Contents

Changes in agriculture and forestry policies have indicated massive changes in land use in the UK. The impact of this form of human pressure on biodiversity, and the need to conserve species richness at many agricultural and spatial species scales, have been a major force for our research.

Biodiversity and land use

Since its inception ITE has been at the heart of research into the ecology of populations and community of species, and how the processes that result in biological diversity are influenced by land management and land use change in the UK. This work has benefited greatly from the interaction of theoretical, empirical and applied approaches, and has resulted not only in a series of landmark studies, but also in the generation of large-scale, long-term data which are only now being fully explored.

Animal and plant abundance

The mechanisms limiting animal and plant populations have been a major component of our research. Particular emphasis has been placed on the role of social organisation, predator-prey interactions and population responses to changing environments associated with man's activities. Many of our model systems have been centred around understanding the dynamics of bird populations, but also including seminal studies on invertebrates including the Butterfly Monitoring Scheme data. This latter study provided the first empirical confirmation that populations of insects fluctuate more dramatically and more erratically towards the northern edges of the species' ranges. On plants a pioneering study of marsh grass (*Gentiana pnemonanthe*) remains the most detailed autecological study of the functional and population ecology of any heathland species. Increasingly ITE research has included important insights into the genetic structure of natural plant populations, especially those in coastal environments. These studies have focussed on gene flow. They have helped to provide a more rigorous science-based assessment of the risks of releasing genetically modified crops.

Interactions between populations and the land

Agri-environment schemes such as Countryside Stewardship and Scottish Environmentally Sensitive Areas (the subject of monitoring by ITE in association with the Macaulay Land Use Research Institute), require the definition of appropriate techniques for delivering biodiversity benefits. Such definition is aided by long-term studies on the management of:

- lowland, species-rich grassland
- relationships between grazing pressures and upland vegetation dynamics
- establishment and dynamics of upland forests.

Techniques for habitat restoration have been developed to the point where Twyford Down now has a greater abundance and diversity of wildlife than before the M3 motorway was constructed.

One of ITE's largest research programmes, Countryside Survey, is becoming a benchmark for the large-scale assessment of land use and biodiversity The repeated survey of sample areas of land has shown clearly the changes in both species and landscapes associated with developments in agriculture and forestry These changes have influenced government policy on hedgerows and are feeding in to the Biodiversity Action Plan process The statistical techniques developed to underpin this work (TWINSPAN, DECORANA) are now standard worldwide

Managing the landscape to help conserve biodiversity

ITE's work is increasingly concerned with developing tools to assess and improve policies and practices that will shape the land and its biodiversity well into the future Large-scale relationships between species distribution and land use have been developed by combining species data held at the Biological Records Centre and elsewhere with ITE's remotely-sensed Land Cover Map of Great Britain At a smaller scale, medium-term population studies of birds in woodland fragments have been used to develop a GIS-based system to evaluate the design of lowland farmed landscapes Detailed behavioural studies of oystercatchers (*Haematopus ostralegus*) and other shorebirds have been used to develop models that can predict large-scale population effects of habitat loss, which has itself been predicted by another suite of models analysing the results of proposed estuarine developments The Dorset Heath study is a classic example of how long-term integrated study of species, changes in land use and climate provide both theoretical insights and practical guidelines for conservation within a living, dynamic landscape

Looking to the future

Recently the work on both land use and animal abundance and population processes has been re-organised across the component institutes that make up the Centre for Ecology and Hydrology (CEH) These two topics each form one of the 10 CEH Strategic Science Programmes

CEH Strategic Science Programme 2 – ***Land Use Science*** promotes an integrated approach to understanding the processes driving land use change, and enable the wide user community to ameliorate the impacts on the landscape and society through four major themes

- *Long term and large scale monitoring of land use* including the techniques for collection, integration, provision and interpretation of land use data and putting them into practice
- *Land use systems* aims to develop a fuller understanding of the processes operating in forest and agricultural land, so that they can be better managed to meet local, national and global needs for both sustainable production ecosystem conservation and management of water resources
- *Management of ecosystems in tropical regions* involves the application of land use research to the particular needs of sustainable management of forest and agricultural land in the tropics
- *Landscape function and modelling* involves mathematical analysis of environmental and socio-economic systems to provide a basis for the integration of environmental and other criteria in land use planning and management

CEH Strategic Science Programme 5 – ***Biodiversity and Population Processes*** addresses important issues of biodiversity, the earth's capital In particular, it considers the underlying processes and resulting functions, and directs knowledge to the sustainable management of biodiversity through four major themes

- *Biodiversity characterisation, pattern and monitoring* aims to develop techniques for defining and measuring biodiversity, especially at the genetic level, monitoring changes and identifying patterns against environmental gradients, over both time and space
- *Ecosystem function and biodiversity* aims to determine the reciprocal interactions between biodiversity and the functioning of ecosystems by investigating processes involved in the maintenance of diversity, (including microbial diversity)
- *Population processes underlying biodiversity* aims to identify the population processes, including population genetics, at the level of single species and groups of interacting species that influence abundance and underpin the maintenance of biodiversity
- *Conservation and restoration of biodiversity* is based on the application of the principles established through the above research, in order to manage ecological systems for conservation, restoration and sustainable use of biodiversity

ITE's work is addressing gaps in our knowledge of critical processes in ecological ecosystems.

We are increasingly concerned with developing tools to assess and inform policies and practices that will shape the land and its biodiversity well into the future.

S D Albon and L G Firbank

Plate 1. The Countryside Surveys have recorded both length and botanical composition of hedgerows using standard procedures. The results show a progressive decline in length, which is matched by a loss of plant species in pastural landscapes between 1978 and 1990

Land use research has grown in importance in parallel with intensification of agriculture and pressure on habitats.

Land use and vegetation change

Land use research has grown in importance in parallel with intensification of agriculture and pressure on habitats. There has also been a progressive increase in policy interest in land use change reflecting public concern. This paper describes how ITE have developed the application of objective methods of sampling, combined with quantitative analysis, in order to provide the basis for independent estimates of stock and change. Table 1 shows examples of these surveys and how they have been applied in the policy arena.

In 1968 the Research Branch of the former Nature Conservancy (NC) was organised on the basis of habitats. The woodland sections at Merlewood and Monks Wood were responsible for fundamental research and advice to the Conservation Branch on site selection for conservation designation. Following a habitat team meeting at Merlewood, after the appointment of John Jeffers as Director in 1968, it was decided that a National Woodland Classification was required primarily to provide an objective system for the selection of representative sites.

At that time, data were being collected from woodland sites as part of the *Nature Conservation Review,* using cards with a list of 136 plant and tree species from throughout GB. It was decided to use the 2 500 woodlands available from this survey, cartographically defined, as the base data to select sites. Association Analysis (Williams & Lambert 1959) was used in 1970 to produce 103 groups using a standard stopping rule, following a pilot project in 1969 in the Lake District. A representative site was selected from each group using an objective procedure. Therefore, during 1971, a total of 103 woods were surveyed throughout GB, as well as 34 Native Pinewoods in Scotland, using a standard procedure of vegetation survey (Bunce & Shaw 1973). Although this survey was solely concerned with woodlands, the structure of the project provided the basis for future land use research at ITE. In addition, it provided the stimulus for developing a new set of vegetation classification algorithms because, although Association Analysis

Table 1. Examples of policy applications of national and regional surveys between 1968 and 1998

1970–1972	Nature Conservancy (National Woodlands Survey)	Advice on woodland site selection
1970–1978	Nature Conservancy Council (Native Pinewoods Survey)	Advice on conservation of Native Pinewoods
1975–1978	Cumbria County Council (Cumbria Survey)	Contribution to Structure Plan
1978–1985	Energy Technology Support Unit (Ecological Survey of Great Britain)	Potential contribution of wood for biofuels
1984–1997	Department of the Environment (ITE National Land Use Survey /Countryside Survey 1990)	Estimates of hedgerow loss (incl. Rural White Paper and Hedgerow Protection Bill)
1985–1989	Bristol University – Zoology Department (Survey of badgers using the Land Classification)	Estimate of badger numbers (Badger Protection Bill)
1986–present	Ministry of Agriculture, Fisheries and Food/Department of the Environment (now DETR) (Land Use Allocation Model)	Implications of agricultural policy scenarios
1987–present	Ministry of Agriculture, Fisheries and Food (ITE survey of Chernobyl fallout)	Restrictions on human consumption of sheep meat
1987–1991	Highland Regional Council (HRC) (HRC Rural Land Use Information System)	Areas of land use and land cover in the Region
1987–present	Department of the Environment (now DETR) (Countryside Information System)	Accessible information on the British countryside
1990–present	Department of the Environment, Transport and the Regions (DETR)/Scottish Office, Agriculture, Environment and Fisheries Dept (SOAEFD) (Countryside Survey 1990 and Countryside Survey 2000)	Contribution to British obligations under the Rio Convention, Agenda 21 and the UK Convention on biological diversity
1998	European Environment Agency (Models for Integrated Review and Assessment of Biodiversity in European landscapes)	State of the Environment Report

had proved to be a useful technique, it had a high mis-classification rate Mark Hill (ITE) was, therefore, consulted about the improvement of this method as he had become interested in an ordination technique now known as correspondence analysis (previously called reciprocal averaging)

For a multivariate method to be applicable to the analysis of extensive survey data, the crucial requirement is that the computation should not increase excessively in magnitude when the size of the dataset is enlarged Most methods available in the early 1970s had computational requirements rising as the square of the number of plots or even faster Moreover, they were wasteful of computer memory ITE developed an algorithm for correspondence analysis that rises only linearly in proportion to the size of dataset This was the key technical breakthrough, leading to efficient computer programs for ordination (Hill 1973) and classification (Hill *et al* 1975) The programs were subsequently developed into DECORANA (Hill 1979a) and TWINSPAN (Hill 1979b) These programs have now been used widely for vegetation analysis throughout the world

The results from the National Woodlands Survey were published by ITE in various documents (eg Bunce 1982) and provided the first national classification of a vegetation resource based on stratified random sampling and statistical analysis The initial Association Analysis results were used to assess the nature conservation significance of woodland sites Following the split of NC and the setting up of ITE, the new Chief Scientist's team did not adopt the site classification In Scotland, however, the classification of Native Pinewoods set the conservation agenda following a successful symposium in 1975 (Bunce & Jeffers 1977) The rigorous approach both to sampling and data analysis in the woodlands project formed the basis of the approach developed for land use studies and epitomised the divergence between ITE and the Nature Conservancy Council (NCC) following their separation

In later work, the concept of a woodland site – and subsequently a 1 km square – comprising of mixtures of vegetation sampled at random, proved important and contrasted with most vegetation surveys that have used individual species records within selected areas of vegetation The work on the woodland classification showed the power of the new multivariate techniques to analyse large vegetation data sets, which was to increase as computer technology developed A series of small projects were carried out to assess the application of such methods to environmental data at the 1 km square landscape scale (Bunce, *et al* 1975) Ecological data were collected to test the validity of the land classifications produced However, it was soon realised that they could also be used to stratify samples in order to obtain resource estimates Ecological parameters such as vegetation composition or soil character are related to underlying environmental factors, such as climate and altitude (ie the model is based on regression theory) The difference in the present approach from traditional methods is that the relationships are formalised through statistical analysis

The first major project to test the methodology of land classification and resource accounting was the Cumbria Survey (Bunce & Smith 1978) which was a joint project between ITE, Cumbria County Council and the National Park Special Planning Board A classification was constructed by applying TWINSPAN to environmental data from 1 km squares such as altitude and geology Sixteen classes were constructed for Cumbria and some 7 000 1 km squares were classified The sampling of resources within the squares drew upon the woodland work, in that samples were taken from complex elements, thus allowing the variability within and between sites to be quantified To this end, both the squares themselves, and the position of the vegetation sampling points were selected at random The correlation between the observed vegetation and underlying environment was highly significant with r = 0 75, confirming the validity of the approach The results were used in various planning exercises such as the zonation of nature conservation in the county In addition, linear programming was used to assess policy scenarios for the first time

Although the Cumbria classification was not published until 1978, the then Director of ITE, Martin Holdgate, saw the potential of a national classification and this led to his decision to set up the Ecological Survey of GB in 1975 This coincided with the increased policy interest in land use change and culminated in the formation of the Land Use Section at Merlewood The main objectives were to provide a framework for environmental/ecological monitoring and to provide a computer system for access to the data

The ITE Land Classification produced for this project defined 32 land classes derived from TWINSPAN analysis of environmental attributes from a grid sample of 1212 x 1 km squares This classification was subsequently extended in 1990 to all 234 000 km squares in GB (Bunce, Barr *et al* 1996) The first field survey was carried out in 1978, with John Jeffers and Fred Last providing management support Eleven sample plots were placed in each 1 km square, five at random and six along linear features In addition, soil pits were dug, and the profiles of the soils described, under the guidance of Mike Hornung (ITE) Furthermore, for the first time, the land cover was mapped in the individual 1 km squares, with 79 categories of semi-natural vegetation being recognised

High correlations were shown between the underlying classification and land use (r = 0 82) and as well as

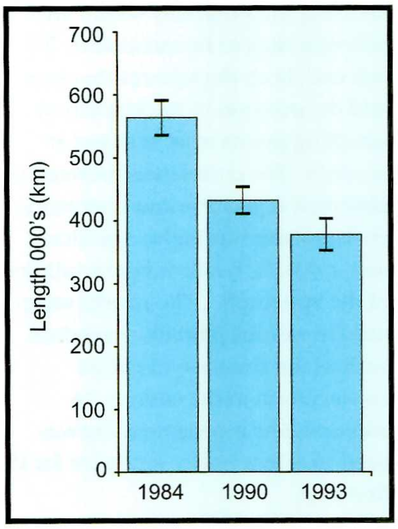

Figure 1. Estimates of length of hedgerows in England and Wales between 1984, 1990 and 1993 (with standard errors) which shows a continuing decline

soils (r = 0.92). The areas of crops and grass also agreed with independent data from the Ministry of Agriculture's agricultural census. The areal extent of the 79 land cover categories also provided, for the first time, complete national estimates for semi-natural vegetation in GB. The Land Classification was also used for other research projects, for example, to estimate badger populations and to assess the representativeness of the Common Bird Census.

In 1984, stimulated by the widely reported losses of many habitats, a further survey was carried out increasing the sample number from 256 to 384 with mainly landscape features being recorded. The results from the 1984 survey showed that there had been a 28 000 km loss of hedgerows since 1978 and provided the basis for more accurate estimates of stock and change in 1990 and 1993 as shown in Figure 1. In addition, other estimates of change were produced that had not previously been available, (eg for new agricultural buildings).

The work was originally funded by the Natural Environment Research Council (NERC), but in 1986 the Department of the Environment (DOE) became interested in the changes of quality that might be taking place within habitats. The vegetation data collected in 1978 provided a unique source of information to measure such changes in quality. John Peters (DOE) and Bill Heal (ITE) therefore instigated the ECOLUC project (Ecological Consequences Of Land Use Change (Bunce *et al.* 1993)) with the following major objectives:

- to examine the ways in which change could be estimated
- to assess the potential of satellite imagery in producing national maps of land cover
- to examine the potential of expert systems as tools for applying ITE's developing information base.

It was concluded that the Land Classification provided the best way of coordinating the disparate ecological information across GB, and that it could be used to integrate surveys of other species groups (eg freshwater invertebrates and moths). It was also shown that the re-recording of the vegetation plots could be used to identify statistically significant change. Much of the botanical variation was found to reside in linear features especially in lowland landscapes, a conclusion that had important policy implications. It was also demonstrated that satellite imagery could produce land cover maps across large areas, as shown by the mapping of heather in England and Wales. However, expert systems were not sufficiently advanced to inform policy decisions. Instead, a pilot information system, based on a project in the Highland Region of Scotland, led to the production of the Countryside Information System for the dissemination of information at the 1 km square scale, from ITE, and from other relevant data sources (Haines-

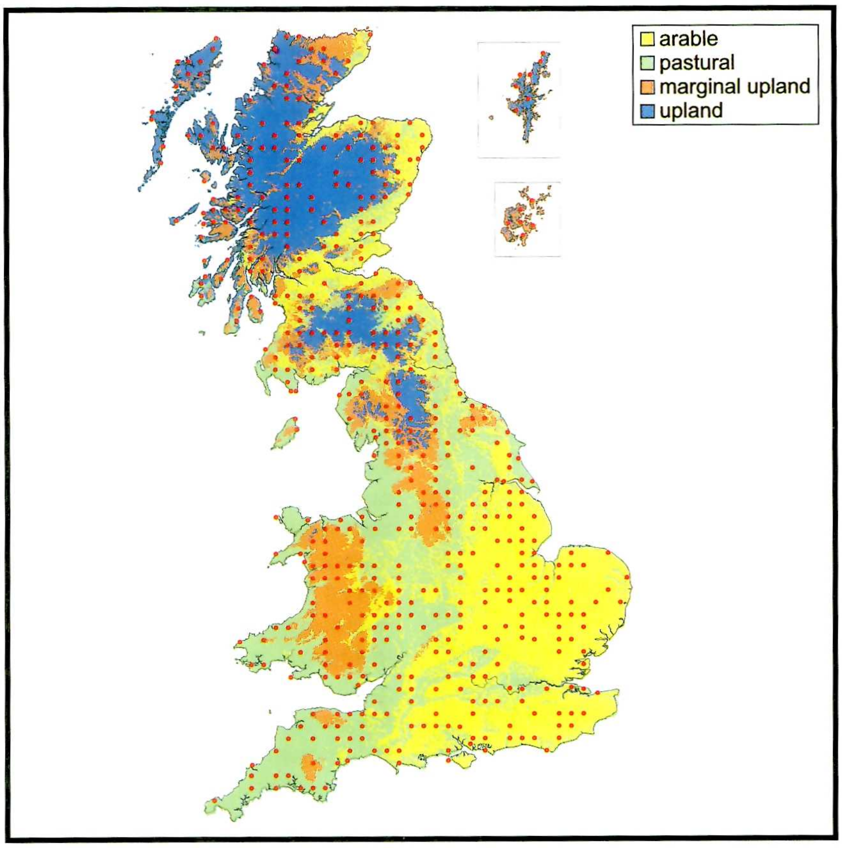

Figure 2. Distribution of the 1 km squares in the four landscape types together with the 1 km squares surveyed in 1990. Arable landscape: land classes 2, 3, 4, 9, 11, 12, 14, 25 and 26; pastural landscape: land classes 1, 5, 6, 7, 8, 10, 13, 15, 16 and 27; marginal upland landscape: land classes 17, 18, 19, 20, 28 and 31; upland landscape: land classes 21, 22, 23, 24, 29, 30 and 32. The derivation of the land classes is described by Bunce *et al.* 1996. The landscapes are used for summarising the results of changes in land cover and land use and for structuring the analysis of changes in species and vegetation

Young *et al.* 1994). This system of spatially referenced data was marketed in 1994 and has become an important means of delivery of environmental information.

The field survey data were appropriate for modelling land use options. One of the first examples started in 1981 to identify the potential for growing wood energy plantations in GB. Maps of the land cover categories from ITE surveys were annotated with financial returns for forestry and agriculture, in order to compare relative performance using a sieve-mapping technique. This technique has been widely applied and is currently being further developed.

ITE also became involved with the development of the Land Use Allocation Model (LUAM), in cooperation with the Centre for Agricultural Strategy at Reading University. This model is based on the structure of the Land Classification and, although primarily directed towards testing the agricultural implications of policy scenarios, it has the potential for being extended into the environmental policy arena. The integration of agriculture and ecological data provides a powerful basis for modelling, which is currently being developed by ITE on the basis of species/landscape relationships.

Following the successful conclusion of the ECOLUC project, it was decided to proceed with the Countryside Survey 1990 (CS1990). This was a joint programme of work between ITE and the DOE with some assistance from the NCC. The number of 1 km squares was increased from 384 to 508 and all the plots surveyed in 1978 were repeated (Figure 2). In addition, further plots were placed along linear features with five additional habitat plots being placed in areas that were considered of nature conservation interest. Although aerial extent of the habitat plots cannot be estimated, they provide a description of additional botanical variation in the landscape.

The results from CS1990 were reported in Barr *et al.* (1993) and showed that the major losses of habitats had slowed, with the exception of hedgerows where a 22% decline was reported. However, the most striking results concerned the general loss of species in many classes of vegetation, as shown in Figure 3. For example, infertile grassland lost up to 20% of species between 1978 and 1990. Of the 65 comparisons in the separate plot types that could be made with adequate sample replication, only eight increased in diversity, whereas 18 declined. CS1990 posed many questions about the causes of landscape change and whether a loss of habitat quality was also involved. A new project called ECOFACT (Ecological Factors controlling biodiversity in the British landscape) was, therefore, set up jointly between DOE; Ministry of Agriculture, Fisheries and Food; Scottish Office of Agriculture, Environment and Fisheries Department; and ITE. The objectives were to extend the analysis of change, to examine the associated causes, to assess pattern in the landscape and to prepare for a possible re-survey.

An important new tool produced in this work was a new single vegetation classification for GB constructed from all the vegetation data available. The results from this classification will be published as *The Countryside Vegetation System* (CVS) (Bunce *et al. in press*). This used a standard stopping rule to group the 100 vegetation classes statistically into eight aggregate classes (Figure 4). The individual classes have subsequently been described in terms of a range of characteristics including soil types, species number and species composition. This classification will be used as the framework for changes in habitat quality. Access to the classification algorithm will be available on the World Wide Web.

This classification has been used to assess botanical diversity at the landscape level. The vegetation in the lowlands is mainly in highly-managed habitats or in linear features and small fragments, whereas in the uplands the vegetation is mainly semi-natural and extensive. Linear habitats make a major contribution to diversity in all landscapes. In lowland landscapes, small patches of semi-natural habitats contain the highest diversity of CVS classes as well as species. This data base will be important in assessing change and will inform policies for the maintenance of botanical diversity at the landscape scale.

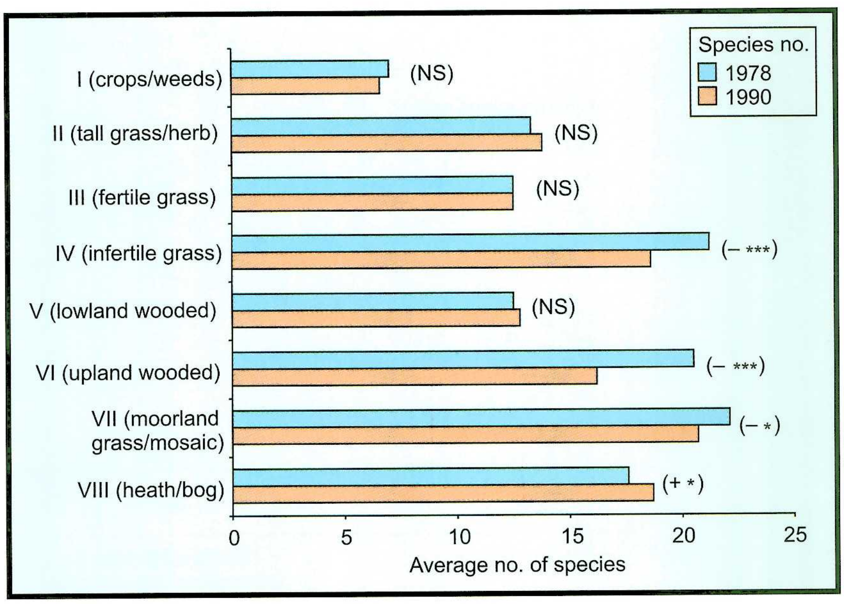

Figure 3. Change in plant diversity within the eight aggregate classes of the Countryside Vegetation System. * = P <0.1; ** = P <0.01; *** = P <0.001; NS = not significant.
The graph shows that botanical diversity declined in the aggregate vegetation classes for infertile grasslands, upland wood and moorland grass/mosaic, but increased in heath/bog. Crops/weeds lost species significantly in arable landscapes only

Plate 2. ITE statistician Tim Sparks with the author Bill Bryson, discussing the ancient hedge at ITE Monks Wood (in the background) which was established to mark the manoral boundary in Norman times

Previous analyses of botanical data have relied upon ecological interpretation for the assessment of the relationships between the principle gradients and environmental factors. Now, however, statistical analysis has shown that the vegetation gradients are highly correlated with environment, the primary gradient with fertility (r = 0.98), the secondary with shade (r = 0.61) and the third with soil wetness (r = 0.82). Shifts between vegetation classes from 1978 to 1990 can, therefore, be interpreted in terms of environmental change. The dominant trend has been shown to be eutrophication, due to a complex of inter-related factors, including aerial deposition of nitrogen, fertiliser and slurry application. Nitrogen was shown to be especially important in neutral grassland systems in reducing plant diversity. By contrast in upland wooded vegetation, the shading effect of increasing conifer canopy was the main cause of species loss.

More subtle changes in vegetation can also affect quality, as considered by the conservation agencies. For example, common assemblages of plant species often form important food resources for many animals. Changes in the distribution and abundance of the groups of these species can, therefore, have consequential impacts on faunal populations. Analyses carried out in the ECOFACT project have explored correlations between the status of a number of butterfly, bird and bumblebee species and their foodplants. The results suggest that the reduction in the food resource, as shown by the 1978 and 1990 vegetation data, may have been an important factor in the recorded decline of these animals.

Following preparatory work in ECOFACT and a scoping study carried out for the Department of the Environment, Transport and the Regions (DETR), it was decided to proceed with Countryside Survey 2000 (CS2000). Field work for this project is currently underway and will be

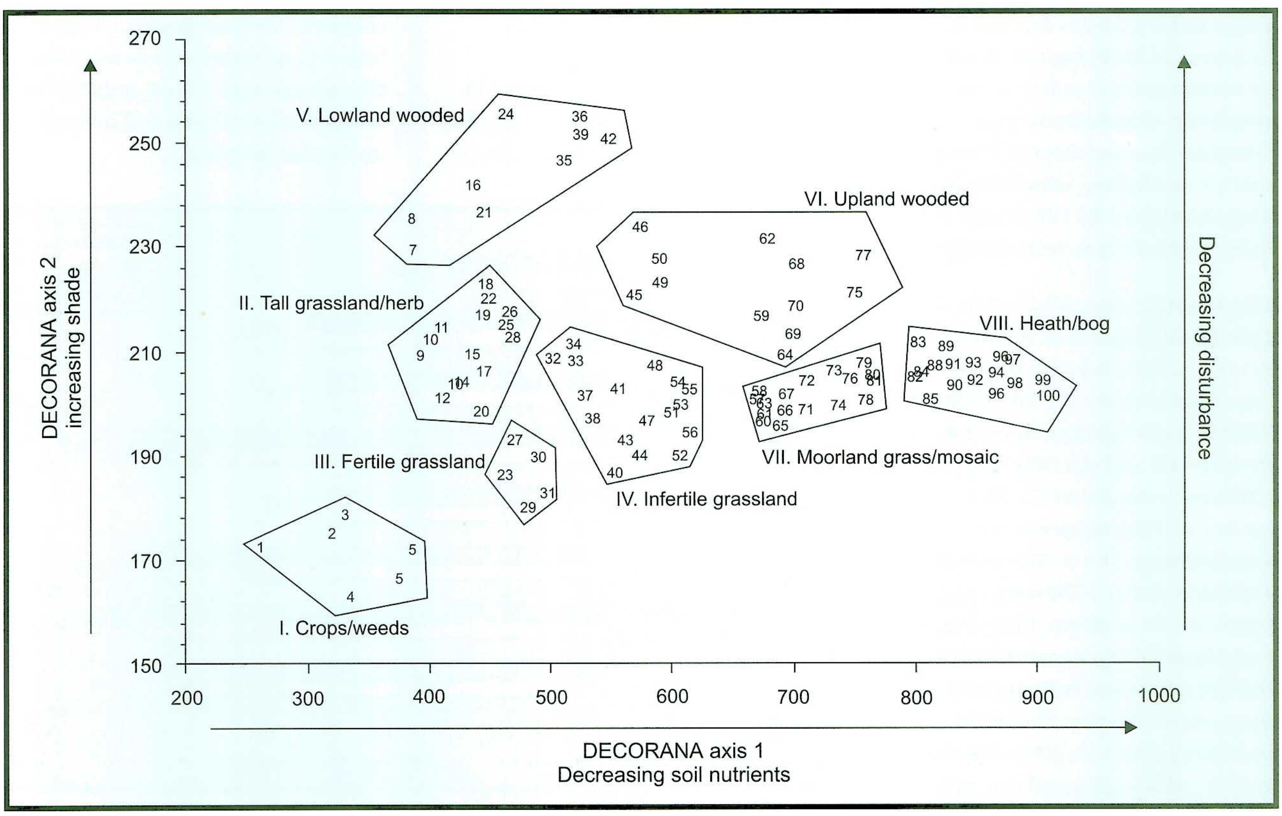

Figure 4. Distribution of the 100 vegetation classes grouped by the eight aggregate classes on the first two axes of the DECORANA ordination. This figure shows that the primary vegetation gradient is correlated with an environmental trend from fertile to infertile soils and the secondary with light and indirectly, disturbance. This graph will be used to show the trajectory of change in vegetation from 1978 to 1990 and 1998

reporting in 2000 The survey will provide a major overview of the habitats, plants, landscape features and land types throughout GB It will provide important information on the current state of the countryside and indicators of the changes that are happening there The survey has two main components

- a field survey of broad habitats, land cover, vegetation, freshwater habitats and linear features including hedges and walls, at over 500 randomly located 1 km squares
- a map and database derived from satellite images showing land cover on a field by field basis across the whole country

The analytical procedures to be used will be those developed in ECOFACT It is intended that further work will be taking place after 2000 to exploit fully the data base for a variety of objectives (eg in assessing the environmental impacts of global warming and detecting the impacts of land use change on biodiversity) The adoption of the Broad Habitats of the UK Biodiversity Steering Group will enable DETR to monitor progress in meeting obligations under the Rio Convention on Biological Diversity New data on the number of woody species in hedgerows will also help to assess the resource of ancient hedgerows (Plate 2) For the first time, reporting will be possible for the whole of the UK, as results from the Northern Ireland Countryside Survey (NICS) will also be coincident with the Broad Habitat categories

ITE's approach to monitoring ecological resources using repeated samples of land, stratified on the basis of environmental variables, will prove increasingly powerful It has now been adopted in several countries (eg Spain, Germany and Austria) and is being developed elsewhere An environmental land classification has now been produced for Europe (Bunce, Watkins *et al* 1996) and has been used to identify ecological regions across the continent These have provided the basis for an ITE-led assessment of pressures on biodiversity, which is being used in the 1998 State of the Environment report by the European Environment Agency A proposal for a European network of land use, land cover and biodiversity monitoring is also under development (EUROLUS), namely *"An integrated monitoring system for strategic assessment of land use, landscape and biodiversity across Europe"*

Countryside Survey now plays a major role in rural policy development, and provides the standard against which new policies can be set It also provides a uniquely rich database for theoretical research and development Whilst ITE has moved a long way from the National Woodland Survey in 1971, that beginning has not been forgotten A pilot for the repeat of this survey has taken place and has confirmed that it provides a valuable baseline for the detection of change in woodland vegetation

R G H Bunce, C J Barr, L G Firbank and M O Hill

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The ITE Countryside Survey now plays a major role in auditing the environmental benefits of land use policies in the UK.

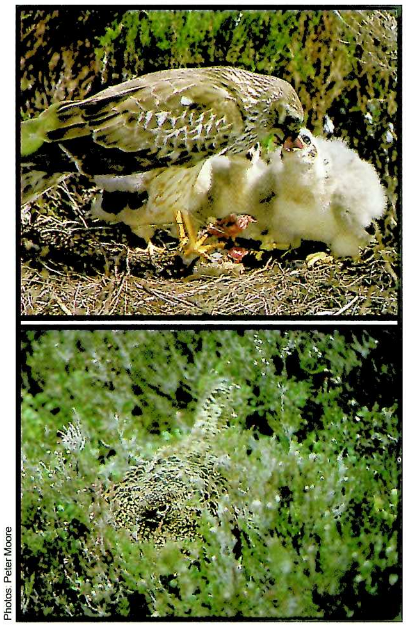

Plate 1. (Top) Female hen harrier feeding her chicks. (Bottom) Female red grouse incubating her eggs

ITE scientists have played an important role in understanding the factors that affect the abundance and reproductive success of bird populations.

Long-term studies of avian population dynamics

The last 25 years have seen major developments in our understanding of the factors that affect the population levels of birds (Dunnet 1991, Perrins *et al.* 1991, Newton 1998), and ITE scientists have played an important role in these developments. The research has been motivated by the need to understand why bird populations fluctuate in the way they do, why so many species are declining, and increasingly, by the need to predict the effects on bird populations of environmental change, whether natural or man-made. The main advances fall into four main categories, namely an understanding of:

- the factors that limit the numbers of particular species, and cause these numbers to go up or down
- the role of behaviour in the limitation of bird numbers
- the performance of individual birds, notably age-related trends in reproduction and survival, and lifetime reproductive rates
- the use of mathematical models for predicting how populations are likely to respond to environmental change.

The following four long-term ITE projects on particular bird species illustrate these aspects.

Sparrowhawks: decline and recovery

Sparrowhawks (*Accipiter nisus*) usually breed at greater densities in areas where their small bird prey are most plentiful, implying that food supply has a major influence on their numbers. In the late-1950s, however, sparrowhawks declined in numbers, disappearing altogether from eastern arable regions. The cause was found to be organochlorine pesticides, which the hawks accumulated from their prey. The insecticide DDT and its metabolites caused shell-thinning, egg-breakage and reduced reproduction, while the more toxic aldrin and dieldrin pesticides killed the hawks directly.

These findings formed part of a large body of information that eventually led to the banning of these chemicals in Europe, North America and elsewhere in the 1970s. Subsequently, ITE scientists helped to monitor the recovery of hawks and other affected species (Newton & Wyllie 1992, Newton & Haas 1984).

After recovery, sparrowhawk numbers in several study areas became relatively stable, and pesticides no longer had an obvious effect on their numbers or breeding. In one area where the hawks had been ringed, it became possible to measure the total number of young raised by 194 different breeding females (Newton 1985). These females showed enormous variation in their lifetime production, ranging from 0 to 24 young (mean 5.0 young). Much of this could be attributed to individual variation in longevity (1–10 years) and to variation in the age of first breeding (1–3 years), which together determined the length of breeding life (1–8 years).

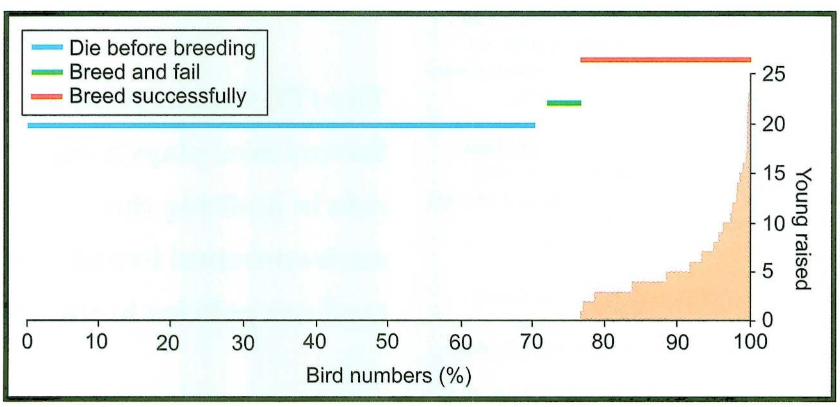

Figure 1. Lifetime reproduction in female sparrowhawks. The diagram shows the percentage of individuals in each cohort that raises different numbers of young, based on data collected over a 25-year period in south Scotland

From knowledge of mortality at different ages, it was possible to calculate the lifetime production of a whole generation of female sparrowhawks, including those that died before breeding (Figure 1). Less than 5% of fledglings (or 20% of breeders) produced half the next generation, and 7% of fledglings (or 30% or breeders) produced 90% of the next generation. The pattern of gene flow from one generation to the next was, therefore, enormously skewed, and repeated in each generation. Comparable measures of lifetime reproduction, now available for more than 20 bird species, show a similar pattern. In a stable population these measures provide a close approximation to Darwinian fitness, a hitherto elusive measure in biology.

Red grouse: population cycles

In many northern areas, the numbers of certain kinds of animals – notably voles, hares and grouse – fluctuate with fairly regular periodicity. They undergo cycles of abundance, in which peaks and troughs in numbers occur at fairly consistent intervals of 3–10 years, depending on area. The red grouse (*Lagopus lagopus scoticus*) is cyclic over much of its range in Britain, as is the conspecific Willow Ptarmigan (*Lagopus lagopus lagopus*) in Eurasia and north America. It is important to understand the basis of cycles in red grouse, not only because they have intrinsic interest, but also because they have economic consequences for many moorland owners.

Two possible explanations for cycles in grouse numbers are that they result from interactions between the grouse and its parasitic worm (*Trichostrongylus tenuis*) or, its food plant, heather (*Calluna vulgaris*). These issues have been tested and shown to be unlikely general causes of cycles (Moss *et al.* 1996). Research in ITE is now centred on testing a different explanation, namely that cycles result from intrinsic social and demographic factors (Watson *et al.* 1994).

A model shown in Figure 2i proposes that population cycles in red grouse can be explained by the joint action of territoriality and differential behaviour between kin and non-kin. It can account for cyclic population fluctuations, without the need to invoke interaction with some other organism.

Future work will entail experiments involving the selective removal of birds, and further studies of the

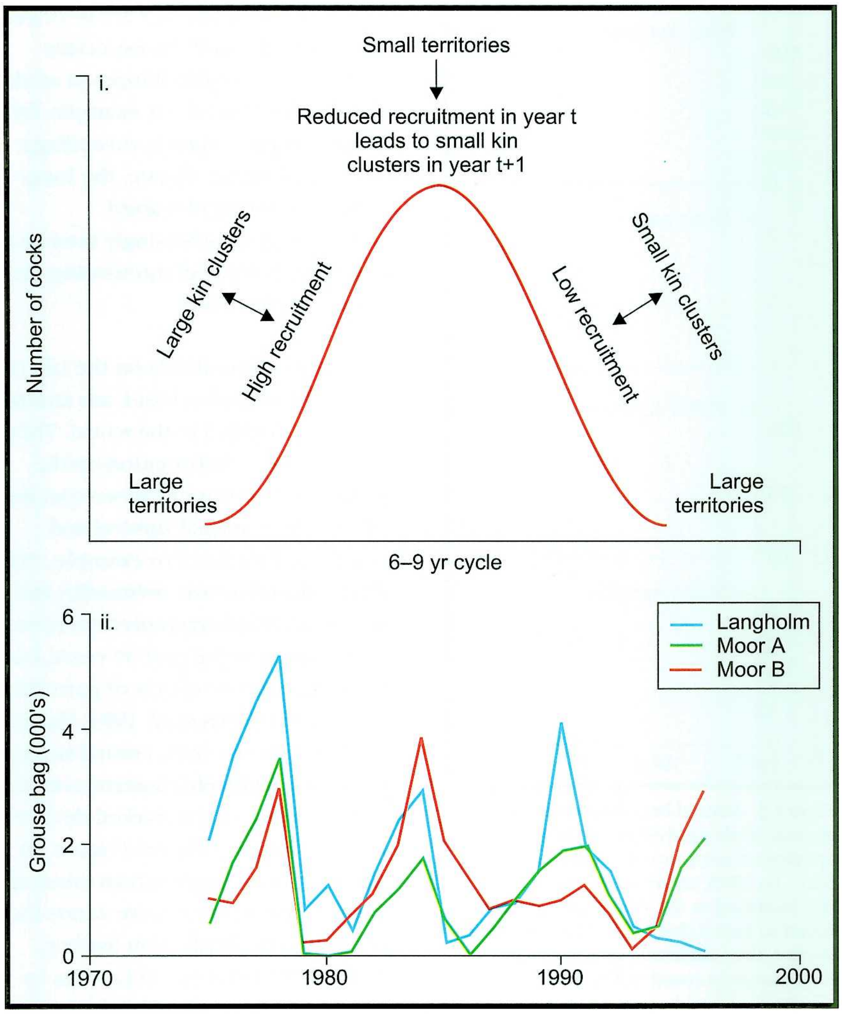

Figure 2i. Model showing how changes in behaviour might cause cyclic changes in the numbers of red grouse. The model is based on six observations: (1) Red grouse numbers are limited by the territorial behaviour of the cocks, who attract hens to their territories, any surplus birds of both sexes being excluded. (2) Changes in population density are accompanied by inverse changes in territory sizes. (3) Territories tend to occur in philopatric family clusters, with sons settling next to their fathers. (4) The offspring of bigger clusters have a better chance of being recruited into the breeding population. (5) Year-to-year changes in numbers are due largely to annual variations in the local recruitment of young birds to the territorial population. (6) Clusters are bigger in the increase than in the decrease phase of a cycle.
ii. Fluctuations in red grouse population, as shown by the numbers shot each year on three moors in northern England and south Scotland. Up until 1991 raptor prediction was very low on all three moors but at Langholm, during 1992–96, raptor predation was high, resulting in reduced grouse shooting bags

differential behaviour of kin and non-kin. The latter aspect is helped by the fact that the degree of relatedness between individuals can now be measured using new molecular techniques.

The grouse research aims not only to understand cycles but also to provide information for the effective management of grouse moors. One important topical issue is the impact of raptor predation on grouse numbers and the shooting bag. This problem was examined in a study based at Langholme moor in south-west Scotland during 1992–96 (Redpath & Thirgood 1997). Unrestrained raptor predation from hen harriers (*Circus cyaneu*) and peregrines reduced the potential breeding stock of grouse, and the number of chicks. Grouse bags failed to increase to a peak in 1996 as expected from past records and events on nearby moors where raptor predation was absent (Figure 2ii).

Seabirds: population change and environmental variation

Most seabird species are long-lived, have low breeding rates, and do not

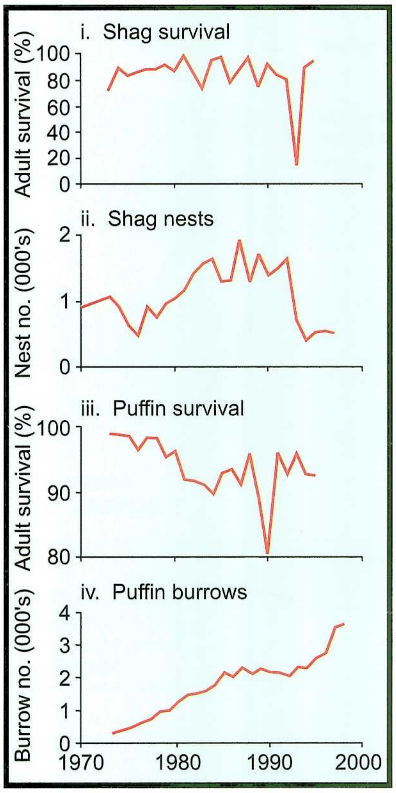

Figure 3. Annual breeding numbers and annual adult survival in two seabird species on study areas on the Isle of May. In 1993, many adult shags were not included in the nest count as they failed to breed that year. The following winter, they suffered heavy mortality, so nest numbers could not recover

ITE studies of seabird and shorebird populations are among the most detailed in the world.

Plate 2. Oystercatcher feeding on mussels

start to breed until they are 6–10 years old. This makes them especially vulnerable to slight changes in adult survival, as caused, for example, by human impacts such as oil-spillage and over-fishing. Hence, the long-term monitoring of seabird populations is increasingly seen as a cost-effective way of monitoring the marine environment.

ITE studies of seabirds on the Isle of May, off eastern Scotland, are among the most detailed in the world. They have provided information on the population trends of various species and on their annual survival and reproductive rates. For example, the shag (*Phalacrocorax aristotelis*) and the puffin (*Fratercula arctica*) have increased over the past 30 years, but both have shown effects of perturbing influences (Harris *et al.* 1994, Harris *et al.* 1997). In the shag, annual survival remained relatively constant over this period, except for a marked decline over the winter 1993–94 (Figure 3i). This was associated with an unusual 2-week period of onshore winds that prevented the birds from feeding. The effect of this one event was to cancel the population gains accrued over the previous 30 years (Figure 3ii). In the puffin, survival showed a stepped decline around 1980, to a lower level that persisted for the next ten years (Figure 3iii). The effect of this period of reduced survival was to halt the population growth (Figure 3iv). This constraining factor was transient, however, as population growth has resumed and there are the first suggestions that adult survival might be improving.

This last event illustrates a problem that often confronts the seabird ecologist, namely that potentially revealing changes in bird demography cannot always be linked to the changes in marine conditions that cause them. For this reason, emphasis is increasingly shifting to international and interdisciplinary research, in which seabirds form only one component in more broadly-based studies aimed to better understand the natural and human-induced phenomena that affect populations of fish, marine mammals and seabirds.

Shorebirds: environmental change and behavioural population models

In recent years, biologists have begun to combine behavioural and population studies, in order to predict what might happen to populations if they were exposed to some environmental change that is outside our range of experience.

The oystercatcher (*Haematopus ostralegus*) has proved an ideal subject for such work, because it is easy to observe, and at the same time continues to be under threat on its estuarine wintering areas from disturbance, land claim and removal of shellfish food-supplies by fishermen (Goss-Custard 1996). All these human impacts serve to reduce the feeding areas or food-supplies of the birds, or reduce the birds' access to food supply. This, therefore, intensifies competition between individuals, which in turn affects survival and eventually numbers. A mathematical model, based on field measurements of feeding rates, movements and survival under different conditions, was developed to predict the effects of these various human impacts on overwinter survival, and on subsequent trends in numbers (Stillman *et al.* submitted). The approach uses computer simulation to model the outcome of decisions made by thousands of individual birds differing in competitive ability (Figure 4).

The value of this approach is in showing how behavioural and demographic information obtained by long-term field study can be combined to construct realistic population models that can be applied to conservation problems. Such models are needed for future applications where the focus is likely to be rather less on reversing population declines (a major preoccupation of recent conservation efforts), and rather more on scenario prediction, often for species which are currently abundant. For example, the UK has been active in implementing policies to conserve the value of estuaries for the millions of migratory shorebirds and waterfowl that depend on them, while the demands from other sectors of the public for using estuaries for recreation and wealth creation have remained high.

Conclusions

The ITE studies mentioned above were started in response to an applied problem:

- to discover the cause of an unexpected population decline
- to find ways of more effectively managing a population for human benefit
- to predict the effects of some proposed human-impact.

At the same time, however, they have contributed greatly to our understanding of the factors that influence the population sizes of birds, as well as the performance of individual birds. These developments all help to put us in a better position to predict and mitigate the increasing effects of human activities on birds, and to conserve bird populations in the future.

P Rothery, J D Goss-Custard, M P Harris, R Moss and I Newton

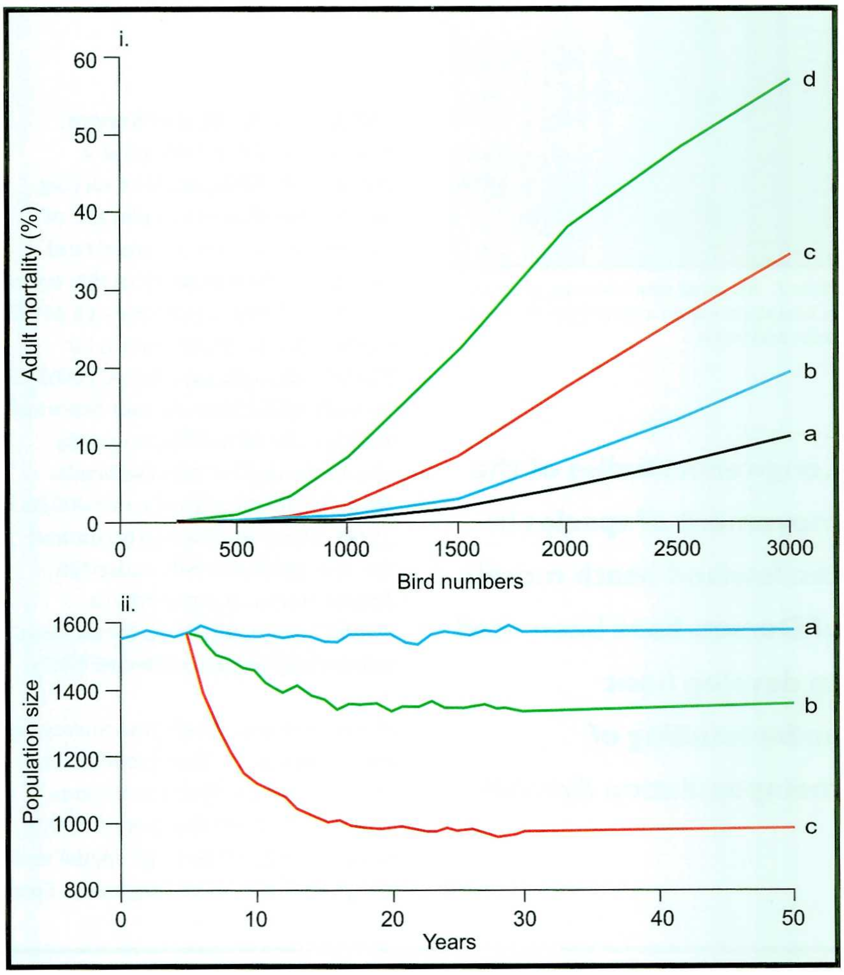

Figure 4i. Predicted adult overwinter mortality rates of oystercatchers derived from the behaviour-based model in present-day conditions and different scenarios involving 200 fishermen, with high-tide fields used by oystercatchers either unrestricted, removed for two frosty weeks or removed throughout winter: (a) present-day, fields throughout; (b) 200 fishermen, present-day, fields throughout; (c) 200 fishermen, two weeks frost; (d) 200 fishermen, no fields.
ii. Predicted effect on size of the Exe estuary oystercatcher population of 200 fishermen introduced in year 5 using density-dependent mortality functions derived from the behaviour-based model: (a) no fishermen, present-day conditions, fields available throughout winter; (b) 200 fishermen, fields throughout; (c) 200 fishermen, two weeks frost

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Photo: British Petroleum

Plate 1. An aerial view showing patches of heathland within a mixed landscape of fields and forest

Long-term studies of the movement of species in the lowland heath mosaic of Dorset, have been used to develop basic understanding of metapopulation dynamics.

Large-scale dynamics of heathland

Like most semi-natural biotopes, lowland heathland occurs as a patchwork of fragments of varying sizes embedded in a landscape of other biotopes and managed land (Plate 1). The dynamics of this system has been the focus for research at ITE Furzebrook Research Station for almost half a century. Moore (1962) in an early application of both historical ecology and island biogeography, traced the decline of these heaths from 30 000 ha in 1811 to 10 000 ha in 1960. These studies also quantified the loss of biodiversity caused by fragmentation and provided a scientifically sound basis for modern conservation practice (Moore 1987).

A formal Dorset Heathland Survey was established in 1978 and repeated in 1987 and 1996 (Webb & Haskins 1980, Webb 1990 Webb *et al.* 1997), and is unique in the large spatial and temporal scales it encompasses. From field survey, quantitative data in digital form have been collected from over 3 000 grid squares (each 200 x 200 m) which covered the entire area of the Dorset heathlands. Records were accumulated for 184 attributes describing the composition and structure of the vegetation, the presence of selected rare species, topography and land use. The Survey is technically a census and was designed to ensure repeatability.

Patch dynamics

Using the 1978 Survey, a population of 141 heathland patches was defined (Figure 1) and the richness of invertebrates and vegetation examined. Where a set of specialist heathland species could be defined within a taxonomic group (eg heathland spiders) there were positive correlations between the point species richness (ie alpha diversity) and heath patch area or degree of isolation (Webb & Hopkins 1984) (Figure 2). However, when all species in a taxonomic group were considered (eg beetles) the small heaths had a greater point species richness than large heaths because of invasion from the edges (Webb *et al.* 1984, Webb & Vermatt 1990). The edges of large heaths had greater overall invertebrate diversity than the centres, but fewer of the species were heathland specialists (Figure 2). Edge effects on invertebrate richness were positively correlated with the structural diversity of the surrounding vegetation, richness being greatest on heaths surrounded by woodland (Webb *et al.* 1984, Webb 1989). Edge effects, which exist in other biotopes, were evident because heathland patches have a lower species richness than their surroundings. The strong interactions between the fragments and their surroundings were of fundamental importance. Previously, it had been held that such patches were analogous to islands. This view emphasised within-patch dynamics but ITE studies showed between-patch dynamics to be of greater significance. The conclusion of this work was that conservation effort was best concentrated on the large or less isolated fragments.

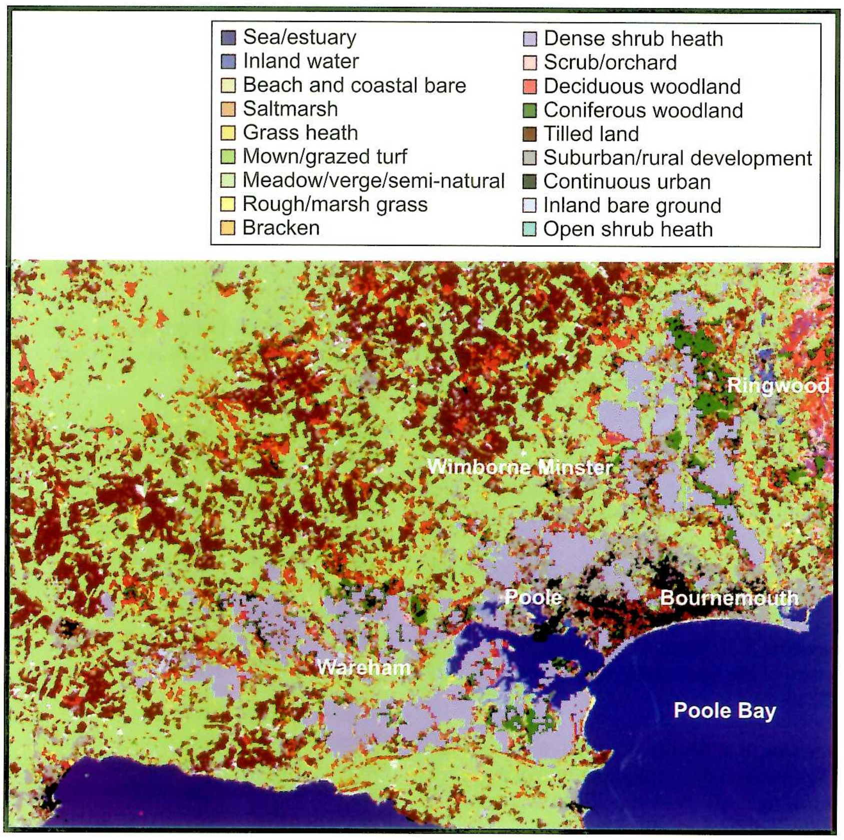

Figure 1. A plot showing some of the 25 classes from the Land Cover Map highlighting the distribution of heathland in Dorset, which has been surveyed in 1978, 1987 and 1996. The Heathland Survey collected vegetation, topography and land use data for each 200 x 200 m (4 ha) square

It is important to distinguish between patches of heathland (ie patches of the biotope) and patches of habitat of individual species. The former, referred to as heaths, are delimited at the human scale whereas habitat patches are at the scale of individual species and represent the landscape as perceived by them. Analysis of the spatial and temporal changes affecting both types of patch enabled the availability and persistence of habitat patches to be calculated. From these data, the problem that the individual species faced in tracking the occurrence and availability of their habitats across the heathland landscape can be estimated. Because of successional change on heathland, the location of habitat for a species continually changes. Effective conservation ensures that successional change is managed to meet the requirements of the species and to provide its habitat at the right time and in the right place. For some species under the current management, new patches occur sufficiently frequently and within distances which the species can colonise (Webb & Thomas 1994).

It is now possible to assume various management policies and map their consequences for the persistence of metapopulations of individual species. This analysis of habitat availability also showed how small patches of habitat enabled a species to maintain metapopulations within the landscape by promoting dispersal. The heathland biotope is not stable because of the successional changes and interactions with the surroundings of patches. There is continuous flux – a fact often overlooked in conservation science that tends to see protected areas as static entities (Webb & Thomas 1994). Previously, it was the view that conservation management should be devoted to large patches, but now it is clear that the edges of patches and patches forming stepping stones are also important.

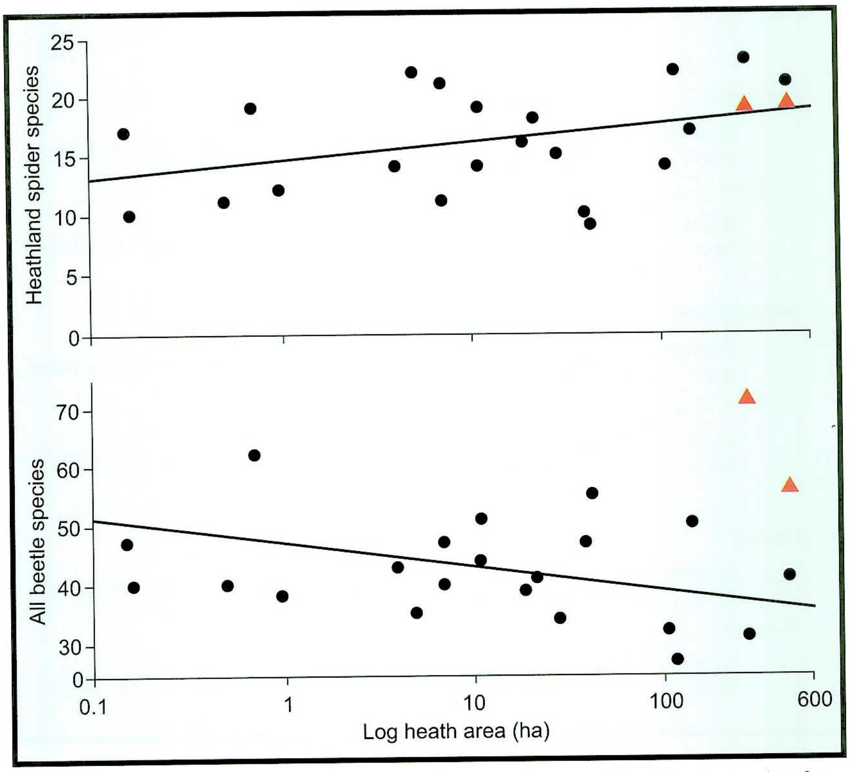

Figure 2. Point species richness (alpha diversity) S in relation to heathland area (ha) for all heathland spider species (fitted line $S = 14.4 + 1.59 \log_{10}$ area, $r = 0.42$) and all beetle species (fitted line $S = 47.2 + 4.13 \log_{10}$ area, $r = 0.45$. Red triangles denote supplementary sample points on the edge of the two largest heaths

Impacts of climate change

It is possible to vary the habitat requirements of a species as if they were living under a different climate and model the consequences of the changing climate. The exact habitat requirements of four ectothermic species – the silver-studded blue butterfly (*Plebejus argus*), the red ant (*Myrmica sabuleti*), the heath grasshopper (*Chorthippus vagans*) and the sand lizard (*Lacerta agilis*) – were defined at their northern limits and 200–400 km further south in their ranges where mean summer temperatures are 2–3 °C warmer (Thomas *et al.* in press). These models predicted that were such warming to occur there would be:

- a large increase in the area of habitat available
- an increase in the length of time the patches may be occupied
- a decrease in the distance between the habitat patches within the biotope
- and that metapopulation structure was more stable (Figure 3).

This implies that species at the northern edge-of-range in lowland heathlands will benefit from increased temperatures. These predictions do not, however, account for random events such as fires or droughts.

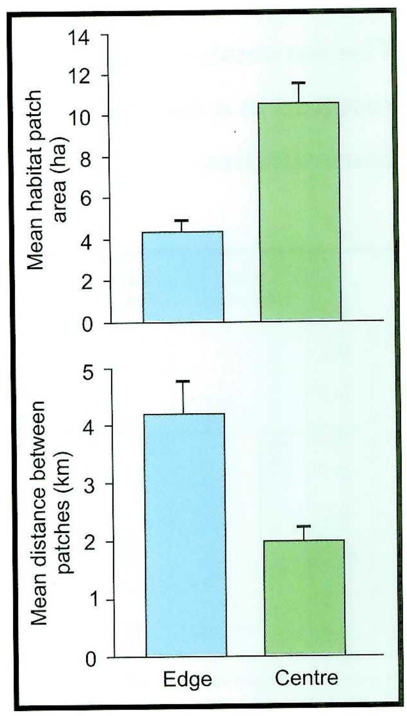

Figure 3. Comparison of the mean area (ha) of habitat patches and mean distance (km) between habitat patches for the silver-studded blue butterfly (*Plebejus argus*) if the same landscape of Dorset heathland were situated near the species northern limit (edge) or more centrally in its range (centre), where summer temperatures are 2–3°C warmer, with standard errors shown as bars

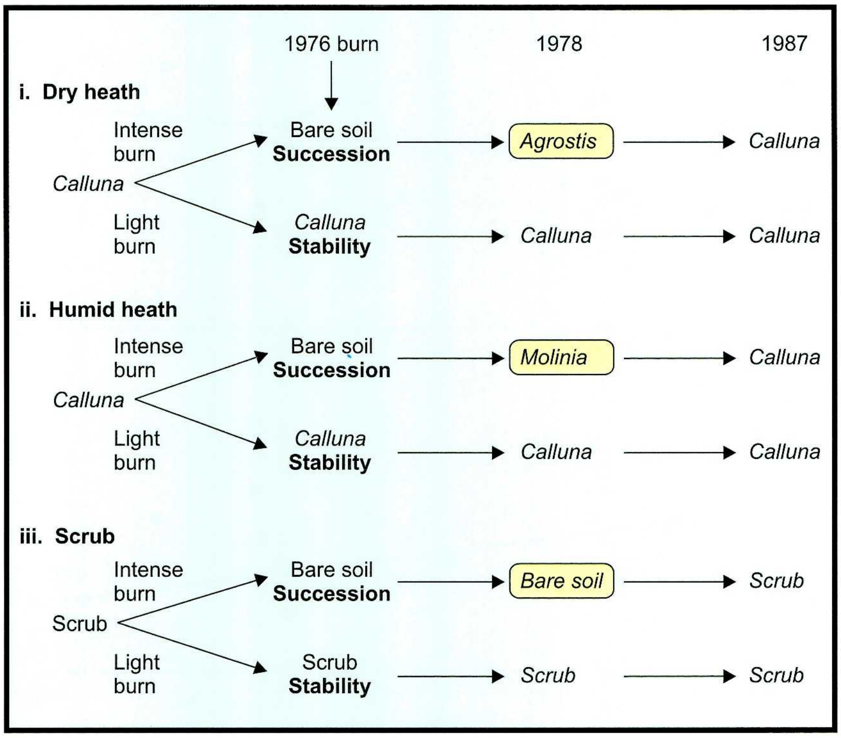

Figure 4. Vegetation responses to wildfires as shown by surveys in 1978 and 1987 (Bullock & Webb 1995). Dry and humid heath did not change in area in response to fires, but the most severely burnt areas underwent succession from bare soil, through grass (*Agrostis curtisii* or *Molinea caerulea*), back to heather (*Calluna*) vegetation in 1986. Over half of the scrub (eg *Betula* spp and *Ulex europaeus*) was burnt out, but this regenerated directly as scrub, and did not go through a *Calluna* phase

The succession of dry years in the last decade may have resulted in a decline in wet heath and peatland communities.

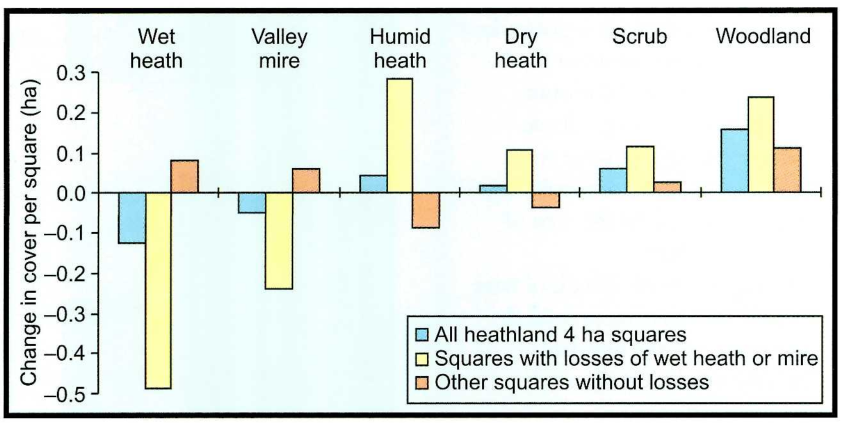

Figure 5. Changes in the heathland vegetation of Dorset between 1987 and 1996. During which, 3 100 4 ha squares were surveyed and these ("All squares") showed declines in wet heath and valley mire vegetation, and increases in dry and humid heath, scrub and woodland. This suggests that the wetter communities (wet heath and valley mire) may be drying out and changing to humid and dry heath. However, due to a lack of management, the humid and dry heath is also undergoing succession to scrub and woodland. These hypotheses were tested by dividing the survey squares into those showing losses of wetter communities and those "other" squares which showed no losses of these two categories. If wetter communities were drying out and turning into humid or dry heath vegetation, we would expect increases in these drier communities in the squares with losses of wet heath or mire, but no increases in the "other" squares. This is what was found and, therefore, the hypothesis is supported

Successional processes

In the hot dry summers of 1975 and 1976 uncontrolled fires burnt some 775 ha (9.8%) of Dorset heathland. Comparisons between burnt and unburnt zones in 1978, just after the fires, and 1987 (Bullock & Webb 1995) showed that the unburnt areas did not change over this period. In the burnt areas the effects of the fires were transitory and all type of heathland vegetation recovered. Scrub areas changed composition in some instances but, contrary to expectation, regenerated directly as scrub without passing through a heathland phase (Figure 4). When viewed over a decade and at the landscape scale, these fires had negligible effect on the heathland vegetation, yet at the time they had been considered catastrophic at individual locations.

The widespread encroachment of scrub and trees on to these heathlands can be attributed to the lack of fires over the last 20 years. In the past the heaths were grazed and burnt regularly but after the severe fires in 1975/76, stringent protection measures were introduced. Surprisingly, no adequate alternative form of vegetation management was substituted. Today, these heaths carry more vegetation and a greater fuel-load. Accidental fires now burn more fiercely, cover larger areas, and are more difficult to control. The increased temperatures during these fires may impede the recovery of heathland vegetation. For management a 20–25-year fire cycle is recommended (Chapman & Webb 1978) but today the frequency of fires is equivalent to a 60-year cycle.

The 1996 survey showed that wet heath and peatland vegetation had declined (Figure 5). This may be due to recent changes in weather patterns and a general increase in vegetation cover and biomass within the heathland catchments, resulting in increased interception of precipitation and evapo-transpiration (Webb *et al.* 1997). The rapid response of heathland vegetation detectable over the entire landscape, is remarkable in view of the low growth rates of the plants A series of wet years may simply reverse these changes, although, wet heath and peatland vegetation may develop in a different direction in the future

Management implications

The recent surveys have shown that planning legislation can control direct losses of heathland, but there is clearly a lack of conservation management Succession on open heathland to scrub and trees occurs at a rate of about 1 7% per year and exceeds other forms of loss Three major policy initiatives have been based on the survey findings

- The Dorset Heathland Forum was established by Dorset County Council, which prepared and published the Dorset Heathland Strategy – a series of policies adopted as non-statutory planning guidance
- The Forest Enterprise established a Heathland Project in which their re-planting programme was modified to provide linkages within the forest between heathlands
- The Royal Society for the Protection of Birds established a Heathland Management Project with joint funding from British Petroleum and latterly from the EU Life Programme

In parallel with research and management of the dynamics of the heathland ecosystem, there has been a programme on restoring heathland patches The spatially referenced data in the surveys have been applied using GIS techniques to identify where new areas of heathland should be created to meet biodiversity targets These areas will link unconnected heaths, infill patches to produce more regular boundaries, maintain species dynamics, reconstruct hydrological units and promote visual amenity (Rose & Webb 1995)

Studies of the dynamics of Dorset heathland have fulfilled a dual role for more than twenty years contributing to both ecological science and the development of conservation policy and management They have shown the biotope to be more dynamic than expected, with greater interactions with the surrounding landscape and climate In addition, this research has been incorporated in to the development of management policies

N R Webb, R T Clarke, J Bullock, R J Rose and J A Thomas

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Future research will focus on the responses of species to heathland restoration at the metopopulation level.

Plate 1. Wild cabbage and black mustard growing on sea cliffs at Kimmeridge in Dorset. Collaborative research at ITE Furzebrook and IVEM Oxford has revealed significant differences in the proportion of cabbage and mustard plants infected with each of six viruses

ITE has had a major role in the scientific research necessary to inform and improve risk assessment for genetically modified plants.

Developing risk assessments for genetically modified crops

A relatively small but important part of ITE's legacy of research on wildlife conservation was an interest in the distribution and maintenance of genetic diversity in natural populations of plants. Concerned with the determinants of population genetic structure and gene flow, this work focused on relatively short-lived (sometimes rare) species behaving as colonisers or occupying early successional phases of environmental gradients such as saltmarshes (eg Gray & Scott 1980, Gray 1986, 1987, 1988, Gray *et al.* 1991). The theoretical framework and practical techniques required for this research has positioned the Institute to tackle the relatively recent issue of assessing the potential environmental risks from genetically modified crops.

Under the genetically modified organisms (GMOs) (Deliberate Release) Regulations 1992 and 1995, organisations proposing to release or market a GMO in the UK are required to evaluate the impact and risk of the intended release to human health and the environment. The risk assessment, made in the application for consent to release the GMO, must address a wide range of questions relating to the effect of the introduced gene (transgene) on the organism and of the altered (transgenic) organism on the environment. Of particular concern is the possibility that the transgene might 'escape'. For crop plants this could be by hybridisation with a wild relative or the establishment and spread of feral populations.

ITE has had a major role in the scientific research necessary to inform and improve risk assessment for genetically modified plants. A report to the former Department of the Environment (DOE) in 1992 which reviewed the genetic transformation of UK crops, the distribution and biology of their wild relatives and the potential for hybridisation, identified three major groups of plants differing in the likelihood of transgene escape (Raybould & Gray 1992, 1993). These groups, by recognising different categories of risk, formed the basis for changes in the UK regulatory process (Table 1). In particular, the identification of low risk GMOs enabled the development of Fast Track Procedures (FTP) (in which applications for consent to release specific crop/gene combinations are processed in a shorter time period – DOE/ACRE 1994). More recently, a review of FTP in the light of experience in the field trials and new developments (Gray & Raybould 1997) has led to extensive revision of the regulations, mainly by adding more crop/trait combinations to the list (DETR/ACRE 1997).

Table 1. Categorisation of UK genetically modified crops by risk of gene flow to wild relatives (modified from Raybould & Gray 1993)

Probability of gene flow to wild relatives	Status of wild relatives	Crops
Minimal	No sexually compatible wild relatives in the UK	Potato, tomato, maize, rye, wheat, peas & beans, cucumber, strawberry, grapevine
Low	Wild relatives in the same genus as the crop (congeneric) – limited sexual compatibility between the crop and wild relative	Oilseed rape, barley, lettuce, flax, blackcurrant, raspberry
High	Wild relatives are the same species as the crop (conspecific), or congenerics – high sexual compatibility with the crop species	Sugar beet, cabbage, ryegrass, white clover, carrot, poplar, apple, plum

For those crops where transgene escape is likely, it becomes essential to understand the factors affecting gene movement from the crop to the recipient natural or feral populations and the subsequent spread of genes among these populations. Although the spread of a gene will depend strongly on how it alters plant fitness, other factors such as rates of gene flow from the crop, and between natural populations, will also be important. Rates of gene flow in natural populations can be estimated either directly (eg by observing pollinators) or indirectly from the distribution of variation at molecular marker loci. ITE has used both methods, but particularly the latter, to investigate gene flow in natural populations of two species in the 'high-risk' category: sea beet (*Beta vulgaris* ssp. *maritima*) and wild cabbage (*Brassica oleracea*). Both are conspecifics of common crop plants.

ITE has estimated gene flow among sea beet populations in Dorset, by measuring variation in soluble enzymes (isozymes), lengths of fragments produced by digesting DNA with specific enzymes (Restriction Fragment Length Polymorphisms – RFLPs) and in the number of times a short sequence of DNA is repeated at various sites in the plant genome (microsatellites). Isozymes and RFLPs gave very different estimates of gene flow among beet populations on sea walls and shingle in Poole Harbour, possibly because of selection at one or more isozyme loci (Raybould *et al.* 1996, 1997). In contrast, both of these markers, and microsatellites, showed similar patterns of gene flow among cliff-top populations (Raybould *et al.* 1998a). The data imply that significant amounts of gene flow (one or more migrants per generation) occur between beet populations up to 14 km apart (Figure 1). (Methods are being developed to generate confidence intervals of this estimate.) Gene flow on this scale means that transgenes will spread widely among beet populations unless they are at a strong selective disadvantage.

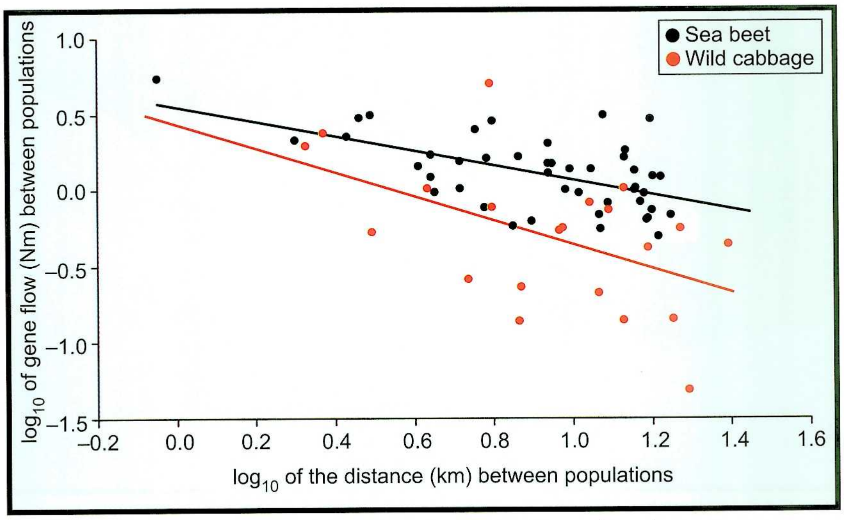

Figure 1. Gene flow among populations is estimated as the number of migrants per population per generation (Nm). As a rule of thumb, if Nm <1 (in other words $\log_{10}$Nm <0) populations are considered to be more or less isolated genetically. At any given distance, estimates of gene flow between pairs of sea beet populations are much higher than those between wild cabbage populations, probably because dispersal of beet pollen by wind is greater than the dispersal of cabbage pollen by insects

Observations of pollinators of wild cabbage (mainly queen bumblebees) indicate that most cross-pollination occurs between near neighbours (<20 m apart). Significant variation in the frequency of alleles at isozyme loci within populations (Mithen *et al.* 1995) also suggests gene flow is limited in wild cabbage. However, there is no such spatial variation within populations at microsatellite loci, and significant gene flow between populations up to 4 km apart is indicated by these data (Figure 1). Further research is required to find the reasons for this discrepancy.

The potential environmental impact of particular transgenes will be related chiefly to the way they alter plant fitness. By focusing on the trait and its effect on the plant and the population, studies have moved on to ask the 'what if?', 'so what?' questions which lie along the critical path of risk assessment. This has involved combining three approaches:

- the study of similar traits under selection in natural populations (analogue genes)
- controlled experiments testing the effects of particular traits on the population dynamics of selected species
- modelling of the impact on population growth rates of traits that change particular demographic parameters.

Glucosinolates are sulphur-containing compounds that mediate interactions between *Brassica* crops and herbivores. High concentrations deter generalist herbivores, such as birds, slugs and generalist insects, but attract and stimulate feeding and egg-laying by specialist *Brassica* feeders such as flea beetles (*Chrysomelidae: Halticinae*), *Pieris* butterflies and various weevils. It is known that there are significant differences in glucosinolate concentrations among wild cabbage populations in Dorset (Mithen *et al.* 1995) (Figure 2). These differences could offer insights into the effects of herbivore-resistance transgenes in natural populations. It has been discovered that cabbage seed weevil is most prevalent in populations where glucosinolate concentrations are highest. Weevil infestation also results in reduced production of viable seeds (Moyes & Raybould 1998). Using glucosinolate concentration as an analogue of a gene for weevil-resistance, it can be suggested that such a gene would increase seed output. However, it is not known whether population growth rate of wild cabbage is limited by seed production. We cannot be sure that weevil-resistant plants would be fitter than susceptible plants.

A concern that applies to all crops engineered for pest- and disease-resistance is that it may enable populations of resistant species to become more persistent or weedy. To understand if this is possible, we must identify the factors that regulate population size and, especially, the major causes of

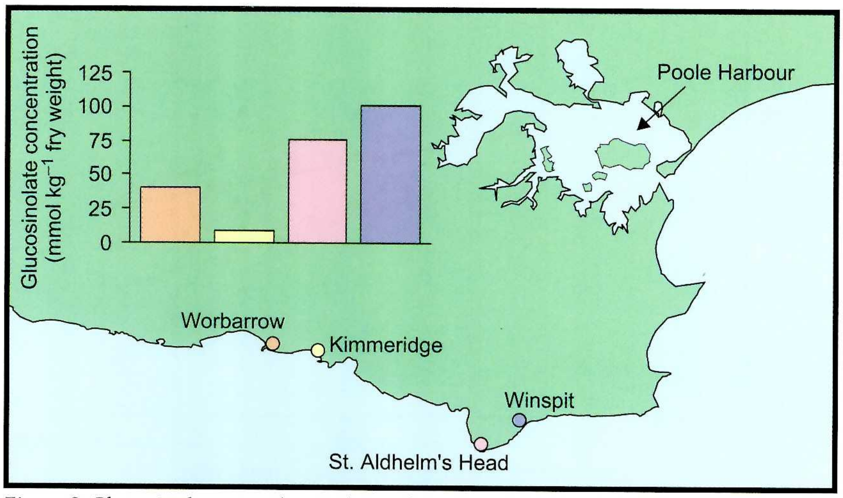

Figure 2. Glucosinolates are chemicals produced by cabbages and other *Brassica* species. They deter feeding by generalist herbivores (such as slugs) whereas they stimulate feeding and egg-laying by insects that specialise on *Brassicas*. This Figure shows the large variation in the concentration of aliphatic glucosinolates (those produced from the amino acid methionine) among wild cabbage populations on the Dorset coast

In collaboration with IVEM, ITE has studied the prevalence of six viruses in Dorset populations of wild cabbage and black mustard.

mortality. Two approaches have been tried:

- to establish experimental populations – in this case "feral" oilseed rape (*Brassica napus*) treated with insecticides (Raybould *et al.* in press) – in which the impact of the trait on reproductive rates is assessed
- to use population models to identify those demographic parameters which, if changed by modification, will most affect the rate of population increase.

Results of these studies clearly indicate, for example, that any trait affecting seed survival in oilseed rape would most strongly influence the persistence of feral populations. High seed mortality in natural populations indicates that even increasing seed production more than threefold by protecting against herbivores does not increase population growth rate.

Potential risks of releasing virus-resistant crops include the evolution of new virus types and, as with insect-resistance, the creation of plants with greater weediness because their population growth rate would not be suppressed by pest pressure (in this case, virus disease). The likelihood of these events occurring is, at least in part, related to the frequency of virus infections in wild relatives of virus-resistant crops. In collaboration with the Institute of Virology and Environmental Microbiology (IVEM), ITE has studied the prevalence of six viruses in Dorset populations of wild cabbage and black mustard (*Brassica nigra*), both relatives of oilseed rape (Plate 1). The key finding of this research is that virus prevalence varies significantly between species and among sites (Figure 3). Risk assessment must, therefore, be species-specific and site-specific.

ITE's research in this field continues to demonstrate the importance of a crop-by-crop, trait-by-trait, step-by-step approach to GMO risk assessment and, in considering the wider implications of the commercialisation of GMO crops, to target research efforts to key ecological processes. The numerous potential interactions and the long-term nature of many effects demand that in taking this work forward we concentrate on areas, such as virus-resistance and biopesticides, where there is the greatest uncertainty in the risk assessment.

The results of ITE's research are made available directly to relevant government departments and can both inform the risk assessment process in particular cases dealt with by the Advisory Committee on Releases to the Environment, and also help determine policy.

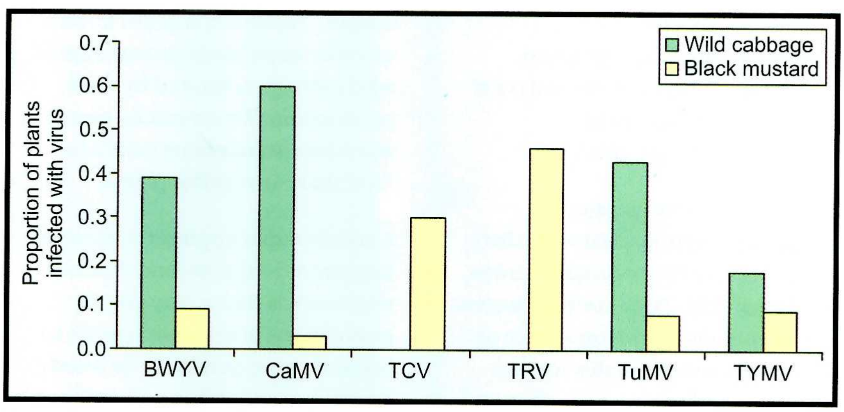

Figure 3. There are significant differences in the proportion of wild cabbage and black mustard plants in Dorset infected with each of six viruses. BWYV = beet western yellows virus; CaMV = cauliflower mosaic virus; TCV = turnip crinkle virus; TRV = turnip rosette virus; TuMV = turnip mosaic virus; TYMV = turnip yellow mosaic virus

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Future research will focus on the potential impact of transgenes for resistance to viruses (and other pathogens and herbivores) occurring in natural populations.