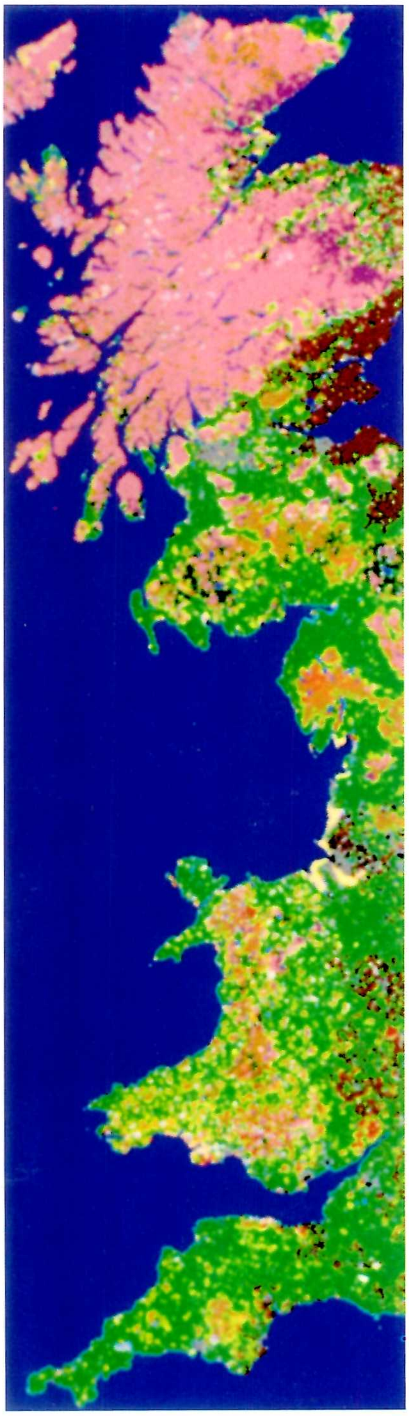
1992 — 1993
REPORT



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 Institute of Terrestrial Ecology 1992–93

Natural Environment Research Council

CONTENTS - Science Reports 1

Forest science

This year has seen the completion of many of the projects in the NERC Special Topic programme on Farm Forestry, funded by members of the Forestry Research Co-ordinating Committee A synthesis meeting was held in London in September 1992 One of the projects is described below, showing that the diversity of insects found in beech woods in Scotland is greatly affected by the microclimate of the woods, especially their exposure to wind, irrespective of their degree of isolation or size This work added a new dimension to ideas on island biogeography, which consider only the size and isolation of the island Other projects within the Special Topic extended our knowledge about colonisation and succession in new woodlands, our ability to introduce a woodland ground flora, and the role of farm woodlands as reservoirs for flower-visiting insects One notable study indicated that sycamore (a non-native species) is unlikely to replace native ash, but that there could be an alternation of these species over time the crucial findings were that the growth of sycamore seedlings is suppressed by sycamore shade, while the growth of ash seedlings is inhibited by weeds that grow beneath ash Much of the Special Topic concerned socio-economic aspects of farm forestry One study clearly showed that the reason why only 12 000 ha of farm woodlands have been planted since 1988, compared to 110 000 ha of golf courses, is directly related to farmers indebtedness and income, only the more wealthy farmers have been interested in tree planting, generally for amenity or sporting purposes

The forestry programme now includes a growing team of mathematical modellers, who are developing models to answer particular questions, and using the models to gain insight into the working of complex ecosystems Last year we referred to the **Edinburgh Forest** model and the **Hybrid** model, which assemble, in different ways, what we know about forest ecosystems The complex structure of the **Edinburgh**

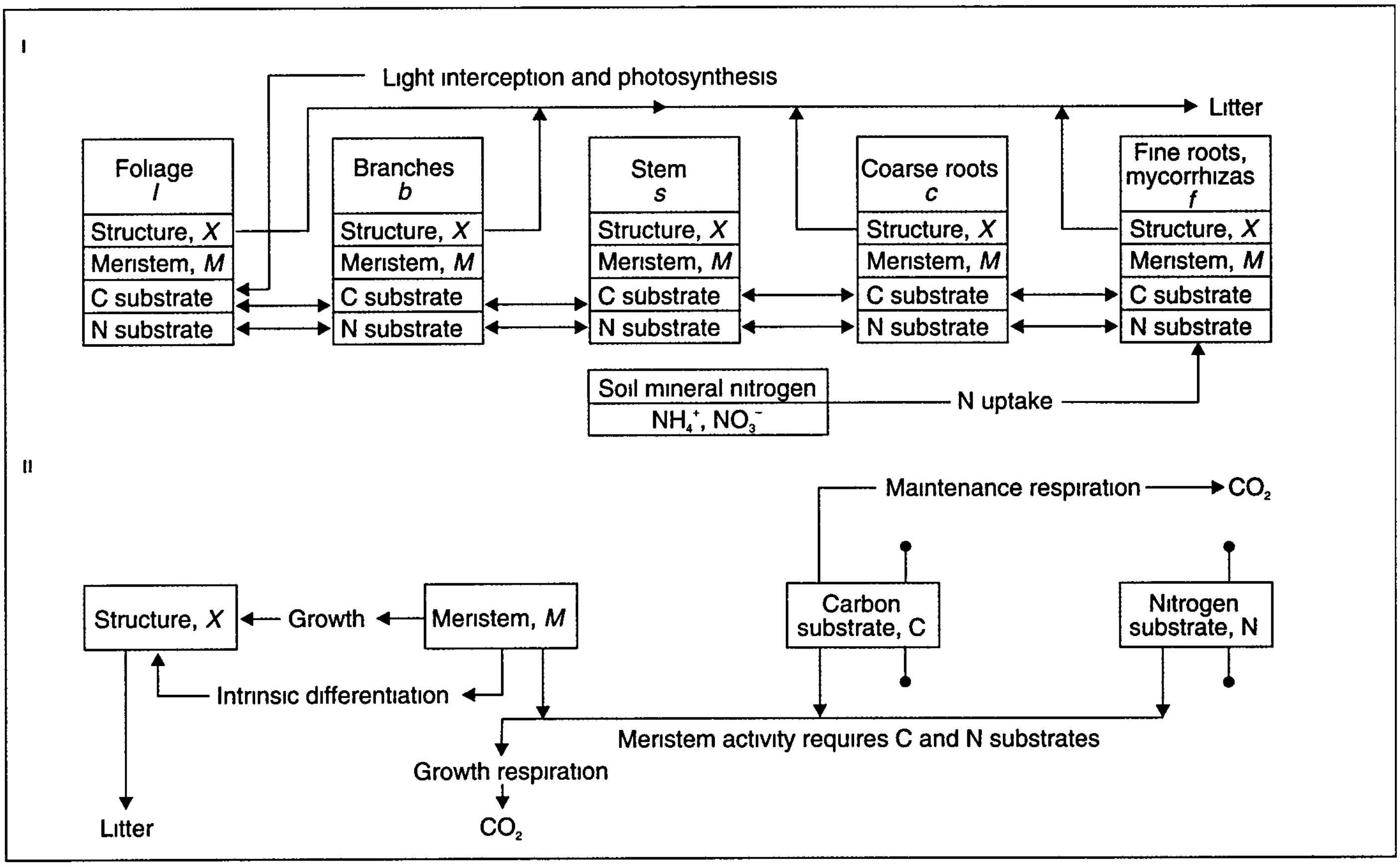

Figure 1 The structure of the **Edinburgh Forest** model (Thornley 1991, Thornley & Cannell 1992, Dewar 1993)
i The five main structural components showing the basic flows of carbon and nitrogen substrates
ii The four parts (*X*, *M*, C and N) of each component

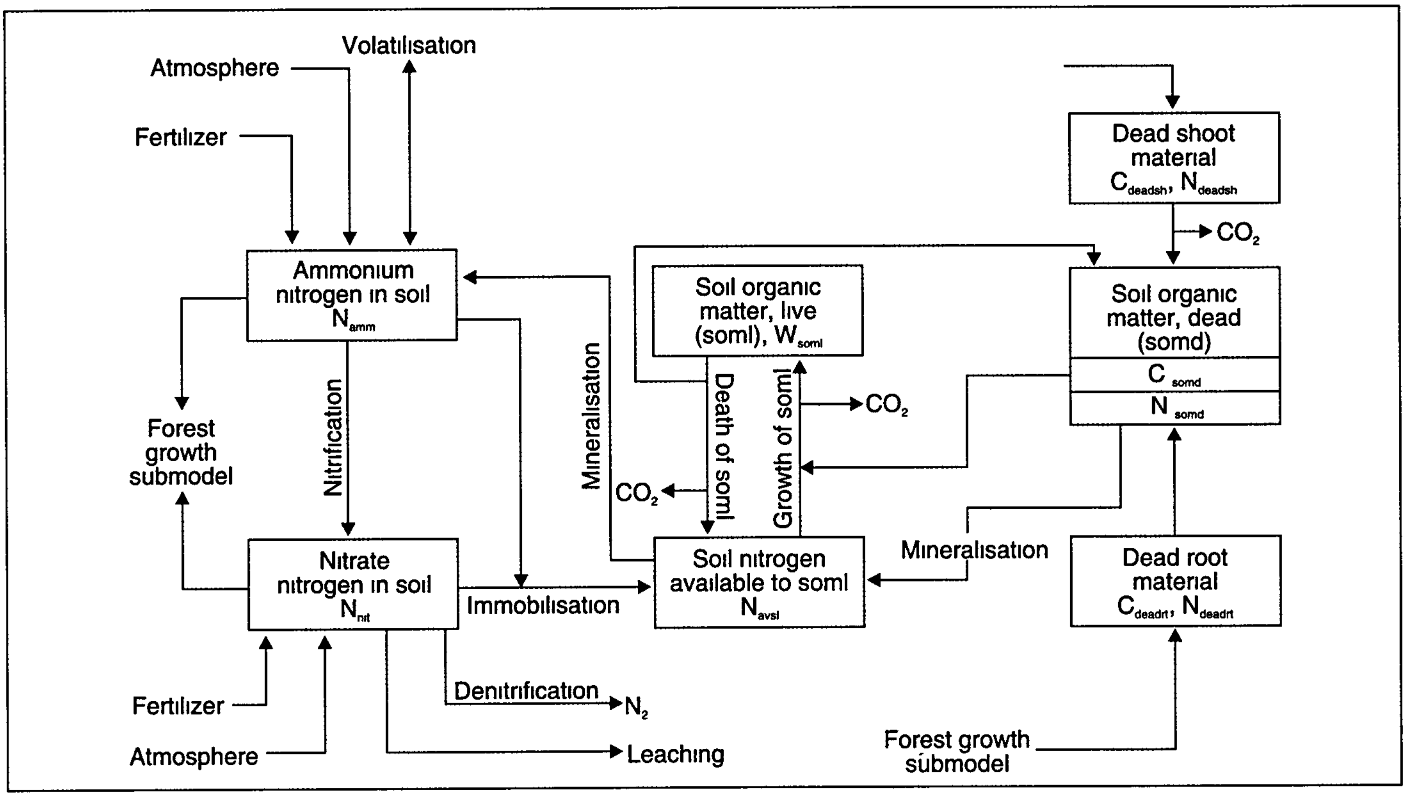

Figure 2 The soil submodel of the **Edinburgh Forest** Model

Forest model is shown in Figures 1 and 2 This year, more emphasis has been placed on understanding and modelling the component processes In particular, a photosynthesis model which couples the water and carbon dioxide (CO_2) exchange of leaves and canopies (PGEN) has been evaluated against published data and examined by deriving an analytical solution Similarly, the Thornley mechanistic model of carbon and nitrogen partitioning has been evaluated and improved At the same time, the models have been used to show how vegetation that responds to elevated CO_2 alters the predictions of climate change and carbon sequestration

Work on tropical forestry has expanded to Indonesia, Costa Rica, Senegal and Chile, as well as Cameroon ITE staff are working on secondment in Indonesia and Cameroon The thrust of the work has been to improve the process of forest regeneration, either by providing techniques of propagation, mycorrhizal inoculum, genetically improved germplasm, or by understanding the ecological processes that govern successful tree establishment Both the ecto- and endomycorrhizal flora have been found to depend upon the land use and vegetation found in any region of the tropics For instance, ectomycorrhizal species differ on *Eucalyptus*, *Nothofagus* and pine in China, while endomycorrhizal species differ in farm and forest soils in Kenya New developments in tropical forestry research include the work reported here on insect diversity, the use of molecular techniques to distinguish mahogany genotypes, the discovery of three-fold variation in *Hypsiphyla* insect resistance in mahoganies, and a growing involvement in dryland degradation

The soil science work has made progress in understanding the impact of nitrification (transforming ammonium into nitrate) on the acidification and release of aluminium in European soils A model which takes meteorological data and outputs soil temperatures and hydrologic conditions may enable the nitrification rates to be determined from basic soil and weather data Other highlights of the soil science work include the successful application of the ^{32}P-bioassay technique to mycorrhizal fungi (as opposed to roots), and the discovery of live rhizobium, mycorrhizal spores and high nitrate levels at 30 m depth beneath *Acacia* in Senegal

M G R Cannell

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Replanting degraded forest in Cameroon: productivity and insect ecology

(This work was funded by the Overseas Development Administration (ODA) and the government of Cameroon)

Deforestation and the role of plantations in West Africa

The average annual rate of deforestation in West Africa from 1981 to 1985 (the period with the most recent reliable data) was 2 2% overall, and 4 1% in closed forest These are the highest regional figures in the world and compare with an average annual loss of closed forest of 0 6% in Africa and 0 3% globally In response to this level of deforestation, only 36 000 ha of plantations were established annually in West Africa during the mid-1980s This figure is very small compared to the 1 7 million ha of forest which were being lost annually at the time It is even less significant when one considers the poor maintenance and survival of these plantations, and the fact that they were usually established in areas where natural forest existed before Furthermore, there is little doubt that the rate of plantation establishment has declined considerably since the mid-1980s

Three indigenous species have been planted widely in West Africa *Triplochiton scleroxylon* (obeche, samba, wawa, ayous), *Terminalia ivorensis* (black afara, framiré) and *Terminalia superba* (white afara, frake, limba) However, many of these plantations were established on a small scale, and few analyses exist of their establishment costs, yields and likely profitability Several hundred sample plots have been established in research and commercial plantations, but these have often been destroyed by fire, logging and/or neglect Results are extremely variable, and differences in soil type, planting stock, planting methods, disease attack and subsequent thinning make it often difficult to draw conclusions

T ivorensis has been widely planted in Côte d'Ivoire, Cameroon, Ghana and Nigeria When well managed (good light and adequate weeding), this species achieves volume increments of 10–12 m^3 ha^{-1} yr^{-1}, and a rotation length of around 25–30 years (to 60 cm diameter breast height (dbh)), although there are major concerns over the 'dieback' of middle-aged plantations in Ghana and Côte d'Ivoire In Cameroon, 4120 ha of *T ivorensis* has been established, with a mean annual diameter increment (mai) of 2 3 cm yr^{-1} The best 50% of plantations achieved 3 0 cm yr^{-1} Ten permanent sample plots have been established by the Forest Management and Regeneration Project (FMRP) in plantations situated in the Mbalmayo Forest Reserve, and diameter increments ranging from 1 3 to 2 9 cm yr^{-1} have been recorded A particularly encouraging plantation was established at Mbalmayo in 1972 It has achieved an average diameter of 60 cm after 20 years, despite damage from a serious fire after ten years

T superba has been widely planted in Congo and Zaire, usually in association with plantains, and it is also an important plantation species in Côte d'Ivoire and Cameroon, 532 ha have been planted in Cameroon, with a mean annual diameter increment of 2 4 yr^{-1} Yields are likely to be in the range 8–10 m^3 ha^{-1} yr^{-1} over a 30–35 year rotation

Triplochiton scleroxylon has been planted in most West African countries, where it also represents the most popular export species Its use has been restricted by difficulties in obtaining seed, although almost 1600 ha have been planted in Cameroon Well-managed plantations in Côte d'Ivoire should yield 8–12 m^3 ha^{-1} yr^{-1} over a 40-year rotation Plantations in central Cameroon are performing less well, however, with 53 cm dbh after 46 years at Makak and 1 7 cm yr^{-1} over the first 15 years at Mbalmayo A recent vegetative propagation trial at South Bakundu, SW province, is recording an encouraging 14 cm after six years

The growth rate of these three native species, and others like *Nauclea diderichii* and *Mansonia altissima*, enables plantations to be harvested after only 25–30 years, and internal rates of return between 9% and 18% to be derived Returns are particularly high when some of the medium-sized trees of valuable species are retained to form part of the final harvest, and when plantations can be combined with agriculture, at least for the first 3–5 years

The Cameroon Forest Management and Regeneration Project (FMRP)

The FMRP is a bilateral Cameroon (Office National de Devéloppement des Forêts (ONADEF))/British (ODA) programme, with the general aim of improving the capacity of Cameroon to carry out wise management and conservation of its moist high-forest areas The Project started in July 1991, with an emphasis on the use of genetically improved indigenous hardwood species in artificial plantations It is based at Mbalmayo, about 50 km south of the capital, Yaoundé, in the semi-deciduous moist forest zone

ITE staff are involved in

- the development of techniques and facilities for the provision of genetically improved planting stock of selected moist forest species,
- the acquisition of growth and cost data for the establishment and management of plantations using different silvicultural techniques,
- the acquisition of data on biological and ecological changes resulting from different silvicultural treatments

The FMRP's planting programme provides an opportunity to demonstrate and study a number of silvicultural options for regenerating degraded forest These options consist of the establishment of *T ivorensis, T scleroxylon* or *Lovoa trichilioides* using the

- *manual regrowth method,* with complete manual clearance of the original canopy, and cutting of undergrowth at knee height,
- *enrichment planting method,* with some well-formed individuals of high-value species in the 29–50 cm diameter class retained to form part of the final harvest of the underplanted fast-rotation species,
- *mechanical complete clearance method,* where large trees are felled by chainsaw and pushed, together with smaller trees, into windrows at a spacing of 40–50 m,
- *line planting method,* where V-shaped lines are cut at wide spacing (determined by the ultimate diameter of the planted trees), and existing trees are heavily cleared,
- *taungya method,* where the Project undertakes forest clearance and burning, and the villagers hoe, plant and cultivate crops for an initial 2–4 year period

This study to compare silvicultural treatments for the growth of indigenous hardwoods builds on preliminary

Plate 1. The non-mist vegetative propagation facility at the Parc de Bouturage of FMRP, Mbalmayo

investigations of the effects of some site preparation techniques on the physical and chemical properties of the soil, the spore populations of endomycorrhizal fungi, and the physiology of the planted trees. This work was part of a reforestation programme linked to the vegetative propagation of indigenous hardwoods and to the development of an appropriate silvicultural system for planting clonal material. The current investigation adds a study to determine the effects of silvicultural treatments on the populations of insects, especially the potential pests and their predators and parasites. The philosophy is that, in order to maximise the productivity from genetically selected planting stock, it is important to minimise risk by the retention of biological diversity in the plantation (Leakey *et al.* 1993).

Tree improvement

The tree improvement component of the FMRP has restored the vegetative propagation (Parc de Bouturage) facilities established under a previous World Bank programme at a 7 ha site in the Mbalmayo Forest Reserve (Plate 1). A mist area containing 2540 m^2 of beds, 40 non-mist propagators (120 m^2), coppice-bed areas, and a drip irrigation system for up to 4 ha of stockplants has now been established. Approximately 4000 m^2 have been planted with 357 clones of *Triplochiton scleroxylon*, 129 clones of *L. trichilioides* and 24 clones of *Terminalia ivorensis*; 1700 *T. ivorensis* plants have been established as stockplants.

The first stage of a genetic selection programme is underway, using a test which measures the response of seedlings to decapitation at 60 cm and partial defoliation. Only two leaves are retained per plant (Plate 2). The number of lateral shoots produced in these standardised conditions and the time required to reassert apical dominance appear to be well related to the growth and form of the tree after four years, and hopefully also in later life. This predictive test is being used to select 2% of the 14 000 *T. scleroxylon* seedlings currently in the nursery. These selected seedlings will be established as stockplants, and rooted cuttings from them used in the field screening phase.

Using this method it is hoped to improved yield and tree form by at least 30% (a level achieved in Côte d'Ivoire). Potentially, as illustrated in Nigeria, these gains could be as high as 80–100%, while following a safe strategy to minimise risk (Leakey 1991).

Insect abundance and diversity

The different site preparation techniques provide plantation plots with contrasting amounts of natural vegetation. The complete clearance plots have only young trees of pioneer species, such as *Musanga cecropioides* and *Trema* spp., other than the planted *Terminalia ivorensis*. Other plots have varied amounts of woody vegetation in addition to the plantation trees. This variability has several possible consequences for insect pests. The diversity of woody plant species in a manual regrowth of line planting system may:

- lead to an increase in potential insect pests and increase the risk of damage; or
- lead to an increase in natural enemies, dampen the fluctuations in the abundance of potential insect pests, and decrease the risk of damage.

There has been little research on the ways that tree species diversity affects damage by temperate and tropical forest pests, but there is circumstantial evidence to suggest that pest problems are, in general, less significant in forests with a high diversity of plant species. Thus, it appears that, although diverse

Plate 2. The implementation of a nursery-based genetic screening programme for *Triplochiton scleroxylon*. This predictive test developed by ITE staff in collaboration with Nigerian scientists identifies trees which will have the desirable characteristic of a low branching frequency over the first 4–5 years of plantation growth

Plate 3. The use of 'knockdown' insecticide in the canopy of an arboretum plot 35-year-old planting of *T. ivorensis*

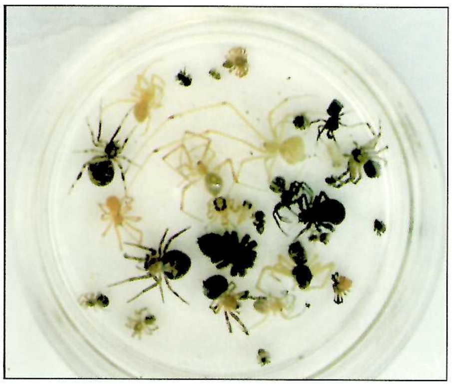

Plate 4. A sample of the spiders collected by 'knockdown' insecticide fogging from 1 m of the canopy of *T. ivorensis* planting in Plate 3

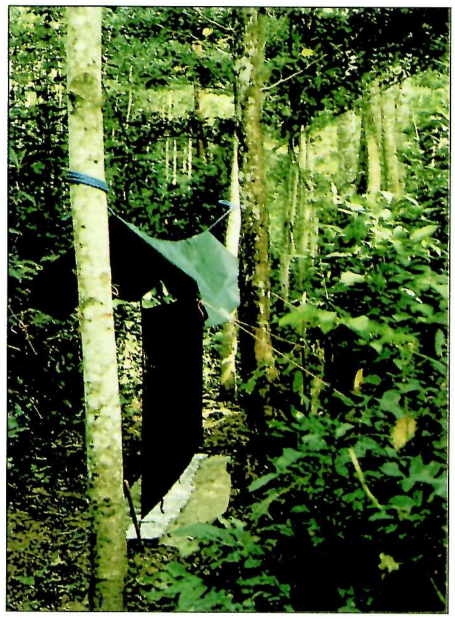

Plate 5. A flight intercept trap in a *T. ivorensis* plantation established after manual canopy opening of logged secondary forest

forests or plantations will contain insect species which are able to feed on and damage a range of host plants, they also contain a far greater diversity of predators and insect parasitoids which will control the potentially damaging fluctuations in insect abundance that occur in many forest (and agricultural) ecosystems.

The first results using 'knockdown' insecticides (Plates 3 & 4), as well as flight intercept (Plate 5) and malaise trapping, indicate that different plantation treatments may bring about differences in the abundance of Homoptera, Coleoptera, Acari and ants.

Thirty-eight species of ants were recorded at Bilik, but only two species (*Crematogaster striatula* and *Oecophylla longinoda*) made up almost 50% of the total. Ants dominated the knockdown samples, whereas the intercept traps caught mostly Collembola, Coleoptera and Diptera. The overall composition of different invertebrate groups sampled by the two techniques is shown in Figure 3.

Improvements in the statistical design of the sampling programmes from 1992 onwards will provide a more reliable standard of monitoring. It must be emphasised that the results from the monitoring of insect damage, abundance and diversity will lack full credibility until the seasonal component is quantified.

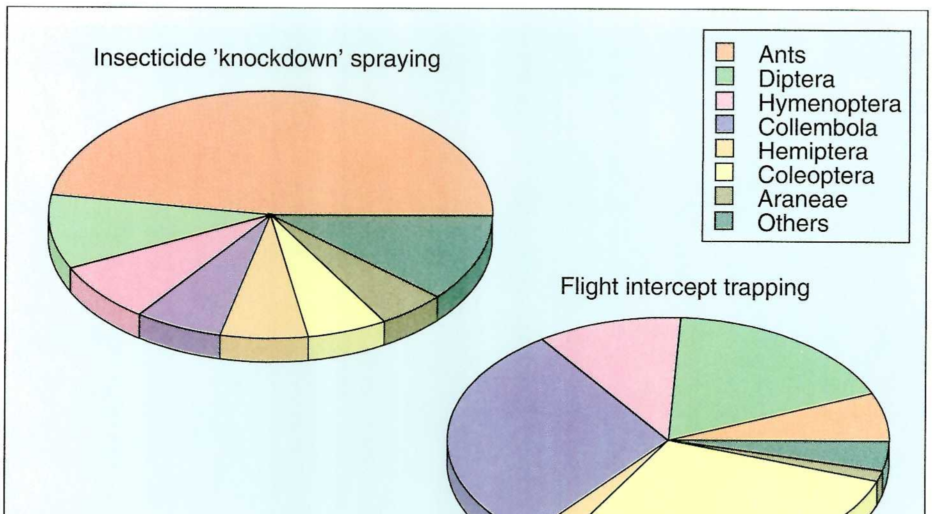

Figure 3. Percentage composition of different invertebrate groups sampled by insecticide 'knockdown' spraying and flight intercept trapping in *Terminalia ivorensis* at Ebogo (planted 1987) and Bilik (planted 1988)

Conclusion

ITE staff are contributing to the FMRP's attempts to develop methods of restocking heavily logged tropical forest in a manner that improves the quantity and quality of timber trees, ensuring that a functional and biologically diverse ecosystem is maintained in both industrial-scale plantations and village-based woodlots. The Project also has a unique opportunity to use its forest management, tree improvement, silvicultural research, training and extension components to assist Cameroon in improving the management of its forest resources in general.

R R B Leakey, G J Lawson* and A D Watt

*ONADEF/ODA Forest Management and Regeneration Project, BP163, Mbalmayo, Cameroon

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The Tropical Soil Biology and Fertility programme (TSBF)

One of the objectives in the Natural Environment Research Council's Corporate Plan for 1993 is 'to encourage international collaboration in environmental research' Like most Institutes in NERC, ITE participates in many international programmes One of these (TSBF) illustrates the long timespan of a research programme between its inception and maturity

In 1984, a group of 20 scientists met in Lancaster to consider how to improve soil biology research in the tropics The meeting was provoked by the recognition that much tropical research was using out-of-date methods to approach the problems of soil fertility, and by the realisation that understanding the processes by which nutrients are efficiently recycled in natural ecosystems could assist agricultural and forest management Encouraged by the UNESCO Man and Biosphere (MAB) Programme and the International Union of Biological Sciences, a network of collaborators was developed and the central concepts of a research programme were identified

- *Synchrony* The release of nutrients from decomposing organic residues can be synchronised with plant growth demand by manipulating the quality and timing of inputs
- *Soil organic matter* The composition and quantity of soil organic matter affects nutrient availability, cation exchange capacity, and soil structure, and can be controlled by management of organic inputs
- *Soil fauna* Soil fauna can be manipulated to improve the physical properties of soil and to regulate decomposition processes

Building on existing research in the tropics, TSBF defined specific methods and experiments to explore these concepts and facilitate inter-site comparisons The TSBF *Handbook of methods,* first published in 1989, has been substantially revised and republished (Anderson & Ingram 1993) These methods and concepts have been incorporated into research projects throughout the tropics, three examples illustrate the type of results

Nutrition of rubber plantations
In Sri Lanka, Prof J M Anderson, of Exeter, has analysed the nutrient use efficiency of young rubber plantations Application of slow-decomposing coconut coir dust, a local waste product, enhanced the retention of fertilizer nitrogen by inhibiting nitrification and reducing leaching Use of expensive fertilizers on small plantations can now be improved

Legume-based agroforestry systems
At Yurimaguas in Peru, researchers from North Carolina State University have shown that nutrient release from surface mulches derived from different leguminous trees and shrubs can sustain upland rice production at the same level as fertilizer application

Management of savanna and derived agriculture
In Zimbabwe, research based at the University in Harare has focused on small farm systems where manure from cattle-grazed savanna is used as fertilizer for arable fields Nitrate leaching, a major loss of nitrogen when inorganic fertilizers are used, is reduced when combined with manure application Manure from 14 ha of savanna can support production of 2 tonnes on a single hectare of arable land At lower savanna/arable ratios, inorganic fertilizer input is necessary to sustain productivity

Research projects and co-ordination across the network of sites has been assisted by grant funding from the UK Overseas Development Administration (ODA) to NERC for work related to MAB, from direct funding from NERC to TSBF, and from participation by ITE staff Regional networks in Africa and India have now been established, and a full review of tropical soil biology management is in press (Woomer & Swift 1993)

TSBF is now a fully fledged organisation in its own right, receiving funding from the Rockefeller Foundation, ODA, and other sources, and with its headquarters in Nairobi It is an equal partner with a number of International Agriculture Centres in a new project funded by the Global Environment Facility of the World Bank on alternatives to slash-and-burn, and the first full-time Director, Prof M J Swift, took up his post in January 1993

O W Heal, P L Woomer and J S I Ingram

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Mechanistic modelling at the leaf, plant and ecosystem scales

How do leaf stomata regulate the flow of carbon dioxide (CO_2) and water vapour into and out of leaves, in response to changes in leaf environment? How do plants regulate the distribution of their carbohydrate and nutrient resources between leaves, stem and roots, in response to changes in the availability of these resources in the plant's environment? What are the likely effects of increasing CO_2 levels on the carbon storage of forest and grassland ecosystems? To answer these and similar questions, we need mechanistic models which adequately describe the various processes involved, on scales ranging from a single leaf to the entire plant/soil system Our aim is to develop models which couple together the flows of carbon, nutrients and water in a mechanistic way, and apply them to the questions outlined above

Modelling leaf stomatal behaviour

The fluxes of carbon and water exchanged between plants and the atmosphere are intimately coupled by virtue of the fact that they share a common pathway for diffusion through the stomatal pores on leaf surfaces Understanding how stomatal aperture responds to changes in temperature, atmospheric CO_2 level, light intensity, air humidity and soil water content is crucial to many questions at the plant and ecosystem scales The PGEN model (Friend 1991) assumes that stomata open or close so as to maximise the rate of leaf photosynthesis under given environmental conditions Photosynthesis increases with leaf water content as well as with the CO_2 concentration inside the leaf The optimal stomatal conductance (g_o) then represents a compromise between allowing more CO_2 to diffuse

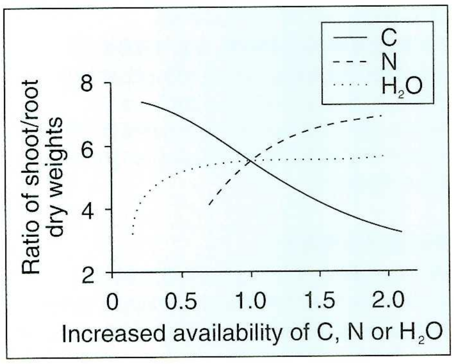

Figure 6. Responses of the shoot/root dry weight ratio to changes in the availability of carbon (C), nitrogen (N) or water (H_2O), predicted by the allocation model (Figure 5) in simulations of balanced exponential growth. Resource availability is defined as photosynthesis per unit shoot mass (for C), nitrogen uptake per unit root mass (for N), or soil water potential (for H_2O), relative to standard values

transported to the root along a sucrose concentration gradient set up by a resistance in the phloem. Roots take up and reduce N, a fraction of which is transported directly to the shoot in the xylem transpiration stream, and some of this shoot N is then transported back to the root along with sucrose in the phloem. Sucrose and reduced N (amino-acids) are both incorporated into shoot and root dry matter during growth, the rate of which depends on the local concentrations of each substrate.

This simple scheme mimics observed allocation responses to changes in the availability of C and N. Figure 6 illustrates this behaviour, including the response to changes in soil water availability obtained by incorporating an effect of water content on growth. As the availability of a particular resource declines, the model predicts that growth is preferentially allocated to the part of the plant responsible for uptake of that resource (the shoot for C, the root for N and H_2O). A crucial feature of the model, which ultimately explains these responses, is that opposing gradients in C and N substrate concentration are set up between the shoot and the root which lead to differential growth effects.

This model provides a theoretical basis for understanding the response shown in Plate 6. However, part of this response may have been due to an observed reduction in the period of active shoot growth under elevated CO_2, an effect not currently represented in the model. Further work needs to be done to understand the role played by such changes in shoot phenology.

Modelling ecosystem responses

Moving up to the ecosystem level requires the inclusion of carbon, nutrient and water fluxes in the soil system, involving processes such as plant litter turnover, microbial growth, soil decomposition, N mineralisation, and nutrient leaching by rainwater runoff. Two models are being developed at this scale: the ITE **Edinburgh Forest** model (Thornley & Cannell 1992) and the Hurley **Grassland** model (Thornley, Fowler & Cannell 1991).

The **Forest** model describes the coupled C and N fluxes in a stand-level plantation/soil ecosystem. Work to date has concentrated on exploring the general behaviour of the plantation/soil model through sensitivity analyses, to gain insight into how the model's responses relate to the underlying processes. Water fluxes have not yet been incorporated.

The **Forest** model has been used to examine the relations between plantation growth, soil organic matter content, atmospheric N deposition, N uptake by the plantation, and the timing and quantity of fertilizer application. Soil organic matter decreases when trees are grown on carbon-rich soils, but increases when trees are grown on infertile (carbon-poor) soils and given large inputs of nitrogen. The potential growth of even-aged plantations may be greater than that realised in poor soils with common levels of atmospheric N deposition and normal fertilizer regimes. Simulations show how soil mineral N concentrations change during stand development, and point to the importance of N application during the period of canopy building when plant demand for nitrogen is highest.

The **Forest** model has also been extended to include the birth and death of trees in order to describe the population dynamics of natural stands (Dewar 1993b). The model has been used to predict the development of a dense stand of small seedlings as it thins out to become a sparse stand of large trees. Simulations show how the rate of thinning is governed by the balance between the increasing amount of light intercepted by each surviving tree as crowding decreases, and the increasing cost of maintenance respiration as the trees become larger.

The **Grassland** model describes the coupled C, N and water fluxes in a crop/soil ecosystem, including the effect of grazing animals. The model has been used to simulate dynamic as well as steady-state responses of carbon storage to various environmental scenarios (including the IPCC 'business-as-usual' scenario for CO_2 and temperature), and to various management and experimental treatments.

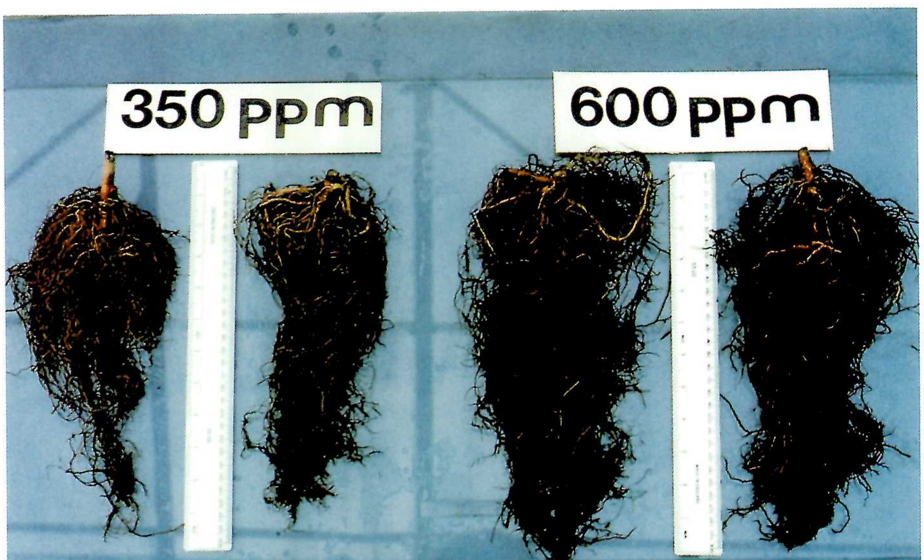

Plate 6. Comparison of root growth in Sitka spruce seedlings grown at atmospheric CO_2 concentrations of 350 ppm and 600 ppm. Shoot growth (not shown) was found to be the same (or even slightly reduced) at 600 ppm, implying increased allocation of total growth to roots

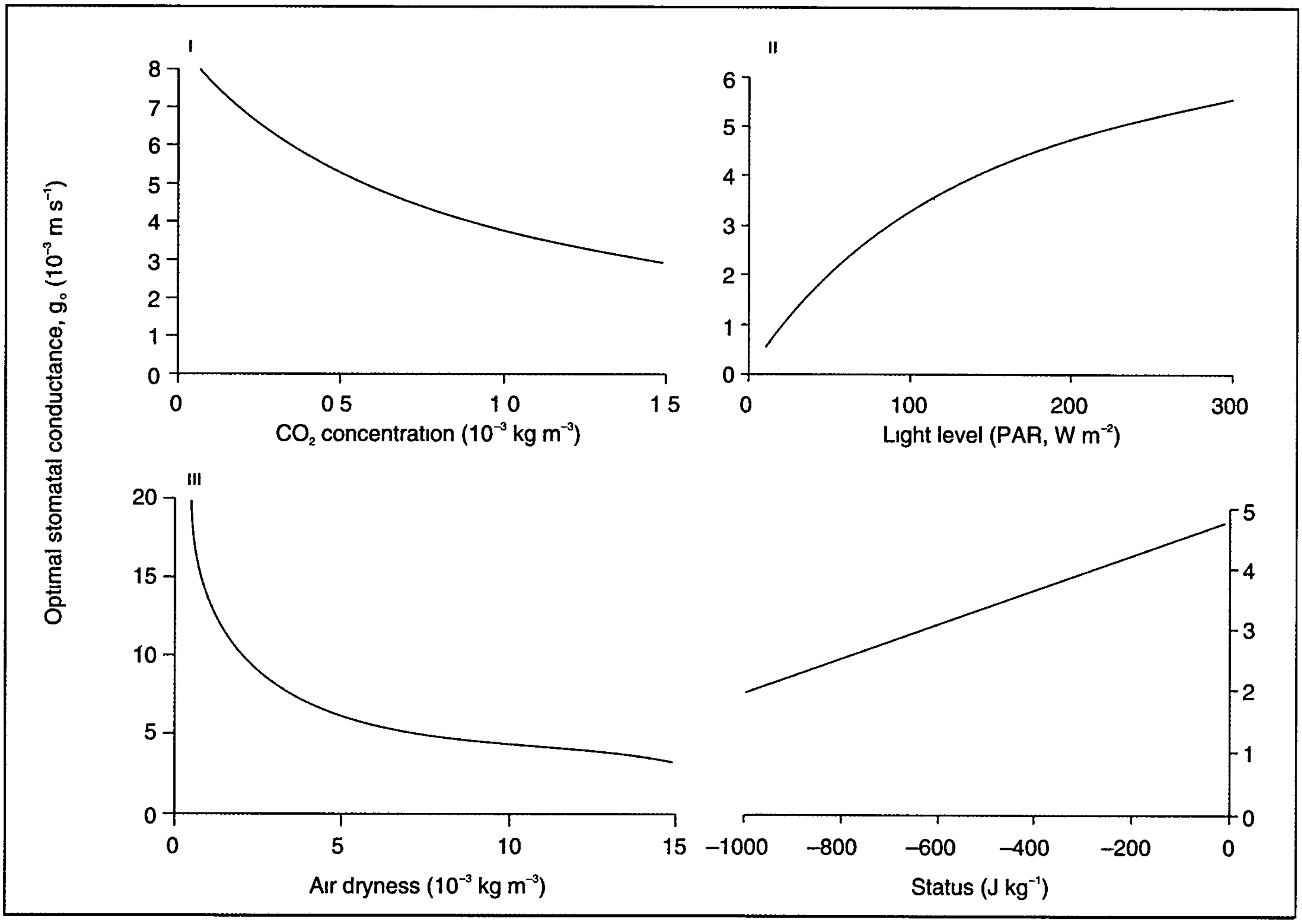

Figure 4 Responses of optimal stomatal conductance (g_o) to changes in (i) atmospheric CO_2 concentration, (ii) light level, (iii) air dryness, and (iv) soil water status, predicted by the PGEN model

into the leaf from the atmosphere (so increasing photosynthesis) and allowing more water to escape from the leaf through transpiration (so reducing photosynthesis) The model quantifies the costs and benefits in terms of what we know (or hypothesise) about the details of leaf photosynthesis, and calculates g_o for a given environment

The predicted responses of g_o to changes in the environment (Figure 4) agree well with measured responses, implying that stomatal mechanisms have, indeed, evolved through natural selection to behave in an optimal way This means that we can now incorporate PGEN into larger-scale models without having to represent explicitly the actual mechanisms which control stomatal aperture Such simplifications are a great advantage when attempting to model the complexity of real plants and ecosystems In their article in this Report (pp36–37), Friend, Stevens and Cox describe how optimal stomatal behaviour may affect climate warming at the global scale, by regulating the exchange of CO_2 and water vapour between vegetation and the atmosphere

Modelling plant growth allocation

Plate 6 strikingly illustrates the increased root allocation of Sitka spruce (*Picea sitchensis*) seedlings subjected to elevated CO_2 levels, observed during a three-year experiment conducted at ITE Edinburgh Because more root allocation may increase the transfer of plant litter to the soil, a mechanistic understanding of this response is needed in order to predict longer-term ecosystem responses to elevated CO_2 Increased root allocation has also been observed in many species when plant nutrient or water supply is reduced, so the underlying mechanisms must involve processes which couple together the carbon, nutrient and water dynamics within the plant

We have examined a simple plant model (Dewar 1993a) consisting of just a root and a shoot (Figure 5) The purpose of this type of model is to try to understand allocation responses qualitatively in terms of what is known about the internal pathways of mobile carbon (C) and nitrogen (N), rather than to make quantitatively accurate predictions In the model, labile C (mainly sucrose) is assimilated by shoot photosynthesis and

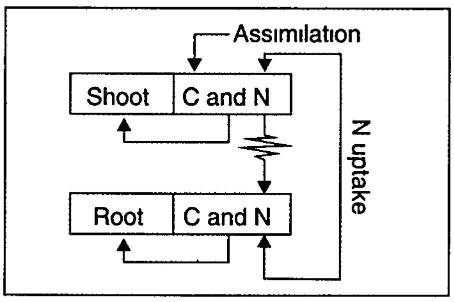

Figure 5 Basic structure of the shoot/root allocation model, in which shoot and root growth are determined by the product of carbon (C) and nitrogen (N) substrate concentrations in each compartment An effect of water content on growth (not illustrated) is also included in the model

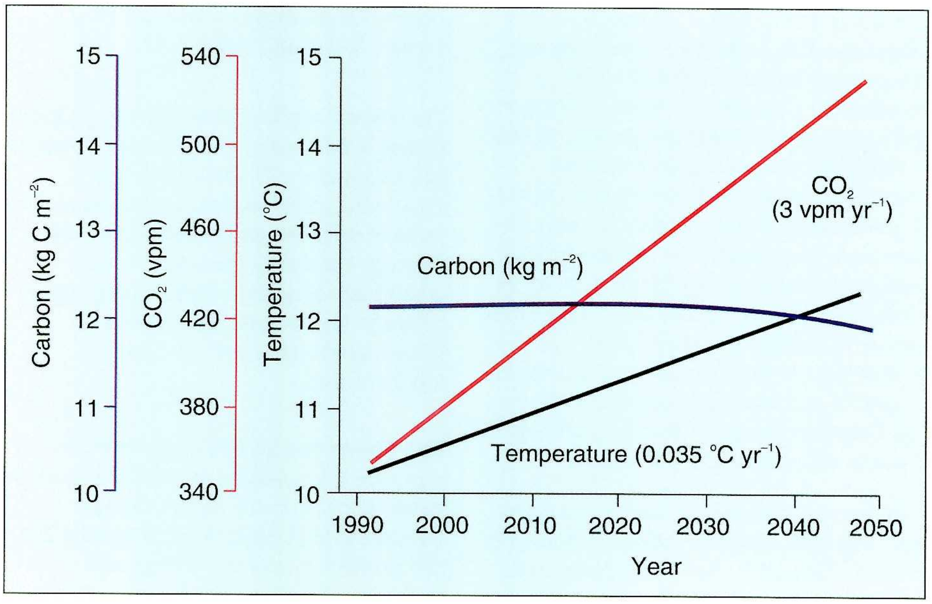

Figure 7. Response of the carbon storage of a temperate grassland ecosystem to simultaneous rises in atmospheric CO_2 and temperature over the next 60 years (the IPCC 'business-as-usual' scenario), predicted by the Hurley **Grassland** model. Almost all of the carbon is stored as soil organic matter, with very little (<1%) contained in the grass itself

Because all processes in the model are temperature-dependent with different sensitivities, the predicted relationships between net annual primary productivity, temperature and total ecosystem carbon storage turn out to be more complex than is sometimes simplistically assumed. For example, simulations suggest that the effects of elevated CO_2 (+3 vpm yr^{-1}) and rising temperature (+0.035°C yr^{-1}) on total ecosystem carbon storage will almost cancel each other out (Figure 9), because, in the model, a rise in CO_2 level stimulates photosynthesis and hence plant litter input to the soil (so increasing carbon storage), while a temperature rise increases plant respiration and soil decomposition more than it increases photosynthesis (so decreasing carbon storage).

In some environments, carbon storage is predicted to decrease as rainfall increases, because of an increase in nutrient leaching.

Multiple-harvest experiments, in which a grass sward is cut down to the same height at regular intervals over periods of weeks to months, are now often performed to study grassland productivity under different conditions of CO_2 and temperature. Simulations using the **Grassland** model suggest that experiments of this type measure transient responses well removed from the steady state, and may therefore give results which are misleading with respect to the longer-term responses to climate change over periods of decades or centuries. This case illustrates that models have as much to contribute to the design and interpretation of experiments as experiments have to contribute to the testing of models.

R C Dewar, J H M Thornley and A D Friend

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Effect of woodland fragmentation on insect abundance and diversity

(This work was funded by the Forestry Research Coordination Committee (FRCC) as part of the NERC Special Topic programme on Farm Forestry)

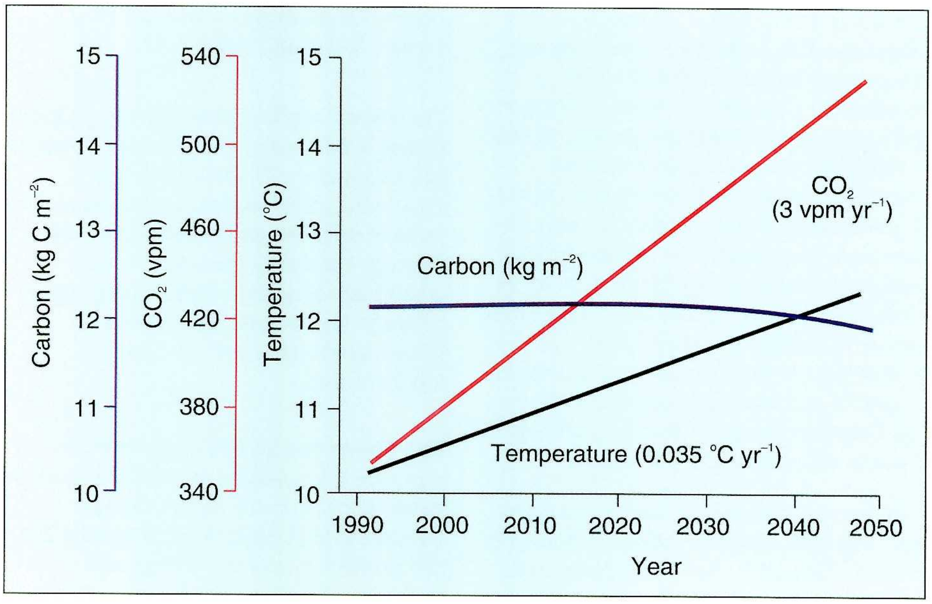
Introduction

Arboreal insects represent a key component of the nature conservation value of woodland habitats, both directly and through their contribution to the food chain (Warren & Key 1991). Although particular species of tree are known to have a greater potential number of insect species associated with them (Strong, Lawton & Southwood 1984), the influence of factors such as woodland size, shape and distribution is poorly understood. ITE has investigated the contribution of these features of farm woodlands to species diversity, and hence the value of farm woods for nature conservation. The ultimate aim of this work is to contribute towards a scientific basis for the management of existing and new woodlands for wildlife.

In the Annual Report for 1991–92, we showed how different factors operate at different spatial scales (tree, wood and woodland system) and have different effects on insects with different life history strategies. Here, we concentrate on the results of further work on insects which mine and gall leaves (endophage insects) and insects which feed externally on foliage (ectophage insects), identifying mechanisms that account for the observed distribution and abundance of insect species on beech (*Fagus sylvatica*).

Methods

Insect species were sampled from beech in and around Bush Estate, near Edinburgh, Midlothian. Three beech trees were sampled in 15 blocks of woodland and nine hedgerows. We sampled insects by physical 'knockdown' and canopy searching in mid-summer, and leaf collection from the canopy in late summer. The structure and position of each tree and adjacent vegetation cover were recorded in the field, and the extent of woodland cover and the pattern of woodlands in the landscape were measured from maps and aerial photographs. The leaf litter that remained under each tree after winter and the draughtiness of each woodland were measured because we believed these factors could result in a reduction



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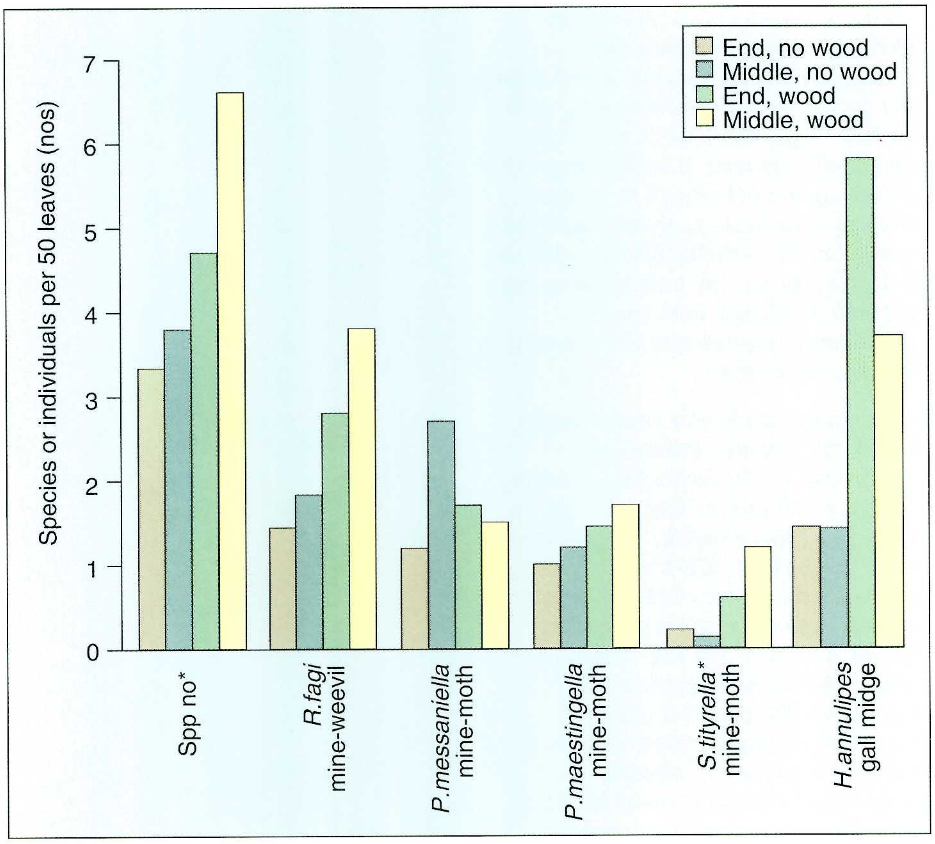

Figure 8. Mean number of species and abundance of five leaf mining and galling species in four hedgerow categories: hedgerow end, unconnected to woodland; hedgerow middle, unconnected to woodland; hedgerow end, connected to woodland; hedgerow middle, connected to woodland. Statistically significant results are marked with an asterisk

in the species diversity and abundance of leaf mining and galling insects in small, isolated woods. Draughtiness was measured as an index, incorporating estimates of the size of gaps between tree canopies and the size of the gaps between the field layer and the base of the tree canopies, for both the south-west and north-east side of each wood.

Results

Data collected in 1990 and 1991 were analysed, first, to assess which factors affected the distribution of species, and, second, to assess which factors affected insect abundance. The data were also analysed separately by woodland and by tree. Differences in sampling intensity meant that the data from 1990 and 1991 had to be analysed separately.

The following factors accounted for 74–78% of the variation between woods in the distribution of leaf mining and galling species:

- area of wood,
- distance south-west (the prevailing wind) to a shelterbelt (as opposed to woods that contained beech), and
- draughtiness of the woodland,

while 40–54% of their distribution between individual trees within a woodland was explained by:

- density of leaf litter,
- tree height, and
- date of budburst.

For the abundance of leaf mining and galling insects between woods, 67–82% of the variation was accounted for by:

- draughtiness of the woodland,

whilst 37–58% of the variation in the abundance of endophages between trees was explained by:

- density of leaf litter,
- date of budburst, and
- plant species richness in tree and field layer.

The leaf mining and galling insect species on beech canopies in woodlands were also found in hedgerows. The number of these species in samples taken from beech in hedgerow networks was greatest where they were connected to woodland, and greater in the centre of a length of hedgerow than at the end. The abundance of some of the individual species roughly followed the same pattern (Figure 8).

Larger woodlands were found to support most species in the study area. Smaller, insular woods, in contrast, were found to have much fewer species: leaf mining micromoths, for example, were absent from these woods. Their absence may be due to a relative lack of insects immigrating into these woods, but the woods are not completely isolated from dispersing insects. The activity of the adult stages of insects with leaf mining larvae were surveyed in the spring and summer dispersal periods, with sticky traps suspended in each tree (Plate 7).

Plate 7. Sticky traps suspended in beech canopies to detect the activity of adult micromoths, weevils and gall midges

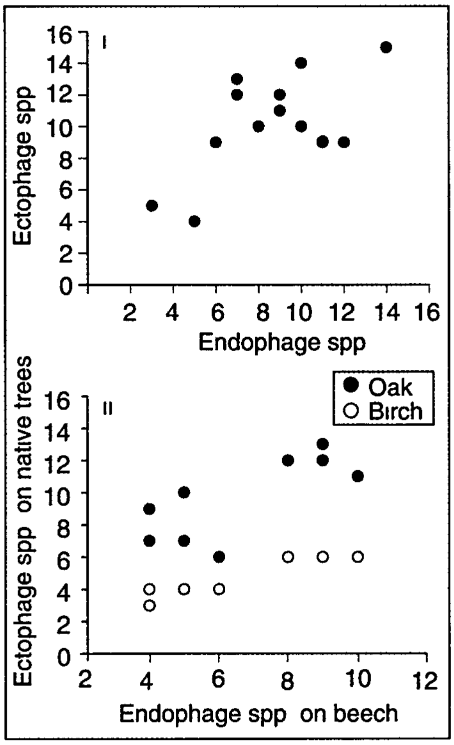

Figure 9 i Comparison of the species richness of endophage (leaf mining and galling) species, with ectophage (externally feeding) species on beech in different woodlands in Midlothian
ii Comparison of the species richness of oak and birch with beech in different woodlands in Midlothian (birch and oak data, G B Usher)

Although an average of 28 5 adult moths per trap were caught in larger woodlands where trees had high densities of micromoth mines in their leaves, small woods which lacked micromoth mines had a detectable level of emigration of 0 1 adult moths per trap

Discussion and conclusions

Although rare or absent in small isolated woodlands (defined as smaller than about 5 ha and further than about 2 km from another woodland along the line of the prevailing wind), the dispersal stages of micromoth species (from the Nepticulidae and Gracillariidae families) were found to be able to reach woodlands of all sizes Their distribution may, however, be limited later by factors which affect the non-dispersing stages of these insects These factors may also account for the similar pattern of distribution of ectophage species collected by 'knockdown' methods (Figure 9 i)

A high proportion of trees in small woods is exposed to the weather The leaves of these trees provide a poor habitat in summer, and the leaf litter is depleted in winter to a greater degree than trees in larger woods Leaf loss due to wind exposure is probably a mechanism which detrimentally affects the abundance and distribution of leaf mining and galling insects overwintering within the leaf Thus, new woods should be designed to be near enough (along the prevailing wind direction) to existing areas of woodlands to obtain dispersing insects and to minimise the draughtiness in the new wood, and both large enough and with a sufficient field layer or understorey vegetation to allow insects to become established

Although this study was conducted on beech, the principal mechanisms responsible for the restriction of insect species on beech are likely to apply to other tree species which occur in the same types of woodland system Many species of micromoth and gall midge on different tree hosts share similar life history strategies and are, therefore, vulnerable to the same physical processes The potential range of micromoth and gall midge species on native tree species in wooded landscapes in Scotland could be much diminished if many of the woods are small (*ca* 1 ha), draughty and exposed A study by G B Usher (pers comm) demonstrated a similar pattern of response of leaf mining and galling invertebrate species found on silver birch (*Betula pendula*) and oak (*Quercus robur*) to that shown for leaf mining and galling on beech in the same types of woods (Figure 9 ii)

In conclusion, this study indicates that small woodlands (*ca* 1–5 ha) should be located within 15–20 h (h =tree height) of woodlands in areas of high woodland cover, preferably linked by hedgerow or shelterbelt networks, and in the prevailing wind direction In addition, a subcanopy and field layer should be encouraged to provide winter shelter for arboreal insects, as well as a suitable habitat for species living on the ground and field layer

P Dennis and A D Watt

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Land use, agriculture and the environment

This year has seen several important landmarks in the progress of research on land use within the Institute. Perhaps foremost among these has been the completion and launch of the ITE land cover map of Britain, progress on which was reported in detail in the Annual Report for 1991–92. The land cover map is a comprehensive data base of the land cover of Great Britain. It is the first major national mapping programme since the Second Land Utilisation Survey of the 1960s, and the first to be based primarily upon remotely sensed imagery. The map has been produced using cloud-free winter and summer imagery from the Landsat Thematic Mapper, based as nearly as possible on a 1990 datum. Three spectral bands from each scene were combined for classification, using the known cover type of selected areas to help control the process. The resulting classified scenes have been harmonised to give 25 standard categories across the whole of Britain, at a resolution of 25 m. The map offers a practical level of discrimination between the major cover types of both upland and lowland areas, and promises to be a useful tool in resource assessment, management and monitoring studies.

The land cover map is one major output from the 1990 Countryside Survey project. Another is the final report to the Department of the Environment, which was launched at a seminar at Edinburgh in February 1993. The Countryside Information System (CIS), developed on the basis of knowledge obtained from earlier ITE land use surveys of Britain, has continued to grow, taking full advantage of the information obtained during the 1990 survey. It has now entered its second phase of collaborative development which involves testing by potential user organisations whose experience will help to improve its practical usefulness. The CIS has strategic importance as the vehicle through which users may gain access to distilled information from the various surveys and data sets accumulated over the last two decades.

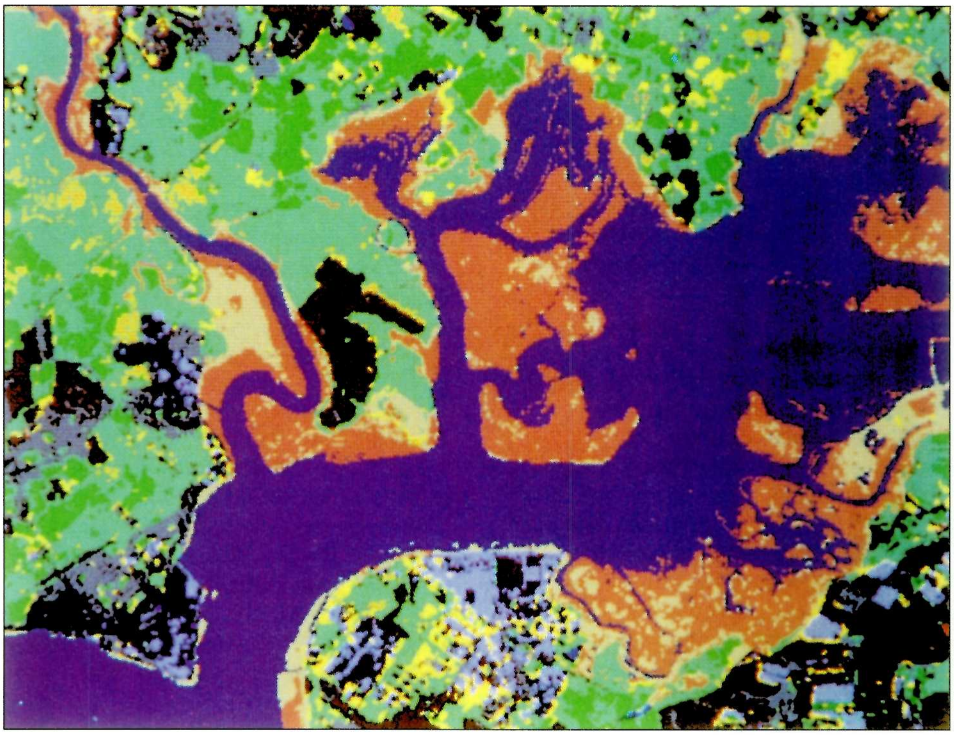

Plate 8. The land cover map – the Medway Estuary, north Kent. This section, roughly 150 km^2 in extent, shows a clear differentiation of the major cover types associated with urban and industrial development on soft coastline. Sheerness is on the eastern tip of the Estuary and the Isle of Grain refinery and power station opposite (grey shades). Most of the agriculture is permanent grassland (green shades), but arable areas occur at top left and bottom centre (red-brown). Saltmarsh is the most extensive semi-natural habitat (pink)

The impacts of land use on biodiversity are of special interest at a time when land use is changing in response to the remodelling of agricultural policy, and there is a possibility of further more drastic change resulting from climatic perturbation associated with global warming. The Institute is making an important contribution to our understanding of these relationships through its exciting research on spatial relationships between land use and biodiversity. Work described in this Report shows, for example, that, while general trends in species richness can often be accounted for by climate, local variations reflect local patterns of habitat and land use history.

Understanding successional processes in vegetation is an area of key importance in plant ecology, and one which has received a great deal of attention over the years. The Institute is making a major contribution in this field by developing mathematical models which enable species changes during succession to be predicted on the basis of a few of their basic ecological characteristics. It has been shown that a mathematical model developed to predict successions in arable fields entering set-aside can be used equally well to describe succession in a range of other ecosystems.

As a result of having long-established research stations located throughout Britain, ITE has developed unique expertise and data bases that are of great value when attempting to predict the effects of policy changes which affect land use and hence the environment (eg agricultural extensification, community forestry). The review by Firbank which follows uses this information and expertise to underpin an assessment of the likely environmental benefits associated with one aspect of agricultural extensification, long-term set-aside.

The Environmentally Sensitive Area (ESA) scheme is a key instrument of UK government policy in implementing agricultural extensification in England and Wales which enhances environmental quality. In order to determine the benefits to flora and fauna of ESAs, it is necessary to monitor the changes occurring in response to the altered land use prescriptions. This information can then be used to improve these prescriptions so as to enhance further the benefits provided by the scheme. ITE is actively involved in developing appropriate methodologies for assessing both the effects of current ESA policies and those likely to be developed in the near future. Research is described which determines the potential benefits to wetland flora and fauna from reinstatement of less intensive farming methods.

J E Good

Biogeographic research in the Biological Records Centre

(This work was partly funded by the Joint Nature Conservation Committee, and involved collaboration with the NERC Centre for Population Biology)

Introduction

The Biological Records Centre (BRC), set up in 1964, is Britain's national biodiversity data centre. Its development and applications during the first 25 years are described by Harding (1992). BRC's computerised data sets include about 6 million individual records (minimum data = species, location, date) of some 10 000 taxa. These data have been used to prepare maps summarising the national distribution of species, which have been published in atlases, taxonomic treatises and studies of individual taxa, and have been used in the preparation of Red Data Books and national reviews of threatened and uncommon species.

The availability of comprehensive data sets on many biotic groups, together with the ability to access other environmental data sets held by the Environmental Information Centre at ITE Monks Wood, provides unrivalled opportunities for examining the relationships between taxa and topography, geology, soils, climate and land use (both past and present).

The BRC data sets now underpin research activities throughout the Institute. Recent examples include studies of the ecological impacts of climate change, determining priorities to maximise the benefits of agricultural set-aside, and assessing the role of habitat corridors for wildlife. The range of research applications using BRC data has been reviewed by Eversham *et al* (1993).

Biodiversity studies

Global concern for biodiversity conservation (Groombridge 1992) has already led to attempts to identify key regions of high diversity – 'hotspots' – for conservation in the tropics (International Council for Bird Preservation 1992). However, the objective analysis of patterns of species richness has seldom been attempted using precise and comprehensive biotic and environmental data, such as exist for Britain. The broad trend in species richness in most groups – a concentration of species in the south-east, and gradually fewer species north-westward – can now be quantified, and local departures from the trend assessed. Figure 10 illustrates the trend for the vascular plants: to remove fine-scale variation, the data have been 'smoothed' by averaging species richness over 30 km squares.

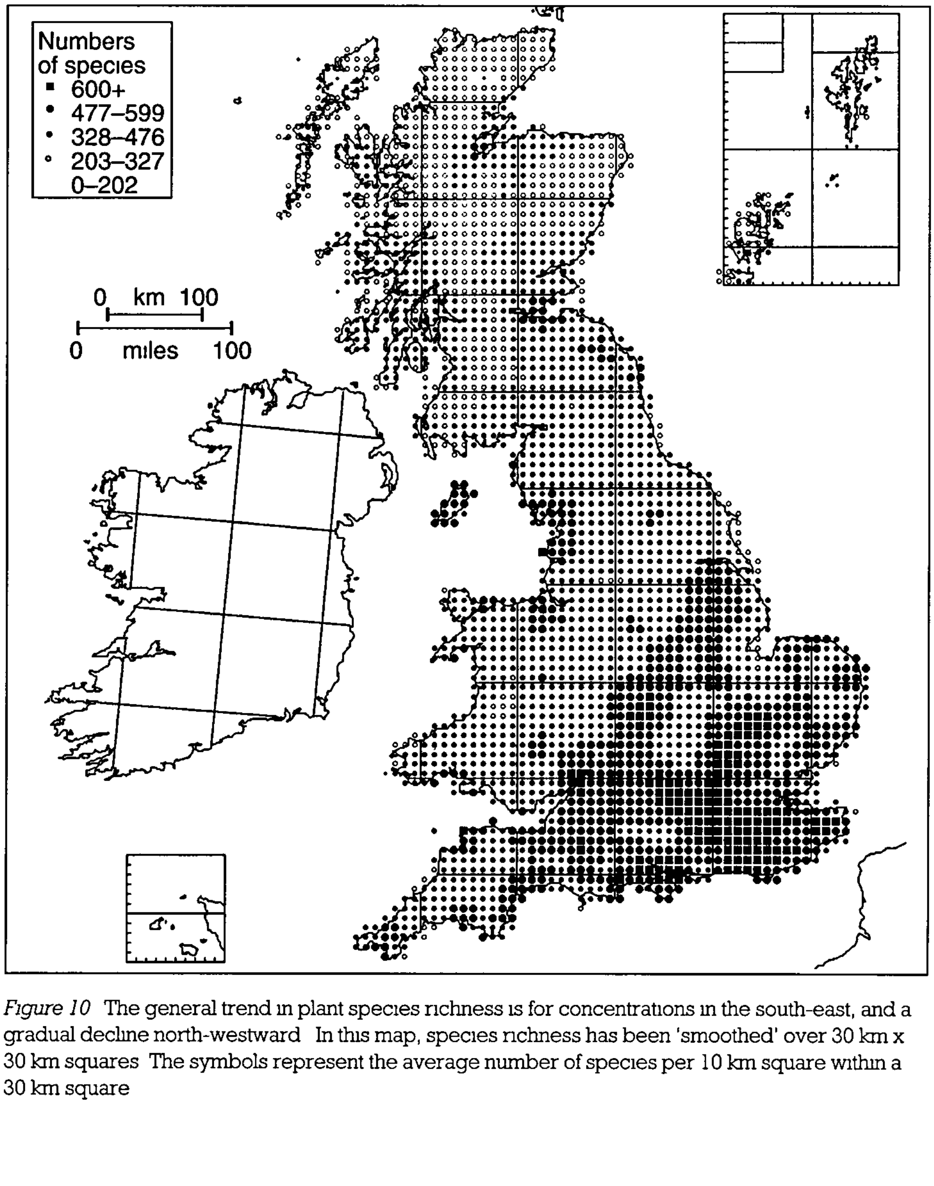

Figure 10 The general trend in plant species richness is for concentrations in the south-east, and a gradual decline north-westward. In this map, species richness has been 'smoothed' over 30 km x 30 km squares. The symbols represent the average number of species per 10 km square within a 30 km square

A further analysis, focusing on 'biodiversity hotspots' (Lawton, Prendergast & Eversham 1993), suggests that there is little coincidence between centres of species richness and concentrations of rare species, and that hotspots for one group do not often coincide with hotspots for another. Such observations have far-reaching implications for conservation strategies, survey methods and evaluation criteria.

Figure 11 shows a pair of transects across Britain. The general trend in species richness can be accounted for by climate, but local variations reflect local patterns of habitat and land use history. For instance, the peak of dragonfly diversity in the Norfolk Broads is due to the extensive wetlands resulting from medieval peat digging, which support populations of several species on the edge of their range, and one, the Norfolk hawker (*Aeshna isosceles*) (Plate 9), which is found nowhere else in Britain (Merritt, Moore & Eversham 1993). The extensive chalk downland of Salisbury Plain represents a peak for butterfly species richness, but the lack of freshwater habitats here accounts for a trough in dragonfly diversity.

Biotope classification and biotope mapping

The Biotope Occupancy Database (BOD) has been derived from an extensive literature search, and consultation with a wide range of specialists in the different groups of plants and animals being considered (Eversham *et al* 1992). All the major biotopes (habitats and land management classes) within which each species has regularly been reported in the literature are coded, using the

Table 1. Numbers of characteristic and Red Data Book (RDB) species associated with selected major biotopes, derived from the Biotope Occupancy Database

Biotope	Character-istic	RDB	% RDB
Raised bogs and blanket bogs	65	18	28
Sand dunes and shingle	185	9	7
Fens and reed beds	232	57	25
Arable	87	20	23
Calcareous grassland	337	61	18
Sandy grassland	182	32	18
Montane grassland	38	6	16
Coastal and estuarine	93	14	15
Dry heathland	233	28	12
Broadleaf woodland	441	53	12
Wet heath and upland moorland	228	22	10
Flowing freshwater	203	18	9
Urban and industrial land	88	18	9
Eutrophic freshwater	66	2	3

conservation. Figure 13 shows the distribution of calcareous grassland using this technique.

Quantification of recorder effort and removal of recorder bias

One problem which needs to be addressed when analysing BRC data is the unevenness of recorder activity in different parts of Britain. Computer programs have already been developed to provide unbiased comparisons of species richness, so that hotspot analysis can proceed (Prendergast *et al.* 1993). Further work will assess the importance of the field-craft of individual recorders, and then compute an index of recorder effort which reflects both the number of visits and the effectiveness of the individual recorders visiting the area.

Changes in species and habitat distributions

The distribution of many species is changing. Most are declining, mainly because of the loss of semi-natural habitats. Habitat loss varies between regions, and can be detected using past and present species distributions. A few species ranges are changing very rapidly. In response to the hot summers of 1989 and 1990, the Roesel's bush-cricket (*Metrioptera roeselii*) and the long-winged conehead (*Conocephalus discolor*) have expanded northwards. These two species are of particular interest, as much of their expansion is into newly created habitats resulting from agricultural set-aside. Continued monitoring will show whether the expansions are maintained.

Future work of the Biological Records Centre

The maintenance and enhancement of the BRC data bases are a shared commitment of the Natural Environment Research Council and the statutory Nature Conservation Agencies.

Research applications using the data bases will develop partly in response to commissions, and partly as a programme of strategic research underpinning Britain's biodiversity action plan. An accurate and up-to-date national biological survey provides a vital resource for land use planning in the UK, for illustrating responses to environmental change, and in all aspects

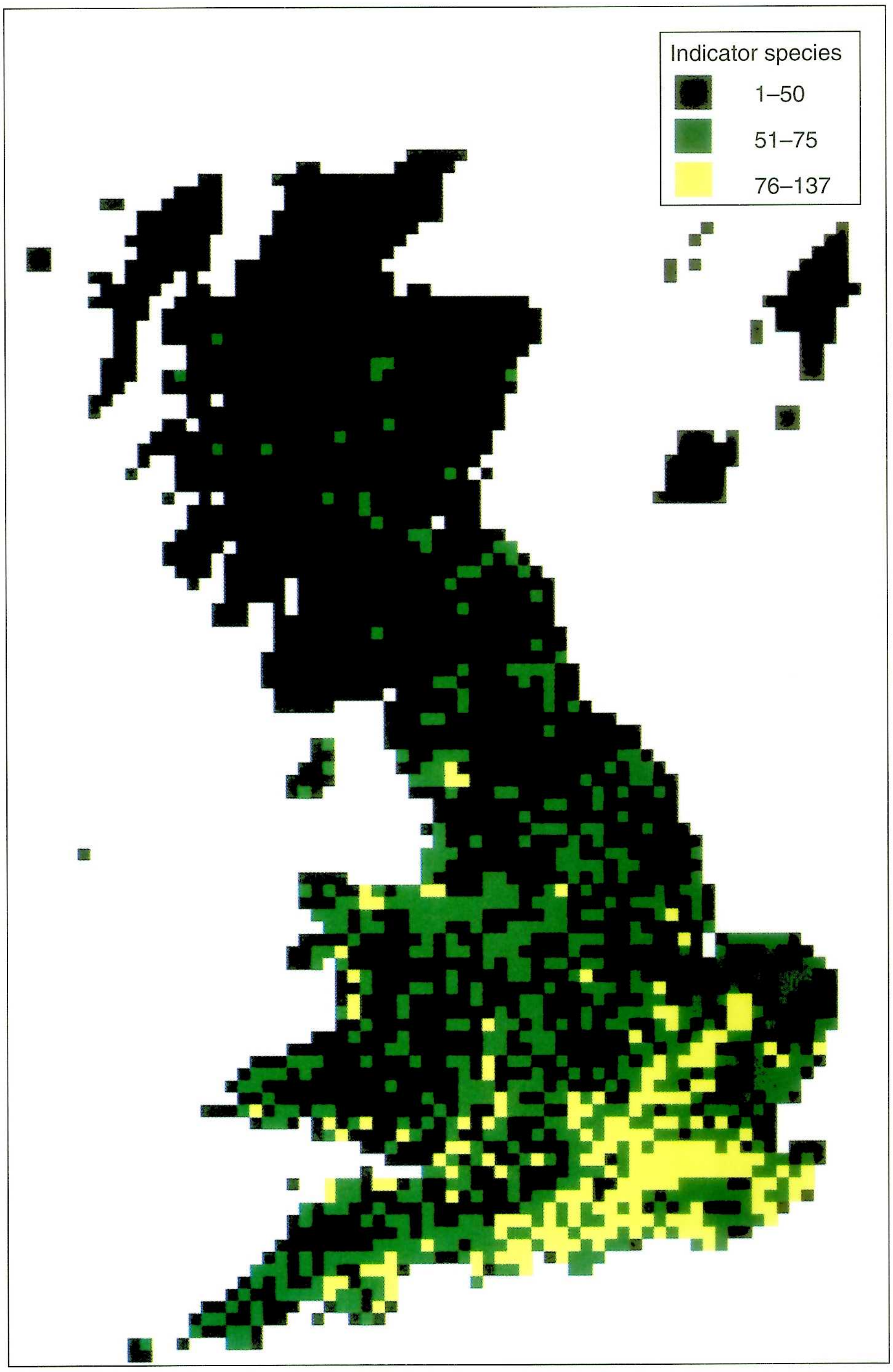

Figure 12. The distribution of calcareous grassland as shown by mapping the species richness of an assemblage of species characteristic of the biotope, taken from the BOD. The pattern revealed not only shows where a biotope occurs, but gives an indication of the most important areas for conservation

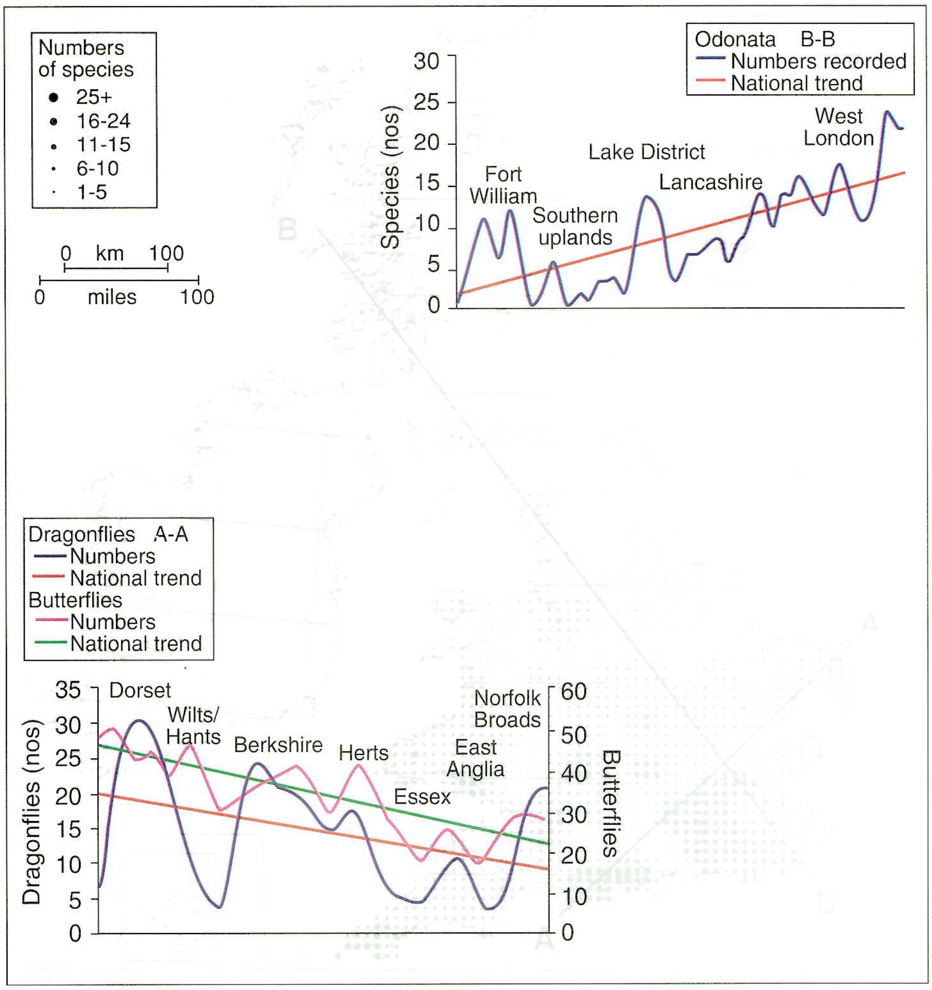

Figure 11. The map shows dragonfly species richness, smoothed over 30 km squares (as in Figure 10), on which are shown two transects, from Dorset to Norfolk (A–A) and from Kent to north-west Scotland (B–B). The graphs show species richness of dragonflies along these transects, and that for A–A also shows butterfly diversity

European standard developed by ITE – the CORINE (Co-ordinated Environmental Information in the European Community) biotopes classification (Commission of the European Communities 1991).

The CORINE system of biotope coding is hierarchical, so it is possible to specify the biotopes of a species to varying degrees of precision, eg:

31 HEATH AND SCRUB
- 31.2 Dry heath
  - 31.22 Sub-Atlantic *Calluna-Genista* heaths
    - 31.225 British *Calluna-Genista* heaths
      - 31.2251 East Anglian *Calluna-Festuca* heath
      - 31.2252 Spring squill (*Scilla verna*) heath

As a generalisation, the scarcer the species, the more precisely it has been possible to delimit its biotope occupancy. Rare and specialised species may occupy a single biotope. More widespread 'eurytopic' species may have a list of five or more biotopes.

BOD now contains biotope data for all the Red Data Book species for which BRC has adequate distribution data – the nationally scarce vascular plants, the breeding birds, mammals, reptiles and amphibians, the butterflies, moths, dragonflies, grasshoppers, molluscs and a range of other invertebrates, the liverworts, and a selection of vascular plants which are particularly characteristic of natural habitats. BOD has already been used to help guide the priorities for long-term set-aside and in the study of rare and declining species in relation to climate change.

For a selection of major biotopes, the numbers of species from BOD associated with each are summarised in Table 1. This Table gives a clear picture of the relative species richness of each biotope, and also of the importance of these biotopes for threatened species: the two do not coincide.

By mapping the species richness of an assemblage of species characteristic of a particular biotope, one can depict the national distribution of the biotope. Because species richness is a key criterion in conservation evaluation, the pattern revealed not only shows where a biotope occurs, but gives an indication of the most important areas for

Plate 9. The Norfolk hawker dragonfly is confined in Britain to a small area of Norfolk and Suffolk, which shows as a peak of dragonfly species richness in Figure 11. The dragonfly breeds in unpolluted ditches and broads

of biogeographic research. It will become even more important when links are developed to Europe-wide data bases.

B C Eversham

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Modelling species changes during ecological succession

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

Ecological succession occurs when one type of vegetation progresses to another through processes of invasion, maturation and competition. The course of succession is often predictable in that communities of annuals progress to perennials, and these may in turn progress to woodland. Where successions are initiated as a result of disturbance, eg by fire, ploughing or clearfelling, the course of events depends strongly on the initial floristic composition, ie on propagules available on the site at the time of the disturbance. Very few species are capable of both immigrating and then playing a large part in the succession.

Succession in set-aside fields

Successions in abandoned fields have attracted interest since at least 1882, when a field called Broadbalk was taken out of cultivation at Rothamsted in Hertfordshire. However, the older studies, such as those at Rothamsted and in the eastern USA, were in fields that were initially much weedier than is now usual in the developed world. In the past, there was almost always a good supply of propagules to initiate the succession. Nowadays, with selective herbicides and efficient seed cleaning, the weed flora often consists of little except a few annual and grass weeds.

The problem of predicting the course of succession in set-aside fields is therefore not easy. The pattern of future successions will not necessarily resemble that of the past, because the initial floristic composition is impoverished.

Predicting the future

The problem of prediction can be solved if the 'rules' of succession can be expressed as a mathematical model. In the forest context, successional models have simulated the fates of individual trees in small 'gaps'. Such forest simulations rarely continue beyond 300 years, representing perhaps three generations of trees. In the case of abandoned arable land, annuals will achieve as many generations in three years, by which time clonal plants such as couch (*Agropyron repens*) will form extensive patches in which individuals are not readily distinguished.

Table 2. Transitions in life stages from one season (columns) to the next (rows). The coefficients are non-zero when a transition is possible

Life stage	Seed	Seed bank	First year	Older	Dormant
Seed	a_{11}	a_{12}	a_{13}	a_{14}	–
Seed bank	a_{21}	a_{22}	–	–	–
First year	a_{31}	–	a_{33}	–	–
Older	–	–	a_{43}	a_{44}	a_{45}
Dormant	–	–	a_{53}	a_{54}	-

A mathematical model

A mathematical model called SETSARIO has been developed to predict succession from an initial floristic composition (Hill 1993). SETSARIO represents species abundance in five life stages, whose temporal dynamics are followed through a year with four seasons. Each species has various attributes, such as seed mass and stem height, which are used to predict how it will increase or die back from one season to the next. The possible transitions are shown in Table 2. These transitions depend on the species and on the season. For example, a winter perennial such as cow parsley (*Anthriscus sylvestris*), dying back in summer, will produce seeds and dormant plants, but will have zero transition coefficients to the other life stages.

Plants compete for space in the model, as this is the basic resource that they require. Layer structure is not represented, except that tall plants are damaged by mowing operations more than short ones. However, the more competitive species (the C strategists of

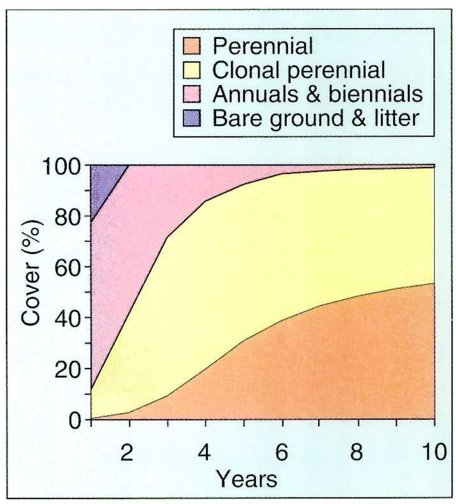

Figure 13. Composition of vegetation predicted by computer model for a set-aside field

of biogeographic research. It will become even more important when links are developed to Europe-wide data bases.

B C Eversham

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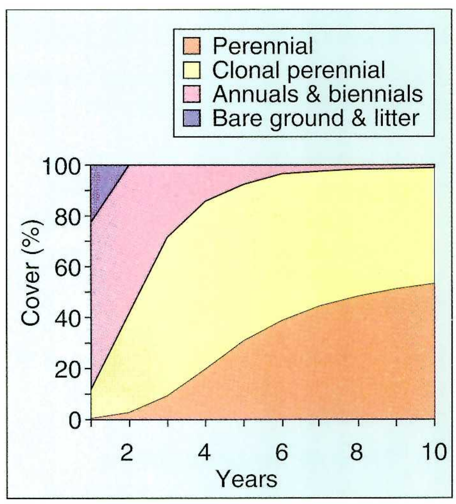

Figure 13. Composition of vegetation predicted by computer model for a set-aside field

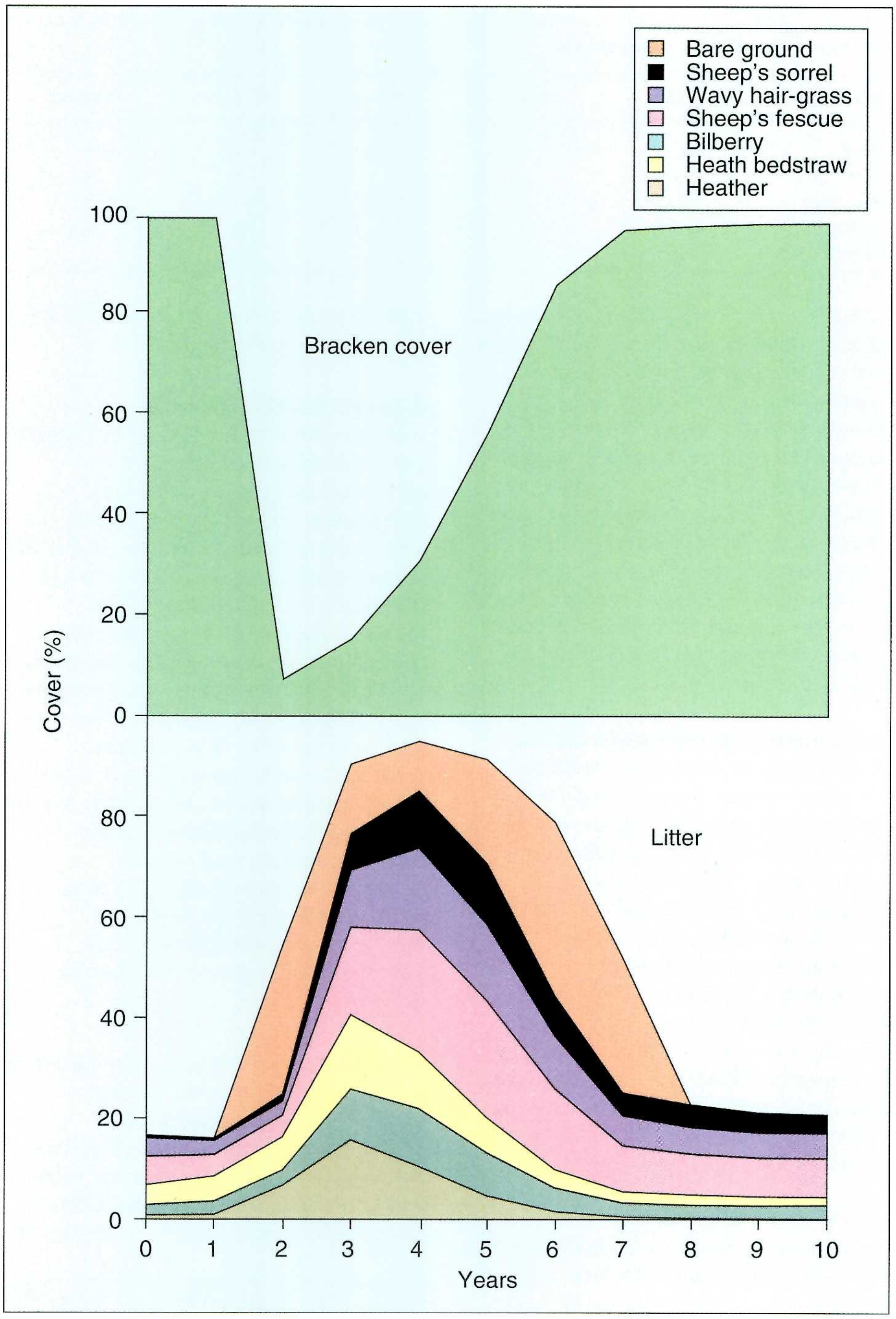

Figure 14. Composition and development of vegetation in a typical bracken stand after a single application of asulam followed by a litter burn in the autumn of year 1

Grime, Hodgson & Hunt 1988) are represented as growing faster. They will, therefore, occupy more space and will eventually out-compete the less vigorous species, unless they are damaged by grazing or mowing.

The outcome of competition for space is decided by a series of bids, taken in order as follows.

i. Green (ie non-seed and non-dormant) plants claim vegetation space that is already occupied (possession is two-thirds of the law).

ii. Plants claim space adjacent to that already occupied (vegetative expansion).

iii. Plants claim less accessible space; this is available mainly to clonal species (vegetative spread by rhizomes or stolons).

iv. Seedlings claim remaining space, but are excluded if there is a mat of dead material.

These rules, combined with seasonal dynamics, can be expected to explain the tendency for annuals to be replaced by perennials. Annuals, which have to reproduce from seed, have a low priority in the claims hierarchy when they germinate. By being annual, they temporarily lose control of their space and are liable to lose ground to perennials.

Applications

SETSARIO was originally written to predict successions in arable fields that are entering set-aside (Hill 1993; Figure 13), but the ecological principles on which it is based are quite general. It can, therefore, be applied to other types of ecosystem – such as moorlands after treatment with the herbicide asulam (Figure 14). In the Figure, the bracken (*Pteridium aquilinum*) has been reduced by the herbicide to 1% of its original frond biomass and its litter has subsequently been burnt to expose bare ground. This treatment results in a substantial growth of moorland ground vegetation, including some heather (*Calluna vulgaris*). Eventually, however, the bracken canopy reasserts itself and the other species are reduced again to low levels.

Testing the model

Like all computer models, SETSARIO makes many simplifying assumptions. In its present form, it has no explicit representation either of the soil type or of the climate. The model simply assumes that propagules present at the site are suited to local conditions. This assumption will often be correct, as propagules, except for those of a few species that are wind-borne, rarely originate from more than a few metres away.

Other simplifying assumptions are that the study area is homogeneous and that plants do not occur in spatially distinct patches. These assumptions are often

Plate 10. Patches of the perennial creeping couch grass, suppressing annual grasses after three seasons of set-aside, show up clearly when the annual grasses turn brown at maturity

violated For example, even dense stands of bracken have gaps, either because of trampling or because of shallow or wet soil Likewise, in arable fields, propagules are typically clustered, so that patchiness may soon result from apparently quite uniform beginnings

When SETSARIO was applied to the vegetation cover of whole fields, it predicted that the perennials would have ousted the annuals by about the fourth year of set-aside However, in one field where observations have been made over a period of five years, large areas were still dominated by annual grasses at the end There was, however, an almost total dichotomy between parts of the field where perennial grasses were present and those where they were absent The model was right in predicting that where such grasses were present they would eliminate the annuals (Plate 10) However, the data supplied to it ignored the fact that perennial grasses were absent from the initial floristic composition of some parts of the field, so that the annuals could dominate for more than five years

M O Hill and R J Pakeman

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The potential uses of set-aside land to benefit wildlife

(This work was funded by the Ministry of Agriculture, Fisheries and Food)

The European Community introduced a five-year voluntary set-aside programme in 1988 as part of a package of measures, with the main aim of reducing overproduction under the Common Agricultural Policy (CAP) However, the response was quite low, and the impact on production was not great In 1992, set-aside was introduced on a much wider scale as part of the reform of the arable sector under the CAP Under the new arable scheme, support for producers is switched from prices to direct payments on the area cropped, and all but the smallest producers are required to set-aside some land as a condition of receiving support The primary objective of set-aside is therefore economic, to reduce production while supporting farmers during a period of adjustment to world prices

The rules of the new programme allow farmers to set-aside 15% of their arable land on a six-year rotational basis, so that most of their land is set-aside at some point in time From the autumn of 1993, they should be able to opt to set-aside land on a non-rotational basis, and they will also be able to take advantage of the new agri-environment package of measures, including the possibility of taking areas of farmland out of production for longer-term habitat restoration Experience from the 1988 set-aside scheme (Clarke 1992) and other programmes shows that all of these kinds of set-aside can benefit wildlife – *as long as the set-aside land is managed appropriately*

Targetting benefits to wildlife

ITE was contracted to review available data to help define priorities for using set-aside land for wildlife, and to use these priorities to draw up a series of management options The starting point was that set-aside is, on the whole, not well suited to the conservation of rare species, which often have precise habitat requirements difficult to include in a national scheme However, set-aside represents a valuable opportunity to raise the levels of those species which, although not threatened with extinction, have nevertheless declined in numbers as farming has intensified

Our analysis of declines in numbers of mammals, some invertebrate groups and scarce plants (Firbank *et al* 1992) showed that these species were found in a range of habitat types, a conclusion supported by the British Trust for Ornithology's analysis of changes in bird distribution and abundance (Marchant *et al* 1990) We concluded that a diversity of set-aside management options would be best suited to help wildlife, each option having clearly defined objectives in terms of the kinds of species and communities that should result under a given regime

A range of set-aside programmes

We identified a range of options to encompass a wide variety of habitat requirements that can be met on farmland, and we produced management protocols on the basis of literature review, experimental data, and ITE's experience of farmland ecology and habitat restoration

Rotational set-aside for birds and rare weeds

The first year of natural regeneration on set-aside land is often dominated by crop volunteers, but with enhanced weed populations because of the lack of herbicide and fertilizer applications The field, therefore, is very similar to an unkempt crop Farmers are understandably concerned at this prospect, and worried about increases in noxious weeds, pests and diseases On the whole, these fears have not been justified by experience, while the benefits to wildlife can be great (Clarke 1992) The wildlife of cereal fields has been undervalued by ecologists (Firbank *et al* 1991) Many of our rarest plants were once regarded as arable weeds, and common broadleaved weeds provide food for overwintering finches (Fringillidae) and other birds The insect fauna is of value for its own sake, as food for birds and mammals, and as beneficial agents for crop protection Increases in the levels of rotational set-aside may prove highly beneficial to wildlife, as long as the benefits are not cancelled by unsympathetic timing of cutting We recommended particular management schemes for birds and rare weeds

Non-rotational set-aside – natural regeneration and sown cover

If natural regeneration is allowed to continue, a successional sequence of plant communities develops to perennial swards and eventually to scrub, depending on the species able to colonise and the choice of management (see Hill & Pakeman, pp25-27) This sequence provides a range of habitats for animals as well as plants, and, by using different cutting regimes, the habitats can be varied within the field at any one time This variation is important for species which benefit from a combination of habitats, such as owls (Strigidae), which hunt in short grass, but whose prey need areas of long grass to provide cover for breeding Some fields would become dominated by perennial weeds, such as couch-grass (*Elymus repens*), a problem for the farmer and of little value to wildlife In such cases, the field would be better sown with a mixture of grasses and wild flowers violated For example, even dense stands of bracken have gaps, either because of trampling or because of shallow or wet soil Likewise, in arable fields, propagules are typically clustered, so that patchiness may soon result from apparently quite uniform beginnings

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Plate 11. Field margins with grass swards rich in wild flowers can be achieved by sowing seeds directly into the old cropped area, as shown by this ITE experimental plot which was sown in 1985 and photographed in 1992

Non-rotational field boundary

Parts of fields can be set-aside, as well as whole fields. We therefore proposed a field boundary option, which envisages three types of management: the boundary itself – the hedge or ditch, then a tall grass and herb strip, and then a strip of natural regeneration or sown cover nearest to the crop (Plate 11). Damaging actions on the field are thus kept well away from the field boundary, which is managed in a way designed to encourage wildlife. This option also allows for the widening of ditches into small areas of fen-like vegetation, and for the development of scrub from hedgerow. It can also be used to enhance public access to the countryside.

Longer-term habitat creation schemes

The schemes described above can be applied widely and easily, and allow an easy return to arable farming. However, under the agri-environment programme, longer-term schemes are possible – up to 20 years, and so it becomes worth considering more specialist habitat restoration programmes. We proposed using set-aside for the recreation of calcareous grassland, damp lowland grassland, saltmarsh, lowland heath and sandy grassland, and upland grassland, woodland and heath. These options are not always suitable, and would not recreate the full variety of species present on well-established habitats of the same type, but they can provide valuable buffer habitats and allow more mobile species to extend their range. The key element is to restore the vegetation. The species may exist in the seed bank if the land has only recently been used for cropping, or may exist in or just beyond the field boundary, in which case some will spread into the field (Plate 12). Otherwise, the plants must be sown into the field.

Species-specific conservation programmes

While set-aside land is by-and-large not suitable to being managed for particular species, there are important exceptions. In England, we identified three. Grazing pastures for brent geese (*Branta bernicla*) have been successfully created under the 1988 scheme, and have diverted the geese from feeding on crops. We recommended that this option be continued, and revised in the light of experience to date. Stone curlew (*Burhinus oedicnemus*) areas are also suitable for set-aside land. These rare birds are site-faithful, and require open landscapes with areas of open, stoney ground for nesting and areas of grass for feeding. Non-rotational set-aside can be used to maintain these habitats by regular cutting in some areas of the field and annual cultivation in the field centre. Finally, the field margin option can be readily modified along some rivers and streams to provide habitat for otters (*Lutra lutra*).

Will set-aside help wildlife?

There is now more area set-aside in the UK than in all of our nature reserves (Andrews 1992). The possibilities of using set-aside land to benefit wildlife are, therefore, great. However, there are ecological limits; restored habitats are rarely as rich as ancient ones, and mobile groups such as birds are more likely to benefit than more site-faithful species, such as the plants of chalk grassland.

There are many other potential limits to the scheme. First of all, at the time of writing, the management rules for the 1993 scheme have not been announced. While most of our proposals have been incorporated into the consultation

Plate 12. Natural regeneration can result in the expansion of important habitats. In this case, lowland heath vegetation is invading the former arable land in the foreground

documents recently released (Ministry of Agriculture, Fisheries and Food 1993a, b), and so may well be approved, issues of funding under different options and the European Commission (EC) non-rotational rules have not yet been decided The EC has not yet agreed on whether farmers should be allowed to mix non-rotational and rotational set-aside on the same farm – this mix is important to encourage longer-term set-aside on field boundaries and near existing high-quality habitats Neither has it agreed whether longer-term habitat creation options on arable land under the 20-year scheme can be counted towards the set-aside requirement, where all the set-aside eligibility criteria are met

Another set of limitations concerns the availability of advice and training Experience from the Countryside Premium Scheme suggests that many farmers lack confidence when dealing with farming for wildlife, and need substantial support This support will be provided by advisors from groups such as the Royal Society for the Protection of Birds, the Game Conservancy, and the Farming and Wildlife Advisory Groups, but the advisors themselves need support In ITE we are preparing a book to help meet this need However, we are the first to recognise that the information we have is often extrapolated from a few studies, and that there are areas of doubt, a continual programme of monitoring and review is needed

Set-aside remains a controversial measure, being widely regarded as payment for farmers to do nothing If set-aside is used widely and successfully to benefit wildlife, then it may be seen as an important step in sustaining our rural environment, while supporting the only group in a position to manage our countryside – the farmers

L G Firbank

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Wetland restoration

(This study was partly funded by the Ministry of Agriculture, Fisheries and Food (MAFF), and involved collaboration with the Agricultural Development and Advisory Service (ADAS) and the Department of Land Economy, University of Cambridge)

Background

Land drainage and the associated intensification of farming practice have caused widespread losses of wetland habitats from the British countryside Many characteristic wetland communities and species have become rare and threatened The Environmentally Sensitive Area (ESA) and Countryside Stewardship schemes have provided new opportunities for the restoration of wetland habitats in farmed landscapes, by subsidising farmers to return to more traditional methods Such schemes could have particular benefits in the English lowlands, where the extent of wetland habitats has become increasingly restricted, and where many individual species have steeply declined in abundance or been lost altogether

On behalf of MAFF, ITE has been carrying out research on wetland restoration techniques in order to determine whether reinstatement of less intensive farming methods will be sufficient to ensure the return of wetland species to the farmed countryside A desk study by ITE, the former ADAS Field Drainage Experimental Unit (now the Soil and Water Research Centre) and the Department of Land Economy at the University of Cambridge demonstrated the potential for successful combination of agricultural and ecological objectives in preserving, enhancing and restoring the wildlife value of wetlands, but also highlighted a number of areas where further field and experimental studies would be crucial in developing suitable techniques (Treweek & Sheail 1991)

In particular, a review of practical experience of wetland restoration in this country and abroad suggested that chances of success were likely to be improved by defining clear ecological objectives and identifying appropriate management strategies for their achievement Subsequent studies have, therefore, been carried out to identify suitable ecological objectives for wetland restoration schemes in England and Wales, to define areas where restoration would be feasible in terms of physical site factors, current drainage infrastructure and existing plant and animal communities, and to assess the financial implications of implementing wetland restoration schemes

Definition of objectives on the basis of vegetational characteristics

The range of wetland habitats and species represented in agricultural landscapes in England and Wales was identified, together with the abiotic and biotic variables determining their occurrence The following wetland habitat types were distinguished

- Wet woodland
- Acid bog, poor fen and wet heath
- Tall-herb fen, small-sedge fen and fen meadow (Plate 13)
- Old, moist mesotrophic grassland
- Open water and margins, including
  - Open water and margins (general)
  - Ditches and pools of grazing marsh and fen
  - Shallow water of springs and rills
- Bare wet mud and peat
- Saline habitats

Possible sources of information for establishing the current status of wetland habitats and species were then explored with a view to identifying those requiring priority action The National Vegetation Classification (Rodwell 1991) communities and associated vulnerable wetland plant species known to occur in these habitats were identified within nine existing and proposed ESAs in lowland documents recently released (Ministry of Agriculture, Fisheries and Food 1993a, b), and so may well be approved, issues of funding under different options and the European Commission (EC) non-rotational rules have not yet been decided The EC has not yet agreed on whether farmers should be allowed to mix non-rotational and rotational set-aside on the same farm – this mix is important to encourage longer-term set-aside on field boundaries and near existing high-quality habitats Neither has it agreed whether longer-term habitat creation options on arable land under the 20-year scheme can be counted towards the set-aside requirement, where all the set-aside eligibility criteria are met

Another set of limitations concerns the availability of advice and training Experience from the Countryside Premium Scheme suggests that many farmers lack confidence when dealing with farming for wildlife, and need substantial support This support will be provided by advisors from groups such as the Royal Society for the Protection of Birds, the Game Conservancy, and the Farming and Wildlife Advisory Groups, but the advisors themselves need support In ITE we are preparing a book to help meet this need However, we are the first to recognise that the information we have is often extrapolated from a few studies, and that there are areas of doubt, a continual programme of monitoring and review is needed

Set-aside remains a controversial measure, being widely regarded as payment for farmers to do nothing If set-aside is used widely and successfully to benefit wildlife, then it may be seen as an important step in sustaining our rural environment, while supporting the only group in a position to manage our countryside – the farmers

L G Firbank

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Wetland restoration

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Background

Land drainage and the associated intensification of farming practice have caused widespread losses of wetland habitats from the British countryside Many characteristic wetland communities and species have become rare and threatened The Environmentally Sensitive Area (ESA) and Countryside Stewardship schemes have provided new opportunities for the restoration of wetland habitats in farmed landscapes, by subsidising farmers to return to more traditional methods Such schemes could have particular benefits in the English lowlands, where the extent of wetland habitats has become increasingly restricted, and where many individual species have steeply declined in abundance or been lost altogether

On behalf of MAFF, ITE has been carrying out research on wetland restoration techniques in order to determine whether reinstatement of less intensive farming methods will be sufficient to ensure the return of wetland species to the farmed countryside A desk study by ITE, the former ADAS Field Drainage Experimental Unit (now the Soil and Water Research Centre) and the Department of Land Economy at the University of Cambridge demonstrated the potential for successful combination of agricultural and ecological objectives in preserving, enhancing and restoring the wildlife value of wetlands, but also highlighted a number of areas where further field and experimental studies would be crucial in developing suitable techniques (Treweek & Sheail 1991)

In particular, a review of practical experience of wetland restoration in this country and abroad suggested that chances of success were likely to be improved by defining clear ecological objectives and identifying appropriate management strategies for their achievement Subsequent studies have, therefore, been carried out to identify suitable ecological objectives for wetland restoration schemes in England and Wales, to define areas where restoration would be feasible in terms of physical site factors, current drainage infrastructure and existing plant and animal communities, and to assess the financial implications of implementing wetland restoration schemes

Definition of objectives on the basis of vegetational characteristics

The range of wetland habitats and species represented in agricultural landscapes in England and Wales was identified, together with the abiotic and biotic variables determining their occurrence The following wetland habitat types were distinguished

- Wet woodland
- Acid bog, poor fen and wet heath
- Tall-herb fen, small-sedge fen and fen meadow (Plate 13)
- Old, moist mesotrophic grassland
- Open water and margins, including
  - Open water and margins (general)
  - Ditches and pools of grazing marsh and fen
  - Shallow water of springs and rills
- Bare wet mud and peat
- Saline habitats

Possible sources of information for establishing the current status of wetland habitats and species were then explored with a view to identifying those requiring priority action The National Vegetation Classification (Rodwell 1991) communities and associated vulnerable wetland plant species known to occur in these habitats were identified within nine existing and proposed ESAs in lowland

Table 3 Total number of species shown to have declined in population size and distribution in at least one of three grazing marshes studied in England and Wales, classified in terms of typical habitat and suspected cause of decline. Information derived from a wide range of archive and published sources (Mountford 1993)

Preferred habitat or vegetation type	Suspected cause of decline	Total no of species
Wet woodland	Felling and drainage	21
Acid bog and heath	Peat cutting and drainage	76
Rich fen and tall wet meadow	Drainage and conversion to pasture or arable	60
Old wet grassland	Drainage and conversion to intensive grassland or arable	55
Grazing marsh ditches and pools	1 Regrading, conversion to trapezoidal section 2 Overgrowing, increased shade and siltation 3 Elimination due to field rationalisation	73
Open water	Aquatic herbicides	28
	Pollution and increased turbidity	39
Bare wet mud and peat	Fencing of ditches control of water levels	13
Saline habitats	Tidal control and sea defence improvement	17
Varied	Urbanisation and industrial development	17
	Weed control and collection by botanists	8
	No clear cause	7

characteristic of old, moist mesotrophic grasslands and their drainage networks (Mountford 1993). Table 3 summarises the results from a study of three English grazing marshes, describing the main causes of decline suspected for different wetland habitat types, and the number of associated species known to have decreased in population size and abundance in at least one of the grazing marshes studied. Results from recently completed studies on a further grazing marsh at Swavesey, Cambridgeshire, support the interpretation of Table 3 that drainage can grossly alter the composition of communities. Four years after the installation of pump drainage in part of the catchment at Swavesey, plant species characteristic of wetlands had become significantly less common than in adjacent undrained areas. Clear changes were observed in the flora of grassland, ditches and ponds following the lowering of the water table (Mountford & Chapman 1993).

Many studies have demonstrated the adverse effects of land drainage on wetland plant species. One of the most obvious approaches to wetland restoration is, therefore, to restore water levels on selected areas. However, for many important wetland plant species, it is not possible at present to specify the precise water level they need. Current research on behalf of MAFF by ITE and Silsoe College seeks to define the water regime requirements of a wide range of individual plant species found in moist, mesotrophic grassland and tall-herb fens. Species occurrence and water table have been compared at sites in Cambridgeshire, Somerset, Wiltshire and Yorkshire (Mountford & Chapman 1993). The results at Tadham Moor in Somerset, an area of old hay meadows on peat, were typical in that the distribution of plant species was found to be controlled partly by water table and microtopography (Table 4).

The technical feasibility of restoring wetlands is determined by topography, soil, hydrological management and climate. The past distribution of wetlands was determined both by the shape of the land and the movement of water. Landscape topography and underlying geology strongly influence the type and occurrence of wetlands. Large areas of fen or wet grassland can potentially be restored on a river floodplain, whilst small hollows may be most appropriate for the creation of new pools. Soil type affects not only the incidence of waterlogging, but also the nutrient level and the acidity/alkalinity of any water body. Drainage works have altered the natural pattern of wetlands, but can provide the mechanisms for reversing the process of water removal. Successful wetland restoration requires adequate water, but the timing and form of the water supply will depend upon which communities and species are targetted for restoration.

Restoration of wetlands on agricultural land has economic implications for the farmer. Restoration might only be funded in the context of ESA or similar schemes, yet suitable sites and enthusiastic farmers may occur elsewhere. The creation of wet conditions on one part of a farm might adversely affect other intensively farmed parts. The relationship between the Common Agricultural Policy and planned habitat creation could be a source of concern for farmers, particularly in terms of any changes to quotas. Despite such caution, successful restoration campaigns in the lowlands will, to a large extent, be dependent on the continued viability of farm systems. The most appropriate wetland habitat types for restoration are probably those traditionally associated with farmed land, which may be restored under viable agricultural regimes or which depend upon agricultural land use for their maintenance and survival.

Certain threatened species require detailed study to establish their habitat requirements. English Nature has commissioned the Institute to investigate

Table 4 Tadham Moor, Somerset: plant species showing a strong association with particular ranges of water table

Species most abundant under two depths of mean summer water table: 20–45 cm	45–65 cm
Marsh foxtail (*Alopecurus geniculatus*)	Lop-grass (*Bromus hordeaceus*)
Kingcup (*Caltha palustris*)	Hammer sedge (*Carex hirta*)
Common spike-rush (*Eleocharis palustris*)	Common mouse-ear chickweed (*Cerastium fontanum*)
Lesser marsh bedstraw (*Galium palustre*)	Meadow fescue (*Festuca pratensis*)
Reed-grass (*Glyceria maxima*)	Smooth-stalked meadow-grass (*Poa pratensis*)
Water dropwort (*Oenanthe fistulosa*)	Dandelion (*Taraxacum* agg.)

Plate 13. Tall-herb fen in Broadland, a rich mixture of grasses, sedges, herbs and mosses. Opportunities for restoring fen and wet grassland exist in several English ESAs, where most areas of fen have been drained and converted to arable agriculture

Plate 14. Bog pimpernel (*Anagallis tenella*), an attractive flower of wet peaty turf, which has declined in southern and eastern Britain, wherever bogs and fens have been drained or where old wet grassland is ploughed or reseeded

England. Species were included if they were known to be largely restricted to wetland habitats and vulnerable to changes in habitat conditions, such as a lowering of the water table. Particular attention was paid to those species and communities where analysis of data held by the Biological Records Centre (BRC) suggested a decline in range or abundance (Plate 14), or where field and/or literature surveys carried out by ITE implied more localised declines (Figure 15). Nationally scarce and rare species were also catalogued. For most areas likely to remain under continued agricultural use, 'old, moist mesotrophic grassland' and associated 'ditches and pools' will be the priority habitat types for restoration.

Where possible, the primary threat to each main wetland habitat type was identified. Review of published accounts, and of land use and drainage data has demonstrated the overriding importance of land drainage in causing the decline of many of the plant species

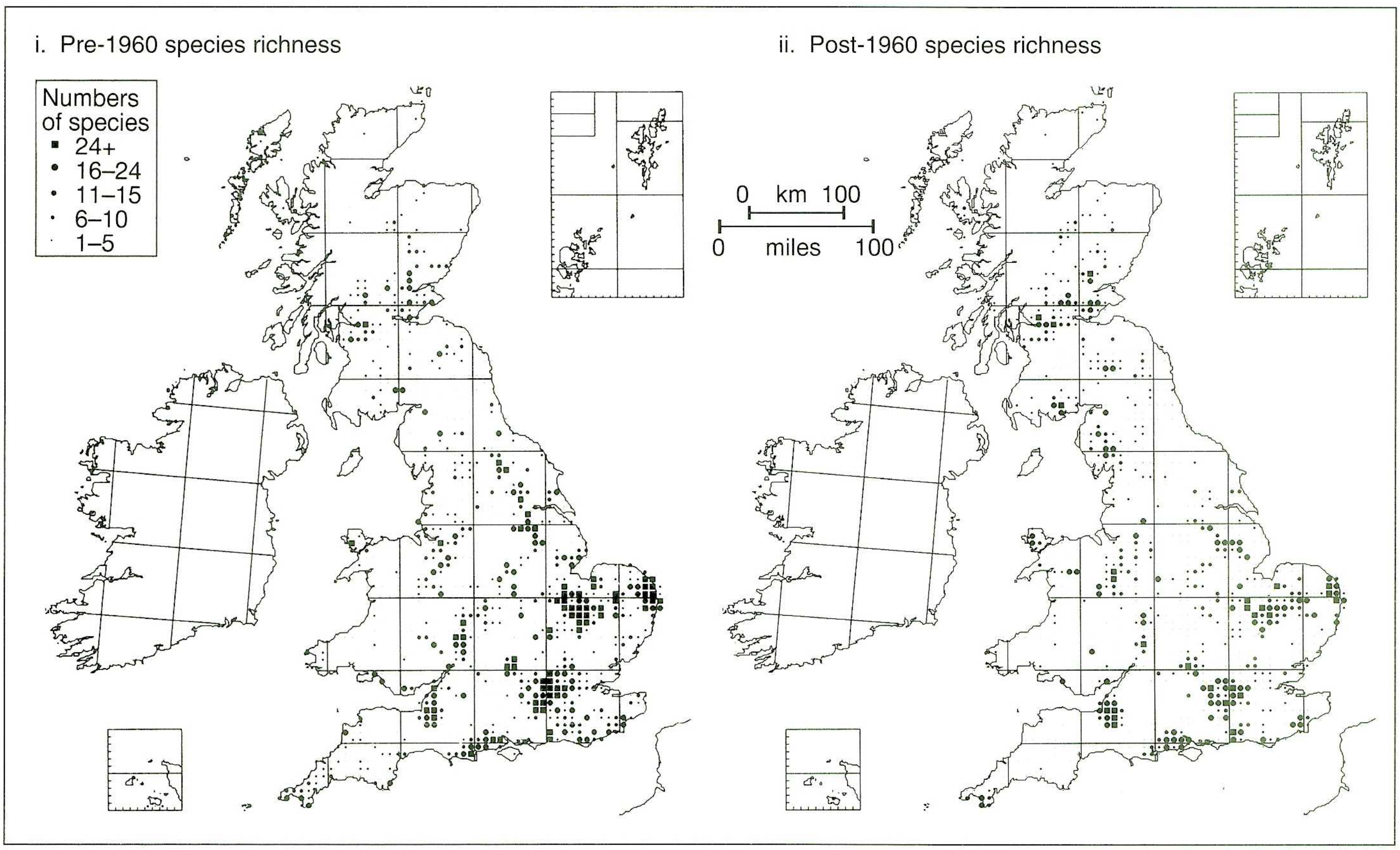

Figure 15. The extent of wetland vegetation has contracted, and, even where it survives, species have been lost as communities are modified by drainage and intensive land management. When the species richness of scarce plants occurring in water-fringe vegetation is mapped for two periods – (i) pre-1960 and (ii) post-1960, it is clear that high-quality wetland vegetation has become increasingly confined to a few prime areas, eg Broadland, Fenland and the Somerset Levels and Moors. (Maps prepared by BRC using the Biotope Occupancy Database)

methods for restoring populations of fen violet (*Viola persicifolia*) under its Species Recovery Programme. Species-based research must be complemented by an investigation of the effect of changing water levels on the composition of the whole plant community. Field experiments have been initiated to establish baseline data on ecological, hydrological and socio-economic factors for further, more detailed studies on wetland restoration techniques. Case study sites have been chosen in the proposed Upper Thames Tributaries ESA and at Tadham Moor in the Somerset Levels and Moors ESA, where the water level will be raised and the changes in sward composition monitored over subsequent years.

J O Mountford and J R Treweek

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