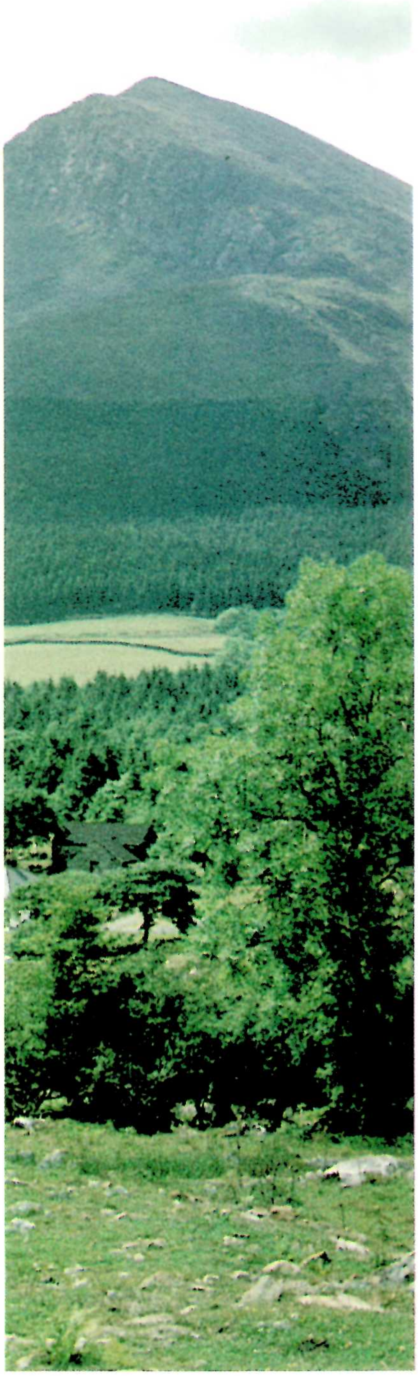
1988 – 1989

REPORT



Institute of
Terrestrial
Ecology
Natural Environment Research Council

Foreword

The Natural Environment Research Council produces an Annual Report summarising the activities across the organisation Such an Annual Report can only provide selected information on the scientific activities of individual Institutes It is therefore important for each Institute to produce its own Report which gives a full account of its research, its structure and its finances

The Institute of Terrestrial Ecology is part of the Terrestrial and Freshwater Sciences Directorate of NERC The Directorate's in-house capability also comprises the Institutes of Freshwater Ecology (formed in April 1989 from the staff and laboratories of the Freshwater Biological Association), Hydrology, and Virology and Environmental Microbiology (formerly the Institute of Virology but renamed in April 1989), the Unit of Comparative Plant Ecology (Sheffield University), the Water Resource Systems Research Unit (Newcastle University) and the Interdisciplinary Research Centre for Population Biology (Imperial College London)

The Institute of Terrestrial Ecology has a wide span of skills and disciplines and forms a core component of the Directorate As noted in the Directors' report, the year has been active and eventful In particular, it has been marked by the retirement of Dr Jack Dempster, its Director (South) I would like to take this opportunity to express my appreciation of his great contribution to the scientific reputation and management of ITE, and to welcome his successor Dr Mike Roberts with all good wishes for his future work with NERC

P B Tinker
Director of Terrestrial and Freshwater Sciences
Natural Environment Research Council

Front Cover Illustration Upland landscape near Beddgelert, North Wales (Photograph Ken Walton, ITE Bangor)

The Natural Environment Research Council

Report of the Institute of Terrestrial Ecology for 1988/89

Contents

Environmental pollution

The programme of research on environmental pollution aims to understand and quantify (i) the input of pollutants to terrestrial ecosystems, (ii) their transfer through ecosystems and foodchains, (iii) the impact of the pollutants on plants and animals, and (iv) methods of ameliorating these impacts.

The following articles illustrate these various threads in current ITE research. Thus, the report on radionuclides focuses on their transfer through upland ecosystems and on research to determine how long the radiocaesium from the Chernobyl fallout will remain available to plant uptake, and possible transfer to grazing animals. The reports on acid mists and pesticides are mainly concerned with the impact of pollutants and with the mechanisms by which the trees, or birds, are affected. The tree work has shown the potential importance of acid mists in forest dieback, while the research on pesticides demonstrates how different pesticides can interact to affect partridges.

ITE research on climatic change and soil protection concerns both causes and impacts. The work on climatic change is planned to expand considerably over the coming years, and will involve both experimental studies and computer modelling. Soil protection concerns the development of guidelines and legislation to reduce the detrimental impacts of man's activities on soils, essential in a crowded island. ITE's involvement in the *Phragmites* work covers the ecology and establishment of the reed beds which provide an ecological method of pollution control.

Acid mist, frost hardiness and the decline of red spruce in the Appalachians

(This work was supported by funds from the United States Department of Agriculture/United States Forest Service)

During the last decade, a decline in the health of fir (*Abies* spp.), spruce (*Picea* spp.), and beech (*Betula* spp.) has been observed in parts of Europe, particularly in West Germany, and in North America. Many hypotheses have been proposed linking these forest problems with air pollution, but no single hypothesis has successfuly withstood experimental tests. As 'forest decline' is used to describe a range of forest problems with different species and in different countries, it seems unlikely that the same agent and mechanism are responsible for all the observed problems.

One species which has shown a marked decline in its native habitat in the last few years is red spruce (*Picea rubens*), in the Appalachians of eastern North America. This species occupies a restricted altitude range (700–1000 m), but is commonly exposed to low cloud at many sites. As a result of the long-range transport of sulphur and nitrogen oxides, the cloudwater contains high sulphate and nitrate concentrations, and has a pH in the range 2.5–4.0.

Staff at ITE Edinburgh have worked in collaboration with the Universities of Nottingham and Lancaster to test the hypothesis that the interception of polluted cloudwater reduces the winter hardiness of red spruce.

Red spruce seedlings grown in clean air were placed in open-top chambers (Plate 16), and were subjected to six acid mist treatments in the pH range 2.5–5.0. This wide range of concentrations for the treatments spans the extreme events observed in the field, but in its mid-range has two treatments (at pH 3.0 and pH 3.5) which approximate the 'average' cloudwater deposited on red spruce in the Appalachians. The acid mist was applied twice each week throughout the summer, and in the frost hardening period (May–December). At intervals during the autumn, shoots were detached from the seedlings in the different treatments and subjected to a simulated night air frost in a programmable freezing cabinet. At each harvest date, a range of freezing temperatures were simulated for different shoots. In this way, the lethal temperature for 50% of the shoots (LT_{50}) was estimated. The techniques used to determine the shoot damage and LT_{50} were based on electrolyte leakage.

Damage estimates using electrolyte leakage

Following freezing, the middle section of shoot was placed in a 20 ml vial with an aliquot of deionised water, and solution conductivities were measured during the following seven days to follow the change in electrolyte concentration. After 14 days, the shoots were scored for visible damage, on a scale 0 = no needles damaged, 1 = <50% needles damaged, 2 = >50% needles damaged, and 3 = shoot brown, assumed dead. Conductivity values were used to derive a normalised leakage rate (k), by fitting the conductivities (c) to the equation:

$$c(t) = c\ (auto) \times (1-e^{-kt})$$

where c(auto) was the conductivity of the autoclaved solutions. The comparison of k values with visible damage showed that

Plate 16 Open-top chambers used for studies of air pollutant effects on trees at ITE Edinburgh

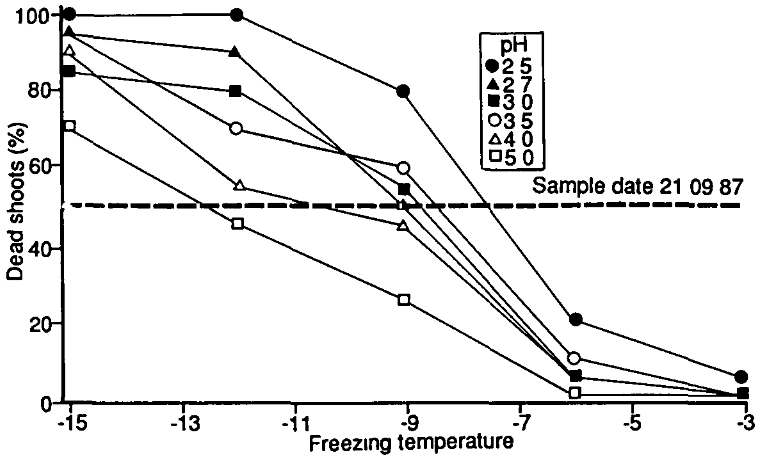


Figure 24 Proportion of red spruce shoots killed in the frost hardiness assessments following exposure to six different acid mist treatments

shoots with values $<0.4\%$ h^{-1} would die, while shoots with values $>0.4\%$ h^{-1} would have little or no damage to their needles. These critical values were used to assess shoots as 'dead' or 'alive'. The percentages of dead shoots for each acid mist treatment were then fitted as a function of temperature, using a probit function to derive an LT_{50} value for each acid treatment, ie the freezing temperature at which half the shoots in the sample population were killed.

The measurements of lower lethal temperatures for the needles allowed the progress of frost hardiness of the seedlings to be followed throughout the autumn.

On 21 September, when the majority of trees had set bud, the lethal temperature for the death of 50% of needles (LT_{50}) was highest (–8°C) in the pH 2.5 treatment and lowest (–13°C) at pH 4.0 (Figure 24), although the only significant difference ($P>0.05$) was between pH 2.5 and the other treatments. By the time of the next assessment, many of the laterals used in the freezing tests from the pH 2.5 and 2.7 treatments bore visibly damaged needles. These needles were not removed on this occasion prior to the measurement of conductivity, and it is likely that their significantly higher leakage rate accounted for the apparent dehardening seen on the 5 October (Figure 25). Between 21 September and 5 October, when night screen temperatures fell below 5°C for the first time and to 2°C or below on two occasions, the shoots from the pH 3.0–5.0 treatments acquired about 5°C more hardiness, but maintained the initial treatment differences. By the third sampling date (19 October), differences in the LT_{50} were quite marked, with shoots from the pH 2.5 treatments having an LT_{50} of –16°C, compared with that of nearly –30°C for the pH 5.0 treatment.

In later tests in November, it became increasingly difficult to estimate the LT_{50} accurately for pH treatments 3.5–5.0. The reason is apparent in Figure 24, which shows the percentage of shoots killed in relation to freezing temperatures for the shoots sampled on 30 November. The freezing cabinet has a capacity to cool down to –39°C and, by the end of November, very few shoots were being irreversibly damaged at –36°C, >30% from the pH 3.0–5.0 treatments.

The results from the frost hardiness testing may be summarised as follows.

1. Frost hardiness increased in all shoots from mid-September, at a rate of about 0.5°C per day, although there was a delay in hardiness in those shoots exposed to the most acid treatments.

2. At any sampling date, the shoots receiving the greatest concentrations of acidity, nitrogen and sulphate were most susceptible to frost injury, with LT_{50} values up to 15°C warmer than for those shoots receiving the smallest concentrations.

3. Although there was not always a significant difference in LT_{50} values between successive levels of acidity, the ranking of the six levels of treatment was reflected in the ranking of the response.

Plants from all treatments were scored for visible injury throughout the experiment, and the results from these measurements are shown in Figure 26.

A clear effect of the acid mist treatment was observed with the LT_{50} between the control and most acidic treatment, differing by as much as 15°C during October. Such differences in field conditions would predispose trees receiving large impacts of polluted cloudwater to autumn frost injury. Although there are difficulties in extrapolating to mature trees in the field,

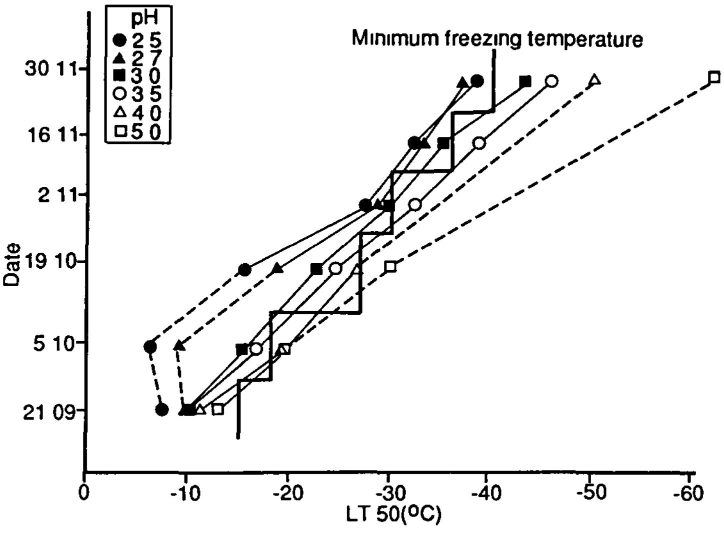


Figure 25 Development of frost hardiness in red spruce exposed to six different acid mist treatments expressed as LT50 for shoot death

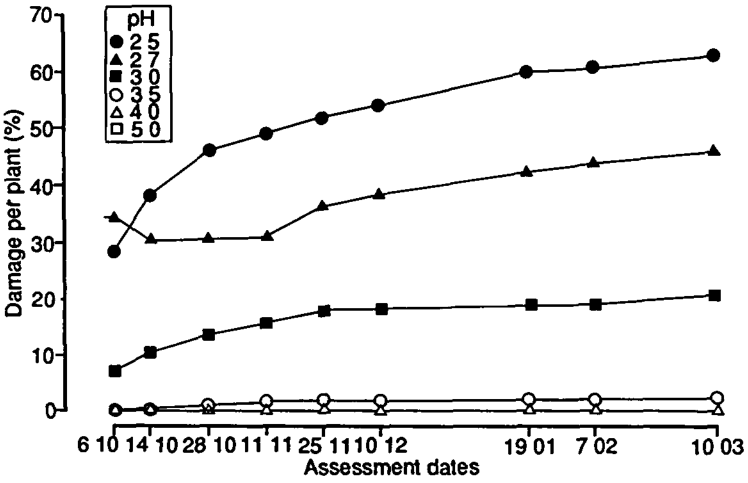


Figure 26 The development of visible injury on acid mist treated red spruce seedlings with time following the first signs of injury on 4 October By 4 October the seedlings had received twice weekly applications of acid mist for 16 weeks

two related studies make such extrapolation simpler In the first study, red spruce shoots were taken from mature trees at two high-elevation sites in the Appalachians and shipped by air to the ITE laboratory for frost hardiness tests These samples showed a pattern of frost hardening and absolute levels of hardiness similar to young plants from the open-top chamber experiments The second study of the meteorology and air chemistry of high-elevation 'red spruce' sites by the University of Nottingham formed part of the ITE collaborative project Rates of deposition of the major ions were established at mountain sites, and were shown to be within the range of the pH 3 0 and 3 5 treatments in the open-top chamber study It seems plausible, therefore, that the pollutants captured in cloud droplets by the red spruce are a predisposing factor in the observed decline The visible injury observed on foliage from the different treatments was linearly related to the concentration of applied mist (Figure 27) The straight line response was an unexpected feature of the results, and one that had not been noted by earlier studies at ITE

In addition to the frost hardiness and visible injury work, a range of plant physiological measurements were made to establish likely damage mechanisms

Water relations

Measurements taken in October/ November 1987 showed that acidic mists decreased the relative water content associated with zero turgor and increased the cell wall elasticity In consequence, the treated seedlings suffered *mild* water stress, evidenced by a reduction in shoot water potential Acidic treatments also affected the stomatal response to CO_2, such that the normal stomatal closure in response to CO_2 was absent This result may have important implications for mechanistic studies, and is to be investigated further during 1989

Photosynthesis and stomatal conductance

Gas exchange was measured in March 1988 on seedlings treated in 1987 Acidic mist (pH 2 5) increased the chlorophyll content of the remaining needles over two-fold, and the rate of photosynthesis per unit area by about 70% (at light or CO_2 saturation) However, the rate of photosynthesis per unit chlorophyll was reduced

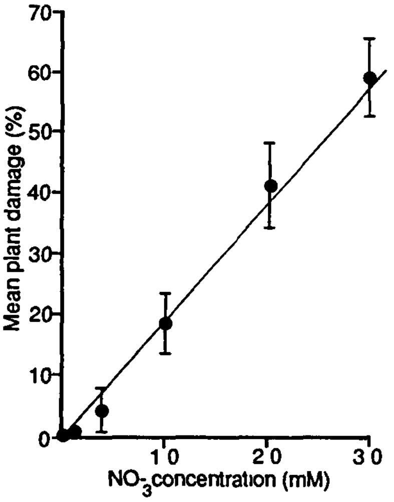


Figure 27 The relationship between visible injury on red spruce seedlings following six months of treatments with concentrations of the major ions in the

Acidic mist made the stomata more sensitive to low light levels and insensitive to CO_2 concentrations

These measurements show a range of treatment responses by physiological processes, and have identified, in particular, the changes in cell wall properties and normal stomatal function They represent an important step in locating physiological damage mechanisms, and will form the basis of further study

D Fowler

Pollution control by *Phragmites*

(This work was supported by funds from the Water Research Centre)

Recent advances in the use of the common reed *(Phragmites australis)* for wastewater treatment could soon give a new meaning to the term 'sewage treatment plant' The reeds are grown in specially constructed beds through which wastewater is passed Compared to conventional methods of sewage treatment, these reed bed treatment systems (RBTS) are just as effective, cheaper to construct and maintain, and more in keeping with the natural environment (Brix & Schierup 1989) They are particularly appropriate for small, rural communities, where a bed of 600 m^2 could treat the sewage from a population of up to 200 people Over the past four years, reed bed treatment systems have been constructed at 27 sites in the UK, mainly by Water Authorities (Plate 17) The wastewater is usually from domestic sewage, but the system also has considerable potential as a means of cleaning up farm effluents and some industrial discharges

The theory behind RBTS is neat and simple (Figure 28) The extensive root and rhizome system of the reeds provides a hydraulic pathway along which wastewater flows Atmospheric oxygen (5–50 g O_2 m^2 day^{-1}) passes down the hollow stems and rhizomes, and diffuses

Plate 17 New technology sewage treatment? A reed bed treatment system at Kingstone and Madley (Welsh Water Authority)

into the rhizosphere and soil around the roots. In this aerobic zone, the wastewater is treated by microbial action and ammonium is oxidised to nitrate (nitrification). Anaerobic treatment of the wastewater and the reduction of nitrates to nitrogen (denitrification) occur in the anaerobic areas in the surrounding soil. In addition, phosphates are adsorbed by the soils, and some additional aerobic composting of sludges occurs on the ground surface. The net result of these processes is, in theory, an effluent of consistent quality, with reported decreases of up to 95% in biological oxygen demand, 94% in phosphorus and 88% in nitrogen (Brix 1987).

However, this 'back to nature' method has not been without its problems or its critics. In practice, the performance of RBTS in the UK and on the continent has rarely lived up to the expectations of theory. The problems have included: failure of the reeds to grow, wastewater flowing over the surface of the bed rather than through it, no nitrification suggesting little oxygen transfer into the system, and generally lower standards of performance than were initially anticipated. To help overcome these problems, the Water Research Centre has been co-ordinating research and development in the UK. The eventual aim is to produce management guidelines for reed bed treatment systems in the UK, based on practical experience being gained by the Water Authorities at existing RBTS sites, and on programmes of research in three main areas:

1. studies on the decomposition processes in RBTS beds, including work on the cycling of nitrogen (University of Bath, Portsmouth Polytechnic);

2. studies on the mechanisms and rates of oxygen transfer into the rhizosphere (University of Hull);

3. studies on the ecology, establishment and management of reeds (ITE).

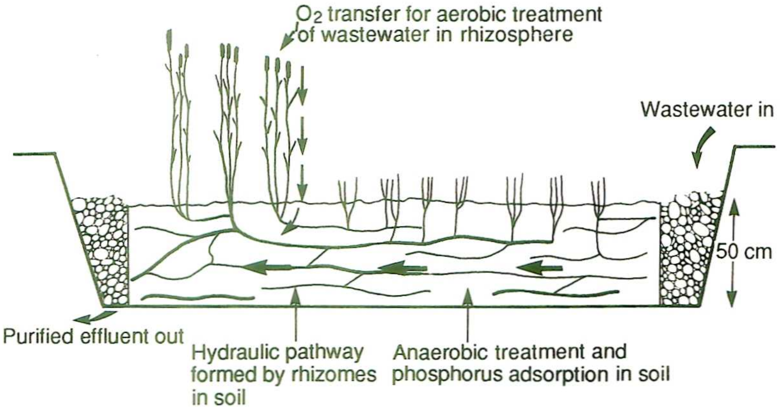


Figure 28 Key features of a typical reed bed treatment system

Staff at ITE Monks Wood have mainly been involved in the work on reed establishment and management (Parr 1987). A good growth of reeds, particularly below ground, is an essential prerequisite of RBTS, but, in practice, there have been frequent failures of reed establishment. In a survey of reed growth in UK beds, growth was found to be unsatisfactory in 73% of cases (Parr 1989a). Research on the germination ecology of the reed and into the effects of water levels on the growth and establishment of reeds has already helped avoid further failures, and some of the previous recommendations on reed bed establishment have been substantially revised. In the past, the recommended method was to use reed rhizomes transplanted in the autumn. However, the work has shown that planting in spring or early summer is preferable to autumn, and that reed seedlings should be used in preference to rhizomes.

Reed seedlings are rarely observed in natural reed beds in the UK, a fact which has given rise to a common misconception that reed stands in the UK cannot regenerate from seed. However, ITE research has confirmed that, in many reed stands, seed production is plentiful, the seed is viable, and seedling growth in a moist and weed-free environment is vigorous. A survey of 32 UK reed beds showed that, although there was considerable variation in seed production, seed was produced at 23 of the sites, with eight sites producing over 200 seeds per flower head. Maximum germination was attained at a fluctuating day/night temperature regime of 30°C/20°C, with germination rates ranging from 37% to 100% (mean = 81%). Most seed germinated within seven days.

Seedlings grown from seed germinated outside, on moist soil, in mid-May had produced an average of 10.9 g (±0.8 g) of shoots and 140 cm (±8 cm of rhizome by the autumn. However, small seedlings are susceptible to competition from other species and to fluctuations in water level, causing high mortality. To overcome this problem, seedlings were cultivated in glasshouses and planted out in mid-May, by which time the plants had already begun to produce rhizomes. By mid-September, these plants had produced an average of 38 g of shoots and 440 cm of rhizomes. Their rate of growth exceeded that achieved by transplanted

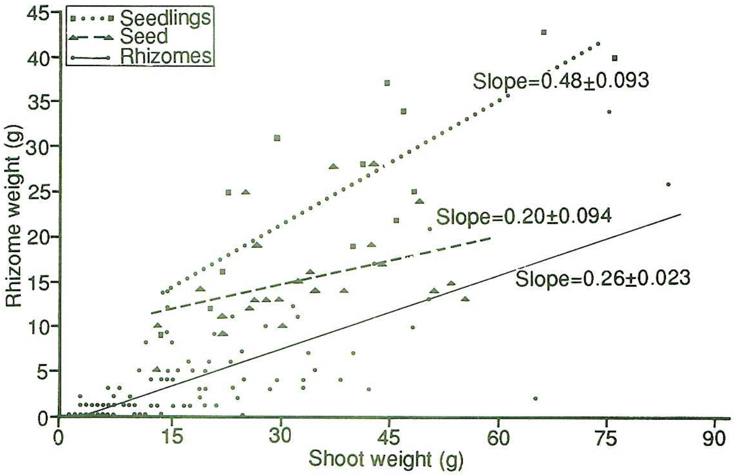


Figure 29 Reed seedlings provide the most effective means of establishing beds for reed bed treatment systems. After one growing season, seedlings produced consistently more rhizomes and had higher rhizome/shoot ratios than plants cultivated from seed or transplanted rhizomes

rhizomes grown under the most favourable conditions (Figure 29).

Reed seedlings have now been used to establish new reed beds successfully in RBTS beds at Little Stretton (Severn Trent Water Authority) and Freethorpe (Anglian Water Authority) (Plate 18). On the basis of these trials and from the results of the ITE research, the use of reed seedlings is now considered to be the quickest and most reliable method of establishing a new reed bed.

One of the main factors associated with poor reed growth in RBTS systems is the growth of weed species, especially sorrell *(Rumex* spp.), stinging nettle (*Urtica dioica*), great hairy willow-herb (*Epilobium hirsutum*), and grasses (*Poa* spp. and *Agrostis stolonifera*). Some experiments have been started to evaluate the long-term effects of weed populations on reed growth (Parr 1989b). The objectives are to quantify the effects of some major weed species on the growth and establishment of reeds, and to assess the benefit of control measures, including, flooding, chemical control and cutting. The effect of varying water levels on rhizome growth is also being investigated. At present, although a good cover of reed shoots can be achieved within two or three years, it may take twice that time for the root and rhizome system to mature. Work at ITE Furzebrook on genotypic variation in reeds is looking for varieties which are best adapted to the RBTS environment. Use of such varieties should further improve the rate of reed establishment and reed performance as sewage treatment plants.

Despite the problems of RBTS, and it is probably too soon to make a reliable judgement about the performance of existing beds in the UK, early results have been sufficiently encouraging to justify continued research and development. Furthermore, interest in using natural communities of plants to purify wastewaters should not be confined to these artificially constructed systems. It is important to understand and appreciate fully the role of naturally occurring wetland communities in keeping waters clean. There may be much to gain from allowing reeds and other wetland plants to thrive in drainage ditches, streams and rivers.

T W Parr

Plate 18. A farm sewer dyke used to clean wastewater before it is discharged into a local stream. The dyke is shown eight weeks after planting with reed seedlings (Severn Trent Water Authority)

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Radionuclide transfer in terrestrial ecosystems

(This work was supported by funds from the Department of the Environment, the Ministry of Agriculture, Fisheries and Food, the Scottish Development Department, the Commission of the European Communities, and the Central Electricity Generating Board)

Merlewood Radioecology Group

The Radioecology Group at ITE's Merlewood Research Station was formed as a result of the publication in 1978 of the report of *The Windscale Enquiry* The aims of the Group are to study the factors and mechanisms which control the movement and deposition of radionuclides in the terrestrial environment

Initially, work was concentrated on the Sellafield area of Cumbria and on radionuclides released to the environment by the reprocessing plant Involvement with the Chernobyl accident began in April 1986, when gamma-emitting fission products were deposited over large areas of the uplands in western Britain Whilst those radionuclides with short half-lives decayed rapidly, the caesium isotopes with their longer half-lives (Cs-137 half-life *c*30 years, Cs-134 half-life *c*2 years) have remained actively recycling in the upland environment

Work within the Group now covers a range of radionuclides emitting alpha (plutonium, americium) and gamma (Cs-134, Cs-137 and silver-110 m) radiation Research on radionuclides emitting beta radiation will become important in the future as changes in fuel reprocessing take place at Sellafield, and studies have been initiated through a CASE studentship with the University of Lancaster, awarded under the NERC Special Topic programme

Fallout from the Chernobyl accident

The first stage of all the investigations carried out by the Radioecology Group has involved a detailed field survey to establish the spatial distribution of the radionuclides and the degree of variability found in the ecosystems studied The initial phase of the work on the Chernobyl deposit produced a map for the UK of the activities of grassy vegetation and the underlying soils, this map showed the highest activities to be where heavy rainfall coincided with the passage of the Chernobyl cloud These areas were concentrated in the north and west of Britain The initial survey provided an incomplete cover of the country, and it has been followed by more detailed surveys, to increase the resolution, in selected areas A recent survey in Scotland has identified an area of heavy contamination at the eastern end of Glean Spean, which was not located by the coarser original survey Many of the results from the surveys relevant to the Chernobyl deposit were used to define areas where restrictions on the movement and slaughter of sheep were required

Radioecology of Chernobyl fallout

Current research on the Chernobyl deposit is concentrating on the mechanisms involved in and the factors controlling radiocaesium transfers in upland ecosystems Much more of the radiocaesium has remained available for plant uptake in the organic soils of the uplands, compared to lowland regions where mineral soils predominate In Scotland, plant uptake from organic soils was, on average, ten times that from mineral soils The clays and micas of mineral soils bind radiocaesium very strongly, making it largely unavailable to plants The organic soils of the upland regions, however, which received high levels of Chernobyl fallout, contain little clay and are acidic in nature, as a consequence, they do not immobilise radiocaesium in the same way as mineral soils Radiocaesium can, therefore, be recycled in the upland systems, from soils to vegetation, and then back to the soil via plant litter It is this cycling which is maintaining high levels of radiocaesium in vegetation and concentrations in tissue of domestic stock (sheep) and wild animals (red deer (*Cervus elaphus*), grouse (*Lagopus lagopus scoticus*) and hares (*Lepus timidus*)) above the 1000 Bq kg^{-1} fresh weight (fw) declared for sheep Recent laboratory studies conducted with soil scientists at ITE Merlewood have shown that over 80% of the radiocaesium in bent-grass (*Agrostis* spp) litter is available for recycling, whilst field studies have indicated that the radiocaesium litter accounts for more than 10% of the total radiocaesium in heather (*Calluna vulgaris*) ecosystems

The concentrations of radiocaesium found in wild plants growing on the acidic upland soils vary considerably, as Table 11 shows for a selection of species from Corney Fell, Cumbria Plants in the Ericaceae family (the heaths) are reported as containing the highest concentrations At Corney, both heather and bilberry (*Vaccinium myrtillus*) contain over 5000 Bq kg^{-1} dry weight (dw) of radiocaesium Uptake of radiocaesium varies, therefore, with soil type and between plant species on a given soil type The potassium status of a soil also influences radiocaesuum uptake, because the two elements are chemically similar and behave in a similar manner in biological systems As a result, high levels of available potassium in a soil reduce the plant uptake of radiocaesium in effect by diluting its concentration in the soil Significantly, levels of potassium in organic upland soils are often low Bryophytes (mosses) obtain the bulk of their water by capillary action, so their

Table 11 The activity concentrations of radiocaesium in vegetation on Corney Fell, Cumbria, in July 1987, showing the marked variation in uptake between plant species

	Cs-137	Cs-134
	(Bq kg^{-1} dw)	
Higher plants		
Heather (*Calluna vulgaris*)	6590	2075
Bilberry (*Vaccinium myrtillus*)	3964	1194
Brown bent-grass (*Agrostis canina*)	1247	379
Heath rush (*Juncus squarrosus*)	1132	303
Soft rush (*Juncus effusus*)	936	295
Common cotton-grass (*Eriophorum angustifolium*)	595	121
Mat-grass (*Nardus stricta*)	514	153
Bryophytes		
Sphagnum spp	7472	2813
Polytrichum commune	4026	1445
Polytrichum alpestre	3543	1187

mechanisms for concentrating radionuclides are different to the higher plants which depend on the absorption of soil water

The levels of radiocaesium in grazing animals reflect those in the vegetation being eaten Therefore, the varying concentrations of radiocaesium in different plant species must be considered in relation to the grazing preferences of the different animals For instance, in some areas sheep and red deer may graze heather more heavily during the winter months, whereas heather is the main item of diet throughout the year for grouse Radiocaesium levels in animals also vary as they move between different grazing areas and with the seasonal patterns of vegetation growth These patterns of variation have been studied on an upland sheep farm within the restricted area of Cumbria

The radiocaesium activity of ewes at the farm declined when they were brought on to the farm's enclosed pastures, and rose when they were returned to the open fell (Figure 30) where the radiocaesium content of vegetation remained higher than on the pastures

Despite the reduction in radiocaesium activity of the mixed grassland vegetation grazed by sheep over the study period (Figure 31), the radiocaesium activity of the ewes grazing on the fell was higher in the summer and autumn of 1987 and 1988 than in the autumn of 1986 This rise appears to be due to the radiocaesium originating from the Chernobyl fallout becoming more readily available as it has been incorporated into plant material, by the cycling processes mentioned above, rather than when it was present as a direct deposit on the surface of the vegetation, as would have been the case in 1986

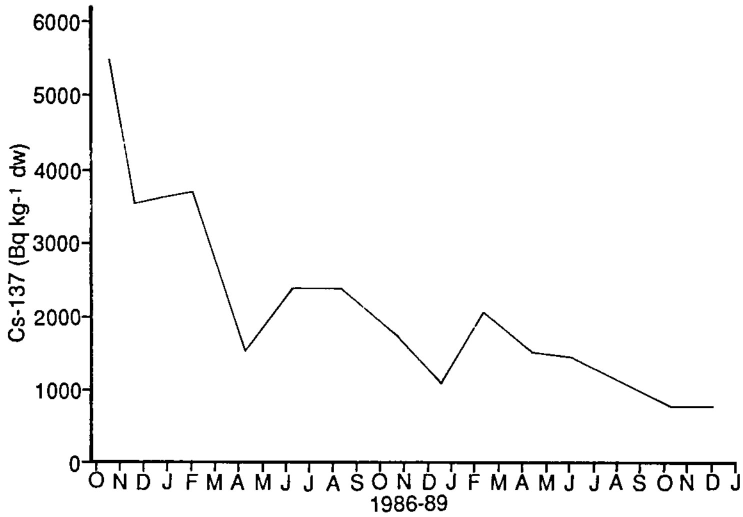

Figure 31 The Cs 137 activity concentration of vegetation samples taken from unimproved grazing land showing an overall decrease in the level of contamination

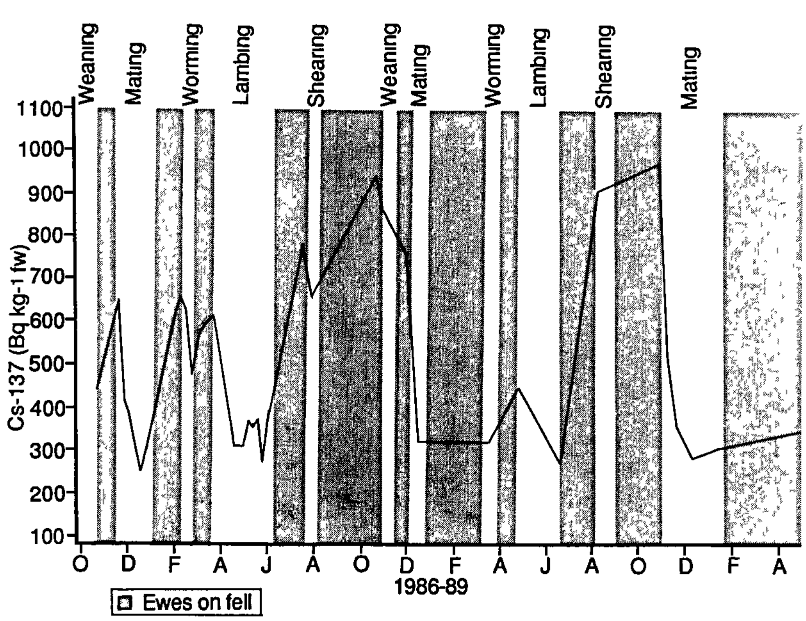

Figure 30 Changes in the Cs-137 activity concentration in the muscle of ewes grazing at the study farm in west Cumbria The effect on their radiocaesium burden as they moved from enclosed pasture to open fell is clearly shown

A rise in activity does not always follow the transfer of the sheep on to the fell During the winters of 1987–88 and 1988–89 when the ewes returned to the fell after mating on the enclosed pastures, their radiocaesium activity did not rise as at other times when they were moved from the pastures to the fell The digestibility of herbage is reduced during the winter, and this factor may cause a reduction in radiocaesium transfer Also, the intake of similar vegetation to that in the study area is known to be considerably higher in the summer than at other times of the year, so that radiocaesium intake would increase during the summer The measurements from the first winter (1986–87) after deposition of fallout from the Chernobyl accident are obviously different from the successive years, as the radiocaesium activity of the ewes rose when they were returned to the fell At present, the reasons are unclear, although the rise may have been associated with the presence of residual direct deposit on the vegetation surface

The addition to the sheep feed of radiocaesium binders, such as the clay mineral bentonite, zeolites and iron-hexacyanoferrates, to reduce radiocaesium uptake by housed animals is well documented The use of counter-measures to reduce levels in free-ranging animals, however, is not so simple In co-operation with the Macaulay Land Use Research Institute (MLURI), pastures at the study farm were treated with powdered bentonite Results looked promising, with a 40% reduction in the radiocaesium activity of ewes grazing the treated pastures after four weeks However, the ewes' herbage intake and body weight were considerably reduced, and this option does not appear realistic The Norwegian School of Agriculture has successfully reduced radiocaesium levels in free-ranging sheep and reindeer using saltlicks and slow-release rumen boli impregnated with ammonium iron-hexacyanoferrate complex (ACFC) In a joint study with Norwegian scientists, the effectiveness of these counter-measures will be assessed under the agricultural regimes of upland Britain

An alternative method of reducing radiocaesium levels is to remove the animals from the contaminated areas With the help of the National Radiological Protection Board and the Ministry of Agriculture, Fisheries and Food, ITE has established that, once removed from upland farms to uncontaminated lowland pastures, lambs lose their radiocaesium body burden with a biological half-life of approximately ten days Such a move is part of the normal management practice because, with the relatively severe climate of the regions which received the heavy deposition of Chernobyl fallout, very few sheep are sold ready for slaughter Instead, they are sold to lowland farmers for fattening This movement of sheep has led to concern that radiocaesium in excreta deposited by lambs when they arrived at the lowland farms would significantly increase the radiocaesium activity of vegetation at these farms In a lysimeter study, the uptake from urine and faeces by vegetation growing on both mineral and organic soils has been assessed On both soil types, less than 1% of the radiocaesium in faeces and less than 0 3% in urine were recycled to vegetation over a twelve-month period

Freshwater radioecology

Prediction of the likely duration of the cycling of the radiocaesium requires information on the temporal changes in its availability within soils This aspect is being investigated as part of the ITE programme of work on the geochemistry of radionuclides in soils, which is concentrating on the higher organic upland soils in Cumbria, typical of those found in the high-deposition areas of north Wales, north-west England and Scotland (ie rankers, podzols, peats and peaty gleys)

The Cs-134/Cs-137 ratio in these soils reflects the ratio present in each contributory source (weapons fallout, industrial discharges and accidental release), the magnitude at each source, and the time since deposition It is fair to say that the pre-Chernobyl Cs-134 activity was negligible in all these soils, and it is thus possible to distinguish between Chernobyl-derived and 'non-Chernobyl' components Chernobyl-derived radiocaesium comprises from 30% to 50% of the total at these sites However, early measurement of the isotope ratio in the 'exchangeable' fraction of the radiocaesium has shown that this fraction consisted almost entirely of Chernobyl-derived radiocaesium, in other words, the Chernobyl-derived radiocaesium was, initially, less firmly bound in these soils than the older radiocaesium Over time, however, the composition of the exchangeable fraction has changed, and the Cs-134/Cs-137 ratio has fallen to the same value as it is in the whole soil This result suggests that the Chernobyl-derived radiocaesium has been redistributed within the soil into the same 'pools' in which the older caesium is held This hypothesis is presently being tested by isolating various soil fractions (clay minerals, humic/fulvic acids, cellulose residues) from samples collected in both October 1986 and March 1989, in an attempt to define the changes over time

Long-term availability of radiocaesium in upland ecosystems

The Chernobyl fallout is also being used as a marker for freshwater cycling processes in a joint study with the Institute of Freshwater Ecology (Ferry House) and the University of Lancaster Studies in two contrasting lakes, Windermere and Esthwaite, have determined the magnitude of both direct deposition to the lake surface and indirect input from the catchment Measurements of dissolved and particulate radiocaesium concentrations over time and throughout the water column, together with an analysis of a time series of sediment cores, have been integrated into a numerical model describing radiocaesium dynamics in the lakes The main findings are that sedimentation in association with algae is a dominant pathway for radiocaesium transport in the lakes, and that the majority of the radiocaesium deposited on to the catchments has been retained in the soils

Current studies on the behaviour of radionuclides released by the Sellafield reprocessing plant

Although the Chernobyl accident resulted in a change in emphasis in the work of the Group, research is continuing on the fate of past and current releases from the Sellafield reprocessing plant This research is concentrated on the long-lived actinide elements which present a potential risk to man, and one study is investigating the uptake of plutonium by plants In order to simulate soil pore water, a hydroponic system has been constructed Water is pumped through silt obtained from the Ravenglass estuary, and a continuous low concentration of 3–18 mBq l^{-1} has been measured After filtration to remove suspended particulates, this water is circulated with nutrients through a series of growth troughs containing plants After a growth period of one month, measurable concentrations of both plutonium and americium have been found in the upper plant tissues of 0 2–0 5 Bq kg^{-1} This work initially used rye-grass (*Lolium perenne*) and is continuing to investigate the mechanisms of uptake using clover (*Trifolium* spp) and barley, in collaboration with the University of Newcastle

Research into the physicochemical associations of the actinide elements in soil is also continuing to identify mechanisms of immobilisation Plutonium and americium are associated with humic and fulvic acid fractions, and the majority of the actinide activity in a humic fraction of a gley soil has been found to be high in molecular weight material, together with iron and manganese Both this fraction and the lower molecular weight material have been separated by gel permentation chromatography and isolated, and it appears that the high molecular weight, actinide-rich fraction consists of colloidal clay/humic acid aggregates The effects of humate and fulvate complexing on the availability of the actinide elements to the plants will be tested

Direction of future research

Data from earlier studies are now being

collated, and mechanistic and predictive models are being developed In collaboration with Sutton Bonington School of Agriculture (University of Nottingham), data from both field and laboratory sheep studies are being used to develop a 'sheep ecosystem model' Further data are being obtained in joint experiments with MLURI on the behaviour in sheep of other nuclides likely to be released from nuclear installations (H-3, C-14, ruthenium, Ce-139, S-35, Ag-110, Zn-65 and Co-60) Together with the Soil Survey and Land Research Centre, the potential recycling of radiocaesium has been assessed from the different soils found in Cumbria It is hoped that this area of research will be expanded jointly with the Land Use Study Team at ITE Merlewood Data obtained from Cumbria before the deposition of Chernobyl fallout have been modelled with the University of Lancaster to show the distribution of radionuclides released from the Sellafield plant throughout the country

Studies of the behaviour of radiocaesium in different 'natural' or 'semi-natural' ecosystems affected by the Chernobyl accident have just begun Field studies will be conducted in Scotland (with the help of ITE Banchory), Norway (with the Norwegian School of Agriculture) and northern Italy (with the Italian Research Institute ENEA) The transfer of radiocaesium through the different ecosystems to a variety of grazing animals will be compared

The ITE studies, and those of others, have shown that a number of factors may affect the transfer of radionuclides to grazing animals However, most of these factors have not been fully investigated Staff at ITE Merlewood have prepared a joint proposal to the Commission of the European Communities, involving Belgian, Italian, Irish, Greek, Norwegian and other UK laboratories, to study the effect of such factors as plant species, animal age, animal breed, physiological condition, and the soil contamination of vegetation on the transfer of radionuclides to grazing animals

As mentioned, the importance of work into beta-emitting radioisotopes will become increasingly important when new reprocessing equipment at the Sellafield site comes into operation In order to investigate the behaviour of these isotopes in the environment, it is hoped to expand ITE's analytical facilities to include the capability for low-level beta counting

A D Horrill, F R Livens and N A Beresford

Scientific principles of soil protection in the UK

(A joint study with the Soil Survey and Land Research Centre, funded by the Department of the Environment)

Many countries have long had policies, and associated legislation, designed to maintain the productive potential of the soil resource Much of the legislation refers to 'soil conservation', but actually focuses almost entirely on the prevention or limitation of soil erosion In fact, the term 'soil conservation' has become virtually synonymous with the control of soil erosion

In the past, there has been little explicit legislation to protect soils in north-west Europe However, in recent years, there have been increasing pressures for measures to protect and conserve soil resources for use by present and future generations These pressures have arisen from a realisation that there are increasing threats to the ability of soils, and not only agricultural soils, to fulfil the functions on which man's use of soils depends The main concerns are the sterilisation of soils by urbanisation, physical depletion (erosion), chemical depletion (leaching), acidification, contamination (by chemical and toxic wastes), and the effects on the soil fauna and microflora of the overuse of pesticides and herbicides Some countries are also concerned about the problems of compaction, drainage, and salinisation

Some of the concerns relate to problems of water pollution, because soils have become increasingly important for their ability to act as filters to remove solid matter from percolating water, to act as buffers to absorb rainwater and control its transport to the groundwater table or streams, rivers, and lakes, and to protect groundwater and food chains against pollution by physicochemical and chemical processes Hence, problems of water pollution by nitrate, phosphate, heavy metals, herbicides and pesticides are considered amenable to control by measures which protect soils

Any soil protection policy would need to recognise the types of soil occurring in the UK and their differences from those in other countries, such as those in southern Europe Thus, soils in the UK are young and still evolving, many have impeded drainage in a cool, wet climate, and most have been influenced by man for many hundreds of years

Soil protection *versus* soil conservation

The use of the term 'soil protection', as distinct from 'soil conservation', is relatively recent, and seems to have originated in Europe, and particularly within the European Community 'Soil protection' is generally used to indicate a broader approach to the maintenance of the soil resource which considers all possible threats, including erosion There would appear to be further differences the existing soil conservation policies throughout the world are aimed primarily at maintaining agricultural or forest productivity However, current ideas about soil protection are not linked to any particular use of soils, but are incorporated in the view of soil as a complex system which carries out various functions

Soil protection in the European Community

In Europe, the first moves towards the development of a soil protection policy were made by the Federal Republic of Germany and the Netherlands In 1985, the Federal Republic of Germany published its *Bodenschutzkonzeption*, essentially a set of principles that the Federal Government would like to see adopted into the legislation of the Lander In 1987, the Dutch Soil Protection Act became operative, and was the first explicit soil protection legislation in north-west Europe

At present, the UK has no such soil protection legislation, although a number of laws and regulations provide implicit protection However, the UK recognises the need to establish the basic principles of soil protection, with a view to optimising the management of its soil resource This recognition implies the consideration of issues other than those covered by the traditional ones of agriculture and forestry There is a need for (i) sound advice on the basic principles of soil protection which might be appropriate to the UK, and (ii) recommendations on what may be the best use of soil in terms of minimal risk and its location in relation to designated areas where there may be restrictions

The importance of the definition of 'soil'

A soil protection policy would protect anything defined as 'soil' However, 'soil' may be defined in a number of ways for different purposes The definition used in a soil protection policy will have a major influence on the structure and implementation of that policy Protection policies being developed in mainland Europe use a broad definition, stressing that soils are complex, dynamic systems In these cases, soil protection aims to protect the soil as a functional system

Aims of a soil protection policy

Soil protection policies do not aim to prevent natural changes or the natural evolution of soils, but, rather, aim to protect soils against adverse changes resulting from man's activities In this context, 'adverse changes' are those which impair a soil's ability to carry out its normal range of functions The central aim of the Dutch soil protection policy is the maintenance of 'good soil quality' The prevention of adverse changes can be seen as the mirror image of that

However, a policy based solely on the prevention of adverse changes in soils would be too restrictive, as areas of soils exist which have already suffered adverse changes and can expect more in the future A soil protection policy should also be concerned with the restoration of damaged soils It should be realised that such a policy could not realistically aim to protect soils against all man-induced changes

The prevention of adverse changes and the restoration of damaged soils could form the basis of a UK soil protection policy However, problems could arise if a soil protection policy was based on the prevention of 'soil degradation', because that term has come to be linked with the maintenance of the productive potential of soils for agriculture and forestry, and a soil protection policy should have broader aims Furthermore, current concerns about the leaching of nitrate, organic pollutants, and phosphate from soils to groundwaters are not considered in discussions on degradation

The concepts 'soil quality' and 'adverse changes' require definition in the context of a soil protection policy In the Netherlands, it has been suggested that reference values for 'good soil quality' should be such that the soil poses no harm to any use by human beings or animals, can function in natural cycles without restriction, and does not contaminate other parts of the environment Problems arise in attempting a quantitative definition of 'soil quality' because of the natural complexity of soils and their heterogeneity at a range of scales from millimetres, through metres, to kilometres There is no single parameter which can be used to define 'soil quality' or 'adverse changes' A series of reference parameters are required, but, even given such a series, there is no single set of reference values for those parameters which might define 'quality' because of the natural variability between and within soils and the variation in impact of given stresses on soil processes and functions Reference values could really only be set with respect to a given end use, eg growing winter wheat, to the ability of a soil to perform certain functions, eg to supply plant nutrients, or to the operation of certain soil processes Any quantitative definition of soil quality which is relevant to several functions or uses will only be possible for a few parameters, eg heavy metals

Similar problems arise with the quantitative definition of 'adverse changes' However, in this context, an alternative approach would be to aim to prevent changes in soils which cannot be reversed naturally or by ecological

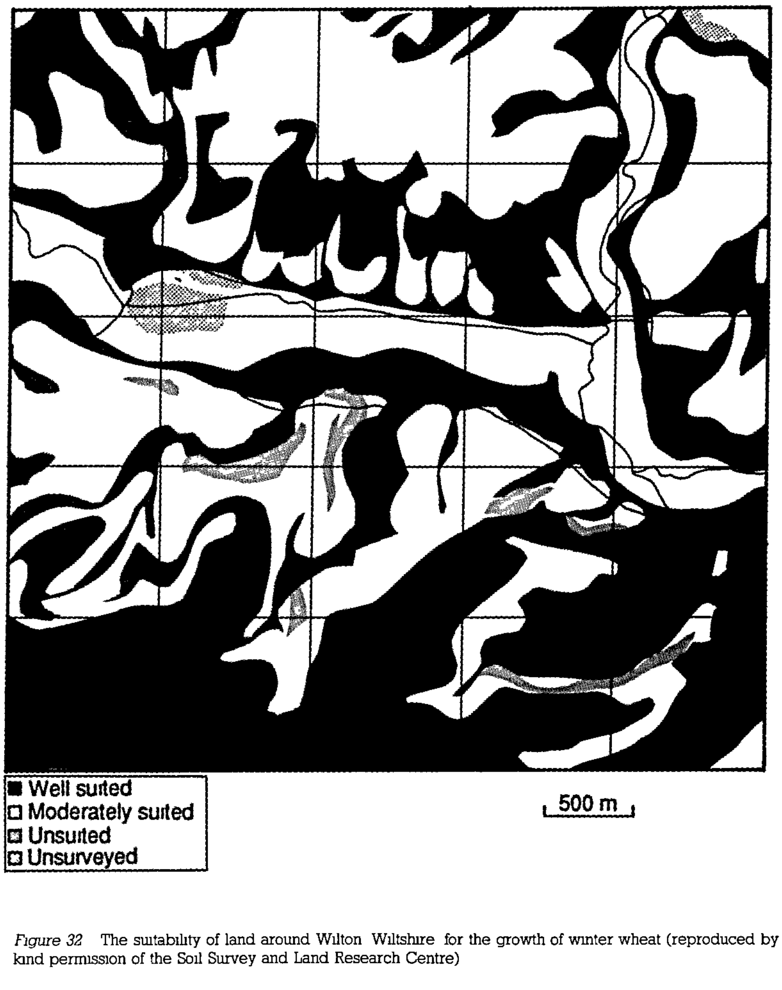

Figure 32 The suitability of land around Wilton Wiltshire for the growth of winter wheat (reproduced by kind permission of the Soil Survey and Land Research Centre)

management, or to prevent changes in soils greater than those which occur as a result of natural variations in other environmental factors, such as climate. Currently, it is not possible to define the limits of change of most reference parameters which are naturally reversible or are within the range resulting from environmental variation. However, in some cases, it is possible to identify, qualitatively, changes which are not reversible naturally.

Susceptibility and sensitivity of soils to stress

Although quantitative definitions of 'soil quality' or of rates of 'adverse' or 'undesirable' changes may not be possible at present, soils can be ranked in terms of their susceptibility and sensitivity to given stresses. In this context, soil sensitivity can be seen as the magnitude of the response of a soil to a given stress, or the rate of that response. The susceptibility of a soil system to stress may be defined as the likelihood of a given form of degradation occurring as the result of that stress. The ranking of sensitivity requires a conceptual model incorporating those factors which control the response of a soil. For example, a soil may be susceptible to erosion, and erosion results from a soil's sensitivity to rainfall. That sensitivity is determined largely by soil texture, slope, and surface cover.

A soil which is well suited to a particular use will have low susceptibility and sensitivity to stresses imposed by that use. Changes induced in such a soil will not be greater than those which are easily reversible. Hence, one aim of a soil protection policy should be to use land for the purpose for which it is best suited. For example, although soil may be suitable for growing winter wheat (Figure 32), a high susceptibility of the soil to nitrate leaching (Figure 33) would make that use unsuitable in the context of a broadly based soil protection policy. A similar approach can be applied to dispersed, as opposed to localised, stresses. Thus, soils can be ranked in terms of their sensitivity to acidic deposition; in this case, the controlling factors would be cation exchange capacity, base saturation, and texture.

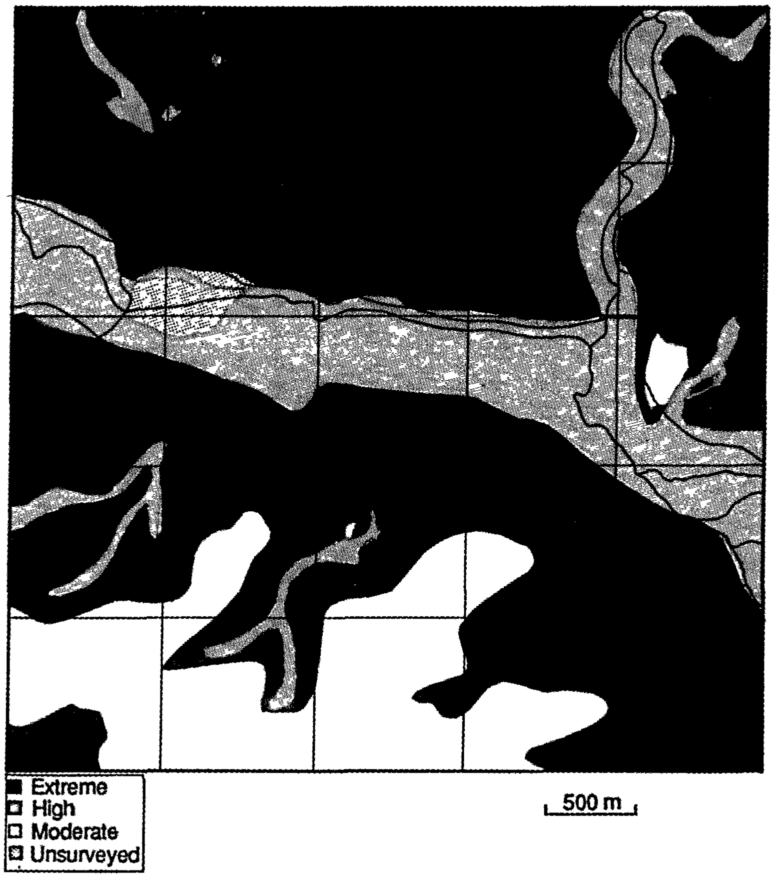

Figure 33 The potential nitrate leaching risk of soils around Wilton, Wiltshire (reproduced by kind permission of the Soil Survey and Land Research Centre)

Soil buffering capacity, resilience, and the reversibility of changes

The concepts of buffering capacity, resilience, and reversibility are related to sensitivity, and may also be useful in formulating soil protection policies. The buffering capacity of a soil is its ability to absorb or neutralise the impact of a given threat or stress, and hence to delay the effect. Resilience is a measure of the ability of a soil system to recover naturally once a threat or stress is removed or the loading of the given stress or threat is reduced. The effect produced by a stress is reversible if the property or properties which have changed can be returned to their original values. Soils and ecosystems are generally resilient within certain limits, but, if the property of interest moves outside those limits, the soil will not recover naturally. The effect may still, however, be reversed by management measures. Some effects are irreversible – the accumulation of heavy metals in soils is generally irreversible.

The implementation of a UK soil protection policy

The implementation of a soil protection policy for the UK would require:

1. characterisation of the soils in the UK and their current properties, followed by an assessment of their degree of degradation;
2. monitoring of changes in soils over time;
3. assessment of the impact of man's activities on soils, particularly the impact of changes in land use and management on their characteristics and functioning;
4. definition of acceptable loads of man-induced stresses and means of controlling those stresses;
5. development of alternative management methods and techniques to reduce the impact of man's activities on soils;
6. definition of target values of soil parameters for the rehabilitation of damaged soils.

The data bases held by the Soil Survey and Land Research Centre and the Macaulay Land Use Research Institute clearly form the basis of the required information on the soils of the UK However, the resolution of those data bases, and the information they contain, may necessitate further input Considerable soil information for semi-natural sites is held by organisations such as the Nature Conservancy Council The national, or regional, assessment of such change would require a network of long-term monitoring sites, such as those which are being established in other European countries The value of these long-term monitoring sites has been demonstrated by the classical plots at Rothamsted Experimental Station

The impact of man's activity on soils could be included in the Environmental Assessment Regulations, which implement the EC Directive no 85/337 While it might not be possible, at present, to produce quantitative assessments of impacts, soils could be ranked in terms of their sensitivity, as a first stage Critical, or acceptable, loads provide a means of linking a soil protection policy with legislation for the control of activities which may have adverse effects on soils The development of less-damaging land management strategies has been referred to as 'optimisation' in the Netherlands, where great efforts have been made to develop models for matching nitrate fertiliser inputs to plant demand Parallel work is in progress in the UK Another aspect of less-damaging land management would be the introduction of new technology, eg wider tractor wheels to reduce the loading on the soil The evaluation of the success of any restoration measures should include reference parameters which cover biological, chemical, and physical aspects of soils and their functioning Wherever possible, reference or target values should be assigned to each parameter

The key question is 'how could a soil protection policy be implemented in the UK?' An important requirement of the Town and Country Planning Act is that, in deciding whether or not to give planning permission, the planning authority 'shall have regard to the development plan for the area and to any other material considerations' The value of the soil for any purpose, or its susceptibility to damage by the proposed development, in any location may be regarded by the planning authority as a 'material consideration', if the value, quality, or susceptibility of that soil could be demonstrated Maps providing such information would be of value to planning authorities if the required data were accessible In the UK, various legal instruments are available for protecting the environment However, they are not linked or co-ordinated under a broad policy, and responsibilities are spread between departments Furthermore, three-quarters of the UK, or at least of England and Wales, is excluded from planning control by virtue of its use for agriculture or forestry Any soil protection policy would require links with general environmental policies and legislation, such as those concerning controls on emissions, pollution of waters, and planning legislation, and with agriculture and forestry policies and legislation

P J A Howard

Interactive effects of pesticides in partridges

Most studies to assess the potential hazards of pesticides to birds and other animals are restricted to the effects of a single chemical in isolation This is the only legal requirement However, in the field, birds may be exposed to a number of different pesticides, because more than one pesticide has been used at the same time in a 'cocktail', because several chemicals have been used sequentially, or because the bird has moved from an area where one pesticide has been used to an area where another has been applied Studies on possible interactions between combinations of pesticides have received scant attention, particularly in birds (Ludke 1977) The paucity of such information was the reason for this study, which was done at the School of Animal and Microbial Sciences, University of Reading, by G Johnston and Dr C Walker, in collaboration with ITE Monks Wood, as part of the NERC Special Topic on Animal Ecotoxicology The red-legged partridge *(Alectoris rufa)* was chosen for the study because it occurs widely on agricultural land and is, therefore, likely to be exposed to a range of pesticides, and also because it is easily kept in captivity and is available commercially

In view of the large number of possible combinations of pesticides to which birds may be exposed, it is obviously desirable in such a study to select combinations which may be expected to interact in some way, particularly those which may result in increased toxicity There are two main mechanisms by which the toxicity of one pesticide may be increased by another by the induction of an enzyme which activates one of the pesticides, or by the inhibition of an enzyme which detoxifies it The study has so far been mainly concerned with the former mechanism

Enzyme induction

The aims of the first part of this study were two-fold First, to examine the effectiveness of the environmentally persistent organochlorine DDE, the major metabolite of DDT, and the fungicide prochloraz, to act as inducing agents (ie their ability to promote the production of various enzymes, some of which are involved with destroying these 'foreign' compounds) (Riviere 1983), second, to

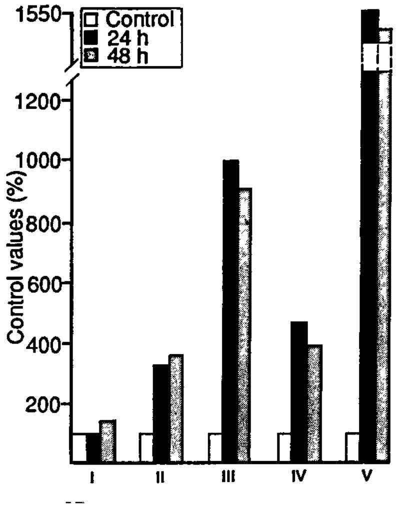

Figure 34 The effects of prochloraz on various liver parameters in partridges. Birds were given an oral dose of corn-oil alone (controls) or 180 mg kg^{-1} body weight prochloraz in corn-oil and killed 24 h or 48 h later The Figure shows (i) liver weight (g) (ii) microsomal protein (mg g^{-1}) (iii) the amount of the enzyme cytochrome P-450 (nmol kg^{-1} body weight) and the activities of two other enzymes; (iv) aldrin epoxidase (nmol kg^{-1} body weight min^{-1}) and (v) EROD (nmol kg^{-1} body weight min^{-1})

All values are expressed as means of values in control birds 24 h and 48 h after dosing Treatment with prochloraz markedly increased all of these parameters determine the effects of prochloraz pretreatment on the subsequent toxicity of the organophosphorus insecticide, malathion, once induction has occurred Prochloraz on its own is not particularly toxic to vertebrates

DDE was found not to be an effective inducer in the partridge, whereas prochloraz was found to be a potent inducer of mono-oxygenase enzymes in the liver There was an increase in liver weight and nearly a four-fold increase in liver microsomal protein content The activities of several enzymes in the liver, including cytochrome P-450, were increased several-fold above those of the controls, when expressed in terms of body weight (Figure 34)

Pretreatment with prochloraz in corn-oil caused a dramatic increase in the toxicity of malathion to partridges, three out of four pretreated birds died within ten minutes of receiving low intraperitoneal doses of malathion The activities of the enzyme cholinesterase in both serum and brain were depressed by 100% in two of these birds, whilst the third showed depressions of 100% and 82%, respectively Significant increases in liver weight, liver microsomal protein and cytochrome P-450 content confirmed that these birds were in the induced state at the time of malathion administration In contrast, birds treated with corn-oil alone and given the same doses of malathion displayed a slight elevation of serum cholinesterase after one hour, and only a 25% inhibition after four hours Prochloraz pretreatment also resulted in a significant increase in susceptibility to low oral doses of malathion (Figure 35)

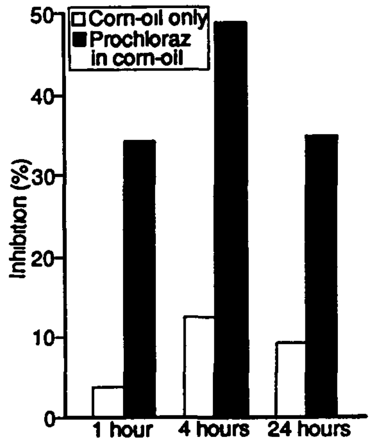

Figure 35. The effect of pretreatment with prochloraz on malathion induced inhibition of the activity of the enzyme serum cholinesterase Partridges were treated orally with corn-oil alone or 180 mg kg^{-1} body weight prochloraz in corn-oil. *After 24 h, all birds were given 11 mg* kg^{-1} body weight malathion orally Blood samples were taken before dosing with malathion and 1 h, 4 h and 24 h later The Figure shows % inhibition of cholinesterase activity compared to activity before dosing with malathion. In birds pretreated with prochloraz malathion caused a much greater inhibition of cholinesterase activity

Malathion itself is inactive within the animal's body, but it is activated by the mono-oxygenase enzymes to produce malaoxon, which is very toxic because it inhibits the activity of the cholinesterase enzymes In mammals and birds, but not insects, most malathion is rapidly detoxified by another enzyme to produce malathion monoacid and diacid, so preventing the accumulation of the toxic malaoxon Thus, malathion is much more toxic to insects than to birds and mammals

To determine why prochloraz increased the toxicity of malathion to birds, the metabolism of malathion was compared *in vitro* by microsomes from the livers of two groups of birds One group had previously been dosed with prochloraz in corn-oil, while the other group was given corn-oil alone Microsomes from both groups were incubated with C^{14}-labelled malathion, and the resulting metabolites were separated by thin-layer chromatography before using a linear analyser to locate the radioactive areas Microsomes from the control birds yielded only one major metabolite, identified as malathion monoacid (Figure 36) In contrast, microsomes from the prochloraz-treated group yielded three distinct metabolites, the most prominent of which was malaoxon The others were malathion monoacid and diacid Thus, in control microsomes, malathion is rapidly detoxified to the malathion monoacid, whereas in induced microsomes metabolism is predominantly to the toxic malaoxon, brought about by one or more forms of cytochrome P-450 induced by prochloraz So, although both prochloraz and malathion alone are fairly safe for birds, the combination of the two becomes lethal

The toxicity of other organophosphorus compounds following pretreatment with prochloraz is currently being assessed Dimethoate and chlorpyriphos have been selected because they require metabolic activation for toxicity Preliminary results suggest that there is also a potentiation of toxicity of these compounds in prochloraz-treated birds Several other fungicides, such as myclobutanil, propiconazole and penconazole, are being investigated in combination with malathion, and results suggest that all of these compounds are capable of causing an increased susceptibility to malathion toxicity in the partridge

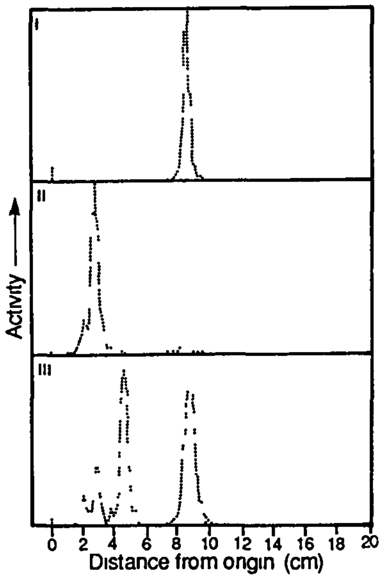

Figure 36 Traces from a linear analyser Microsomes were prepared from the livers of partridges which had been treated with corn-oil alone or with prochloraz in corn-oil 24 h earlier Microsomes were incubated *in vitro* with C^{14}-labelled malathion. The resulting metabolites were separated by thin-layer chromatography and run on a linear analyser to locate the radioactive areas. The Figure shows (i) the trace from C^{14}-labelled malathion standard, (ii) the trace from control microsomes showing only one major metabolite malathion monoacid, (iii) the trace from microsomes from prochloraz-pretreated birds showing three metabolites of which the most prominent is the toxic malaoxon

Enzyme inhibition

The results described so far have dealt with the increased toxicity of insecticides brought about by pretreatment with a fungicide which increased the activity of the enzymes needed to activate the insecticide A further study is concerned with increased toxicity caused by an inhibition of the enzymes involved with detoxifying a pesticide, and, in particular the effects of partial inhibition of blood esterase enzymes on the toxicity of the carbamate insecticide, carbaryl Carbaryl was given orally at a dose corresponding to either 20% or 10% of the lethal dose to control birds, and to birds which had previously received low doses of malathion Although there were no significant differences between malathion-pretreated and control birds in either the concentration of carbaryl detected in the blood or in the degree of inhibition of cholinesterase enzymes, three of four malathion-pretreated birds showed symptoms of poisoning, and one of these birds died As no signs of toxicity were observed in four control birds, it appeared that an interactive effect had occurred which was not apparent from blood analysis Further work aims to confirm this observation and to establish the mechanism

Effects on reproduction

A collaborative study with the Karolinska Institute, Stockholm, showed that treatment with prochloraz induced several forms of cytochrome P-450 enzymes in the livers of partridges Because gonadal steroid hormones, essential in reproduction, are metabolised by cytochrome P-450 enzymes, it is possible that prochloraz could affect the normal reproductive function This possibility was investigated Birds were treated with repeated oral administration of prochloraz and malathion, alone or in combination, throughout the breeding season and data were obtained at successive stages on induction and reproductive status in males and females Results showed that all birds which received repeated prochloraz treatment were maintained in an induced state for the three months of the experiment There were no significant differences between any of the experimental groups and controls in terms of testis, ovary or oviduct weights, or plasma concentrations of luteinising hormone or testosterone However, it must be pointed out that, in retrospect, the birds used in this study were too young Many of the control birds did not become fully sexually mature, and there was a great deal of variation between individuals The negative result is, therefore, not conclusive Further work will investigate whether prochloraz-stimulated induction does alter the metabolism of gonadal steroid hormones

Little attention has been paid to the possible interactive effects of pesticides Results show that such effects can be important, and this conclusion gives some cause for concern It is unclear if such interactions have ever been a major cause of mortality Because the levels of each pesticide involved in such synergisms may be well below their individual lethal levels, and because these pesticides are often rapidly metabolised in any case, post-mortem analysis of tissue residues would not have pinpointed this factor as the cause of death

A S Dawson

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Ecological impacts of climatic change

(This work was partly supported by funds from the Department of the Environment)

Several recent observations have revived concern that emissions of 'greenhouse' gases could change the world's climate dramatically in the coming 50–100 years These observations are that (i) concentrations of radiatively active gases (RAGS) other than CO_2 are increasing rapidly, especially methane, nitrogen oxide, tropospheric ozone and chlorofluorocarbons, (ii) historic temperature data have now been critically analysed, and there is agreement that the world has warmed by about 0 5°C in the past 100 years, with five of the ten warmest years in the last 100 having been in the 1980s, and (iii) all five major General Circulation Models of the atmosphere predict a global warming of 2–5°C resulting from effective CO_2 doubling

The scenario

'Effective CO_2 doubling' means that the combined effect of all the greenhouse gases in trapping infra-red radiation (heat) on the earth is equal to the effect of doubling the CO_2 concentration Such a doubling is likely to occur by the year 2050 AD CO_2 concentrations themselves are likely to double towards the end of the next century The predicted warming of 2–5°C by 2050 AD is the warming to which the earth will be committed over the long term, once the oceans have warmed The actual global warming by 2050 AD is likely to be 1 0–2 5°C, and high latitudes will warm more than tropical latitudes The global increase in mean sea level is likely to be about 35± 20 cm by 2050 AD (less than previously predicted) There are no reliable predictions for particular regions of the world, but it is assumed that the UK will follow the global trend Rainfall may increase, but evapotranspiration could increase faster There is no evidence that the UK will suffer more extreme weather

Over the past year, ITE staff have undertaken desk studies and planning exercises, and begun new projects on (i) land/atmosphere exchange of RAGS, especially methane and the nitrogen oxides, and (ii) the impact of increased CO_2 levels and temperature rise on terrestrial ecosystems

Desk studies for the Department of the Environment

In 1988, the Department of the Environment and NERC commissioned six desk studies of the impact of increases by 2050 AD of CO_2 to 540 ppmv (parts per million by volume), mean temperatures of 3°±1 5°C, rainfall ±20%, and a sea level rise of 80 cm (all somewhat larger values than in current scenarios)

The subjects and main conclusions were as follows

1 *Direct effects of CO_2 increases on trees and forests* (ITE and the University of Edinburgh)

   In general, increased CO_2 levels will promote photosynthesis and decrease the loss of water through stomatal pores in leaves However, over several years, plants may adapt to high CO_2 levels and then respond less than in short-term experiments Seedlings and young trees grow 20–120% faster at doubled CO_2 concentrations, but no experiments have been done on mature trees or on trees without nutrient or other limitations No information is available on stand responses, which can only be assessed using mathematical models

2 *Effects of climatic change on trees and forests* (ITE and University of Edinburgh)

   Trees are vulnerable to climatic

changes which occur within their lifespan, and are especially vulnerable to winds, fires and pest outbreaks In the absence of water stress, spruce at 400 m altitude could grow up to 40% faster, following a 1°C rise in temperature, and tree rings show increased pine growth at 1–2°C warmer temperatures However, with increased water stress, conifers would be adversely affected, and more broadleaved tree species could be grown Also, peaty upland soils will improve in the long term

3 *Effects of CO_2 and climatic change on agriculture* (University of Nottingham)

Doubled CO_2 levels might increase crop yield by an average of 30%, and reduce water loss per unit of yield Increased temperatures (3–4°C) would accelerate the development of crops such as wheat, leading to lower yields, but would increase the yields of crops which grow into the autumn, like sugar beet and potato, by 50–70% The geographical distributions of crops would change, and large, but uncertain, changes could occur in pest and disease incidence

4 *Effects of climatic change on species, ecosystems and processes of conservation and amenity interest* (ITE and Unit of Comparative Plant Ecology, University of Sheffield)

The relative abundance of plant species will change, especially in southern Britain, with grasses and early-flowering bulbous plants (like bluebells *(Hyacinthoides non-scripta)*) becoming less common except in dry places Many species will expand northwards, on to north-facing slopes, and to higher altitudes These changes will occur in spurts, in particular years, and could be altered by land use practices The most threatened plant species will be those currently growing in wetlands and on mountains and heathlands

5 *Impacts of climatic change on freshwater ecosystems* (Institute of Freshwater Ecology)

Most UK lakes will not be seriously affected, but many nutrient-rich lakes may produce more algal blooms Many fish will be adversely affected, especially the northern cold-water species like Arctic charr *(Salvelinus alpinus)* and whitefish *(Coregonus* spp), but also trout *(Trutta* spp) in southern streams

6 *Effects of sea level rise on coastal ecosystems of conservation and amenity value* (ITE)

A sea level rise of 20–165 cm by 2050 AD would cost about £5–8 billion in sea defences Sea walls would not be protected by salt marshes on the seaward side All invertebrate and bird species that depend on marshes and mudflats would suffer

Highlights of the ITE research programme

1 *Radiatively active gases*

There are great uncertainties about the sources of methane, including releases from the boreal wetlands Two methods will be employed to measure the methane given off by wetlands The first is to place boxes (cuvettes) upside down over the ground and to measure the rate at which methane accumulates inside them The second is to measure the increase in concentration of methane in the air from high up towards the ground (the gradient), and the micrometeorological processes that make it possible to calculate the rate at which methane is released to produce the measured gradient (the flux gradient) In addition, experiments will be done in open-top chambers (small glasshouses with no roof) to determine the effect of temperature on methane emissions from wet organic soils A second subject of concern is the build-up of ozone in tropical regions this is the ozone near the ground (not stratospheric ozone), and is produced by the action of light on nitrogen oxide gases that are emitted from agricultural soils, as well as from cars and power stations

2 *Impacts on forests*

Impacts of climatic change on forest growth and water use will be assessed by a combination of experimental studies (in open-top chambers), the use and development of mathematical models of tree and forest growth, and the use of historic and spatial information on changes or differences in tree growth (using tree ring records and site differences)

3 *Impacts on natural vegetation*

Changes in natural vegetation will be determined by using historic records, by monitoring change (especially in montane communities), by screening species for responses to temperatures, and by developing models of the population dynamics of plants having different life forms (including Arctic plants)

4 *Impacts on soils*

Increases in temperature will change the rate of decomposition of organic matter and alter the rate of release of nutrients Many of the changes in natural vegetation may result indirectly from changes in soil properties Information will be obtained by measuring the decomposition of standard litters in different climates, by using heating cables to warm soils in the field, and by experiments in laboratory microcosm units In addition, work will be done to determine the impact of elevated CO_2 levels on nutrient release from soils

5 *Impact on invertebrates*

Invertebrates are very responsive to small changes in weather patterns The ITE data bases will be used to relate past changes in species distribution to climate, and existing and new models are being developed for key species to show how climatic change alters insect fecundity/mortality, insect/plant and insect/natural enemy relationships

6 *Impacts on coastal ecosystems*

In order to predict the impact of sea level rise on coastal ecosystems, more needs to be known about salt marsh physical processes across the zones from mudflats to marshland, the dynamics of salt marsh vegetation, the methods of stabilising coastal structures with vegetation, and the patterns of sediment erosion and accretion on soft coasts A review is planned of the wildlife dependent on low-lying areas, and the impact on conservation of different strategies for coastal defence

M G R Cannell

Population ecology

Work in this programme area is concerned with understanding what determines the distribution and abundance of plants and animals. A knowledge of the factors that influence population levels is necessary for the successful management of plants and animals, whether for conservation reasons, for human use, or for pest control. Such knowledge is also helpful in understanding and predicting the effects of environmental change on populations.

The projects described below fall within the general theme of population ecology, and illustrate part of the current range of work within this programme.

Population dynamics of radio-tagged goshawks

(This work was partly supported by the Swedish Sportsman's Association, Conseil International de la Chasse, and a Swedish charitable trust)

The northern goshawk (*Accipiter gentilis*) is a subject of controversy in many countries. As a result of predation on game and poultry, it is frequently killed by hunters and farmers. On the other hand, because goshawks are shy and elusive by nature, bird-watchers tend to underestimate their abundance and object to any exploitation by man. Despite a European population of at least 40 000, European Commission legislation for the Convention on International Trade in Endangered Species (CITES) now effectively treats the goshawk as an endangered species. If it had been enacted before 1970, this legislation would have prevented the imports for falconry which re-established a small British goshawk population (Marquiss & Newton 1982).

Population models can help to reconcile divergent views on problem species, by predicting the impacts of human exploitation and thus enabling effective management. Previous attempts to model goshawk populations were based on ring recoveries, which suggested a first-year mortality of 60–70%, and indicated slow population growth, even if all birds bred from their second year onwards (Mueller, Berger & Allez 1977). However, a high proportion of ringing recoveries came from hawks killed by man: this fact can seriously overestimate first-year mortality if dispersing juveniles are prone to encounter humans, whereas adults tend to die in the forest. At pheasant farms in Sweden 70–80% of killed hawks were juveniles (Marcström & Kenward 1981a).

Plate 19 Juvenile goshawks trapped near the nest for radio-tagging. A male (left) is 65% the weight of a female (right)

In 1980, a collaborative project was set up between ITE and Uppsala University to build a population model by radio-tagging goshawks on Gotland, a 3100 km^2 Baltic island about 100 km from mainland Sweden. Gotland was chosen because it was large enough for up to 200 active goshawk nests, but small enough to search for radio-tags in two days by road or three to four hours by air, and isolated enough for ringing to suggest that only 2–4% of hawks immigrated or emigrated to the mainland.

In each of six years, up to 35 juvenile hawks were caught near nests after their feathers were full grown (Plate 19), and equipped with 14 g tail-mounted radios. These radios lasted 8–12 months, and contained mercury switches which altered the rate of their signal pulses to help indicate whether a bird was perched in a tree, feeding, flying, or lying dead on the ground. The tags, which were ultimately shed by moulting, were 1–2% of each bird's weight (typically 700–1000 g for males, 1000–1600 g for females), and did not influence weights or dispersal tendency (Kenward 1978). Including older hawks, a total of 352 goshawks were radio-tagged to measure survival and breeding performance at different ages, and causes of death.

Plate 20. Goshawks were radio-tracked using a minibus with a direction-finding antenna

The location of each tagged hawk was usually checked at least once a week, using a minibus equipped with a mast-mounted directional antenna and repeater compass (Plate 20). Checks were made at night, because at that time live hawks were in trees, giving a slow signal pulse with a good detection range. During the day, hawks were sometimes feeding on the ground in hollows, in which case they were hard to detect. The whole island could be covered in two nights. If a hawk was missing, its previous range was checked more thoroughly for the weak, fast signals typical of a dead hawk. The whole island was covered by air up to twice a year for birds whose signals had been lost.

Survival estimates were complicated, because hawks could leave the tagged population through tag failure as well as death. Survival over a long period was, therefore, estimated as the product of survival in many consecutive short periods, 'censoring' tags whose signals were lost from all subsequent periods. However, this procedure overestimates survival if tag failure was sometimes associated with death, eg if tags were chewed by a scavenger. A correction could be applied by dividing censored tags into those moulted or known to fail without death of the bird, and those with unexplained signal loss. The proportion of hawks that were later recaught was very similar in both categories: 17 of 70 birds whose tags were moulted or otherwise known to fail, compared with 16 of 68 birds whose signals were lost inexplicably. This showed that there was little tendency for hawks to die at the time that their signals were lost. An independent checking technique supported this conclusion, so the recorded survival was not an overestimate.

On this basis, 51% of male hawks died in their first year, compared with only 36% of females (Figure 37). There was a similar sex-linked difference in mortality in the second year of life, but from then on mortality was estimated at 21% for both sexes.

Of 67 dead hawks, 36% were killed by man (which was legitimate for birds attacking poultry), and 13% were killed by other hawks or impacts. Fifteen per cent had starved to death, another 9% were starved with evidence of disease, and only 3% had definitely succumbed to disease. The other 24% died of starvation or disease, but were not recovered fresh enough for autopsy.

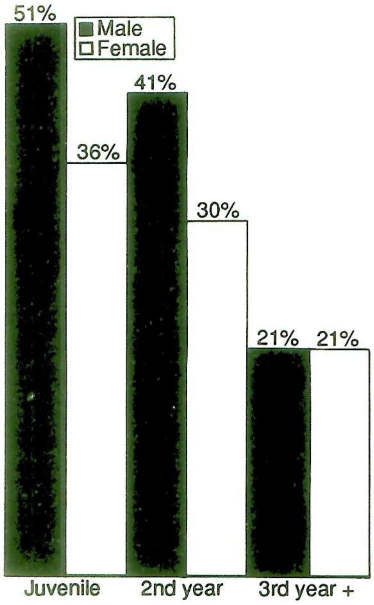

Figure 37. The annual mortality of goshawks on Gotland was higher for males than for females in both their first and second year of life, but was similar for both sexes in adults

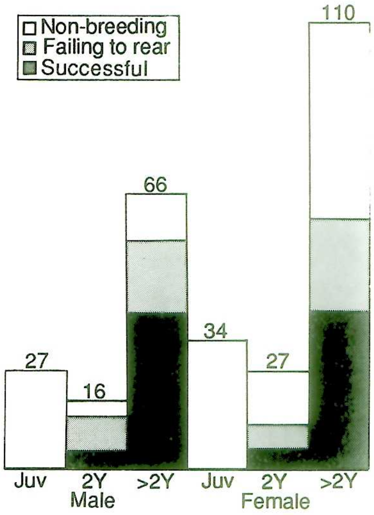

Figure 38. Because fewer males than females survived for two years, the adult goshawk population on Gotland contained a large excess of females, with many more non-breeders. Although many males nested in their second year, most failed to rear young. A higher proportion of older hawks was successful in both sexes

On Gotland, no birds attempted to breed in their first year, although Ziesemer (1983) estimated that 21% of juveniles did so in Schleswig-Holstein. Even in their second year, only 25% of females laid eggs, and 53% each year thereafter, largely because the females outnumbered males by 1.56:1 as a result of the differences in prebreeding mortality (Figure 38). A similar excess of adult female sparrowhawks (*Accipiter nisus*) has been estimated from ringing data by Newton (1986), and may in part result from female hawks being larger than males, and therefore having more reserves for surviving periods of food shortage. Moreover, only female goshawks can take adult hares (*Lepus timidus*), and a higher proportion of females than males killed rabbits (*Oryctolagus cuniculus*) on Gotland.

Using uncorrected estimates of survival and breeding success for each sex, the goshawk population model predicted a 17% per annum decline in numbers on Gotland, but was stable if adult survival was increased by 4% and the proportion of adult females breeding by 6%. These were reasonable corrections, as trapping of adults in winter selects poorer individuals (Marcstrom & Kenward 1981b), whereas the whole brood was marked at nests The model showed that the high first-year survival, compared with previous estimates, was balanced by a relatively high proportion of unbreeding adults, especially females If the data on juvenile breeding from Ziesemer (1983) were included in the model, the population would have increased by 27% per annum, despite 36% being removed by man It seems that goshawk populations can tolerate quite a high level of mortality caused by humans

This work provided much new information on goshawk predation, post-fledging behaviour and dispersal mechanisms Similar work is needed for other large raptors which are thought to suffer high prebreeding mortality, and are therefore managed conservatively, despite protests about predation on game and livestock Uncompromising protection can result in illegal, unselective forms of management, such as poisoning, which may well be more detrimental to raptor populations than the legal killing of some goshawks in Sweden

R E Kenward

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Changes in numbers and breeding performance of seabirds: evidence for changing conditions in the northern North Sea

(This work was partly supported by funds from the Nature Conservancy Council)

Many seabirds feed in the upper trophic levels of marine food webs, and are both numerous and conspicuous In comparison to other top marine predators such as whales, seals and fish, they are relatively easy to study and thus can be used as indicators of the health of the marine environment Seabirds have been used widely to monitor the incidence of pollutants, eg organochlorines, heavy metals, oil and plastics, throughout the oceans and, to a somewhat lesser extent, as indicators of large-scale changes in fish stocks

Sandeels (*Ammodytes* spp), particularly *Ammodytes marinus*, are a key component of the North Sea ecosystem, and form a large part of the diet of many commercially important fish, such as cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*), seabirds and seals, and are also the target of a substantial industrial fishery The potential for competition between seabirds, marine mammals, fish and the fishery has been recognised since the 1970s

Many of the North Sea's seabirds breed in colonies on mainland cliffs or on offshore islands along the coast of eastern Britain During the last 20 years, considerable effort has been directed at monitoring changes in the numbers of many species, but much less attention has been paid to determining the biological processes involved or the causal factors Parameters such as adult survival, breeding success, chick growth rate, and time spent by adults at the colony are all likely to be related to food availability, and are, therefore, potential indicators of trends in prey populations Over the past three years, work has been in progress to develop low-input techniques for the routine monitoring of some of these parameters in a range of seabird species over a wide geographical area

Changes in breeding success

In a recent survey by ITE and the Nature Conservancy Council (NCC), data on breeding success from 23 kittiwake (*Rissa tridactyla*) colonies bordering the North

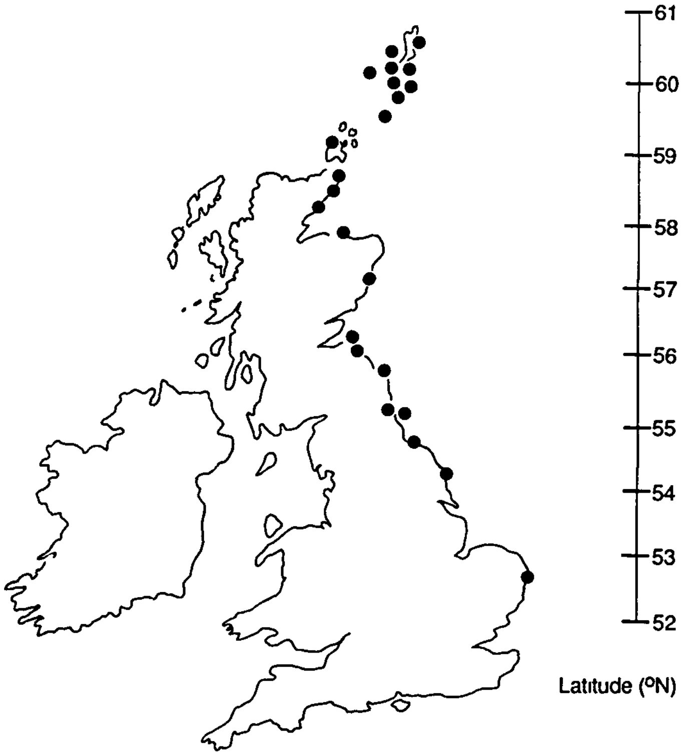

Figure 39 Locations of kittiwake colonies in east Britain where breeding success was recorded in 1986–88

Plate 21. Kittiwake on nest

Sea were collected between 1986 and 1988 (Figure 39). This small gull, which feeds at, or just under, the surface of the sea, is particularly suitable as a monitoring species because (i) it is common and widespread, (ii) it breeds on cliffs where its nests and young can easily be counted without causing disturbance to the birds or danger to the observer, (iii) it has a clutch of one to three eggs so that there is potential for variation in breeding success, (iv) it feeds its young mainly on sandeels, (v) a 'short-cut' method had already been developed (by ITE) to measure its breeding output, and (vi) much is already known about its population trends and biology from research by J Clarkson and colleagues at the University of Durham.

The results indicated considerable spatial and temporal variation in kittiwake reproductive success in north and east Britain. In 1986 and 1987, breeding success was generally high, with about one young fledged per breeding pair, but colonies in Shetland produced few young. In contrast, breeding success in 1988 was also lower in colonies well south in the North Sea, and the situation in Shetland had deteriorated to such an extent that all (or nearly all) of the chicks died (Figure 40) at eight colonies monitored by M Heubeck (Shetland Oil Terminal Environmental Advisory Group). Overall, there was a significant north/south trend in breeding success over the whole range, with success declining by 0.18 chicks fledged per completed nest for every 1° shift north.

The reduction in breeding success in 1988 was due mainly to chicks dying, although, in the northernmost colonies, some pairs deserted their eggs. Changes in the extent and severity of the breeding failures were matched by changes in the timing of the main period of loss. Thus, in Shetland, losses occurred earlier in 1988, when there was almost complete breeding failure, than in 1986 or 1987 when some chicks fledged, although relatively few by British standards. Similarly, in 1988, losses occurred earlier and were more severe in the most northerly colonies, whilst further south failures occurred later and were less extreme.

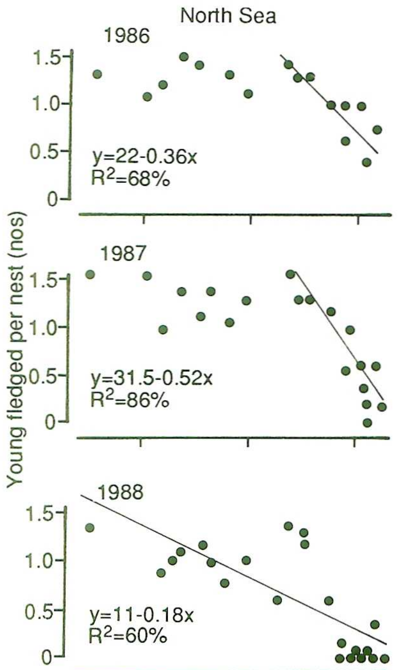

Figure 40 Breeding success of kittiwakes at the colonies plotted in Figure 39, showing a latitudinal decline within Shetland, Orkney and Caithness in 1986 and 1987 and throughout the western North Sea in 1988. The lines indicate significant linear relationships between young fledged per completed nest and latitude over the latitudinal ranges shown

Sandeel shortage

Sandeels were by far the most important item in the chicks' diet, but, in several colonies where food samples were collected, the proportion of sandeels present was markedly lower in 1988 than had been recorded previously. Also, there were fewer 0 group fish (ie fish hatched in the current year). Thus, there was a suggestion of a link between the availability of 0 group sandeels and kittiwake breeding success.

The evidence that food shortage was responsible for the low breeding success was mostly circumstantial, but, taken as a whole, compelling. First, the reduction in reproductive output coincided with a marked increase in the frequency with which young, including small, chicks were left unattended. Normally, small nestlings always have one or other of the adults with them, although larger chicks are occasionally left alone. There was no evidence that adult kittiwakes were just sitting on ledges away from their nests or occupying loafing areas, and the inference was that they were at sea trying to find food. Second, several other seabird species, which also depend on sandeels to feed their young, reared few or no chicks in Shetland in 1988. The species most severely affected were small-sized, inshore, surface or near-surface feeders, such as Arctic tern (*Sterna paradisaea*) and puffin (*Fratercula arctica*), or those which klepto-parasitise these species, ie the Arctic skua (*Stercorarius parasiticus*) and great skua (*Catharacta skua*). In contrast, deep-diving species, such as the guillemot (*Uria aalge*) and shag (*Phalacrocorax aristotelis*) were largely unaffected.

The stocks of sandeels around Shetland have declined in recent years, and this decline has been attributed to overfishing by a local fishery, which started in 1974 and reached a peak in 1982, and/or to natural factors. The available data from fishery research tend to support the latter cause for, although sandeel numbers have certainly declined, the spawning stock in 1986 was reported by P A Kunzlik (Department of Agriculture and Fisheries for Scotland) to be still more than 60% of the maximum recorded in 1984. A series of years when relatively few young sandeels recruited into the population appears to have resulted in a decrease in smaller-sized sandeels, on which many of the seabird species depend for food for their young It is possible that adverse environmental factors could be influencing the survival of larval sandeels and/or the transport of larvae into and out of the Shetland area However, the results of the survey of kittiwake breeding success suggest that the situation in Shetland, although more severe, is part of a more widespread change which extends well south into the North Sea

Additional evidence for a north/south gradient in conditions in the North Sea is provided by a series of counts of 18 guillemot colonies made over the past 15–20 years by the organisations listed in the acknowledgements These counts show that numbers increased at all the colonies during the 1960s and 1970s but the most northerly colonies started to decline about 1980, and, by 1988, numbers at all but the two most southern colonies counted, those at St Abb's Head and the Farne Islands, were decreasing

Poor recruitment

Long-term, detailed studies by ITE on the Isle of May, Firth of Forth, have revealed changes in the demography of the guillemot and puffin populations there, which occurred in the early 1980s and coincided with the levelling off in numbers after two decades of continuous steady increase In the guillemot the number of immatures recruiting into the population fell, although adult survival remained high, whilst in the puffin survival of both adults and immatures was reduced. However, in contrast to the kittiwake, neither species has, as yet, shown a reduction in breeding success, although adult guillemots in 1988 spent as little time as possible with their young One adult must remain with the chick to protect it from predators but, whereas in 1983 the pair spent an average of 60 minutes together while changing over, in 1988 the period was only seven minutes These observations indicate that the duration of a feeding trip had increased, and birds were having to travel further to feed and/or taking longer to catch prey in the feeding area

The future

There is, therefore, growing evidence of widespread changes in the population processes of a variety of seabirds breeding in colonies bordering the North Sea, and there is strong circumstantial evidence that these changes are associated, at least in part, with a reduction in food availability during the breeding season While it is as yet impossible to confirm a link with any specific environmental change, and indeed it is likely that the causal factors involved will be complex, long-term studies of the demography, feeding ecology and behaviour of seabirds and sandeels will provide essential information for the development of a realistic multi-species model of the North Sea ecosystem

Acknowledgements

ITE is grateful to the many observers who undertook much of the fieldwork, and to their parent organisations, principally the Royal Society for the Protection of Birds, the Shetland Oil Terminal Environmental Advisory Group, Britoil plc, the Universities of Aberdeen and Glasgow, and the Nature Conservancy Council, for fruitful collaboration

M P Harris and S Wanless

Declining fritillaries: the next challenge in the conservation of Britain's butterflies

(This work was partly supported by funds from the Nature Conservancy Council)

British butterflies have experienced enormous declines over the past 40 years Many sites have been destroyed, but, for conservationists, the most worrying feature has been the fact that many rarer species have also disappeared from Nature Reserves and land where foodplants remained abundant Indeed, it looked as if the British populations were following the pattern of those in the Netherlands, where more then 20% of all resident species have recently become extinct

Experience has shown that most attempts to conserve scarce butterflies fail, unless they are based on a detailed knowledge of each species' ecological requirements (Thomas 1984a) Considerable progress has been made with a few rarities (Thomas 1983, 1984b, 1989, Thomas *et al* 1986, Warren 1987), but there remain many declining species that cannot be conserved because they have not been studied at all The most urgent recent case involved certain butterflies that breed in woodland, notably five species of fritillary whose larvae feed on violets (*Viola* spp) The high brown fritillary *(Argynnis adippe)* is the most acutely threatened Colonies once bred in most large southern woods, but are now restricted to a handful of western sites even the recent map (Figure 40), based on data from ITE's Biological Records Centre and local surveys, greatly overemphasises the current status, for most of the remaining colonies in central England disappeared during the 1980s (Thomas & Webb 1984) The pearl-bordered fritillary *(Boloria euphrosyne)* has declined almost as rapidly, but from a higher baseline, whilst the small pearl-bordered *(B selene)* (Plate 22), dark green *(A. aglaja)* and silver-washed *(A paphia)* fritillaries have fared only slightly better

It has long been recognised that these declines were associated with the

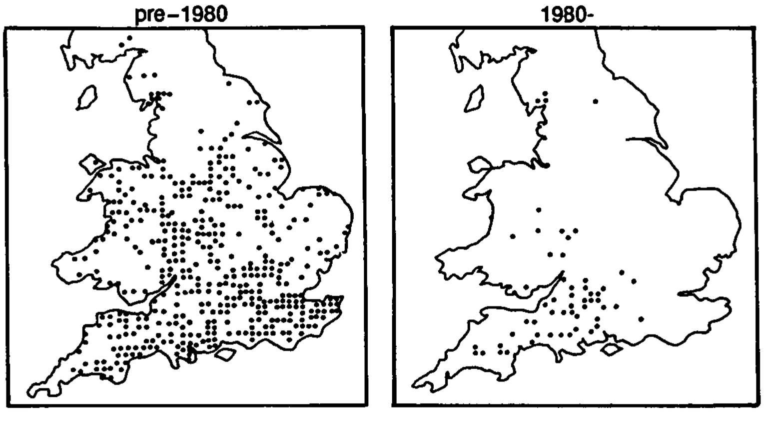

Figure 40. Changes in the status of the high brown fritillary

Plate 22. Small pearl-bordered fritillary

replacement of coppicing in British woods by modern forms of silviculture, which result in shadier conditions and fewer violets on the forest floor. However, most fritillary colonies have disappeared from woods that still contain a great abundance of violets, and losses have been particularly severe in broadleaved woods, including Nature Reserves. Most remaining populations are confined to young conifer plantations, but are likely to become extinct as the trees mature.

Research into the requirements of the violet-feeding fritillaries started in 1984 in an attempt to define the exact conditions needed by each species. This research has involved making intensive studies of the behaviour and habitat preference of each butterfly within two heterogeneous sites, coupled with more superficial analyses of a range of woods that held various-sized (or no) populations of the different species. Adult fritillaries were individually marked, released and recaught in order to assess their ability to disperse and colonise new habitats, and measurements were made of the features of each site that were used by every stage of each life cycle. Particular attention was paid to an analysis of the precise places chosen for egg-laying: the species, density and growth form of violets were recorded where eggs were laid, together with measurements of the incidence of direct and indirect light, the integrated temperatures at ground level, and the stage of each microhabitat within the woodland succession.

As with earlier studies of butterflies, the needs of each fritillary's young stages proved to be much more specific than had previously been thought. Although a variety of violet species can be eaten, all fritillaries usually eat the same violet on a particular site. However, there is little overlap between the plants that are chosen. The pearl-bordered fritillary uses young violets that have recently sprung up in bare ground, or which are growing in a warm, sheltered microclimate. The small pearl-bordered fritillary lays on the same violets a year or two later, when the plants are larger and surrounded by lusher growth, whilst the dark green fritillary – which is more characteristic of open grassland – uses large-leaved clumps that are partly choked by grass and yet not shaded by trees. The silver-washed fritillary breeds within the body of a wood on clumps of violets growing in sunny patches beneath a thin cover of trees, but even this species requires direct sunlight to reach at least 25% of the woodland floor. More research is needed on the high brown fritillary, but it appears to need large clumps of established violets growing in bare, open ground by the edge of shrub.

The five fritillaries, therefore, use violets at different stages quite early in the woodland succession. Suitable conditions can be short-lived for any particular species, especially on soils where there is a vigorous regrowth after a clearing. A complicating factor is that these butterflies also have limited powers of dispersal (Figures 41 & 42): marking experiments have shown that the silver-washed fritillary flies freely throughout a wood, but appears reluctant to cross farmland to reach neighbouring sites. The small pearl-bordered fritillary is considerably more sedentary; recent clearings that contain ideal breeding conditions are not necessarily colonised, if there is a barrier of a few hundred metres of shady woodland to cross.

The implications of this research are that woods need more frequent small-scale clearings than they currently receive, if they are to contain continuity of the breeding habitats of every violet-feeding fritillary; a break of perhaps three to five years between clearings can be fatal for the pearl-bordered fritillary, and, once lost, there is little chance that a site will be recolonised when suitable conditions

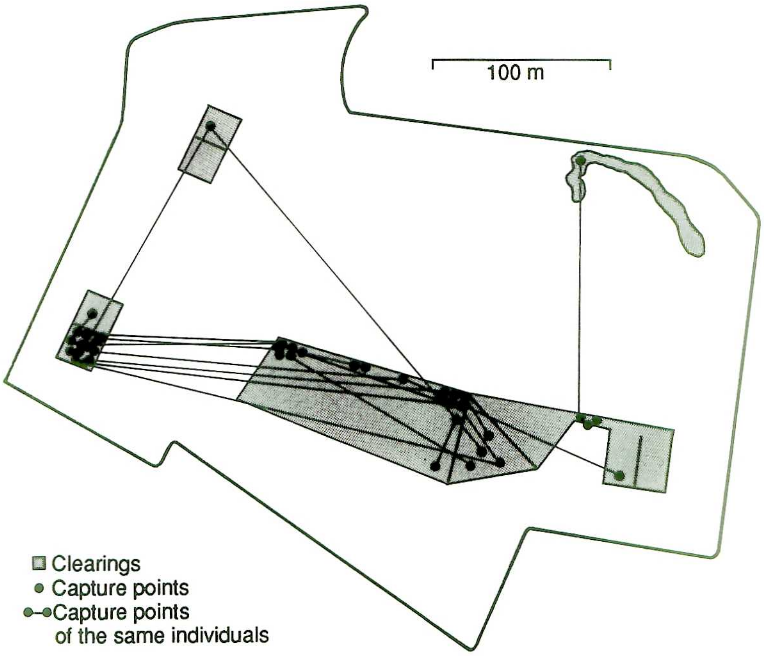

Figure 41. Movements of the silver-washed fritillary between clearings in an isolated wood. (o——o) represent captures of the same individual over a period of two weeks; the butterflies are moving freely through the wood

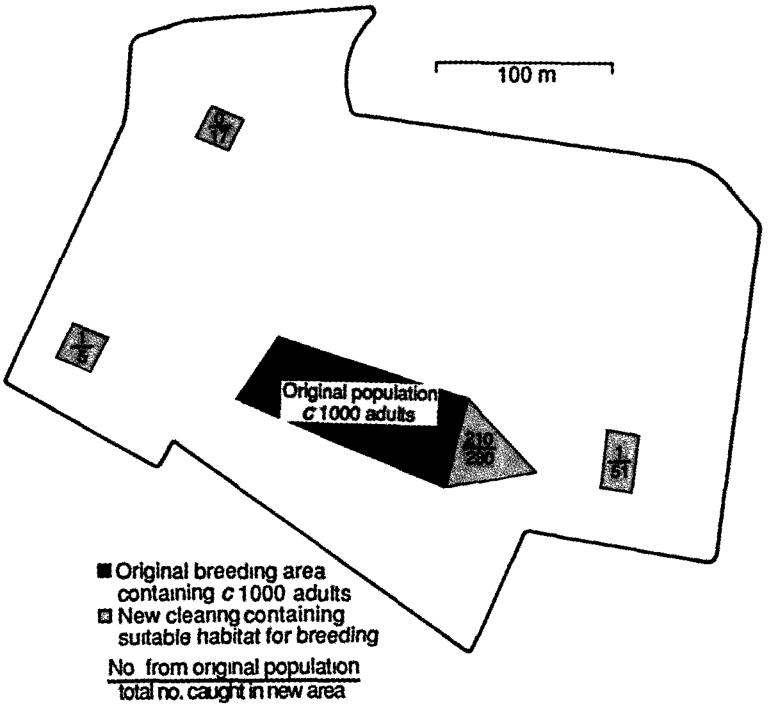

Figure 42 Movements of the small pearl-bordered fritillary between its breeding areas within the isolated wood shown in Figure 41 The original population was confined to a large clearing shown in black. Four new clearings were made, all of which contained abundant violets suitable for egg-laying during the experiment Twenty marked adults were introduced to each new clearing the figures represent the number of captures made in each clearing in the following two weeks and the proportion of these that were immigrants from the original population Only two immigrants were caught in the three clearings that were 100–150 m from the old population whereas 210 captures of immigrants were made in the clearing that adjoined the old area

recur, unless another colony exists nearby This possibility is becoming remote as the remaining populations become more isolated

Although most modern woods are too shady to support any species of fritillary, it seems likely that it will be possible to conserve populations on Nature Reserves and in commercial woodland, if small areas of land are suitably managed Encouragement can be taken from the case of another fritillary, the heath *(Mellicta thalia)*, which also breeds on early successional plants in fresh clearings Ten years ago, this rarity was reduced to about eight British sites and had disappeared from both the Nature Reserves that had been established to save it Research at ITE Furzebrook (Warren 1987) showed that this species had similar requirements to the pearl-bordered fritillary, and that all known remaining colonies were doomed to extinction in the near future if management plans were not changed An emergency programme was introduced, and within five years each of its two Reserves were again supporting colonies of several thousand adults Other Reserves were also established and have responded similarly to science-based management, whereas the few sites that were left to normal forestry practices have already lost their heath fritillary populations

J A Thomas and R G Snazell

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Population dynamics of estuarine mussels

Estuaries are important breeding areas for fish, they support shell fisheries, and they are important winter feeding areas for migratory wading birds and wildfowl They are also prime targets for land claim, various forms of development, and waste disposal Ecologists are often asked to comment or advise on the likely outcome of such schemes While it may be possible to answer in general terms, it is difficult to make predictions because the mathematical relationships describing the interactions within and between the various biological components are lacking or incomplete The factors which determine the density of one of the most important species (in terms of biomass), the mussel (*Mytilus edulis*), have been studied in the River Exe estuary in Devon These factors have been incorporated into a mathematical model which can be used as a predictive tool There is also a parallel study of the main winter predator of adult mussels on the Exe, the oystercatcher (*Haematopus ostralegus*), and the two studies will be combined to model the predator/prey system

The entire intertidal mussel population was studied because mussels are known to move voluntarily when young, and storm-driven immigration or emigration can cause errors in studies restricted to one location The population was sampled in March and September over a seven-year period from September 1976 to 1983 Each survey consisted of 600 samples (each 0 04 m^2), distributed over

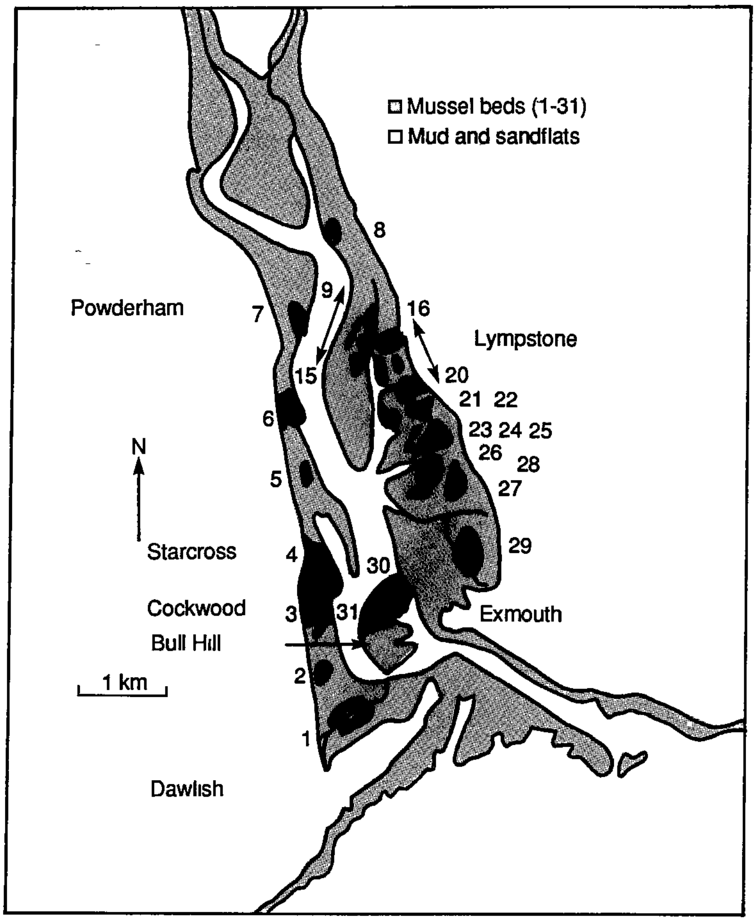

Figure 43 Map of the River Exe estuary, showing the location of the mussel beds (numbered 1–31) in September 1976 Not all of the beds are shown as separate areas Some areas of mussels were divided into two beds along natural boundaries, such as freshwater streams (beds 3 & 4) or deep channels (beds 30 & 31) Only twelve beds remained at the end of the study

the mussel beds according to a stratified random sampling scheme The number of samples allocated to each bed was in proportion to its area, weighted by the standard deviation of the density estimates of the most abundant age classes of mussels present The mussels were counted and measured, and their age distribution was determined from a subsample (40%), for which the winter spawning rings on the shells were identified and counted The areas of the mussel beds were determined by walking 9–20 lines at right angles to a fixed baseline, measuring distances with a one m pacing stick and noting when boundaries were crossed This method was preferred to more conventional mapping techniques because the surface topography of some beds was uneven

Of the 31 mussel beds sampled in September 1976 (Figure 43), 12 contained 82% of the mussels, the remainder were either very small or contained only a low density of widely scattered mussel clumps By March 1980, only the 12 major beds remained, the others having been destroyed by storms However, the decline in mussel bed area (24%) was countered by an equivalent increase (36%) in mussel density in the remaining beds, so that the numbers of adult mussels showed no significant trend (Figure 44i) It seems, therefore, that most of the mussels from the smaller beds were incorporated into the larger beds

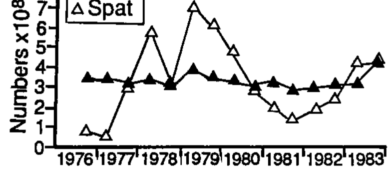

Figure 44 The numbers of (i) adult mussels 1–9+ years old, and (ii) mussel spat, 0 year in the estuary between 1976 and 1983 The numbers of adults varied little and showed no significant trend whereas the numbers of spat mussels varied widely within and between years, suggesting that a strong regulatory factor acted upon the mussels in their first year on the beds in the estuary

In contrast to the stability of the adult density, which only varied between years by a factor of 1 5, spat mussel (0 year) density varied widely (17-fold) throughout the study (Figure 44ii) This variation indicates that a strong damping process was acting in the first year

Density-dependent mortality in the first year and the period when it occurred were investigated by key factor analysis This analysis divided the lifespan into a number of stages (egg, larva 1, , adult), and determined (i) the stage at which mortalities were density-dependent, and (ii) the greatest influence on changes in the total generation mortality (called the key factor) These mortalities need not be the same, and rarely are

It was possible to measure five stage mortalities within the first (0) year k_1 and k_2 were losses of potential eggs due to the failure of the adult females to grow to the maximum possible size at each age, on the different beds and in different years, respectively k_3 was the losses in the plankton and primary settlement stages, or the failure of plantigrade larvae to settle on the adult mussel beds k_4 was the losses in the first summer, and k_5 the losses in the first winter, on the mussel beds

In their second summer, mussels develop a gonad and are regarded as adults The lifespan of mussels in the Exe is about ten years, but the study lasted only seven years, so the key factor analysis could not be applied beyond the first year

The analysis showed that only losses during the first winter on the mussel beds (k_5) were density-dependent (Figure 45), and operated in a strongly regulatory manner Above the critical density of 57 m^{-2}, few extra mussels survived as density increased, resulting in the damping seen in Figure 44 The mortality agent was probably predation by juvenile shore crabs (*Carcinus maenas*)

Losses in the plankton and primary settlement stages (k_3) were identified as the key factor in the first year, having the greatest influence on changes in the total

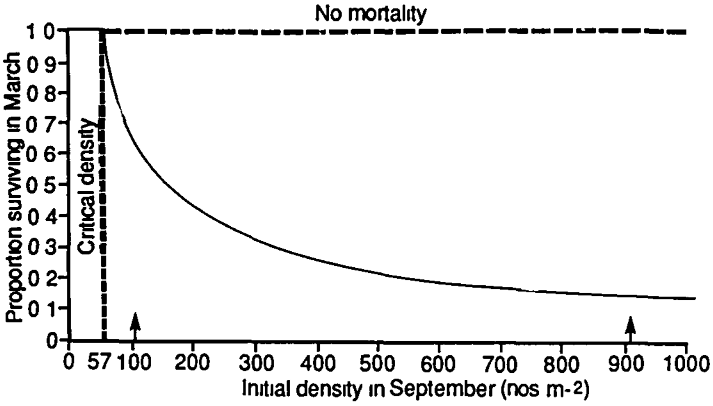

Figure 45 The effect of the first-winter density-dependent mortality k_5, on the proportion surviving in March, as the initial density in September (N_5) increased The curve was calculated using the equation, $k_5=0\ 685 \log N_5-1\ 204$ The arrows indicate the range of densities recorded As the initial density increased, few extra individuals survived, and the numbers entering the adult population were regulated within narrow limits

mortality (K) between years These losses were also by far the largest, and had, therefore, the greatest influence on the level of K

k_3 was inversely density-dependent in six out of seven years The 1977 cohort suffered twice the normal winter and spring rainfall, and the spring spat fall failed, despite the potential egg production in September 1976 being the largest recorded This failure was probably due to both lowered salinities in the estuary and the large amounts of liquid mud deposited on the mussel beds by the flooded River Exe

The other losses in the first year, k_1, k_2 and k_4, were independent of density It was possible, therefore, to develop a predictive model, incorporating the density-dependent relationship for k_5, the inverse density-dependent relationship for k_3, and mean values for the density-independent mortalities, k_1, k_2 and k_4, which explained *c*90% of the variability in the total losses in year 0

The total density of adults was remarkably stable (Figure 44), but did vary a little, for example, density increased in spring 1979 following the large spat fall in 1978, but then declined through 1980, despite an even larger spat fall in 1979 This evidence suggested the possibility of density regulation within the adult population

The pattern of mortality varied with season (summer or winter) and with increasing age Following the large loss during the first winter (mean 68%), there were only small gains in the summer and losses in the winter for the next four years Only the summer immigration of three-year-old animals (mean +10%) was statistically significant From their sixth year onward, there were increasingly large losses each year in summer after spawning (mean 39%) and in winter, as a result of predation by oystercatchers (24%)

However, density-dependent mortality was detected only in the second winter and tenth summer, ie in the youngest and the oldest adults The mathematical relationship describing the tenth-summer mortality indicated an almost perfect density dependence, but this could not be an important population regulatory mechanism, as few animals reached this age The second-winter mortality had the potential to operate in a strongly regulatory manner, but there were significant losses of second-winter mussels in only three of the seven years studied

The second-winter mortality was also related to the total density of 'all' (1–9+ year) adults (r^2=72%) and, more specifically, to the density of 'young' (1–4 year) adults (r^2=75%), perhaps indicating competition among adults for food or space Mortalities during the fourth, fifth and sixth summers were also related to the total densities of young or all mussels The equations describing these relationships indicated that these were overcompensating mortalities, which means that, above the critical densities at which these relationships operated, two or more mussels died for every one recruited to the adult population Potentially, this behaviour could have caused violent fluctuations in density, but, in reality, did not do so because the total density of adults did not greatly exceed the critical densities (mean values +7% to +30%) and soon fell below them These relationships could, therefore, do no more than act as a 'fine-tuning' mechanism, retaining adult densities within narrow limits

The study has shown that the greatest mortality of mussels occurs in the plankton/settlement stages However, the population was regulated by the mortality of spat mussels in their first winter on the mussel beds, not by oystercatchers eating adult mussels So, what part do oystercatchers play in the population dynamics of the mussels? On average, they ate 24% of the adult mussels each winter, but, because their preferred size range included the most fecund mussels, egg production was reduced in spring by 37% However, more importantly, mussel spat in the Exe only settled within the byssus threads of adults By removing adult mussels, oystercatchers could reduce the amount of space for spat to settle On the other hand, 'thinning out' the adults could reduce competition for food for those spat which do settle, and could enhance their chances of survival These subtle effects require an experimental approach to unravel, and will be the subject of further studies

S McGrorty

The Arctic: a stressed environment for plant growth and reproduction

Global warming and climate change are probably the greatest environmental problems currently facing mankind Predictions from the various General Circulation Models (GCM) generally agree that the greatest changes will occur at the highest latitudes Temperatures between latitudes 60° and 90° could increase by aboout 3°C and 4°C in winter, and by about 0 5° and 0 9° in summer by the year 2040 The impacts of global warming on vegetation are, therefore, likely to be recognised at high latitudes sooner than elsewhere

While the predictions of climate change are uncertain, it is clear that we are in a poor position to predict the extent, nature, mechanisms and speed of the impacts on plant populations and communities ITE is collaborating with scientists at Abisko in Swedish Lapland and on Svalbard, in an attempt to understand and model the relationships between the population dynamics and environment of species near their distributional limits By considering the responses of a plant to its environment at all stages of its life cycle, it should be possible to relate climatic change impacts to the populations and abundance of a species, and to identify sensitive stages and processes

Arctic environments

Arctic environments have long, dark winters and short growing seasons with continuous, but low intensity, daylight Growing seasons are short because of low air and soil temperatures in exposed habitats, and the long duration of the snow cover in sheltered habitats Plants usually have developmental processes extended over more than one season, and perennials with pre-formed flowers and evergreen leaves are common

Decomposition rates are slow, and freeze/thaw cycles in moist soils with permafrost create disturbance through the repeated frost-heave of soils The associated meso- and microtopographical features lead to a pronounced microclimatic and edaphic patchiness both in space and time, and plants compensate for this patchiness and generally low soil fertility in many ways, such as conserving, storing and recycling nutrients As temperatures in the Arctic increase, much of the permafrost will thaw and the patchiness will decrease, thus enabling the development of a more uniform vegetation core

The vegetation of the Arctic varies from aggregations of few species into islands surrounded by bare ground in the high Arctic to continuous two-storied canopies in the forest tundra of the sub-Arctic In the most extreme and exposed habitats with open vegetation, non-clonal cushion plants which propagate either by seeds or viviparous propagules are the dominant life form among vascular plants. In less extreme habitats with closed vegetation, however, clonal plants which maintain their populations by vegetative spread rather than seed recruitment are common.

Case studies

Cassiope tetragona

On high Arctic Svalbard, studies of a slow-growing ericaceous dwarf shrub have revealed an historical record of leaf production, leaf extension growth and flowering over a 20-year period

Cassiope tetragona is evergreen. Its leaves photosynthesise for up to five years but remain attached to stems for 15 or more years, and two patterns of leaf length are evident Short leaves alternate with longer leaves on a regular and annual basis, and there is an overall trend of increasing leaf length as the shoot develops (Figure 46) By removing this developmental trend, it is possible to correlate the number of leaves produced each year and leaf length with climate These correlations show that leaves are formed one year before they open, and that temperature and precipitation in the spring of the current and preceding years correlate significantly with leaf production (Figure 46) Thus, poor leaf length in 1981 and 1982 was associated with cold summers, whereas an increased number of large leaves was associated with higher summer temperatures and precipitation between 1978 and 1980

Such studies establish baselines of plant responses to climate in recent times in those areas where dendrochronology is often impractical Future changes in leaf production and development can then be interpreted as either a new response to a changing climate, or transient variation similar to that in the past The data are also being used to investigate fluctuations in reindeer (*Rangifer tarandus*) populations on Svalbard related to the amount of plant food available, and to identify years in which flowering occurred

Lycopodium annotinum and *Carex bigelowii*

In the closed vegetation of the Arctic, recruitment to populations from sexual reproduction often occurs only after disturbance, eg fire, frost-heave or overgrazing, and then clones may maintain themselves indefinitely, and certainly for hundreds of years

The production of annual segments of growth in the creeping *L annotinum* enables clones to be treated as populations of parts, each with probabilities of survival and fecundity related to age Population growth models developed during collaborative studies with the Universities of Lund and Lancaster show that the growth of clones was most sensitive to changes in survival probabilities, particularly in the youngest age classes

In the locations where the clonal sedge *C bigelowii* has been studied, no

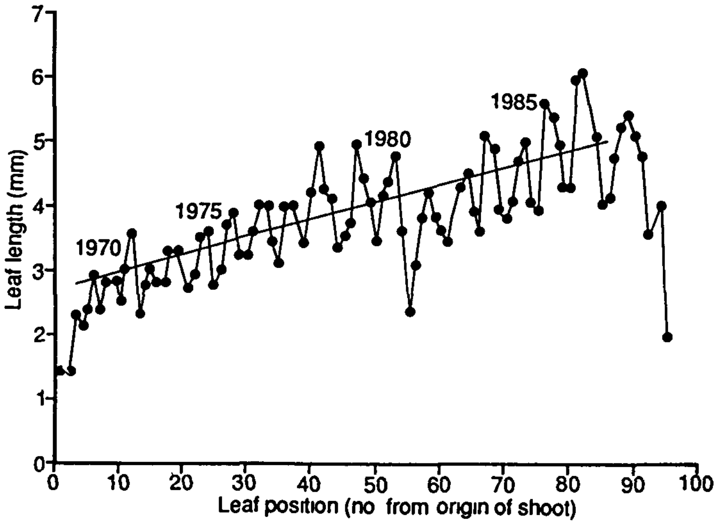

Figure 46. Example of variations in leaf lengths related to their position on shoots of *Cassiope tetragona* The thick line represents the general developmental trend, and each peak represents one growing season's production of leaves. Thus, in 1979 six large leaves were produced in a warm summer whereas in the cooler summer of 1982 only four small leaves were produced

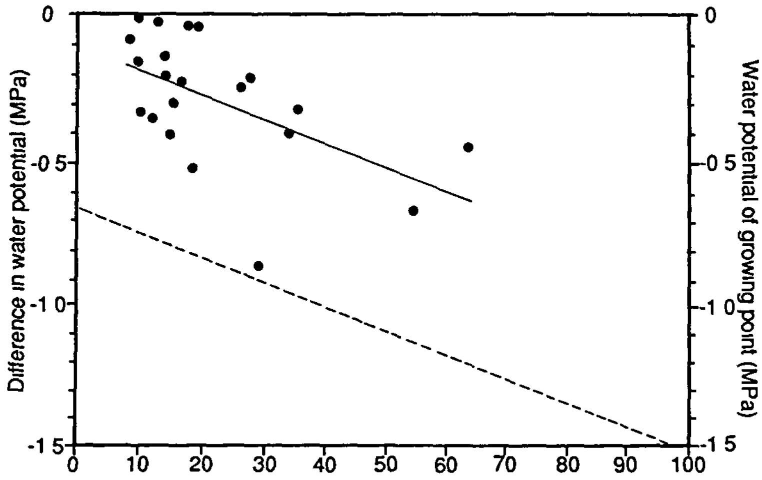

Figure 47 The water potential of the growing point of *Lycopodium annotinum* related to the distance between it and the nearest root The negative values indicate that the growing point has a lower water potential than the root and that water will flow from the root to the growing point The broken line represents distances predicted by assuming a mean root water potential of –0 62 MPa and shows the predicted maximum distance (97 cm) when the growing point dies at – 1 4 MPa As temperatures increase with climate change this distance will decrease

seedlings have been found However, the populations of tillers are still controlled by flowering Flowering occurs in older tillers, which then die, and varies in frequency from year to year After a peak in flowering frequency, the population of tillers crashes due to the death of flowering tillers, but then increases as buds break dormancy This pattern appears to create cycles in tiller densities which must be understood if the climatic effects are to be interpreted, particularly the relationship between flowering and climate

Within *L annotinum*, the growing points of the horizontally creeping branches, or stolons, are the priority sinks for water, nitrogen, phosphorus and potassium There is a gradient of decreasing water potentials from old to young tissues, which ensures a flow of water and nutrients to the growing point

This subsidisation of the growing points allows the horizontal branches to cross unfavourable microsites where roots cannot develop However, as the distance between the growing point and nearest root increases, the water potential of the growing point decreases (Figure 47) Eventually, the water deficit of the growing point becomes too great, and it dies It is, therefore, possible to calculate the maximum patch size (97 cm) in which *L annotinum* can survive (Figure 47) If temperature increases as the climate changes, however, the growing points will experience water stress sooner, the patch size which *L annotinum* can tolerate will decrease, and its distribution will become limited

While the growing points are important sinks for water and some nutrients, they are also important sources of hormones, which control the number of side branches and their rates of development This control is sensitive to nitrogen supply As the climate changes and decomposition rates increase, the control system will break down and parts of the same plant will begin to compete with each other for resources, thereby damaging their chances of survival As there is no bank of dormant buds in *L annotinum*, it is sensitive to such damage

The persistence of connections between old and young branches enables the efficient recyling of scarce nutrients to priority sinks Approximately 63%, 64% and 90% of nitrogen, phosphorus and potassium respectively are recycled, and the plant can survive with only 5% of its total dry weight invested in roots However, if nutrients become more available as decomposition rates increase with increasing temperatures, the small roots will be unable to compete with the larger roots of other species, and *L annotinum* will be displaced

C bigelowii forms extensive tiller systems, and there is a division of labour between tiller generations Young tillers possess leaves and export energy-containing compounds to older leafless generations at least eleven years older (Figure 48i), while these old leafless generations retain active roots, and take up and translocate nitrogen to the young photosynthesising tissues (Figure 48ii)

The young tillers of *C bigelowii* suppress the growth of many buds on the older attached tillers, but, when connections between the young and old tillers are broken, old dormant buds begin to develop *C bigelowii* is tolerant of grazing and disturbance when a tiller is defoliated, there is increased translocation of photoassimilates from neighbouring tillers, but this translocation decreases if damage continues These two mechanisms ensure that *C bigelowii* will be able to buffer changes in climate or disturbance to some degree, but not indefinitely

A deterministic, or unvarying, growth model of the architecture of *L annotinum*, based on population dynamics data, showed that the observed mean angle of branching and the presence of apical dominance decreased the risk of overlap between branches within the clone In the field, however, each plant has a different form (Figure 49i,ii) For example, the direction of growth can soon be diverted from the initial direction by microtopography The apparent chaos of the architecture found in the field can be simulated by introducing random elements into the architectural model (Figure 49iii,iv)

This model includes the possibilities for growing points to survive and die at different ages, for branching to occur and direction of growth to change, for roots to be produced, and for clones to fractionate into separate plants The model has identified features and age classes sensitive to change, and has provided long-term predictions of how clones develop However, the random variations are unintelligent, and a process-related model is being developed in which the death of growing points, root production, direction of growth, etc, are related to the environment For example, *L annotinum* seems unable to respond to nutrient-rich pockets, and its clonal architecture seems to be suited to continuous mobility This characteristic may serve to reduce competitive encounters, which will increase as more opportunistic species respond rapidly to climate change

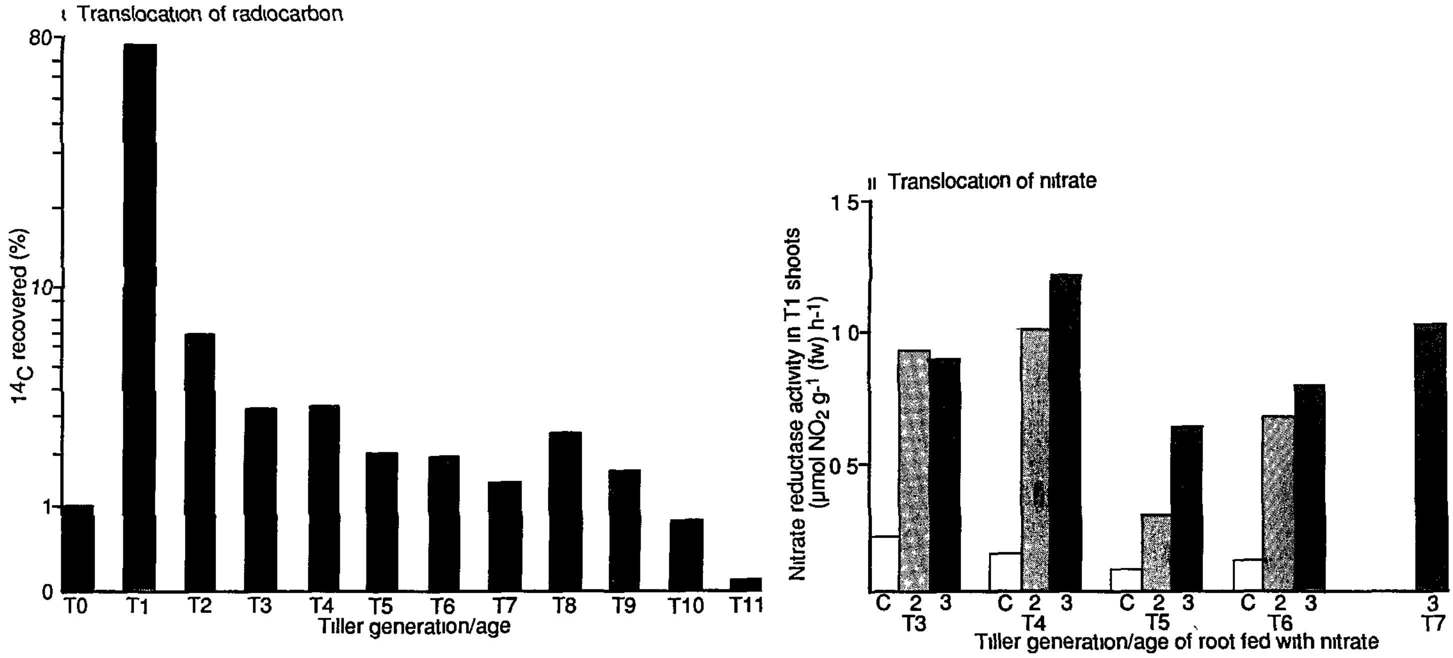

Figure 48 The different functions of different tiller generations in *Carex bigelowii*, illustrated by translocation between them This is one of the processes which will help *C bigelowii* initially to accommodate the impact of climate change NB (i) shows ^{14}C in each tiller generation, whereas (ii) shows nitrate only in the T1 generation

i Translocation of radiocarbon from a young photosynthesising tiller (T1) labelled with $^{14}CO_2$ to older leafless generations

ii Translocation of nitrate, determined by assaying the activity of the inducible enzyme nitrate reductase to the young T1 tiller from older tillers whose roots were incubated in nitrate

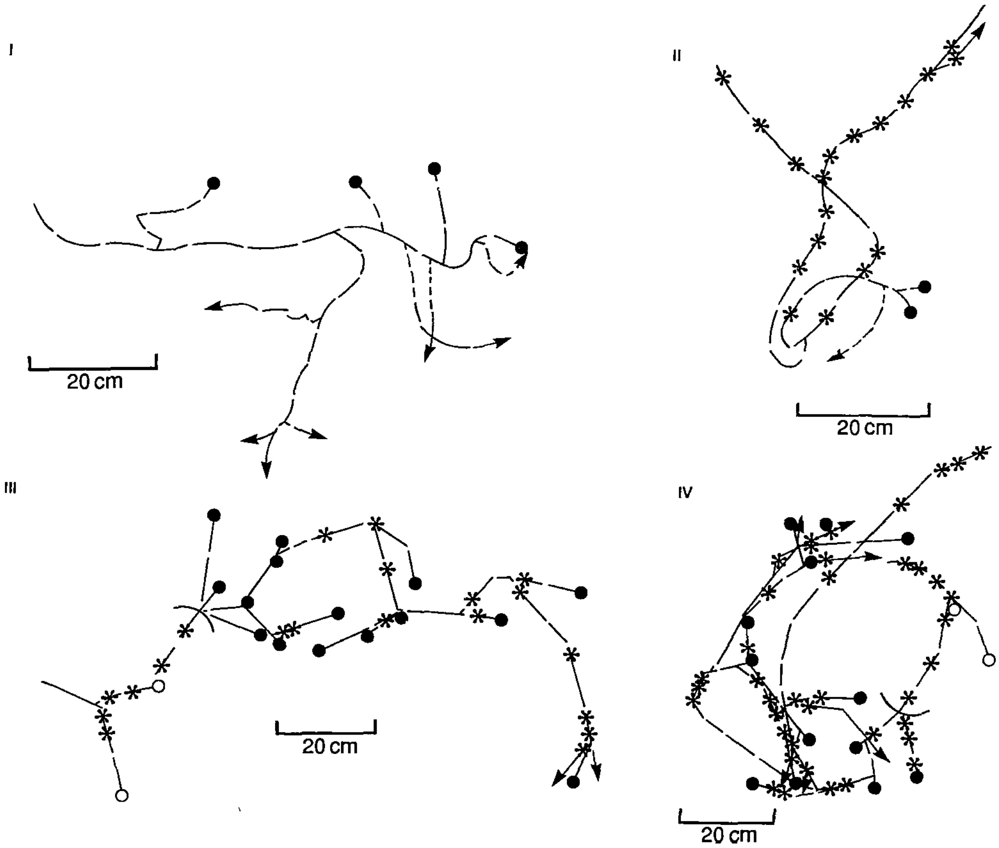

Figure 49 Maps of the horizontal branch systems of *Lycopodium annotinum*

i-ii Examples of plants mapped in the field

iii-iv Examples of plants simulated by the random architectural model for 25 years After 25 years, (iii) had two living growing points 19 dead and 17 roots shared between four plants, three of which died. (iv) shows the ability of the plant to turn through 360° (see also (ii)) It has six living growing points 22 dead and 34 roots shared between two plants, one of which survived.

Gaps delimit annual segments
Circles = dead growing points
Arrows = living growing points
Stars = roots
Thin lines bounded by arcs = senescent parts of the clones
Large arrows = start and initial direction of clone

Such models of clonal growth will enable us to predict some responses to climate change

In contrast to *L annotinum*, *C bigelowii* responds to patchy soil fertility and light penetration Two types of tiller are produced, one with long and one with short rhizomes When growing in nutrient-rich pockets, more short-rhizome tillers are produced, thus maximising the exploitation of the resource This opportunistic response is accompanied by aggressive competitiveness, and dense swards may be produced Thus, as nutrient availability and temperatures increase due to the change in climate, *C bigelowii* will be able to take advantage of the improved conditions

Conclusions

In the high Arctic where climate change will be greatest, the prevalence of slow growth and reproduction by seed and bulbils will lead to early impacts on plants such as *Cassiope tetragona* Such species should be targeted for monitoring

At lower latitudes in the Arctic, clonal integration may provide a buffer against the patchiness of the habitat, and against such impacts as grazing and climate change Clones may respond slowly at first to climate change, and then the impacts may be sudden Monitoring the impacts on clonal plants may, therefore, be inappropriate, and predictive models are required

The two totally unrelated species, *Lycopodium annotinum* and *Carex bigelowii*, share many attributes of clonality which are successful in Arctic environments However, the opportunistic responses of *C bigelowii* and its ability to tolerate disturbance may favour its initial ability to withstand climate change, in contrast to the relatively inflexible *L annotinum*

The stress-tolerant strategies of Arctic plants are mirrored by species from alpine and montane areas further south Similar responses to climate change could, therefore, be expected However, in the alpine and montane areas of temperate regions, the degree of change will not be as great as that in the Arctic and will be slower Thus, an early understanding of plant responses in the Arctic should enable the prediction of the type of change which will occur in related environments further south

T V Callaghan

Community ecology

The understanding of successions is fundamental to community ecology, and the following three articles illustrate different aspects of ITE work.

The report on phosphorus and successional changes in lowland heaths uses the PCAL model to investigate not only the relationship between nutrient status and successions, but also the perturbations caused by different management regimes, notably grazing. The analysis is used for determining suitable methods for heathland conservation. The second report also uses an ITE-developed computer program (TABLEFIT), to provide an objective numerical method for classifying vegetation types even with incomplete data sets. The automated identification of types provides the ability to specify likely trends in succession, soil and other factors, that can then be used for site evaluation and management.

The third report considers the possible effects of climate change on populations and the more subtle changes within communities. It emphasises the problems in separating directional change from background fluctuations, and illustrates how long-term data sets can be invaluable for separating cause and effect (especially through simulation modelling), whilst recognising the need for controlled experiments of comparative ecophysiology.

Plate 23. Great Ovens Hill, Dorset, where open heathland has survived in the absence of grazing, but with some invasion by Scots pine (*Pinus sylvestris*) from an adjacent plantation

Phosphorus and successional change in heathland vegetation

Heathland undergoes continual change, and management decisions must consider both structural and functional relationships. Common heather *(Calluna vulgaris)* dominates the vegetation when there are low levels of plant nutrients in soil with a pH between 3.5 and 6.7, the climate is oceanic, and there is protection from low temperatures by snow cover during the winter. Factors such as grazing and burning must also be sufficient to arrest natural succession to scrub and woodland. Most heathlands were once subject to 'rights of common', where grazing in combination with heather burning maintained a low nutrient status in the soil and prevented the establishment of trees and scrub. Unfortunately, grazing by stock has now ceased in many areas, and the loss of rabbits (*Oryctolagus cuniculus)* by myxomatosis has reduced grazing pressure, with the result that many heathland areas have now become birch (*Betula* spp.) woodland.

Studies of production and nutrient budgets (Gimingham, Chapman & Webb, 1979) have tended to consider *Calluna* heathlands as a single entity. However, lowland heathlands in southern England are characterised by higher temperatures, lower rainfall, and lower soil nutrients, whilst upland heaths are characterised by lower temperatures, higher rainfall and generally higher nutrient levels in the soil (Chapman & Clarke 1980). Lowland heathlands in Britain occur on a variety of soils, and show a range of vegetation from open *Calluna* to woodland containing only relict areas of heathland. Many such sites have been open heathland in living memory. Sites can be placed within three broad vegetation categories:

1. *Calluna* heathland with little or no invasion by scrub or trees;
2. sites which are still *Calluna* heathland, but with invasion by gorse (*Ulex europaeus*);
3. sites where there has been extensive invasion by birch, and where *Calluna* now only survives in small patches.

A model (PCAL), developed by Chapman, Rose and Clarke (1989) and based upon data from dry heathland in Dorset, has been used to examine the long-term consequences of management techniques and the importance of specific factors in the phosphorus economy of *Calluna* heathlands. This model is controlled by the growth of the vegetation described by the Gompertz function, but is limited by the availability of inorganic phosphorus in the soil. Root production has been assumed to be directly proportional to above-ground

Plate 24. Bramshot Heath, Hampshire – an area subject to colonisation by birch and gorse, and open heathland now restricted to small areas

production Inputs to the system are in the form of carbon by photosynthesis, and phosphorus from atmospheric deposition and mineral sources

Available inorganic phosphorus is assumed to be present in the soil either as adsorbed phosphorus or within the soil solution The equilibrium between these two forms is described by the Langmuir equation

$$y = a\,s\,x/(1+ax)$$

where y = adsorbed phosphorus ($\mu g\ P\ g^{-1}$),
x = soluble phosphorus ($\mu g\ P\ ml^{-1}$ soil solution,
s = adsorption maximum in $\mu g\ P\ g^{-1}$ soil, and
a = constant defining the rate of equilibrium

The concentration of phosphorus in the soil solution predicted by this equation, the volume of water draining from the root zone, and the soil moisture equivalent are used to calculate drainage losses of inorganic phosphorus from the system

The losses of phosphorus predicted by the model depend upon the constants in the Langmuir equation Soils from a range of heathlands in southern England have been examined in relation to their phosphorus adsorption characteristics, and placed in one of the three vegetation categories described above (Chapman, Rose & Bassanta 1989)

The soils examined showed a range of adsorption curves At one extreme were soils derived from Tertiary sands, with adsorption maxima of less than 100 μl P g^{-1} soil, while at the other extreme were soils from Dartmoor with adsorption maxima in the order of 4000 $\mu g\ P\ g^{-1}$ soil Soils from other heathlands in lowland Britain produced values between these two extremes

When the phosphorus adsorption maxima for each site were plotted against levels of isotopically exchangeable phosphorus, there was a clear relationship with vegetation type In the absence of grazing, or alternative management, open *Calluna*-dominated heathland can persist where the phosphorus adsorption of the soil is less than about 70 $\mu g\ P\ g^{-1}$ soil However, in the absence of grazing, invasion by gorse is likely where the adsorption maximum lies between about 70 and 700 $\mu g\ P\ g^{-1}$ soil Where it exceeds 700 $\mu g\ P\ g^{-1}$ soil, succession to birch wood is probable, if grazing or management is not maintained Sites, such as Dartmoor, Exmoor and the New Forest, that remain as open *Calluna* heathland despite phosphorus adsorption levels over 300 $\mu g\ P\ g^{-1}$ soil, are all still grazed, or managed by burning or mowing Climate might retard the development of woodland on Dartmoor and Exmoor, but it is unlikely that the New Forest would remain as open heathland, if grazing or management were discontinued

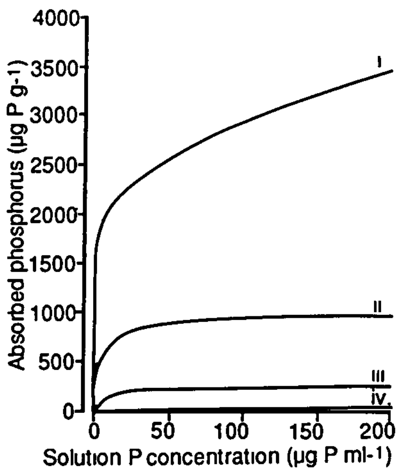

Figure 50. Adsorption curves fitted to data from (i) Headland Warren, Dartmoor – an area with high soil phosphorus adsorption capacity, but maintained as open heathland by grazing, (ii) Langford Heathfield, Somerset – an ungrazed site subject to invasion by trees (iii) Clayhiddon Turbary, Devon – an ungrazed site with areas invaded by gorse, (iv) Hartland Moor NNR, Dorset – an ungrazed heathland with low soil phosphorus adsorption capacity, where successional change is slow

The range of phosphorus adsorption maxima shows that soils from Dorset are not typical of heathlands in general Whilst the concept and assumptions made in the model remain valid, it is probable that leaching of phosphorus will be lower on many other sites (Gimingham & de Smidt 1983) Thus, greater proportions of the phosphorus released by burning and decomposition would be retained in the soil Hence, the rate of change of vegetation, in the absence of grazing or management, might be more rapid than in Dorset

Heathlands in lowland Britain are, largely, the result of particular forms of land use on suitable soils Changes in land use have led to marked changes in both the structure and composition of the vegetation and associated fauna of many British heathlands The maintenance of representative areas of heathland in some areas of lowland Britain is an immediate problem

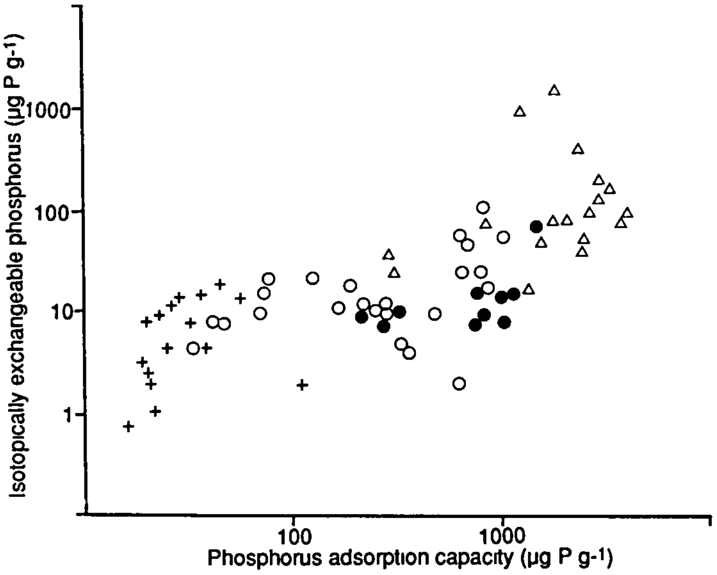

Figure 51 The relationship between the vegetational state of heathland sites in southern England, phosphorus adsorption capacity, and levels of isotopically exchangeable phosphorus in the soil
+ Ungrazed *Calluna* heathland with little or no invasion by scrub or trees
▲ Grazed heathland with little or no invasion by scrub or trees.
O *Calluna* heathland with invasion by gorse
● Heathland with extensive invasion by birch and where *Calluna* now only survives in small areas

Decreased rabbit grazing and, in many areas, the decline of common rights have led to an invasion of heathland by gorse, birch, bracken *(Pteridium aquilinum)* and other species As suggested here, the rate of succession from open heathland to scrub and woodland will be related to nutrient status Several of these invasive species have been associated with improved soil nutrient status Thus, the control of such species is essential, if successional change is not to be further accelerated

Whilst the arrest of succession is important in the management of most heathland sites, the requirements of individual sites must be considered because of variations in soil and climate The loss of traditional forms of land use on some sites will require drastic alternatives The use of herbicides for the control of birch and bracken has been investigated by Marrs (1987), but methods of reducing the nutrient capital contained in some heathlands must be considered, if the long-term future of such sites is to be assured Mowing and the removal of the cut heather as bales, as has been done in the New Forest, may be more effective than burning for removing nutrients Mowing may be more practical on many smaller sites, where the nature of adjacent land may preclude the use of fire, it has the advantage that it is less dependent upon weather conditions, requires less manpower, and can be applied throughout a greater period of the year than heather burning

A more drastic, but even more effective, treatment in reducing nutrient capital is that of sod-cutting, as practised in the Netherlands However, the characteristics of the soil profile must be examined, especially with regard to phosphorus adsorption before any such disturbance is undertaken The removal of surface layers may deplete soil phosphorus, but, in some situations, the exposure of the deeper soil horizons may accelerate undesirable succession

Further work is required into the energy of adsorption, and into the relative availability of phosphorus in different heathland soils Similarly, the different forms of heathland management, such as burning, grazing and mowing, should be examined further for their effects upon maintaining the low nutrient status of lowland heathlands

S B Chapman and R J Rose

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Computer programs for identifying vegetation types

Suppose that you visit a Pennine moorland and find that it has dominant heather (*Calluna vulgaris*) and cloudberry (*Rubus chamaemorus*), with an admixture of hare's-tail and common cotton-grass (*Eriophorum* spp) This information about the vegetation can (if you are an ecologist) tell you a great deal about the environment Probably the soil has impeded drainage, with peat exceeding 30 cm thickness, the site sheds water in wet weather, so there are no permanent pools or runnels, the soil is exceedingly acid, with a pH of about 3 8, the climate is cool and moist, and sheep grazing, if present at all, is light

The ability of the experienced ecologist to 'read off' environmental information from vegetation is derived from years of field experience With simple vegetation such as that on a Pennine blanket bog, the signals may be quite easy to read, with complex vegetation, the signals may be apparently conflicting, and much harder to interpret Only a really good field ecologist can make sense of them How can his knowledge of vegetation be simplified so that it is available to an investigator with less experience?

The standard approach to this problem is to classify vegetation into types The subject of vegetation classification (as opposed to habitat classification) is called phytosociology In the past, authors such as Tansley (1939) used attributes both of vegetation and of habitat to define plant communities Nowadays, a phytosociological approach is favoured, whereby the vegetation is classified first and its environmental relations are investigated afterwards For example, a blanket bog is a physical object composed mainly of peat It is defined by its physical attributes, not in terms of its vegetation It may support any of several kinds of vegetation, some of which may also occur on other types of bog

In practice, the range of habitats that can support a given type of vegetation is quite limited Indeed, the species composition of most semi-natural vegetation conveys enough information to say how it should be managed for nature conservation, and sometimes for other purposes Approximate limits can also be put on its productivity

Vegetation classifications are often made automatically, by means of a computer The starting point is typically a phytosociological table of the occurrence of species in quadrat samples (Table 12) The classification seeks to group the samples so that like assemblages of species are classified with like Almost all current numerical methods for classification of vegetation are 'unsupervised', ie they do not use previous classifications as input data Each problem is examined afresh from first principles

Once a classification has been set up, there remains the problem of how to assign a new sample to a vegetation type that has been defined previously This is the problem of allocation or identification Identification has received far less attention from numerical ecologists than classification

Each numerical classification must be based on a set of data If the input data are comprehensive, then the resulting classification will suffice for all new samples of vegetation However, such an

Table 12 Phytosociological table specifying the occurrence and abundance of species in samples Absence is denoted by a dot, numbers denote abundance on the Domin scale, which specifies categories of ground cover ranging in this example from 1 for a species with negligible cover to 8 for a species covering 50–75% of the ground

	Sample					
Species	1	2	3	4	5	6
Brown bent-grass (*Agrostis vinealis*)	3	1		2	3	3
Heather (*Calluna vulgaris*)	6	8	8	5	3	3
Common sedge (*Carex nigra*)		2	4	3	4	
Wavy hair-grass (*Deschampsia flexuosa)*	3	3	2	3	4	
Crowberry (*Empetrum nigrum*)	3	3	3	3	3	3
Common cotton-grass (*Eriophorum angustifolium*)	3	3	3			
Hare's tail (*E vaginatum*)	4	5	5		5	5
Cloudberry (*Rubus chamaemorus*)	5					
Bilberry (*Vaccinium myrtillus*)				5	6	

Table 13 Association table summarising data in Table 12 Key to frequency classes I, 0 0–0 2, II, 0 2–0 4, III, 0 4–0 6, IV, 0 6–0 8, V, 0 8–1 0

Species	Frequency	Median Domin value
Brown bent-grass (*Agrostis vinealis*)	V	3
Heather (*Calluna vulgaris*)	V	5
Common sedge (*Carex nigra*)	IV	3
Wavy hair-grass (*Deschampsia flexuosa)*	V	3
Crowberry (*Empetrum nigrum*)	V	3
Common cotton-grass (*Eriophorum angustifolium*)	III	3
Hare's tail (*E vaginatum*)	V	5
Cloudberry (*Rubus chamaemorus*)	I	5
Bilberry (*Vaccinium myrtillus*)	II	5

ideal is unattainable, as all knowledge and all data are partial

A major problem now presents itself Given that no scheme of classification is comprehensive, how can partial information be used? It is impracticable to maintain an ever-growing and increasingly bulky data base, which is repeatedly re-analysed However, established vegetation types can be published in summary form as 'association tables' (Table 13) New samples can then be compared with association tables, rather as one compares a plant specimen with its description in a *Flora* In the terminology of image classification, the association tables serve as a summarised training set of data to generate a 'supervised' classification of vegetation

In order to produce repeatable results, the process of matching samples to association tables needs to be automated ITE has recently developed a computer program called TABLEFIT (Hill 1989), designed for this purpose Written in the FORTRAN programming language, it can run on most desktop and all larger computers The input data are (i) a set of association tables describing vegetation types, and (ii) the composition of a vegetation sample (either a complete species list, or a list with measures of species abundance, or just the dominant species) From these data, TABLEFIT calculates a measure of the goodness-of-fit of the sample to the vegetation type

The measure used is a composite, consisting of the mean of three coefficients which answer the following questions

1 How closely do the species present match those that would be expected in the vegetation type?

2 How well does species abundance coincide with that described for the type?

3 Taking the four most abundant species in the sample, what is their frequency in the vegetation type (the best score being when all four occur in frequency class V)?

The best-fitting vegetation types are then listed in descending order of preference

The new thing about TABLEFIT is that it provides a numerical method of generating supervised classifications from published data It can be applied to any vegetation classification for which association tables are available It is just as suitable for use with traditional non-numerical systems of classification as it is for computer-generated numerical classifications It has been tried on the mire types defined in NCC's *National vegetation classification* (Rodwell 1986–87) User reaction has been favourable, and it is hoped to develop it further

Automated identification of vegetation types presents exciting possibilities for the future For each vegetation type, it is possible to specify the likely soil, grazing pressure, management history and successional trends, together with the type's rarity, geographical distribution and conservation value Given a data base with this information, TABLEFIT can be used for site evaluation by suggesting whether vegetation present at the site is unusual or rare in a given district, and whether the site is likely to be a habitat for valuable species It can also be used for site management, either by suggesting species suitable for introduction or by indicating how the vegetation is likely to change if the management regime is altered

M O Hill

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Assessing effects of climatic change on vegetation

(This work was partly supported by funds from the Nature Conservancy Council)

If current forecasts of climatic change are accurate, then there will be significant effects on the structure and species composition of many natural and semi-natural plant communities within the next 100–150 years Clearly, these changes must be identified before they occur (prediction), or as they occur (measurement) Studies have begun in ITE to identify the possible areas where change is most likely to be detected This work has highlighted some of the difficulties in detecting change *per se* and the subsequent problems in determining cause/effect relationships

Change: where will it be most easily detected?

Basically, for the purposes of monitoring the effects of climate, vegetation change can be classified into three main groups (i) where the mean regional climate has a direct effect on species, (ii) where climatic extremes affect vegetation change through disturbance, and (iii) where the climate exerts an indirect effect through other ecosystem processes, such as increasing net primary production, modifying competitive interactions between species, or accelerating habitat change through succession

Direct climatic effects on species

Vegetation change will involve either the colonisation of new species typical of warmer climates, or the extinction of species typical of colder climates It is difficult to predict which species are likely to be the best indicators of climatic change, because distribution maps show a plethora of species whose British distribution is apparently limited by some aspect of climate (Perring & Walters 1962) However, there are three broad groups of species which are likely candidates for initial study the Lusitanian flora, alien species with a southern distribution, and the Arctic-alpine flora

Lusitanian species, such as the Cornish and Dorset heaths (*Erica ciliaris* and *E vagans*), reach their northern limits in the south-west of England and/or western Ireland, and may expand their British range if the climate becomes warmer and wetter Introduced alien species from warmer climates, such as the holm oak (*Quercus ilex*) and the Hottentot fig (*Carpobrotus edulis*), are already established in the south-west of Britain, and are obvious candidates for study Arctic-alpine species, on the other hand, are found mainly in montane areas, where the climate is harsh, and the British distribution of these species is likely to contract if the climate becomes warmer, with the possible extinction of some species

An example of one group of plants that could be considered for further study are the saxifrages (*Saxifraga* spp), because of their current British distributions

1 Lusitanian species the kidney saxifrage and St Patrick's cabbage (*Saxifraga hirsuta, S spathularis*),

2 widely distributed/lowland species meadow and rue-leaved saxifrage (S *granulata, S tridactylites)*

3 Arctic-alpine/montane species starry, mossy, yellow and purple saxifrage (*S stellaris, S hypnoides, S aizoides, S oppositifolia)*

The distribution of one member from each of these groups shows the clearcut nature of the distributions, and there is obvious potential for mapping their spread as climate changes (Figure 52) Although it may be possible to predict the likely change in distribution of the Lusitanian and Arctic-alpine species in response to climate change, it is much more difficult to forecast what might happen to *S granulata* or *S tridactylites*

Gross change in these species may be detected by mapping their distributions at regular intervals, as is done within the Biological Records Centre (BRC) at ITE Monks Wood However, accurate assessments of the effects of climatic change will require detailed autecological studies of existing populations, so that range expansion and contraction can be measured For example, a detailed baseline study of the Dorset heath (*Erica ciliaris)* (a Lusitanian species) and its hybrid with the cross-leaved heath (*Erica tetralix*), a widely distributed species, has already been established, and has indicated that these species are expanding their ranges (Chapman 1975)

Effects of extreme events

When extreme climatic events occur, there is often catastrophic death of individuals and populations Recent examples in Britain include the October gales of 1987 affecting the southern woodlands, and the hot dry summer of 1976 affecting heathlands, directly through heather (*Calluna vulgaris)* death (Marrs 1986), and indirectly through increased 'accidental' fires The important feature of such a catastrophe is that it is an initiator of change, and the community regenerates, either cyclically to replace the original community (cyclic regeneration), or by the invasion of new species Good examples of such change occur in Breckland where heather death started in 1976 during the hot summer, and increased in the following two to three years after outbreaks of insect herbivores In the affected area, there was immediate large-scale invasion by birch (*Betula* spp) (Marrs 1986) Such data emphasise the importance of catastrophes in initiating new successions Studies of patch dynamics in sensitive communities, where the normal periodicity and return interval of such catastrophes is known, may help detect important influences of climate Moreover, this type of catastrophic disturbance may be an important factor allowing bursts of invasion by species typical of warmer habitats As information is already available on the Breckland heaths, a southern habitat with a continental climate (by British standards), and the cycles are not too long (15 years), these heaths are likely 'pressure point' communities Baseline monitoring and extensive study of community dynamics are currently in progress

Indirect effects through ecosystem processes

These vegetation changes are likely to be much more subtle than those described above, because the same species may persist, but at markedly altered rank abundance As the productivity of most ecosystems is likely to increase, because of higher temperatures, higher or modified rainfall, at least in some areas, and higher CO_2 concentrations, an approximation can be obtained of the likely effects of increased vegetation growth, using experiments where other growth-limiting factors are alleviated, as a model Fertiliser addition is often used to increase vegetation

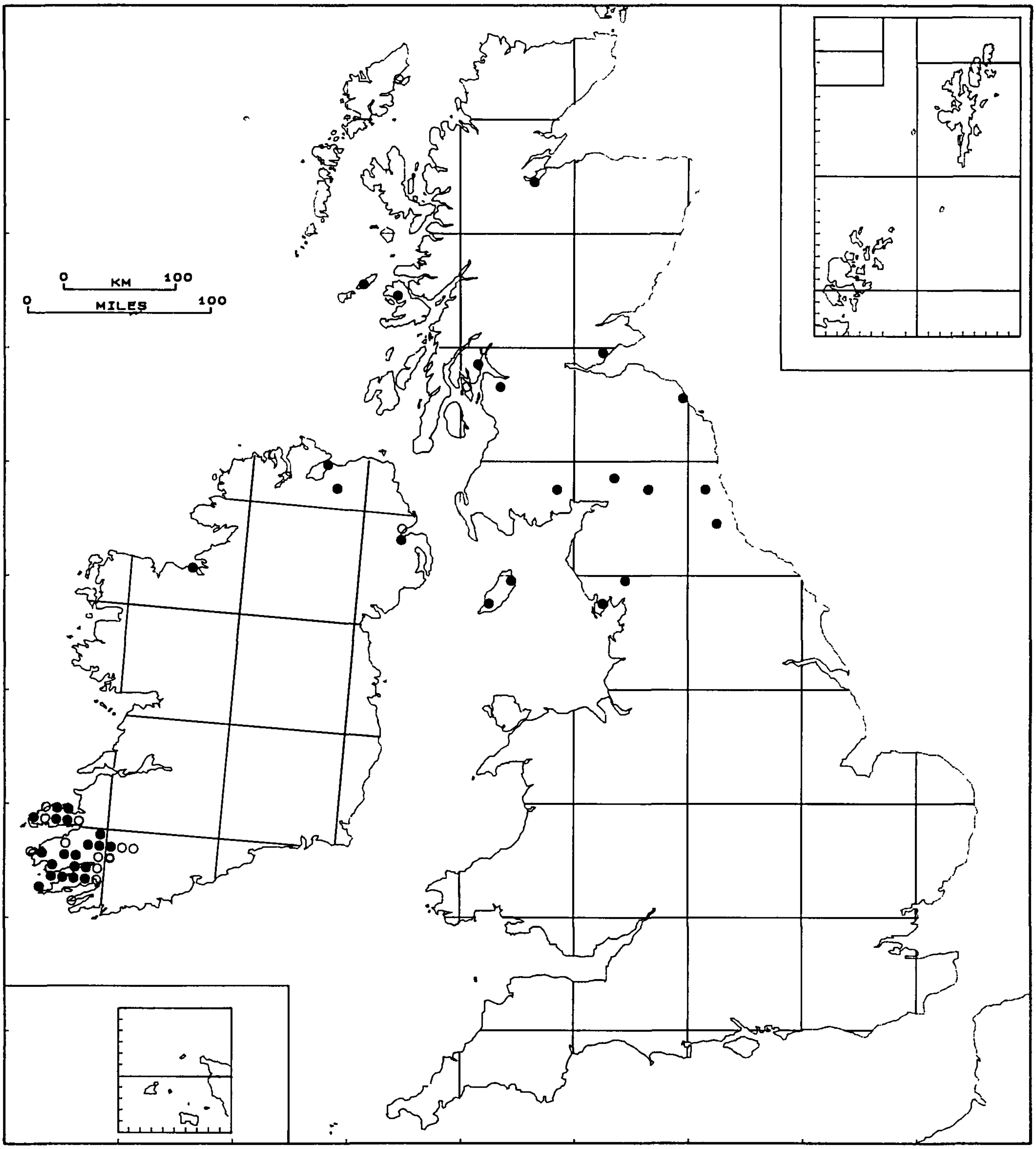

Figure 52 The current distribution of three saxifrages from the data base held in the ITE Biological Records Centre These species would be ideal candidates for studying response to changing climate because of their contrasting distributions (i) a Lusitanian distribution

productivity, and, when applied to semi-natural communities at high rates (agricultural rates), the growth of aggressive productive species has been promoted at the expense of subordinate ones which do not respond to fertiliser addition However, recent research in Europe suggests that, even where much lower amounts of nutrients are added in polluted rain, similar effects occur, with increasing dominance of competitive grasses on infertile heathlands and chalk grasslands (Heil & Diemont 1983, Bobbink & Willems 1987), and a dramatic loss of bryophytes and lichens (During & Willems 1986) Thus, if climate does tend to increase the productivity of natural and semi-natural vegetation, then some competitive species are likely to flourish, but at the expense of the understorey species, and especially the lower plants

Problems in detecting vegetation change

There are two fundamental problems in detecting vegetation change first, the separation of significant directional change (ie the signal) from background fluctuations (noise), and, second, the identification of cause/effect relationships These two problems are illustrated using real data collected in a long-term monitoring scheme at Moor House International Biosphere Reserve, an upland reserve which is likely to be vulnerable to climate change The data presented here are from one experiment (heath rush (*Juncus squarrosus*) grassland experiment) in a set of ten established between 1954 and 1972 by the Nature Conservancy, and continued first by NCC, and, since 1982, by ITE (Marrs *et al* 1986) The experiments were set up to cover the range of upland vegetation found on the Reserve, and, in each experiment, the effects of sheep grazing *versus* no sheep grazing are compared

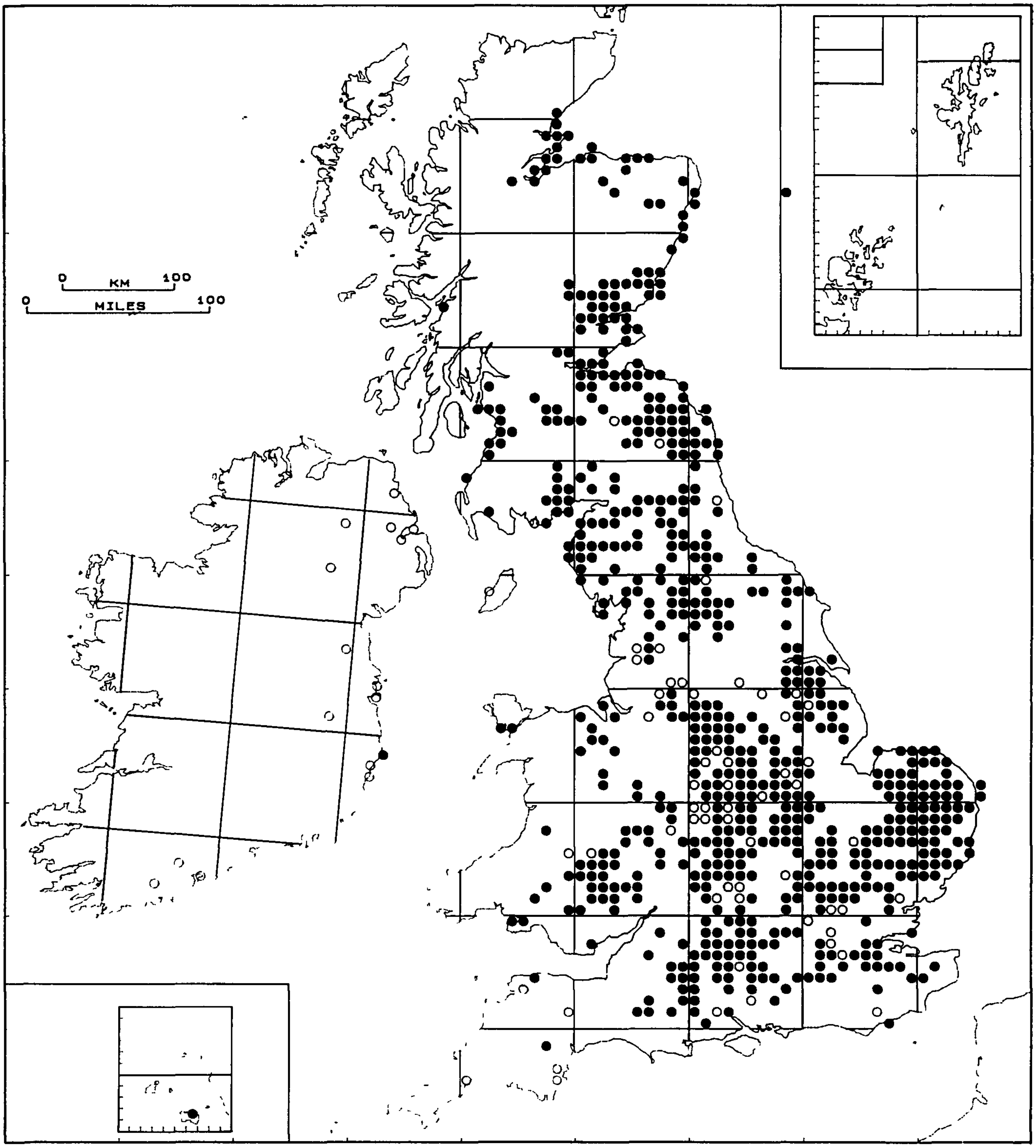

Figure 52 The current distribution of three saxifrages from the data base held in the ITE Biological Records Centre These species would be ideal candidates for studying response to changing climate because of their contrasting distributions (ii) a widely distributed species

At one blanket bog site, a rotational burning sequence is also included The general aim of the study is to measure vegetation change, and identify important signals (ie changes induced by management) from background noise (species fluctuations in abundance that are not accounted for by known events)

Separation of signal from noise

In the heath rush grassland experiment, four typical examples of species response through time are shown in Figure 53 Obviously, common sedge (*Carex nigra)* was increasing and common cotton-grass (*Eriophorum angustifolium)* was decreasing, but *Pohlia nutans* showed a curvilinear response and bilberry (*Vaccinium myrtillus)* was erratic Clearly, the first two species are showing a consistent directional change over the period examined, but the latter two must be viewed as noise Where such noise occurs, measuring change in abundance from a few points is impossible (Figure 54), and, moreover, long-term data are essential even to determine that they are noisy! Thus, the current classification of common sedge and cotton-grass may prove erroneous when data for a longer period become available

It is possible to use multivariate ordinations for data from all species to assess change, and comparisons can be made between sites (Figure 55) In this example, the grazed *versus* ungrazed plots are changing in both treatments in the same direction, but at different rates, the enclosed plots are changing towards blanket bog much faster Rates of change on the ordination axes may provide a useful, albeit crude, method for assessing climatic change impacts

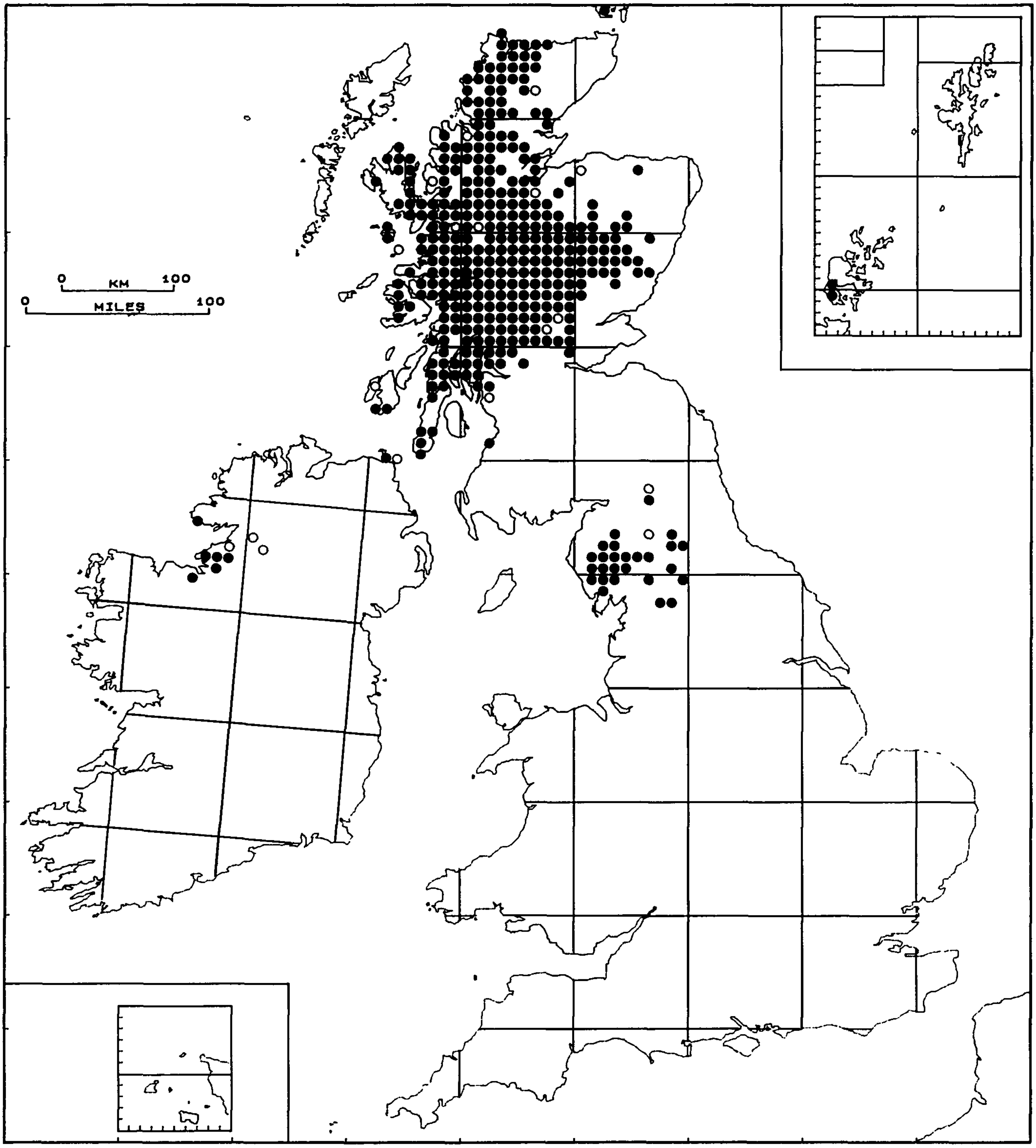

Figure 52 The current distribution of three saxifrages from the data base held in the ITE Biological Records Centre These species would be ideal candidates for studying response to changing climate, because of their contrasting distributions (iii) a montane/northern species

Cause/effect relationships

It is impossible to separate cause/effect relationships without detailed experiments where the causal factors of interest are manipulated For example, the results in Figure 55 show that both grazed and ungrazed heath rush grassland changed towards blanket bog between 1966 and 1984, but the trend was faster when grazing was removed However, directional change in other unknown environmental factors may also have occurred during this period, and these covariates with time complicate the interpretation of cause/effect relationships Thus, the general trend in the grazed plots towards blanket bog could be the result of

- unknown vagaries of the climate, eg individual extreme events, some periods favouring certain species at the expense of others,
- a possible increase of nutrient inputs, particularly nitrogen, through rainfall deposition and cloud capture,
- possible slight reductions in grazing pressure on the grazed site, through changes in stocking density or animal preferences,
- changes in unknown variables

What has been determined is that this background change is slower if sheep grazing is continued

Clearly, the best way of separating cause/effect relationships is through experiments where the causal factors are manipulated However, it may be possible to obtain pointers using the newer methods of multivariate analysis (Ter Braak 1986), where community trends can be related to measured environmental variables, eg time To be successful, this approach requires measurements of the environmental factors of interest throughout the study period

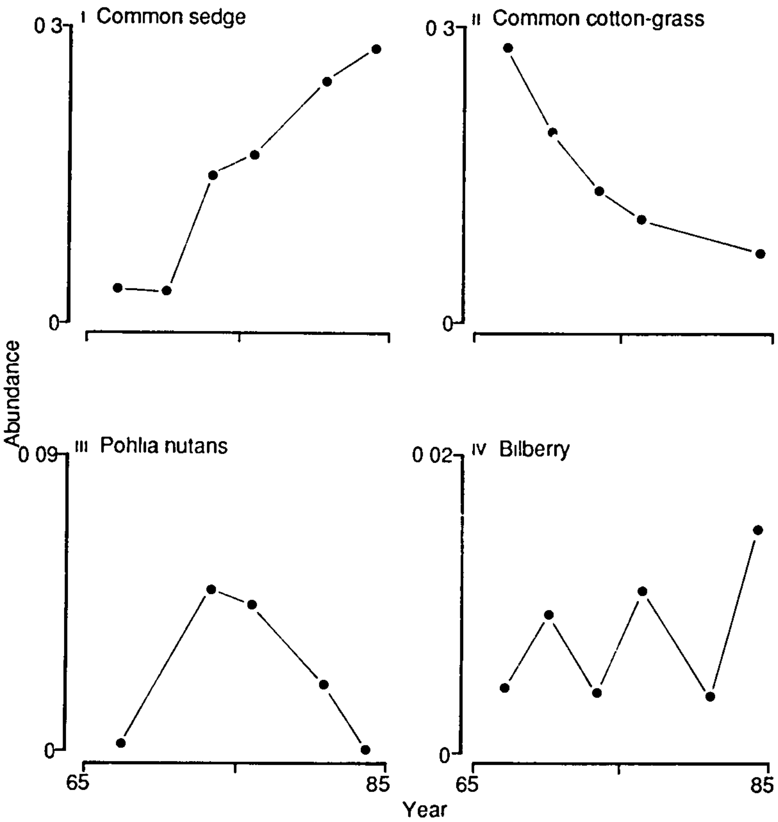

Figure 53 Observed change in abundance of four species in the heath rush grassland experiment at Moor House International Biosphere Reserve between 1965 and 1985 showing examples of directional change (i ii) and fluctuations/noise (iii iv)

So far, the difficulties in showing that vegetation change has been caused by changes in major driving variables have been considered However, change can also be initiated by secondary effects that may be promoted by climatic change or its interaction with other major driving variables, such as pollution and grazing pressure Secondary effects that might occur are the increased productivity of dominant species, and hence a lower resource availability (light and nutrients) for subordinate species, or responses induced by changed invertebrate herbivory

Conclusions

Although it is possible to detect the effects of climatic change for certain 'pressure point' communities where species may be gained or lost, for most communities separation of signal from noise and the isolation of causal factors are likely to be major problems In order to detect the subtle effects of climate change on vegetation, an expanded system of long-term site monitoring must be set up, and linked intimately to (i) experimental studies of comparative plant ecophysiology, the competitive relationships between species under various management scenarios, and (ii) simulation modelling

R H Marrs

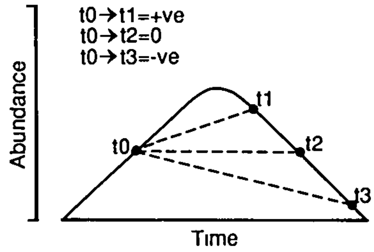

Figure 54 Hypothetical diagram illustrating the problem of detecting change when there are few sampling points and change is curvilinear Opposite results are obtained depending on the time interval between sampling points

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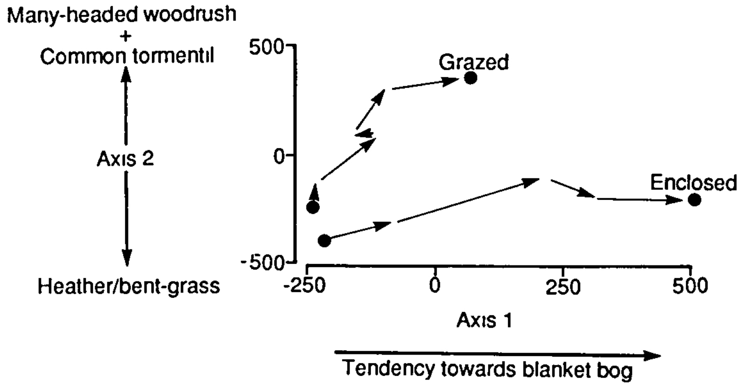

Figure 55 Trajectories through time for the sheep grazed and enclosed (no sheep grazing) plots of the heath rush grassland experiment at Moor House International Biosphere Reserve between 1965 and 1986 using multivariate analysis

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