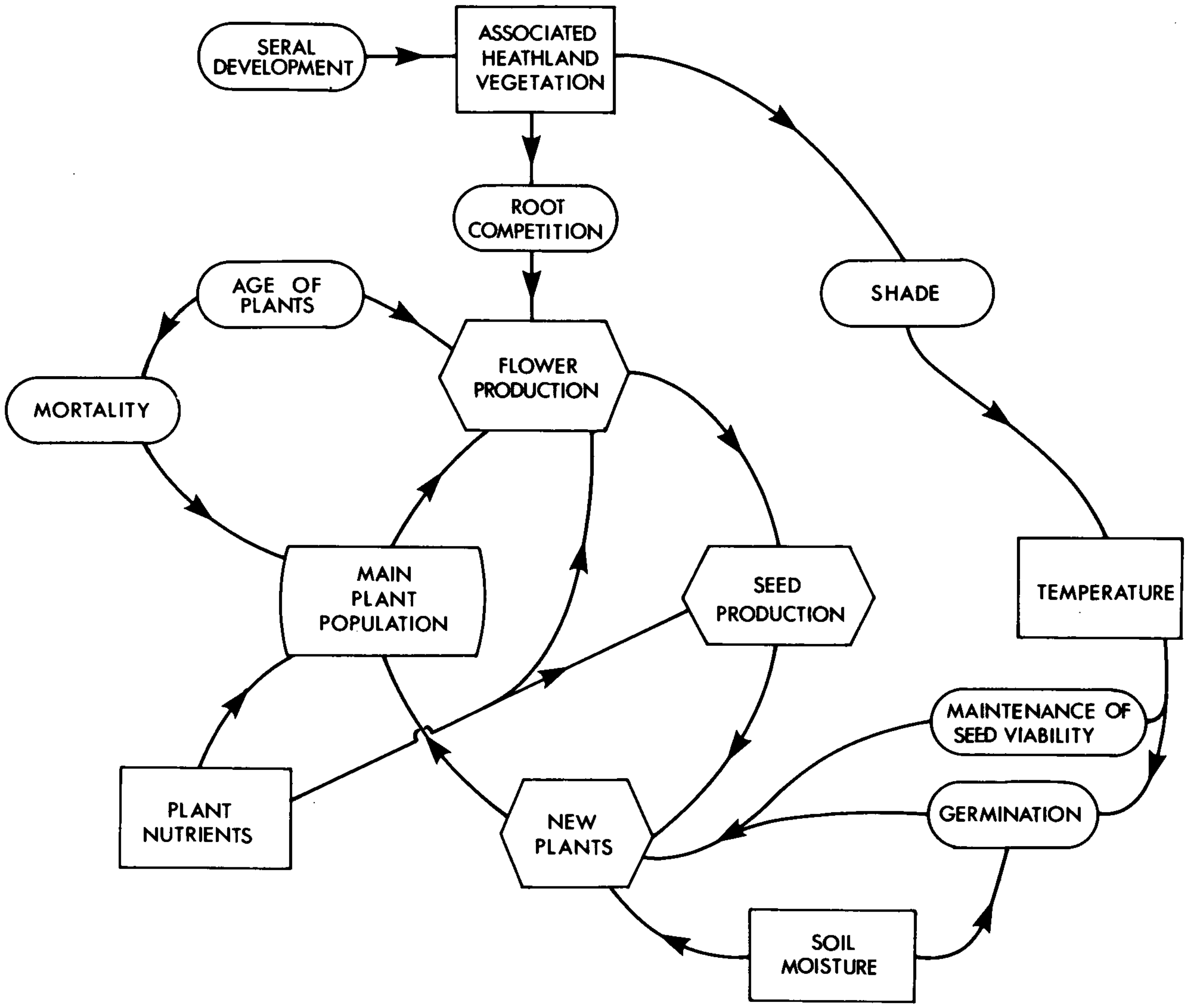


*Figure 42 Factors and relationships in the ecology of the marsh gentian.*

*Ecology of the marsh gentian*

*Table 27.* Effects of seasons and sites on numbers of shoots and flowers of plants recorded in the same 4 replicate 10 metre squares.

| Location | 1977 Plants | 1977 Numbers of Shoots | 1977 Flowers | 1978 Plants | 1978 Numbers of Shoots | 1978 Flowers | 1979 Plants | 1979 Numbers of Shoots | 1979 Flowers |
|---|---|---|---|---|---|---|---|---|---|
| Hartland Moor (burnt 1976) | 175 | 291 | 295 | 180 | 305 | 50 | 169 | 235 | 34 |
| New Forest | | | | | | | | | |
| A | 69 | 98 | 94 | 90 | 121 | 47 | 75 | 134 | 37 |
| B | 61 | 81 | 86 | 63 | 93 | 46 | 81 | 120 | 63 |

germination was significantly increased after either removing litter or disturbing the soil, but that the biggest increase occurred after killing existing vegetation by applying the herbicide 'Paraquat' (Figure 43).

Problems of re-establishment are not confined to the routine management of heathlands: they are paramount in eroded areas, which are becoming increasingly frequent as areas of lowland heathland are decreased (Webb & Haskins in press), and as a result become subject to intensifying recreational pressures. In these circumstances, where soil profiles may have been severely modified, seedling establishment must be considered in relation to the supply of nutrients, the accumulation of organic matter, and the redevelopment of soil profiles.

*S.B. Chapman and R.J. Rose*

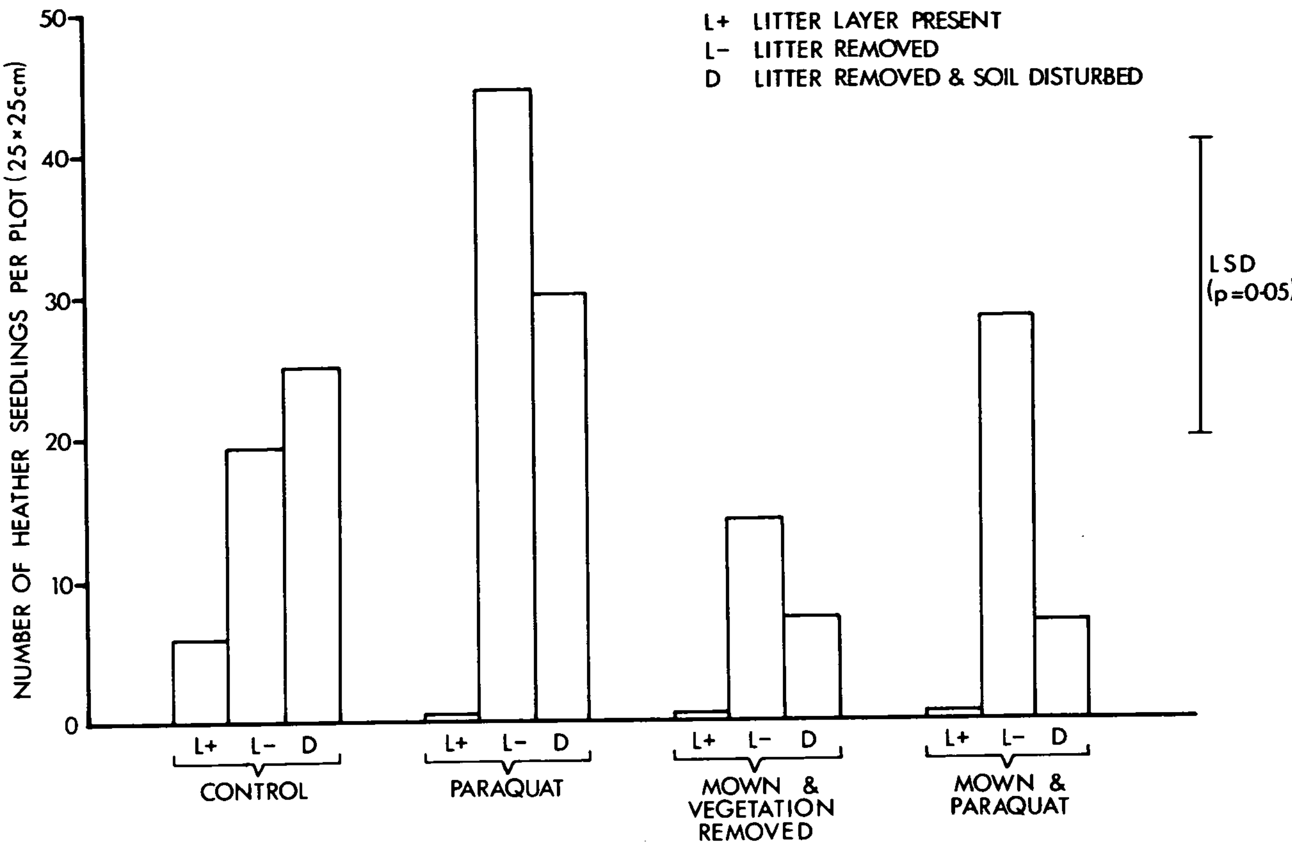


*Figure 43 Effects of mowing and/or the application of Paraquat (main-plot treatments), and litter removal and soil disturbance (split-plot) treatments, on the emergence of heather seedlings on a lowland heath.*


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STANDING CROP AND ORGANIC MATTER ACCUMULATION ON BRITISH HEATHLANDS

Analysis of data, from a wide range of British heathlands, has suggested the division of *Calluna* heathlands into 2 main groups: (i) lowland sites characterised by higher soil and air temperatures, lower annual rainfall and small amounts of available plant nutrients than (ii) upland sites with lower air temperatures, larger rainfall and generally greater amounts of available nutrients. However, with the accumulation of detailed information about growth, standing crop and organic matter accumulation from a restricted number of heather *Calluna vulgaris* dominated heaths and moorlands, it seems, surprisingly, that heather grows nearly as well in grouse moors in Scotland (Miller 1979) as on lowland heathland in southern England (Chapman *et al.* 1975).

A predictive equation, linking logarithms of weights of above ground standing crop with age, temperature, rainfall, extractable soil magnesium and extractable soil potassium, accounts for 81% of the variation. An analysis restricted to data from lowland sites emphasised the importance of age and rainfall, and highlighted that of soil phosphorus instead of extractable magnesium and potassium. The usefulness of the present equations is restricted to stands of heather up to 20 years old: if predictions are needed for older stands of heathland, then a more sophisticated asymptotic model must be developed.

While it is difficult to compare standing crops of sites of different ages, it is even more difficult to make valid comparisons of surface litter accumulations. Estimates have been made of the total weights of litter that might have accumulated if none had been decomposed. These estimates have then been compared with actual weights of litter found at different sites. Differences between these 2 weights have enabled estimates to be made of rates of decomposition which, in turn, were related to climate and the chemical composition of the litter layer. Despite the shortcomings of working with a set of data that does not encompass the complete range of variation found within British heathlands, some interesting results have been obtained which have led to suggestions of ways in which information should be collected when further comparative studies of heathland are made.

*S.B. Chapman and R.T. Clarke*

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## DYNAMICS OF HEATHER STRIPES

On exposed hill shoulders in the Cairngorms, near the altitudinal limit for growth, heather *Calluna vulgaris* sometimes grows in regular stripes or waves, separated by bare ground (Metcalfe 1950). The stripes occur where the surface is flat or convex, but reasonably smooth, and the wind either funnelled or at least unrestricted by the terrain (Plate 15). In these situations, the heather grows asymetrically with the windward side eroding away and showing generally stunted growth, and the sheltered side creeping forward and growing more vigorously. Similarly eroding and advancing communities formed of *Juncus trifidus* and *Racomitrium lanuginosum* are frequent on higher ground in the Cairngorms, and elsewhere, though they rarely form as well defined wave patterns as heather (Burges 1951; Ingram 1958).
Twelve heather stripe sites in the Cairngorms were monitored from 1975–79 to examine the dynamics of the *Calluna*, and the fate of germinating seedlings.

Wind blew predominantly from the west (King 1971). The stripes were, on average, oriented at 251°, but there were considerable site differences (range 189–355°), apparently related to local channelling of wind by features of adjacent hills. Although not smooth like sand dunes, heather stripes are nevertheless similar topographically, with a slightly convex surface on the eroding side and a concave surface on the advancing face, although the latter is to some extent concealed by the heather itself (Figure 44). Wavelengths (85–138 cm) and amplitudes (5·1–9·7 cm) were, like those of sand dunes, relatively constant.

*Wave movement*
There was considerable variation, both between sites and from year to year, in the movement of the waves: in a small number of instances, waves even moved towards the prevailing wind, presumably because of particularly favourable growing conditions. On average, advancing heather moved 08·2 cm $yr^{-1}$ and the eroding front face withdrew 0·88 cm $yr^{-1}$. During the 5-year period of study, the width of the stripes decreased at half of the sites and increased at the others. Rates of heather 'erosion' varied little from year to year, the small differences seeming to reflect patterns of windiness. In contrast, the rates of advance were appreciably slower from 1975–77 than from 1977–79, possibly because of the warmer drier conditions.

Shoot elongation was noticeably less at the (exposed) eroding front than at the (sheltered) advancing front. Within a heather clone, extension growth was inversely related to shoot water potential (Figure 45), but the absolute values of this relation differed considerably between clones.

*Seed production and seedling survival*
Flowering was very variable, some heather plants producing an abundance of flowers, others few or none, with a tendency for slightly more flowers in sheltered than exposed parts of waves. Although the seed 'rain' was sparse, about 40–200 seeds $m^{-2}$, large numbers of seeds were found in soil (up to 4 500 $m^{-2}$), presumably accumulations over several years. The largest concentrations were found in cores from bare soil from near the eroding front, where exposure minimized seedling emergence, the seedlings rarely producing more than a few pairs of leaves. Seedling survival decreased at increasing distances from the advancing front, the longest lived seedling, in marked plots, being

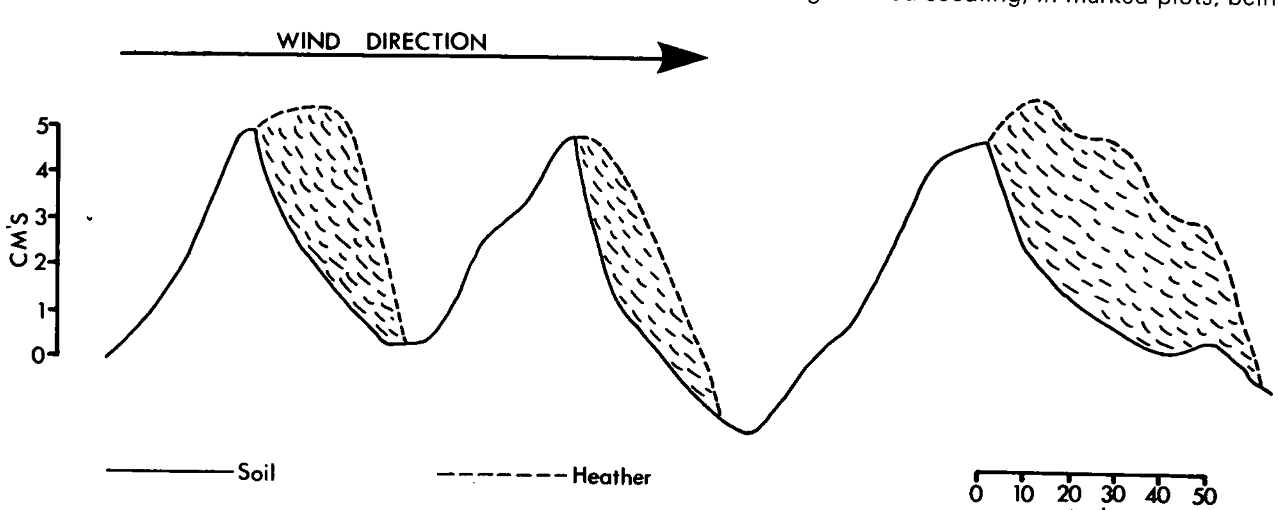


*Figure 44 Profile across 3 heather stripes at An t-Aonach showing the relative heights of soil (continuous line) and heather (dotted line) surfaces.*

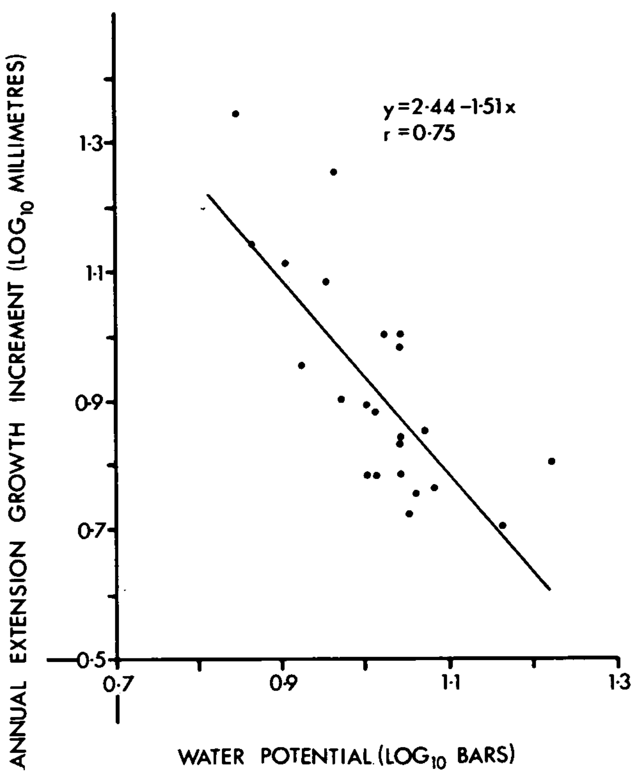


*Figure 45 Relationship between water potential and annual extension growth increments of long shoots of a single clone of* Calluna vulgaris *in a heather stripe.*

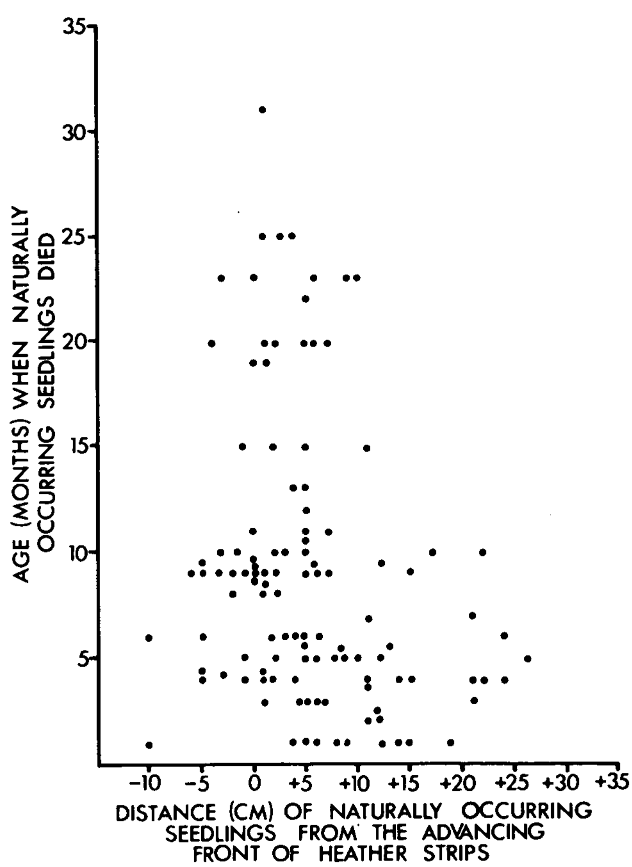


*Figure 46 Age when naturally occurring heather seedlings died related to the advancing fronts of heather stripes at An t-Aonach, 1971-77.*

31 months old at the time of death (Figure 46). Mortalities were most numerous during spring, presumably as a result of increased evaporative demand and root damage attributable to winter frost heave.

Heather stripes in the Cairngorms appear at present to form stable systems, with erosion more or less balanced by annual growth increments. The failure of seedlings to survive for more than a few years suggests that heather plants in the stripes may be of great age. The long term stability of the community is however less certain, nor is it clear how this form of patterned ground originated. The 2 most likely possibilities are that bare ground was invaded by heather which coalesced into stripes under the influence of wind, or else that a previously intact area of heather was eroded into stripes during a period of severe wind blast, with the pattern subsequently being self-maintaining.

The latter seems the more likely explanation: long strips of heather torn out by storms have been recorded by Metcalfe (1950). If invasion of bare ground by individual plants took place, it would probably result in crescent-shaped patches such as are a feature of *Juncus trifidus* heaths.

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## GROWTH RESPONSE OF SCOTS PINE TO SITE FACTORS OVER GREAT BRITAIN

As the growth rates of trees depend on site factors, it is not surprising that predictive equations of growth can be calculated as an aid to decisions about land use. The calculation of these equations has been relatively straightforward in homogeneous areas where few factors need to be taken into account, as for example in semi-arid areas where moisture availability is of main importance. In temperate areas, however, there are many problems to be overcome, not the least being the need to take many factors into consideration, but, even here, success has been achieved where the predictions are limited to restricted geographical areas (Fourt *et al.* 1971; Malcolm 1976; Mayhead & Broad 1978).

Two attempts have been made within ITE to obtain predictive equations for (i) Forestry Commission sample plots of Scots pine ranging from 29–109 years old, and (ii) individual trees of different ages, in open range situations and in closed plantations. Site factors were recorded at each of the many sites spread over Great Britain. They included topography, competition, the chemical and physical properties of soil at 2 depths, estimates of climatic variables (White 1979) and, in addition, concentrations of monoterpenes in needles of Scots pine as possible indicators of genetic origin. These variables were analysed against deviations calculated from a logarithmic relationship between tree height and age.

Growth in the UK was associated with amounts of solar radiation, soil texture as expressed by silt and stone content, amounts of soil moisture, soil water-holding capacity, wind direction and topographical factors, these variables accounting for 75% of the variation. The addition of a complex of soil variables increased the percentage of variation explained to 69%. The difficulty of reaching this level of success probably reflects the heterogeneous character of Scots pine sites and the interplay of site factors in temperate areas.

By restricting predictive equations to parts, instead of the whole, of Great Britain, it was relatively easy to account for between 62 and 99% of the variation in growth rates. Summer soil moisture at a depth of 5–25 cm was the most important factor in the south of the country, although slope to the west superseded it in one equation. In the north, exposure was the most important factor. The different origins of Scots pine, as indicated by their monoterpenes, seemed to be generally unimportant but limonene was the most important variable in the south-west.

When analysing the height growth of individual trees, 63% of the variation was associated with 'competition', rainfall and soil water-holding capacity.

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THE INITIAL ESTABLISHMENT AND EARLY SURVIVAL OF SCOTS PINE *PINUS SYLVESTRIS*

The native pinewood of Glen Tanar, Aberdeenshire, like many of the other native pinewoods of Scotland, is dominated by Scots pine of the older age classes (120+ years), although there are extensive areas outside the present forest limits which have regenerated in the last 40 years. Regeneration inside the forest is usually absent or held 'in check' at the height of the ground vegetation.

As part of an investigation of factors involved in the establishment of seedlings beneath a stand of mature pine, experiments were done to determine the effects of 5 ground treatments that varied in the intensity of disturbance to the vegetation soil on germination and survival of pine seedlings. Seed-traps showed that seedfall in the study area amounted to 114 seeds $m^{-2}$. Where the ground treatment involved the removal (screefing) of ground cover, including the bryophyte mat and litter, so exposing a bare humus surface, emergence increased from 2–22 $m^{-2}$; shallow ploughing, which exposed the mineral soil in places, increased emergence to 25 $m^{-2}$. Burning, cutting and spraying with herbicide (2,4,2-D) did not significantly affect germination.

Even on the most favourable seedbed, only a small proportion of the seedfall germinated. The others were colonised by fungi, destroyed by insects and small mammals, etc. Estimates of seed losses attributable to small mammals were made by comparing germination inside and outside wire mesh exclosures. Seed was sown at a density of 300 $m^{-2}$ on small screefed and unscreefed plots inside and outside the exclosures. Small mammals destroyed about 90% of the seed which would otherwise have germinated. Of those that germinated, some succumbed to browsing by slugs or stresses imposed by drought during the 3 weeks following germination. Thereafter, losses decreased.

The seedlings established from seed during these experiments did not attain sufficient height to attract browsing by larger mammals. To assess the effect of browsing by deer, hares and rabbits, young pines and birches (2–4 years old) planted inside exclosures grew well; pines and birches, outside the exclosures, were severely browsed by deer, hares and rabbits, and, as a result, height increments were adversely affected.

*Conclusions*

Successful regeneration depends on an adequate seed supply, favourable ground conditions for germination, and low seedling mortality. Seed is destroyed by small mammals, but, in a good 'seed year', sufficient remains undamaged. Germination can be improved by removing the ground vegetation and litter; seeds rarely germinate on an undisturbed bryophyte mat. Mortality was greatest during the few weeks after germination. Thereafter, losses decreased, although the growth of survivors was notably retarded.

*I.D. Edwards*

## AN AUTOMATIC SYSTEM FOR MEASURING SHOOT LENGTH IN SITKA SPRUCE

To aid the assessment of the effects of weather on the growth of Sitka spruce, a device was designed to measure shoot lengths repetitively over short periods (Milne *et al.* 1977). The device minimises physical contact with shoot apices (Plate 16).

An electric motor periodically repositions a light transmitter-receiver system and an associated multi-turn potentiometer so that the light beam is just clear of the shoot tip. The readjusted position of the beam, and hence of the shoot tip, is inferred from the changed resistance of the potentiometer. The sensor head, consisting of a light-weight tubular steel framework, is usually clamped to the previous season's section of hardened stem, the frame supporting a light-emitting diode (LED) on one side of the shoot opposite a light receiver on the other side. The LED emits beams of near infra-red radiation at 900 nm, outside the action spectra of plants, for 40 $\mu$s at intervals of 7 ms. When the device is being reset, which at most occurs every few minutes, this pulsed light is emitted for periods of only ~10 s. The light receiver is a phototransistor with a Kodak 87C filter to block ambient light below 850 nm. The light emitter/receiver pair is mounted on an assembly which is moved along a screwed rod by a motor mounted at the base of the sensor head framework. The housing for the motor also encloses the multi-turn potentiometer which is geared to the motor. A multiway cable connects the sensor to the electronics, including bias voltage for the potentiometer control logic, a pulse oscillator and drive interfaces for the LED and motor, which may be some distance away. When a new assessment of shoot length is required, after a period of extension or shrinkage, the electronics generate signals which cause the light beam assembly to be positioned at the tip of the shoot and in such a way that the final position is always approached from below. The device has a resolution of $\pm 0{\cdot}1$ mm at constant temperature and $\pm 0{\cdot}2$ mm over the range 10–40°C. It can record contraction as well as extension, and can accommodate shoot length changes up to 250 mm without remounting. The prototype instrument, and others built on the same principles by the Wolfson Microelectronics Liaison Unit, University of Edinburgh, showed that the hourly growth rates of leading shoots of Sitka spruce varied through the day, being maximal in late evening (Figure 47), which is some 5 hours after the daily temperature peak and about 8 hours after the incoming radiation maximum. There are thus significant short term variations in shoot growth rates, and also in the internal water status of trees. Changes in growth rate or water status usually occur some time after changes in weather. The exact temporal relationships are those to be expected in a dynamic system; they need further investigation using time series analysis.

*R. Milne and E.D. Ford*

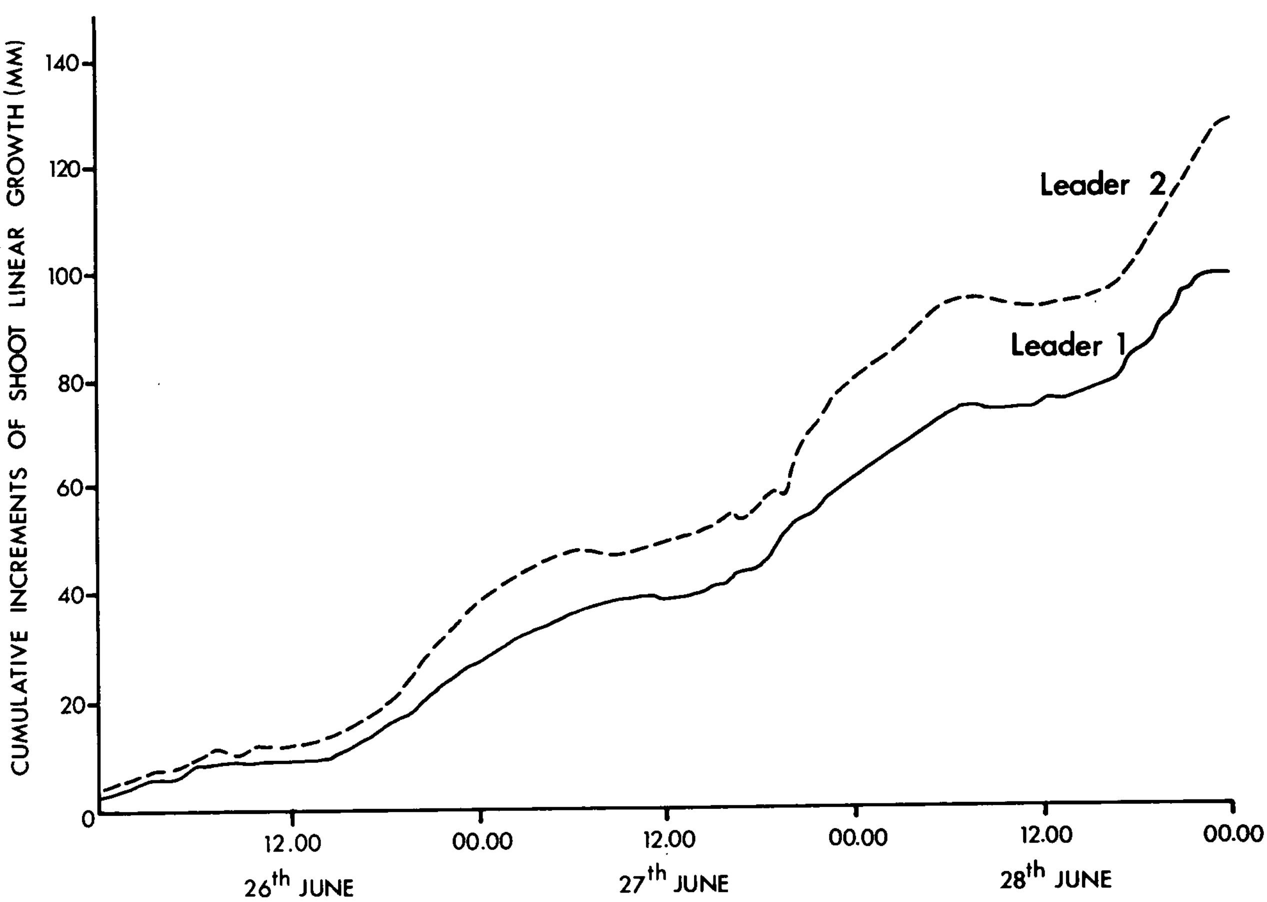



*Figure 47 Short term patterns of growth when the leading shoots of 2 Sitka spruces were monitored in forest conditions with an automatic measuring device.*

*Reference*

**Milne, R., Smith, S.K. & Ford, E.D.** 1977. An automatic system for measuring shoot length in Sitka spruce and other plant species. *J. appl. Ecol.*, **14**, 523-529.

## TREES FOR PLANTING ON COAL WASTE

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

Coal waste, often with a variety of undesirable physical and chemical factors, can pose problems for the cultivation of trees. Current reclamation practices usually seek to ameliorate these adverse factors, but, while being costly, these practices are not always successful. However, other approaches can be adopted, for instance by the selection of within-species variants that are better able to tolerate difficult conditions, an approach that may lessen the need for expensive site improvement and aftercare. To this end, seeds and cuttings of hairy and silver birch *Betula pubescens* and *B. pendula* and grey and common alder *Alnus incana* and *A. glutinosa* have been collected from specimens found growing successfully on coal waste. Subsequently, stocks of these plants have been built-up for assessments of tolerance.

During the winter of 1978-79, 3 field trials were planted with a variety of clones whose performance will be tested against that of plants obtained from commercial nurseries. The characteristics of the 3 trial sites, Easthouses, Bilston and Bush, differ appreciably (Table 28).

At the alkaline Easthouses site, with a small water-holding capacity, there was a severe early water shortage. Although performance was generally poor, the percentage survival of *Betula* clones was greater than those of *Alnus*. At Bilston, pH 6.0, water stress was less severe but, nevertheless, there were conspicuous dry spells during the growing season.

*Table 29.* Mean relative rates of height growth, cm cm$^{-1}$ yr$^{-1}$, of *Alnus* and *Betula* clones of coal waste origin at 2 sites (a) Bilston and (b) Bush, both near Edinburgh.

(a) Bilston

| | g m$^{-2}$ of Enmag 0 | 36* | 73 |
|---|---|---|---|
| *Alnus* | 0·224 | 0·437 | 0·316 |
| *Betula* | 0·105 | 0·193 | 0·175 |

* equivalent to 20 kg N, 75 kg $P_2O_5$, 33 kg $K_2O$, 29 kg Mg ha$^{-1}$

(b) Bush

| | Coal spoil I | Coal spoil II | 'Control' nursery soil |
|---|---|---|---|
| *Alnus* | 0·568 | 0·587 | 0·609 |
| *Betula* | 0·116 | 0·135 | 0·272 |

Generally, the relative height growth rates were greater among clones of *Alnus* than of *Betula* (Table 29), with one of *Alnus* appearing to withstand early season drought particularly effectively. This initial advantage seemed to lessen in the moister conditions later in the season. Applying fertilizers appreciably increased mean rates of growth, but that of *Alnus* clones remained twice as large as that of *Betula* clones.

At Bush, tree growth is being assessed on 3 substrates, 2 spoils, one alkaline and the other acid, and a nursery soil 'control'. Overall, the growth of *Alnus* clones was conspicuously faster than that of *Betula*. However, while the *Alnus* clones grew rapidly irrespective of the nature of the subtrate, those of *Betula* were significantly influenced. Growth of *Betula* in both acid and alkaline coal waste was halved when compared with growth on the 'control' nursery soil. Some *Alnus* clones grew more on spoil than in the control substrate.

Assessments of growth during the first year of these trials are regarded as indicators of performance during establishment. Except in extremely dry conditions,

*Table 28.* Characteristics of substrates at 3 sites where attempts are being made to identify tolerant clones of *Alnus and Betula*.

| Site | pH | Conductivity µS | K (mg 100$^{-1}$g) | Ca | Mg | Mn | P | $NO_3$-N + $NO_2$-N | $NH_4$N |
|---|---|---|---|---|---|---|---|---|---|
| Easthouses (extremely coarse, alkaline coal spoil) | 8·6 | 100 | 1·70 | 2·3 | 0·76 | <0·002 | 0·23 | 0·30 | 0·30 |
| Bilston (coal spoil) | 6·0 | 110 | 0·82 | 1·3 | 1·00 | 0·002 | <0·05 | 0·19 | 0·37 |
| Bush | | | | | | | | | |
| (a) Coal spoil I | 3·7 | 646 | 0·84 | 16·6 | 4·60 | 1·3 | 0·06 | 0·03 | 1·60 |
| (b) Coal spoil II | 8·6 | 112 | 1·70 | 4·2 | 0·71 | 0·018 | 0·03 | 0·08 | <0·02 |
| (c) 'Control'—nursery soil | 5·8 | 81 | 0·66 | 2·3 | 0·18 | 0·004 | 0·06 | <0·02 | 0·12 |

*Plate 4. The upland area used to examine the distribution of beetles in a range of habitat types. Photograph: A. Buse.*

*Plate 15. Heather stripes, and aeolian erosion feature in the Cairngorm mountains. Hill shoulder at An t-Aonach (780m). Photograph: N G Bayfield.*

*Plate 16. An automatic system for measuring shoot length in Sitka spruce. Photograph: R Milne.*

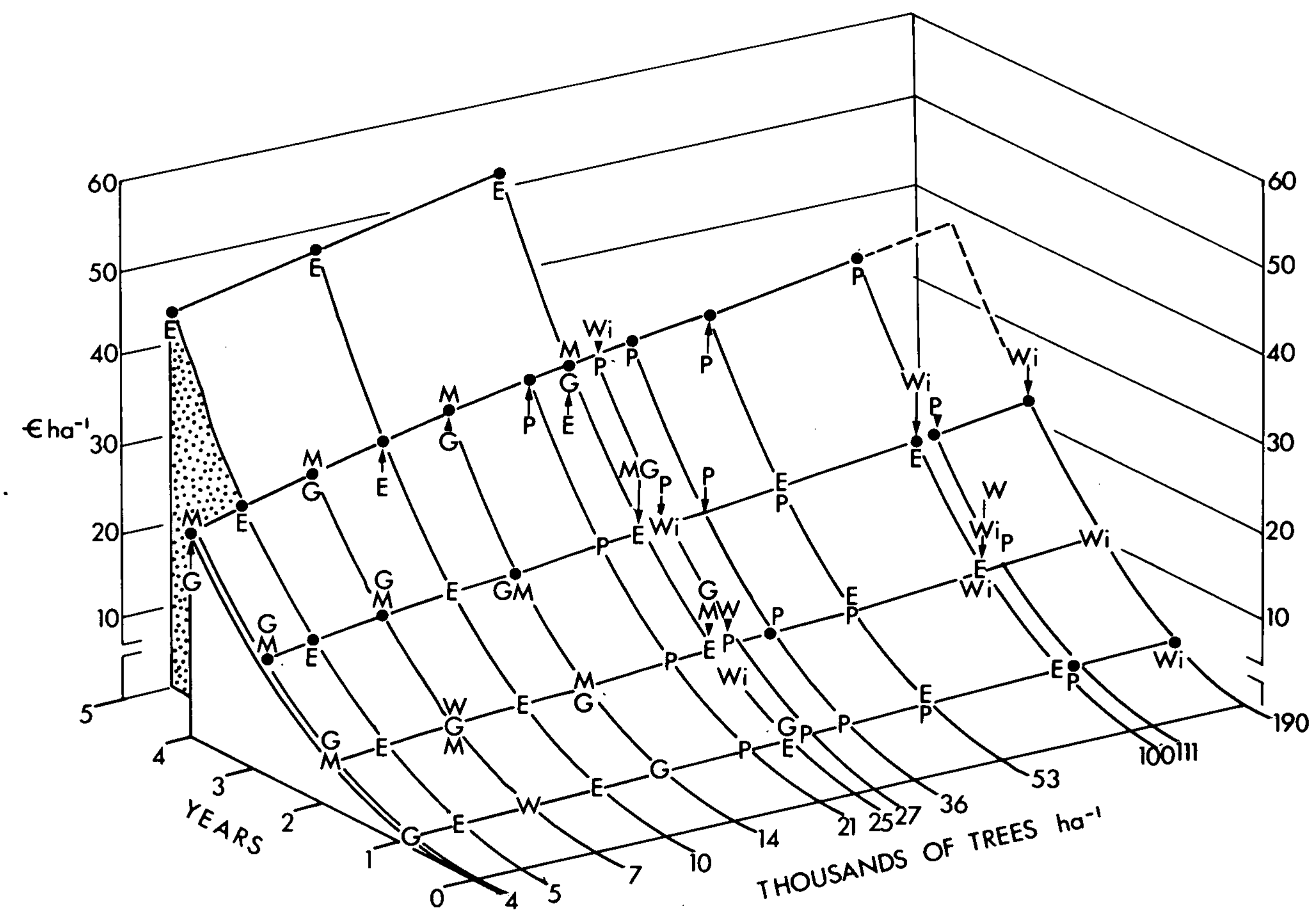
some of the *Alnus* clones appear to have promise. However, while concentrating on physico-chemical aspects of these difficult sites, the continuing damage done by sheep, rabbits and children emphasises the need to ensure that favoured clones regrow readily after this type of damage.

*Julia Wilson*

## APPRAISAL OF MINI-ROTATION FORESTRY

There has been considerable interest in temperate regions in cultivating trees which have rapid juvenile growth at close spacings on fertile soils for periods of only 1–6 years, that is like field crops, the end-product being hardwood fibre, for use as pulp, chips or fuel. It has been claimed that yields of dry wood, including branches and bark, could be in the range 15–20 t $ha^{-1}yr^{-1}$ (Swedish workers alone claim 30 t $ha^{-1}yr^{-1}$). However, yields of ITE trials with *Populus trichocarpa* grown at various locations in Britain have averaged only 6-8 t $ha^{-1}yr^{-1}$ over 5 years; even at the best site, in Gloucestershire, they did not exceed 10 t $ha^{-1}yr^{-1}$ (Cannell 1980) (Cover photograph). A critical review was therefore made of yields recorded in similar studies in other countries: 11 other research groups were located mostly in North America. Critical attention was given to possible effects of edge bias, competitive interaction between plots, definitions and methods of estimating yields. All recorded *reliable* yield data were then examined with respect to age and spacing (Figure 48, Cannell & Smith in press). Excepting one group of studies in which trees were repeatedly irrigated and given regular foliar applications of nutrients, there were 83 records of high yields of mini-rotation closely-spaced hardwoods in temperate regions. These yields were regarded as the 'working maxima'. A single multiple regression of yield on age and spacing accounted for 90% of the total variation among these 83 records, the remaining 10% being due to species (either *Populus* spp or *Platanus occidentalis* L.), site and error (Figure 48).

The maximum mean annual yield of dry stems and branches plus bark was in the range 10-12 t $ha^{-1}yr^{-1}$ at age 4·5 years (Figure 48), much less than the 15-20 t $ha^{-1}yr^{-1}$ claimed by advocates of silage and fuel forestry. Although the data refer to yields in the first rotation after planting, and somewhat greater yields




G= *Platanus Occidentalis*, Georgia, USA. M = *P. Occidentalis*, Mississippi. W = *Populus*, Washington State.
E = *Populus*, England. P = *Populus*, Pennsylvania. Wi = *Populus*, Wisconsin

*Figure 48 Yields of dry stems and branches, with bark, of closely-spaced hardwoods in the first 4-5 years after planting cuttings* (Populus) *or one year old seedlings* (Platanus). *The lines are drawn through values fitted to 83 records taken from 6 studies in temperate regions. G =* Platanus occidentalis, *Georgia, USA; M =* P. occidentalis, *Mississippi; E =* Populus, *England; P =* Populus, *Pennsylvania; W =* Populus, *Washington State; Wi =* Populus, *Wisconsin (From Cannell & Smith 1980).*

may be expected after coppicing, there is as yet no convincing evidence that coppice yields will be as large as 15-20 t $ha^{-1}$ $yr^{-1}$. Mini-rotation forests seem to be no more efficient at converting solar energy into woody fibre than more conventional hardwood plantations with rotations of 11-26 years, which, on good sites in temperate regions, can also produce 10-12 t $ha^{-1}$ $yr^{-1}$ of dry stems and branches with bark (Cannell & Smith in press).

Given 'operational' coppice-wood yields of 6-8 t $ha^{-1}$ $yr^{-1}$ of dry combustible material, containing $20 \times 10^9$ J per tonne, converted to energy as efficiently as coal, it would need 56–75 million hectares of coppice to meet the total UK energy demand of about $9 \times 10^{18}$ J per year. This is 2·3 times the total land area of the UK. If the 1·5 million hectares considered potentially available for fuel forestry were to yield 6-8 t $ha^{-1}yr^{-1}$, this production would meet only 2·0–2·7% of current national energy consumption. Short rotation coppices will probably be more valuable nationally as a substitute for imported hardwood pulp and chips.

*M.G.R. Cannell*

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APICAL DOMINANCE IN TROPICAL TREES

(This work was supported by Overseas Development Administration funds)

The relative ease with which the West African timber tree *Triplochiton scleroxylon* can be propagated vegetatively provides an opportunity to test the growth of clones. Specimens of *T. scleroxylon* are usually single-stemmed, with a small compact crown topping a straight 'clear-stemmed' bole; however, occasionally they are either multi-stemmed, or have a lax crown, at the same time retaining lower branches. The production of many stems possibly indicates a tendency to weak apical dominance and, perhaps, forking. If this, and other undesirable branching habits, could be predicted, the quality of forest plantations would be greatly enhanced.

It is likely that the degree of apical dominance, where terminal buds inhibit the extension of axillary buds, reflects the ever-changing balance of plant hormones whose concentrations are likely to be determined genetically, while also being very sensitive to environmental influences, particularly of nutrient availability water stress and light.

Studies with *T. scleroxylon* are being made in field experiments in Nigeria, using a wide range of clones representing the range of the species in West Africa. In these studies, numbers and sizes of branches produced per season, and their relationship to mainstem growth, have been assessed. This relationship is complicated by :

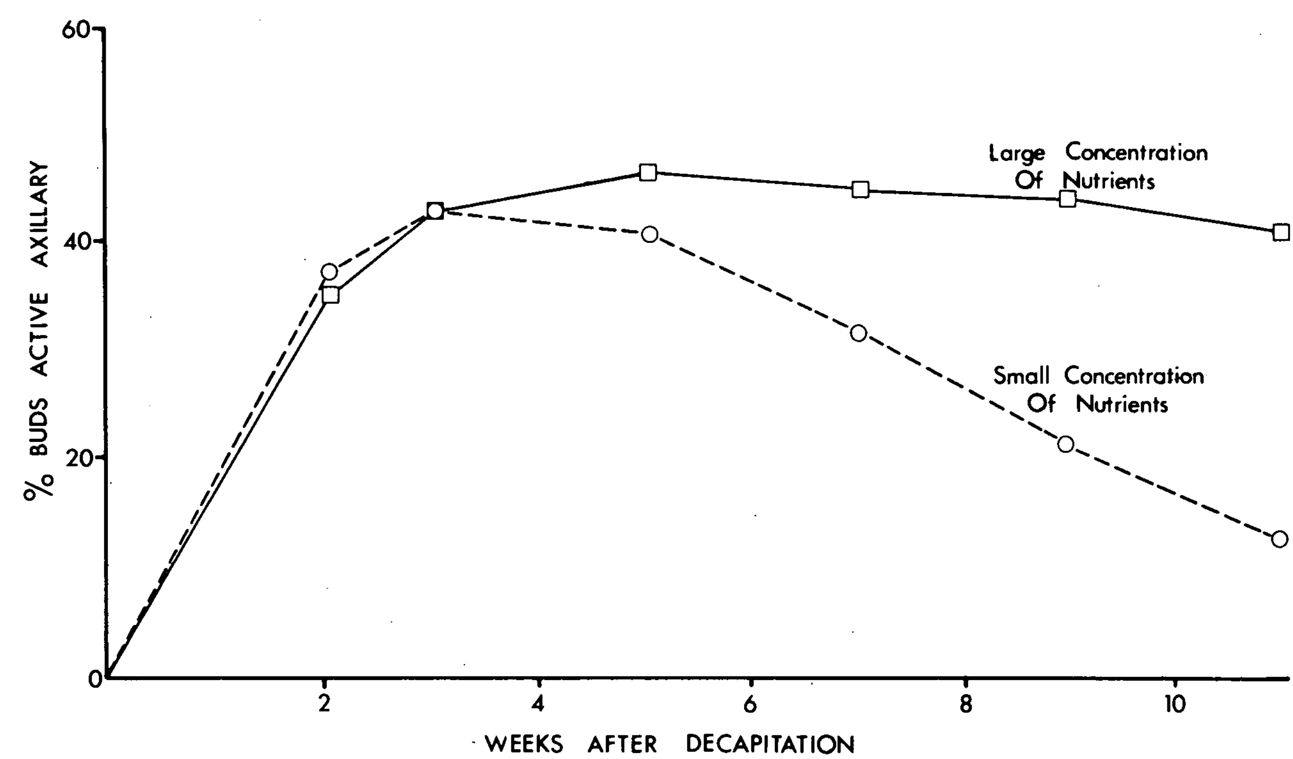


*Figure 49 Effects of nutrient supply on the proportions of lateral shoots actively growing after removing the mainstem apical bud (decapitating) of vegetatively propagated plants of* Triplochiton scleroxylon.

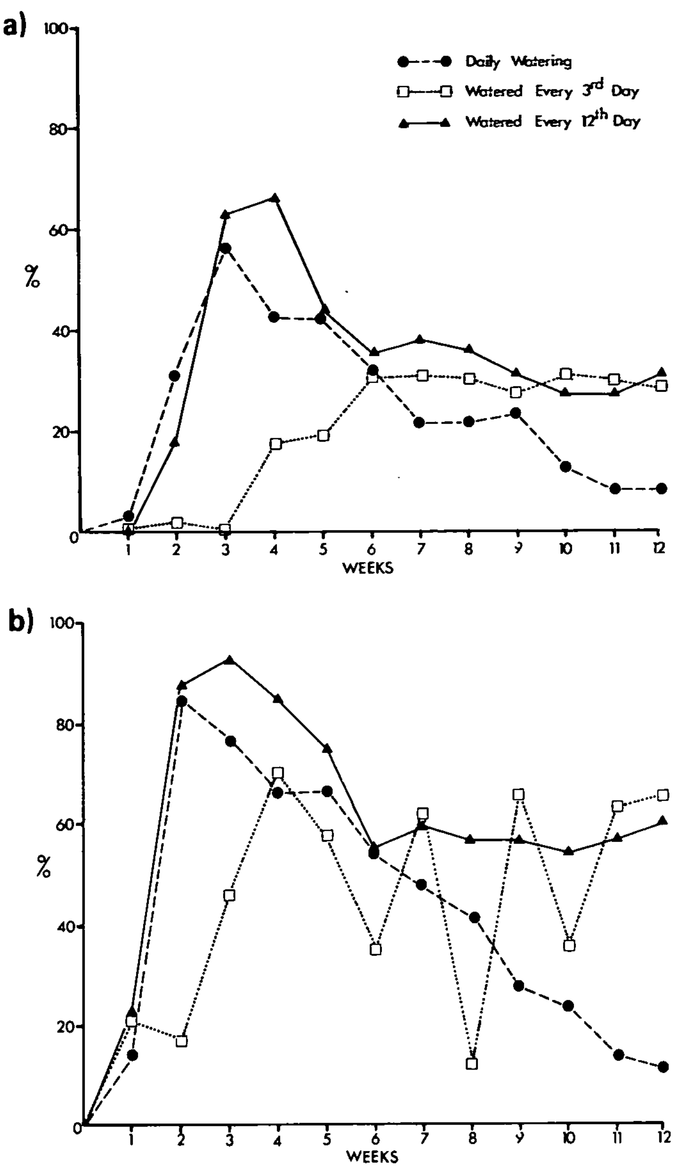


*Figure 50 Effects of water stress, imposed by different watering regimes on the percentage of lateral shoots growing from decapitated* T. scleroxylon *plants.*

1. The production of 2 types of branches: (i) proleptic or 'whorl' branches which appear to develop early in the season from inactive axillary buds immediately behind 'resting' terminal buds, and (ii) sylleptic or 'feather' branches which grow behind very active terminal apices.

2. The relationship between apical dominance and apical control. Apical dominance refers to the inhibition of axillary buds on the current year's growth, whereas apical control, which is often inversely related with apical dominance, refers to the suppression of previous years' shoot apices.

Our understanding of how these processes govern branch development in field-grown *T. scleroxylon* is still rudimentary. In contrast, glasshouse experiments to identify the genetic component of apical dominance are relatively advanced, the aim being to develop a test enabling the branching habit of *T. scleroxylon* to be predicted. It has been found, after decapitating vegetatively propagated plants, that numbers of activated axillary buds and their patterns of growth differ greatly from clone to clone—this response being susceptible to environmental modification. The extent of apical dominance is known to be particularly influenced by the supply of nutrients, especially nitrogen. In *T. scleroxylon*, a copious supply of nutrients enabled a greater number of axillary shoots to remain active after decapitation than happened when nutrients were restricted (Figure 49).

Water stress, developing after controlling the water supply 12 days prior to decapitation, had different effects on different clones. On clone 8047, it restricted the proportion of axillary buds which became activated (Figure 50a), whereas there was virtually no effect on the immediate stimulation of axillary buds on clone 8038, but, thereafter, water stress delayed the re-establishment of dominance (Figure 50b).

Light intensity and spectral composition usually influence apical dominance. When pot-grown *T. scleroxylon* were subject to shade in Nigeria, the proportion of active axillary buds, after decapitation, was appreciably decreased. Interestingly, the positions of the active buds differed on different clones, a feature possibly influencing the nature of 'multi-stemming'. Because the effects of decapitation are affected by a range of factors broadly concerned with plant condition, experiments are being done to investigate the role of different plant hormones. Auxins enhance apical dominance by inhibiting axillary bud growth; gibberellins have the same effect, but achieve it by favouring the vigorous growth of the dominant lateral shoot.

Having elucidated many of the factors controlling apical dominance and patterns of branching, attempts are being made at Ibadan, Nigeria, and Edinburgh to correlate the data from predictive glasshouse tests with the actual field performance of an array of clones. It is hoped that these experiments will confirm that patterns of mature growth can be anticipated with reasonable precision, thus safeguarding the future of *T. scleroxylon* as a commercially important timber tree.

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## Plant Community Ecology

ECOLOGY OF RAILWAY LAND

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

As a result of discussions between the Nature Conservancy Council (NCC) and British Rail (BR) (Way & Sheail 1977), it was recognised that insufficient was known about the ecology of railway land. To rectify this deficiency and to identify areas of particular (i) biological value and (ii) sensitivity, a survey was structured for the 5 Regions of BR, comprising some 11 300 miles of active line with fenced verges supporting an estimated 135 000 acres of grass, scrub and woodland.

Because of the scale of the exercise and the absence of detailed relevant information (pH, drainage, railway formation type), a stratification, while considered to be extremely important, was initially impracticable. Thus, the surveys of Eastern (completed in 1977) and Southern and Western (1978) Regions were based on random samples, whose numbers were calculated, *pro rata*, from the number of track miles in the different BR subdivisions. However, with the recent classification of rural BR track using a method described by Bunce *et al.* (1975), the track in the London Midland Region (LMR) was allocated to an array of classes (strata) before selecting random sites with the strata. The same sampling procedure will be used for the survey of the Scottish Region in 1980.

The classification, because it includes all Regions, enables sites visited in 1977 and 1978 to be ascribed *post-hoc* to a stratum. In addition to the randomly selected sites, others were surveyed because of their known, or suspected, scientific interest.

Site and vegetation data collected to date have been classified with Indicator Species Analysis (Hill *et al.* 1975). Already it is apparent that the assemblages of plants alongside railways are zoned, the zones running parallel to the track. In all the areas so far surveyed, the vegetation immediately adjacent to the permanent way, where the habitat has been enriched and conspicuously disturbed, is very similar. However, at a distance from the track, plant assemblages increasingly reflect local conditions. The effects of disturbance and nutrient enrichment are most extensive on embankments where spent ballast is often tipped, and where drainage patterns assist the spread of chemicals, sometimes including weed killers. Disturbance is minimal in cuttings, particularly those cut through rock.

The greater part of BR property would be considered to consist of slightly disturbed habitats, and these could be put at risk by changes in management policies. They are usually dominated by *Arrhenatherum elatius*, which gives way to a finer-leaved turf in chalk and limestone regions and to associations including *Agrostis tenuis* and *Deschampsia flexuosa* in the more acid parts of the north-west of England. Since the virtual discontinuance of hand cutting and clearing during the early 1960's, areas of scrub and woodland have increased.

*Caroline Sargent and J.O. Mountford*

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## BRACKEN AND SCRUB CONTROL ON LOWLAND HEATHS

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

Since 1945, the traditional agricultural management of lowland heaths of marginal economic value by controlled burning and grazing has virtually ceased to be practised. As a result, adverse vegetational changes have occurred, jeopardizing the interests of wildlife conservation and adding to the problems created by habitat loss and fragmentation (Moore 1962; Armstrong 1975). In some areas, there has been substantial invasion by bracken *Pteridium aquilinum*, birch *Betula pendula* and *B. pubescens*, and Scots pine *Pinus sylvestris*, at the expense of heather *Calluna vulgaris* and grass heaths (Plates 17 and 18). To conserve open *Calluna* and grass-dominated plant communities, different methods of controlling bracken and scrub are being investigated.

Experiments testing the use of selective herbicides, burning and cutting as management tools were set up in 1979. Earlier experiments on the control of bracken in both heather- and grass-dominated heaths in the Brecklands of East Anglia, threatened by bracken invasion, have tested the effects of (i) annual and biannual cutting of bracken, (ii) application of the herbicide Asulam, and (iii) reseeding with locally collected seed.

A single application of Asulam in July reduced bracken frond density (fronds $m^{-2}$) by 96%, frond height by 85%, and standing crop by 99%. Cutting once a year in late July reduced the frond height, but this reduction was compensated by an increased frond density, so that there was a negligible effect on standing crop. Cutting twice each year exaggerated these responses, although the final standing crop was reduced.

Very little grows, particularly at Weeting, beneath bracken fronds, possibly because of the effects of litter accumulation and allelopathic properties of bracken. Where the bracken canopy was removed by cutting, therefore, the incidence of *Aira praecox* and *Rumex acetosella* was increased. No similar response was observed on plots treated with Asulam.

*J.E. Lowday and R.H. Marrs*

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EFFECTS OF SIMULATED 'ACID RAIN' ON FOLIAR LEACHING

(This work has been largely supported by Department of Environment funds)

'Acid rain' is a widespread phenomenon, occurring in areas often remote from sources emitting $SO_2$ and other acid-forming air pollutants. The pH of rain, in Britain, is often <4·5 and occasionally <3·0. While recognising that acid precipitation may be altered while passing through forest canopies, the effects of precipitation with different degrees of acidity on leaf leaching have not previously been studied intensively.

In a preliminary study, samples of freshly detached foliage of ash *Fraxinus excelsior*, birch *Betula pubescens* Scots pine *Pinus sylvestris* and bracken *Pteridium aquilinum* were taken from trees growing in an unpolluted area. Each of the replicate samples—about 100 g of foliage, comprising separate leaves or young shoots with leaves attached, and with cut ends sealed with nail varnish to prevent leakage—was washed for 4 hours in 300 ml of tap water acidified with $H_2SO_4$ to pHs ranging from 2·8 to 4·5 and 6·9.

Whereas the acidity of solutions initially pH 2·8 remained virtually unchanged, those of pH 4·5 and 6·9 were altered during washing. The acidity of the latter solutions was consistently increased when foliage of birch and Scots pine was washed; bracken and ash foliage increased the acidity of solutions initially pH 6·9, but decreased the acidity of solutions initially pH 4·5 (Figure 51).

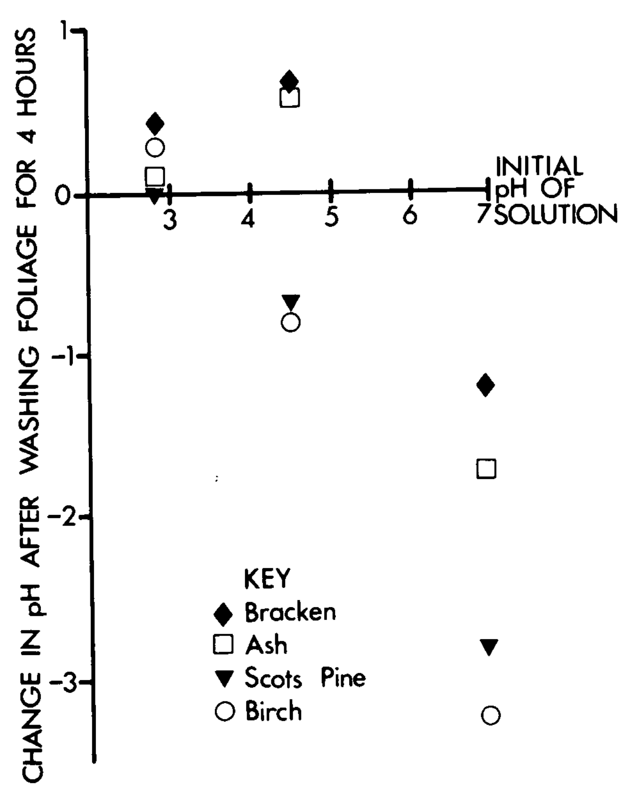



*Figure 51 Changes in pH of solutions used for washing/immersing foliage of 4 plant species for 4h.*

In addition to affecting the pH of simulated acid rain, leaves influenced the concentrations of $Ca^{2+}$ and $K^{+}$. Larger concentrations of both ions were found in washing solutions initially at pH 2·8 than in those at 4·5 and 6·9, with amounts of $K^{+}$ usually exceeding those of $Ca^{2+}$ (Figure 52). Irrespective of pH, larger amounts of $Ca^{2+}$ and $K^{+}$ were generally leached from foliage of bracken and ash than from birch and pine—clear evidence that different species respond differently when wetted. Thus, it seems that the pH of incident rain determines amounts of different ions released into solution (throughfall and stemflow) from foliage; the amounts also differ from one plant species to another.

*I.A. Nicholson, J.W. Kinnaird and I.S. Paterson*

GASEOUS POLLUTANTS AND ACID RAIN: PROGRESS TOWARDS UNDERSTANDING EFFECTS ON FOREST TREES

Although pollution-induced injury to plants has often been ascribed to sulphur pollutants, the latter usually occur in mixtures with other substances released by the combustion of fossil fuels, or from a variety of industrial processes. Additionally, toxic secondary pollutants are formed in the atmosphere, often by photochemical reactions, eg ozone. This being so, pollution research is progressively moving to a study of mixtures of pollutants, and, in this context, there has been an increasing awareness of the occurrence of acid rain, in part attributable to particulate sulphate formed by the oxidation of gaseous sulphur dioxide, and which is of greater importance at increasing distances from sources of emission.

Over extensive areas, concentrations of gaseous pollutants occur which are too small to produce observable injury to plants, eg leaf blemishes. 'Hidden' effects, which may impair growth and which are intrinsically difficult to identify, may have important economic consequences for agricultural and forest production.

In determining the direct and indirect effects of atmospheric pollutants on forest ecosystems, it is desirable to be aware of the spatial and temporal distribution of pollutants, gaseous and particulate.

The Institute's study is centred on a stand of Scots pine planted in the Forestry Commission's Devilla Forest in 1952. According to wind direction, the stand is swept

*Table 30.* Mean atmospheric concentrations of $SO_2$, $O_3$ and NOx above Scots pines growing in Devilla Forest, 1978.

| | Atmospheric pollutant | | |
|---|---|---|---|
| | $SO_2$ | $O_3$ | $NO_+$ $(NO+NO_2)$ |
| Annual mean concentration (Parts per $10^9$ by volume) | 10·5 | 22·0 | 19·1 |
| Range of monthly concentrations | 6·5–21·0 | 7·9–32·8 | 3·4–40·8 |

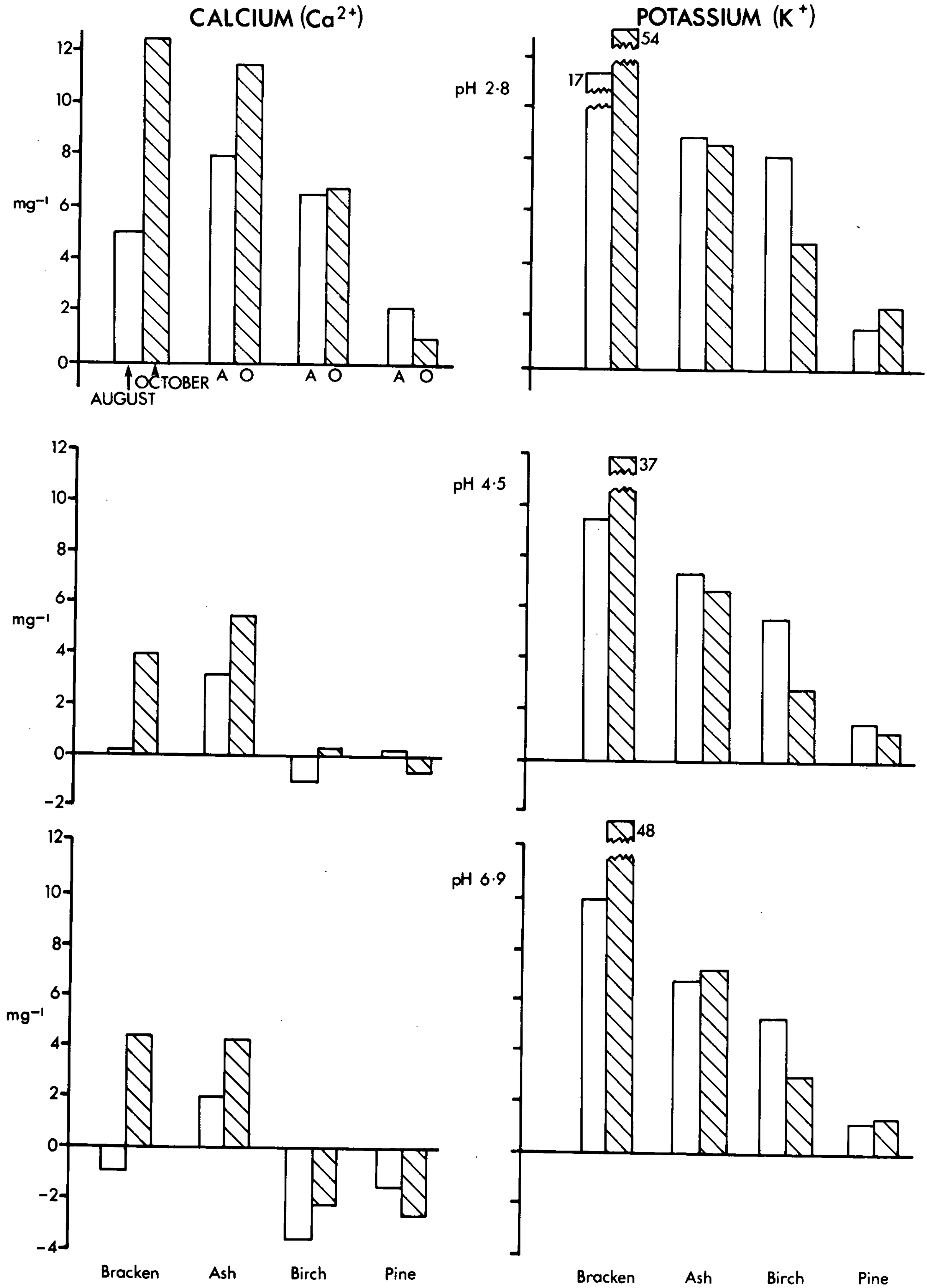



*Figure 52* Changes in concentrations of calcium and potassium in simulated acid rain when detached leaves were washed/immersed for 4 h. (Duplicate experiments done in August (□) and October (▧).

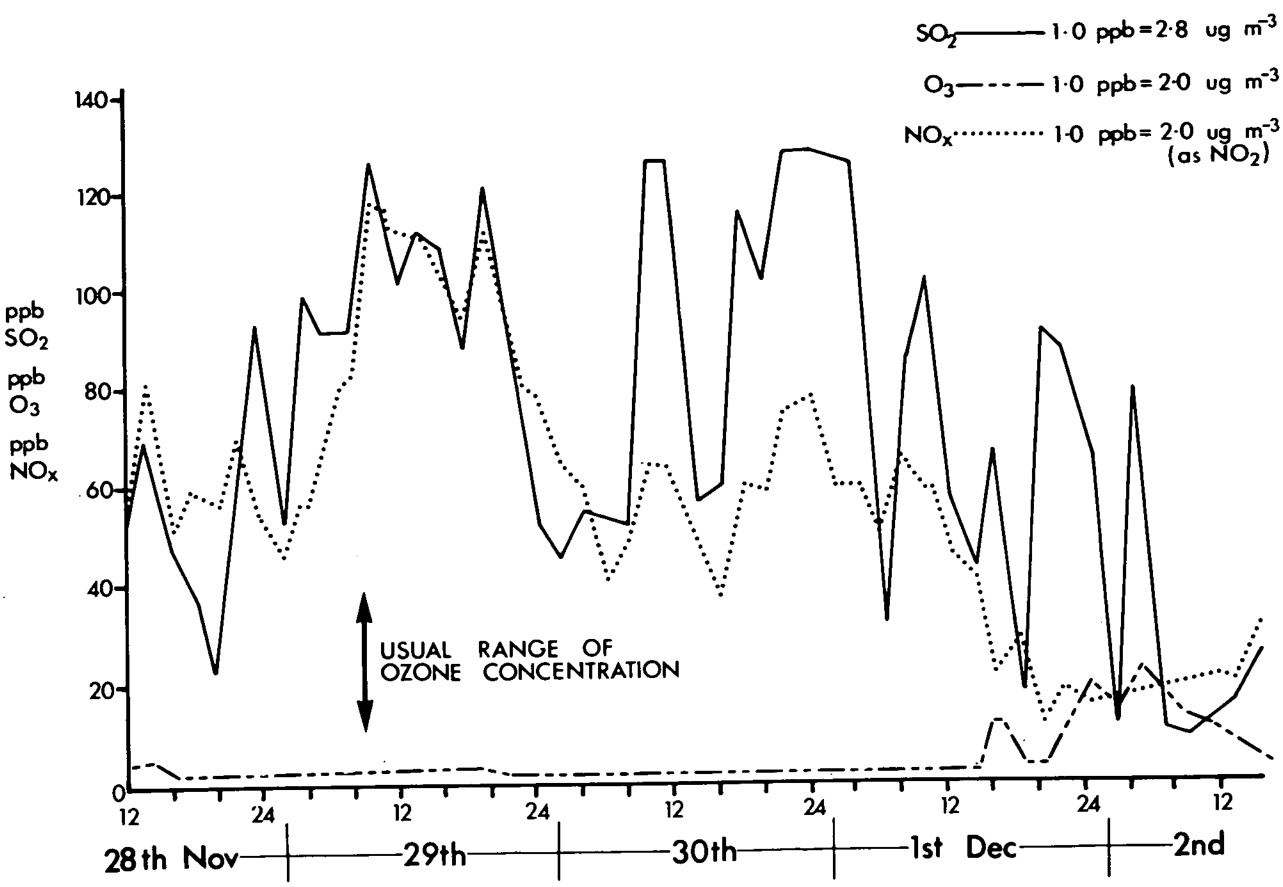



*Figure 53 Short-term changes in concentrations of $SO_2$, $O_3$ and $NO_x$ measured over Devilla forest (28 November–22 December 1977).*

by relatively 'clean' air, by air with pollutants from distant sources, or by air with pollutants from local sources. (Table 30).

*Atmospheric concentrations of gaseous pollutants*

Atmospheric concentrations of gaseous pollutants Concentrations of sulphur dioxide, $NO_x$ and $O_3$, just above the forest canopy, have been measured at intervals of 10 minutes. Data for 2 years indicate that $SO_2$ concentrations of >100 ppb (280 ug $m^{-3}$) have been measured for over 40 hours and of >50 ppb for *c* 300 hours: concentrations of $NO_x$ have exceeded 100 ppb for 45 hours.

*Table 31.* The concentrating effects of tree stems in a Scots pine plantation, 27 years old, on S reaching the ground in stemflow. The area of ground affected around stem bases has been arbitrarily selected as 3 × stem basal area. The means are shown by quartiles for the period 29 March–14 June 1979.

| | Mean stem diameter (cm) | | | |
|---|---|---|---|---|
| | 6·3 | 8·5 | 10·8 | 13·3 |
| Stem flow ($l$ $m^{-2}$ $wk^{-1}$)* | 107 | 97 | 91 | 61 |
| $SO_4$-S deposited (mg $m^{-2}$ $wk^{-1}$)* | 2429 | 1837 | 1950 | 1272 |

Throughfall during the same period carried 43 mg $SO_4$-S $m^{-2}$ $wk^{-1}$

* Quantities calculated assuming area of ground affected was 3 × the stem basal areas in the different size classes.

Amounts of $SO_2$ and $NO_x$ are positively correlated, large concentrations occurring (i) when winds blow from the south-west, and (ii) during low level temperature inversions, when forests may be exposed to concentrations exceeding 300 ug $m^{-3}$ for protracted periods (Figure 53). Large concentrations of ozone have occurred during the summer months, being associated with conditions favouring photochemical reactions, as occurred during 1978 when concentrations exceeded 50 ppb on 20 days. On these occasions, the interplay between the different pollutants might be unexpectedly damaging.

*Acid precipitation*

At Devilla, for example, precipitation had a mean pH during 1978 of 3·95, ranging from 3·3 to 5·4. In total, 7·5 kg S $ha^{-1}$ was brought down in rain, and, of this amount, 95% was attributed to the activities of man [ thus only 5%, an exceptionally small percentage, was of oceanic origin (estimated by Mg sulphate ratio)]. The rain collectors at Devilla form part of a network which includes 16 other stations in northern Britain. The acidity of rain at Devilla is similar to that measured at other eastern locations, pH tending to increase northwards and westwards (Figure 54). Daily measurements indicate that rain more acid than pH 4·0 is not uncommon; at Banchory, in the north-east, a pH of <4·5 has been recorded on 50% of rain events.

*Wet and dry deposition*

At a rural location south of Edinburgh, total sulphur deposition has been estimated at 32 kg $ha^{-1}$ per annum,

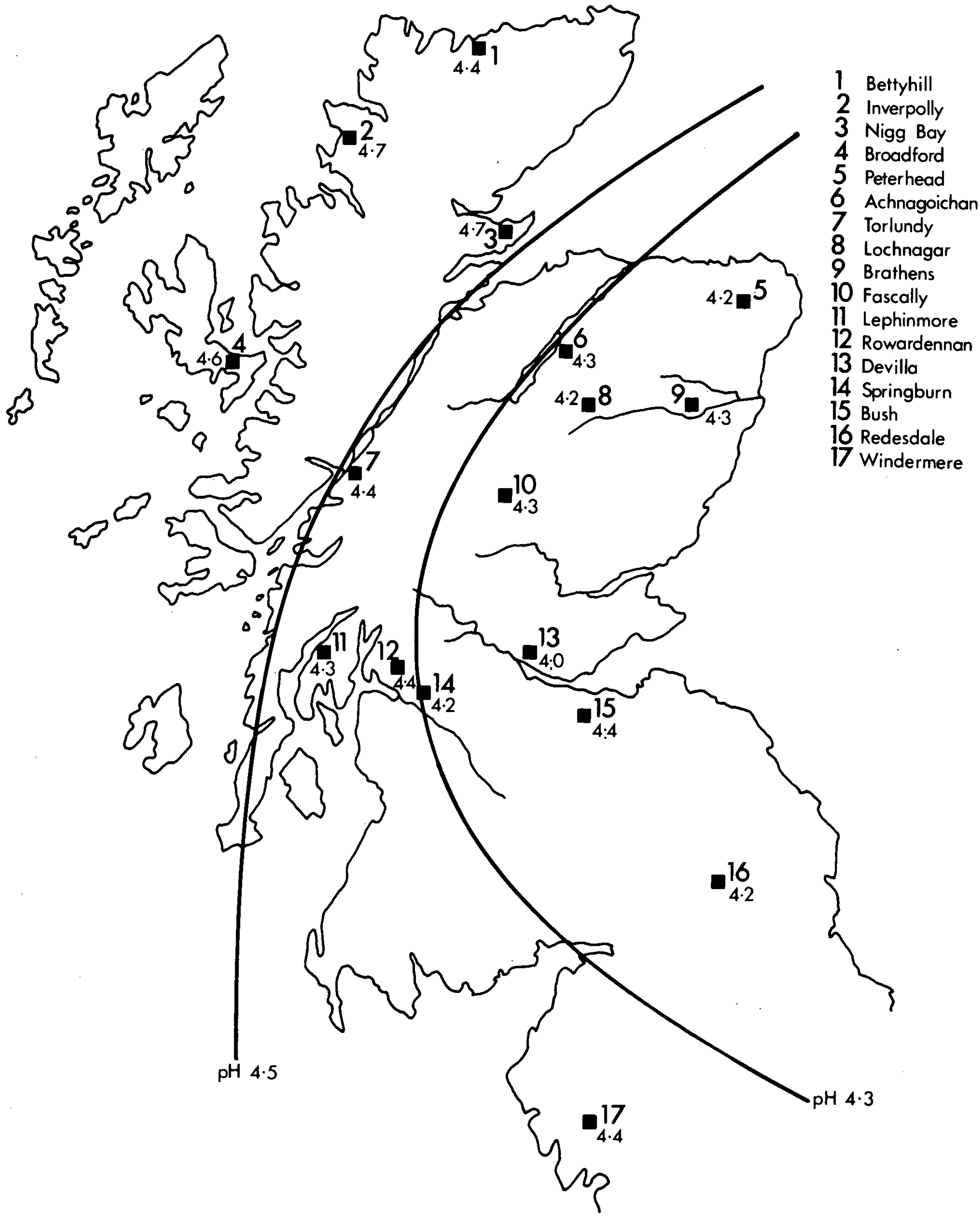



*Figure 54 The mean pH during 1978 of precipitation collected at 17 locations in northern Britain.*

66% originating from dry deposition. Thus, in areas where acid precipitation is thought to be of importance, the contributions made by the dry deposition of $SO_2$ should not be overlooked. For the future, it is essential to gain a better understanding of the transfer (dry deposition) of sulphur dioxide to forest ecosystems—for this purpose a 'fluxatron' with a responsive sulphur sensor is being developed. At the same time, the impact of leaf surface chemistry on deposition is being explored.

*Control of deposition pattern on soil by forest structure*
The fate of incident precipitation (rain) is determined by forest structure. During a period of 10 weeks in 1979, amounts of sulphate—sulphur reaching the ground in stemflow seemed to be at least × 40 greater

than amounts in throughfall (Table 31). The pH of incident precipitation changed from 4·4 to 4·0 and 3·3 in throughfall and stemflow respectively. Thus, the forest floor and its underlying soils are influenced by a highly structured patchwork of different precipitation inputs. These inputs contain not only particulate pollutants washed from the atmosphere by rain, but also pollutants washed from foliage, having been earlier accumulated by dry deposition and leaf leachates, the release of the latter being, to some extent, influenced by the chemical nature of precipitation.

*Effects of polluted atmospheres on leaf surfaces*

Studies with the scanning electron microscope on Scots pine needles, taken from trees of the same age and provenance growing in polluted and 'clean' air conditions, have shown that atmospheric pollutants accelerate the erosion of surface epicuticular waxes. While the effect can be mimicked by fumigations with $SO_2$, the part played by other substances has not been elucidated. There is reason to believe that the accelerated erosion of waxes, and therefore the disruption of leaf surfaces, may have important implications for the loss of water from trees.

*I.A. Nicholson, N. Cape, D. Fowler, J.W. Kinnaird and I.S. Paterson*

SCOTTISH DECIDUOUS WOODLANDS

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

Observations made when surveying Scottish deciduous woodlands have been stored in a computer data bank, so facilitating data retrieval and analysis. The survey was based on deciduous woodlands, 5 ha or more in extent, identified by the appropriate symbol on the seventh series Ordnance Survey maps. In addition to recording details of their altitude, area, geology and location, field assessments were made of canopy composition: a 'delete' record was entered for woods that were no longer in existence or that contained more than 50% of exotic conifers. Of 3 188 woods marked on OS maps, 752 were recorded as 'delete'. The remaining 2 436 woods totalled 61 600 ha, or just under 1% of the land area of Scotland. Of this woodland area, birch, oak and beech account for 45%, 19% and 8% respectively. Woods in which birch is the dominant tree are widely distributed, only being absent from the higher mountainous areas. Oak-dominated woods (Figure 55) are concentrated in central Scotland, Argyll and Dumfries and decrease in abundance in the north (Figure 55). In contrast, the distribution of beech, which was introduced into Scotland, reflects the planting of policy woods in the eastern coastal fringe and in lowland areas of the central valley (Figure 56).

Of the 752 'deleted' woods, 97% are now dominated by conifers. Most were originally scrub which has been cleared and replanted with conifers. These losses have been compensated, to some degree, by increases in the areas of some of the surviving woods. Although there is a clear indication that the intermingling of conifers has been responsible for the decline in the area of deciduous woodland cover, it would be unwise to use Ordnance Survey maps for the accurate assessment of rates of change, simply because its woodland symbols are not necessarily updated with each map revision. However, a direct comparison of this survey with one done in 1947-49 by the Forestry Commission suggests that the area of deciduous woodland in Scotland has decreased by 56% in the past 30 years. Some counties have suffered very small losses (Caithness and Sutherland), whereas others, including Kincardine and Selkirk, have been seriously depleted, with losses of up to 80%. Detailed assessments of change in Nairn and Selkirk stress that these assessments are probably overestimates, with a figure of 40% being closer to the actual losses. Comparisons with data forming part of the 1947–49 Forestry Commission survey suggest that all types of deciduous woodlands have been equally at risk.

The present survey has established a baseline against which future changes can be readily judged. It has also provided staff of the Nature Conservancy Council with a compelling indicator of relatively recent changes whose implications for conservation should not pass unnoticed.

*R.G.H. Bunce, R.C. Munro and T.W. Parr*

REGENERATION OF NATIVE PINEWOODS

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

A number of the formerly extensive Caledonian pinewoods *Pinus sylvestris* have been in decline for several centuries because natural regeneration has been left to chance, and has been largely unsuccessful (see Plate 1). For regeneration to be successful, the principal requirements are an adequate seed supply and suitable site conditions for the establishment and continued growth of seedlings. Both deer and domestic sheep use pinewoods for shelter and as a source of food; in areas where populations are temporarily or permanently large, these animals can endanger tree regeneration.

The effects of excluding large mammals from small areas of pinewood are being monitored in Coille Coire Chuilc (Tyndrum) and in the Black Wood of Rannoch. At the former, an area of 12 ha was fenced in late 1974, since when a number of permanently marked transects and quadrats have been searched annually for tree seedlings; seedlings have been given identifying number tags, their heights being measured and their fate, from year to year, being documented. The annual seed production potential of the mother trees in the enclosures has also been assessed. Similar records have been compiled from 3 smaller enclosures in the Black Wood, established in 1976.

DISTRIBUTION OF OAK DOMINANT WOODS

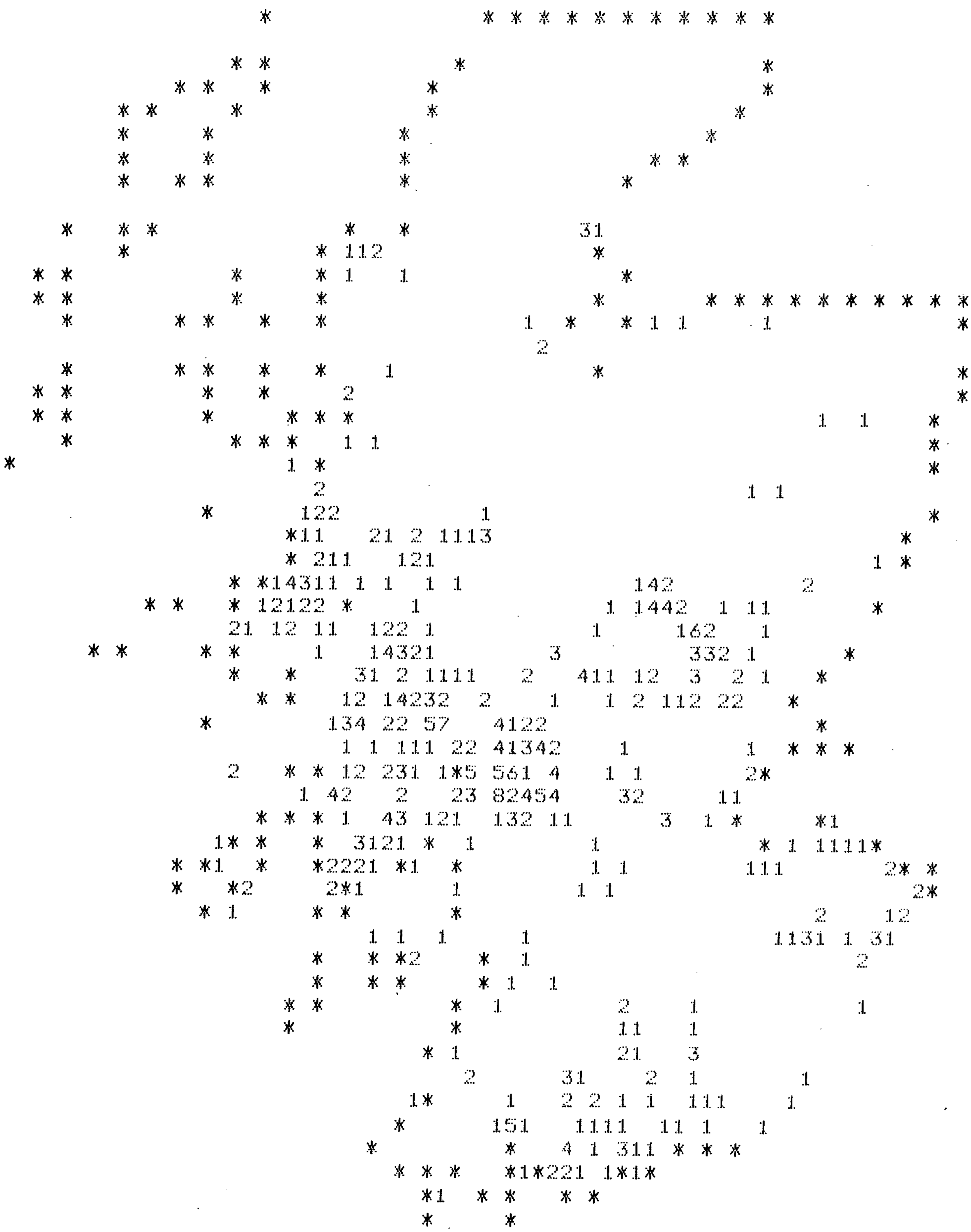


*Figure 55* A computer produced map of Scotland (coastline indicated by asterisks) showing the distribution of woods in which oak is dominant. Each figure gives the numbers of woods in a rectangular area of approximately 45 $km^2$.

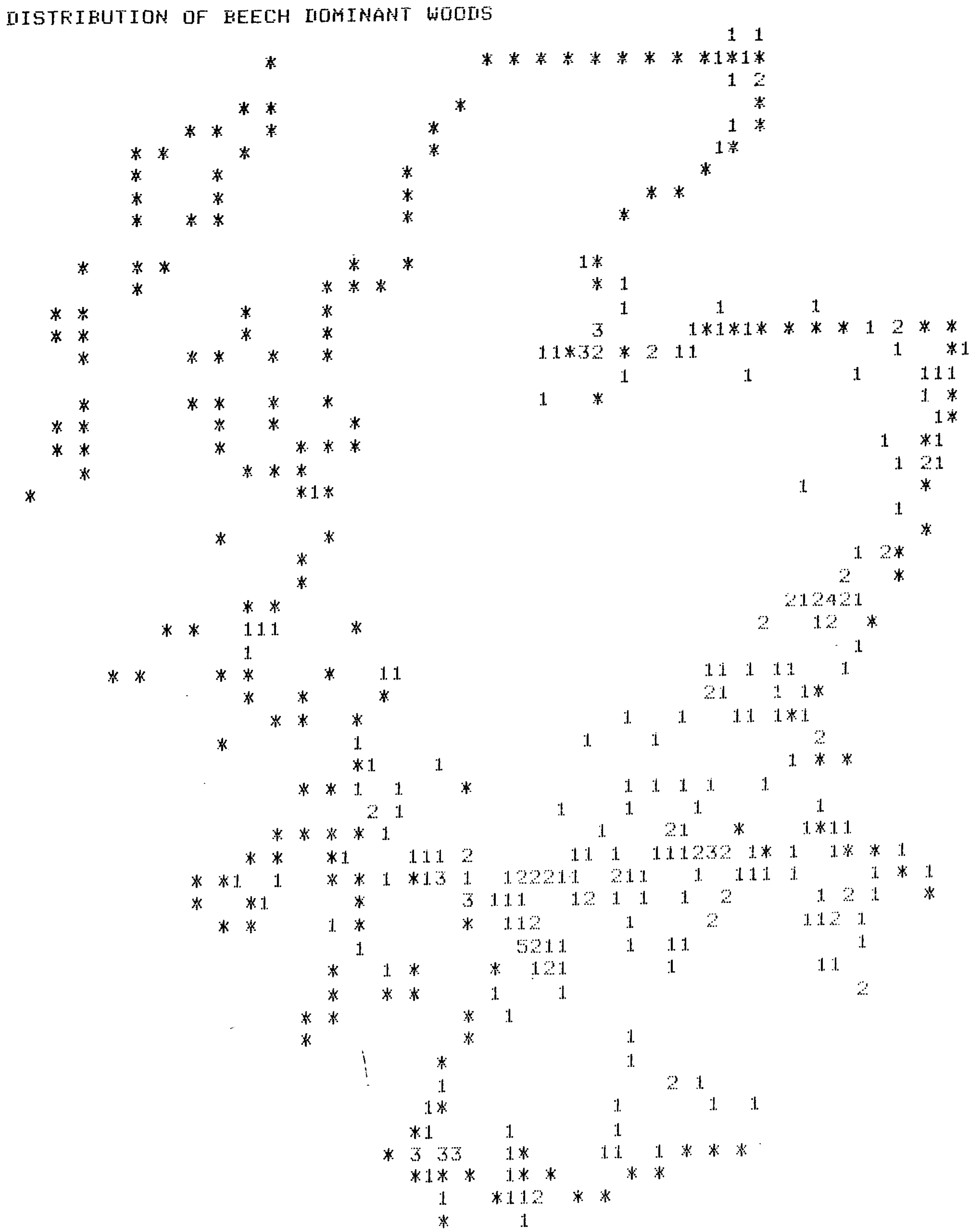



*Figure 56* A computer produced map of Scotland (coastline indicated by asterisks) showing the distribution of woods in which beech is dominant. Each figure gives the numbers of woods in a rectangular area of approximately 45 $km^2$.

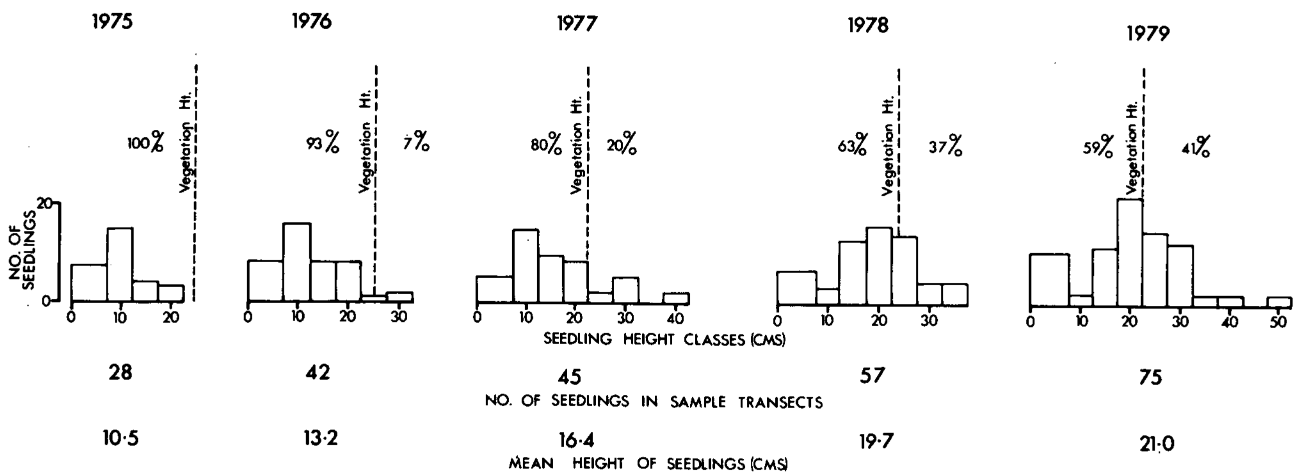



*Figure 57 Height of Scots pine seedlings inside a stock-proof enclosure at Coille Coire Chuilc in relation to height of surrounding vegetation, 1975-79.*

The majority of Scots pine, birch and rowan seedlings now present in both woods were already there before the fencing was erected, though they were not necessarily discovered in the first search. These seedlings were heavily browsed prior to fencing and were almost invariably shorter than the surrounding vegetation which afforded them some protection. Some seedlings have emerged since fencing, but few have survived. The increasing height of Scots pine seedlings at Coille Coire Chuilc, in relation to the surrounding vegetation, is shown in Figure 57 for the years 1975 to 1979. Mean seedling height doubled during the 4-year period and, by 1979, 40% of seedlings were taller than the surrounding vegetation.

At Coille Coire Chuilc, the crops of *P. sylvestris* cones, assessed by eye on a 4-point scale, have differed considerably from year to year, though some individuals are consistently prolific or sparse producers. The germination percentage of seeds, collected from different trees within the enclosure, ranged from 24 to 72, with a mean of 47%, a figure consistent with, but slightly larger than, the mean for western pinewoods as reported by other authors. The evidence suggests that the exclusion of large mammals, including red deer, would enable the establishment of sufficient *P. sylvestris* seedlings to ensure the continuance of British native pinewoods.

*J.M. Sykes and A.D. Horrill*

NATIONAL WOODLAND CLASSIFICATION

Over the years, botanical and habitat data have been obtained from 16 plots, each 200 m², selected at random in each of 103 woodlands thought to encompass the range of variation among British woodlands.

Although the main analyses were completed some time ago, one major problem remained to be surmounted, namely the presentation of results of multivariate analyses in a format which is readily comprehended by scientists not familiar with such procedures and by laymen. There have been 2 aspects—first, a summary of the principal features distinguishing one type of woodland from another, and, second, a means of comparing the relationships of the types of woodlands produced in the presence exercise with those evolved by other systems of classification. The approach adopted for the former problem has involved the production of keys, backed by succinct descriptions of woodlands in terms of (i) ground flora assemblages, (ii) species forming woodland canopies, and (iii) associated environmental features—woodland type 12 is illustrated in Plate 19 and described in Table 32. The summaries will be produced in A5 format; they will have English common names and Latin binomials of the indicator, diagnostic, species, so enhancing the usefulness of the keys. In the first instance, the different assemblages will be described; a second publication will follow. Accepting that an area of woodland is rarely homogenous—it contains a mosaic of different, but usually closely related, types of woodland—the second publication will outline the procedures for attaching a name (classifying) to the sum of the heterogenous components within a woodland.

To set the multivariate classification in context with other systems— the traditional British Tansleyan and the Braun-Blanquet, Zurich-Montpellier system details of these classifications have been added to the type summaries, recognising that the Norwegian interpretation of the Braun-Blanquet system that was used can be interpreted in different ways.

*R. G. H. Bunce and M. W. Shaw*

*Table 32.*
Type 12
Vegetation

| | |
|---|---|
| *Ground flora* | |
| Constant species: (in more than 75% of plots) | Fraxinus excelsior (ash) Rubus fruticosus (bramble)<br>Viola riviniana (violet) Dryopteris filix-mas (male fern)<br>Geum urbanum (herb bennet) Oxalis acetosella (wood sorrel)<br>Crataegus monogyna (hawthorn) Deschampsia cespitosa (tufted hair grass) |
| Plot dominants: (species that have over 10% cover in 15% of plots) | Mercurialis perennis (dog's mercury)<br>Rubus fruticosus (bramble) |
| Selective species: (species tested as being characteristic of the type) | Geum urbanum (herb bennet) Sanicula europea (sanicle)<br>Brachypodium sylvaticum (wood false brome)<br>Fragaria vesça (wild strawberry) Viola riviniana (violet)<br>Deschampsia cespitosa (tufted hair grass) |

*Constant trees* (present in over 20% of plots)
ash, oak, birch, sycamore, hawthorn, alder

*Constant saplings* (present in over 20% of plots)
ash, hawthorn, sycamore

*Constant shrubs* (present in over 20% of plots)
hazel

*Main trees* ((with a basal area over 0·1 $m^2$)
oak, ash

*Environment*
Mainly distributed in north-east England but also throughout Britain.
Occurs mainly on Millstone grit and coal measures but also on other strata.

| *Altitude* (m) | *Slope* (°) | *Rainfall* (cm) | *pH* |
|---|---|---|---|
| 102 (average) | 19 (steep) | 102 (average) | 5·3 (average) |

A type of medium heterogeneity with a high species complement, most closely related to types 11, 10 and 13. There is usually a low ground cover, with much rock and bare ground.

This type belongs to the broad range of pedunculate oak-ash woodland growing on steep valley sides. The soils are mainly brown earths, although sometimes skeletal and very stony and sometimes gleyed.

Phytosociology:
Class: Querco-Fagetea Br. Bl. et Vl. 1937.
Order: Fagetalia sylvaticae. Pawlowski 1928.
Alliance: Ulmo-Fraxinetum Kielland-Lund 1971.
or Dryopterido-Fraxinetum Klötzli 1970.
or Fraxinus-Brachypodium nodum McVean & Ratcliffe 1962.

EFFECTS OF DIFFERENT TREE SPECIES ON SOIL AT GISBURN

The Gisburn experiment was established in 1955 to study the effects of oak, alder, Scots pine and Norway spruce in pure and mixed stands on soil and naturally occurring vegetation. Successive assessments have been made of vegetation and soil chemistry in the differing replicate plots (0·2 ha) and the activity of soil micro-organisms in the single species stands has recently attracted interest.

Earlier studies of the loss in tensile strength of buried cotton strips—an index of cellulose decomposition—have been extended to include:

1. Measurements of the effects of tree species on the physical environments of soils which are likely, in turn, to influence microbial activity. Measurements included soil temperatures (sucrose inversion method), soil moistures, pHs, and organic matter contents.
2. Seasonal assessments of rates of cotton strip decomposition, soil respiration, and amounts of fungal mycelium (Jones and Mollison method).

Although analyses are incomplete, it is already apparent that trees, especially conifers, decrease soil surface temperatures in summer (Table 33). At depths from 5·20 cm, this effect was reversed, less markedly with alder than with oak, pine and spruce. The soils in unplanted and alder plots have more clay than the others, and show greater lags when warming in the summer and cooling in the autumn. It is uncertain whether the apparent differences in soil texture are effects of treatment or merely reflect initial site heterogeneity.

The pHs of the surface (0–6 cm) mineral soils are very similar under all treatments in the summer (pH ± 5·0), but fall to about 4·0 and become more variable in winter. This seasonality in soil pH contrasts with the findings of Frankland *et al.* (1963), who showed seasonal differences only in the pH of vegetation and litter, but not in mineral soils.

Surface soils (0–6 cm) become drier under most species of trees during summer. Drying was greatest under pine and spruce (to 60% oven dry weight) and least beneath oak (to 140% oven dry weight) which did not differ greatly from conditions in unplanted soil. The present studies of cotton strip decomposition indicate that rates of decomposition are decreased when soil moistures fall below 80%. Although moisture regimes beneath spruce and pine were similar, rates of cotton strip decomposition differed.

*Table 33.* Effects of different trees on soil temperatures (°C) at different depths at Gisburn during the period 11 May-2 August 1978.

| | | Soil depths | | |
|---|---|---|---|---|
| Tree species | Surface | 5 cm | 10 cm | 20 cm |
| Unplanted | 20·4 | 6·2 | 4·6 | 4·1 |
| Oak | 13·2 | 8·2 | 7·7 | 7·2 |
| Alder | 11·7 | 5·8 | 4·9 | 4·0 |
| Pine | 11·3 | 8·0 | 7·2 | 7·0 |
| Spruce | 8·5 | 6·9 | 6·0 | 6·0 |

These cotton strip results are broadly in agreement with the preliminary findings that decomposition is fastest under alder and slowest beneath Norway spruce, but decomposition rates beneath Scots pine did not differ appreciably from those beneath alder. Whereas lengths of fungal mycelium were 22 km $g^{-1}$ dry soil for most of the year beneath Scots pine, they had noticeable summer maxima beneath oak, alder and spruce. The largest maximum, 40 km $g^{-1}$, was associated with oak. Soil respiration in the 0·5 cm horizon ranged from 5–15 $\mu l$ $O_2$ $g^{-1}$ organic matter $hr^{-1}$ at 10°C, being low in pine, and higher in oak and spruce soils.

*Gillian Howson and A.H.F. Brown*

*Reference*

**Frankland, J.C., Ovington, J.D. & Macrae, C.** 1963. Spatial and seasonal variations in soil, litter and ground vegetation in some Lake District woodlands. *J. Ecol.*, **51**, 97–112.

## Soil Science

SOIL AND MARGINAL UPLAND IN CUMBRIA

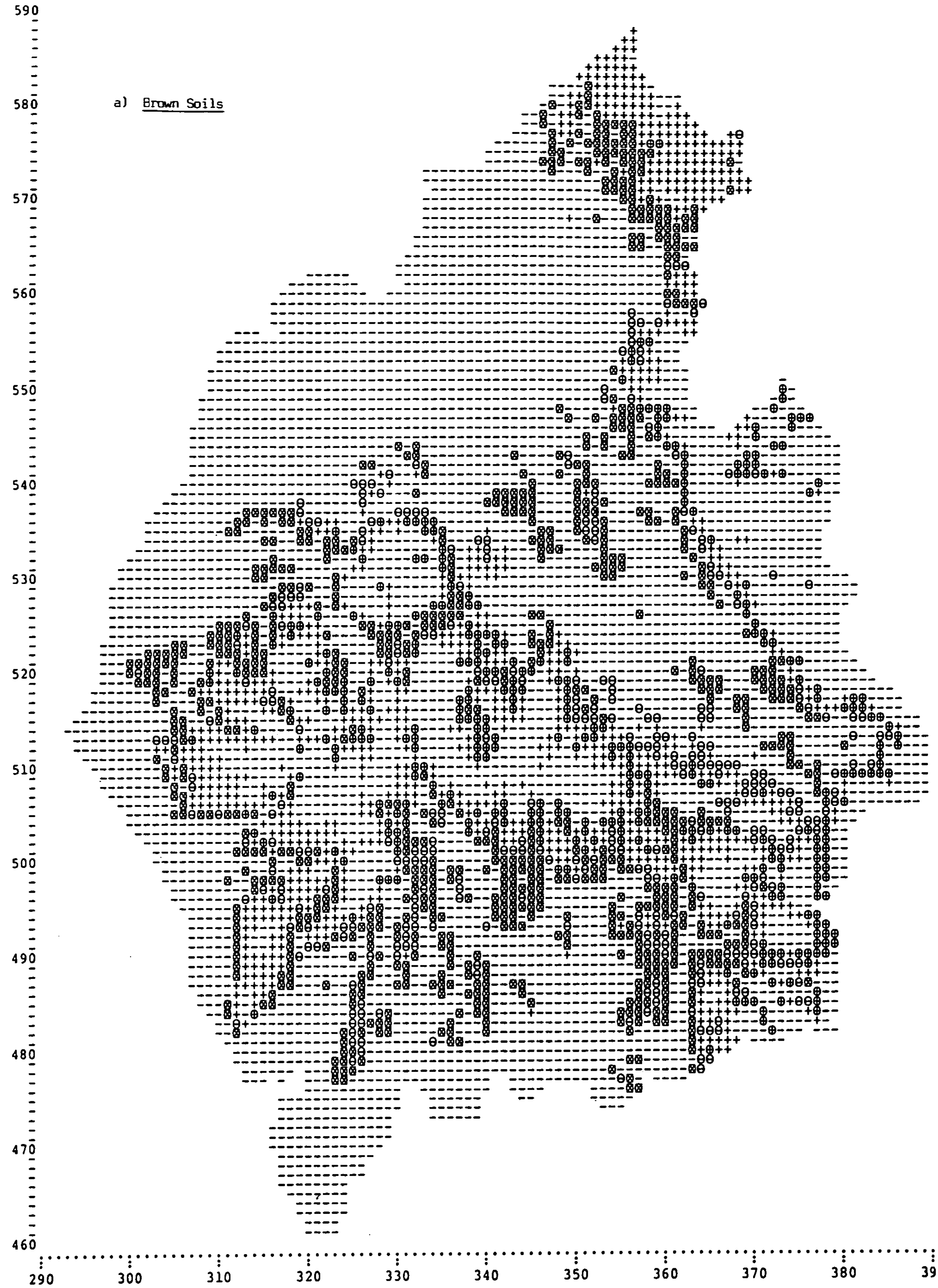
A land classification based on the analysis of information taken from existing maps, principally the 1:50,000 Ordnance Survey series, has shown that land in Cumbria, using one km squares as the descriptive unit, can be apportioned in terms of environmental features, to 16 land classes (Bunce & Smith 1978). This classification provides a data base to which other information may be added and, perhaps more usefully, it provides a framework for sampling specific features which are related to, or determined by, the type of land, including hedgerows, landscape characteristics, the frequency and distribution of elm trees, and possible sites for refuse disposal. Additionally, surveys concerned with soils and vegetation of marginal upland have been investigated in Cumbria, using the land classification as a sampling framework.

To examine the relationship between soil types and 16 land classes, random samples of kilometre squares of each land class were visited. In each kilometre square, 8 soil profiles were described and assigned to a Soil Group of the Soil Survey classification (Avery 1973). For these data, it has been possible to determine the proportion of different soil groups within each land class, and, as a result, maps of Cumbria showing the *probable* occurrence of the different Major Soil Groups have been produced. The probable nature of these maps must be emphasised; they await confirmation by traditional methods of soil survey.

*Table 34.* The probability of different soil characteristics, regarded as constraints to agricultural improvement, occurring in the marginal uplands of Cumbria.

| Constraint | % occurrence |
|---|---|
| Soil depth < 20 cm | 3 |
| Stoniness prohibitive to ploughing | 60 |
| Peaty topsoil | 18 |
| Slope > 13° (conventional tractor) | 32 |
| Slope > 20° (crawler tractor) | 18 |
| Profile drainage poor | 20 |

The marginal areas, represented by land classes 4, 9, 10, 11 and 12, and constituting 33% of Cumbria, are subject to appreciable alterations in agricultural practice with consequent effects on vegetation, fauna and soils. To enable predictions, and to monitor these changes, a detailed survey was made of soils, vegetation, and environmental parameters. Soil profile, vegetation and habitat data were collected from each of 72 randomly selected kilometre squares, the methods used being the same as those employed in the Ecological Survey of Britain. As a result, it is possible to compare and reconcile Cumbria data with those for Britain. After analysis, maps have been produced showing the likely occurrence of different soil types and vegetation assemblages. Potentially productive brown soils occupy 26% of the marginal land of Cumbria but their distribution is complex (Figure 58). The intermingling




**KEY**

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Symbol | +++ | OOO | ϴϴϴ | ⊕⊕⊕ | ⊠⊠⊠ | ▩▩▩ | ■■■ | ●●● |
| Range | 0-9 | 10-19 | 20-29 | 30-39 | 40-49 | 50-59 | 60-69 | 70-100 % occurrence |

Non-marginal land ---

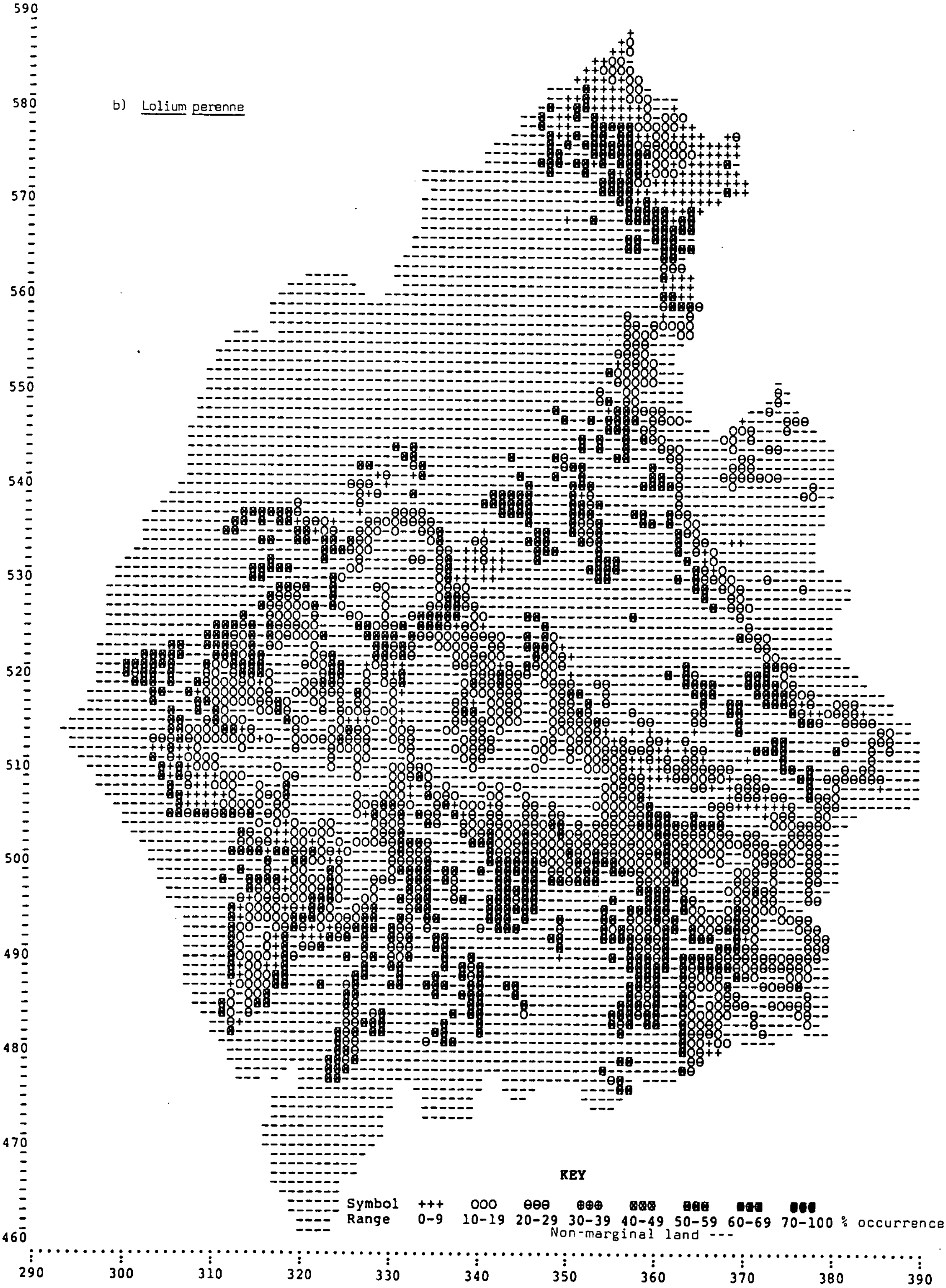



*Figure 58 The distribution and frequency of (a) brown soils and (b)* Lolium perenne *in land classes 5, 9-12, which together constitute the marginal lands of Cumbria (non-marginal lands are denoted - -; probabilities of occurrence are shown below map a).*

*Plate 17. Silver birch* Betula pendula *invading heather* Calluna vulgaris *dominated lowland heath, Frensham Common, Surrey, October 1978.*
*Photograph: J E Lowday.*

*Plate 18. Bracken* Pteridium aquilinum *invading heather* Calluna vulgaris *dominated lowland heath, Cavenham Heath, Suffolk, July 1978.*
*Photograph: J E Lowday.*

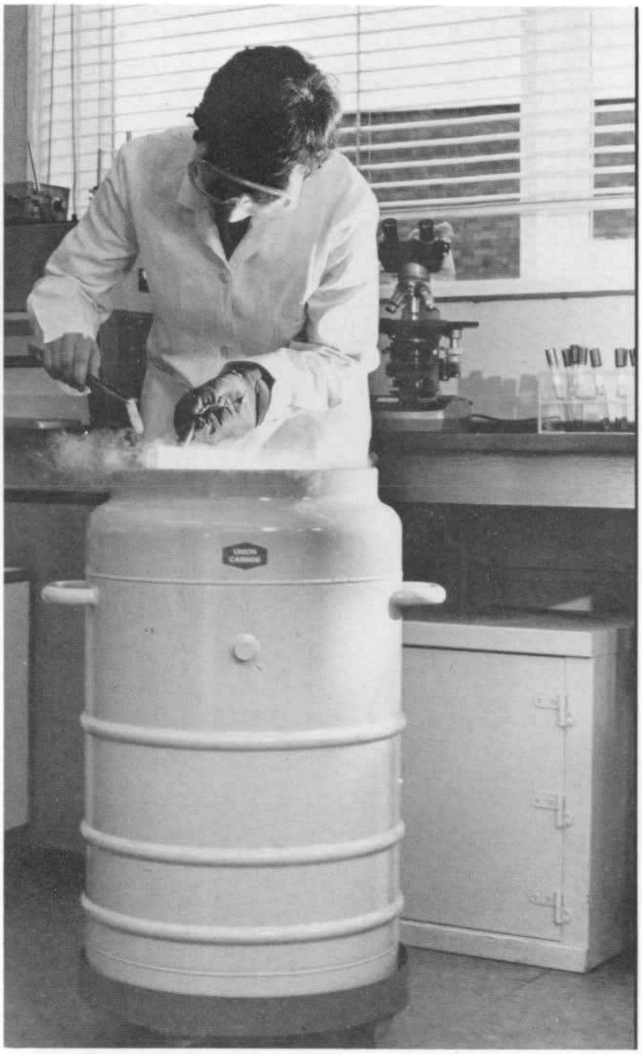


*Plate 20. Removal of an algal culture from liquid nitrogen (-196°C).*
*Photograph: C Chalk.*

*Plate 19. Plot type 12. Ground flora species:* Rubus fruticosus, Athyrium filix femina, Dryopteris filix-mas, Brachypodium sylvaticum. *Woody species:* Quercus *spp.,* excelsior, Betula *spp.,* Corylus avellana, *Reins, near Thirsk, Fraxinus, Yorkshire, NGR GE 569850..*
*Photograph: R G H Bunce.*

(mosaic) of brown soils with other less productive soil types provides the basis for considering combined and integrated forestry and agriculture enterprises. However, in the marginal upland areas the extreme stoniness at ploughing depths is likely to be a more important constraint on pasture improvement than soil type (Table 34). Rye-grass *Lolium perenne* is characteristic of the better grazings in the floors of the valleys (Figure 58) contrasting with the 'poorer' swards of mat-grass *Nardus stricta* at higher altitudes on the central Cumbrian fells and the Pennine scarp. By comparing the distribution maps of brown soils and rye-grass, it is apparent that large areas of marginal uplands do not support the 'quality grazings' that would be predicted as being feasible from soils data. Thus, if economic conditions were to favour expenditure on improvement, large increases in grassland productivity would be expected (Plate 12).

In the immediate future, the variety, extent, and distribution of land use practices in marginal upland areas of Cumbria will be summarised; it is also planned to monitor changes in soil and vegetation as a result of bracken invasion and abrupt changes in drainage conditions, to mention but 2 of many regulating factors.

*C.B. Benefield and J.K. Adamson*

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## MICROBIAL CHARACTERISTICS OF SOILS.

Microbial characteristics of soils have been studied extensively but they have seldom been considered in direct relation to plant productivity—a relationship is assumed but not proven. In 1978, an opportunity arose to examine 76 soils from 8 major soil types being used by Drs. M. Hornung and A.F. Harrison in their study relating plant production to the chemical and physical characteristics of different soils.

The decomposition of litter (leaves of cotton-grass), 2 nitrogen-containing substances (chitin and gelatin), and some plant cell wall components (pectin, cellulose and wood) was assessed by separately inserting these different substrates in pots of sieved soil placed outdoors. With the exception of litter and wood, the substrates were contained in 2 × 5 cm nylon mesh bags, with 5 $\mu$ mesh. Plant productivity was assessed by measuring the growth of radish *Raphanus sativus* seedlings—it does not seem to be complicated by the formation of mycorrhiza.

Pectin, as judged by weight losses, was decomposed more rapidly than chitin (Figure 59). Preliminary results suggest that plant growth and the rate of chitin breakdown are positively related whereas, in the conditions of this experiment, growth and rates of pectin breakdown are independent of each other. Although further analyses need to be made of the varying responses among replicate samples of soils within the same group, it has been decided to concentrate future tests on soils from a woodland on limestone (Merlewood); permanent pasture (Ravenstonedale, Cumbria); spruce forest (Gisburn, Yorkshire); blanket peat (Moor House NNR, Cumbria); and heath on podzolic soil (Banchory, Scotland). Decomposition and plant growth are again being assessed, but, on this occasion, after storing the soils with different amounts of (i) moisture and (ii) added phosphate.

*Pamela M. Latter*

## MINERALOGICAL INDICATORS TO DETERMINE HOMOGENEITY OF SOIL PARENT MATERIAL

In determining the influence of birch invasion on soils of heather moorland, it has been important to ensure that the effects of birch could be dissociated from those of other soil-forming factors. Of these, the nature of the soil parent material is of major importance, its uniformity having been assessed at the different sites from estimates of the content of stones, particle size distributions and the occurrence of heavy minerals. 'Heavy' minerals are minerals having specific gravities greater than 2·89: they occur in sedimentary deposits in distinctive and diagnostic arrays depending on the types of parent rocks.

In his study, Dr. Miles is using 13 sites in Scotland and north Yorkshire. At each, the heavy minerals in the fine sand (63–105$\mu$) fraction of the soil parent material in each of his experimental plots including adjacent heather moorland were separated using bromoform (S.G.2.89). The heavy minerals were then identified microscopically and the proportions in the different samples calculated. Within-site differences were negligible, except at Advie, Highland Region, and Craggan, Grampian Region. At the former, the soil of one plot of birch had more amphibole and less biotite and apatite than soils in other plots at the same location with birch of different age classes. At Craggan, one plot had more biotite and less zircon than other plots. From assessments of 'repeat' samples of soil parent material, it seems that analyses of heavy minerals can indicate the degree of within- and between-site homogeneity; statistical aspects of interpretation are being further examined.

Soils derived from Jurassic grit at Silpho, north Yorkshire, and Silurian sandstone at Kill Burn, Borders Region, had arrays of heavy minerals dominated by zircon, tourmaline, rutile, garnet and opaque minerals, whereas those derived from Moine schists at Advie, Craggan and Kerrow in the Highland Region contained

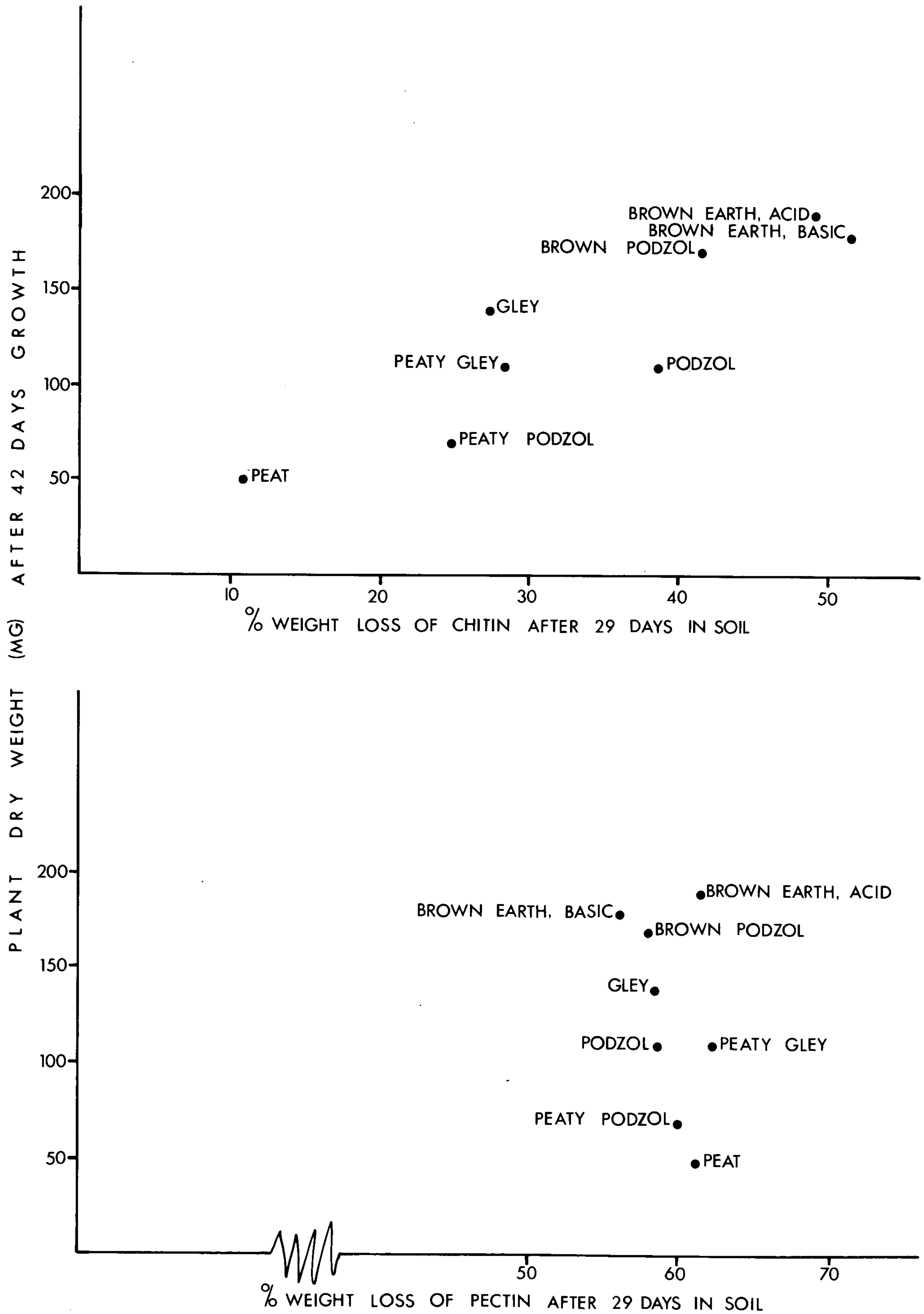


*Figure 59 The relation between the growth of radishes and the decomposition of a) chitin and b) pectin, when tests were done with 8 different types of soils (peat, peaty podzol....). (The growth and decomposition assays were subject to the same weather conditions).*

a wider range of minerals including amphibole, pyroxene, biotite, chlorite, apatite, garnet, kyanite, tourmaline, zircon, zoisite and opaques.

*Aldyth A. Hatton*

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CELLULOSE DECOMPOSITION: SOME TECHNICAL ASPECTS OF THE COTTON STRIP METHOD

Losses in tensile strength of standard strips of cotton placed in soil (Latter & Howson 1977), now assessed with a Monsanto Type W tensometer, are being used increasingly as simple assessments of cellulose decomposition in management and land use studies (see the Gisburn forest project (p 106). These assessments can integrate decomposition over a period of months but methodological problems have arisen. For instance, if cotton strips are to be stored after being subject to the activity of microbes and before having their tensile strengths measured, they must be washed. Washing in a jet of water is sufficient: scrubbing can be deleterious, the magnitude of the damage differing according to the type of soil in which the strips were placed. Scrubbing strips taken from a coarse-particled sandy soil decreased tensile strengths by 25–30%, whereas scrubbing strips from clay and limestone soils nearly doubled tensile strengths. If washed strips have to be stored, they should be kept dry; periods of storage should be minimized because tensile strengths tend to decrease in

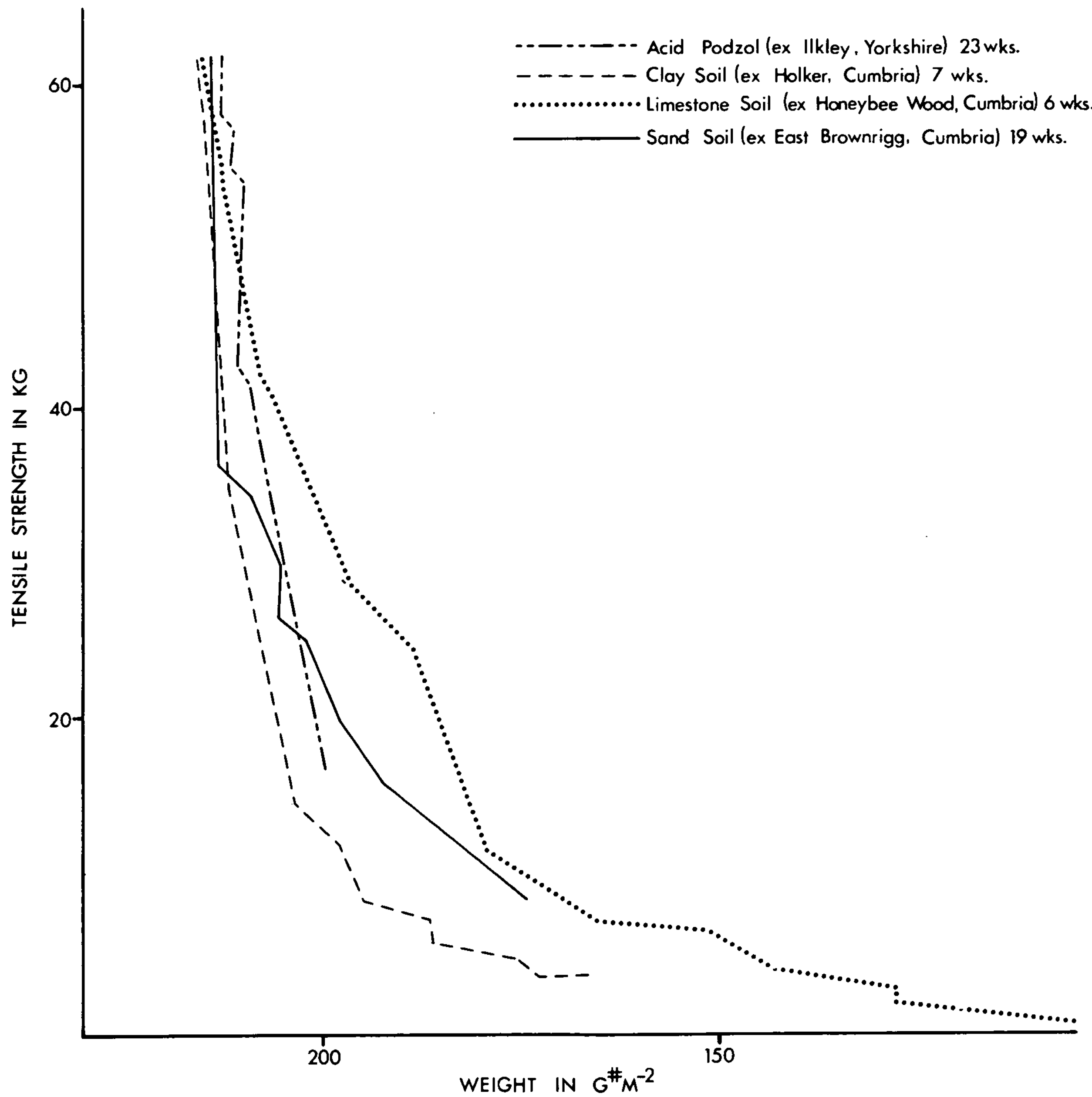


*Figure 60 Relation between losses of (i) tensile strength and (ii) dry weight, of cotton strips placed in trays of soil outdoors. Strips in acid peat had neither decomposed nor lost tensile strength at 9 weeks. (214 g m⁻² = initial weight of strips, 62.0 = initial tensile strength of strips).*

store. For instance, strips previously subjected to rotting lost 27% of their residual tensile strength when stored unwashed for 4 weeks.

When strips were placed in different soils, the relation between weight losses and decreases in tensile strength were broadly similar (Figure 60), initial small losses in weight being associated with large decreases in tensile strength.

Remembering that the fluidity (an inverse measure of molecular size or chain length) of cotton remains constant when subject to microbiological attack but increases during chemical and photochemical degradation, an attempt was made to separate chemical from microbiological factors during the degradation of strips in acid soils. With the help of the Shirley Institute, Manchester, where fluidity tests were made on decomposed and undecomposed cotton strips, it was found that losses of tensile strength in acid soils were attributable to microbial, and not acid, attack.

*Pamela M. Latter, G. Bancroft (a sandwich course student from Manchester Polytechnic), and Gillian Howson*

*Reference*

**Latter, P.M. & Howson, G.** 1977. The use of cotton strips to indicate cellulose decomposition in the field. *Pedobiologia*, **17**, 145–55.

## FACTORS INFLUENCING THE PRODUCTION OF SPOROCARPS (TOADSTOOLS) OF THE FLY AGARIC, A MYCORRHIZAL ASSOCIATE OF MANY TREES

As world-wide interest increases in the use of forest tree transplants inoculated with selected isolates of mycorrhizal fungi, it is becoming increasingly evident that much more needs to be known about the ecology of the fungi in question. In recent years, factors affecting the occurrence and distribution of sporocarps of fungi forming sheathing mycorrhizas with species of birch have been examined in a field planting near Edinburgh, the fungi including species of *Hebeloma, Inocybe, Laccaria, Lactarius*, etc. As yet, sporocarps of *Amanita muscaria* (L. ex Fr.) Hooker, the fly agaric (Cover photograph), which is associated with ageing trees, have not appeared, but an opportunity arose to consider the factors influencing this fungus when associated with plantations of *Pinus patula* growing at high altitude near Kodaikanal, southern India.

Having counted numbers of sporocarps, from February to December 1977, in plantations of different ages, it was found that their production was strongly affected by monthly rainfall and plantation age (Figure 61). During the 11 months, numbers of sporocarps per 1 000 trees ranged from 150–11 000 in plantations 5 and 16 years old respectively. In plantations less than 7 years old, new sporocarps were not recorded during the 4 months without rain, viz February, March, June and August: in older plantations, some sporocarps emerged during June. On average, numbers of sporocarps were increased 10-fold when monthly rainfall increased from 30–300 mm. However, young plantations, judged by the production of *A. muscaria* sporocarps, were more responsive to additional rain than older plantations. In plantations less than 7 years old, numbers of sporocarps increased by a factor of $\times$ 5·5 from 4–22 when monthly rainfall increased from 100–300 mm; in plantations 14–16 years old, numbers increased by $\times$ 1·8 from 610–1 100 per 1 000 trees.

*F.T. Last, P.A. Mason, R. Smith and J. Pelham*

## SELECTION PRESSURES IN EARTHWORM EVOLUTION

Adaptive radiation in terrestrial annelids proceeded concurrently with the spread of angiosperm plants during the Cretaceous period. It seems likely, because of their basically aquatic form of organisation, that the first lumbricids were mud-dwellers with low reproductive rates, low metabolic rates, small population densities, and an ability to utilise low-grade organic matter for food. From this form of organisation, it is perhaps a short evolutionary step to that of a soil-dwelling earthworm, and thence to life on the soil surface.

Because the most nutritious and abundant foods occur in surface organic horizons rather than in mineral horizons, selection pressures seem likely to have favoured forms which could actively seek out, and consume, surface organic matter. Colonising species would have required a high metabolic rate sufficient to maintain the mobility required for food searching. It would have been advantageous to develop behaviour patterns serving to keep the population in the vicinity of these food sources and to develop sensory mechanisms for selecting them. Organic horizons are best developed today in tundra and boreal vegetation, and, in earlier periods, similar habitats with cold winters occurred at high altitudes and nearer to the equator. Because few worms can survive freezing, the evolving species would have overwintered as cocoons and would have required the metabolic capacity to grow and reproduce rapidly during the favourable season. Because surface feeding carries the penalties of exposure to predators, ultraviolet irradiation and desiccation, it would have been advantageous to be pigmented, hence camouflaged, to develop nocturnal surface activity, surface movement during rain, and means of moistening the respiratory surface with secretions. Tolerance to the acidity of many types of litter layer would also have been required.

### *r and K selection in earthworms*

One of the main debates amongst evolutionary-

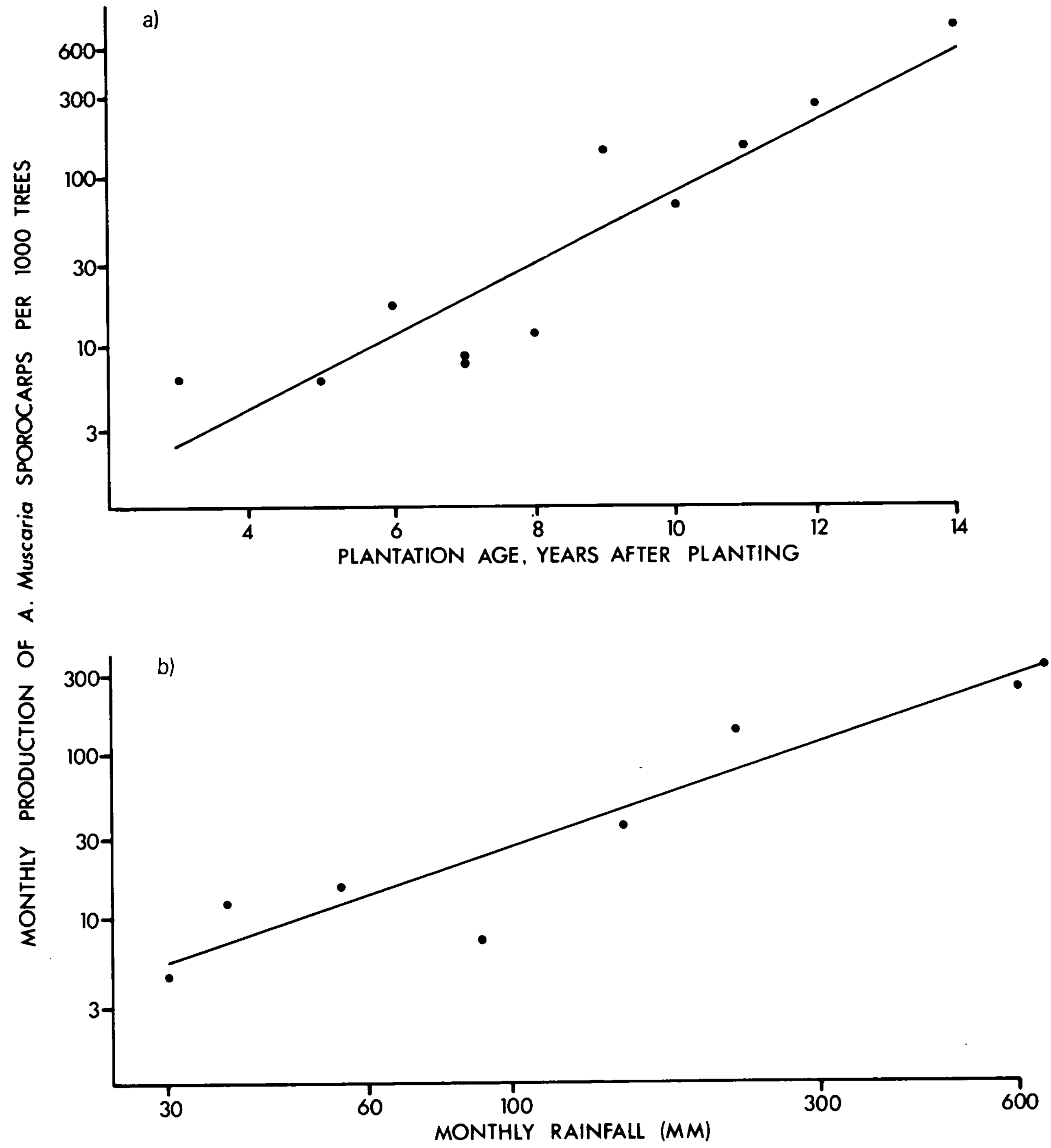


*Figure 61 Associations between the monthly production during 1978 of* Amanita muscaria *sporocarps in stands of* Pinus patula *at Kodaikanal, India, and a. plantation age and b. monthly rainfall (monthly rainfall and numbers of sporophores plotted on* $log_e$ *scale).*

minded ecologists in the 1970's has been the value of the concept of r and K selection. Coined by MacArthur and Wilson in 1967, these terms described the different ways in which populations might function in uncrowded and crowded environments. In an environment with no crowding, genotypes which devour most of the food and/or selectively take the most nutritious will rear the largest families and be most fit, evolution favouring productivity—r selection; but, in a crowded environment, genotypes which can at least replace themselves with a small family with the minimum of food will win, the food density being lowered so that large families cannot be fed—K selection. Where climates are rigorously seasonal, and winter survivors recolonise each spring in the presence of abundant food, r selection will operate favouring high productivity, but, where seasons are more uniformly benign, K selection favouring efficiency of conversion of food into offspring will result. Newly colonising species will be subject to r selection, but, once safely established, will tend to become K selected.

As related to earthworms, the attributes distinguishing r and K life forms may be considered as those concerning reproduction and productivity; those related to the feeding behaviour associated with different levels of

*Table 35*. Summary of attributes of r and K selected earthworms.

| | | r | K |
|---|---|---|---|
| A. | Directly related to fecundity and length of life cycle: | | |
| 1. | Number of cocoons produced per worm | Higher | Lower |
| 2. | Number of embryos produced per cocoon | Higher | Lower |
| 3. | Incubation time of cocoons | Shorter | Longer |
| 4. | Maturation time from hatching | Shorter | Longer |
| 5. | Duration of reproductive life | Shorter | Longer |
| 6. | Time distribution of mortality | Shorter | Longer |
| 7. | Form of survivorship curve* | Type III | Type I or II |
| 8. | Seasonal stability of population density | Lower | Higher |
| B. | Related to the feeding behaviour required to sustain different reproductive rates: | | |
| 9. | Surface or subsurface dwelling | Surface | Subsurface |
| 10. | Metabolic rate | Faster | Slower |
| 11. | Mobility | Higher | Lower |
| 12. | Sensitivity to pH | Lower | Higher |
| 13. | Sensitivity to light | Higher | Lower |
| 14. | Pigmentation | Pigmented | Unpigmented |
| 15. | Avoidance of desiccation | Quiescence | Diapause |
| 16. | Size | Smaller | Larger |
| 17. | Morphological adaptations to burrowing | Poorly developed | Well developed |
| 18. | Form of prostomium | Tanylobic | Epilobic or proepilobic |
| 19. | Form of typhlosole | Smaller, unfolded | Larger, folded |
| C. | Related to metabolic rate | | |
| 20. | Nitrogen excretion rate | Faster | Slower |
| 21. | Intestinal transit rate | Faster | Slower |
| 22. | Oxygen affinity of haemoglobin | Lower | Higher |

* See Deevey, E.S. 1947. Life tables for natural populations of animals. *Q. Rev. Biol.*, **22**, 283–314.

productivity, including adaptations to surface living or burrowing; and those which may be adaptive or may be associated with different metabolic rates as either causes or effects. These attributes are summarised in Table 35.

As the group spread, and as competition for food intensified, adaptations to pioneer conditions would tend to have been replaced by new adaptations to survival on the lower grade food material of soil organic matter and by the return of the burrowing habit. Survival through the cold season below ground-level creates the possibility of extending the life span beyond one season. A large biomass can then exist throughout the year ready to exploit the available food supply whenever temperature and moisture constraints permit. The need for rapid maturation and reproduction decreases and the reduction in mortality from surface hazards reduces the rate at which cocoons must be produced to maintain the population density. Having overcome the need to seek out a nitrogen-rich food source in order to produce a big seasonal batch of cocoons, it becomes possible to conserve energy by reducing the rate of body metabolism and to adopt a more sedentary life.

By the operation of surface laws, reductions in metabolic rates permit increases in body sizes and hence the power to form burrows. Subsurface feeding on soil organic matter can then be combined with feeding on surface plant remains from below, or collecting materials on the surface close to burrow openings. Exclusively subsurface feeding patterns may also develop, including subsoil feeding. It then becomes prudent, so to speak, to maximise resource conservation by combining low metabolic rate with protracted longevity. Adaptive radiation into a variety of niches in both organic and mineral horizons could be expected to produce specialists in dung, corticolous, subsoil, amphibiotic and other habitats. If selection forces did indeed operate broadly as outlined, it seems that the Lumbricidae may have evolved from life in the soil to life on the surface and back again, and that species with adaptations to soil dwelling are not necessarily older than species adapted to life on the soil surface.

In the northern hemisphere, the most important recent event in lumbricid evolution has been the obliteration of the endemic populations of earthworms in large areas by glaciation and the post-glacial recolonisation of these areas by species from elsewhere. It can be inferred from the absence of new species since the glacial periods that these events are too recent for them to have evolved. Nevertheless, the changing selection pressures, exerted on the existing stock of species as the tundra-like habitats of the immediate post-glacial period were succeeded by temperate ecosystems, determined the species composition of the present-day lumbricids. Selection pressures favouring initially the short, fast life style of the surface feeder must have swung, as the climate ameliorated, to favour the slow, resource-conserving

*Table 36.* Adaptive radiation of some lumbricid earthworms

Adaptive strategy

| | r <——— | | | ———> K |
|---|---|---|---|---|
| **Surface feeders** | | | | |
| Litter layers | *D. octaedra* | | | |
| Litter and subcortical | *B. eiseni*<br>*D. subrubicunda* | | | |
| Litter and dung pats | *L. castaneus* | | | |
| Litter and dung heaps | *E. foetida* | | | |
| **Surface and subsurface feeders** | | | | |
| Semi-aquatic | *E. tetraedra* | | | |
| Litter, dung pats and subsurface | | *L. rubellus* | | |
| Litter and soil organic matter | | | *L. terrestris* | |
| **Subsurface feeders** | | | | |
| Surface soil | | | *A. chlorotica* | |
| Soil organic matter and litter | | | | *A. nocturna*<br>*A. longa* |
| Soil organic matter | | | | *A. caliginosa*<br>*E. rosea* |
| Aquatic muds and subsoil | | | | *H. oculatus*<br>*B. muldali* |
| Subsoil | | | | *O. cyaneum*<br>*O. lacteum* |

life style of the soil dweller. The earthworm's answer to the question of whether it is better to live like a lion for a day or a lamb forever is, on this interpretation, partly historical and partly geographical.

*Adaptive radiation within r and K strategists*

Within the confines of the r strategy, several variations in life style are possible (Table 36). *Dendrobaena octaedra* and *Bismastos eiseni*, living in forest or heathland litter layers, are seen as predominantly r selected. *Lumbricus castaneus* occurs in litter layers but more abundantly in grassland where it is adapted to exploit ephemeral dung pats. *Eisenia foetida*, originally a corticolous litter-layer species, is now also adapted to man-made habitats in nitrogen-rich organic matter. *Lumbricus rubellus*, primarily an r strategist, lives in forest litter or in grassland as a partial coprophage. In some sites with a thin litter layer, it burrows into the mineral soil and seems part way along the route to a K strategy. *Lumbricus terrestris*, further along the same route, has the reproductive features of a K life form but, having retained the r selected habits of feeding and mating on the surface, also retains the pigmentation of the r strategist. *Eiseniella tetraedra* is perhaps an r strategist that has become semi-aquatic.

Predominantly K selected types, including *Allolobophora caliginosa* and *Eisenia rosea*, while living in the A horizon of mull soils, reproduce slowly and maintain a large biomass throughout the year. *Allolobophora chlorotica*, also a mull-soil dweller, lives just below the soil surface where it is exposed to bird predation. Its pigmentation, thought to have camouflage value, is of an entirely different composition from that of r strategists. *A. longa* and *A. nocturna* are 2 typical K strategists which in their exploitation of the full depth of the A horizon have developed the behaviour of defaecating on the surface. Their distal pigmentation differs from that of r strategists. *Octolasion cyaneum* and *O. lacteum* are K strategists adapted to exploit permanently moist subsoil. The latter has a weak ability to diapause, but is enabled, by a well-developed network of subcutaneous blood vessels and a high concentration of haemoglobin, to inhabit poorly aerated soils.

Within the main division of r and K strategists, many forms of adaptive radiation are thus seen to be possible, and this can be expected to apply not only to the lumbricid species which migrated into Britain, but also to endemic species. Where winter temperatures or summer drought do not permit survival of post-embryonic worms, r life forms may be expected—where adult or juvenile worms can survive throughout the year, a variety of adaptations within the K life form will occur.

Recent work in the Ivory Coast has shown that small species of megascolecid earthworms living close to the surface have a fast rate of multiplication and are more productive (P/B) and less efficient (P/I) than large species living deep in the soil. It seems therefore that, although some differences may be found among their r and K attributes, Megascolecidae and possibly other earthworm groups may, like the Lumbricidae, be capable of analysis in terms of r and K selection.

*J. E. Satchell*

## Data and Information

SERVICES

*Computing*

The development of computing within the Institute is closely linked with that of the NERC Computing Service. Within this context, the PDP–11/10 systems at Monks Wood and Bangor have both been upgraded to PDP–11/34 systems and are running under the RSX–11M operating software. Merlewood is expected to use this system as soon as practicable. Monks Wood is also linked by private line to the SRC computing system at the Rutherford Laboratory. New computing accommodation has been provided at Merlewood and Bangor.

The software developments at Merlewood have concentrated on producing an efficient word processor for the station and expanding the existing software for handling extensive bibliographic references. The purchase of a VDU and a high quality printer have greatly enhanced the ability to handle textual material at Merlewood.

Bangor has continued to explore the use of the G-EXEC data base management system at the Rutherford Laboratory as a way of handling extensive ecological data bases in relation to the Terrestrial Environment Information System. This data base system is being used by a number of groups within NERC, and by the Biological Records Centre at Monks Wood. TEIS has a role in providing information on and access to data sets relevant to ITE's work and G-EXEC has been selected as the most suitable system through which to pursue this objective. It will allow considerable scope for analytical studies which will involve ITE's own data collected in such projects as the Fluorine Pollution Studies and the National Land Characterisation study.

The 2 ITE stations at Edinburgh (Bush Estate and Craighall Road) have a programmable calculator with graph plotter which is used for tackling problems with small data sets. The staff also have access to the computer systems and related facilities run by the Edinburgh Regional Computing Centre. Terminals on the stations communicate with an interactive system, EMAS, which has batch processing ability. These links are supplemented by a frequent van service for large volumes of input and output. A wide variety of computer packages supplemented by a number of locally written programs are used, mainly for the analysis of data and the development of mathematical models. These arrangements are under review in consultation with the NERC Computer Service.

Until this year, computing at Furzebrook was dependent upon the use of a terminal to external computers. The addition of an Olivetti P6060 mini-computer greatly improves the computing power. This machine is single-user, works in extended BASIC and has good plotting facilities. Programs can be interchanged between similar machines at Furzebrook, Merlewood, ITE Cambridge, CCAP, and the FBA River Laboratory. The G-EXEC data base is also used for information storage and retrieval.

The Banchory PDP–11/10 continues to be used for a wide range of tasks for which an extensive program library exists.

*D.K. Lindley, G.L. Radford, R.T. Clarke and R. I. Smith*

*Biometrics*

The small Biometrics staff has been fully extended in providing a statistical service to meet the increasing demand by ITE biologists for guidance over a wide variety of biometrical problems which includes analyses of experimental and survey data, development of methodology to solve problems arising from ecological studies, ecological modelling and simulation, systems analysis and the computerisation of data banking and information retrieval.

Some examples of specialist consultancy activities are given below.

The statistical analysis of red grouse populations has included studies on the inheritance of aggression; the survival of chicks in relation to clutch size, egg size and laying date; the modelling of fluctuations in numbers; and the measurements of dominance within and between clutches. The last has resulted in the publication of an important methodological paper (Rothery 1979).

A numerical classification based on a sample survey of the environmental and vegetation characteristics of the United Arab Emirates has been made. The final classification was arrived at by selecting the grouping which picked out the features common to 7 different numerical methods of classification.

Work has continued on the Phytophagous Insects Data Bank. A major task has been the conversion of the data bank's software from the obsolescent ICL 1906A machine at the SRC Rutherford Laboratory to the University of Cambridge IBM 370 computer. Particular difficulties arose from the difference of job control languages, file organisation, character codes, library software, and FORTRAN dialects. Some 6 main programs, 18 sub-programs, and 5 megabytes of data have been tested and converted to the IBM conventions.

The international wildfowl count data organised by the Wildfowl Trust are being analysed to estimate annual fluctuations in the sizes of wintering populations over the period 1967/76. The estimation is presenting a number of problems such as non-orthogonality of the data, as not all sites were counted in every year, non-random dispersion of wildfowl which tend to move in flocks, and the dependence of their distribution in a given winter on the weather conditions. Initial tests indicate that the estimation of numbers is improving by subdividing north-west Europe into 20 separate sub-areas.

A multivariate analysis of variance is being applied to measurements made on the ant *Myrmica ruginodis*, collected from various sites and countries in order to identify the major sources of environmental and geographical variation. Size is the major component in the variation; another major component is expected to be between colonies with normal sized queens and microgynes (small queens).

As so much research effort is put into carrying out large-scale land surveys, an experiment has been set up to test the validity of the survey methods, and, in particular, to measure the variability between observers in their assessment of the cover values of plant species. Preliminary analyses indicate considerable differences between observers. However, the assessments of a given observer tend to be consistent over time.

An improved method of estimating the contribution of crown leachates to the chemical composition of rain collected beneath trees has been developed. A joint paper on this subject (Lakhani & Miller in press) has been accepted for publication.

*M.D. Mountford, K.H. Lakhani, P. Rothery, D.F. Spalding, D. Moss and R.T. Clarke*

*References*

**Rothery, P.** 1979. A non parametric measure of intraclass correlation. *Biometrika*, **66**, 629–640.

**Lakhani, K.H. & Miller, H.G.** In press. Assessing the contribution of crown leaching to the element content of rainwater beneath trees. In: *Effects of acid precipitation on terrestrial ecosystems*, edited by T.C. Hutchinson and M. Havas. New York: Plenum.

*Biological Records Centre*

Much of the work of the Biological Records Centre (BRC) was commissioned by the Nature Conservancy Council as part of its programme of research into nature conservation. The work of BRC has been re-organised during the year, with the object of improving both the flow and quality of data being acquired from the national recording schemes, of which there are now 45. Liaison with each scheme organiser is now the specific responsibility of one of the biologists in BRC, and 20 scheme organisers have been visited during the year. New schemes have been initiated for Aquatic Coleoptera, Coleoptera Ptilidae, Hemiptera Auchenorhyncha, Trichoptera and Tardigrades in the invertebrates, and Characeae in the plants, with appropriate specialists as scheme organisers. Species list cards have been produced for most of these schemes. The freshwater fish scheme has been completely re-organised.

Optical Machine Reading (Opscan) forms have been prepared for the mammals, Odonata, Orthoptera and Hymenoptera Formicidae schemes, and these forms will enable entry of the data for these groups in the data bank at the SRC Rutherford Laboratory. The addition of these data will greatly extend the range of animal groups for which data are available for analytical studies.

Distribution maps have been produced for the Lepidoptera Geometridae (ca 300), which are currently being edited, thus completing the maps for this group; 50 species of *Carex* and 118 Welsh plants. Entering data from the 80-column plant individual record cards into the plant data bank has been completed. Revised editions of the Provisional Atlases of Odonata, Orthoptera, Hymenoptera Vespidae and Formicidae have been prepared and are at press, whilst maps for the Lepidoptera Sphingidae, Notodontidae, Lymantriidae, Arctuidae, Nolidae and Noctuidae have been published in Volume 9 of *Moths and butterflies of Great Britain and Ireland*.

The entries for the Vertebrate Red Data Book have been completed, as has the listing of the candidate species for the Insect Red Data Book. A study of the *Threatened Rhopalocera (butterflies) in Europe* is being carried out under contract from the Council of Europe. This study will result in a publication in their *Nature and Environment Series*.

The International Commission for Invertebrate Survey (IUBS), for which BRC provides the secretariat, held its 4th International Symposium of the European Invertebrate Survey in Saarbrucken, Germany, from 25–26 June 1979. This symposium was attended by J. Heath who also, under the aegis of IUBS, visited the USA in May in order to initiate the formation of a North American Invertebrate Survey organisation. During this visit, discussions were held with the organisers of several regional distribution mapping schemes in the

USA, as well as with interested scientists at a number of US Government research institutions.

Routine enquiries have been received from numerous sources, including the Nature Conservancy Council, research scientists, regional records centres and individuals. In response to these enquiries, some 100 maps and 50 sets of data have been provided.

*J. Heath, P.T. Harding, H.R. Arnold, Diana W. Awdry and Dorothy M. Greene*

*Terrestrial Environment Information System (TEIS)*

The Terrestrial Environment Information System (TEIS) is under development at ITE Bangor with the aim of facilitating access to relevant data holdings within ITE and elsewhere for applications in ecological research and for environmental management purposes. TEIS is introducing standards for data storage and exchange at 3 levels:

1. Standard logical formats are being developed for recording ecological data. As far as possible, these formats will follow existing practice, but will seek to achieve consistency and compatibility of data management practices throughout ITE.

2. Standard aids for data characterisation (eg indexing vocabularies, species lists, coding systems) are being introduced so that data sets which share common attributes may be recorded consistently and reproducibly.

3. Computer systems are being developed (using existing packages as far as possible) to assist the transformation of data into the standard format, to facilitate data exchange and to provide comprehensive facilities for data retrieval, analysis and presentation.

TEIS will thus function as a link between independent data sets, making it possible to identify relevant data from a number of different sources and to bring them together for purposes of analysis or comparison.

The groundwork for this has already been laid by the incorporation of the National Land Characteristics Data Bank (ITE Project 534) into the NERC G-EXEC data management system on the IBM 360–195 computers at Rutherford Laboratory. This system is already used to operate the BRC data bank, and both BRC and the National Land Characteristics Data are based on a 10 km × 10 km recording grid. It is, therefore, now possible to analyse directly these independent data sources and to look for correlations between species distribution and environmental factors such as topography, meteorology and soil type. The G-EXEC system provides sophisticated data retrieval and presentation facilities, typified by Figure , which consists of an overlay of the occurrence of land with slope >5° (the denser the background, the greater the proportion of sloping ground) on a standard BRC species distribution plot of *Pinus sylvestris*.

An *ad hoc* advisory service covering all aspects of data management is being provided locally at Bangor. This function will be developed into a more formal service available throughout ITE. TEIS will also provide channels through which requests for information or advice can be referred to suitable data sources or directed to the most appropriate experts in ITE. This role will be developed in the course of the next year with the compilation of a comprehensive directory of ITE's data holdings, and with the publication of promotional literature to encourage the use of TEIS services internally and externally.

*B.K. Wyatt*

*Publications*

The Institute published 10 items up to November 1979 and has another 5 in the final stages of printing. A list of ITE publications for sale is given at the end of this Report.

ITE have published 27 books, booklets, leaflets and final atlases over the last 4 years, covering a wide range of ecological subjects in formats suitable for the material. Our guiding principle has been three-fold: to make readers aware of the work and aims of the Institute as a component body of the Natural Environment Research Council; to provide a service to professional biologists in their special and technical subjects; and to give a wider public a chance to make use of research results and information normally presented in scientific papers.

*M.J. Woodman*

*Education*

When Monks Wood was built in 1962/63, its educational possibilities were very much in mind. Fourteen study bedrooms were provided, and these have been in regular use. During 1979, the following institutes have visited Monks Wood for periods ranging from one to 9 days:

University College London
Imperial College London
Sheffield University
University College of North Wales, Bangor
Aberdeen University
Oxford Polytechnic
Bucks College of Higher Education
Wye College
Brunel University
Leicester Polytechnic
City of London Polytechnic
University of East Anglia

North East London Polytechnic
Cambridge College of Arts and Technology
Cambridge University Geographical Society
Botanical Society of the British Isles
Isopod Study Group
British Arachnological Society

Courses varied in size from 9–40 people, and, altogether, some 300 students and tutors were accommodated. Thirty-four members of staff gave 89 lectures and demonstrations, and field visits were also arranged. Many of these institutions are regular visitors who prefer to make their visits at much the same time and the main problem is to fit them all in.

Sixteen seminars for ITE staff were held at Monks Wood in 1979, as well as an NERC Health and Safety Course. A special 2-day course on public speaking was arranged for ITE staff by the NERC Training Section.

A large number of postal and telephone enquiries come to the Education Officer each year. These vary from organisations seeking general information on ITE, specialists wanting more specific details, and school children wanting help with projects or information on ecology. The Education Officer also gives evening talks to a variety of local organisations.

*Joan M. Welch*

*Library*

A continuing shortage of staff has meant that the ITE library has had to continue to concentrate on providing a basic library service. The *Current contents of journals received* continues to be produced weekly. This service is widely used and generates a considerable amount of photocopying and lending between the different locations of the Institute library. A revision of the *Serials list* was produced, and is available to other libraries on request. ITE is very dependent upon the goodwill of other libraries in lending items and the number of inter-library loans requested is about 7 000 annually, mostly from the British Library Lending Division.

Book cataloguing is recorded on the PDP–11 computer at Merlewood, and a project was initiated using labour provided under the Short-Term Employment Measures of the Manpower Commission to produce a union catalogue of all books in ITE libraries. First steps were also taken towards using a computer to store serial records. A library service was established for scientific staff at Craighall Road, Edinburgh, where the library is concerned mainly with freshwater ecology.

During the year there was some development of on-line literature search services for scientific staff, and it is hoped to develop these services as resources permit.

*J. Beckett*

RESEARCH

*Island biogeography*

Since the publication in 1880 of *Island life* by Alfred Wallace, a friend of Charles Darwin, islands have been used increasingly for ecological and biogeographical studies. The British Isles are 'continental' islands separated from the mainland of Europe about 7 000 years ago. As well as the main islands of Great Britain and Ireland, 88 797 and 32 020 square miles in area respectively, there are, offshore and mainly in the west and north-west, at least 6 000 smaller islands ranging in size from the largest, the 825 square miles of Lewis/ Harris in the Outer Hebrides, to the multitude of small rocks and reefs located around the coasts. Many of these small islands are important as breeding groups for seals and seabirds. However, if one criterion used to define a 'true' island, namely an area sufficient to support one sheep, in winter, is used, it is estimated that there are fewer than 2 000 islands off Britain and Ireland.

When an island first separates, it possesses a biota like that of similar situations on the mainland. This biota is influenced both quantitatively and qualitatively by the habitats available. These, as elsewhere, depend on the interaction of factors such as area, altitude, geology and pedology, geographical position and climate, but an additional factor is the increasing effect of isolation. Islands are, therefore, very appropriate for the study of processes such as colonisation, depopulation, speciation, and species/area relationships.

It is against this background that work on a comparative biogeographical assessment of the British and Irish offshore islands is being undertaken. As a first step, all islands shown on the 'one inch' and 'half inch' Ordnance Survey Maps of Britain and Ireland were listed. The names of these islands, National Grid references, vice-county numbers and relevant biological and physical data are stored in a data bank. A catalogue of islands with a statement of what is known of their biota and physical attributes is being produced. A comparative biogeographical assessment will then be based on those groups of plants and animals for which there are reliable and reasonably comprehensive distributional data. These groups include the flowering plants, mosses, lichens, seabirds, non-marine molluscs and spiders.

*Noelle M. Hamilton*

## Chemistry and Instrumentation

SERVICES

*Chemistry at Merlewood and Monks Wood*

ITE services for analytical chemistry are provided through 2 centres, Merlewood and Monks Wood. The laboratories at these stations have been organised, and facilities provided, so that, as far as practicable, the 2 laboratories complement each other. The Merlewood laboratory concentrates on the natural constituents to be found in biological materials, soils and waters, whereas the emphasis at Monks Wood is on pollutant chemicals, notably heavy metals and organic pesticides. There are, of course, exceptions; for example, it is more appropriate to use facilities at Merlewood for the determination of sulphur and fluorine pollutants, whilst the gas chromatographic expertise at Monks Wood can be put to good use for the examination of some natural organic constituents, as in the case of monoterpenes.

Altogether, the 2 chemical laboratories provided analytical support during the year for over 50 of the ITE projects. Total sample numbers processed were approximately 4 000 vegetation, 3 000 waters, 2 500 soils and 1 500 animal specimens. Some 60 separate constituents were determined as routine, in some cases as many as 15 on the same sample. Important factors in enabling this large amount of work to be processed so smoothly were the new data handling systems, described later.

Although no one project alone accounted for more than 5% of the work of the analytical services, the projects concerned with geochemical cycling (ITE 594), sulphur pollution (ITE 380) and coppice woodland management (ITE 389) made heavy demands on Merlewood laboratory time. Most of the work at Monks Wood was carried out in support of the Animal Function Subdivision, based entirely at that station. Projects 455 (heavy metals) and 181 (organochlorines), in particular, called for frequent support.

Apart from the service provided for ITE's research staff, some work was also carried out for other NERC establishments and grant-aided individuals. Most of this work was done for the British Antarctic Survey and for the Unit of Comparative Plant Ecology at Sheffield. Analyses carried out for the Sheffield Unit concluded a 3-year contract with them for the provision of nutrient data in vegetation samples. In the present year, 1 500 of these samples were analysed, with 10 elements being determined on each sample.

It was not possible to take on so many of the requests for analytical assistance received from non-NERC organisations as in previous years, because of pressure from internal commitments. An exception was made for the Nature Conservancy Council because of the close working relations between the 2 organisations. For separate financial reasons, however, even work from this source was less than hitherto. The only 2 other external contracts of any significance involved analyses for the Firth of Forth Pollution Unit at Napier College, Edinburgh (nitrogen and phosphorus fractions), and for the United Kingdom Atomic Energy Research Establishment (soil particle and exchange analyses).

The dominant practical problem of the year in the Merlewood laboratory was the handling of water samples and the development of practical procedures to fit them into the laboratory routine. Most of the waters originated from regular monitoring studies, and, because of the labile nature of some of the constituents, they have to be processed immediately. In the early part of the year, most of these samples originated from the sulphur pollution programme based on Devilla Forest, Fife (ITE 380). Later in the year, the geochemical cycling project provided samples of stream and soil leachate waters from the Plynlimon catchment for analysis at 2-weekly intervals.

Because many of these waters required 2 separate wet oxidation procedures, one for total nutrient elements and one for total sulphur, and, with similar equipment being required for vegetation analyses, the existing digestion equipment could not cope. Two further digestion units were, therefore, designed and constructed in the station workshop. Two routine teams were also established in the Merlewood laboratory and facilities rearranged so that one group could concentrate on water analyses without disturbing the main production team dealing with all other samples.

Waters also constituted a considerable fraction of the work of the Monks Wood analytical chemists. However, these samples were mainly generated by the studies dealing with the effects of heavy metals on aquatic organisms (ITE 289, 482) also at Monks Wood, and it was convenient to match the analytical contribution with field collection and experiments.

Most of the routine methods at present in use by both the service laboratories have now been well tested and documented, and less time needs to be spent on technique development work than in the past. At Merlewood, 2 new methods were investigated. One was a method for the determination of organic carbon in soils derived from the well-known wet oxidation/titrimetric method of Tinsley. A new procedure for estimating mineralisable nitrogen in soils, designed to replace the traditional time-consuming and labour intensive incubation technique with a simpler chemical extraction procedure, is still being studied.

There was continued interest during 1979 in the effects on freshwater organisms of Eulan WA, a chemical used for processing textiles. The need for an improved analytical method for this substance was discussed at a meeting at Monks Wood between representatives of different organisations and a co-operative analytical test programme was subsequently set up.

For instrumental development, 1979 was mainly a year of consolidation after the acquisition of new equipment late in the previous year. In particular, the purchase by both the Merlewood and Monks Wood sections of similar on-line data processing systems were major innovations that had to be assimilated.

The preparation of operating programs, modifications of instruments and work routines, and staff training occupied much of the early part of the year. It was not until the middle of the year that the substantial benefits conferred by these instrument-linked systems were obtained.

The Merlewood data processing equipment was linked first to 2 flame instruments and 2 continuous flow colorimeters. Recently, the system has been extended with the addition of 2 electronic balances and an extra dual floppy disk unit. The Monks Wood data equipment is linked to atomic absorption and gas chromatography equipment.

A new autosampler and injector for the electrothermal atomisation equipment employed at Monks Wood for heavy metal analysis was also introduced. This equipment has been found to give erratic responses when used manually, especially with low concentration samples. Using automatic injection, this problem is largely overcome, and there is also the added advantage of being able to process samples overnight.

*J.A. Parkinson and M.C. French*

*Radiochemistry*

This new service section was established late in the year to look after the analytical requirements of the radionuclide research projects and general radiotracer requirements. Accommodation, formerly occupied by the Nature Conservancy Council's North-West Regional Office which has now moved to Windermere, is being converted into radiochemical laboratories.

A number of major instruments have been purchased in addition to the normal range of chemical equipment. These include 2 GeLi and one sodium gamma detector and 8 surface barrier alpha detectors, all coupled with a multi-channel analyser. In addition, a separate image analyser has been installed for alpha track counting. The separate radiotracer building referred to houses the beta scintillation equipment.

*A.R. Byrne*

*Engineering*

The engineering section continued to provide support for the research staff both in instrument development and the routine maintenance and repair of equipment. All of ITE's research stations, except Furzebrook and CCAP, have a resident engineer. The engineers are mainly concerned with the requirements at their own stations, but there is co-operation for major construction jobs and the particular skills of an engineer may be used whenever necessary (Cover photograph). The central engineering unit at Bangor provides an Institute-wide service.

The nature of the routine duties of the different engineers varied considerably in 1979. Bangor and Monks Wood staff had a mixed spread of tasks, but work at Bush was dominated by the need to maintain and modify the growth cabinets and equipment in the glasshouses. Boats and other associated sampling equipment used by the aquatic biologists at Craighall Road also needed constant attention. At Merlewood, the resident engineer spent much time maintaining instruments in the chemical laboratories and the new engineer at Brathens was mostly occupied with developing and repairing radio transmitters used in animal tracking experiments. An additional engineer was appointed to Bangor to work both as a station engineer and to assist with the work of the central engineering unit.

The fitting of the new workshop, erected at Brathens towards the end of the previous year, was completed, but financial restrictions meant that little other new equipment could be obtained.

*G.H. Owen*

*Plant culture*

The construction of new glasshouses at Bush (3 units), Merlewood, Furzebrook and Banchory (1 unit each) was completed during the year. These provide protected environment facilities with a moderate degree of automation, and in some cases day length extension by MBER/U lamps. The Furzebrook glasshouse, the second one for that station, is split into separate units, and is equipped with air conditioning.

The 50% increase in the glasshouse facilities at Bush necessitated a change in arrangements and project staff now carry out much of their own production work under the supervision of the nursery staff. During the year, 34 000 plants, of which 16 000 originated from other stations, were reared in the Bush glasshouses.

The production of *Betula* specimens for the National Birch Collection is now complete. These plants were grown from seed collected from Scandinavia, Holland, Kashmir, Japan, Alaska, Canada and the USA. Plants from seed obtained in Russia and Germany have been grown for planting in 1980.

The second half of the amenity grass mixture trial (the effect of establishment period on tolerance to wear) was sown in spring and progressively mown to a 2 cm high sward during the summer. Trials of the 2 areas commenced in October, using an artificial wear machine. This work was done in association with Monks Wood staff and with the Sports Turf Research Institute. The Scottish Institute of Agricultural Engineering at Bush Estate has also been involved in monitoring the performance of the wear machine.

Additional land suitable for field plots has been allocated for ITE use by the Edinburgh Centre for Rural Economy. This is a part of the Glencorse Mains farm which lies south of the research estate, and 1·5 ha of this new area has been taken into immediate use for field trials and clone banks. Part of the original nursery field close to the station has been adapted for use as a second irrigated plunge and standing area.

The nursery unit was fortunate in being able to acquire a mini-tractor in 1979, following the closure of ITE's Colney Research Station, and this machine has proved specially valuable, in combination with a rotary grass cutter, for mowing around older trees where space is limited. The problem of preparing large quantities of potting composts, the total volume of which exceed 50 m$^3$ in most years, was eased by the acquisition of another piece of relatively simple equipment, namely a cement mixer.

The planting and final phase of the contract for landscaping the land around NERC Headquarters at Swindon was completed during the year. This phase was the culmination of 2 years' planning which has had to deal with such diverse problems as site topography, local authority planning requirements and chemical pollution from the previous railway and industrial occupation of the site. Advice and designs on landscaping were also produced for the Edinburgh Centre for Rural Economy and for the Scottish Institute of Agricultural Engineering.

*R.F. Ottley*

*Photography*

The photographic unit has continued to provide developing and printing, colour processing and slide copying services to the Institute. Additionally, photographs of field sites and experiments are also taken on request and illustrations were prepared for 16 sites.

Most of the work has been black/white printing, but there was also a steady demand for colour prints from slides, using the Cibachrome reversal system. Most of this work was for inclusion in scientific papers and reports. Material was also provided for 'Open Day' displays at Merlewood and Furzebrook and involved the production of 100 black/white prints and 300 colour prints. The purchase of an automatic variable speed paper processor with thermostatically controlled baths, suitable for both colour and resin-coated black/white paper processing, and a resin-coated print dryer, has helped to increase print production.

*P.G. Ainsworth*

## RESEARCH AND DEVELOPMENT

*On-line data processing*

The installation of an on-line data processing system in the Merlewood laboratory has speeded the rate at which chemical analyses can be made and also much facilitated the processing of analytical data. Although the system was initially designed to meet ITE specifications, certain aspects of the system have proved inadequate. Initially, only 20% of each floppy disk was available to BASIC, limiting the range of manipulations possible using one disk. The addition of an extra dual floppy disk unit has provided 2 complete disks for BASIC; one is used for software and the other provides sufficient storage space for one month's data. All data from a batch of samples can now be contained on a single floppy disk, and software is available to compile a customer report from the disk. The extra disk unit allows the chemical data bank (see 1978 Annual Report) to be used simultaneously with the on-line data collection facilities.

The data processing system includes software to process the raw peak height data to correct for baseline and instrumental drift. BASIC software, now fully developed, processes this drift-corrected data on the system master disk and stores it on the BASIC data disk. Additionally, BASIC programs to perform linear, curvilinear and logarithmic regressions on data from off-line instruments have been designed for manual input. The suite of programs also contains management software to provide listings from the floppy disks and relevant statistical programs are available.

The connection of 2 electronic digital balances to an on-line system has also improved laboratory automation. Operator errors have been much reduced, as has the time spent in weighing batches of samples. Programs have been developed to relate the balance data to the results from the regression programs, and to increase the efficiency of the data processing. Other programs combine weight files in various ways, eg for moisture determination by weight difference.

*A.P. Rowland*

*Long-term nutrient status of soils*

This research is intended to develop an index to measure the reserve nutrients in soils. Exhaustive cropping techniques have been used by some workers for this purpose, but these techniques are too laborious for routine measurements. Different physical and chemical methods are now being examined and compared with exhaustive cropping techniques using *Holcus lanatus* and *Rumex acetosa* in the search for a rapid, simple, but biologically sensible technique. The main elements considered in the initial study are potassium, calcium and magnesium, but it is hoped to include other essential elements, eg iron, manganese and zinc, and to see whether a similar approach is appropriate for phosphorus. An important consideration is the need to adapt any procedure to the automated techniques in routine use in the Merlewood laboratory.

Several processes which facilitate a breakdown of soil structure leading to the release of nutrient elements are being examined. In particular, the effects of storing at high temperatures for short periods, in conjunction with various extraction treatments, have been found, for some soils, to give results which may be useful in predicting nutrient availability in the long term.

Chemical methods have long been in use to assess readily available plant nutrients, and, initially, the fractions released and mechanisms of release were evaluated. The use of cation exchange resins at elevated temperatures was also investigated. Results were good, but the practical problems involved made the method unsuitable for routine use.

Extraction of soils with boiling molar acids is so far the most promising approach and contrasting test soils of known mineralogical and particle size contents are being used in the investigations. The extraction data will be assessed in relation to mineral and organic composition, to the exchange properties of these constituents, and to their elemental composition and stability.

*S.E. Allen and A.P. Rowland*

*The application of isoelectric focusing to isoenzyme separation*

The net charge on an amphoteric molecule is governed by the pH of the surrounding medium: the lower the pH the more positive the charge and vice versa. In electrophoresis, the region between the electrodes is being maintained at constant pH and separation of the molecules depends only on mobility, each molecular species retaining the same overall charge throughout the experiment. In the related technique of isoelectric focusing, a linear pH gradient is set up between the electrodes, the lower pH towards the anode. Under these conditions, each molecular species will migrate towards the appropriate electrode, but its charge will fall as it migrates through the pH gradient. At zero potential, the isoelectric point, the molecule is no longer influenced by the electric field. Moreover, should a molecule diffuse from its equilibrium position, it is automatically returned to it by the field. This process is in marked contrast to electrophoresis where bands continue to broaden the further they travel.

Gel electrophoresis has been used in a number of ITE projects for the determination of isoenzymes for genetic purposes. However, the range of enzymes which can be studied is limited by the chromogenic techniques available for the detection of bands. In general, detection must be done directly, multi-enzyme chain reactions (which are perfectly possible in aqueous solution) being too difficult to perform on the surface of a gel. In addition, quantitative measurements are difficult to make and kinetic determinations virtually impossible. In order to extend the range of enzyme systems which could be studied and to improve the quantitative aspect of the work, the bands need to be eluted after separation, preferably whilst still under the influence of the electric field to reduce loss of resolution by diffusion. A continuous flow, flat-bed, gel-stabilised system originally described by Fawcett (1973) and used for the preparative separation of single proteins was used as the basis for the work (Figure 62). The electrode holders containing the semi-permeable membranes were redesigned to operate with plain dialysis tubing for ease of replacement. The principal difficulty, however, was to construct a manifold for the collection of the final fractions, but which would maintain the high resolution achieved by the separation process. Also, each fraction needed to be pumped from the bottom of the cell to maintain an even, laminar flow in the cell itself, which would normally call for the use of a large number of specially adapted peristaltic pumps. Both problems were eventually solved, and a system developed which allowed collection of fractions at a resolution 3 times greater than anything previously reported and which could be used in standard peristaltic pumps. After modification to run at lower speeds than normal, such a system would pump 32 channel per inch width of the pump platten with a coefficient of variance between channels of 0·6%.

Initial tests have been carried out using a preparation of carboxyhaemoglobin; this preparation allowed the progress of the separation to be followed visually. Using an ampholyte gradient of pH 3·5–9·5 at 1% final concentration, a field strength of 100 volts $cm^{-1}$ and a residence time of 120 mins, 2 principal bands were clearly resolved and collected 0·5 pH units apart. The bands showed no tendency to drift sideways over a period of several hours.

These tests suggest that the apparatus should be suitable for the separation of isoenzymes without further modification. The resolution of fine detail in the pattern of the bands will not match that of the commonly-used polacrylamide gel method, but this disadvantage will be more than offset by the better quantitative assessment of band densities and by making available for analysis a much larger range of enzyme systems.

*C. Quarmby*

*Reference*

**Fawcett, J.S.** 1973. Continuous flow isoelectric focusing and isotachophoresis. *Ann. N.Y. Acad. Sci.*, **209**, 112–126.

*Radionuclides in terrestrial ecosystems*

ITE's Annual Report for 1978 included a summary of the main findings of a desk study which was carried out for the Department of the Environment, and dealt with the fate of radionuclides in the ecosystem. This study identified a number of research areas which needed further examination and work on 2 of these commenced during the current year.

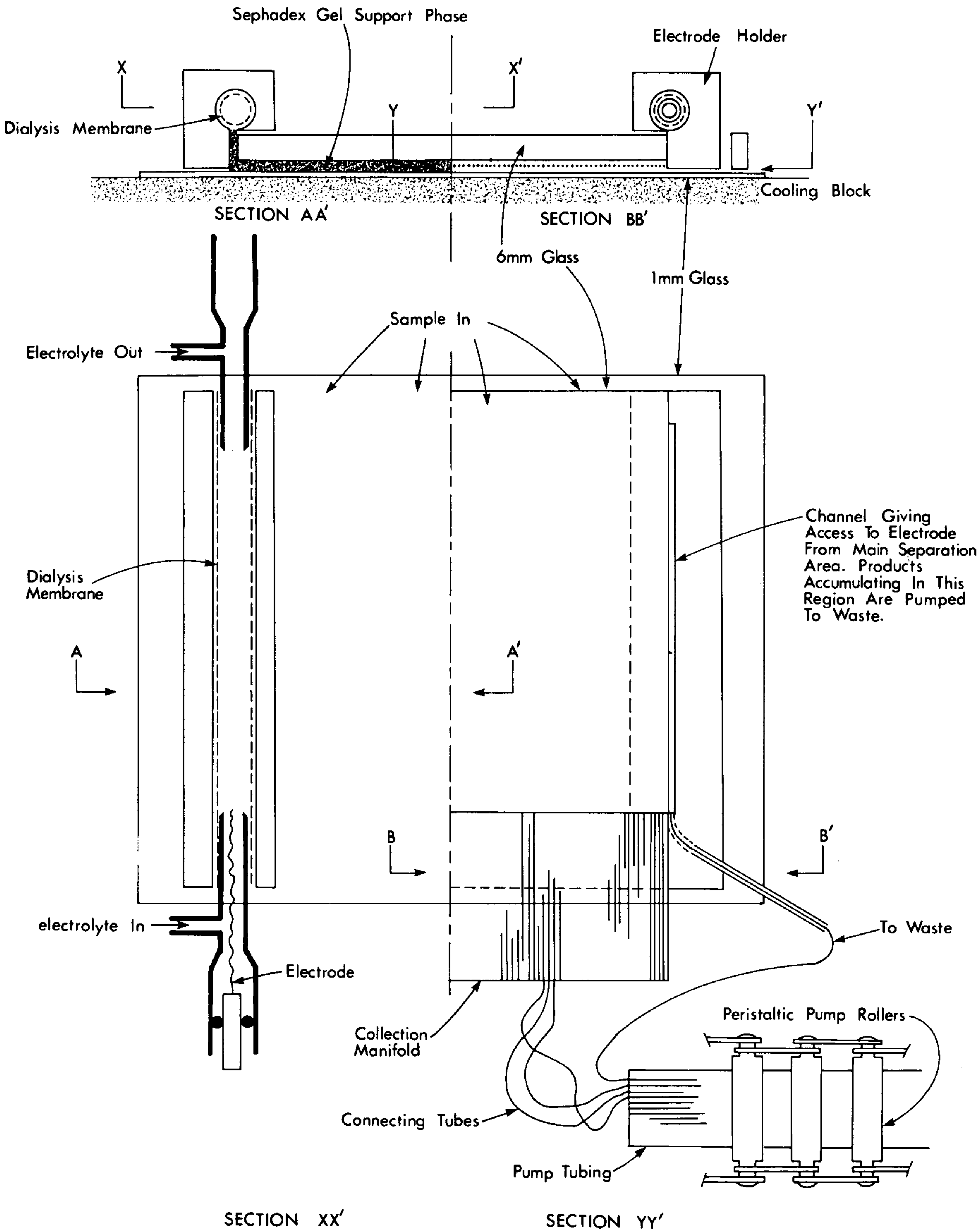


*Figure 62 Continuous-flow separation cell.*

One of these areas is concerned with the behaviour of radionuclides in a salt marsh. The salt marsh chosen for this study is situated on the north side of the estuary of the river Esk in west Cumbria, about 11 km from the Windscale nuclear processing plant. A sampling grid was established on the marsh and the nature and density of the vegetation were recorded. A total gamma count was made on samples of vegetation, and also on samples taken at 2 depths in the top 10 cm of sediment.

The highest counts occurred amongst sea purslane *Halimione portulacoides*, a straggly plant with many branches, whereas the lowest were in the grassy vegetation above the high tidemark. At least half the radioactivity in the vegetation occurred as superficial contamination which could be removed by brief washing in water. Bare sediments, especially above the high tidemark, were generally low in gamma activity.

The other research area which received attention during the year dealt with the temporal and spatial variation of radionuclides in soils. This work was carried out in association with Dr. P.A. Cawse (AERE, Harwell) who had obtained data on plutonium isotopes and caesium–137 in soils collected throughout Great Britain. These data were examined in conjunction with various environmental and soil chemical and physical variables using multiple regression and principal component analysis. Explanation of 80–90% of the variation in radionuclide concentration was achieved in this way. Of particular interest was the difference in the importance of the regressor variables between grassland and woodland, thus emphasising the importance of the input mechanisms. It is hoped to pursue this aspect, and also to examine the relative degree of radionuclide retention and movement in soil profiles.

*K.L. Bocock and A.D. Horrill*

*Engineering developments*

Work on ageing amenity trees (ITE 463) involved the laborious and time-consuming measurement of annual rings in numerous tree sections and cores to a high degree of accuracy, and a method of automating the procedure was sought. An instrument was produced consisting of a stage, to which the specimen is fixed, capable of being driven by a precision screw under the field of view of a fixed binocular microscope. A high degree of precision/accuracy and readability was built into the mechanical structure. To convert the number of turns of the driving screw into a digital read-out of distance, an opto-electronic transducer together with the necessary decoding logic and display circuitry has been designed and constructed. Measurements can be made in either a total or incremental mode by switch selection. The measuring electronics also drive a paper tape punch interface, which, together with the generation of the appropriate control functions, gives a punched tape output suitable for computer processing. It would be relatively easy to adapt this instrument to other types of work where accurate linear measurement is required.

A microprocessor-based lighting control system was installed at Monks Wood to regulate the lighting in 10 experimental rooms used for bird activity experiments. The design of the bird activity and data recording unit was modified during the year to incorporate a room light failure and dawn/dusk recording system. Modifications have also been made to the activity perches and feeder units used in these experimental rooms.

The following selection of development projects undertaken by the engineering staff during the year illustrate the range of tasks.

1. Stream monitor. A self-contained instrument was required for measuring directly several water parameters in small mountain streams so the detachable sensing probes had to be small. The probes were connected to a recording instrument by 8 m of cable which enabled continuous monitoring to be carried out. The instrument gave direct temperature compensated readings of both oxygen saturation and conductivity, and employed novel circuit design. The liquid crystal digital display provided good resolution and readability for outdoor use.

2. Signal isolating module. Extensive modifications were carried out to limnological monitoring equipment in order to overcome problems associated with signal interaction between transducers. The analogue signal from one of the transducers was electrically isolated from the unit by means of an analogue opto-coupler.

3. Salinity meter. A meter was constructed to meet a requirement for a small field instrument to give a direct reading of water salinity in salt marshes and estuarine brackish water. Temperature and water conductivity measures were also available on the digital display. The sensing probe was of rugged design, unaffected by corrosion or fouling by organic deposits or detritus.

4. Radio location and telemetry transmitters. Development work is being carried out on a radio tracking transmitter of good reliability which can be used in badger and red deer studies. A range of up to 6 miles line-of-sight, long operational life and suitability for use with motion or activity sensors is specified.

5. Hormone extraction columns. A system has been developed for mounting a series of 10 tubes used for extraction and which allows each to be individually connected to a low pressure air manifold. Each tube can be released without general loss of air pressure in order to aid eluting the medium as the extraction proceeds. The application of low pressure air to the upper ends of the tightly packed tubes speeds up the process.

6. Automatic weather stations. Two Epsylon automated weather stations, one at low elevation and one at about 500 m, are currently maintained at 2 sites on Snowdon. It is hoped shortly to commission a new station at 1 000 m. To overcome difficulties caused by battery failure, a wind generator has now been fitted at the 500 m site, and one is planned for the 1 000 m site. Trickle chargers have been prepared so that the batteries can be maintained close to full charge.

*G. H. Owen, D. G. Benham, G. B. Elphinstone, G. Hughes, J. Morris, C. R. Rafarel and V. W. Snapes*

## Culture Centre of Algae and Protozoa

*General review*

The demand for cultures has remained fairly steady over the last 4 years . About 15% go overseas to over 30 different countries (Tables 37 and 38). Unless collected by hand, cultures are dispatched by first-class mail or airmail as appropriate. Postal delays are an increasing source of anxiety, especially for some overseas destinations, and more customers are choosing to pay for the more expensive air freight method.

*Table 37.*

| | 1979 | 1978 | 1977 | 1976 |
|---|---|---|---|---|
| Number of Orders | 990 | 981 | 1090 | 962 |
| Cultures | | | | |
| *United Kingdom* | | | | |
| Academic | 3221 | 3502 | 3214 | 2925 |
| Government and Public Services | 199 | 147 | 73 | 138 |
| Commercial | 128 | 113 | 113 | 77 |
| *Overseas* | | | | |
| EEC | 298 | 463 | 197 | 200 |
| Others | 372 | 426 | 476 | 323 |
| Total | 4218 | 4651 | 4073 | 3663 |

*Table 38.*

| COUNTRIES ORDERING CULTURES DURING 1979 | | |
|---|---|---|
| Australia | Hong Kong | Papua-New Guinea |
| Austria | Hungary | Rhodesia |
| Belgium | Ireland | Singapore |
| Canada | Israel | South Africa |
| China | Iraq | Spain |
| Czechoslovakia | Italy | Sri Lanka |
| Denmark | Japan | Sweden |
| Fiji | Kuwait | Switzerland |
| France | Mexico | Tahiti |
| Germany W | New Zealand | Turkey |
| Holland | Norway | USA |

Several new isolations of amoebae have been added to the Collection during the year. Most have been from marine or brackish habitats, and have included types of 2 newly described genera. Among other acquisitions were several strains of the ciliates *Euplotes* and *Tetrahymena*.

Taxonomic research, aided by electron microscopy, has been pursued in several groups, including the amoebae, Chrysophyceae and diatoms. In conjunction with a French worker, a new genus of amoeboid marine chrysophytes was described. It is remarkable in several respects, chiefly perhaps in the zoospores having only a single detectable flagellum: this feature is interpreted as being the end of a well-known series of organisms ranging from having 2 flagella of more or less equal length, to having only a vestige of the second flagellum.

Work has also continued on the phytoplankton of rivers, resulting in the publication *An illustrated guide to river phytoplankton*, a companion volume to the highly successful *A beginner's guide to freshwater algae*. It is confidently hoped that these 2 works will provide a stimulus to teaching and an aid to workers in the water industry.

Requests for information and advice are a continuing feature and will shortly benefit from a computer-aided information system which is being set up to include both biological and bibliographic data.

*E. A. George*

*Lipids, membranes and freezing*

At CCAP, many cultures of algae are stored under liquid nitrogen with a recovery upon thawing greater than 60% (Plate 20). At this temperature (−196°C), cell survival appears to be independent of the period of storage and biological systems are genetically stable. However, with some species of algae, the survival upon thawing is consistently very low (less than 1%), and no significant improvement is obtained using conventional techniques. There is no generally accepted theory of the mechanism of freezing injury to cellular systems so cryobiological experimentation must be of an empirical nature. It is important, therefore, to understand the biochemistry of cellular freezing injury. Such an understanding helps to evolve specific methods of cryopreservation, but it may also have wider implications. For example, if it were possible to increase the frost hardiness of crop plants, this increase would be of major economic importance as a 2°C increase in the frost hardiness of wheat could extend production to new areas with a potential increase in world wheat production of between 25 and 40%.

The unicellular algae *Chlamydomonas reinhardii* is extremely sensitive to the stresses of freezing and thawing, and is therefore a useful organism for investigating the mechanism of injury. Upon warming from a lethally low temperature, a leakage of intracellular enzymes was observed. Alterations to the selective permeability of the cellular membrane are an early feature of freezing injury. Biochemical analysis of the membrane lipids following freezing and thawing (in collaboration with Dr. A. Clarke, British Antarctic Survey) indicates changes which are consistent with the intracellular activation of phospholipases. However, it became evident that alterations to the membrane lipid composition are a consequence, rather than a specific cause, of cell death. Ultrastructual studies were also of little help as the damage to cells upon thawing was extensive and it was not possible to distinguish between a primary cause and subsequent pathological events. From these studies, it became apparent that the organisation of whole cells was too complex to investigate freezing injury and that a simpler model system was required.

Liposomes (artificial, lipid bilayer vesicles) have been used extensively to examine the structure and function of biological membranes. The response of liposomes to freezing and thawing has, therefore, been investigated. Liposomes have many advantages in cryobiological research as their composition can be easily and reproducibly altered and the effects of these alterations on the biophysics of the bilayer are well understood. Liposomes entrap solutions and the integrity of the bilayer can be assessed by measuring the leakage of entrapped solutes—a principle which is often used to determine the viability of plant material upon thawing. No lytic enzymes are present and pathological events are therefore avoided.

Preliminary studies indicate that, during the freezing and thawing of liposomes, much of the behaviour of intact cells was simulated. Liposomes thus appear to be a valid model system for investigating freezing injury. The composition of the bilayer is critical in determining the response to freezing and thawing. In liposomes composed of one phospholipid and cholesterol, there is a direct correlation between the concentration of cholesterol in the membrane and its sensitivity to stresses of freezing and thawing. This is the first demonstration that the composition of a membrane directly determines freeze-thaw injury. Liposomes were prepared from whole cell lipid extracts of several cell types, and, following freezing and thawing, it was found that the responses of liposomes were different from that of the cells from which they were derived. During extraction and resulting homogenisation of the lipid, the initial cellular response to freezing is lost. It is probable that it is the lipid composition of the membrane at a critical micro-environment that determines the cellular response. These results question the experimental approach of analysing whole cell lipid extracts after different treatments which affect the cellular freezing tolerance, i.e. cold hardening. Finally, evidence of the loss of membrane components during freezing and thawing was obtained. Phospholipids are lost preferentially to cholesterol, and, what is more important, the membrane consequently becomes enriched with respect to cholesterol.

From these early studies, liposomes appear to be a useful model system for determining the biochemistry of freezing injury. Further work should elucidate the primary site of injury, and enable specific methods of overcoming this membrane lesion to be developed. This experimental approach may then be applicable to the protection of sensitive cell types.

*G. J. Morris*

*Diatoms of inland saline habitats*

Certain inland water bodies with an abnormally high concentration of dissolved salts are often referred to as 'saline', though this term can be misleading, as the proportions of ions present may differ considerably from those in sea water. We have been looking at the diatom flora of some sites of this type.

Near Cambridge, high levels of sodium and chloride ions in some ditches appear to be derived from the droppings of water birds, and the run-off pools and channels associated with recently constructed trunk roads are high in dissolved salts, chiefly of calcium, leached from the unweathered chalky boulder clay used in the embankments. Salt from winter gritting operations puts up the ionic level still further in these habitats which, with the ditches, support a diatom flora containing species usually only found in brackish areas near the sea.

Material, collected by Dr. G. Fryer of the Freshwater Biological Association, was also examined from a series of lagoons near Castleford, Yorkshire, in which the dissolved salts are derived from nearby industrial tips. These pools are noteworthy for their brackish-water crustaceans and rotifers, and the diatoms present also contain a proportion of species usually found under brackish conditions. These habitats can be compared with the Thames at Teddington near the upper limit of tidal influence, where characteristic brackish-water diatoms live, often in considerable numbers, in river water containing only a small percentage of sea water.

Attempts to grow some of these brackish water diatoms in culture have been successful, and have also shown that a number of species characteristic of eutrophic (i.e. enriched) water grow much better when 10-25% of sea water is added to the medium. Sea water added to mixed cultures starting from wild material seems both to encourage the diatoms and discourage algae of other systematic groups.

*J. Hilary Belcher and Erica M. F. Swale*

# Projects

**listed by Subdivisions as at 9th January 1980**

*Station code*

1 Monks Wood
2 Merlewood
3 C/o University of East Anglia, Norwich
4 Furzebrook
5 Edinburgh, Bush
6 Edinburgh, Craighall Road
7 Banchory, Brathens
8 Banchory, Blackhall
9 Bangor
10 Biometrics, Cambridge
11 CCAP, Cambridge

*Project status*

@ NCC contract
\+ DOE contract
£ Other contract
! PhD or other student project

VERTEBRATE ECOLOGY SUBDIVISION

| | | | *code* |
|---|---|---|---|
| 54 | Red deer ecology on Rhum | V.P.W. Lowe | 2 |
| 59 | Taxonomy of the red squirrel | V.P.W. Lowe | 2 |
| 67 | Prey selection in redshank | J.D. Goss-Custard | 4 |
| 68 | Dispersion in waders | J.D. Goss-Custard | 4 |
| 104 | Distribution and segregation of red deer | B.W. Staines | 7 |
| 106 | Red deer food studies | B.W. Staines | 7 |
| 109 | Annual cycles in Scottish red deer | B. Mitchell | 7 |
| 111 | Population dynamics of red deer at Glen Feshie | B. Mitchell | 7 |
| 116 | Freshwater survey of Shetland | P.S. Maitland | 6 |
| 117@ | Freshwater survey of Great Britain | P.S. Maitland | 6 |
| 123 | Zoobenthos at Loch Leven | P.S. Maitland | 6 |
| 124 | Distribution & biology of fish in Great Britain | P.S. Maitland | 6 |
| 136 | Hen harrier study in Orkney | N. Picozzi | 8 |
| 138@ | Puffin research | M.P. Harris | 7 |
| 159 | Upland bird project | D.C. Seel | 9 |
| 209@ | Vertebrate recording schemes | H. Arnold | 1 |
| 291@ | Population ecology of bats | R.E. Stebbings | 1 |
| 292@ | Specialist advice on bats | R.E. Stebbings | 1 |
| 322 | Dispersal of otters | D. Jenkins | 7 |
| 363 | Dispersion of field voles in Scotland | N. Charles | 6 |
| 386 | Behaviour and dispersion of badgers | H. Kruuk | 7 |
| 391 | British mammals—the red fox | V.P.W. Lowe | 2 |
| 439 | Red deer on the Isle of Scarba | B. Mitchell | 7 |
| 441 | Oystercatcher & shellfish interaction | J.D. Goss-Custard | 4 |
| 442 | Ecology of capercaillie | R. Moss | 8 |
| 460 | Interaction of gulls and puffins | M.P. Harris | 7 |
| 461@ | Puffins and pollutants | M.P. Harris | 7 |
| 479 | Red deer in production forests | B.W. Staines | 7 |
| 498! | Wildcat studies | L.C. Corbett | 7 |
| 499 | Classification of Cervidae | V.P.W. Lowe | 2 |
| 524 | Fluoride in predatory mammals | K.C. Walton | 9 |
| 525 | Fluoride in predatory birds | D.C. Seel | 9 |
| 528 | Red deer in woodland habitats | B. Mitchell | 7 |
| 543! | Population ecology of the red squirrel | V.P.W. Lowe | 2 |
| 546£ | Impact of Craigroyston scheme on Loch Lomond | P.S. Maitland | 6 |
| 606 | Grey squirrel damage & management | R.E. Kenward | 1 |
| 619 | Small rodents in Sitka spruce plantations | A.G. Thompson | 9 |
| 636 | Song bird density & woodland diversity | D. Jenkins | 7 |
| 638 | Monitoring otters at Dinnet | D. Jenkins | 7 |
| 675£ | Protection against carnivores in N. Kenya | H. Kruuk | 2 |
| 676 | Ecology of lampreys in Loch Lomond | P.S. Maitland | 6 |

INVERTEBRATE ECOLOGY SUBDIVISION

| | | | *code* |
|---|---|---|---|
| 65 | Invertebrate population studies | S. McGrorty | 4 |
| 185 | Effect of urbanisation | B.N.K. Davis | 1 |
| 188 | Woodland invertebrates | R.C. Welch | 1 |
| 202 | The Roman snail | E. Pollard | 1 |
| 204@ | Assessing butterfly abundance | E. Pollard | 1 |
| 211@ | Lepidoptera distribution maps scheme | J. Heath | 1 |
| 223 | European invertebrate survey | J. Heath | 1 |
| 229 | Ecology/taxonomy of Spanish Hemiptera | M.G. Morris | 4 |
| 230 | Cutting experiment (Coleoptera) | M.G. Morris | 4 |
| 231 | Barton Hills grazing experiment (Coleoptera) | M.G. Morris | 4 |
| 232 | Butterfly studies at Porton Range | M.G. Morris | 4 |

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|---|---|---|---|
| 233 | Cutting experiment (Hemiptera) | M.G. Morris | 4 |
| 234 | Grassland management by fire | M.G. Morris | 4 |
| 236 | Invertebrate populations in grass sward | E. Duffey | 1 |
| 241 | The fauna of box | L.K. Ward | 1 |
| 243 | Scrub succession at Aston Rowant NNR | L.K. Ward | 1 |
| 255 | Ecology of Myrmica species | G.W. Elmes | 4 |
| 256 | Protein electrophoresis | B. Pearson | 4 |
| 262 | Digestive enzymes | A. Abbott | 4 |
| 270 | Distributional studies on spiders | P. Merrett | 4 |
| 273 | Productivity of S. Magnus | N.R. Webb | 4 |
| 274 | Physiology of soil fauna | N.R. Webb | 4 |
| 295 | Survey of juniper in N. England | L.K. Ward | 1 |
| 296 | Scrub management at Castor Hanglands | L.K. Ward | 1 |
| 309 | Phytophagous insect data bank | L.K. Ward | 1 |
| 345 | Spiders in East Anglian fens | E. Duffey | 1 |
| 400 | The large blue butterfly | J.A. Thomas | 4 |
| 403 | The black hairstreak butterfly | J.A. Thomas | 4 |
| 404 | The brown hairstreak butterfly | J.A. Thomas | 4 |
| 405 | Fauna of pasture woodlands | P.T. Harding | 1 |
| 406 | Non-marine Isopoda | P.T. Harding | 1 |
| 407 | British Staphylinidae (Coleoptera) | R.C. Welch | 1 |
| 414 | Hartland Moor spider survey | P. Merrett | 4 |
| 437£ | Further ecological studies on the Wash | S. McGrorty | 4 |
| 450 | Ecology of pseudo-scorpions | P.E. Jones | 1 |
| 469 | Scottish invertebrate survey | E. Duffey | 1 |
| 470 | Upland invertebrates | A. Buse | 9 |
| 474 | Breckland open ground fauna | E. Duffey | 1 |
| 500 | Recolonisation by spiders on Hartland Moor | P. Merrett | 4 |
| 509! | Wood white butterfly population ecology | M. Warren | 1 |
| 519 | Myrmica sabuleti and M. scabrinodis | G.W. Elmes | 4 |
| 527 | Long-term changes in zooplankton | D. H. Jones | 6 |
| 547 | Study of the genus Micropteryx | J. Heath | 1 |
| 557@ | Terrestrial & freshwater invertebrate surveys | P.T. Harding | 1 |
| 568 | Subcortical fauna in oak | M.G. Yates | 4 |
| 569 | Insect fauna of Helianthemum & Genista | B.N.K. Davis | 1 |
| 570 | Studies on fritillary butterflies | E. Pollard | 1 |
| 572 | Aldabra management plan | M.G. Morris | 4 |
| 577 | Predation of freshwater zooplankton | D.H. Jones | 6 |
| 592 | Spatial organisation of Zooplankton populations | (Suspended) | |
| 615@ | Fragmentation of heaths & invertebrates | N.R. Webb | 4 |
| 641 | Invertebrate fauna of Nothofagus & Quercus | R.C. Welch | 1 |
| 644 | Breeding success & survival in Anura | C.J. Reading | 4 |
| 656@ | Marine invertebrate recording schemes | H. Arnold | 1 |
| 657 | Biological Records Centre—general | J. Heath | 1 |
| 660 | Simultaneous butterfly population studies | J.A. Thomas | 4 |

ANIMAL FUNCTION SUBDIVISION

| | | | *code* |
|---|---|---|---|
| 137 | Sparrowhawk ecology | I. Newton | 1 |
| 178 | Causes of seabird incidents | I. Newton | 1 |
| 181@ | Birds of prey and pollution | A.A. Bell | 1 |
| 182 | Aquatic herbicides | H.R.A. Scorgie | 1 |
| 193 | Stone curlew and lapwing | N.J. Westwood | 1 |
| 199 | Avian reproduction and pollutants | S. Dobson | 1 |
| 289 | Pollutants in freshwater organisms | F. Moriarty | 1 |
| 325 | Carrion-feeding birds in Wales | I. Newton | 1 |
| 413 | Breeding biology of the cuckoo | I. Wyllie | 1 |
| 444 | Endocrine lesions in birds | S. Dobson | 1 |
| 455 | Heavy metals in avian species | D. Osborn | 1 |
| 473 | Metal residues in birds of prey | A.A. Bell | 1 |
| 559 | Ecophysiology of the rabbit | D.T. Davies | 1 |

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|---|---|---|---|
| 590 | Pollutants and the grey heron | J.W.H. Conroy | 1 |
| 630 | Stress in birds | A. Dawson | 1 |
| 655+ | Biological health monitoring | F. Moriarty | 1 |

| GROUSE AND MOORLAND ECOLOGY | | | code |
|---|---|---|---|
| 129 | Red grouse and ptarmigan populations | A. Watson | 8 |
| 130 | Management of grouse and moorlands | A. Watson | 8 |
| 131 | Golden plover populations | A. Watson | 8 |
| 132 | Monitoring in the Cairngorms | A. Watson | 8 |

| HEATHLAND SOCIAL INSECTS | | | code |
|---|---|---|---|
| 252 | Hartland Moor NNR survey | M.V. Brian | 4 |
| 253 | Tetramorium caespitum populations | M.V. Brian | 4 |
| 258 | Degree of control by queen ants | M.V. Brian | 4 |
| 259 | Larvae and worker communication | M.V. Brian | 4 |
| 263 | Worker ant activity | M.V. Brian | 4 |
| 370 | Inter-species competition in ants | M.V. Brian | 4 |
| 371 | Male production in Myrmica | M.V. Brian | 4 |
| 578 | Modelling an ant population | M.V. Brian | 4 |

| PLANT BIOLOGY SUBDIVISION | | | code |
|---|---|---|---|
| 2 | Meteorological factors in classification | E.J. White | 5 |
| 73 | Puccinellia maritima | A.J. Gray | 4 |
| 82 | Seed produced by montane plants | G.R. Miller | 7 |
| 102 | Mountain vegetation populations | N.G. Bayfield | 7 |
| 158 | Community processes (physiology) | D.F. Perkins | 9 |
| 160 | Fluorine pollution studies | D.F. Perkins | 9 |
| 208@ | Botanical data bank | | 1 |
| 246 | Physical environment, forest structure | E.D. Ford | 5 |
| 247 | Physiology of flowering | K.A. Longman | 5 |
| 248£ | Physiology of tropical tree improvement | K.A. Longman | 5 |
| 249 | Morpho-physiological differences | M.G.R. Cannell | 5 |
| 265 | Regeneration on lowland heaths | S.B. Chapman | 4 |
| 266 | Root dynamics of Calluna vulgaris | S.B. Chapman | 4 |
| 269 | Autecology of Gentiana pneumonanthe | S.B. Chapman | 4 |
| 329 | Response of Scots pine | E.J. White | 5 |
| 346 | Genecology of grass species | A.J. Gray | 4 |
| 359 | Fibre yield of poplar coppice | M.G.R. Cannell | 5 |
| 410 | Tundra plants (bryophytes) | T.V. Callaghan | 2 |
| 411 | Taxonomy of bryophytes | S.W. Greene | 5 |
| 451 | Analysis of S. Georgian graminoids | T.V. Callaghan | 2 |
| 507 | Ecologists' flora | E.M. Field | 5 |
| 552£ | Carbon as a renewable resource | T.V. Callaghan | 2 |
| 575 | Regeneration & growth of bracken rhizomes | R.E. Daniels | 4 |
| 576 | Genecological variation in Sphagnum | R.E. Daniels | 4 |
| 583+ | Scots pine leaves in polluted atmospheres | D. Fowler | 5 |
| 600£ | Conway submerged tunnel | A.J. Gray | 4 |
| 640£ | Field studies on natural vegetation | T.V. Callaghan | 2 |
| 643£ | Mapping primary production in Devon & Cornwall | T.V. Callaghan | 2 |
| 648£ | Highcliffe stabilization trials | A.J. Gray | 4 |
| 649 | Demographic genetics of Agrostis setacea | A.J. Gray | 4 |

| PLANT COMMUNITY ECOLOGY SUBDIVISION | | | code |
|---|---|---|---|
| 1 | Semi-natural woodland classification | R.G.H. Bunce | 2 |
| 9 | Monitoring at Stonechest | J.M. Sykes | 2 |
| 14 | Tree girth changes in 5 NNR's | A.D. Horrill | 2 |
| 75 | Control of Spartina | D.G. Hewett | 9 |
| 77 | Cliff vegetation methods | D.G. Hewett | 9 |

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|---|---|---|---|
| 78 | Management of sand dunes in Wales | D.G. Hewett | 9 |
| 92 | Grazing intensities causing change | D. Welch | 7 |
| 93 | Assessing animal usage in N.E. Scotland | D. Welch | 7 |
| 95 | Importance of dung for botany change | D. Welch | 7 |
| 120 | Phytoplankton grazing & sedimentation | A.E. Bailey-Watts | 6 |
| 163 | Ordination and classification methods | M.O. Hill | 9 |
| 165 | N. Wales bryophyte recording | M.O. Hill | 9 |
| 225 | Population studies on orchids | T.C.E. Wells | 1 |
| 227 | Sheep grazing on chalk grass flora | T.C.E. Wells | 1 |
| 228 | Effect of cutting on chalk grassland | T.C.E. Wells | 1 |
| 242@ | Establishment of herb-rich swards | T.C.E. Wells | 1 |
| 318 | Peat hydrology | | 1 |
| 340 | Survey of Scottish coasts | D.S. Ranwell | 3 |
| 360£ | Trees on industrial spoil | J.E. Good | 9 |
| 367 | The Gisburn experiment | A.H.F. Brown | 2 |
| 374 | Sand dune ecology in East Anglia | L.A. Boorman | 1 |
| 377 | Environmental perception studies | J. Sheail | 1 |
| 380+ | Monitoring of atmospheric $SO_2$ | I.A. Nicholson | 7 |
| 381 | Plankton populations in Loch Leven | (Suspended) | 6 |
| 388 | Rusland Moss NNR survey | J.M. Sykes | 2 |
| 389 | Management effect in lowland coppices | A.H.F. Brown | 2 |
| 417 | Silvicultural systems—N. Ireland experiment | A.H.F. Brown | 2 |
| 424 | Ecological survey of Britain | R.G.H. Bunce | 2 |
| 426 | Modelling of sulphur pollution | I.A. Nicholson | 7 |
| 452+ | Foliar leaching and acid rain | J.W. Kinnaird | 7 |
| 453 | $SO_2$ dry deposition in Scots pine forest | I.A. Nicholson | 7 |
| 454@ | NCC monitoring of woodlands | J.M. Sykes | 2 |
| 463 | Age class of amenity trees | J.E. Good | 9 |
| 466@ | Ecology of railway land | C.M. Sargent | 1 |
| 467 | Roadside experiments | C.M. Sargent | 1 |
| 483 | Scottish deciduous woodlands | R.G.H. Bunce | 2 |
| 539 | Phragmites 'dieback'—Norfolk Broads | L.A. Boorman | 1 |
| 549@ | Monitoring in native pinewoods | J.M. Sykes | 2 |
| 573+ | Amenity grass—stage 2 | | 1 |
| 599@ | Bracken & scrub control on lowland heaths | R.H. Marrs | 1 |
| 602 | Modelling sports turf wear | T.W. Parr | 1 |
| 626£ | Welsh wetlands survey | D.F. Evans | 9 |
| 628! | Colonisation of limestone quarries | D. Park | 1 |
| 633 | Water level & vegetation change—Kirkconnell Flow | J.M. Sykes | 2 |
| 634 | Field plot survey—Monks Wood | | 1 |
| 637 | Word processing | N.J. Pearce | 2 |
| 650 | Amenity grass irrigation | | 1 |
| 665 | Coastal management | D.S. Ranwell | 3 |
| 666 | Coastal publications | D.S. Ranwell | 3 |

SOIL SCIENCE SUBDIVISION

| | | | *code* |
|---|---|---|---|
| 4 | Soil classification methods | P.J.A. Howard | 2 |
| 8 | Radiocarbon analysis of wood humus | A.F. Harrison | 2 |
| 17 | Meathop Wood IBP study | J.E. Satchell | 2 |
| 21 | Decomposition in Meathop Wood | O.W. Heal | 2 |
| 22 | Fungal decomposition of leaf litter | J.C. Frankland | 2 |
| 29 | Phosphorus circulation | A.F. Harrison | 2 |
| 30 | Biomass and decay of Mycena in Meathop Wood | J.C. Frankland | 2 |
| 39 | Phosphorus turnover in soils | A.F. Harrison | 2 |
| 45 | Tundra biome IBP study | O.W. Heal | 2 |
| 61 | Variation in growth of birch and sycamore | A.F. Harrison | 2 |
| 87 | Vegetation potential of upland sites | J. Miles | 7 |
| 88 | Plant establishment in shrubs | J. Miles | 7 |
| 89 | Calluna-Molinia-Trichophorum management | J. Miles | 7 |
| 90 | Birch on moorland soil and vegetation | J. Miles | 7 |

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|---|---|---|---|
| 140 | Weathering and soil formation, Whin Sill | M. Hornung | 9 |
| 148 | Soil erosion on Farne Islands | M. Hornung | 9 |
| 153 | Mineralogical methods | A. Hatton | 9 |
| 154 | Field recording of profile data | M. Hornung | 9 |
| 245 | Genetics of Betula nutrition | J. Pelham | 5 |
| 358 | Earthworm production in organic waste | J.E. Satchell | 2 |
| 364 | Early growth of trees | A.F. Harrison | 2 |
| 384 | Benthic microalgal populations | | 2 |
| 398 | Upland land use | O.W. Heal | 2 |
| 431 | Soil change through afforestation | P.J.A. Howard | 2 |
| 432 | Effect of birch litter on earthworms | J.E. Satchell | 2 |
| 438 | Ecology of Mycena galopus | J.C. Frankland | 2 |
| 471 | Soils of Upper Teesdale | M. Hornung | 9 |
| 521 | Mathematical modelling in Cumbria | O.W. Heal | 2 |
| 522+ | Ecology of vegetation change in uplands | D.F. Ball | 9 |
| 533 | Podzolic soils | P.A. Stevens | 9 |
| 534 | National land characterisation | D.F. Ball | 9 |
| 541 | Marginal land in Cumbria | C.B. Benefield | 2 |
| 551* | Overseas liaison activities | J.E. Satchell | 2 |
| 554 | Cumbria land classes and soil types | J.K. Adamson | 2 |
| 558! | Fauna/mycoflora relationships | K. Newell | 2 |
| 561 | Soil fertility | M. Hornung | 9 |
| 589 | Microbial characteristics in soils | P.M. Latter | 2 |
| 594 | Geochemical cycling | M. Hornung | 9 |
| 607 | Woodland soils conservation | D.F. Ball | 9 |
| 639£ | Heather & grass moorland management—Exmoor | O.W. Heal | 2 |
| 654 | Status of mycorrhizas in soil | J. Dighton | 2 |
| 673 | Nutrient transfer efficiency of mycorrhizas | J. Dighton | 2 |

DATA AND INFORMATION SUBDIVISION

| | | | *code* |
|---|---|---|---|
| 216 | Register of NNRs | G.L. Radford | 9 |
| 218@ | Site management information system | G.L. Radford | 9 |
| 302 | Population growth and regulation | M.D. Mountford | 10 |
| 306 | Spatial process and application | P. Rothery | 10 |
| 307 | Index of eggshell thickness | P.H. Cryer | 10 |
| 308 | Data from multi-compartment systems | P.H. Cryer | 10 |
| 365 | Competition between grass species | H.E. Jones | 2 |
| 376 | Statistical training | C. Milner | 9 |
| 402 | Biometrics advice to NERC | M.D. Mountford | 10 |
| 434 | ITE computing services | C. Milner | 9 |
| 457 | Grazing models | C. Milner | 9 |
| 494 | Computing facilities at Craighall Road | I.R. Smith | 6 |
| 496 | Data processing services at Monks Wood | | 1 |
| 512 | National collection of birch | A.S. Gardiner | 2 |
| 514 | British birch publication | A.S. Gardiner | 2 |
| 529 | Biological data bank | | 1 |
| 530 | Laser scan mapping system | | 1 |
| 531 | Statistical & computing advice, Furzebrook | R.T. Clarke | 4 |
| 548 | Leaf-shape analysis of European birch | A.S. Gardiner | 2 |
| 556 | Estimation in acid rain | K.H. Lakhani | 1 |
| 564 | British Hydracarina—mainly of mosses | N. Hamilton | 2 |
| 565 | Bibliography of Shetland | N. Hamilton | 2 |
| 566 | Islands: biogeographic analysis | N. Hamilton | 2 |
| 574 | Potential for fuel cropping in upland Wales | D.I. Thomas | 9 |
| 579 | Woodland research conference | A.S. Gardiner | 2 |
| 591 | Terrestrial Environment Information System | B. Wyatt | 9 |
| 598 | Information retrieval system for Dorset heaths | R.T. Clarke | 4 |
| 603 | Measures of familial similarity | P. Rothery | 10 |
| 609£ | Biological classification of UK rivers | D. Moss | 9 |
| 612@ | Analysis of common birds census | M.D. Mountford | 10 |

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|---|---|---|---|
| 613 | Computerization of ITE/NERC costing procedure | M.D. Mountford | 10 |
| 614 | Numerical classification | M.D. Mountford | 10 |
| 621 | Models of rabies epidemiology | P.J. Bacon | 2 |
| 622 | Applications of systems analysis | P.J. Bacon | 2 |
| 623 | Entity, attribute, relationship of data bases | P.J. Bacon | 2 |
| 624 | Population genetics | P.J. Bacon | 2 |
| 642 | Physics of freshwater systems | I.R. Smith | 6 |
| 645 | Effects of soil chemistry on decomposition | D.D. French | 7 |
| 646 | Statistical consultancy service at Bangor | D. Moss | 9 |
| 647 | Dipper territory and population models | D. Moss | 9 |
| 668 | Biometrical consultancy | M.D. Mountford | 10 |
| 670 | Statistical advice & computing at Edinburgh | R.I. Smith | 5 |
| 671 | Analysis of BRC data | G.L. Radford | 9 |
| 672 | Computing facilities at Bangor | G.L. Radford | 9 |

CHEMISTRY AND INSTRUMENTATION SUBDIVISION

| | | | code |
|---|---|---|---|
| 23 | Soil temperature in Meathop Wood | K.L. Bocock | 2 |
| 52 | Biological studies of Glomeris | K.L. Bocock | 2 |
| 62 | National plant nutrient survey | H.M. Grimshaw | 2 |
| 378 | Chemical data bank | S.E. Allen | 2 |
| 481 | Monitoring pollutants in natural waters | K. Bull | 1 |
| 482 | Chemistry of aquatic pollutants | K. Bull | 1 |
| 484 | Chemical technique development | Parkinson/French | 2 |
| 485 | Chemical support studies | S.E. Allen | 2 |
| 486 | Engineering development | G.H. Owen | 9 |
| 487 | Microprocessor development studies | C.R. Rafarel | 9 |
| 489 | Glasshouse and nursery maintenance | R.F. Ottley | 5 |
| 490 | Photographic development | P.G. Ainsworth | 1 |
| 491 | Radiochemistry | A.R. Byrne | 2 |
| 553+ | Radionuclide contamination of ecosystems | K.L. Bocock | 2 |
| 667£ | Transfer pathways of radio-iodine in environment | S.E. Allen | 2 |

CULTURE CENTRE OF ALGAE AND PROTOZOA

| | | | code |
|---|---|---|---|
| 445 | Marine flagellates taxonomy | J.H. Belcher | 11 |
| 446 | Freshwater flagellates taxonomy | D.J. Hibberd | 11 |
| 447 | Freshwater and marine amoebae | F.C. Page | 11 |
| 448 | Colourless flagellates taxonomy | E.M.F. Swale | 11 |
| 449 | Preservation of cultures | G.J. Morris | 11 |
| 610 | Computerization of CCAP records | E.A. George | 11 |

DIRECTORATE

| | | | code |
|---|---|---|---|
| 203 | The Cinnabar moth | J.P. Dempster | 1 |
| 393 | Isolation effects in butterfly populations | J.P. Dempster | 1 |
| 408+ | Arboriculture: selection | F.T. Last | 5 |
| 503 | Development of systems analysis | J.N.R. Jeffers | 2 |
| 504 | Markov models | J.N.R. Jeffers | 2 |
| 505 | Ecology of Outer Hebrides | J.N.R. Jeffers | 2 |
| 508 | Botanical variation in elm | J.N.R. Jeffers | 2 |
| 511 | Landscaping at Swindon | F.T. Last | 5 |
| 516 | Forest management for energy | R.C. Steele | 10 |
| 517 | Primary productivity in woodlands | J.N.R. Jeffers | 2 |
| 518£ | UNESCO MAB information system | J.N.R. Jeffers | 2 |
| 526 | Monitoring in Banff and Buchan | F.T. Last | 5 |
| 629£ | Systems analysis of Egyptian deserts | J.N.R. Jeffers | 2 |

# Staff List April 1980

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PS Mrs Waterfall, G.M.

*Institute Secretary*
Prin Mr Ferguson, J.G.

*Administration, Finance and Establishments*
SEO Mr Collins, R.T.
HEO Mr Clapp, E.C.J.
EO Mr Easterbrook, M.J.
CO Miss Barrett, L.M.
CO Miss Hale, K.A.
CO Miss Hunt, R.J.
Aud/t Mrs Chambers, E.M. (PT)
CA Miss Jackson, S.

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PSO Mr Mountford, M.D.
PSO Dr Way, J.M.
SSO Mr Cryer, P.H.
SSO Mr Rothery, P.
SSO Mr Spalding, D.F.

*Publications and Liaison Officer*
PSO Mr Woodman, M.J.

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**University Plain**
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**0603 (Norwich) 56161**

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ASO Mr Storeton-West, R.L.

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**Telex 32416**

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PS Mrs Stocker, B.J.

*Administration*
HEO Mr Abbott, L.F.
CO Mrs Burton, V.J.
CO Mr Cotton, A.E.
CO Mrs Haas, M.B. (PT)
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Charles W.N. North of Scotland Hydro-Electric Board April 79

557 See 211/212/213/557

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Harris M.P. Ministry for Conservation, Victorian State Govt. April 79

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655 POLLUTION AND BIOLOGICAL HEALTH IN GREAT BRITAIN—PRELIMINARY REPORT
Moriarty F. DOE December 79

# Commissioned Research Contracts

**listed by customer organisations for 1979**

COMMISSIONED RESEARCH CONTRACTS UNDERTAKEN DURING 1979

| *Customer* | *Project No* | *Project Title* |
|---|---|---|
| Nature Conservancy Council | 218 | Site management event recording |
| | 117 | Synoptic survey |
| | 454 | Survey methods in woodlands |
| | 549 | Pinewood monitoring |
| | 466 | British Rail land |
| | 242 | Herb rich swards |
| | 204 | Monitoring population changes |
| | 461 | Puffins and pollutants |
| | 138 | Monitoring puffin numbers |
| | 181 (pt) | Birds of prey and pollutants |
| | 291/2 | Bats |
| | 615 | Fragmentation of heaths and invertebrates |
| | 599 | Bracken control on heaths |
| | 208/9/11, 557, 656 | Recording of data—BRC |
| | — | Advice and services |
| | 545 | Lochs Morar and Shiel |
| Department of Environment | 369, 380, 452, 583 | Sulphur pollution |
| | 522 | Ecology of vegetation in upland landscapes |
| | 437 | Ecological study of Wash Borrow Pit |
| | 408 | Arboriculture |
| | 573 | Amenity grasses |
| | 655 | Biological health monitoring review |
| | 553 | Radionuclides in the terrestrial ecosystem |
| | 181 (pt) | Birds of prey analysis |
| | 609 | River communities (joint FBA contract) |
| North Scotland Hydro-Electric Board | 652 | The ecology of Loch Lomond in relation to the Craig Royston pumped storage scheme |
| | 546, 555 | Ecological study of Lochs Lomond and Ness |
| Countryside Commission | 639 | Management of heath and moorland |
| Energy Technology Support Unit | 552 | Natural vegetation as a renewable energy source |
| | 640 | Field studies on natural vegetation |
| Overseas Development Administration | 248 | Tropical hardwoods |
| National Coal Board | 360 | Tree planting project |
| | — | Open cast sites |
| Welsh Office | 160 (pt) | Fluorine pollution |
| National Radiological Protection Board | 667 | Radio-iodine 129 study |
| Travers Morgan/Welsh Office | 600 | Conwy Estuary Tunnel |
| Christchurch Council | 648 | Highcliffe coastal protection |
| Fife/St Andrews<br>Royal Cinque Ports | 665 | Golf course erosion |
| European Economic Community | 369, 380, 452, 583 | Sulphur pollution |
| UNESCO/MAB | 518 | MAB information system |
| Council of Europe for IUCN | 657 | Threatened butterfly species |
| Frankfurt Zoological Society | 627 | Feral dogs in Galapagos |
| Binnie & Partners | 632 | Lima water transfer scheme |

Expected level of income from Commissioned work for the financial year 1979/80

| | £(1,000) |
|---|---|
| Nature Conservancy Council | 290 |
| Department of Environment | 354 |
| Other Government Departments | 82 |
| Other UK Organisations | 65 |
| Overseas Customers and Contracts | 47 |
| | 838 |

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R.T. Collins

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