Institute of Terrestrial Ecology

Annual Report 1994–95

Centre for Ecology and Hydrology

Natural Environment Research Council

The ITE mission

The Institute of Terrestrial Ecology will develop long-term, multidisciplinary research and exploit new technology to advance the science of terrestrial ecology, leading to a better understanding and quantification of the physical, chemical and biological processes of the land.

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 *monitoring*, *modelling* and *predicting* environmental trends to assess past, present and future effects of natural and man-made change

- the securing, expansion and dissemination of ecological data to further scientific research and provide the basis for impartial advice on environmental protection, conservation, and the sustainable use of natural resources to governments and industry.

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

ITE will promote the use of research facilities and data to enhance national prosperity and quality of life.

Report of the Institute of Terrestrial Ecology 1994–1995

Centre for Ecology and Hydrology

Natural Environment Research Council

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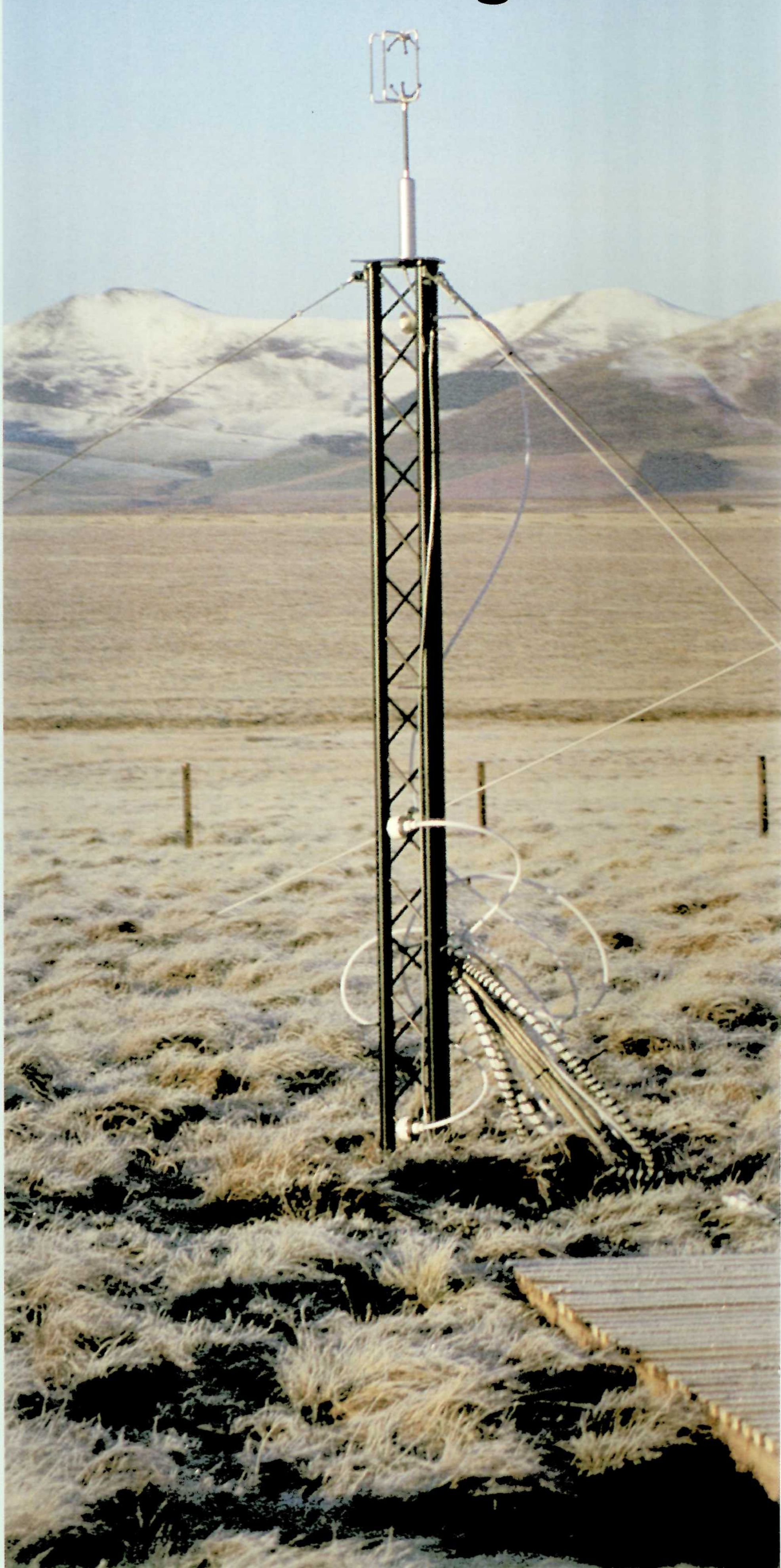


Global change, including prediction on a range of time and space scales

- Research and advanced numerical modelling focusing on key questions concerning the nature, scale and prediction of climate change, weather events and stratospheric ozone depletion, with particular emphasis on atmospheric and global ocean circulation processes.

- Improved understanding of the effect of land and freshwater processes on global climate, leading to incorporation into models; studies of the effects of increased UV-b radiation; large-scale coupling of atmospheric, hydrological and biological models to forecast the impacts of climate change on land-based systems.

- Studies on the influence of polar regions on global systems and their response to environmental change, with particular emphasis on stratospheric ozone depletion, detection of past climate from ice cores and lake sediment records, atmospheric chemistry and ice dynamics including atmosphere/sea ice/ocean interactions.

- Studies of past environmental change in the geological record to reveal feedback mechanisms that amplify or limit them, thus informing predictive studies of future change.

(NERC priorities 1995)

Introduction

The NERC priorities in global change science are:

i. to improve the numerical models of atmosphere and ocean processes,
ii. to understand and model the ways in which processes on land affect the climate and *vice versa*,
iii. to focus on processes in polar regions, and
iv. to use the fossil and geological record to understand the past climate change.

The ITE research programme is mainly in areas (i) and (ii).

ITE research on global change is funded mainly through the NERC Terrestrial Initiative in Global Environmental Research (TIGER) Programme, by the European Union, and the Department of Environment's Global Atmosphere Division. The main areas of work concern the UK and global carbon cycle, land/atmosphere interactions, land/atmosphere exchange of methane and nitrous oxide, and the impacts of climate change and elevated CO_2 on soils and vegetation in the UK. The research reports given below pick out a few of the advances made this year. More comprehensive descriptions of ITE's global change research programme can be obtained from the TIGER co-ordinators, B G Bell at Edinburgh and C P Cummins at Monks Wood.

There have been some notable developments this year. Four can be mentioned here. First, the Meteorological Office general circulation model has been able to replicate the slow rise in global temperature since the middle of the last century, and has thereby effectively shown that the observed increase has been due, at least in part, to human influences on the atmosphere (Hadley Centre for Climate Prediction and Research 1995).

Second, some strange fluctuations have occurred in recent years in the rate of increase of greenhouse gases in the atmosphere. Methane concentrations are increasing more slowly than previously and we do not know whether this is because less is being emitted or more is being destroyed. The lifetime of methane in the atmosphere is certainly longer than it used to be, mainly because it poisons its own sink, which is principally the hydroxyl radical (OH). As more methane is produced, it destroys more OH, so that there is less OH to remove subsequent methane. This aspect of global change research is discussed below by Cape and McFadyen.

Third, notable advances have been made in modelling species distribution in relation to climate, some of which are reported below by Carey *et al.* Analysis of historical vegetation data in East Anglia has shown strong relationships with climatic variables over the last 250 years. Predictive models developed from these relationships suggest that the appearance of 27 common species would advance by 5–25 days in the spring. Models have also shown, for the first time, that vegetation changes caused by climate change can, in turn, affect the climate; this aspect is described in the contribution below by Friend and Stevens.

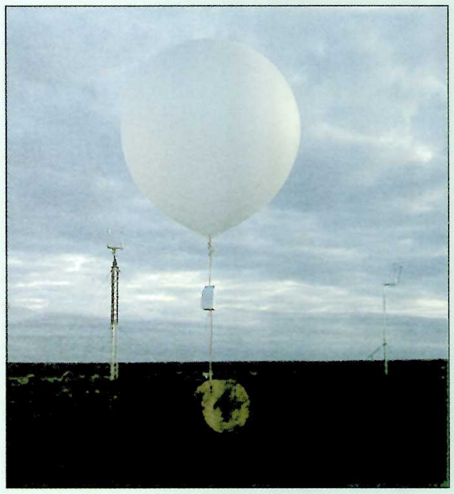
Fourth, during the year, ITE staff contributed to the second (1995) assessment of the Intergovernmental Panel on Climate Change impacts, which condenses an immense amount of new research into statements for policy-makers. In general, that research has confirmed the seriousness of the issue and the need for further research on the dynamics of ecosystem responses.

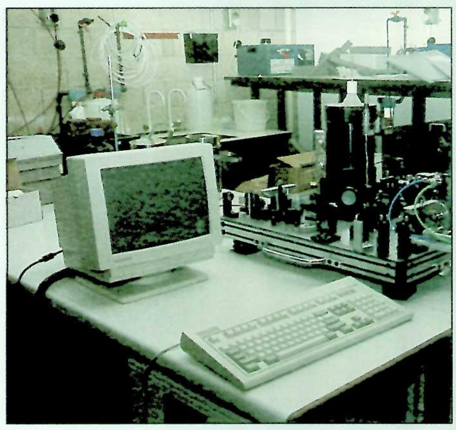
The ITE programme will continue to address the issues concerning causes and impacts of climate change. Continued emphasis will be given to the effects of UV-b on terrestrial ecosystems. In the longer term, global change research will need to incorporate the implications of land use change driven by international trade agreements.

M G R Cannell

Reference

Hadley Centre for Climate Prediction and Research. 1995. *Modelling climate change 1860–2050.* Bracknell: Meteorological Office.





In order to determine the rates at which methane and nitrous oxide are emitted from the land surface, air is collected using masts, fitted with micrometeorological equipment, balloons, which take sampling tubes aloft, and the Hercules aircraft of the Meteorological Office Research Flight. Air samples are then analysed in the field or laboratory using a Tunable Diode Laser

Climate change and UK hill grassland soils

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

It is anticipated that the global mean annual temperature will rise between 2°C to 5°C during the next century, as a consequence of increases in atmospheric concentrations of trace gases (Houghton 1993). There is considerable debate about the effects that such changes will have on terrestrial ecosystems, with particular concern for the fate of the large amounts of carbon currently held in soils, and the feedback effect on climate (Jenkinson, Adams & Wild 1991).

Soils are important reservoirs of carbon, particularly in cooler climates: tundra and cool grassland ecosystems hold as much as 15 kg C m^{-2} below-ground which is commonly more than ten times the amount of C held in these systems above-ground. Additionally, it has long been recognised that the amount of C held in soils can be related to climate, with cold temperatures being associated with greater accumulation of C. The greatest effects of global warming on C fluxes in the UK are likely to occur in hill land regions where there are considerable accumulations of organic C in the soil. These accumulations are the result of centuries of net C input to the soil where net primary productivity exceeds the rate of decomposition. Increases in temperature in such systems, by analogy to existing climatic gradients, should result in a loss of soil organic matter, with an associated release of CO_2 to the environment.

Unfortunately, such simple analogies fail to recognise the importance of other feedbacks and constraints that may operate in these systems. For example, increases in temperature can stimulate the mineralisation of organic matter and release additional nutrients, consequently improving plant growth; two- or three-fold increases in the productivity of hill grasslands have frequently been achieved by simple nutrient additions, indicating that nutrient availability rather than direct effects of temperature restricts production in many hill areas. The extreme soil acidities commonly found in hill systems may also limit decomposition processes, regard-less of temperature.

The outcome of the effect of increased temperatures on the C dynamics of upland temperate ecosystems is, therefore, difficult to predict, and requires the use of experimental manipulations, combined with mathematical modelling approaches. This project has the objective of determining the influence of climate change on the C dynamics of upland soils, and involves a consortium of research groups in the UK. The study was specifically initiated as a contribution to the TIGER Programme, in order to monitor the responses of intact soil/ vegetation systems to warming, with the role of ITE being to co-ordinate, design and implement the experimental framework in which the research consortium operates. The two main objectives of the consortium are to:

- test the hypothesis that atmospheric warming of upland grassland sites will result in a net release of C to the atmosphere and drainage water,
- establish the relative impact of global warming on productivity and decomposition in an upland grassland ecosystem, and
- quantify the feedback effects exerted through changes in nutrient cycling.

The experimental approaches

The effects of global warming on upland grasslands were investigated using two approaches. In the first, climate change was simulated by transposing cores of upland grassland vegetation and surface soils in lysimeter tubes to four selected elevations along an altitudinal transect (Figure 56). There was a difference in mean annual temperature of about 4.5°C between the extreme points of the transect. This approach means that the transported systems are subjected to normal fluctuations in diurnal temperatures as well as seasonal changes, and freeze/thaw cycles. The effects of differences in rainfall were removed at one site by automatic manipulation of rainfall inputs.

In the second experimental approach, two sets of replicate lysimeters (ambient and heated) have been established at the highest site. Electronically controlled cables maintain the soil surface at 3°C above ambient in the heated treatment. The novel soil warming system was based on a stainless steel mesh supporting electric cable heating placed on the soil surface. The meshes were established over lysimeters in order to be able to quantify the effects of warming on gas and solute fluxes. The objective was to warm soil cores within lysimeters, and a proportional control heating technique was used to eliminate excess temperature overshoot inherent in simple on/off systems.

Overall, the changes in C dynamics have been measured for three upland soil types (acid brown earth, peaty gley and micro-podzol), including exchanges of trace gases with the atmosphere, losses

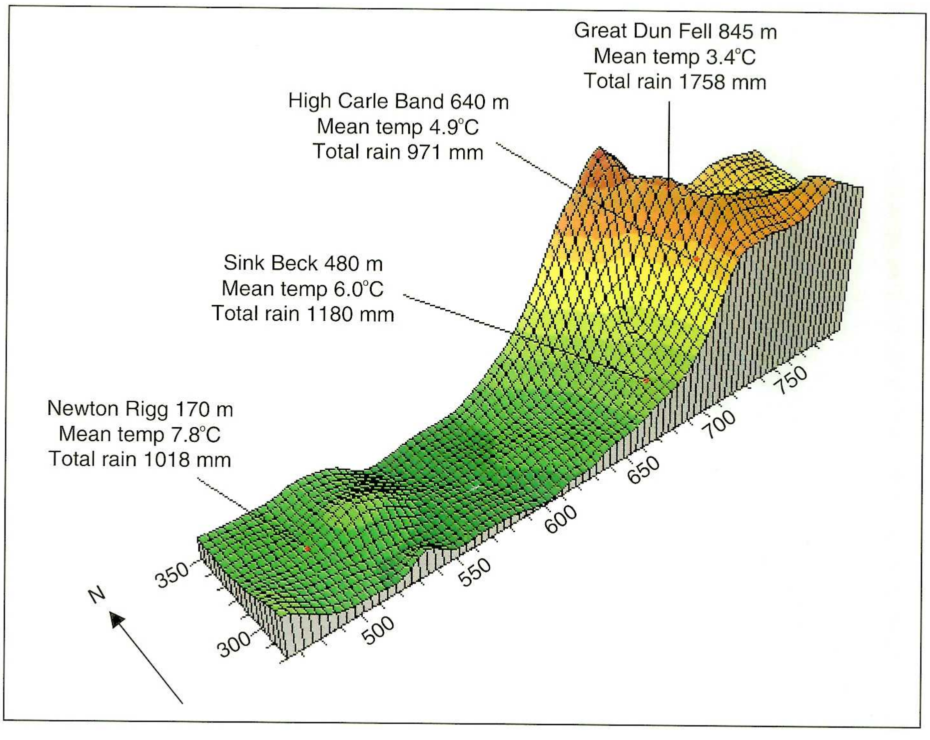


Figure 56. The altitudinal transect at Great Dun Fell

Plate 33. The Great Dun Fell soil warming equipment

The site used for the soil warming experiment was at an elevation of 845 m and close to the summit of Great Dun Fell, Cumbria, UK, which is part of the Moor House and Upper Teesdale National Nature Reserves, currently designated as a TIGER 'flagship' site for research (Plate 33). The Moor House Reserve became a major site of ecological importance during the International Biological Programme (IBP) of the 1970s, when it was used as a principal UK ecosystem study site. The soils represent the types frequently found in hill areas of the UK, and there is a considerable amount of information available on the biological composition of the soils, together with detailed mapping and profile data. The Great Dun Fell site was chosen because of this background of information, together with good vehicular access and electricity supply available at the summit.

of C as dissolved organic carbon (DOC) in soil leachates, and changes in soil and vegetation C pools. Soil fractionation and C isotopic analyses were performed to identify changes in C pools in the soil, and the sources and sinks of C. Air, sward and soil temperatures were monitored at each site, together with other major climate variables. The empirical observations of the responses of these systems to the climatic manipulations provided parameters for models of C dynamics in upland systems and their response to climatic change.

Impacts of climate change

For the year October 1993–October 1994 the soil warming treatment raised the annual mean soil temperature from 4.5°C to 7.4°C at 2 cm depth, and from 4.5°C to 7.5°C at 0.5 cm above the soil surface, within the grass sward. As an example, Figure 57 shows detailed temperature

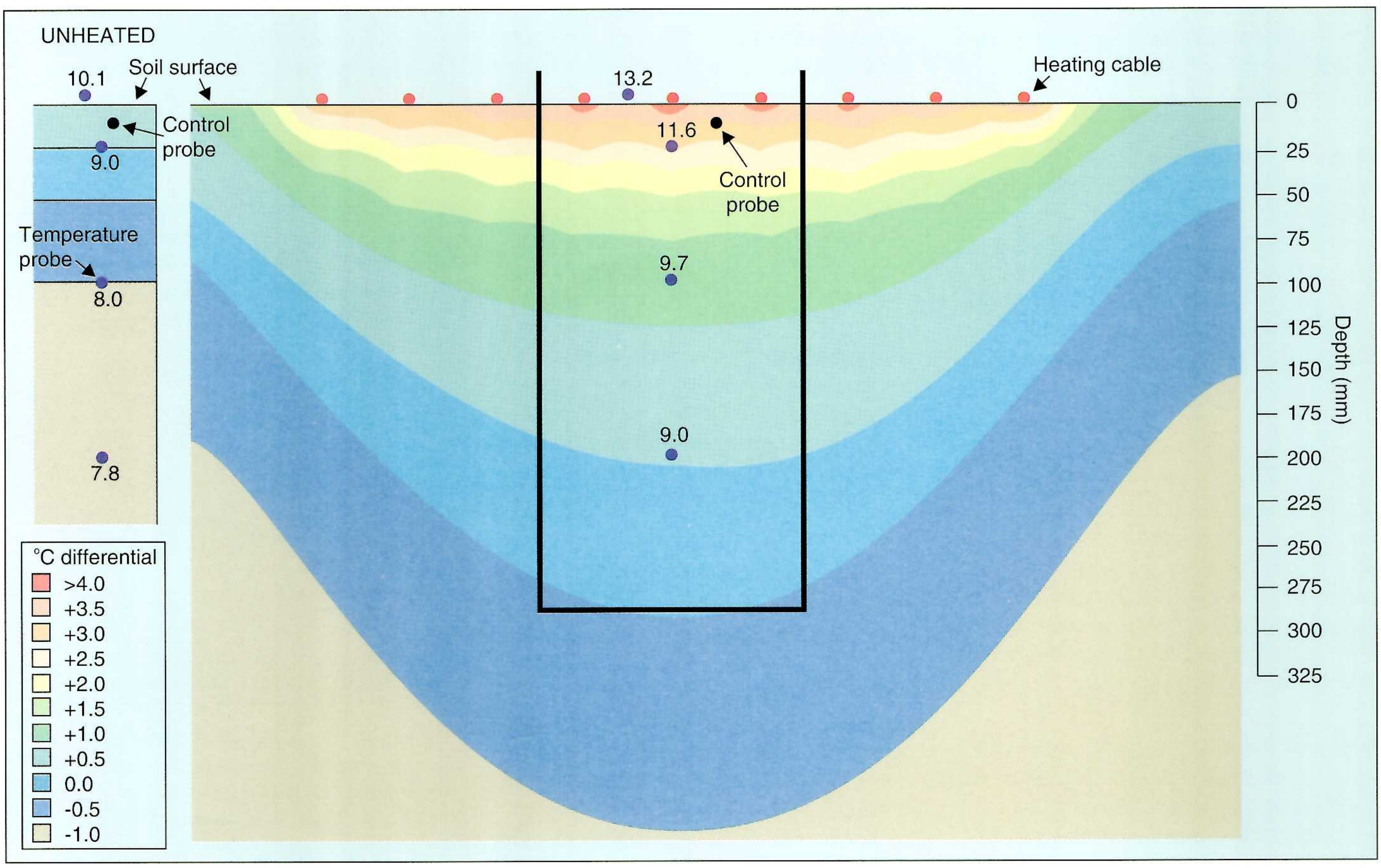


Figure 57. Temperature profile through a heated lysimeter

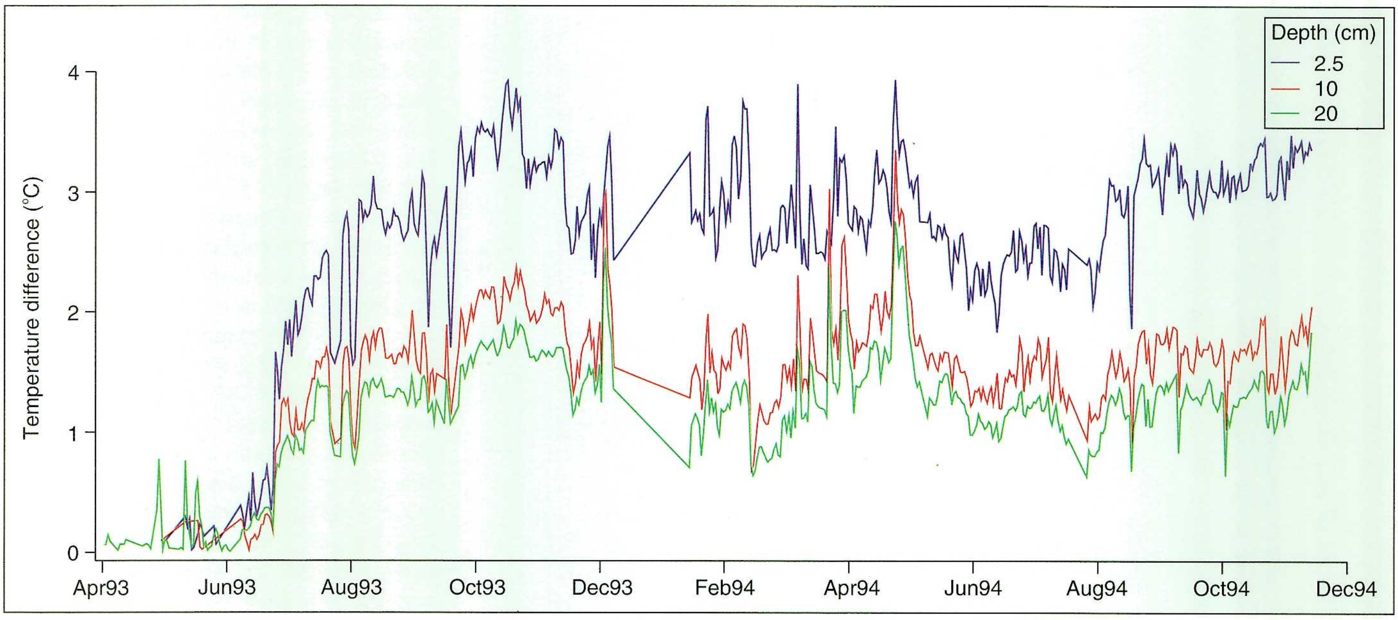


Figure 58. Mean daily temperature for the heated *versus* unheated systems from October 1993 to October 1994. Data are presented as differences in temperature between the unheated and heated lysimeters in the soil at varying depths

measurements taken around mid-day on 27 September 1994, in calm cloudy conditions when the temperature profile was fairly stable. The slight asymmetry shown in the profile was probably caused by variations in contact between the mesh and the soil. The position of the lysimeter and temperature probes in relation to the mesh can clearly be seen, and the need for heating around, as well as within, the lysimeter is well demonstrated.

Figure 58 shows the annual trace for the soil temperature difference between the heated and unheated lysimeters, at 2 cm, 10 cm and 20 cm depth. The heating system was operational for 91% of the time, and the consumption of electricity that was necessary to maintain the observed temperature differences was about 0.1 kW m^{-2}.

The diurnal rhythms of soil temperatures in the unheated cores show all the characteristics of undisturbed soils, and the cores to which surface warming was applied mirrored the temperature patterns of the ambient temperatures measured in the unheated cores, but they were raised throughout by between 2°C and 4°C.

The most dramatic response observed in leachate chemistry for the lysimeters was for dissolved organic carbon (DOC) which showed a significant increase in concentration in the initial months of warming. Figure 59 shows DOC concentrations prior to heating being applied in June 1993, and indicates no significant *a priori* differences between the lysimeters allocated to each treatment. A significant increase in DOC concentrations of nearly 50% was induced within a few months of starting the treatments. Five months after heating began, this initial large difference decreased and became less consistent. However, for the first 17 months during which heating was applied, DOC concentration showed an overall significant increase ($P<0.05$). There were no significant differences in the volumes of water leaving the lysimeters during the first five months, so that the observed concentrations translate to an equivalent increase in total DOC flux. However, during the winter, the volumes of water leaving the heated lysimeters were greater than for the controls, which resulted in considerable variability in DOC flux between samplings; there was a significantly greater total flux for the heated lysimeters over the 17 months **($P<0.05$).**

Similarly, the leaching of NO_3 was not significantly different between the two sets of lysimeters prior to switching on the heat, but responded very rapidly when the temperatures in the two treatments diverged (Figure 60). However, unlike the response for DOC, the quantity of NO_3 leaving the heated lysimeters during the first five months ($P<0.01$) was significantly lower than for the controls. Again, this was reflected directly in terms of total NO_3–N leaching, as volumes were not significantly different. The peak in NO_3 concentration observed in the unheated lysimeters in August 1993 failed to occur in the heated lysimeters. From December 1993 onwards, there was no consistent difference in NO_3 concentration between the two sets of lysimeters. Again, the greater volumes of leachate leaving the heated lysimeters during the winter resulted in greater NO_3 flux.

Conclusions

These results clearly show the efficacy of the soil warming technique on swards of short grass/herbage where good contact can be made between the mesh and the soil. Location of the heating

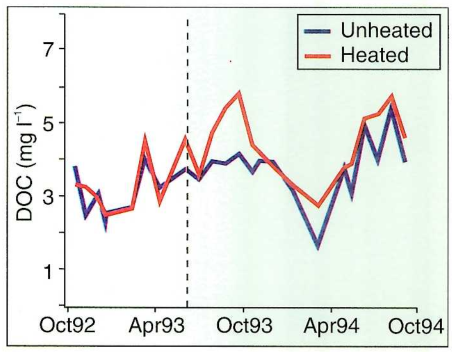


Figure 59. Concentrations of dissolved organic carbon in lysimeter leachate for the acid brown earth between October 1992 and May 1994. Values represent the mean of seven replicates in the unheated and heated treatments. Warming was switched on in June 1993

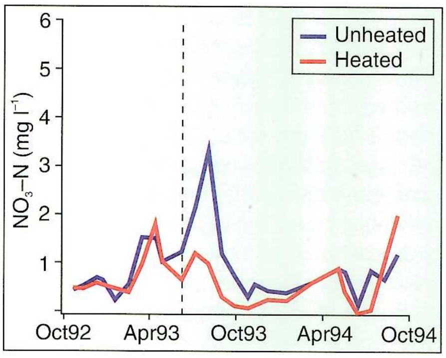


Figure 60. Concentrations of NO_3–N in lysimeter leachate for the acid brown earth between October 1992 and May 1994. Values represent the mean of seven replicates in the unheated and heated treatments. Warming was switched on in June 1993

cable on top of the metal mesh minimised any local heating effect on the soil and had a more natural action in warming the vegetation in the zone where heat exchange normally occurs. Over three years of trials and operation, the mesh heaters have proved completely reliable. Similarly, the recording of soil temperature profiles has been 100% reliable and accurate over three years of continuous use.

The warming of the entire system led to interactions between productivity and decomposition, as evidenced by changes in the chemistry of soil waters. The effect of the 2.9°C temperature increase on DOC production indicated that decomposition increased in response to warming; however, a reverse initial reaction was noted for NO_3 production, suggesting that any increases in decomposition and nutrient release were masked by plant uptake. Although significant increases in denitrification rates have also been observed in the current experiment (data not reported here), the reduction in NO_3 leaching is too great to be explained by denitrification losses, and we must assume that increased plant uptake is causing the reductions. Thus, it appears that DOC is an excellent indicator of increased soil organic matter decomposition because, unlike the essential nutrients, it is not taken up by the plant roots at the rate which it is released. The implication is that future global warming would result in changes in the DOC content of waters draining upland systems in the UK, with the attendant problems which this raises for the water supply industry.

P Ineson, D G Benham, J Poskitt,
A F Harrison and K Taylor

Acknowledgments

We are grateful to English Nature and to the Civil Aviation Authority for practical assistance.

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'Radical' chemistry that determines methane concentrations in the atmosphere

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

The atmospheric concentration of methane is determined by the balance between rates of emission to the atmosphere and rates of removal. The increase in tropospheric methane concentrations over the past century implies that either emission rates have increased, or removal rates have decreased. Over 90% of methane is removed from the atmosphere by the gas-phase reaction with the hydroxyl radical (OH). Although it is possible to measure the concentration of this radical directly, concentrations are so small that direct measurements can explore only a small region of space and time (O'Brien & Hard 1993). Alternatively, concentrations of the OH radical can be inferred from changes in chemical composition of other trace gases in the atmosphere (Plate 34). This has been the approach of a consortium (University of East Anglia, University of Birmingham and ITE Edinburgh) funded under the NERC TIGER Programme.

Of particular interest is the rate of methane removal close to source areas over land. The average OH radical concentrations and methane oxidation rates are fairly well understood over the ocean, remote from pollutants. However, most methane sources are terrestrial, and the atmosphere into which methane is emitted is frequently perturbed by anthropogenic sources of carbon monoxide and nitrogen oxides, both of which play a very important role in regulating the OH radical concentration.

The OH radical drives many of the atmospheric oxidation processes that convert molecules like methane, carbon monoxide, nitrogen dioxide and sulphur dioxide into their oxidised forms (carbon dioxide, nitric and sulphuric acid, respectively). It is formed continuously in sunlight by the fragmentation of ozone by ultraviolet light; the resultant energetically excited oxygen atoms rapidly combine with atmospheric water vapour to give the OH radical. Each OH radical has a rather short lifetime. In clean oceanic air, the OH radical reacts with something else within less than a second, usually to produce a related radical, the hydroperoxy radical (HO_2). This radical, in turn, is a potent oxidising agent, and can be converted back to the OH radical through reaction with molecules such as nitric oxide (NO). The rapid interchange of these free radicals means that the concentrations of one are intimately linked to concentrations of the other, so that they are known collectively as HO_x.

Plate 34. Measurements of trace gas concentrations and photolysis rates are made from masts or towers, to avoid interference from emission or deposition of gases at the earth's surface

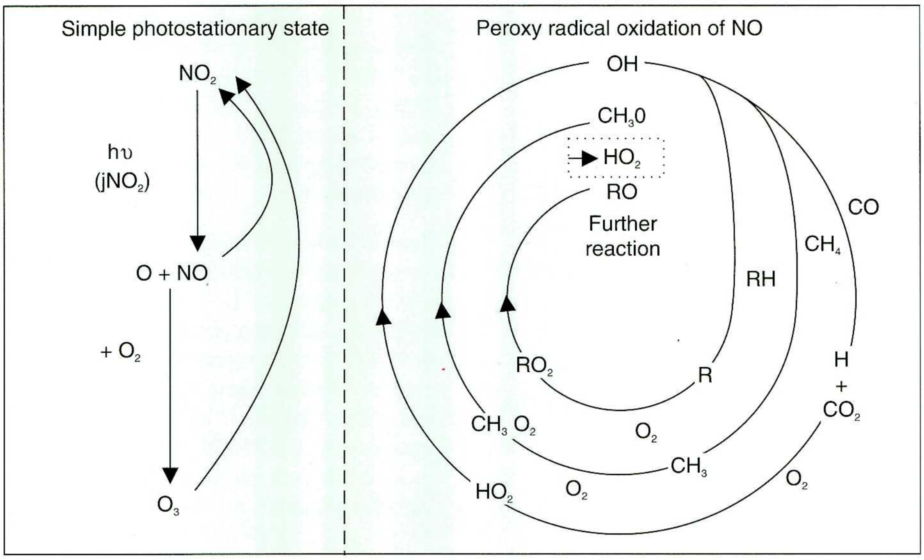

Figure 61. Schematic diagram of NO_x and HO_x chemistry, showing coupling between the conversion of HO_2 to OH and the conversion of NO to NO_2

The importance of nitrogen oxides in regulating the interconversion of OH and HO_2 can be used as a first step in estimating HO_x radical concentrations in the atmosphere. Nitrogen dioxide (NO_2) is photolysed by sunlight (in the ultraviolet) to produce NO, and an oxygen atom which rapidly combines with an oxygen molecule to give ozone (O_3). The resultant ozone can then react with NO to give NO_2, completing a cycle which depends on the rate of photolysis of NO_2 (jNO_2) and the rate of the reverse reaction between O_3 and NO, which has been determined under controlled conditions in the laboratory. All the other components of this simple system, referred to as a 'photostationary state', can be measured in the atmosphere. Any perturbation, for example by the reaction of NO with HO_2 rather than O_3, will produce an imbalance in the 'photostationary state'. The extent of the imbalance can then be used to infer concentrations of HO_2 and other peroxy radicals formed during the oxidation of hydrocarbons, such as methane, in the atmosphere (Figure 61). To use this approach, one must first show that measurement systems are sufficiently good to detect small perturbations to the NO_x photostationary state.

In winter, radical concentrations are very small because of the reduced production of OH, and even on very bright cloudless days calculated peroxy radical concentrations are effectively zero. Under these conditions, there should be no perturbation of the photostationary state, and measured concentrations of any of the gases (eg NO) should be the same as those calculated on the basis of the reaction rates involved. Figure 62 demonstrates this for one cloudless day during the field measurement campaign at the Weybourne Atmospheric Observatory in Norfolk, during December 1994. The rate of the NO+O_3

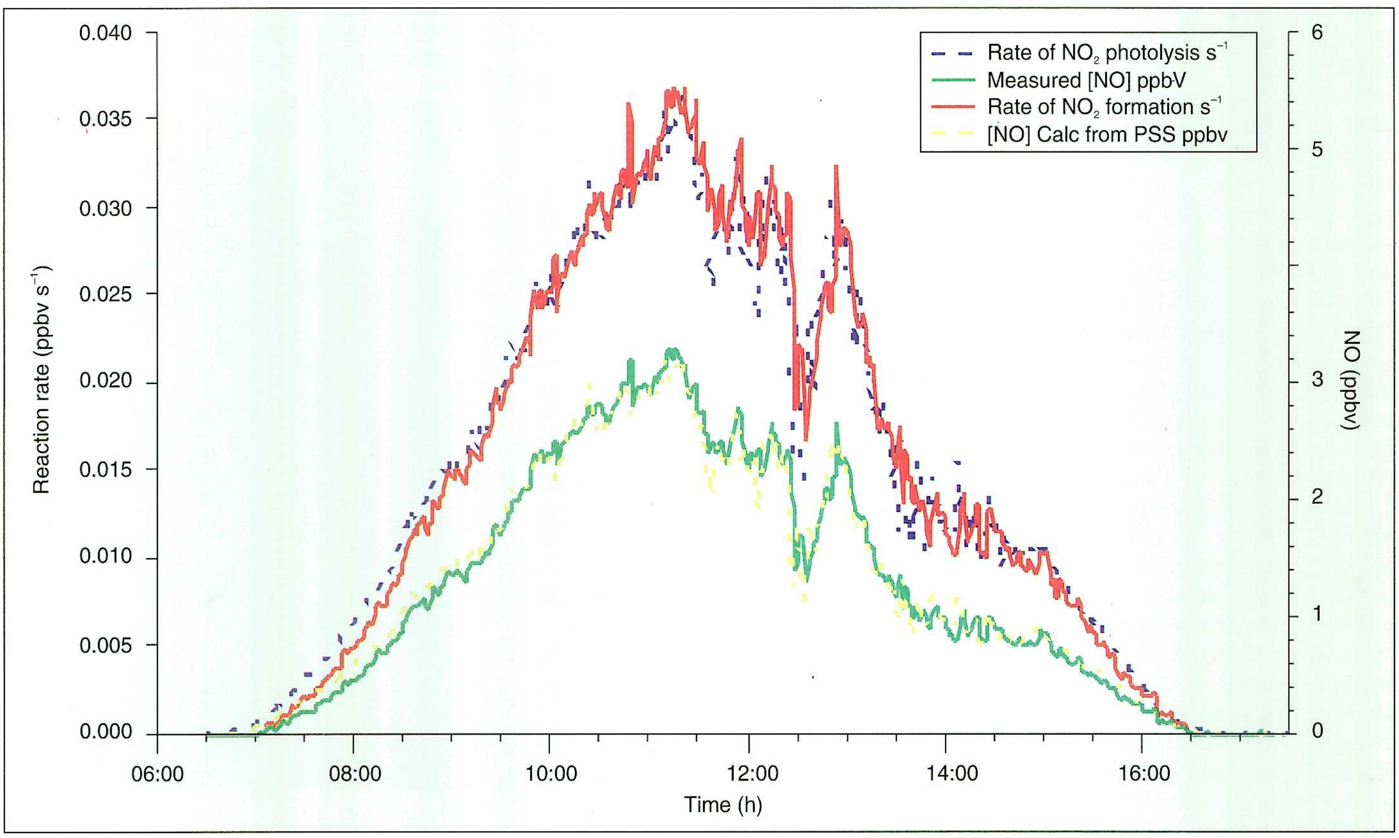

Figure 62. In winter, when photochemical activity is low, the rate of NO_2 photolysis, which follows sunlight intensity through the day, is balanced by the rate of NO_2 production from the reaction of NO with O_3. The measured concentration of NO is compared with that calculated from knowledge of the forward and backward reaction rates, as a check on the existence of the photostationary state

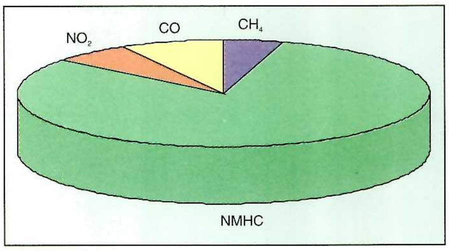

Figure 63. Reactions of the OH radical in summer are dominated, in this example, by reaction with non-methane hydrocarbons (NMHC). The overall oxidation rate of methane (CH_4) is, however, still much greater than would be found in an unpolluted atmosphere. Measured and calculated concentrations of important trace gases and photolysis rates are shown for noon on 12 June 1994 at Bush Estate, Midlothian

reaction was taken from published laboratory data, corrected for the measured temperature through the day. The agreement is remarkable, as the largest source of uncertainty is the laboratory-derived measurement of the $NO+O_3$ reaction rate, which is known to only ±20% (Atkinson *et al.* 1992).

In summer, the rates of formation of OH are greatest, and the presence of reactive hydrocarbons (such as isoprene) in the atmosphere catalyses the radical chemistry of the OH/HO_2 reactions. Concentrations of peroxy radicals inferred from the perturbation of the NO_x photostationary state have been calculated as around 0.01 ppbV (parts in 10^9 by volume). These values agree well with measurements of peroxy radical concentrations made by colleagues from the University of East Anglia using a 'chemical amplifier' (Cantrell & Stedman 1982). Together with measured concentrations of other gases involved in the complex chemistry of the lower

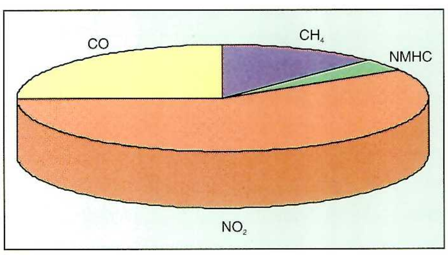

Figure 64. Reactions of the OH radical in winter are dominated, in this example, by reaction with nitrogen dioxide (NO_2) to give nitric acid. The overall oxidation rate of methane (CH_4) is very much smaller than would be found in an unpolluted atmosphere. Measured and calculated concentrations of important trace gases and photolysis rates are shown for noon on 1 November 1994 at Weybourne, Norfolk

atmosphere, it is possible to deduce OH concentrations, and the removal rate of methane by oxidation. Two examples are shown in Figures 63 and 64, for a single set of data in summer (measurements at Bush Estate) and winter (measurements at Weybourne). The examples show how other chemical reactions compete with methane oxidation in terrestrial atmospheres containing hydrocarbons and nitrogen oxides. In summer, although methane oxidation accounts for only a small proportion of the OH radical reactions, overall concentrations of OH radicals are large, and the methane oxidation rate is about twice what would be expected in the remote marine atmosphere. By contrast, in winter, methane oxidation accounts for only a small proportion of the very small concentrations of OH radical present in the atmosphere, and overall oxidation rates are very much slower.

Oxidation rates of methane are slow compared with rates of emission of methane into the atmosphere, so that the perturbations in methane oxidation caused by anthropogenic emissions of nitrogen oxides and hydrocarbons have not only a regional but also a global relevance. Once we have built up a better picture of the factors which influence the production and consumption of OH radicals in polluted atmospheres, models can be developed to estimate the influence of man's activities in determining the rates of methane oxidation at regional and global scales, and to investigate whether the current global increase in atmospheric methane is the result of increased rates of emission or decreased rates of oxidation.

J N Cape and G G McFadyen

Acknowledgments

The results presented above were collected during intensive field measurement campaigns, involving S A Penkett, K C Clemitshaw, L J Carpenter, L Cardenas (University of East Anglia), R M Harrison, S Yamulki, J Peak (University of Birmingham) and J Binnie (ITE Edinburgh). The hydrocarbon measurements at Bush Estate were made by courtesy of AEA NETCEN, with thanks to P Nason for installing the instrument at ITE Edinburgh.

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Developing and testing models of plant distribution in response to climate change

(This work was funded by the NERC Terrestrial Initiative in Global Environment Research (TIGER) Programme)

There is no question that plant distributions are related to climate at the largest scale of resolution, and that they respond to changes in climate. It appears to follow that, if the climatic constraints can be determined for a particular species, then its distribution can be predicted for any given climate scenario for the future.

Perhaps the simplest way of determining climatic constraints is to seek correlations between the occurrence of a species or vegetation type and climatic data. At the moment, suitable climatic data exist only for a few accurately measured and interpolated variables. Regression models may be generated to relate current distribution to current climate for each cell in a spatial grid covering the existing distribution. The climates for each cell are then amended according to some scenario, and the regression model is applied to the new climates to provide a forecast for the species distribution under the new scenario.

It is clear that, in most cases, the correlative models created by this method will only provide a description of a species' distribution and may not indicate the critical climatic factors which affect the physiology or demography of that species. It is only by adopting a more mechanistic approach at a much finer scale that we can hope to determine the critical climatic factors creating distribution limits. Once the limiting factors of species distribution have been found, then they can be used to improve the simple correlative regression models. This will only be possible if the necessary data are available as an accurate large-scale dataset; otherwise, the nearest analogue climatic variable should be used.

As in any regression approach, there are risks that the model will break down when extrapolated. Models looking at species distribution for the UK should, therefore, be developed using data for places which include present-day climatic analogues to those climates expected to be found in the UK in the future. In other words, models forecasting changes in British distribution should be based ideally on data based on a wider geographic range than Britain alone.

Further complications arise because limits of species distribution are caused by a wide range of factors other than climate. In longer-lived plants, for example, the present distribution may reflect past climate regimes and, as a result, the distribution is a function of climatic variables from the past and not the present. The same is true for some species which may take centuries to move only a few metres. Climate is not independent of other aspects of the plants' environment; soils, land use, potential competitors and herbivores are all influenced, as are the responses of the plants to these factors. Finally, the colonisation of new areas may have to await the evolution of populations which can cope with the different patterns of daylength encountered at different latitudes.

Plate 35. Bristle bent (*Agrostis curtisii*)

In this article, we demonstrate the development of several models of species distribution, before discussing how this approach has been used to stimulate experimental programmes. The species chosen for study is bristle bent (*Agrostis curtisii*) (Plate 35), a grass with a Lusitanian distribution in the south-west of England and Wales, western France, Spain, Portugal and the Tangier area of Morocco. In general terms, it is a gap coloniser, establishing quickly to become conspicuous and locally abundant in burnt heathland and in forest gaps created by treefall or clearance

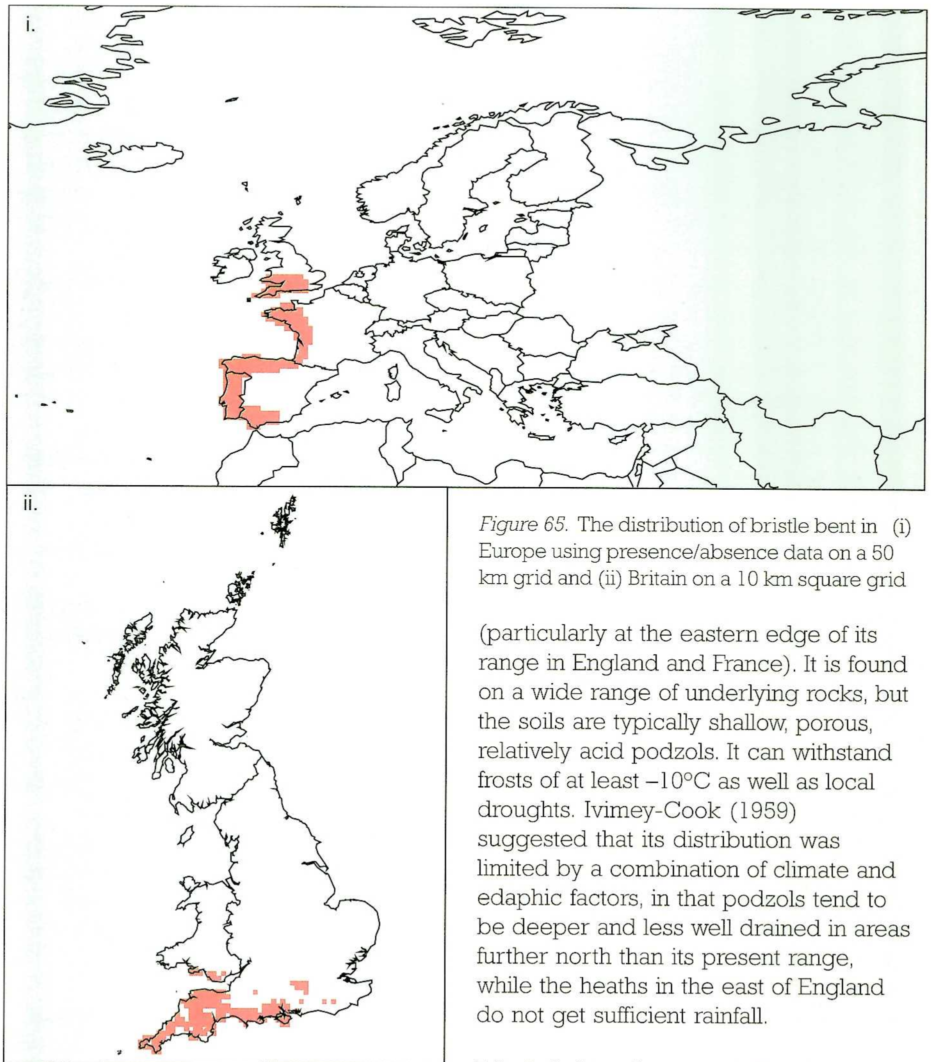

Figure 65. The distribution of bristle bent in (i) Europe using presence/absence data on a 50 km grid and (ii) Britain on a 10 km square grid

(particularly at the eastern edge of its range in England and France). It is found on a wide range of underlying rocks, but the soils are typically shallow, porous, relatively acid podzols. It can withstand frosts of at least −10°C as well as local droughts. Ivimey-Cook (1959) suggested that its distribution was limited by a combination of climate and edaphic factors, in that podzols tend to be deeper and less well drained in areas further north than its present range, while the heaths in the east of England do not get sufficient rainfall.

Model development Europe

The European distribution of bristle bent was digitised to give a presence/absence map, which was converted into a 50 km grid (Figure 65i). This distribution was related to climate by using logistic regression, with the probability of the occurrence of bristle bent in each 50 km square as the dependent variable. This variable was related to the minimum January temperature, the maximum July temperature, and the annual precipitation at the mean altitude of each square, using step-down multiple regression. Models including quadratic variables and cross-products were created but are not included in this article.

Great Britain

The present distribution of bristle bent within Britain was established (Figure 65ii) using the Biological Records Centre database, which identifies species presence and absence within a grid of 10 km squares across Britain. The same

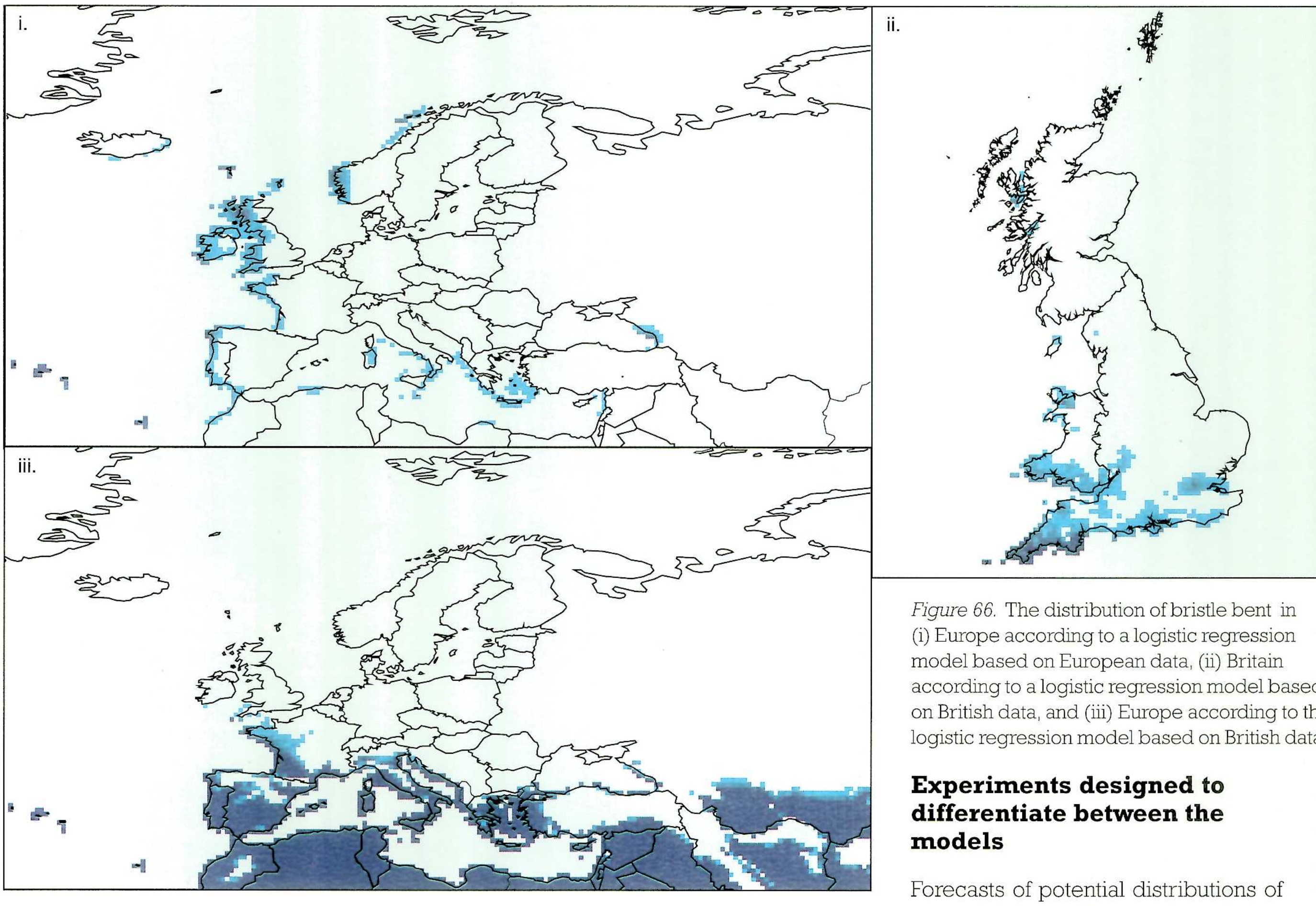

Figure 66. The distribution of bristle bent in (i) Europe according to a logistic regression model based on European data, (ii) Britain according to a logistic regression model based on British data, and (iii) Europe according to the logistic regression model based on British data

procedure used to produce the model on the 50 km European scale was applied to the 10 km British data, and the model produced using the British 10 km climate data was then applied to the European 50 km climate data to extend the modelled distribution into Europe.

Predictive models

All three models were used to forecast climatically suitable areas for bristle bent by assigning climatic variables for each square according to the IS92a scenario of a climate possible for the year 2050 (Houghton, Callander & Varney 1992). This scenario is based on the assumption of little change in the build-up of carbon dioxide and other greenhouse gases, and forecasts a temperature rise of roughly 1–1.5°C across Britain. The probability of bristle bent occurring in each square was recalculated using the original models to give potential future distributions of this species.

Model results

The model of European distribution based on European climate data alone includes areas not presently occupied by bristle bent, notably the western coasts of Mediterranean countries and also south-west Norway. The model also exaggerates the extent of bristle bent in Britain compared with the true situation (Figure 66i). The model of the British distribution based on the British data gives a better fit to the present distribution, but suggests that suitable climates may be found in northern Wales and possibly even Scotland (Figure 66ii). When extended to the European climate dataset, the British model is not as accurate in predicting the Euopean distribution as the model created using the European climate data (Figure 66iii), and over-emphasises the distribution in southern Europe and northern Africa.

The forecasted distribution of suitable climates according to IS92a varies substantially between models. The model based on European data forecasts little change (Figure 67i). The model based on British data forecasts the greatest expansion of suitable climate within Britain and Ireland (Figure 67ii), but suggests that the species will be lost from most of the rest of Europe (Figure 67iii).

Experiments designed to differentiate between the models

Forecasts of potential distributions of suitable climates for bristle bent differed substantially between the models we have described. Other models we have produced differ even more widely in their predictions, some showing a possible expansion in the climatically suitable area for the species and some showing a contraction. Clearly, not all of these models can be correct. One could favour the models based on European data, on the premise that the greater the range of data, the better the regression model. However, this assumption need not hold true if the data are not of uniform quality. The European data used here are of 50 km resolution, while the British data are of 10 km resolution. The accuracy of the model based on the British data extrapolated to the European scale was somewhat unexpected, but can be explained by the fact that much of the climatic variation across the range of bristle bent is encountered within Britain. For species where this is not the case, extrapolation from British data is less likely to be successful. The over-emphasis of southern Europe and northern Africa is indicative of the high winter temperatures required by this species.

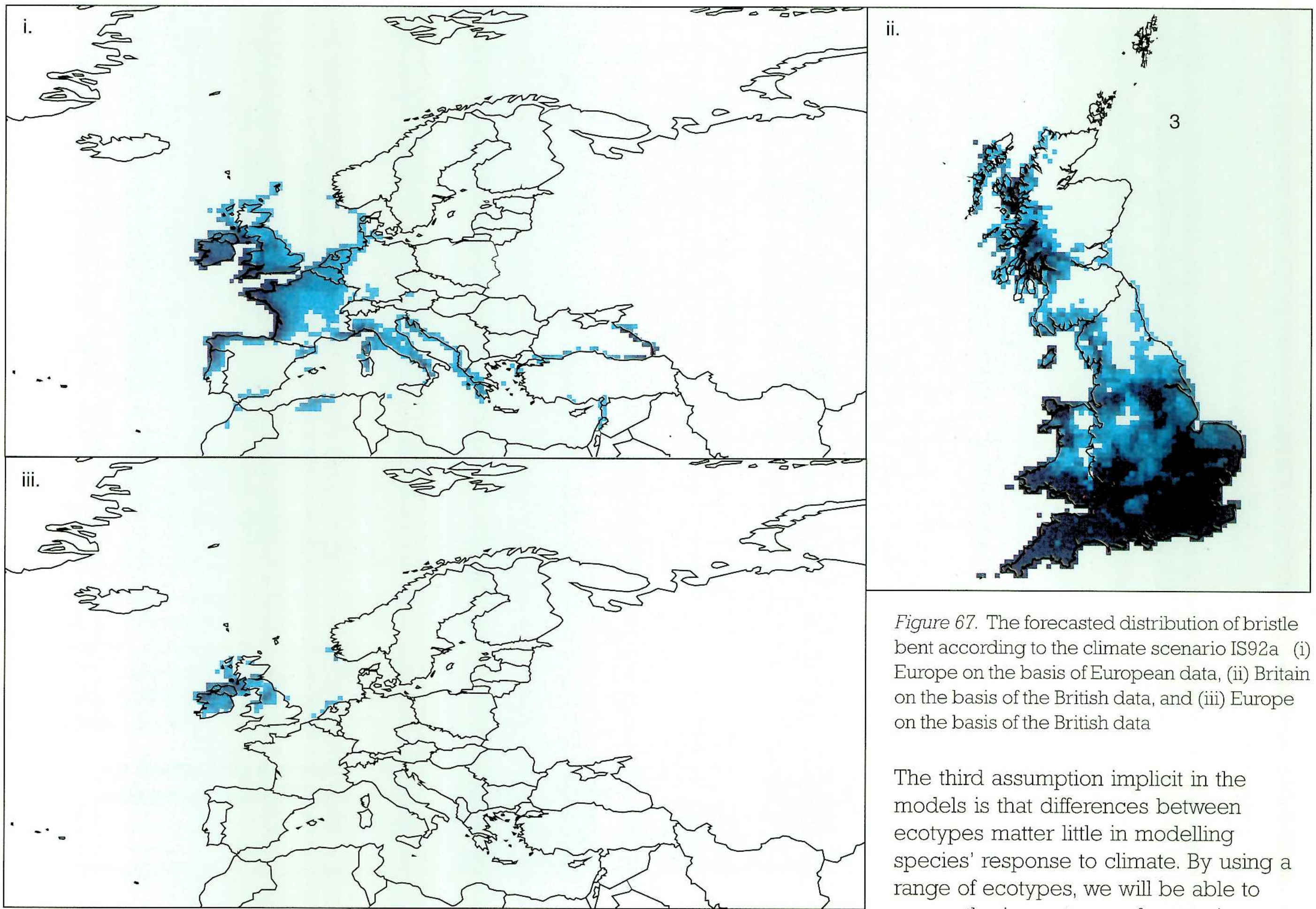

Figure 67. The forecasted distribution of bristle bent according to the climate scenario IS92a (i) Europe on the basis of European data, (ii) Britain on the basis of the British data, and (iii) Europe on the basis of the British data

To help distinguish between the models, and to help assess some of the assumptions behind them, ITE and the University of East Anglia have established a field transplant programme of bristle bent. In the autumn of 1994, populations from UK, France and the Iberian peninsular were transplanted into native soils at four sites to the north-west and north-east of its existing range, and also into pots (as seeds and as young plants) with uniform soil at eight locations throughout the UK. Intra- and inter-population variation in performance can be assessed. As bristle bent is a perennial, the experiments are expected to last until at least late-1996.

The field experiments will test several key questions. First of all, they will test the assumption that the current distribution is in equilibrium with climate. If this assumption is wrong, then the whole basis of extrapolating from present climate/distribution relationships is invalid, and bristle bent is absent from some areas simply because it has failed to colonise them. The transplants into pots or open areas of suitable soils within and beyond the current range will test this hypothesis; the assumption will be tentatively accepted if populations transplanted beyond the current climate space do not persist over several years. Any rejection of the assumption of equilibrium can only be tentative, as the experiment may not include the rare extremes of climate capable of eliminating the populations. Furthermore, while populations may persist for a while beyond current distributions, the local rate of colonising new patches may be less than the local rate of extinction.

The second assumption is that regeneration and persistence are possible within potentially suitable areas, as indicated by a particular model. It may well be that the distribution of bristle bent is limited by soil characteristics or community composition, rather than climate *per se*. If so, then the performance of the transplants into native soils and communities will compare better with the present distribution than transplants into the standard soil in pots and trays.

The third assumption implicit in the models is that differences between ecotypes matter little in modelling species' response to climate. By using a range of ecotypes, we will be able to assess the importance of ecotypic variation to the performance under different climates.

The fact that different models on the same data yield different forecasts is not surprising – it is a typical problem in extrapolating beyond the ranges of current data. That does not mean the correlative models should be rejected as a tool for forecasting the impacts of climate change – it simply means that experimental approaches to distinguish between the models should be adopted wherever possible. The true limiting factors determined by the experimental programme can be used to produce more meaningful correlative models in the future.

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Global modelling of vegetation responses to climate and atmospheric CO_2 change

(This work was funded by the NERC Terrestrial Initiative in Global Environment Research (TIGER) Programme and the EC Environment Research Programme)

During the past year we have concentrated on further development of the ecosystem model HYBRID, and the parameterisation of a global daily weather generator. The ecosystem model is designed to predict the short-term fluxes of carbon, water, and energy between the land surface and the atmosphere, as well as long-term ecosystem development (both of vegetation and soils). It has been built with the aim of simulating the effects of atmospheric CO_2 and climate change on ecosystems, as well as feedbacks between land surface properties and atmospheric processes. Thus, it would be possible to use it to represent the land surface in a general circulation model, and this will be the aim over the next phase of the work.

The version of the ecosystem model resulting from this year's work (HYBRID v3.0) treats the daily cycling of carbon, nitrogen, and water within the biosphere and between the biosphere and the atmosphere. It combines a mass balance approach with the capacity to predict the relative dominance of different species or generalised plant types (such as evergreen needleleaved trees, cold deciduous broadleaved trees, and C3 grasses). The growth of individual trees is simulated on an annual timestep, and the growth of a grass layer is simulated on a daily timestep. The exchange of carbon, nitrogen, and water with the atmosphere and the soil is simulated on a daily timestep (except the flux of tree litter to the soil, which occurs annually). Individual trees and the grass layer compete with each other for light, water, and nitrogen within a 'plot'. Larger and taller plants shade smaller ones; they also take up a greater proportion of the available water and nitrogen. The above-ground space in each plot is divided into 1 m deep layers for the purposes of calculating irradiance interception; horizontal variation in the plot environment is not treated. The soil is represented as a single layer, with a daily hydrological budget. Decomposition of soil organic matter is calculated using an empirical submodel. The initial size of each tree seedling is stochastic. To predict the mean behaviour of the model for a particular boundary condition, it is necessary to simulate a number of plots.

The model has been tested extensively. For a given location, a quasi-equilibrium is usually reached after approximately 250 years with ten plots. We found that more plots are not necessary in order to obtain a reliable estimate of mean behaviour. Predictions of productivity, leaf area index, foliage nitrogen, soil carbon, and biomass carbon are all within expected ranges. Mortality is shown to be a necessary model component; without it, large trees reach a maximum size, and then remain in dynamic equilibrium with the climate, without dying. The model runs at a rate of 0.176 s $plot^{-1}$ yr^{-1} on a workstation (a 500-year simulation, with ten plots, thus takes approximately 15 minutes).

HYBRID v3.0 has been written with the intention of using it to represent the terrestrial biosphere in a total earth system model. This would be achieved by linking it to models of other components of the earth system, such as the climate and the oceans, in a fully coupled manner. This total earth system model could then be used to answer a large range of questions concerning European and global environmental change.

The main areas of development during the last year are outlined below.

Soil dynamics

In HYBRID v3.0, as well as in nature, soil carbon and nitrogen dynamics largely determine the availability of mineral nitrogen to the plants, the rate of heterotrophic respiration by the ecosystem, and the amount of carbon stored in the soil.

We examined several approaches for simulating soil carbon and nitrogen dynamics in HYBRID v3.0, including those described by Thornley and Verberne (1989), Raich *et al.* (1991), and a simplified version of the Century soil submodel developed by ourselves. The full Century soil submodel (Parton *et al.* 1987; Parton *et al.* 1993) was chosen for incorporation into HYBRID because only it gave reasonable predictions of both soil carbon storage and nitrogen mineralisation rate for a wide range of litter input rates and climate conditions, without requiring detailed parameterisation of microbial kinetics (as is required by the model of Thornley and Verberne 1989) or different parameterisations for different vegetation types (as is required by the model of Raich *et al.* 1991). Simplifying Century by reducing the number of pools resulted in good predictions of nitrogen mineralisation, but low estimates of carbon storage.

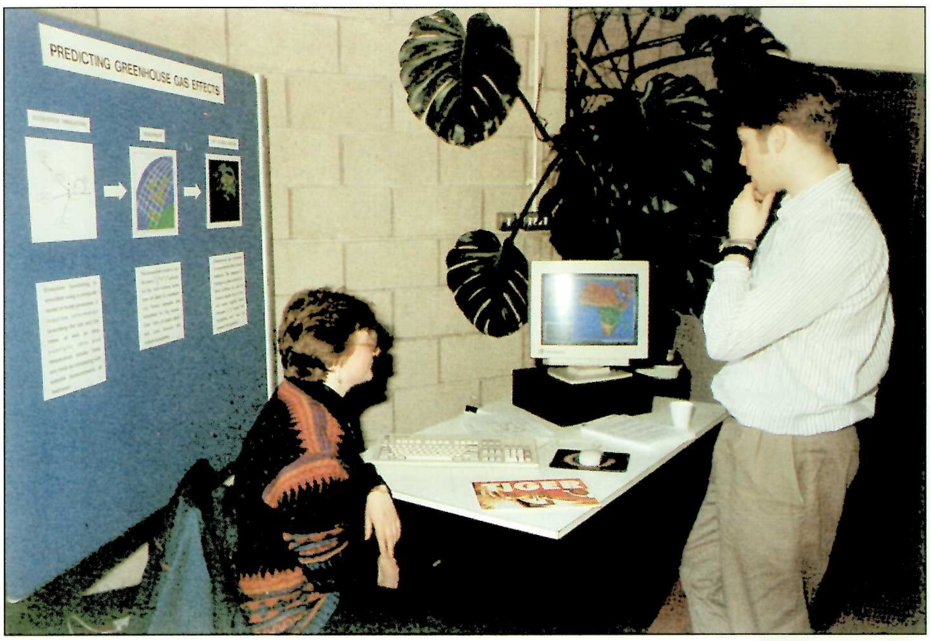

Plate 36. Processing large datasets is a necessary tool for global ecosystem modelling

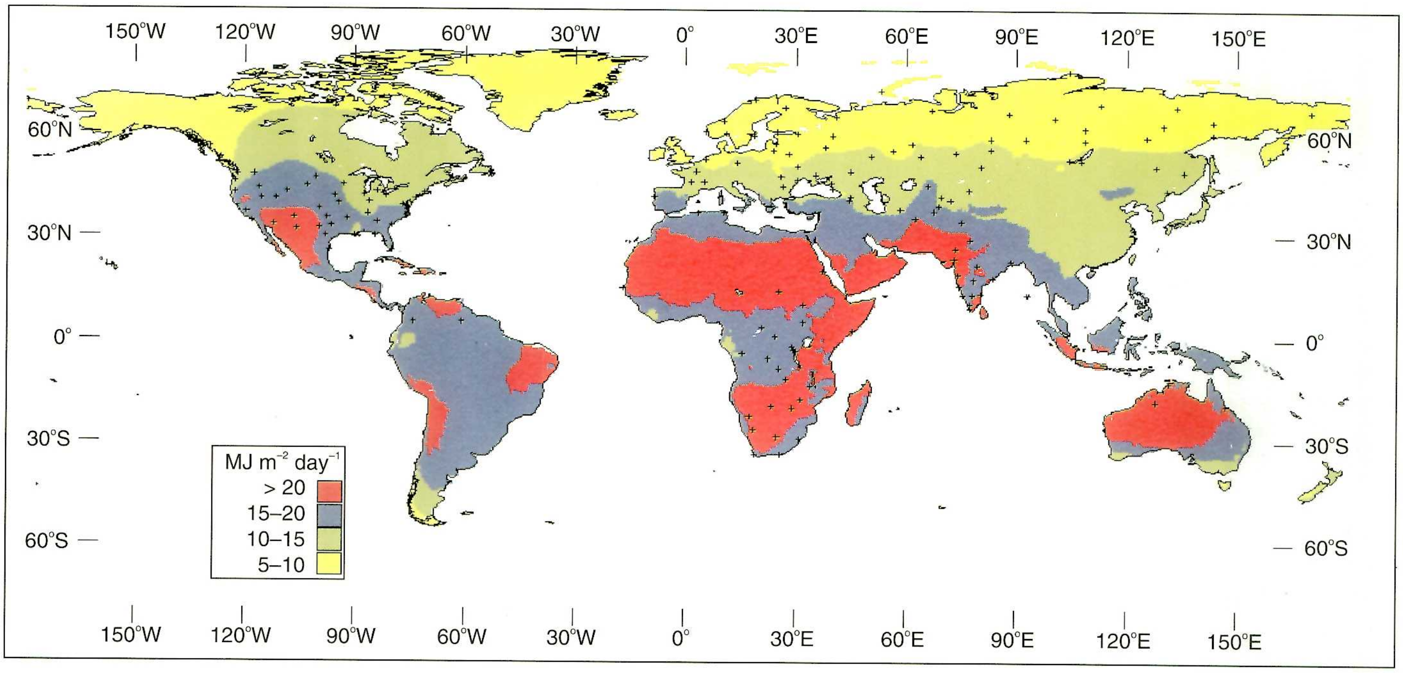

Figure 68. Mean annual solar radiation at the half-degree scale calculated using regression techniques on relative sunshine duration. The regression parameters were derived from station data and interpolated across the land surface

Canopy scaling

A classical problem in modelling fluxes of carbon and water in ecosystems is how to scale from the leaf to the canopy. The seemingly infinitely complex environment of the canopy makes the task daunting. However, recent work has shown that, if it is assumed that the physiological properties of leaves are allocated optimally within the canopy, then the total fluxes scale linearly with the flux of any individual leaf (Sellers *et al.* 1992). This theory has been incorporated into HYBRID v3.0, with significant success.

Phenology

During the year we have also developed a general method for predicting cold deciduous tree phenology based on expected behaviour. We have written a model which uses our daily weather generator (see below) to calculate the degree-day requirement for spring budburst, and the daylength requirement for autumn budset, for any location in Europe, assuming a 1.5% risk of frost whilst the foliage is exposed.

Climate data

A significant problem in using models to investigate the effects of environmental change on ecosystems is the lack of reliable climate data. To obviate this

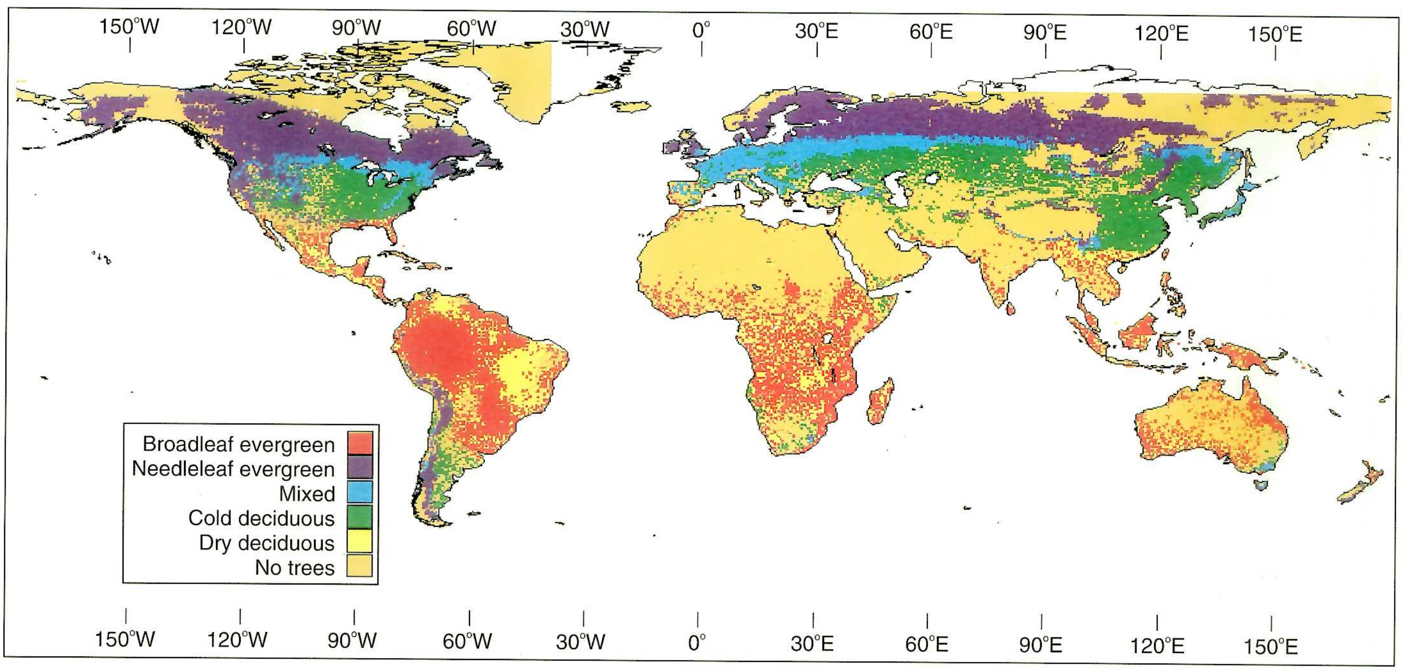

Figure 69. Predicted relative dominance of tree types for each half-degree land pixel in the world, using HYBRID v3.0. The model was run for 200 years with one plot in each pixel

problem we have parameterised a daily weather generator to enable its use at any location in the world, to the nearest half-degree (Friend 1995) This has been achieved by deriving relationships between mean monthly climate variables to enable maximum and minimum 24-hour temperatures, solar radiation, and vapour pressure to be estimated from mean 24-hour temperature, precipitation, and relative sunshine duration These relationships were then gridded across the world and applied to a pre-existing gridded dataset of mean 24-hour temperature, precipitation, and relative sunshine duration The resulting mean monthly values were used to estimate the parameters required by the daily weather generator The resulting generated weather appears realistic, and enables us to concentrate on ecosystem modelling (Plate 36) The derived values of mean annual solar radiation are shown in Figure 68

Physiological parameterisation

A problem in using a detailed physiological model such as HYBRID is that of parameterisation Each species in HYBRID has about 20 parameters These have frequently not been measured and so must be estimated Because many are very important, this estimation presents problems In order to make the task more manageable, we have parameterised four broad categories of tree cold deciduous broadleaf, evergreen needleleaf, dry deciduous broadleaf, and evergreen broadleaf, and one C3 grass type We will also be parameterising a cold deciduous needleleaf tree type We have called these categories generalised plant types (GPTs) Mean estimates of each parameter for each GPT have been obtained from an extensive literature survey The resulting behaviour of each GPT seems realistic, with the key differences between the types in their relative growth in different climates being captured, enabling their relative distributions to be predicted (Figure 69)

A D Friend and A K Stevens

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