



**Institute of
Terrestrial
Ecology**

Annual Report 1994-95

**Centre for Ecology and Hydrology
Natural Environment Research Council**



The ITE mission

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

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

- the factors which determine the *composition, structure, and processes* of terrestrial ecosystems, and the *characteristics* of individual plant and animal species
- the dynamics of *interactions* between atmospheric processes, terrestrial ecosystems, soil properties and surface water quality
- the development of a sound scientific basis for *monitoring, modelling and predicting* environmental trends to assess past, present and future effects of natural and man-made change
- the securing, expansion and dissemination of ecological data to further scientific research and provide the basis for impartial advice on environmental protection, conservation, and the sustainable use of natural resources to governments and industry.

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

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

**Report of the
Institute of Terrestrial Ecology
1994–1995**

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Environmental risks and hazards

Environmental risks and hazards, including release of genetically modified organisms and improved prediction of extreme events

- Monitoring, modelling and prediction of extreme natural events including inland flooding, storm surges, seismic events, storm tracks and monsoons.
- Research and survey underpinning the assessment of environmental hazards such as land instability, the impact of drought conditions, changes in the geographical distribution of pests and diseases.
- Studies and risk assessment of the environmental consequences of the release of genetically modified organisms; research on gene transfer and other ecological and evolutionary impacts.

(NERC priorities 1995)



Introduction

Ecologists are increasingly finding that the dynamics of the systems with which they deal are dominated by the rare, extreme, and often unpredictable, event. Instead of being in equilibrium, populations are discovered to be recovering from some extreme perturbation in their past: the great storm, the extremely cold winter, the drought year, the fire, the oil spill, or the flood. Events such as the cold winter of 1963 or, more recently, the storm in south-east England on 15–16 October 1987 have left their fingerprint both on populations of individual plants and animals and on patterns at the landscape level.

The exact time of occurrence of many of these rare extreme events remains largely unpredictable. However, the fact that in some cases they have occurred in the past, and are likely to occur again in the future, renders tractable a study of their impact or potential impact.

For example, the extent to which intermittent fires, mostly the wildfires of the hot summers of 1976 but also some managed burns, dictate the pattern of successional change in Dorset heathland is described in the first article in this section. Remarkable resilience is seen to be an emergent property of this heathland vegetation mosaic when viewed within an appropriately long timeframe. This is despite periodic local, totally destructive, fires which remove all the vegetation from specific sites, and it emphasises that, however extreme it may seem to us, fire has played a key role in shaping the ecology of many of our natural and semi-natural biotopes. Many early-successional species depend entirely on extreme events such as fire and the windthrow of forest trees. The diversity of the community and the landscape is, perversely, driven by the fairly rare catastrophic event.

The trick, of course, is to predict the rare event. Within NERC as a whole, earth and atmospheric scientists and hydrologists are working to increase our capability of predicting extreme natural geophysical and meteorological events. For the ecologist, there is the prospect that some individual organisms will themselves, by dominance of the communities they invade, constitute a major environmental hazard. Again, we are increasingly finding that non-equilibrium populations display the shadow of a major biological event in the

past: a pest infestation, an outbreak of disease, the death or migration of a major competitor or predator. The impact of events such as the spread of myxomatosis virus in rabbits in the 1960s was both severe, far-reaching and often unexpected (eg the decline and eventual extinction of the large blue butterfly, described in earlier ITE *Annual reports*). The second article characterises the type of scientific understanding which is required to predict the likely impact of an invasive species, in this case bracken, under a range of future management regimes. Here, a knowledge of the plant's ecology is combined with ITE's land classification to identify those areas and conditions under which bracken may constitute a hazard, and hence require control.

Attempting to predict the third sort of hazard, or potential hazard, illustrated in this section – that from the release of genetically modified organisms – brings into play a wide range of ecological skills and research. The problems of making adequate and realistic risk assessments for the products of the new recombinant DNA technology have exercised the minds of industry, the regulatory authorities and scientists around the world. The third article in this section describes some research which is partly funded by the Department of the Environment's Biotechnology Unit and is being carried out in collaboration with the John Innes Centre and the University of Liverpool. It is aimed at identifying the possible risks associated with the widespread cultivation of insect-resistant crops. In this particular example, the factors influencing the distribution and frequency of genes coding for aliphatic glucosinolates, and thus providing defence against certain insect herbivores, are being studied in wild cabbage populations. These genes are among several natural equivalents of the genes being inserted into crops, and understanding their distribution and dynamics will greatly improve the process of risk assessment.

A J Gray



Large-scale dynamics in heathland: effects of wildfires

Large-scale ecology and management

Semi-natural communities are subject to successional change and, to maintain a variety of successional stages, these communities must be disturbed periodically by management. This form of management works on the premise that local extinctions of species occur (because of the disturbance), and the subsequent development of the community on disturbed patches depends on both the initial species composition of the patch and the composition of the surrounding patches. This latter feature reflects the capacity of the surroundings to supply immigrants which either maintain the populations of resident species or introduce novel species, thus determining the direction of the succession. Studies of disturbance regimes have emphasised the temporal features – the frequency of disturbance events and the change in species composition with time – and not the spatial relationships between patches. This is particularly true in conservation management where consideration of the frequency at which patches have been managed has taken precedence over where one should manage in the landscape to allow a dynamic maintenance of the different community types, and of populations and meta-populations of the component species.

This perspective is part of a broader investigation of large-scale processes in the Dorset heathlands, using experimental and modelling studies, and analyses of maps of the vegetation, management and disturbance episodes of the landscape over a long time period. The work will determine the effects of landscape structure on vegetation development and single-species ecology through studies of the dispersal of species among different patches, the effects of patch size and isolation on the survival of populations and community succession, and the effects of disturbance and management of individual patches on these processes. Work already carried out in this area includes:

- the large-scale dynamics of insect habitat (Webb & Thomas 1994),
- the responses of individual species to heathland fragmentation (Bullock & Webb 1995a), and



Plate 28. A wildfire on Dorset heathland

- landscape approaches to planning heathland restoration (Bullock & Webb 1995a; Webb, Veitch & Pywell 1995).

Here, we present an example of our approach – a study of wildfires in the Dorset heathland landscape.

Fires in heathland landscapes

European dwarf shrub heaths are both managed by fires and subject to unplanned fires (Plate 28). There have been a number of long-term fine-scale studies of community development following fires, but there have been no studies of the effect of fires on the stability of the heathland landscape. We have assessed these effects by measuring responses of a variety of vegetation types and plant species to wildfires across several different heaths in the Dorset landscape (Bullock & Webb 1995b).

In 1976 large areas of heathland in Dorset were affected by uncontrolled fires. We analysed the effects of these fires in 11 of the largest heathland fragments ($n=141$) which were distributed over the entire range of the Dorset heaths (Figure 49). Data were collected during surveys in 1978 and 1987 (Webb & Haskins 1980; Webb 1990), and relate to 3100 200 m × 200 m grid squares covering the entire heathland area in Dorset. Four types of heath (dry, humid, wet and peat) and five associated vegetation types (scrub, carr, woodland, grassland and bare ground) were represented. For each of the 11 heaths, we compared the cover values of

the vegetation types and their species compositions in burnt (28% of the area) and unburnt (61%) zones in 1978, shortly after the fires, and again in 1987 (Plate 29).

Five of the nine vegetation types responded to the fires (Figure 50). There was little difference in the proportion of dry heath between the burnt and unburnt zones in 1978, but in 1987 the burnt zones contained more dry heath vegetation. The dry heath decreased by about 5% over the nine years in the unburnt zones as a result of invasion by scrub, but showed little change over the same period in the burnt zones.

A significant proportion of scrub, carr and woodland was removed by the fire and these areas were seen as bare ground in 1978. Much of the former carr and woodland remained as bare ground in 1987, but the scrub regenerated totally. This probably indicates a transitional period in which what will ultimately be woodland is passing through a scrub phase. One might have expected dry heath to increase in the burnt zones as the former scrub and wood areas were converted to early-successional heath. As shown above, this was not the case and areas of burnt scrub and woodland regenerated as this type and not as heathland.

Thus, the proportions of the four heath types were all unaffected by burning and there was no subsequent revegetation of bare areas by heath vegetation. However, in both the dry and humid heath types, we

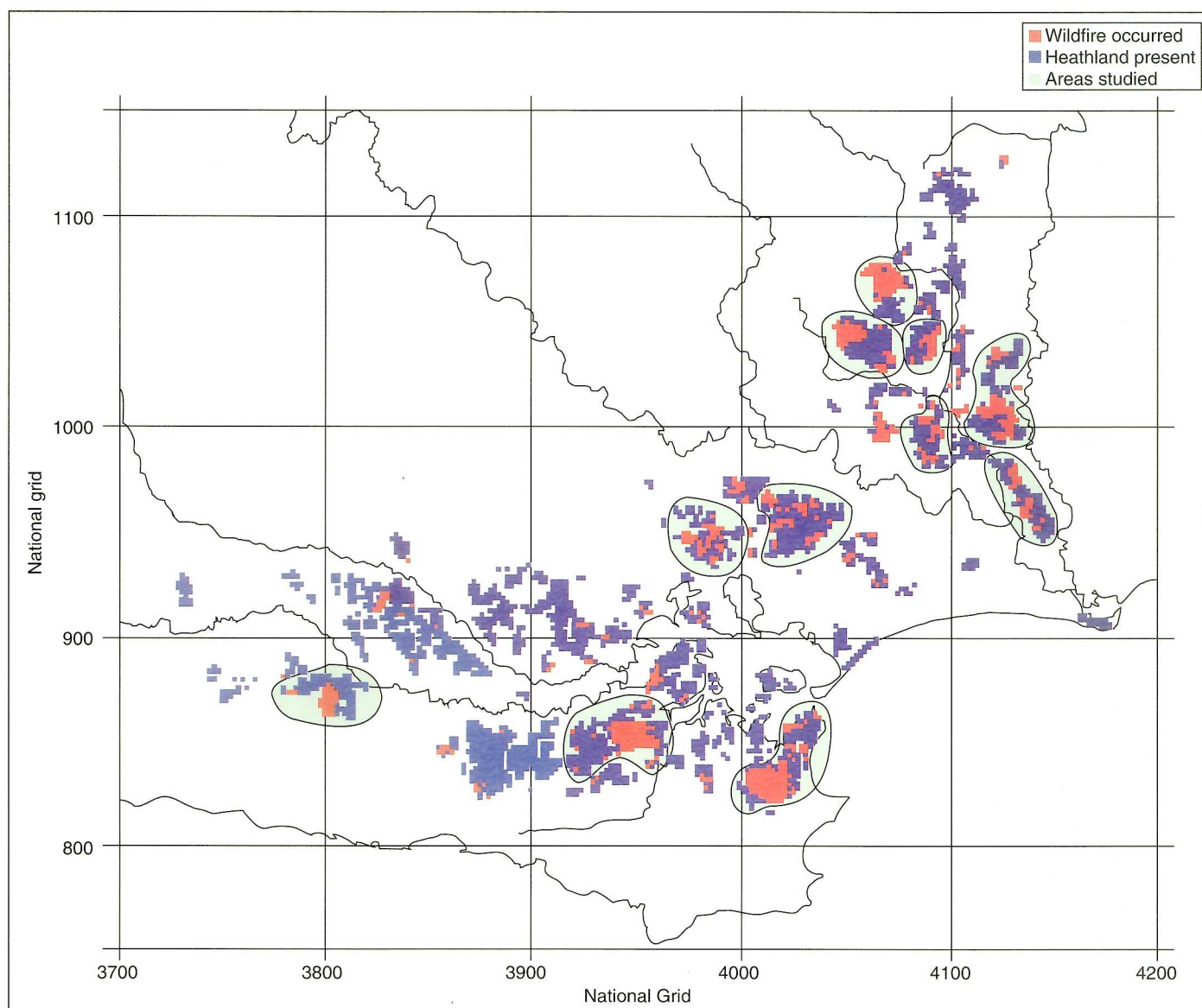


Figure 49. The location of heathland fires in Dorset in 1976. The grid line interval represents 10 km and the map area is 200 km². Heathland was present within every small 200 m × 200 m square marked in blue on the map. Wildfires occurred in the red heathland squares and the shaded areas show each of the 11 large heaths studied

found short-term successional trajectories in response to the fires, resulting in these areas returning to their pre-burnt states by 1987. Burning caused changes in the frequencies of the dominant species in 1978, but these changes were lost by 1987. The dry heath areas of the burnt zones were first colonised by bristle bent (*Agrostis curtisii*)-dominated vegetation which was replaced by heather (*Calluna vulgaris*)-dominated vegetation. Likewise, on the humid heath areas, purple moor-grass (*Molinia caerulea*) established after the fire to be replaced eventually by heather vegetation. This development contrasts with the stability of the unburnt zones.

Although scrub did not change significantly in extent between the two



Plate 29. Heathland regenerating after a fire

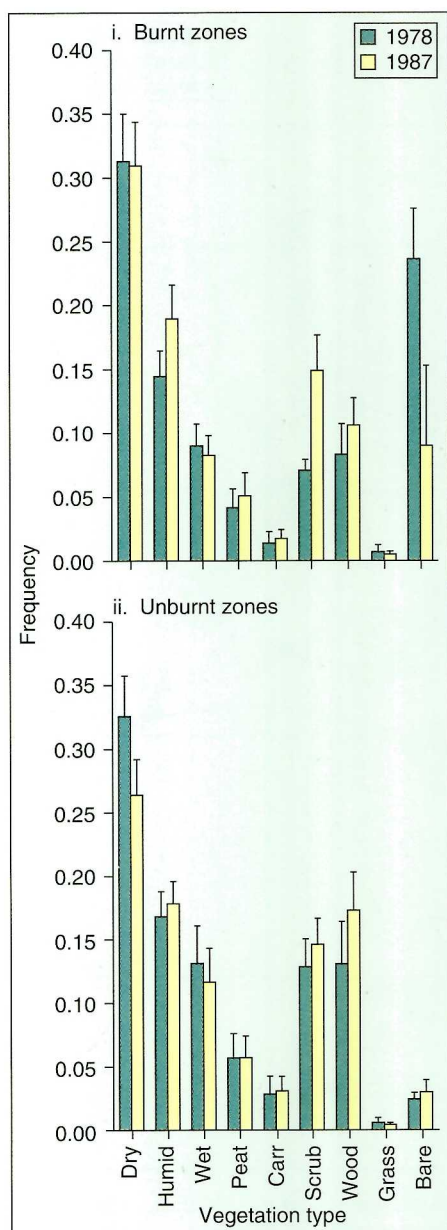


Figure 50. The mean cover frequency ± 1 standard error of each primary vegetation type in 1978 and 1987 in (i) burnt zones and (ii) unburnt zones of the 11 heaths

surveys, the composition on the burnt areas differed from the unburnt, with the proportion of silver birch (*Betula pendula*) increasing and of gorse (*Ulex europaeus*) decreasing. Over the nine years, the total area of bracken (*Pteridium aquilinum*) increased more rapidly in the burnt zones, whereas there was virtually no change in the unburnt zones, which supports anecdotal evidence that bracken tends to spread following fires.

In summary, by 1987 neither the extent nor the composition of the principal heathland types was affected by the fires which had occurred in 1976. The only long-term effect was in the species

composition of scrub. The fires had a beneficial effect in conserving the dynamic mosaic of the heathland vegetation types by preventing the succession of heathland to scrub and by reducing the cover of woodland and carr between 1978 and 1987. However, the observed effect on woodland and carr may reflect the longer timescale over which woodland develops compared with heathland. The only detrimental effect appeared to be the slight spread of bracken into burnt heathland. Overall, one might conclude that the 1976 fires, when viewed at the landscape scale and over a long timescale, had negligible or possibly beneficial effects on the mosaic of heathland communities.

Conclusions

We have deliberately adopted a large-scale approach, enabling us to examine the dynamics of the heathland vegetation mosaic over the entire landscape of the Dorset heathlands, rather than those of a small part of the mosaic. The interesting overall conclusion is that, when the entire heathland area is considered over an appropriately long timescale, the heaths are seen to remain stable, despite catastrophic disturbance at specific locations. Thus, the mosaic of vegetation types on the heathlands promotes resilience. This evidence supports our contention that responses to environmental factors and management planning will require spatial structuring and landscape dynamics to be examined.

N R Webb and J M Bullock

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Bracken spread in Great Britain and the fate of sites after control

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

Bracken (*Pteridium aquilinum*) is well known as a persistent and poisonous weed of grasslands and moorlands, particularly in the north and west of Great Britain. It is thought to have expanded from its past range as a result of many changes in past land use practices. These changes are as diverse as:

- 1 rural depopulation – such as events like the Highland Clearances,
- 1 switches from cattle to sheep as the major grazing animal – emerging fronds are less affected by trampling by lighter animals,
- 1 improved moorland drainage,
- 1 reduction in cutting for agricultural or industrial purposes, and
- 1 a general reduction in the intensity of upland farming.

It is certainly possible that recent and future reform of agricultural policy mainly leading to reduced grazing pressure in the uplands will have similar effects on the expansion of bracken into suitable habitats.

Identification of land at risk from bracken encroachment

A reduction in grazing pressure could have two effects on the current stock of bracken: encroachment from stand edges or linear features presently held in check by grazing could proceed, and bracken currently forming a sparse canopy that is prevented from increasing by grazing or trampling could have that restriction removed. The latter could also be affected by changes in climate (Pakeman & Marrs 1995).



Plate 30. Bracken encroaching into heather moorland in the North York Moors National Park

The availability of data from ITE's Countryside Survey 1990 provides the opportunity to classify land in terms of the risk of bracken encroachment or increasing dominance. Also, because the data on bracken distribution are available in a number of forms – land cover of dense bracken, land where dense bracken and scattered bracken is present, and presence in linear features – a number of classifications are possible. These classifications are based on statistics for each land class, and are hence only an indication of possible trends and do not imply that such changes will occur at a local scale.

Encroachment from linear features

Bracken is most common in linear features in the marginal uplands of the south Pennines and much of Wales, as well as in areas such as Dartmoor, Exmoor and the western coast of Scotland. Hence, the greatest possible loss of grazing land to bracken encroachment from this source could occur in these areas.

Encroachment from stand edges

This risk is very dependent on the characteristics of the neighbouring vegetation. However, if the presence of large areas of bracken can be taken as an indication of the possibility of spread from stand edges, then the greatest problems could occur throughout much of upland Britain at moderate altitude (Plate 30).

Increasing dominance of bracken

Large areas of land currently contain

bracken that is not as dense as possible under current climatic conditions. If contained by grazing/trampling pressure, then a relaxation of this pressure could lead to an increase in density of the bracken canopy and the subsequent loss of grazing value (Miles 1988). This is possible throughout much of Wales, upland England and, particularly, in western Scotland (Figure 51).

Vegetation development after control with herbicide

As bracken has become a problem species, considerable time and effort have been put into its control. Much of this control is done by herbicide application from helicopters, as many areas are inaccessible or impractical for treatment from tractor-mounted equipment (either cutting or spraying). Sites are usually monitored in terms of how effectively the bracken has been controlled; however, little is known about the rate and course of vegetation development after treatment. In 1990 and 1991 a number of sites in the North York Moors were surveyed to monitor the effects of a single application of asulam on both the bracken and the vegetation. The sites were revisited in 1994 as part of a larger national survey (carried out with the University of Liverpool) and the data from the two periods of recording were analysed using a range of techniques.

The species data from each site were subjected to an ordination using

DECORANA (Hill 1979a), and correlation was used to show those species most closely related to each axis of the ordination. The same data were classified using TWINSpan (Hill 1979b) into groups with similar vegetation.

For ease of interpretation, a hybrid diagram showing the two main axes produced by DECORANA and the centroids of the first four categories classified by TWINSpan is presented (Figure 52). Axis 1 was highly positively correlated with the moss *Campylopus introflexus* and negatively correlated with bracken cover. Axis 2 was similarly positively correlated with wavy hair-grass (*Deschampsia flexuosa*) and negatively with bilberry (*Vaccinium myrtillus*). Characteristic sites of the four TWINSpan classes are shown as part of Figure 52. Type 1 sites were mainly unsprayed sites with high bracken cover, type 2 had a substantial cover of bracken but some understorey of grass, type 3 sites had little bracken present but a high cover of mosses and bracken litter, and type 4 had high cover of mosses and grasses.

The trajectories of sites between the two survey periods and data on grazing intensity suggest a number of possible fates for a site after spraying. Where sites are little disturbed, the transition from type 1 to type 2 is observed, and reversed as the bracken recovers from the effect of spraying. Where grazing intensity is higher, then the litter layer is broken up sufficiently to allow the substantial growth of mosses, mainly *Campylopus introflexus*, and the transition 1 to 3 is seen. As the bracken regenerates, then sites may show the reverse transition, or revert via type 2 if there is substantial invasion by grasses before the canopy closes. If grazing and disturbance are sufficiently high, then sites may progress beyond type 3 to type 4. These sites have substantial cover of grasses, mainly wavy hair-grass, as well as *Campylopus introflexus*. Bracken recovery appears to be delayed, and the transition back to type 2 is slow or, in some sites, appears not to occur at all.

Thus, a high grazing pressure appears to delay or even possibly prevent bracken recovery from asulam application. However, in doing so, a grass-dominated community is produced. Though appropriate in some situations, most of the sites in the North

Persistence of heather seed under bracken

In an attempt to answer the first question – do heather seeds persist under bracken after a heathland or moorland site has been invaded – a small study was carried out on three sites across the country: Cavenham Heath in Breckland, Ramsley Moor in the Peak District, and Levisham Moor in the North York Moors.

At each site, soil and litter samples were taken along transects from outside stands of bracken to c 40 m into the interior of the stand. The assumption was made that the bracken stand at each site was actively encroaching, such that, as distance behind the stand edge increased, so did the putative time since invasion. Soil samples were placed in trays and kept well watered in an unheated greenhouse. Germinating seeds were counted as they became recognisable.

Heather seeds germinated in almost all the samples; however, germination was much higher in samples taken from outside or near the edge of the stand (Figure 53). Samples taken from more than 20 m into the patch contained only 21%, 60% and 7% of those outside the stand at Cavenham, Ramsley and Levisham respectively. Similarly, much of the seed was present in the litter layer rather than in the mineral soil in the interior of the stand – 28%, 40% and 35% in the soil respectively.

This result has a number of implications for vegetation development or restoration after control. The low density of heather seed deep inside bracken stands suggests that, after control, there will be little contribution to the vegetation cover from heather germinating from buried seed, even if suitable germination sites are made available by disturbance (whether by grazing animals or by deliberate attempts to break down the litter layer). In most cases, control of large, and therefore old, stands means that some form of propagule addition will be necessary to restore heathland.

The contributions of buried and added seed are being looked at as part of a large project investigating the integration of bracken control and vegetation restoration in collaboration with the University of Liverpool. Different methods of litter treatment (including raking and burning), fertilizer addition, nurse crop

Figure 51. The distribution of land classes with substantial potential for the conversion of sparse bracken to dense bracken as a result of land use change

York Moors are adjacent to heather (*Calluna vulgaris*) moorland, and were controlled specifically to restore this habitat. The absence of heather from these sites could be attributed to one

or more possibilities: the absence or loss of seeds from the seedbank, the lack of regeneration niches in dense bracken litter or in a sward of mosses and grasses, or uprooting by grazing sheep.

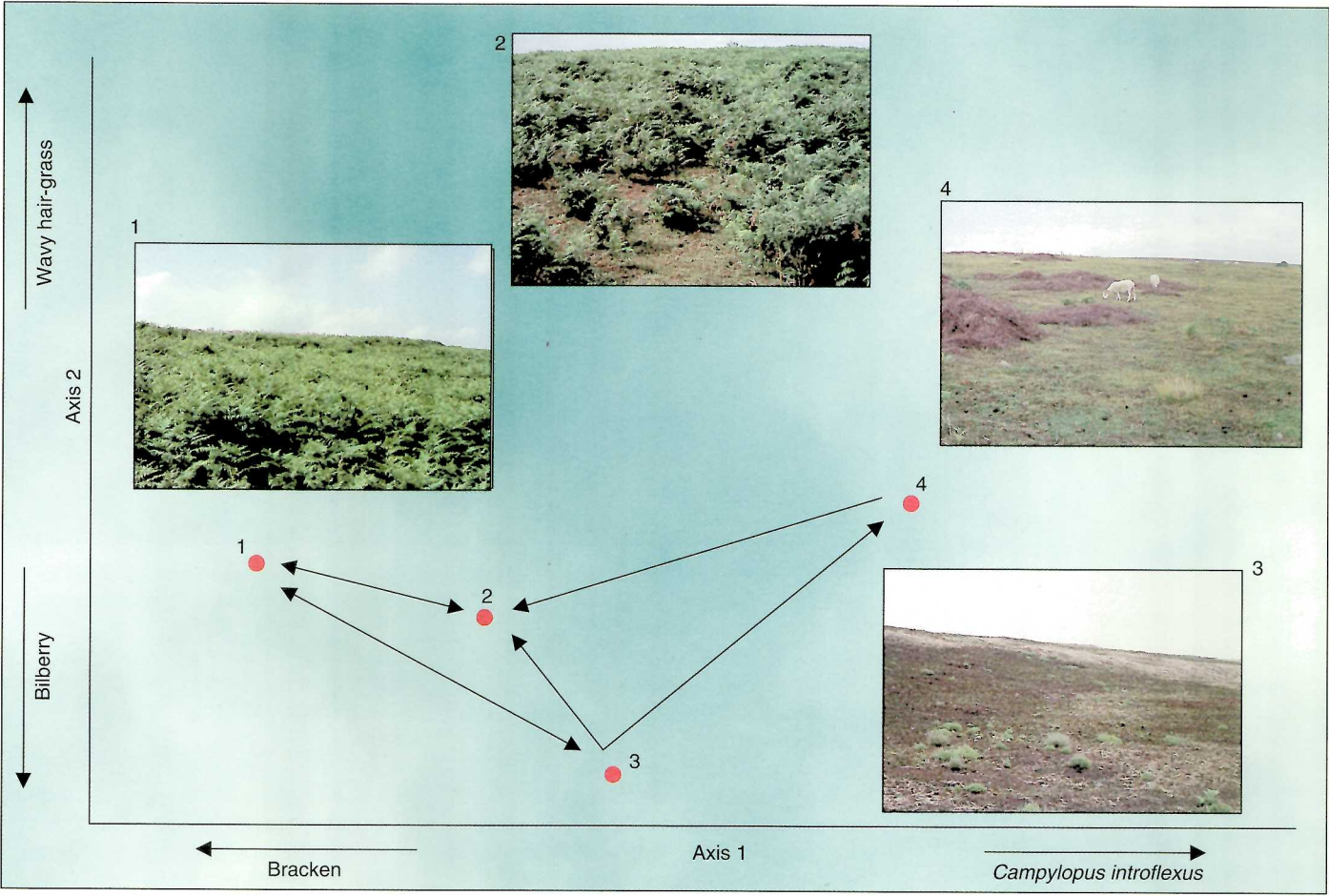


Figure 52. Hypothetical trajectories of sites in species space in the North York Moors subjected to treatment with asulam

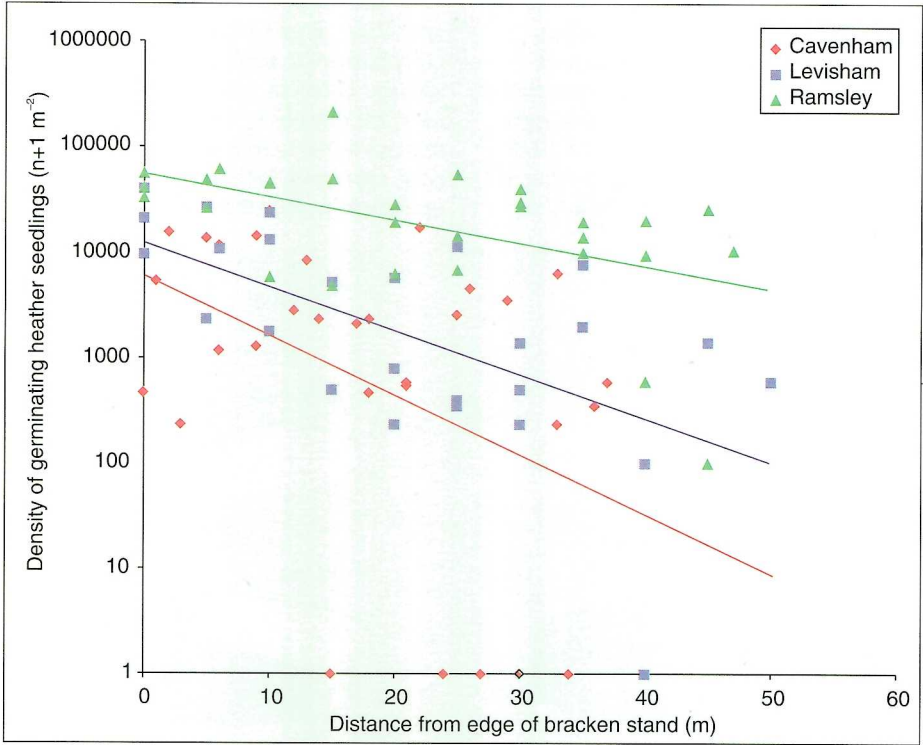


Figure 53. Density of germinating heather as a function of distance from the edge of the bracken patch at three sites. Fitted curves for Ramsley Moor: $r^2=0.26$, $n=30$, $P=0.004$; Levisham Moor: $r^2=0.23$, $n=27$, $P=0.011$; Cavenham Heath: $r^2=0.19$, $n=32$, $P=0.012$

sowing, stock exclosure, as well as different forms of bracken control, are being tested in experiments aimed at untreated stands of bracken and treated stands which have shown little recovery since control. The results from this study will be used to improve and update the advice given by the Ministry of Agriculture, Fisheries and Food to farmers about bracken control. In particular, for the first time the most suitable methods of control will be integrated with techniques for the subsequent restoration and management of the vegetation, with the aim of improving the agricultural or conservation value of the land.

R J Pakeman

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Predicting the environmental impact of genetically modified plants – the example of insect resistance

(This work was partly funded by the Department of the Environment and a CASE award from the Biotechnology and Biological Sciences Research Council, and involved collaboration with the John Innes Centre and the University of Liverpool)

The genetic modification of many crops is now routine, and several genetically modified varieties are nearing the point of commercial-scale release. Up to the end of 1993, 1025 field trials of genetically modified plants (GMPs) had been carried out. More than 38 species, with a wide range of modified phenotypes, and nearly 30 countries were involved in these trials (Ahl Goy & Duesing 1995). Regulators concerned with potential environmental effects cannot hope to scrutinise fully all applications to release GMPs as the number of crop/phenotype/environment combinations increases. Therefore, some categorisation of crops and modifications with regard to environmental risk is desirable.

GMPs could have an impact on non-agricultural ecosystems either by establishing feral populations or through gene flow to wild relatives by sexual hybridisation. In the UK, feral populations of crop species, with the exception of oilseed rape, tend to be very localised and ephemeral. Much of the research into the environmental consequences of GMPs has, therefore, been concentrated on gene flow.

The first step was to identify crop and crop relative pairs between which gene flow is possible (Raybould & Gray 1993). Many common crops, such as maize and potatoes, have no sufficiently close wild



Plate 31. Wild cabbage at St Aldhelm's Head, Dorset. Knowledge of the effects of insect resistance in wild crop relatives will help assess the impact of crops with genetically modified insect resistance

relatives in the UK for gene flow to occur, and several crops have been classified as 'low-hazard' GMPs under a fast-track risk assessment procedure.

What of the crops that can hybridise with wild relatives? Early work on risk assessment of these crops was concerned with isolation distances, and much effort was spent studying and modelling pollen movement. While isolating crops from wild relatives may have been practical with very small trials, commercial release will result in large volumes of pollen. Therefore, it is not realistic to expect isolation by distance to be effective when growing GMPs commercially. The right question to ask about a particular GMP that can hybridise with a wild species is not, therefore, 'how far away from wild

relatives should we grow the crop' but 'what are the consequences of the transfer of the genetic modification to wild relatives'.

One way to assess the impact of a genetic modification on a wild crop relative is to study the selection pressures acting on natural equivalents of the modified phenotype. For example, many crops have been modified with genes from a soil-dwelling bacterium *Bacillus thuringiensis* (Bt). When the bacterium sporulates, it produces an endotoxin that can be lethal to insects that ingest the spores. Different strains of the bacterium produce distinct forms of the endotoxin that are lethal to specific insect groups (Gill, Cowles & Pietrantonio 1992). The endotoxin is, therefore, an attractive

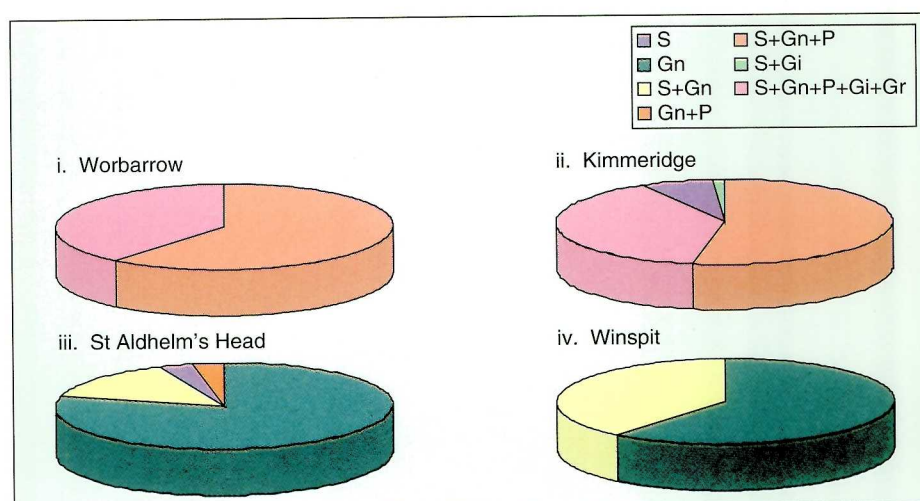


Figure 54. Frequency of glucosinolate phenotypes in Dorset populations of wild cabbage. These data indicate very marked allele frequency differences between populations at the four loci that control glucosinolate profiles (S=sinigrin; Gn=gluconapin; P=progoitrin; Gi=glucoiberin; Gr=glucorapin)

insecticide because it can be used against phytophagous insect pests while leaving beneficial insects unharmed. *B. thuringiensis* has been used as an insecticidal spray on crops for several years, but transferring the endotoxin genes to the crops themselves offers a more reliable method of protection (Lambert & Perferoen 1992).

At ITE Furzebrook we are studying insect resistance in natural populations of wild cabbage (*Brassica oleracea*) (Plate 31) as a model for the effects of the transfer of Bt and other insect resistance genes from modified oilseed rape (*Brassica napus*) to a wild relative. Insect resistance in wild cabbage is believed to be effected, at least in part, by volatile compounds called aliphatic glucosinolates. These compounds deter feeding by generalist insect pests, while attracting and stimulating egg-laying and feeding by insects that specialise on crucifers (Mithen 1992). This characteristic has similarities with the specific nature of the Bt endotoxins in having differential effects on various herbivores. Both the total level of aliphatic glucosinolates and the nature of the side chain modifications are important in producing these effects. Side chain modification is controlled by alleles at four loci, while the total level is under complex control but is highly heritable (Mithen, Raybould & Giamoustaris 1995).

Recent work has shown that clear differences occur in both the total amount of glucosinolates and the presence or absence of individual glucosinolates in Dorset populations of wild cabbage (Mithen *et al.* 1995) (Figures 54 & 55).

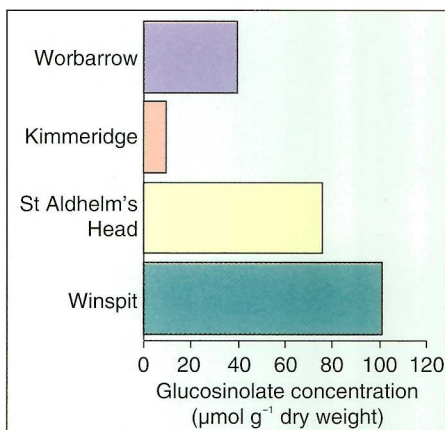


Figure 55. Average total aliphatic glucosinolate concentrations in leaves from wild cabbage populations in Dorset. The differences between populations are also found in plants raised from seed in a glasshouse. This demonstrates a genetic component to the differences



Plate 32. Wild cabbage infested with cabbage aphid. Aphids are a major vector of plant viruses, hence changes in insect resistance could alter the incidence of virus diseases in plant production

However, there are no significant differences in the occurrence of alleles at isozyme loci, which are assumed to be selectively neutral. Therefore, the differences in glucosinolates are unlikely to be the result of random genetic drift or founder effects. We are currently investigating the relationships between glucosinolate profiles and herbivore damage and plant survival and fecundity. New work will focus on the importance of herbivore-transmitted viruses in these relationships (Plate 32). Identification of the key selective agents and their interaction with defence compounds will allow more precise prediction of how new insect resistance genes might affect the dynamics of wild populations of both the plants and herbivores.

Bt genes may also become established in feral oilseed rape populations, either by spillage of genetically modified seed or by gene flow from cultivated to feral populations. To assess the importance of insect resistance on the population dynamics of oilseed rape, ITE has just begun a nationwide survey of the ecology of feral oilseed rape's major insect herbivores. This survey will provide information about the role of insect predation in the population dynamics of feral oilseed rape across a range of different herbivore faunas. Predictions can then be made concerning the introduction of insect-resistant oilseed rape varieties and possible changes in the abundance of feral populations. It will also show whether insects tolerant of insect-resistant GMPs are likely to evolve on modified feral oilseed rape populations.

It is not often realised that, in many cases, there are natural counterparts to the genes currently being transferred to crop plants. For example, as well as insect resistance, there are genes conferring herbicide tolerance, defence against viruses, and tolerance of drought and high salinity. Understanding the causes of the distribution, frequency and dynamics of these genes in natural populations will help us to predict some of the impacts of GMPs.

A F Raybould, C Moyes and A J Gray

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