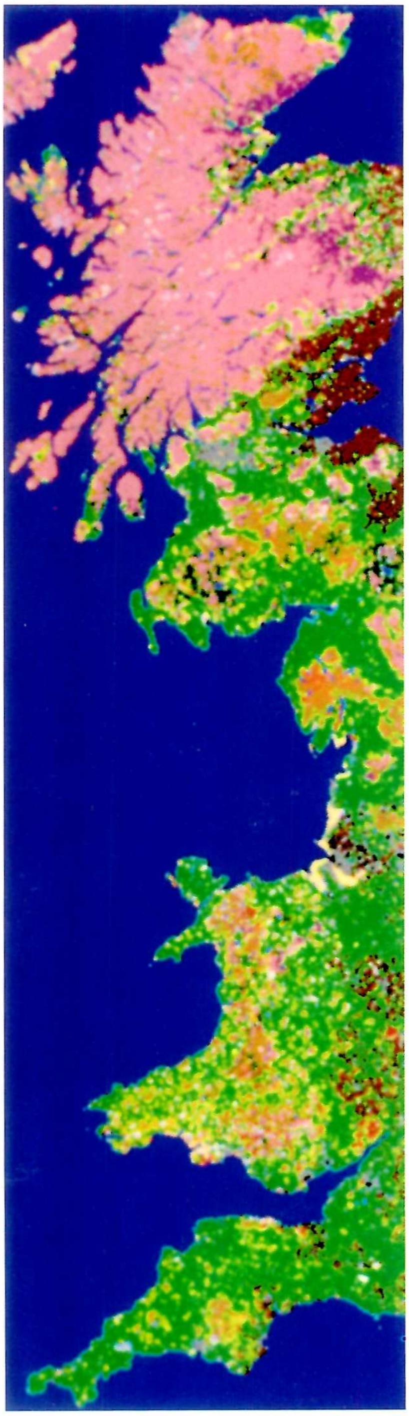
1992—1993
REPORT



Institute of Terrestrial Ecology

Natural Environment Research Council

The ITE mission

The Institute of Terrestrial Ecology will develop long-term, multidisciplinary research and exploit new technology (molecular ecology, information technology, and modelling) to understand the science of the natural environment, with particular emphasis on terrestrial ecosystems

Priority is placed on developing and applying knowledge in the following areas

- the factors which determine the *composition, structure,* and *processes* of terrestrial ecosystems, and the *characteristics* of individual plant and animal species
- the dynamics of *interactions* between atmospheric processes, terrestrial ecosystems, soil properties and surface water quality
- the development of a sound scientific basis for *modelling* and *predicting* environmental trends arising from natural and man-made change
- the *dissemination* of this research to decision-makers, particularly those responsible for environmental protection, conservation, and the sustainable use of natural resources

The Institute will provide training of the highest quality, attract commissioned projects, and contribute to international programmes

By these means, ITE will seek to increase scientific knowledge and skills in terrestrial ecology, and contribute to national prosperity and prestige

Front cover illustration
An overview of the ITE land cover map of Great Britain

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Report of the
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CONTENTS - Science Reports 2

Global environmental change

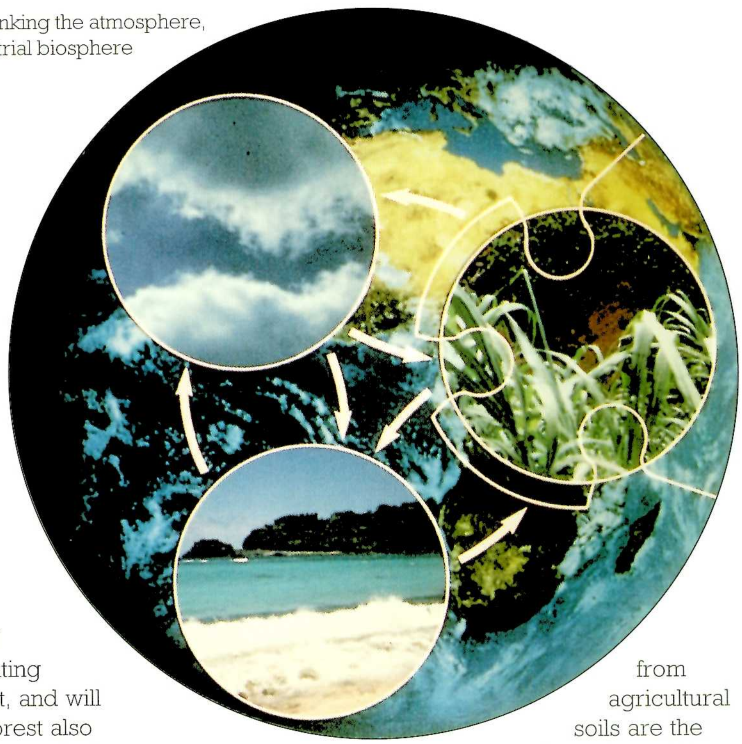

Plate 15. The jigsaw linking the atmosphere, oceans and the terrestrial biosphere

From its inception in 1990, this programme anticipated major initiatives in the field of global environmental research. Consequently, ITE has been well placed to make rapid and significant contributions to the NERC Special Topic programme on Arctic Ecology and the NERC Terrestrial Initiative in Global Environmental Research (TIGER), and to the Department of the Environment's core model for predicting impacts of climate change. Two further initiatives into CO_2 enrichment facilities and UV-B radiation have been funded jointly by NERC and the Agricultural and Food Research Council (AFRC). ITE staff are involved in projects to review and develop CO_2-enrichment facilities, and a system is being constructed at ITE Monks Wood for exposing vegetation to realistic increases in UV-B radiation.

Five of the reports which follow concern work funded under the TIGER programme: three deal with global system processes – carbon cycling and 'greenhouse' gas fluxes – and two with impacts of global change. General circulation models concur in predicting greater climatic changes in polar regions than at lower latitudes, and work on arctic invertebrate ecology has particular relevance to the broader issue of climate change. The last report in this section describes progress in the Environmental Change Network (ECN), which promises to provide an invaluable infrastructure for global change studies and comprehensive data needed for the construction, testing and validation of hypotheses and models.

TIGER I is concerned with carbon cycling, particularly in the UK and in tropical forests. In addition to the reports which follow, a field experiment has been established to determine the effects of warming on carbon turnover in upland soils at three different altitudes at Great Dun Fell, in the northern Pennines, while in Brazil radar satellite images are being used to determine the extent of different stages of regeneration in Amazonian forests. A geographical information system will be used in the estimation of net carbon balance of cleared, regenerating and primary forest, and will include areas of forest also being studied using optical imagery in Brazil and Cameroon. The ultimate aim of these TIGER I studies is to supply data for models to quantify the effects of increasing CO_2 levels on the net flux of carbon between vegetation/soil surfaces and the atmosphere, and to produce sound predictions of CO_2 exchange at scales up to 1000 km (see pp15–18, 34–37).

The measurement of 'greenhouse' gas fluxes forms the basis of TIGER II. This work has involved ITE staff in projects examining methane emissions both from peat monoliths placed in open-top chambers, where it was confirmed that methane concentrations increased with temperature, and at the landscape scale over a peat bog in northern Scotland. The latter study involves personnel from the University of Edinburgh and the University of Manchester Institute of Science and Technology in a consortium led by ITE, using a range of micrometeorological methods to make measurements which integrate net vertical flux over large areas. A field campaign in the summer of 1992 unfortunately followed a drier-than-usual spring, which resulted in unexpectedly low methane concentrations. A repeat campaign in 1993 will be augmented by the availability of a tunable diode laser, which will enable accurate measurement of methane concentrations at the landscape scale.

Substantial emissions of another major 'greenhouse' gas, nitrous oxide, have been measured over upland forest soils on recently felled sites where nitrogen fertilization has taken place. Emissions from agricultural soils are the subject of one of the following reports.

A pervasive issue in global environmental research is the need to integrate impacts and responses over a wide range of spatial scales. In a biological context, it entails discovering how changes in the behaviour and survival of individual organisms affect the geographical ranges of species, the species composition and functioning of ecosystems, and hence the global distribution and feedback effects of forests, savanna and other biome types on the global climate system. Our ability to achieve this integration is currently constrained by the spatial scale and resolution of environmental data. The study on arctic invertebrates shows how population dynamics can be altered by increasing temperature, and allows some prediction of changes *in situ*. In contrast, the modelling of orchid distribution focuses on changes in the availability of suitable climate and habitat, and makes use of data spanning a range of scales. The butterfly study illustrates not only the constraint that temperature places on some species distributions, but also the need to define climate at a scale appropriate to the organism in question.

Bringing together research from diverse fields and integrating results over a wide range of scales is a demanding and challenging task. To this end, ITE staff are working closely with colleagues in other institutes and in universities in the UK and overseas.

B G Bell and C P Cummins

CO_2 fertilization effects on decomposition processes

(This work involved collaboration with the University of Lancaster)

The relentless rise in global atmospheric carbon dioxide (CO_2) levels is arguably the most important long-term change occurring on this planet, and it is becoming clear that the natural sinks and sources of this gas are being overwhelmed by anthropogenic emissions. The single largest contributor to this increase is the combustion of fossil fuels, and the consequences of the rising concentrations of CO_2 for both climate and biological systems are the cause of much concern world-wide. Fundamental information is needed about global carbon (C) stores and how they are changing in response to man's activities.

Most of the carbon held in terrestrial ecosystems is actually in the soil, and is derived from the decomposition of plant and animal materials. There is very little direct evidence of how elevated atmospheric levels of CO_2 will interact with decomposition processes (and therefore soil C stores), yet this limited evidence suggests that decomposition processes can be affected (Couteaux *et al.* 1991). These effects appear to occur because the quality of the organic matter produced by plants grown under normal and elevated CO_2 conditions is different, and alters the rate of attack by decomposer organisms in the soil. On a global scale, such interactions may go some way to compensating for elevated CO_2 concentrations in the atmosphere by resulting in greater storage of C in the soil. This project is designed to quantify these interactions for a variety of plant litters grown under ambient and elevated CO_2 levels. Work with leaf litter derived from tree species is reported here, yet investigations with plant material from other natural plant species are also underway.

CO_2 fumigation

Seedlings of birch (*Betula pendula*) and Sitka spruce (*Picea sitchensis*) were grown in pots in solar domes (Plate 16) at the University of Lancaster under two CO_2 regimes (350 ppm and 600 ppm). Trees were grown within each dome under two different nutrient regimes: with (N+) and without (N–) additional nitrogen.

At the end of the first growing season, the deciduous leaves were collected as they fell, whilst the needles from the spruce were harvested by cutting the branches and drying. The material collected was sampled for chemical composition, and used to establish litter bags and microcosms for decomposition studies.

Chemical analysis

Particular emphasis has been given throughout the study to changes in the nitrogen content of the plant litters derived from the experiments. This is mainly because the C/N ratio is known to be a major controlling factor in the decomposition of plant litters, but also because our work suggests that N is the only major plant nutrient which appears to be strongly influenced by enhanced CO_2 levels. The observed increased C uptake from the atmosphere by plants exposed to elevated CO_2 can cause a 'dilution' of N available from the soil and, as a consequence, the C/N ratios of the plant material and litter may increase.

Plate 16. The solar dome fumigation facilities at the University of Lancaster, where trees have been grown at CO_2 concentrations of 350 and 600 ppm

Table 5. Relationships between CO_2 and nitrogen treatments on nitrogen content and C/N ratio of plant material

Species	Treatment	N (%)	C/N
Birch	350 ppm N+	1.6	30.2
	600 ppm N+	1.6	31.9
	350 ppm N–	1.2	41.9
	600 ppm N–	0.8	65.4
Sitka spruce	350 ppm N+	2.2	22.9
	600 ppm N+	2.1	25.1

The results of our chemical analyses confirmed the hypothesis that, when N availability to plants was low, but not growth-limiting, then CO_2 fumigation significantly increased the C/N ratio of the plant material (Table 5). For birch, the highest values for C/N ratio were observed in the leaves grown at elevated CO_2 (600 ppm) in unfertilized soil.

In the case of Sitka spruce, the CO_2 fumigation did not induce any significant effect on the quality of the litter, as indicated by either the C/N ratio or other mineral nutrient content. One possible explanation is that even the unfertilized treatment provided sufficient N for the spruce, because the N concentrations in the needles from the spruce trees in all the four treatments were consistently high (Table 5).

Decomposition studies

Litter decomposition has been studied both in field litter bags and in laboratory microcosm systems. The litter bags containing birch and spruce litter were placed out at field sites in Cumbria in 1992 in a mixed deciduous woodland (Meathop Wood) and a pure Sitka spruce plantation (Grizedale Forest), respectively. Litter bags are being collected at intervals over a one-year period, and decomposition rate (mass loss) and C and N concentrations of the litters determined. The results of the first samplings are reported in Figure 16. Decomposition rates were strongly correlated with the initial C/N ratio of the material, with the litters having the highest C/N ratios producing the lowest

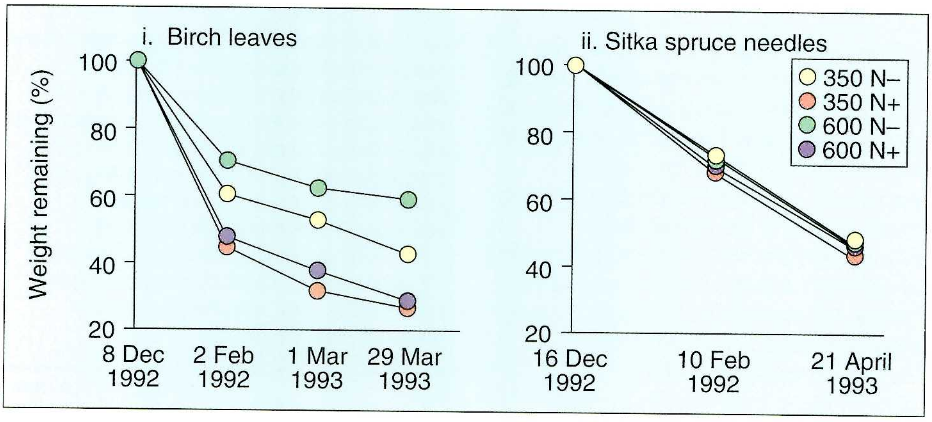

Figure 16. Weight remaining of decomposing (i) birch leaves and (ii) Sitka spruce needles grown under ambient (350 ppm) and elevated (600 ppm) concentrations of CO_2 without (N–) and with (N+) additional nitrogen. Results are from field litter bag experiments

decomposition rates for both species. The effects on birch decomposition were far more pronounced than for spruce, parallelling the changes in C/N ratio resulting from the treatments.

These observations have been investigated further in a separate experiment in which litters derived from birch trees grown in controlled conditions have been used to produce a further series of litter bags. In this second experiment, the C/N ratio of the birch leaves was manipulated by watering the trees with nutrient solutions containing different amounts of mineral N. This resulted in a range of litters grown under identical conditions but with a wide range of C/N ratios. After two months in the field, the effect of the initial C/N ratio on decomposition rate was marked (Plate 17), with the N-rich litter decomposing at a much greater rate than the 'poorer' litters. This experiment clearly demonstrates how litter quality affects C dynamics.

A laboratory microcosm experiment has also been established in order to follow the decomposition of litter under defined laboratory conditions. The plant materials derived from the experiments described above have again been used, and every two weeks, for an experimental period of four months, decomposition rates have been monitored by measuring CO_2 evolution from the litter using infra-red gas analysis (Wookey, Ineson & Mansfield 1991).

The results obtained from this component of the study are shown in Figure 17, and are consistent with the data obtained from the field, the litters having the lowest C/N ratio showing greater decomposition rate. The differences in respiration rates between the treatments declined during the course of the study, with rates becoming more constant towards the end of the experiment.

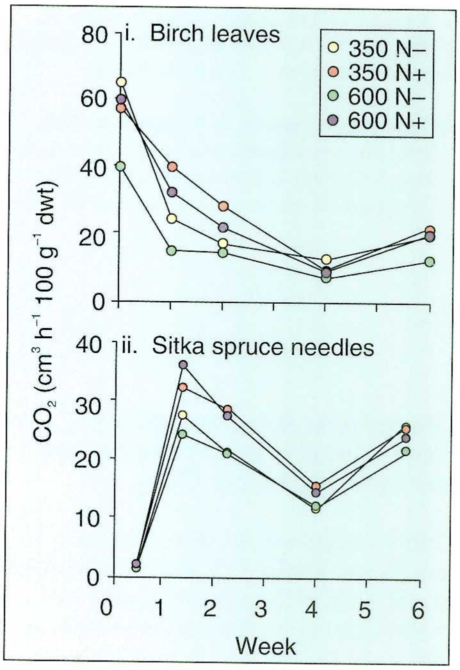

Figure 17. Respiration rates of decomposing (i) birch leaves and (ii) Sitka spruce needles grown under ambient (350 ppm) and elevated (600 ppm) concentrations of CO_2 without (N–) and with (N+) additional nitrogen. The decomposition incubations were performed in laboratory microcosms at 15°C

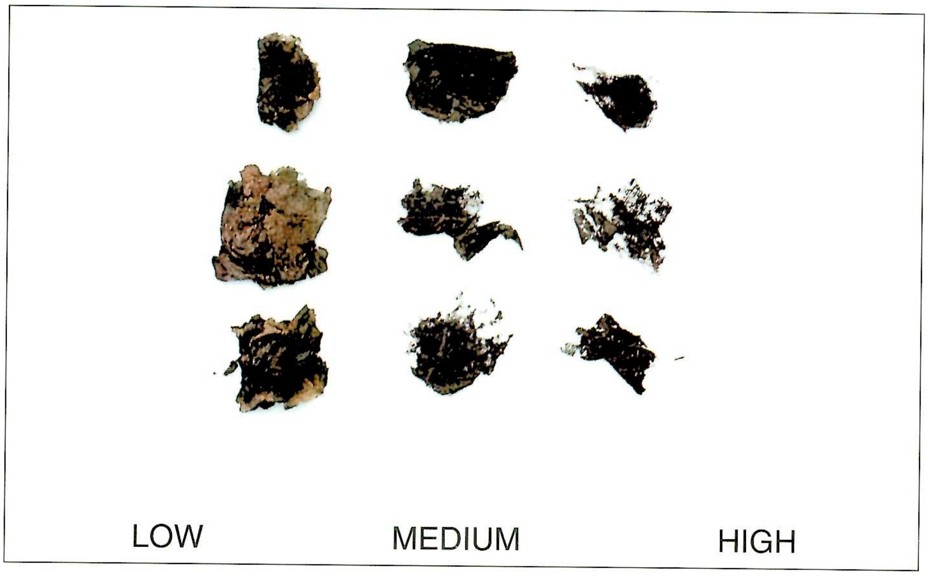

Plate 17. Decomposing leaf litter from birch trees, showing the importance of N content on weight loss. The leaf litter had been decomposing for eight weeks, and each column shows the leaves from three replicate litter bags

Conclusions

Although the work reported here is at an early stage, some general and important conclusions are already emerging from these experiments.

- Plants grown at elevated (600 ppm) CO_2 concentrations tend to produce litter which decomposes more slowly than plants grown under ambient CO_2 levels.
- The interaction between CO_2 concentration and decomposition rate appears to be dominated by the N content of the litter, and does not occur unless enhanced CO_2 fumigation, interacting with the nutrient status of the soil, causes a change in the plant C/N ratio.

M F Cotrufo and P Ineson

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Vegetation/atmosphere interaction and responses to atmospheric CO_2

The Meteorological Office general circulation model (GCM) is used to make predictions of the earth's present and future climate, particularly in relation to the possible effects of increasing levels of atmospheric carbon dioxide (CO_2) and other 'greenhouse' gases. Simulations have predicted the well-known 'greenhouse effect' in response to increasing atmospheric CO_2 concentrations. This effect will be felt most strongly at high latitudes in the northern hemisphere, where more than 4°C warming is predicted. In addition, continental summer soil moisture deficits are predicted to increase, because of changes in the hydrological cycle. This latter effect is one of the most significant changes observed in GCM simulations of climate response to doubled CO_2.

The GCM deals with atmospheric processes in a complex manner, but treats the land surface relatively simply. Each land cell contains a fixed dominant and subdominant vegetation type. Each vegetation type has a fixed set of parameters that enable the flux of water from the soil to the atmosphere (evapotranspiration), and the partitioning of energy between sensible and latent heat to be predicted at each GCM time-step. The most significant of the vegetation parameters for evapotranspiration are the surface resistance to water flux and rooting depth. None of the land surface vegetation parameters is changed in response to changes in temperature or rainfall, neither does the distribution of vegetation change. However, change is to be expected across a wide range of timescales, from stomatal dynamics over a few minutes, to vegetation types over many decades. It is not yet known to what extent the inclusion of vegetation change in the GCM will alter climate change predictions.

Table 16. Sensitivity of predicted responses to doubled atmospheric CO_2 by the single column model of the Meteorological Office for an Amazon rainforest. The model was run with vegetation properties fixed during atmospheric CO_2 changes (fixed resistance) and with the stomatal resistance to water loss changing in response to the environment (variable resistance). Values indicate the change predicted if the present atmospheric level of CO_2 is doubled. In each case the model was run to equilibrium, and predictions were averaged over eight years

	Fixed resistance	Variable resistance
Rain (%)	+2.7	–6.0
Surface temperature (°C)	+1.82	+2.12
Evapotranspiration (%)	+9.6	–9.4
Cloud cover (%)	+0.05	–1.20

ITE has been working on developing an interactive vegetation model to provide the GCM with a dynamic land surface. So far, effort has been concentrated on those processes with short response times: stomatal resistance and leaf area index (LAI). Stomata open and close in response to the environment, regulating the flux of water from the soil to the atmosphere, and the flux of CO_2 into the leaves. We have taken a simplified version of a model of optimal stomatal resistance and photosynthesis, called PGEN (Friend 1991, 1993a, b), and used it to replace the fixed surface resistance currently used in the GCM. PGEN calculates the response of stomatal resistance to the environment in a realistic manner by coupling together water and CO_2 effects on photosynthesis (Friend 1993a, b). The greatest stomatal resistance responses that PGEN predicts are to soil water content, vapour pressure deficit, atmospheric CO_2 concentration, and light. Increasing soil water or light generally decreases stomatal resistance (ie the stomata open),

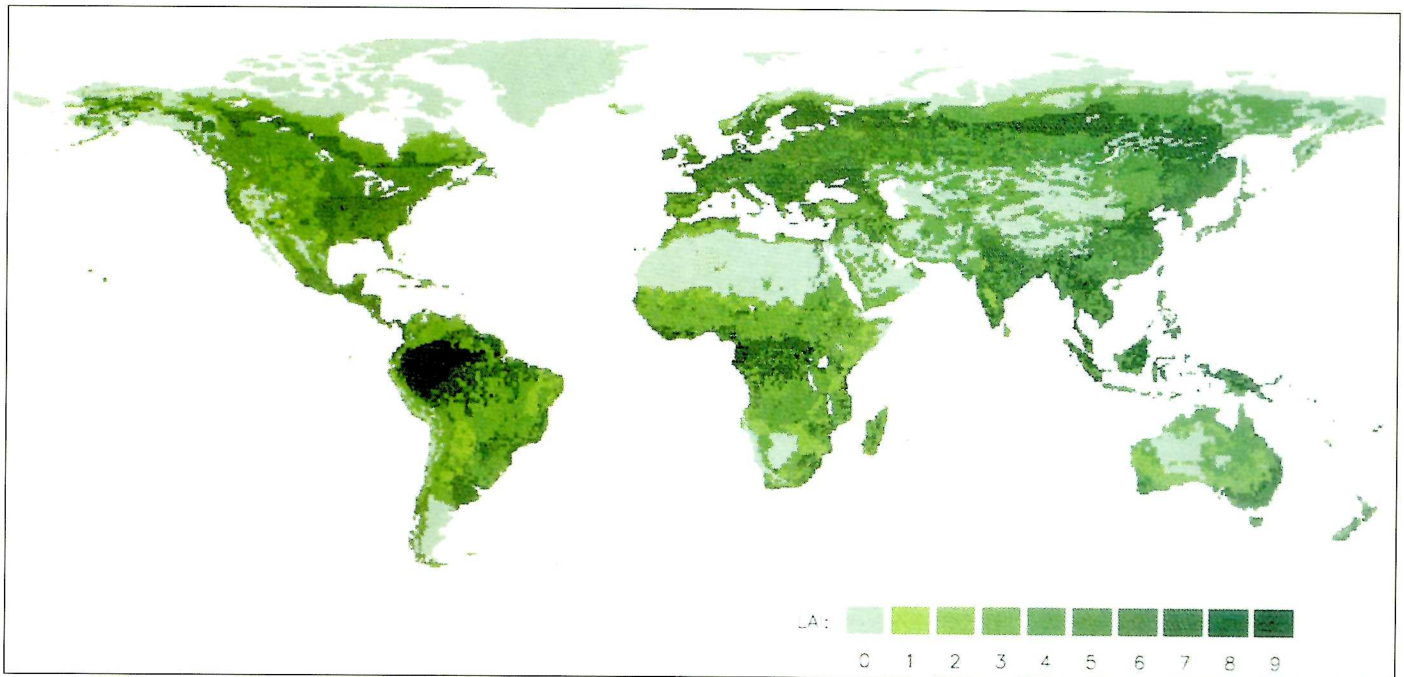

Figure 18. The ITE global map of annual maximum leaf area index. Leaf area index values are assigned to each 0.5° x 0.5° land surface cell, according to the vegetation type defined by Olson, Watts and Allison (1985). This map is being updated from satellite and other data as they become available

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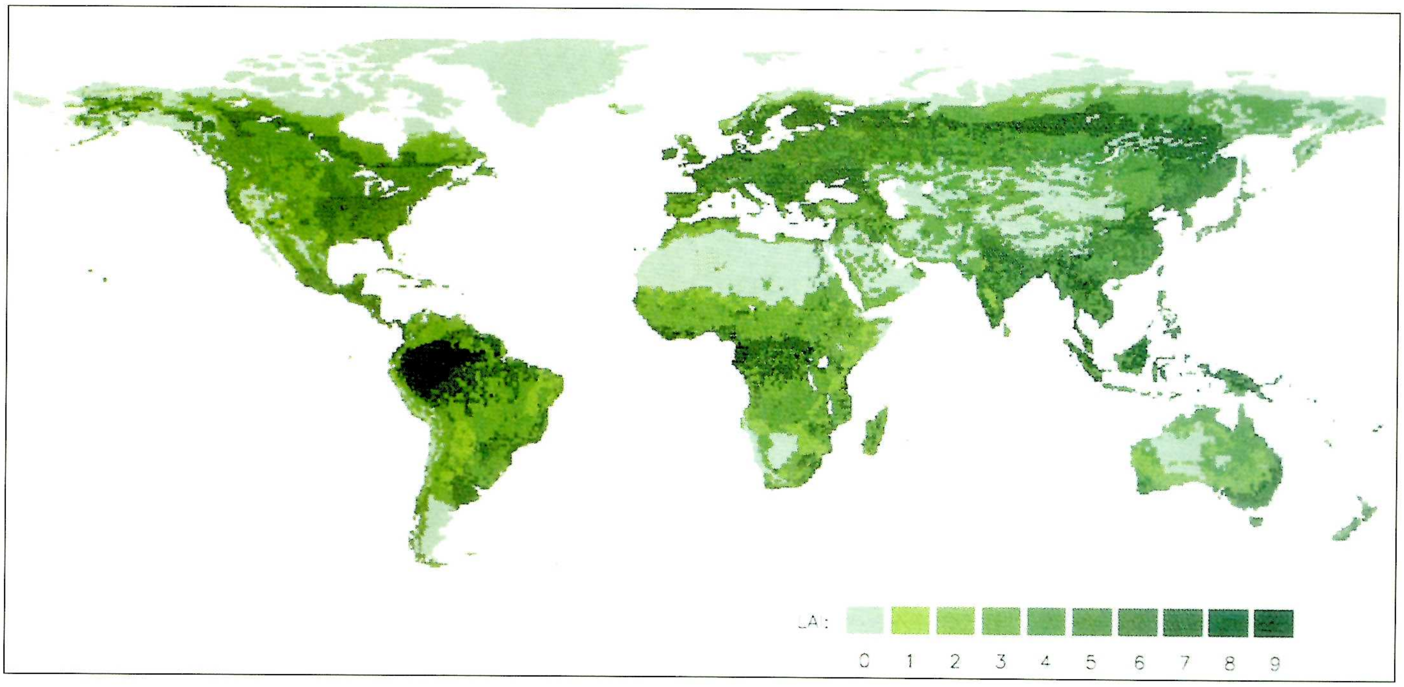

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whereas increasing vapour pressure deficit or atmospheric CO_2 increases stomatal resistance (ie the stomata close)

Using a simplified version of the GCM, known as the single column model, we simulated the effect of doubled CO_2 on the climate over an Amazon rainforest with and without the dynamic stomatal resistance model The results are given in Table 6 Without dynamic stomatal resistance, doubled atmospheric CO_2 is predicted to cause a slight increase in rainfall (2 7%) This increase is due to increased evapotranspiration caused by a rise in surface temperatures However, with the dynamic land surface model, rainfall is markedly reduced (by 6%), and soil water content is increased, because increased atmospheric CO_2 causes the stomata to close, thereby reducing evapotranspiration The effect of this stomatal closure is exacerbated because reduced evapotranspiration increases the vapour pressure deficit (ie the air becomes drier), which then causes a further reduction in evapotranspiration through stomatal closure Thus, the predictions of soil drying under doubled atmospheric CO_2 scenarios may be reversed if the stomatal effect is included

This feedback stresses the need for realistic stomatal responses in all simulations of vegetation/climate interactions Other feedbacks, such as those caused by changes in cloud cover (see Table 6), may also significantly alter the predictions made by the full GCM

It would appear from these initial simulations that 'dynamic' vegetation (ie that with properties that change in response to climate change) is necessary if GCMs are to give accurate predictions of the 'greenhouse effect', particularly with regard to the hydrological cycle

The next stage in our research is to use this stomatal resistance model in the full GCM However, the flux of water from the soil to the atmosphere is also controlled by the total amount of leaf area, and this might also change if atmospheric CO_2 and climate change In order to assess the likely changes in leaf area index, we have developed a more comprehensive ecosystem model (BL-HYBRID) around the stomatal model We have constructed a global map of LAI from a land cover data base (Figure 18) This map will be compared with the predictions of LAI made by BL-HYBRID using real global climate data We will also be using BL-HYBRID to make predictions of global fluxes of carbon and water between the land surface and the atmosphere BL-HYBRID operates on a daily timestep and is based on the forest gap model HYBRID (Friend, Shugart & Running 1993) Among other processes, BL-HYBRID simulates canopy photosynthesis and transpiration, whole plant respiration, dynamic leaf area index and biomass, litter production, and soil respiration We are presently working on the inclusion of nutrient dynamics

A D Friend, A K Stevens, and P Cox*

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Nitrous oxide emissions from soil in the UK

(This work was partly funded by the Commission of the European Communities, and involved collaboration with the Edinburgh School of Agriculture)

The importance of nitrous oxide (N_2O) as a 'greenhouse' gas and its role in the nitrogen chemistry of the stratosphere have stimulated interest in the global source of N_2O Nitrous oxide accounts for 5% of the total 'greenhouse effect', partly because, in the absence of chemical sinks in the troposphere, it has a long tropospheric lifetime of *ca* 150 years The destruction of N_2O in the stratosphere may also lead to the depletion of ozone in the stratosphere Biogenic production of N_2O is the dominant source of atmospheric N_2O, with soils estimated to contribute over 50% of the global annual emission Other sources of atmospheric N_2O are the oceans and estuaries, industry, livestock, road transport and, by orders of magnitude less than earlier anticipated, the combustion of fossil fuel

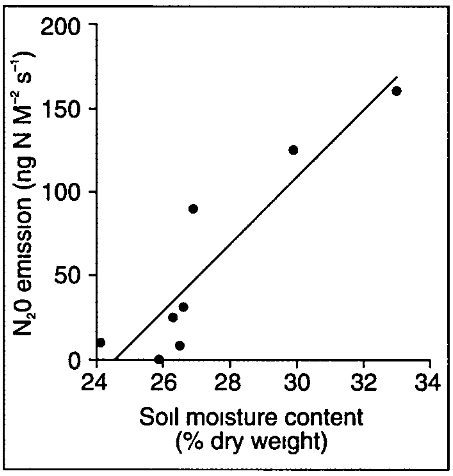

Figure 19 The effect of soil moisture content on the N_2O emission from a fertilized clay loam soil cropped with rye-grass (*Lolium perenne*)

In soil, N_2O is produced during nitrification (the oxidation of ammonia to nitrate) and denitrification (the anaerobic reduction of nitrate to gaseous forms of N) In order to estimate N_2O emissions from soil on a regional or global scale, it is necessary to understand the underlying mechanisms of N_2O production and the size of the emission expected for a particular soil environment Measurements of N_2O emission for soils were made at ITE Edinburgh, using the closed chamber technique A lid (129 mm deep) was placed on to a 1 m x 1 m frame for a period of 1–2 hours Gas samples (1 ml) were taken at intervals and were analysed for N_2O by gas chromatography using an electron capture detector The N_2O flux was calculated from the rate of change in N_2O concentration within the chamber Simultaneous measurements of soil temperature at 30 mm depth and soil surface temperature were made Soil samples were analysed for moisture content, pH and available NH_4^+ and NO_3^-

Nitrous oxide flux measurements were taken from a variety of soil ecosystems agricultural soils, small lowland forest plantations, grassland, an experimental whereas increasing vapour pressure deficit or atmospheric CO_2 increases stomatal resistance (ie the stomata close)

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The importance of nitrous oxide (N_2O) as a 'greenhouse' gas and its role in the nitrogen chemistry of the stratosphere have stimulated interest in the global source of N_2O Nitrous oxide accounts for 5% of the total 'greenhouse effect', partly because, in the absence of chemical sinks in the troposphere, it has a long tropospheric lifetime of *ca* 150 years The destruction of N_2O in the stratosphere may also lead to the depletion of ozone in the stratosphere Biogenic production of N_2O is the dominant source of atmospheric N_2O, with soils estimated to contribute over 50% of the global annual emission Other sources of atmospheric N_2O are the oceans and estuaries, industry, livestock, road transport and, by orders of magnitude less than earlier anticipated, the combustion of fossil fuel

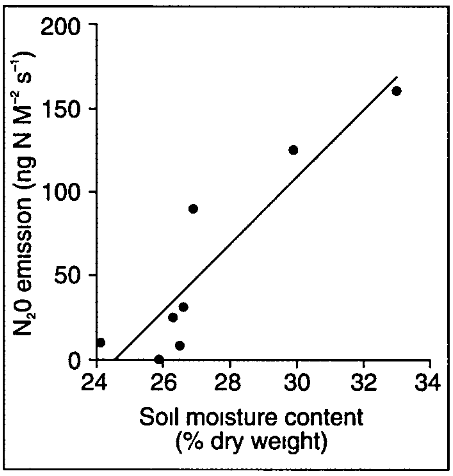

Figure 19 The effect of soil moisture content on the N_2O emission from a fertilized clay loam soil cropped with rye-grass (*Lolium perenne*)

In soil, N_2O is produced during nitrification (the oxidation of ammonia to nitrate) and denitrification (the anaerobic reduction of nitrate to gaseous forms of N) In order to estimate N_2O emissions from soil on a regional or global scale, it is necessary to understand the underlying mechanisms of N_2O production and the size of the emission expected for a particular soil environment Measurements of N_2O emission for soils were made at ITE Edinburgh, using the closed chamber technique A lid (129 mm deep) was placed on to a 1 m x 1 m frame for a period of 1–2 hours Gas samples (1 ml) were taken at intervals and were analysed for N_2O by gas chromatography using an electron capture detector The N_2O flux was calculated from the rate of change in N_2O concentration within the chamber Simultaneous measurements of soil temperature at 30 mm depth and soil surface temperature were made Soil samples were analysed for moisture content, pH and available NH_4^+ and NO_3^-

Nitrous oxide flux measurements were taken from a variety of soil ecosystems agricultural soils, small lowland forest plantations, grassland, an experimental

Plate 18. N_2O flux measurements in the Carse of Stirling using a micrometeorological technique

The wet and dry deposition of nitrogen as HNO_3, NH_4 and NO_x can substantially increase the nitrogen input to a natural non-fertilized ecosystem. At high altitudes (> 400 m), cloudwater deposition significantly increases both sulphur and nitrogen inputs. Furthermore, forests which are commonly planted at high-altitude sites intercept dry deposition very effectively, and therefore can also contribute to an increased input of nitrogen to the soil, as shown at Dunslair Heights in the Borders. Nitrous oxide emissions were comparable to those of the lowland forest plantations and the grassland area, in spite of the much lower soil temperatures measured at Dunslair Heights. Conditions such as on Dunslair Heights are simulated in the ITE large-scale acid mist experiment at Glencorse, near Bush Estate, Midlothian, where mature Sitka spruce trees are currently sprayed with acid mist, pH 2.5, twice a week. The weekly input of nitrogen into the ecosystem is equivalent to 3.4 g N ha^{-1}. It is, therefore, not surprising to observe an approximately four-fold increase in N_2O emission, compared to non-treated neighbouring plots (Table 7). Colleagues at ITE Merlewood observed that clearfelling forests on peat increased N_2O production (Ineson & Dutch 1991). This effect was explained by the tendency for moisture contents to rise after clearfelling, and the decomposition of accumulated forest litter to accelerate, thus increasing the nutrient availability for denitrification.

The enormous variation in the N_2O emission rate observed over all sites (Table 7) was primarily due to variation in soil-available NO_3^- and NH_4^+ concentration, the soil texture and the soil moisture content. Dependence on soil-available N makes agricultural soils receiving N fertilizers clearly the most important source of N_2O. We estimated that fertilized agricultural land in the UK would account for 16–64% of the total annual N_2O emission (Skiba *et al.* 1992).

These estimates have a high degree of uncertainty, mainly because of the high spatial variability in denitrification rates recorded in the field. To account for this spatial variability, it is desirable to measure a flux for considerably larger areas than the 0.5^2 to 1 m^2 areas usually covered by chamber methods. This measurement was attempted in conjunction with colleagues at the Edinburgh School of Agriculture, the Max Planck Institute, Mainz, and the Swedish Environmental Research Institute, Gothenburg, using flux-gradient micrometeorological and conventional chamber techniques. Three separate micrometeorological techniques were employed (gas chromatography, Fourier transform infra-red spectroscopy, and tunable diode laser spectroscopy) to measure small gradients in N_2O concentration close to the surface of a large agricultural grassland (10 ha) in central Scotland (Plate 18). To maximise the success of this experiment, a heavy wet soil was chosen for which denitrification rates are likely to be large. Flux measurements were made immediately after the application of 150 kg NH_4 NO_3 ha^{-1}. Emission fluxes ranged from 0 to 100 ng N_2O–N m^{-2} s^{-1} over the previously ungrazed part of the pasture, and were slightly larger over the grazed area of the pasture (150 ng N_2O–N m^{-2} s^{-1}).

Agreement between the three micrometeorological and the chamber techniques were good, thus establishing the suitability of these methods for measurements of N_2O emissions at the field scale, integrating the great spatial variability in N_2O emission rates (Figure 20) (Hargreaves *et al.* 1993). Flux measurements using micrometeorological methods will be continued by developing the gas chromatography technique and by using a tunable diode laser spectrophotometer purchased jointly with colleagues at the Edinburgh School of Agriculture, with funding from the NERC Terrestrial Initiative in Global Environmental Research (TIGER).

Using our work and data in the literature, we estimated the N_2O emissions from UK soils, based on land area, soil texture, fertilizer application, and typical N_2O

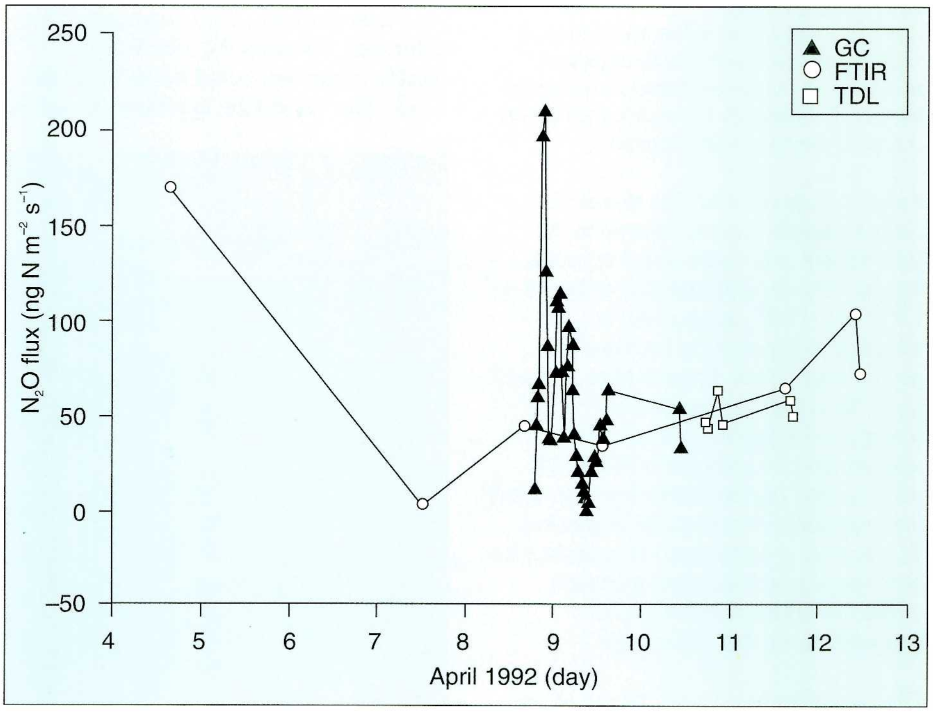

Figure 21. N_2O flux measurements by micrometeorological techniques in the Carse of Stirling, central Scotland, April 1992. GC = gas chromatography, FTIR = Fourier transform infra-red spectroscopy, TDL = tunable diode laser spectroscopy

Table 7. Nitrous oxide emissions from agricultural and natural soil ecosystems in south-east Scotland showing the high variability both within and between soil environments and treatments

Soil texture	Crop/vegetation	Treatment	N_2O emission Median[1] ($ng\ N\ m^{-2}\ s^{-1}$)	sg
Clay loam	Rye-grass	NH_4NO_3, 2 days afa[2]	91	0.26
		NH_4NO_3, 7 weeks afa	0.01	1.77
Clay loam	Rye-grass	NH_4NO_3, 2 days afa	0.01	1.77
		NH_4NO_3, 3 weeks afa	58	0.48
Sandy loam	Winter wheat	NH_4NO_3, 1 week afa	28.2	0.85
		Nitrochalk, 7 weeks afa	0	36.2
Sandy clay loam	Mixture of lawn grasses	Atmospheric input of N: approx. 20 kg N ha^{-1} yr^{-1}	4.33	0.16
	Alder		2.32	23
	Roble beech (*Nothofagus obliqua*)		0.94	0.41
	Downy birch (*Betula pubescens*)		1.31	0.41
	Sitka spruce		2.70	0.18
Sandy clay loam	Sitka spruce	Acid mist N input: 0.85 kg ha^{-1} yr^{-1} in addition to atmospheric input	10.22	0.10
Montaine soil, very peaty	Sitka spruce/ Douglas fir (*Pseudotsuga menziesii*)	Enhanced deposition of N in cloudwater and rainwaters at high elevation: 24.3 kg N ha^{-1} yr^{-1}	1.62	0.84
	Moorland vegetation (heather, grasses, mosses)		3.75	0.32

[1] Median and geometric standard deviation (sg), n = 3
[2] afa = after fertilizer application

Sitka spruce (*Picea sitchensis*) plantation with acid mist, and an upland Sitka spruce plantation and heather (*Calluna vulgaris*) moorland, both about 600 m above sea level. Agricultural soil, immediately after N fertilizer application, emitted the largest concentrations of N_2O (Table 7). Fertilizer application alone, however, did not increase N_2O emissions unless the soil moisture content was high. The dependence of the N_2O emission on the soil moisture content is shown in Figure 19. Considerably larger fluxes were observed for heavy clay loam soil than for light-textured sandy soils (Skiba *et al.* 1992). High soil moisture content and heavy, fine-textured soils promote the development of anaerobic microsites necessary for N_2O production by denitrification. For more aerated light-textured soils and for soils which are dry, nitrification is an important source of N_2O. Application of the nitrification inhibitor dicyandiamide (DCD) inhibited N_2O emissions by 40% in the first week after fertilizer application, suggesting that for this highly aerated sandy loam N_2O was emitted at almost equal rates during nitrification and denitrification (Skiba, Smith & Fowler 1993) (Figure 20).

For the non-fertilized semi-natural and natural ecosystems, it was observed that inputs of N by other means than fertilization increased N_2O emission rates: significantly more N_2O was emitted from plots planted with alder (*Alnus rubra*), a species that develops root nodules in which nitrogen fixation occurs (Table 1).

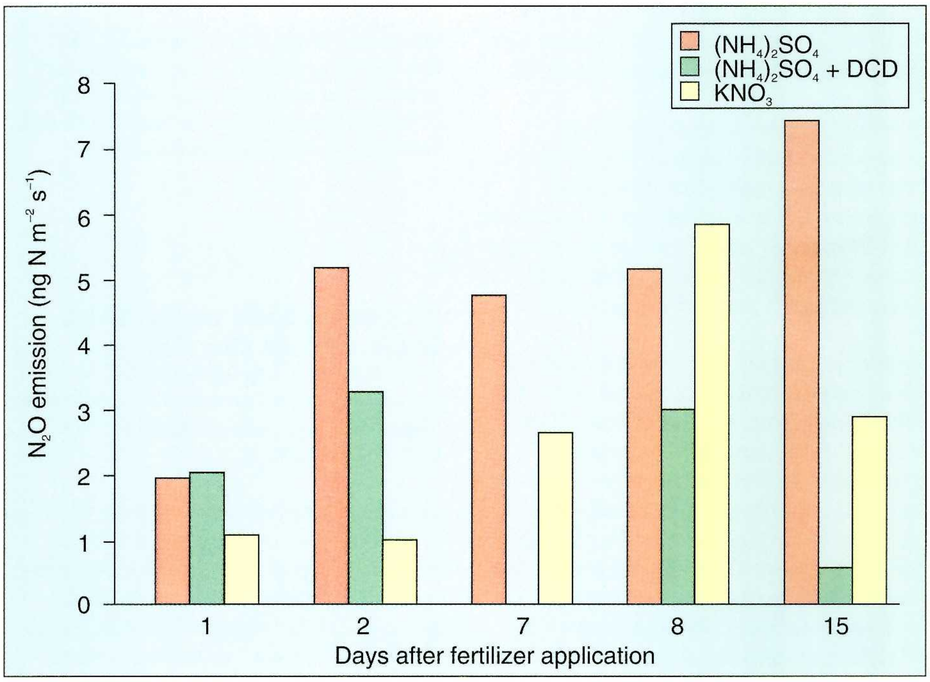

Figure 20. The effect of fertilizer type and the nitrification inhibitor DCD on N_2O emission. This experiment was carried out in a greenhouse containing a freely drained brown earth cropped with rye-grass. Plots were fertilized with $(NH_4)_2\ SO_4$, $(NH_4)_2\ SO_4$ + DCD (10%) or KNO_3 at a rate of 100 kg N ha^{-1}

emissions. Soils emit 13.3–2.5 kt N_2O–N yr^{-1}, which is 28–55% of the total UK emission of N_2O, and 0.3–0.4% of the total annual global N_2O emission.

U Skiba and D Fowler

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Arctic invertebrates and temperature

(This work was funded by the NERC Special Topic programme on Arctic Ecology, and involved collaboration with the Liverpool John Moores University, the British Antarctic Survey, and the University of Birmingham)

It is widely predicted that elevated carbon dioxide concentrations in the atmosphere will cause a rise in mean annual surface temperatures of between 1.5°C and 4.5°C. Such a rise in temperature is likely to be most pronounced in the Arctic where a rise of up to 10°C has been predicted. Manipulative experiments on the undisturbed ecosystems of the Arctic offer unique opportunities for examining the responses of terrestrial organisms. To this end, a consortium of invertebrate ecologists has developed a project within the NERC Special Topic programme on Arctic Ecology.

This invertebrate project, based at the NERC Arctic Research Station at Ny-Alesund, Svalbard, aimed (i) to characterise the thermal environment of common invertebrates; (ii) to conduct, using polythene cloches, a field temperature manipulation experiment to assess the effects of elevated temperatures on invertebrate communities; and (iii) to carry out detailed studies on the ecophysiology and life history responses of selected invertebrates to changing temperatures, making comparisons between the plant-feeding and soil-dwelling communities.

Two characteristic high arctic communities are being studied: a polar semi-desert community in the outer fjord zone (*Dryas octopetala* zone) and tundra heath of the inner fjord zone (*Cassiope tetragona* zone) (Coulson *et al.* 1993). At these sites, 20 geodesic transparent polythene tents, each 1.5 m x 1.5 m, were erected and maintained for the summers of 1991 and 1992 in an experiment to modify the soil and vegetation temperatures, and to assess the responses of the above- and below-ground invertebrate populations (Plate 19).

Temperatures within the tents and in control plots followed similar seasonal and diel patterns. Summer temperatures within the tents were increased by *ca* 5°C in the vegetation, and *ca* 2°C at 3 cm depth in the soil. Cumulative day degrees above zero within the tents were increased by *ca* 35% in the vegetation and *ca* 9% in the soil (Figure 22). On occasions, the maximum difference between the inside and outside of the tent could be as much as 10°C. The vegetation appeared to act as a thermal insulator, preventing the conduction of heat into the soil from above and enhancing the thermal contact with the cooling permafrost below. Although temperatures in the vegetation were similar at both sites, soil temperatures were modified less in the tundra heath than in the polar semi-desert with its sparser vegetation (Coulson *et al.* 1993).

During the first season, there were no detectable differences in either soil mite or collembolan populations between the tented and control plots, but the outer fjord site had the highest densities. In 1992, the mites and Collembola of the inner fjord site remained fairly constant, whereas on the outer fjord site collembolan numbers declined while mite numbers increased on both the tented and control plots. This coincided with an unusually warm dry spell that led to a drying out of the soil at the outer but not at the inner fjord site. These results were surprising; an increase in the thermal budget of 10% produced no measurable response in mite and collembolan populations over two years, but an unexpectedly dry spell enhanced recruitment and increased mortality at the outer fjord site. The effects of temperature appears to interact strongly with soil moisture, and these two factors need to be considered together when modelling the effects of elevated temperatures.

The aphid *Acyrthosiphon svalbardicum* was found to be the most abundant above-ground invertebrate herbivore

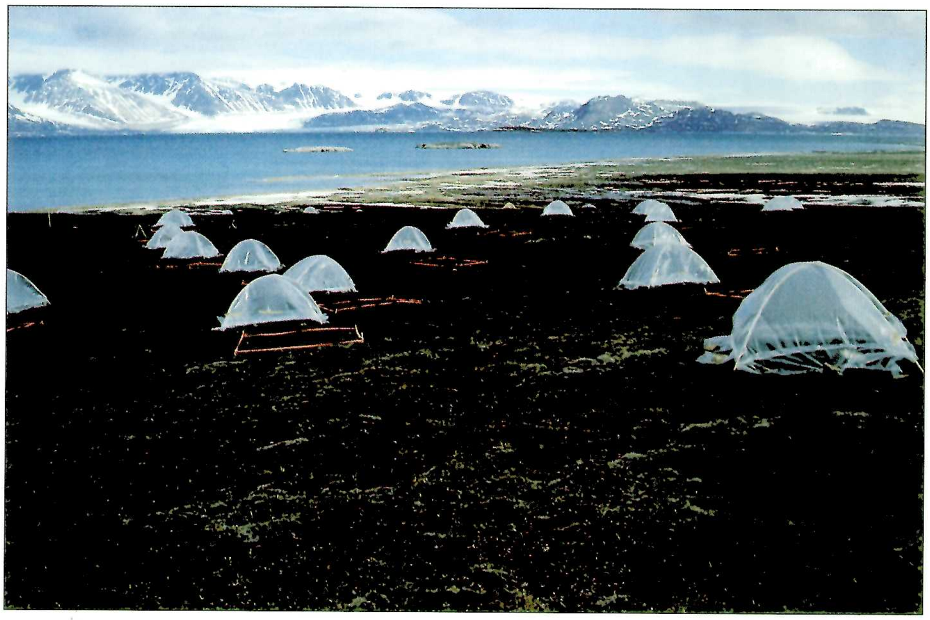

Plate 19. General view of study area at Ny-Alesund with tents in position

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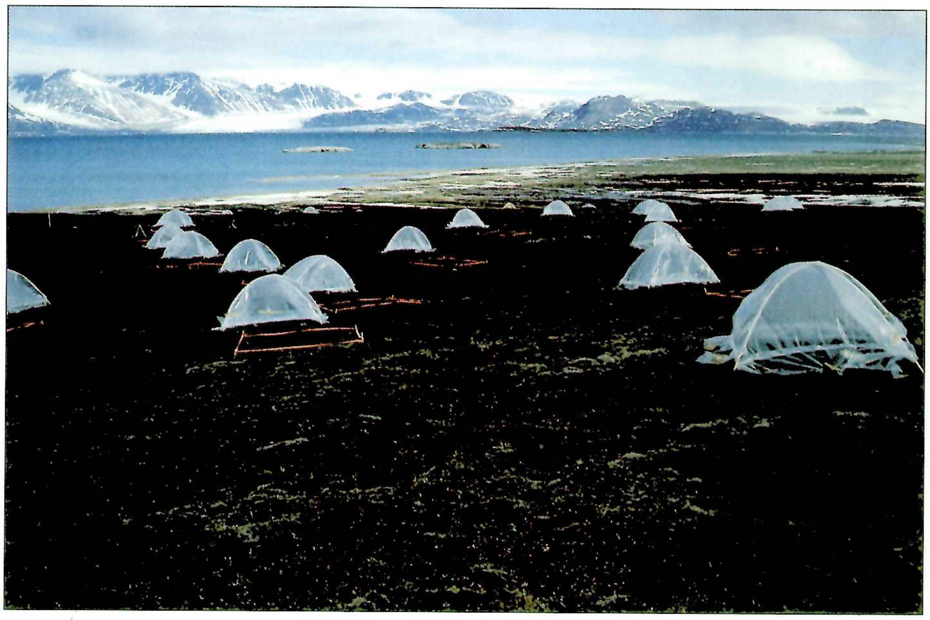

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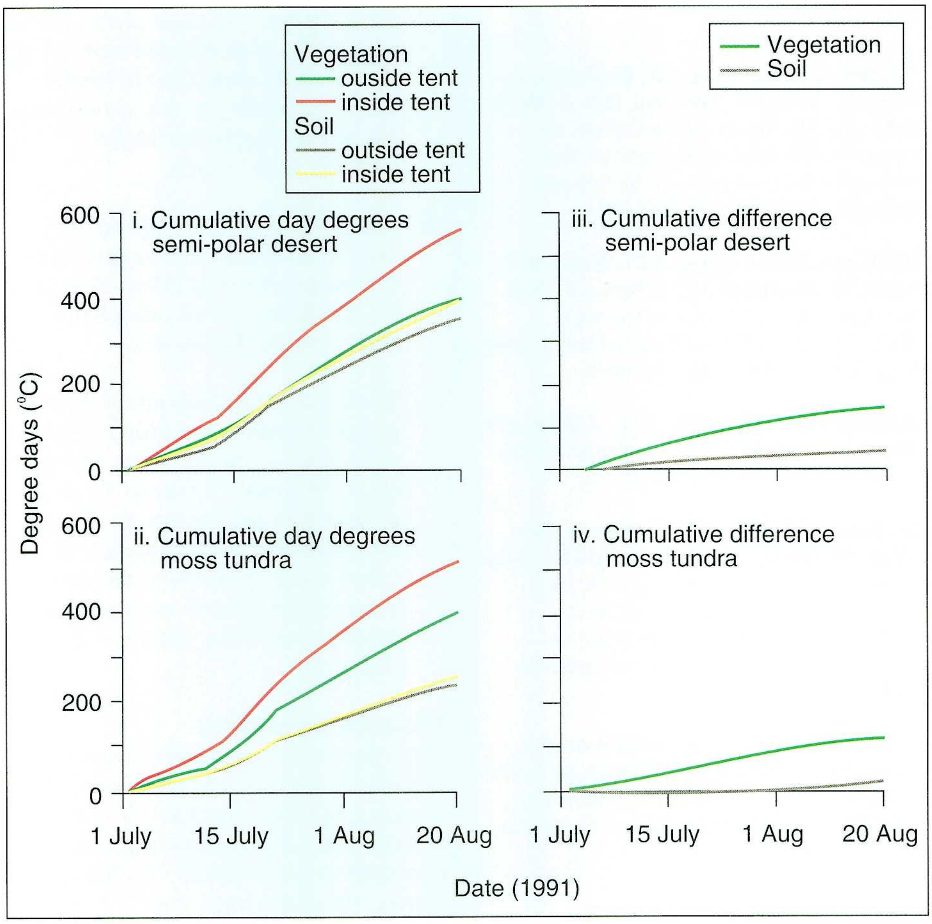

Figure 22. Comparison of cumulative day degrees (°C) at the semi-polar desert (top left) and moss tundra/tundra heath (bottom left) sites. The right-hand diagrams show the cumulative difference in day degrees between the inside and the outside of the tent for probes placed in the vegetation and in the soil

and is monophagous on mountain avens (*Dryas octopetala*) (Plate 20). Although this species had previously been reported from Spitsbergen, its four apterous morphs (fundatrix, vivipara, ovipara and male) were described for the first time (Strathdee *et al.* 1993a). The annual life cycle is genetically determined, unlike temperate aphids in which it is determined by environmental factors. The fundatrix gives birth directly to both sexual morphs (unique in the Aphidinae) which mate and lay eggs, thereby ensuring survival in the following season. The fundatrix also produces some viviparae which in turn produce only sexual morphs; however, under the present climate, this happens rarely (Strathdee *et al* 1993b). When thermal budgets are increased, this flexible life cycle has the potential to increase the number of overwintering eggs. Raising field temperatures by 2.8°C using cloches (Strathdee & Bale 1993) advanced the phenology of both the aphid and the host plant and enabled the aphid to complete three generations in a season; in turn, this led to an 11-fold increase in the number of overwintering eggs. With guaranteed egg production by mid-summer combined with an in-built flexibility to produce an extra generation in favourable seasons, *Acyrthosiphon svalbardicum* is well adapted to respond rapidly to enhanced temperature regimes.

Onychiurus arcticus is a large species of springtail (Collembola) with a maritime distribution in the high Arctic. It is to be found beneath stones on screes, particularly beneath bird cliffs and on glacial outwash fans. This species was found to be unusual among the collembola in feeding on living bryophyes (*Drepanocladus uncinatus, Racomitrium lanuginosum* and *Polytrichum alpinum*) and algae, as well as organic detritus (Hodkinson *et al.* 1993). Detailed ecophysiological studies have shown that this species is active down to –4.0°C. The animals supercooled to –6.0°C before freezing (Figure 23) and this relatively high supercooling point, which was stable throughout the year, was not affected by either starvation or temperature or acclimation. The survival of individuals at sub-zero temperatures showed a similar pattern. At –3.0°C, 60% of the individuals survived for 84 days, but at lower temperatures survival was reduced, with only 35% of the individuals surviving at –5.0°C. In contrast, survival at high temperature was good, and was shown to be dependent on humidity. At 100% humidity, over 80% of the individuals survived for 3 h at 30°C, but there was negligible survival above 32.5°C, and above 35.0°C there was no survival at all.

Oxygen consumption by *O. arcticus* was comparable with that of other surface-dwelling species of Collembola, despite

Plate 20. Mountain avens

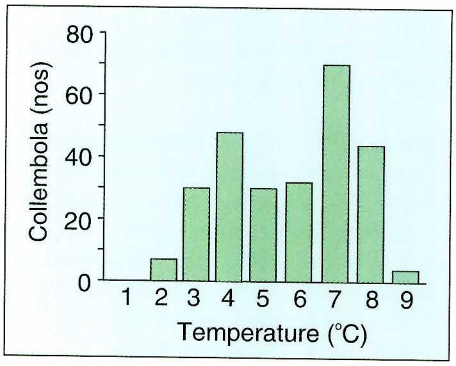

Figure 23. Supercooling points for *Onychiurus arcticus*

O. arcticus being morphologically similar to soil-dwelling species. The relationship between oxygen consumption and temperatures was non-linear over the range 0–30°C. From zero to +10.0°C, the Q_{10} was as high as 7.0, falling to 1.6 over the range 10–30°C, and increasing again above 30°C as the animals suffered heat stress.

The ecophysiological profile of *Onychiurus arcticus* reveals an animal which is poorly adapted for surviving low winter temperatures. It has physiological characteristics suited to living on the soil surface beneath deep snow cover, and is able to select rapidly favourable micro-habitats. Following snowmelt, the springtail is able to take advantage of the warmer conditions, but as temperatures rise its response is dampened; however, this enables it to be active at the relatively high temperatures (up to 30°C) which it might experience living on the soil surface during the summer.

Acyrthosiphon svalbardicum and *Onychiurus arcticus* are examples of the differing adaptations shown by polar invertebrates. The project aims to complete similar profiles for the Collembola *Onychiurus groenlandicus*, *Hypogastura tullbergi* and *Folsomia quadrioculata*, and for the cryptostigmatid mites *Camisia borealis*, *Hermannia reticulata*, *Diapterobates notatus* and *Certoppia hoeli*. These species are present in the sample material from the field temperature manipulation experiments, and changes in population dynamics will be combined with ecophysiological data to predict the responses of these invertebrate populations to changing temperatures.

N R Webb, I D Hodkinson[1], W Block[2], J S Bale[3] and A T Strathdee[3]

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Modelling the effects of climate change on the distribution of lizard orchid

(This work was funded by the Department of the Environment)

Climatologists predict that the flora and fauna of Great Britain are about to experience changes in temperature at an unprecedented rate. ITE has begun to model the impacts of these changes on the distribution of species, and has chosen the lizard orchid (*Himantoglossum hircinum*) (Plate 21) as its first species to develop the models for several reasons.

i. Lizard orchid has a predominantly European distribution (Figure 24) and the area which is climatically suitable for this species is likely to expand northwards.

ii. Most species will not be able instantly to fill the areas which become available to them as the climate changes, mainly because of their inability to disperse and colonise sites which become suitable. Orchids are better adapted for dispersal than most plants, having minute seeds distributed over great distances by wind. Lizard orchid seeds, for example, can quite easily be carried across the English Channel from France.

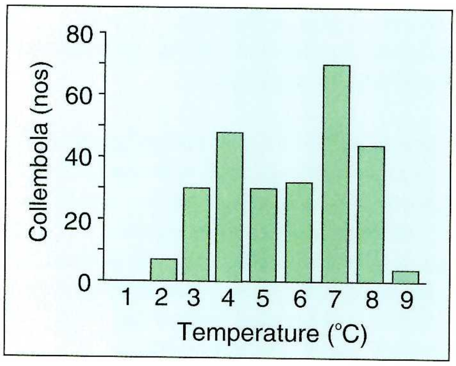
iii. It is one of Britain's rarest species and, as a result of monitoring, there is a large amount of information on the distribution of its populations within Britain (Figure 25).

iv. It has long been recognised that on a global or continental scale species distributions are limited by climate. One of the earliest papers on this relationship was by Good (1936). He suggested that the spread of lizard orchid in Britain in the early years of this century was due to an amelioration of the climate at that time.

Climate suitability

In the past, the correlation between distribution and climatic factors has at least in part been anecdotal. We are now in a position to use a more rigorous approach to this problem. A number of climatic variables were used to explore what might determine the British distribution of lizard orchid (Carey & Ullyett 1993). The distribution of the species in the south-east of England suggested that soil moisture deficit could be an important limiting factor. Therefore, the 12 monthly soil moisture deficits were used as the climate variables in the models shown in this

Plate 21. The lizard orchid



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Modelling the effects of climate change on the distribution of lizard orchid

(This work was funded by the Department of the Environment)

Climatologists predict that the flora and fauna of Great Britain are about to experience changes in temperature at an unprecedented rate. ITE has begun to model the impacts of these changes on the distribution of species, and has chosen the lizard orchid (*Himantoglossum hircinum*) (Plate 21) as its first species to develop the models for several reasons.

i. Lizard orchid has a predominantly European distribution (Figure 24) and the area which is climatically suitable for this species is likely to expand northwards.

ii. Most species will not be able instantly to fill the areas which become available to them as the climate changes, mainly because of their inability to disperse and colonise sites which become suitable. Orchids are better adapted for dispersal than most plants, having minute seeds distributed over great distances by wind. Lizard orchid seeds, for example, can quite easily be carried across the English Channel from France.

iii. It is one of Britain's rarest species and, as a result of monitoring, there is a large amount of information on the distribution of its populations within Britain (Figure 25).

iv. It has long been recognised that on a global or continental scale species distributions are limited by climate. One of the earliest papers on this relationship was by Good (1936). He suggested that the spread of lizard orchid in Britain in the early years of this century was due to an amelioration of the climate at that time.

Climate suitability

In the past, the correlation between distribution and climatic factors has at least in part been anecdotal. We are now in a position to use a more rigorous approach to this problem. A number of climatic variables were used to explore what might determine the British distribution of lizard orchid (Carey & Ullyett 1993). The distribution of the species in the south-east of England suggested that soil moisture deficit could be an important limiting factor. Therefore, the 12 monthly soil moisture deficits were used as the climate variables in the models shown in this

Plate 21. The lizard orchid

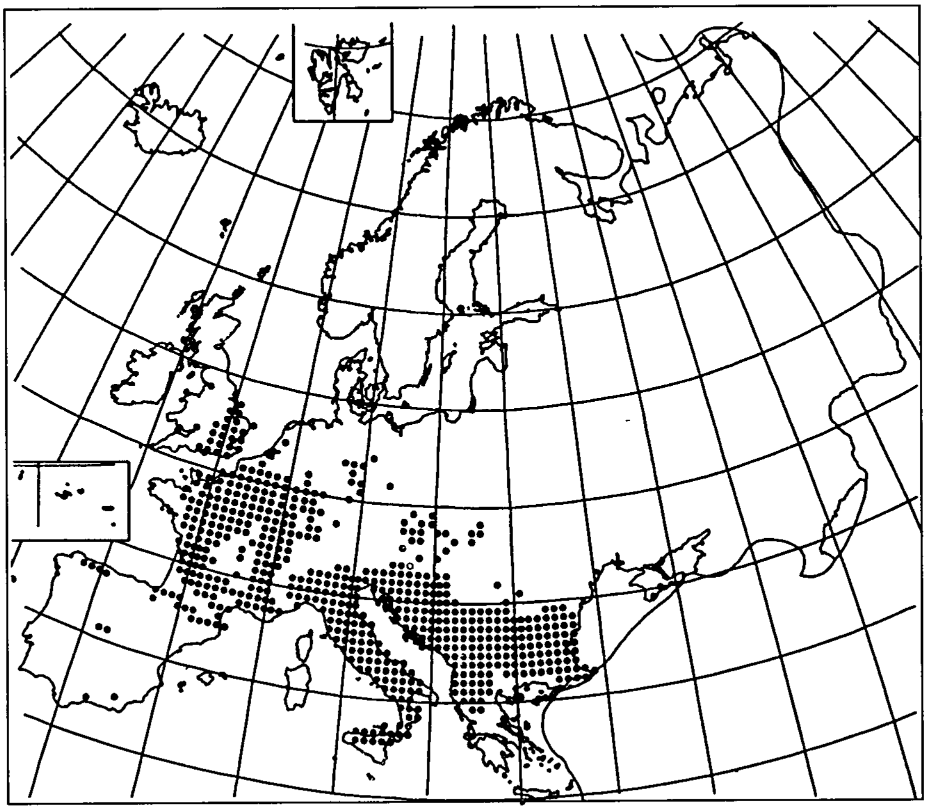

Figure 24 The European distribution of the lizard orchid. This map was produced on a geographical information system by digitising the distribution given by Meusel, Jäger and Weinert (1965) and then overlaying that map on the *Atlas Flora Europaea*, 50 km grid

paper. Step-down multiple linear regression removed the insignificant variables and gave the relationship

$$\mathrm{Ln}(Y) = -6.17 - 0.05X_1 + 0.01X_9 \qquad \text{Equation 1}$$

where Y is the number of lizard orchid populations per 40 km square, X_1 is the soil moisture deficit for January (in mm), and X_9 is the soil moisture deficit for September (in mm). The distribution data come from the Biological Records Centre and the climate data come from the Meteorological Office's MORECS data base. These climate data are limited to an unsatisfactory 40 km grid. We have, however, used this data base to demonstrate our modelling approach.

The equation (Equation 1) was then fitted to the climate data for the 40 km squares of Great Britain, and the likely number of lizard orchid populations in those squares calculated, which is a measure of the climatic suitability of those squares (Figure 26, first map).

Future climatically suitable areas

We can predict the expansion of the climatically suitable area of lizard orchid quantitatively by fitting Equation 1 to the predicted climate for the 40 km squares of Britain. Using this method, we see that the climatically suitable area for lizard orchid should expand quite dramatically (Figure 26, second map) if there is only a 5% increase in the soil moisture deficit in January and September.

Habitat suitability

Within their climatically suitable areas, most species are likely to be limited by the availability of suitable habitat. Lizard orchid, for example, is found on calcareous soils and sands. We have developed a method for producing a habitat density map based on soil types (data used under licence from the Soil Survey and Land Resource Centre and Macaulay Land Use Research Institute). A habitat density map can be produced which shows the number of 1 km squares containing suitable soil types in each 10 km square. The habitat density map for lizard orchid (Figure 27) indicates that there are many areas outside the present climatically suitable area (Figure 26, first map) which apparently have suitable soils for populations of the species.

DISPERSE

We have been developing a model, DISPERSE, which includes the climatically suitable area (Figure 26, first map) and the habitat density map (Figure 27), and which introduces population dynamics. DISPERSE is an aggregated cellular automaton. Cellular automata are models based upon a number of cells on a grid, each cell having its own set of rules which are affected by the neighbouring cells. In an aggregated cellular automaton, cells are grouped together in larger cells which share the same properties. We decided that the spatial unit for the model should be the 1 km square as this is the finest-resolution species distribution data we have. It means that in our model each 1 km square of Britain can support only one population of lizard orchids, which is not necessarily true. The number of 1 km squares in each 10 km square that can have a population is determined by the habitat density (Figure 27). For example, if a 10 km square has a habitat density of 20 suitable 1 km squares, then there can be a maximum number of 20 populations in that 10 km square. All the 1 km squares in each 40 km square have the same climatic suitability, which is equal to that shown in Figure 26, first map.

The position of extant populations was fed into the program at time interval 1. Each population had a probability of surviving (input parameter 1) from time

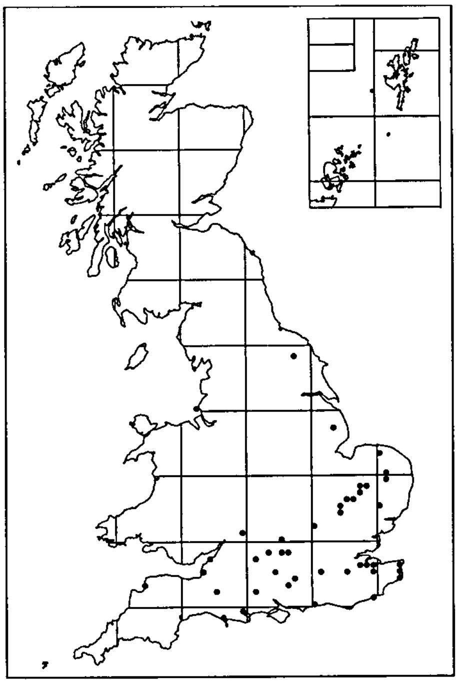

Figure 25 The British distribution of lizard orchid. All records from 1940 onwards are included. Yellow squares have one population, light green squares have two populations, dark green squares three populations

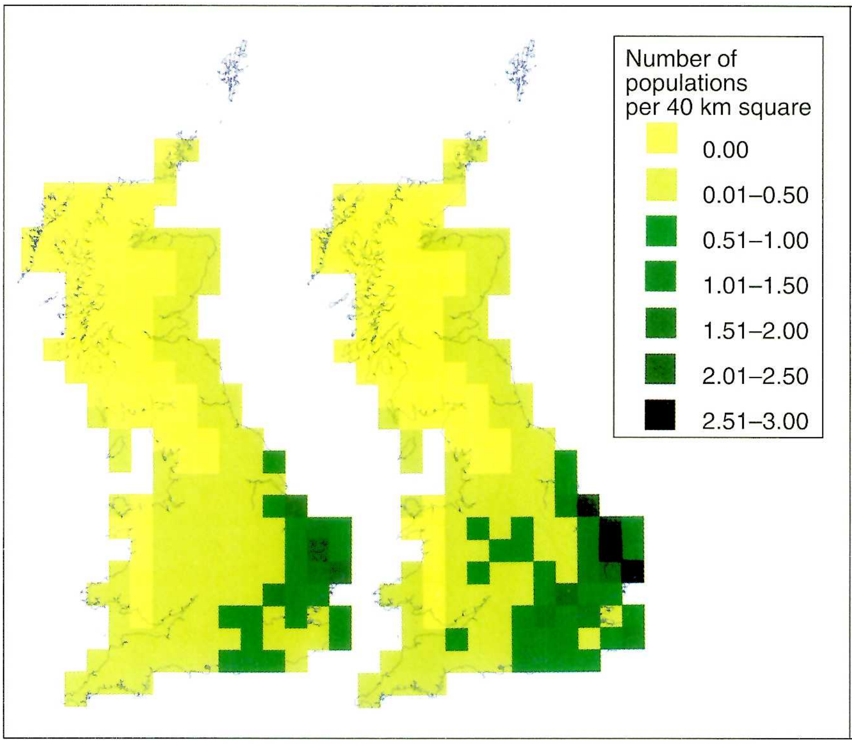

Figure 26. First map: the current climate suitability map for lizard orchid. Climate suitability is expressed in terms of the likely number of populations expected in any 40 km square and is calculated from Equation 1. Second map: the climate suitability map for lizard orchid with a 5% increase in soil moisture deficit

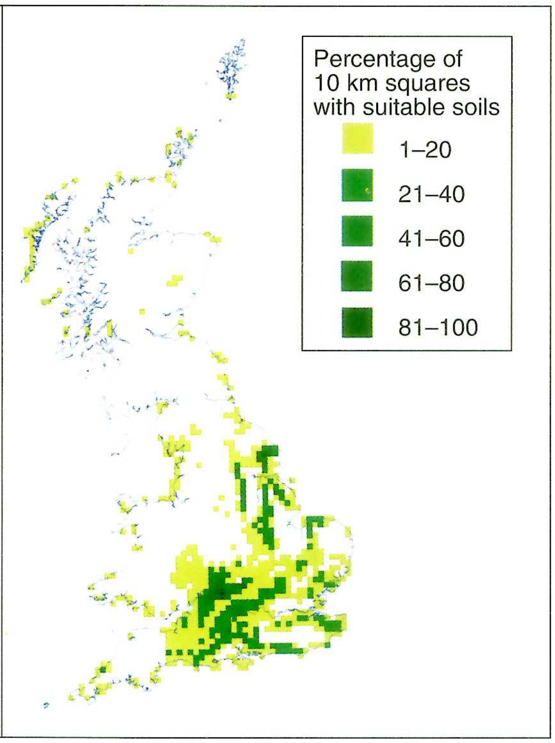

Figure 27. The habitat density map for lizard orchid. Habitat density is expressed as the number of 1 km squares in each 10 km square which have a soil type suitable for lizard orchid

interval 1 to time interval 2. If any population survived, it became a year older. When they reached a specified age of maturity (input parameter 2), they produced a number of long-distance dispersing seeds (input parameter 3) which travelled a random distance from their parent determined by a very simple model, the bivariate normal distribution. The fourth input parameter was the root mean square (rms) deviation of the bivariate normal distribution. The model was allowed to run for 60 time intervals, equivalent to 60 years.

In some runs of the model, the death of one or two critical populations in the first few time intervals can push the species towards extinction, whilst in other runs the chance establishment of a seed in the first few time intervals can lead to the species expanding. We, therefore, ran the model 25 times for each of a variety of combinations of the four input parameters, and produced a probability map of the lizard orchid distribution after 60 time intervals, ie in the year 2050. As a control we assumed that, if there was no climate change, the number of populations of lizard orchid would remain relatively stable. We are currently carrying out sensitivity analyses to determine how the four input parameters interact and control the number of populations of lizard orchid. The most stable result so far was achieved with population survival probability set to 0.95, age to maturity set to ten years, three long-distance dispersing units per time interval per population, and rms dispersal distance set to 40 km.

The model was then rerun 25 times using a changing climate scenario. The climate suitability was increased linearly at each time interval so that there would be a 5% increase in soil moiture deficit by the year 2050. With the four input parameters held as they were in the example above, the number of populations increased slightly but not significantly.

Conclusions

Lizard orchid may not be able to fill the extra area that becomes available to it by 2050, probably because the chances of any seed landing on suitable habitat outside its parent's population are very small. However, a greater expansion than our model suggests may be seen if the ecological niche of the species in Britain becomes wider as the climate becomes more favourable. There is anecdotal evidence that in France, in the centre of the distribution of lizard orchid, it grows in a wide range of habitats.

We are continuing to develop our models with European climate data and detailed studies of population dynamics to give us better models of the climatic and habitat requirements of lizard orchid, while studies of infection theory will improve our understanding of the processes of dispersal.

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Intraspecific variation in fluctuations of butterfly populations towards the edges of range

(This work was funded by the NERC Terrestrial Initiative in Global Environmental Research)

A central problem in ecology is to identify and understand patterns in the distribution and abundance of species (Gaston & Lawton 1988). There has, for example, been much interest in the possibility that animal populations experience greater fluctuations, and may be less stable, towards the edges of species' ranges. However, although this hypothesis is based on sound ecological premises and convincing theoretical deductions, empirical confirmation has been elusive. Interspecific comparisons of population patterns are generally meaningless because of artefacts and incompatible data sets, whereas intraspecific data sets are seldom long or thorough enough for valid comparisons to be made, and may suffer from some of the same artefacts that bedevil interspecific comparisons (McArdle, Gaston & Lawton 1990). Indeed, the only published data known to us that confirm these theoretical predictions are that certain vole populations fluctuate with increased amplitude and more cyclically at higher latitudes in Fennoscandia (Hansson & Hentonnen 1985).

The British Butterfly Monitoring Scheme (BMS) offers a unique opportunity to investigate this phenomenon in cold-blooded animals. The northern limits of most European butterfly species are closely correlated with summer isotherms, and as many as 47 of our 58 resident species reach or approach the northern limits of their ranges somewhere across the 4.5°C gradient in mean summer temperatures that exists between south England and north Scotland. Relative changes in the numbers of most British butterfly species have been monitored since 1976 (ie for 17 or 34 generations) on fixed sites from Cornwall to Sutherland, using a method that ensures – for colonial species – that the same population is monitored in the same way in every year or generation (see ITE Annual Report 1990–91 and Pollard & Yates 1993). Furthermore, enough is known about the phenology and population structure of most British butterflies for a distinction to be made between species whose numbers are enhanced erratically by migrants and the colonial species that experience genuine population changes on each monitored site. It is also possible to distinguish between univoltine species and those that have partial second or third broods, which could distort the size of emergences in alternate years on certain sites.

We restricted our analyses to species with data sets that satisfied three criteria:

i. there must be a valid run of annual population index values for at least eight consecutive years;

ii. the mean index value for each run of years should not be less than 10;

iii. there should be at least seven sites that fulfilled the first two conditions.

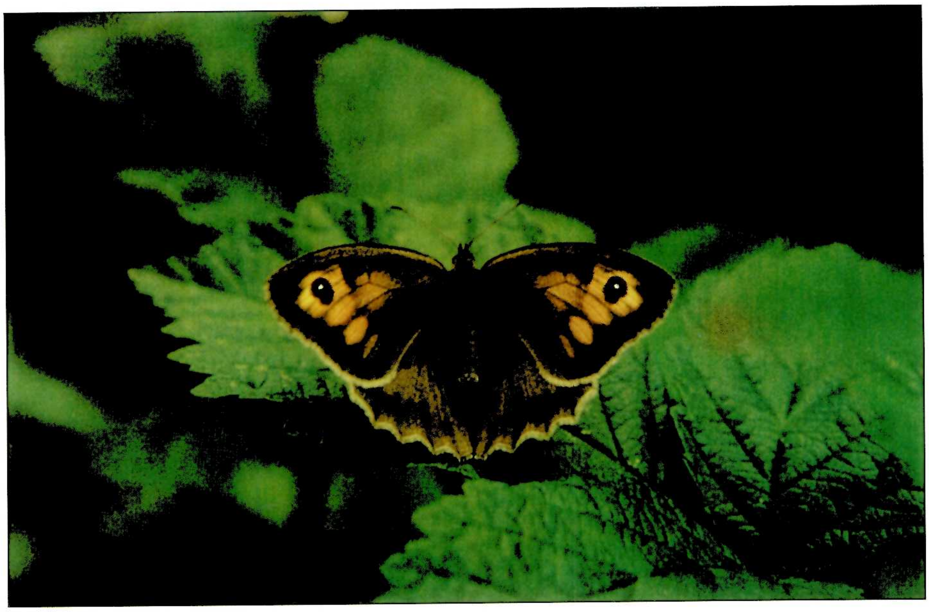

Plate 22. Female meadow brown butterfly

Twenty-seven species met these three conditions, although in some cases the geographical distribution of their sites was small and we would not necessarily expect to detect significant differences in patterns of population changes.

Nevertheless, the results showed that there were significant increases in the amplitude of population fluctuations in nine species towards the northern limits of their ranges. In four cases (and with a fifth species that did not show greater amplitude in the north), fluctuations were also significantly smoother over a period of years on their more northern sites. In addition, five species experienced greater fluctuations the further east that they were monitored in their ranges.

The clearest demonstration of the phenomenon was for the meadow brown (*Maniola jurtina*) (Plate 22), which also had much the largest useful data set: 54 different populations were both large enough and monitored for long enough to be included in the analysis, and the mean population index (507) on these sites was more than double that of any other species. In addition, not only was the meadow brown monitored over a greater geographical range than any other species, but it conveniently reaches the northern limit of its world range in north Scotland. It is also a colonial species and is strictly univoltine.

The mean changes in population size on the six most northerly and six most southerly monitored populations of the meadow brown are shown in Figure 28. Clearly, the amplitude of fluctuations on the northern sites was considerably greater than in the south, and, when the measurements of the meadow brown fluctuations on all 54 sites were plotted against latitude, we found that the increase in amplitude occurred gradually across the country from south to north, and was not confined to a few northern populations. In addition, whereas southern populations fluctuated erratically from one generation to the next, northern ones built up and fell in size gradually over a number of years. This difference in the smoothness and direction of population change is statistically significant, but a longer data set is required before we can say whether northern populations of the meadow brown genuinely oscillate on a 3–4 year cycle, as Figure 28 suggests.

There are several possible explanations for these differences in population

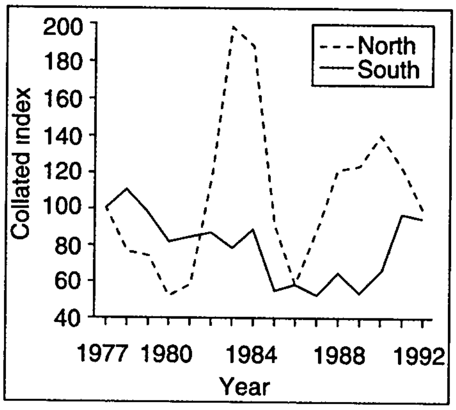

Figure 28 Mean changes in the abundance of the meadow brown butterfly on six northern and six southern sites between 1977 and 1992. Northern populations experienced large oscillations, which are possibly cyclical, with each increase and decrease occurring over 3–4 generations. Fluctuations on southern sites were smaller in amplitude and more erratic.

fluctuations, none of which is mutually exclusive. Two that are particularly pertinent for cold-blooded species are as follows.

i Ectotherms may be living at the limits of their physiological tolerances at the edges of their ranges, and a very small variation in the weather could have dramatic consequences on their fitness. In this respect, it is interesting to note that, although mean summer temperatures are lower at the high latitudes sampled by the BMS, they vary less from year to year. Thus, the increased amplitude of butterfly fluctuations cannot be explained by there being a more variable summer climate in the north: the reverse is true.

ii Some butterflies which inhabit broad niches near the centres of their ranges become increasingly confined to local patches that have unusually warm microclimates further north. Thus, some grassland species oviposit only in short or sparse swards on south-facing slopes in the north, but can also breed in much taller swards and on all aspects in the south (Thomas 1993). For these species, the areas that are suitable for breeding remain more or less constant on sites towards the centres of their ranges, but the colony may temporarily expand into areas that are normally too cool for breeding in the north during years when summer temperatures are one or two degrees warmer than usual, allowing the population to boom for a year or two before crashing when temperatures return to normal.

This description of how certain insect populations fluctuate at different latitudes (or under different climates) has applied aspects, in addition to its intrinsic interest to ecology. Many of the invertebrates that currently live near the edges of their ranges in Britain may be situated nearer the centre if the climate warms through the 'greenhouse effect', and the reverse may be true for some alpine species. It will be important to predict how the dynamics of populations are likely to change, on the one hand to see whether valued local species will need greater or less conservation effort under a different climate, and on the other hand to predict whether species that do not currently cause commercial damage in Britain are likely to experience population patterns that might turn them into pests.

J A Thomas, D Moss and E Pollard

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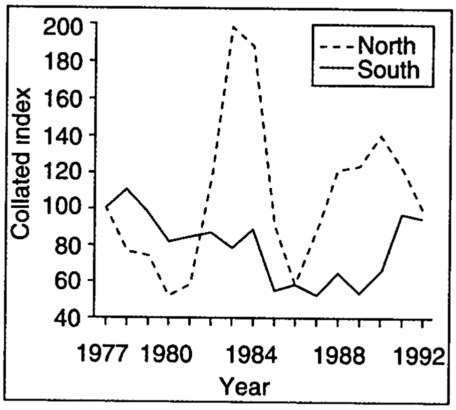
The Environmental Change Network (ECN)

The Natural Environment Research Council (NERC) is one of nine organisations* which are collaborating in sponsoring the United Kingdom Environmental Change Network (ECN). All have a strong commitment to environmental management and research, and to monitoring the changes which may be taking place in UK ecosystems.

The ECN initiative arose from proposals by an NERC Working Group on Long-Term Reference Sites, chaired by Prof O W Heal, which reported in 1989. It recommended that a network of sites should be set up throughout the UK, with the primary purpose of identifying and quantifying environmental changes associated with man's activities, distinguishing man-made change from natural variations and trends, and giving early warning of undesirable effects. The ECN was officially launched by Prof J Knill in January 1992. The operation of the Network depends on the voluntary collaboration of the sponsoring agencies in providing sites and the necessary funding for staff to carry out the monitoring programme. Scientists from a number of research institutes and universities have collaborated in devising protocols intended to ensure that measurements are standardised, with appropriate quality assurance procedures, at all the sites. Site managers will be responsible for ensuring that the protocols are followed at their own site and that the data are sent in a standard format to a central data facility.

The sites

There already exist in the UK many sites with a long history of environmental data collection and where repeated surveys have taken place. In selecting suitable sites it seemed sensible to capitalise, as far as possible, on established sites with their known management history and to take advantage of existing data and understanding. A list of 24 such terrestrial sites was drawn up, representing the broad range of climate, soil, habitat and land management in the UK. It has been possible to recruit nine terrestrial sites into the Network so far; it is expected that two others will be committed in 1993, and that others will join later. The sites range from small, intensively managed lowland agricultural establishments to large, semi-natural upland areas (see Figure 29). A number of internationally important research sites are included in the network, eg Rothamsted Experimental Station which celebrates its 150th anniversary of agricultural research in 1993.



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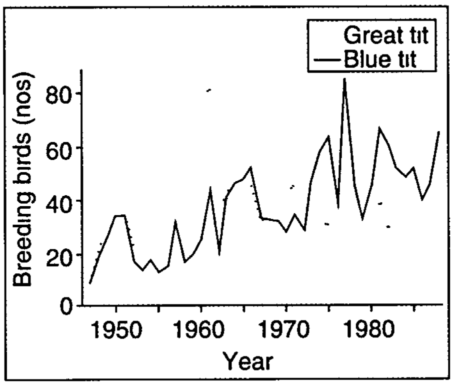

Figure 30 Fluctuations in populations of great and blue tits breeding in Wytham Wood, 1947–88

are also 'flagship' sites for the NERC Terrestrial Initiative in Global Environmental Research (TIGER), and will be used by researchers in that programme for a range of research projects. The links between ECN and TIGER are important – the relatively short-term research from TIGER will provide detailed information on the ecological and environmental processes which are important to ECN, whilst ECN is already providing useful background data on the environment at these sites for TIGER researchers.

The ECN programme is managed by a Central Co-ordination Unit based at ITE Merlewood. In addition to the ECN Co-ordinator, the team consists of a data manager, a statistician, and the managers of the two NERC-sponsored sites.

An ECN data base is being developed at Merlewood to handle and make accessible the large quantities of data produced by the programme. A meta information system will contain vital information describing the origin of the data, and their spatial and temporal characteristics, as well as their quality. Digital map information describing the spatial variability of measurements within and between ECN sites is being established in a geographical information system, this system is integrated with the data base and with the meta information system for spatial analysis and modelling. It is being designed to handle and retrieve the data efficiently, as well as to provide for the wide range of spatial and temporal queries and analyses needed for environmental change research. The data base will be accessible to registered users over the Joint Academic Network (JANET).

Examples of long-term research at Wytham and Moor House ECN sites

Some examples of existing long-term research at the two NERC-sponsored ECN sites indicate the value of long-term observations in clarifying the roles of different environmental factors which could be confused in short-term studies.

At Wytham, a long-term population study of tits, especially the great tit (*Parus major*), started in 1947 and breeding data on these birds have been collected annually ever since by researchers in the Department of Zoology at the University of Oxford (Perrins 1989). Sparrowhawks (*Accipiter nisus*) are a major predator of tits and they hatch their young at about the same time as young tits leave the nest, they feed heavily upon those tits which have recently left the nest and are easily caught. Those hawks which hatch their young later seem unable to catch enough tits, and they cannot find a good alternative prey, they bring fewer prey to the nest and raise fewer young than early nesters. Sparrowhawks became very rare in the late 1950s because of the widespread use of seed dressings, such as dieldrin, they stopped breeding in Wytham in about 1959, and were rarely seen during the 1960s. However, they have been breeding again in the wood since the mid-1970s, which has made it possible to look at tit populations both in the presence and absence of a major predator (see Figure 30). In spite of the heavy predation of up to 30% of the fledglings and further predation throughout the winter, there is little evidence that tits were more common during the 1960s when the hawks were absent than they were either before or after. Tit populations seem to have been affected more by other factors, possibly by year-to-year changes in their own food supply or changing habitat, than by changes in this predator. ECN data will provide background information which will aid in the interpretation of such detailed studies.

A study by Prof J B Whittaker (Whittaker 1971) has linked the Wytham and Moor House ECN sites, and demonstrates the benefits of ecological studies carried out at several sites, this benefit is expected to be multiplied at the network of ECN sites. The study compares and contrasts the changes in two populations of a cercopid, *Neophilaenus lineatus*. This spittle-bug is at the edge of its range at Moor House on the Pennines, in contrast with its status at the southern, lowland site at Wytham. Observations of second instar 'generation mortality' and of second instar density at the two sites show contrasting situations (Figure 31).

At Moor House, the plot of the two variables has a slope not significantly different from zero, and provides no evidence of density-dependent mortality. At Wytham, on the other hand, mortality within a generation is related to the starting density of that population, as shown by the significant slope of the regression line. These results demonstrate that, whilst the effects of climate change may be seen clearly where a species is at the edge of its range, the effects may be masked where fluctuations in numbers are governed by density-dependent factors. The use of a network of sites covering a range of environmental conditions can, in these circumstances, help to distinguish controlling factors.

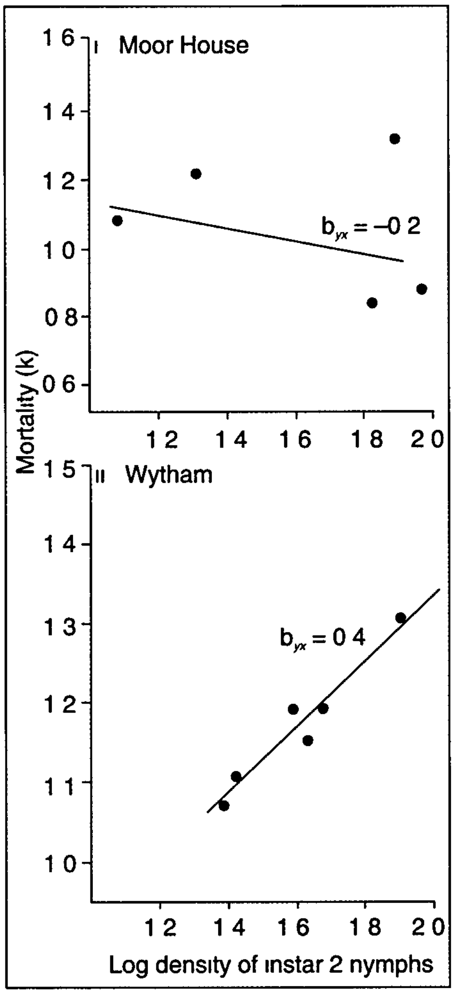

Figure 31 Relationship between the logarithm of the instar 2 numbers in each generation and the subsequent 'generation mortality' (k) (i) at Moor House, and (ii) at Wytham

Figure 29. Map showing the location of ECN terrestrial and freshwater sites in January 1993

The measurements

Standardised recording of an agreed suite of selected environmental attributes and variables started in 1993, with the aim of continued long-term integrated monitoring. A number of physical and chemical features of the environment will be recorded at each site. As well as standard meteorological recording, regular samples of rainwater will be collected for chemical analysis, and diffusion tubes will be used to collect some pollutants such as NO_2; sites with perennial streams will record stream discharge and water quality. Soils will be sampled on a five-year cycle for a number of chemical and physical determinands, and soil water will be extracted for analysis at fortnightly intervals using suction lysimeters. This recording will be automated wherever possible, eg by the use of automatic weather stations.

The biological part of the programme does not lend itself easily to automation and will rely on more traditional methods of data collection. Existing vegetation at the sites will be surveyed, and characterised using the National Vegetation Classification. Permanent quadrats will then be located so as to cover the range of variation and will be recorded at intervals of three and nine years to examine any shifts in species composition and frequency. Linear features such as hedgerows and vegetation boundaries are of particular interest. At agricultural sites, additional measurements will be made of grass and cereal production.

Recording of animals has been directed towards groups considered to be good indicators of environmental change. Animals with wide distributions can be used for inter-site comparisons of possible changes with time; those for which there are already national monitoring schemes into which results from ECN sites can be fed have also been included. Application of the Common Bird Census (and its successor when trials are completed by the British Trust for Ornithology) will provide annual counts of territorial birds matched against the main habitat features at each site. At some upland sites, the application of a recently devised and validated survey method will give an annual assessment of moorland birds. Surveys of changes in rabbit populations should provide information on how changes in weather, disease and land use affect their numbers. Bat surveys will use existing, well-tried techniques to assess year-to-year changes in populations of this climate-sensitive mammal which can be monitored using ultrasonic detectors. Frogs are known to be sensitive to some pollutants, and there is a marked geographical trend in their spawning dates whose pattern may be affected by climatic changes.

A number of invertebrate groups have also been included in the programme. Moths and butterflies already have national monitoring programmes, and it is planned that ECN sites should follow the existing survey methods and contribute data to their programmes. Other groups such as spittle bugs, craneflies and ground beetles, which have no existing national networks, are also included as indicators of environmental change.

NERC's role in ECN

Through ITE, NERC has a special role in ECN as the programme's managing agent. In addition to providing the Chairman of the ECN Steering Committee, it provides the secretariat for both this Committee and the two Working Groups which have been meeting over the past two years to consider the technical and statistical aspects of the Network measurements. Two of the ECN sites are sponsored by NERC – one is at the adjacent Pennine National Nature Reserves of Moor House and Upper Teesdale, which English Nature also supports as an ECN site by providing the necessary access and facilities; the second is at Wytham Estate, near Oxford, owned by the University of Oxford. Both sites have been important in the development of ecological science in the UK during the past 40 years; both

The next phase

ECN recording started in earnest in 1993, in some respects regarded as a trial year during which the measurement protocols will be under test and after which some modifications may be necessary The next phase is the expansion of the Network into the aquatic environment – this has already started with the selection by the National Rivers Authority of seven river sites in different regions of England and Wales at which a wide range of measurements were started in April 1992 (see Figure 29) A Working Group led by Dr S I Heaney of the Department of Agriculture for Northern Ireland (formerly of the Institute of Freshwater Ecology) started work in February 1993 to consider possible sites, measurements and funding mechanisms for other rivers and lakes in the UK At a later stage, it is envisaged that the scope of the programme might be extended by including estuarine and marine sites

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*The other eight sponsoring organisations are the Agricultural and Food Research Council, Department of Agriculture for Northern Ireland, Department of the Environment, English Nature, Forestry Commission, Ministry of Agriculture, Fisheries and Food, National Rivers Authority, Scottish Office, Agriculture and Fisheries Department

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