Gene flow in the environment – genetic pollution?

G.R. Squire, N. Augustin, J. Bown[1], J.W. Crawford, G. Dunlop, J. Graham, J.R. Hillman, B. Marshall, D. Marshall, G. Ramsay, D.J. Robinson, J. Russell, C. Thompson & G. Wright

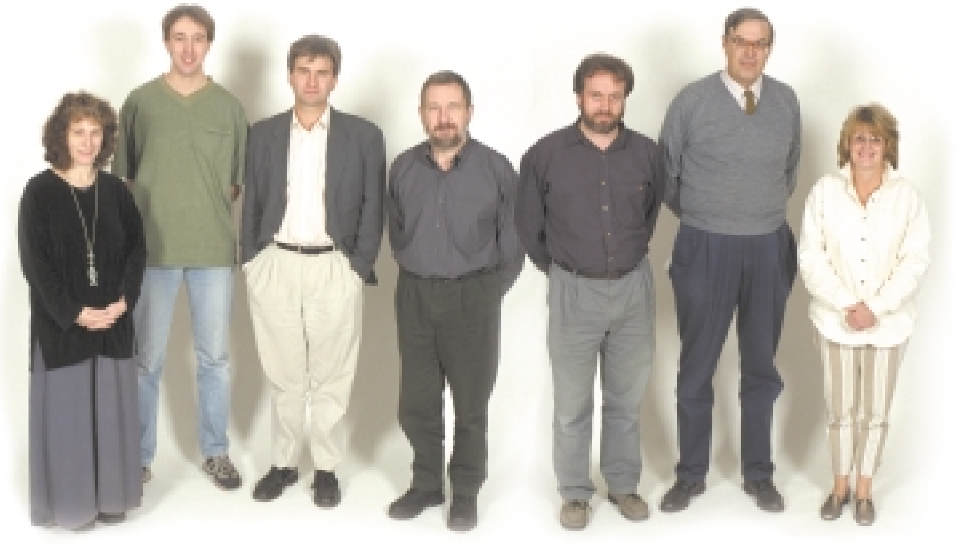
Biological invasions have had profound effects on human society from the earliest times. The spread of the black death in the Middle Ages, the devastations of potato blight, the effects on indigenous species by grey squirrels, dutch elm disease and flatworms have all been seen as detrimental to man or the environment. Others are seen as bringing benefits: most of our crops evolved elsewhere in the world and many culinary and medicinal herbs were brought to Britain by the Romans. Perhaps the greatest invasion is the import of vast numbers of exotic plants to gardens and greenhouses. Ecological invasions are an intrinsic part of ecology and evolution and we only consider them bad if they impoverish our health, livelihood or living conditions.

Recent events brought awareness of a need to be knowledgeable and vigilant about where food comes from, how it is grown and what it might contain. During the 1990s, agriculture and the food chain returned to be daily topics of conversation. In 1998, the concern was for genetically modified crops, and the term ‘genetic pollution’ came into common usage. There is no place in science for such emotive terms but publicly funded science must answer, as far as it can, the public’s fears with facts and sound interpretation.

The questions? Biological science is regularly in the spotlight. Is habitat being destroyed by land management practices? Will GM crops escape from fields, affect plants and animals, injure us? Will crops in general, and GM ones in particular, reduce even more the biological diversity of arable farmland? Will they contaminate other crops, cause more pesticide to be used, rather than less as some companies claim?

An increasing number of people have a stake in the debate - pressure groups, farmers, farm advisers, consumers, agrochemical companies and government. Opinions are too often polarised. In this confrontational atmosphere, the need is for clear, independent fact, answers and comment. A part of the debate is ethical, but independent research is essential on questions that science can legitimately address. This is not to say that scientists should not be ethical, but that the methods of science can only be applied to answer certain types of question through constructing hypotheses and testing them by observation, experiment and modelling. It cannot say, for instance, that grey squirrels or GM herbicide-tolerant crops are ‘good’ or ‘bad’. The answer depends on your standpoint. Science can, however, define what effect such organisms are having or might have on wildlife, habitat and health, and advise government and the public on the risks and hazards.

Invasions are complex biological processes. How do we study them? First there is the movement of plants or seeds, and the transfer of genes by pollen. The organisms have to find and occupy space and grow in their new environment, while the pollen has to find



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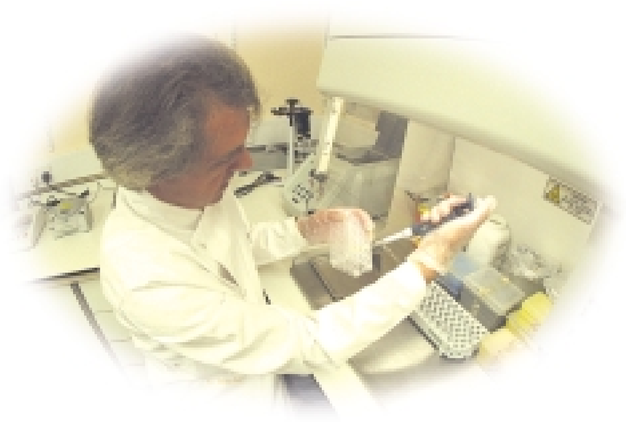
[1] University of Abertay, Dundee

receptive stigmas and create a new organism. Incoming plants have to interact for space and resource with the plants that are already there, and accumulate enough mass to reproduce and maintain a stronghold. The local environment acts on them and sorts out the less able. Exchange of genes creates variants that are continually re-sorted. The nature of the invaded population changes from what it was at the beginning.



The difficulty lies in the range of interacting scales. Growth or death, and exchange of genes, occurs through direct interactions between individuals. The individuals occur in patches or fragments and the fragments are scattered over the landscape. Single fragments evolve their own characteristics that fit them to the local environment. The patches are not independent, but potentially connected through the migration of seed or transfer of pollen. The individuals in distant patches can therefore influence the interactions within any other patch. Clearly, the degree of connectivity will depend on whether the pollen or seed moves by wind or is carried by insects or other animals, and how sexually compatible are the plants in the different patches. This system evolves therefore at scales of both the patch and landscape. This is what makes the study of gene flow and invasions so difficult and so challenging. Very advanced techniques are being developed and used to examine these exchanges.

New methodologies Movement of seed or genes into a fragmented ecosystem usually begins slowly and proceeds gradually. Only when things are well on their way are they generally noticed. The crux is detecting and interpreting rare events and small numbers. Methods and techniques are needed to do three things: to show that an organism or gene has moved from one place to another; to measure its effect on the existing organisms at that place; and (because these two can only be done on a small number of the organisms) to build the greater picture from all the available data. The sciences of plant ecology, genetics, zoology, pathology, mathematics and statistics are all put to use in this work. Research not only has to break new ground in each subject but to find new ways of seaming them together.

Genetic exchange and detection Advances in knowledge of the genetic code have led to robust techniques for genetically typing individuals and for detecting the movement of genetic material from one plant to another. Some of the techniques now in use at the Institute[1,2] are shown in Figure 1. Each is appropriate for a specific purpose. To confirm geneflow, it is essential to observe a transfer of genetic material from one individual or group to the progeny of another. Potential receptors and donors need to be genetically typed to search for distinguishing features in their DNA. Seed is collected from the potential receptor (mother) plants, germinated and the seedlings also genetically typed. The DNA of the mother plant and seedlings are then compared. Gene flow has occurred if a particular DNA sequence is found in a seedling but not in the mother plant. Further, if the number of potential donors is reasonably small, then some of the techniques can trace the plant from which the pollen came. As Figure 1 shows, the approach is being used to detect and quantify gene flow in plants ranging from feral brassicas to tropical trees.

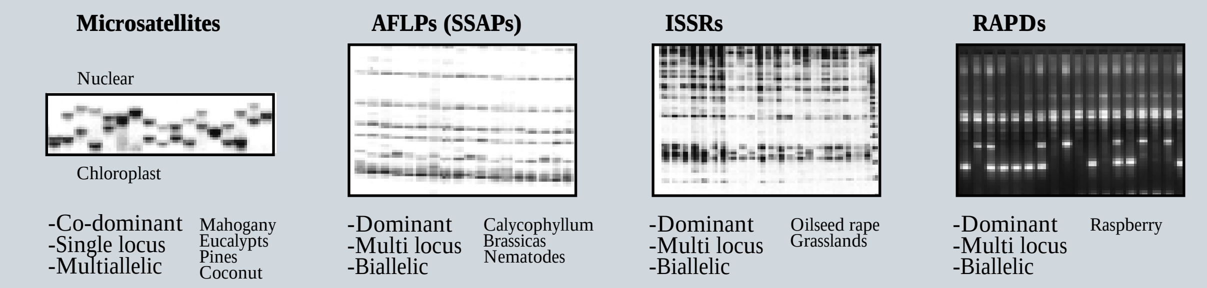


Figure 1 Banding patterns from some genetic technologies, with which it is now possible to assess gene flow and the spatial organisation of genetic variation. The techniques are used at SCRI with the species indicated.

The new genetic enabling technologies allow us to do things that were impossible a few years ago. To answer most questions, further knowledge is needed of how seed or pollen are moved by wind or insects, and whether plants are sexually compatible. This brings in new scales of operation that are influenced by the local weather and the flight paths and foraging behaviour of pollinators. Molecular science can contribute to knowledge at these scales by helping to define the distance over which pollen can move from one plant to another.

Science in this area has recently made major contributions to the topical and contentious issue of gene transfer from GM crops to wild plants. It has been suggested that GM characters will be transferred to weeds giving them resistance to weedkillers and insect pests. The flow of genes from some crops to some wild relatives is possible and will happen if GM crops are deployed on a large scale. Indeed, crops and weeds have exchanged genes since the beginnings of agriculture, so there is nothing new in the process itself. So far, there are few indications in the UK that crops are crossing with other species to increase the latter's ability as a weed. Those crops and wild relatives that are most likely to exchange genes in the UK are known in principle[3]. For instance, the potato has no wild relatives in the UK that are sexually compatible with it, whereas oilseed rape can potentially cross with wild turnip and wild radish. However, gene transfer is much more likely from crops to feral descendants of crops growing as weeds within fields, and could cause problems for the farmer.

Economic issues aside, any transfer from crops to wild relatives might impoverish their diversity, an event unwelcome in itself but which could weigh against crop improvement in the long term if the wild relatives contain potentially useful genes. Again, sexual compatibility is crucial in assessment. The risk in Tayside of cultivated strawberry crossing with wild strawberry is negligible because they are genetically incompatible, while that of cultivated raspberry crossing with wild raspberry is moderate because they can mate freely. Detailed studies at SCRI on wild and cultivated raspberry are given later as a case history.

Sorting, extinction, amplification Seeds or vegetative parts of invasive individuals face not only severe physical and chemical environments but also the competitive influences of other organisms. Seed is attacked by fungi, bugs and birds. If it lives to germinate, it faces an aggressive set of species. An invading organism enters an ecological assemblage that primarily determines its rate of establishment, extinction or amplification. Many factors mitigate against the ingress of an alien organism, and many invasion events and many cycles of reproduction are likely to be required before it gains a secure place.

Invasions and population structure In an established arable field or wayside patch of ground, perhaps 30 weed species cohabit in the soil as dormant seed. Among them are likely to be several of the typical, economically damaging, arable weeds: fat hen, cleavers, blackgrass, wild oat. Each is at least as capable of exploiting time windows in the weather and husbandry as any invading type such as feral oilseed rape or feral beet. The existing seedbank species occur in some hierarchy of abundance, and are distributed over space in characteristic ways. Typical abundance rankings show a wide range from species that are very dominant (10,000 to 100,000 in a square metre down to plough depth) to those that occur relatively scarcely (<1000).Which individuals are dominant depends on the soil, the rotation, the use of herbicide, and other factors. The Institute's unrivalled database on arable buried seed (seedbanks) is continually probed to answer questions on arable diversity[4]. Spatial maps of the seedbank in a field (Fig. 2a) have interesting features, but interpreting 30 or more of these for individual species presents a major problem. Statistical procedures are therefore used to condense the masses of data that accumulate from measuring communities. For example, Principal Co-ordinate Analysis gives a quantitative and also visual summary of the diversity among samples or experimental treatments. The analysis is applied in Figure 2b to compare the assemblage of species that developed in two rotational treatments at three sites[5]. Each symbol represents the arable plant community at a sample point in a field. (The farther apart two symbols are, the greater the difference in the species detected at the two sample points.) The seedbank was small and similar at the start of the experiment (not shown). After 6 years, during which herbicide input was reduced and spring-sown crops were introduced to the winter cereal rotation, a marked divergence of the communities occurred, shown by the spread of symbols and separation of sites. The weed communities were very different at the end, potentially providing contrasting opportunities for an invading species. Land management and location are therefore central to the progress of invasions.

The feral weeds of crops such as oilseed rape, beet and potato, and certain wild relatives, all now inhabit

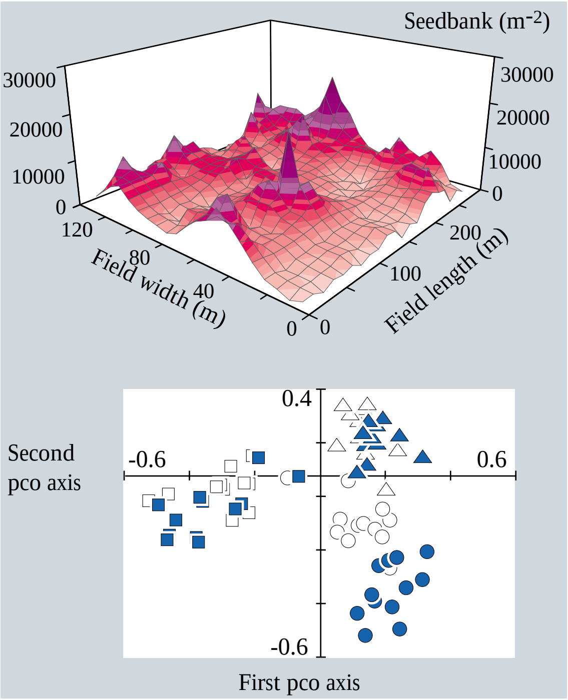


Figure 2 Examples of (A) spatial pattern in a weed community and (B) Principal Co-ordinate Analysis, which condenses information on many species: symbols represent data for experimental plots at three sites (triangles, circles and squares) and two rotations per site (open and closed symbols). The distance apart of any two symbols is a measure of the difference in the species present.

seedbanks of arable and waste land. The significance of the feral plants is that they will emerge with a crop of the same species, are largely indistinguishable from the crop, are difficult to control in that crop, are generally sexually compatible with it, and are close enough to cross-pollinate with it in quantity.

Linking fragments in the landscape The Institute now has an extensive network of sites throughout the UK and overseas where the composition and dynamics of plant communities are studied. More intensive research to link both fragment and landscape scales is concentrated in the Tayside region using 'model' plant systems: the feral brassicas[6], descended mainly from swede and turnip oilseed crops and the wild raspberry[7]. Additionally, and as part of co-ordinated research programmes, the Institute carries out field studies on species-rich grassland, Scot's Pine[8] and a range of tropical trees. Populations are mapped spatially and their origins and persistence inferred. In selected fragments, the genetic markers are used to discover which cultivars they descend from and whether new genes are entering the fragment. This long-term work of plant demography provides a natural laboratory, a sound foundation and a context in which to answer a range of questions on policy and management (examples are given later). Because all these populations are examined with minimal disruption to them, further science is needed to understand how they function.

Detection and quantification of pattern It is imperative to be able to detect small changes in populations so that the impacts of migrating individuals or incoming genes can be judged. It is not usually enough to detect that a particular event has occurred. Migrations and other invasive events have spatial and temporal dimensions: they affect the patterns in existing populations and not just the numbers. For this reason, techniques of spatial statistics are being developed which allow an existing pattern and its change over time to be quantified[9]. The technique is demonstrated by means of four artificial patterns, which were simulated by a computer programme (Fig. 3). The blue and pink squares could, for instance, represent individuals of a different genetic type, and the intensity of colour, their numbers. In the top left pattern, the colours are independent of each other. In the top right, they are arranged along a gradient with more

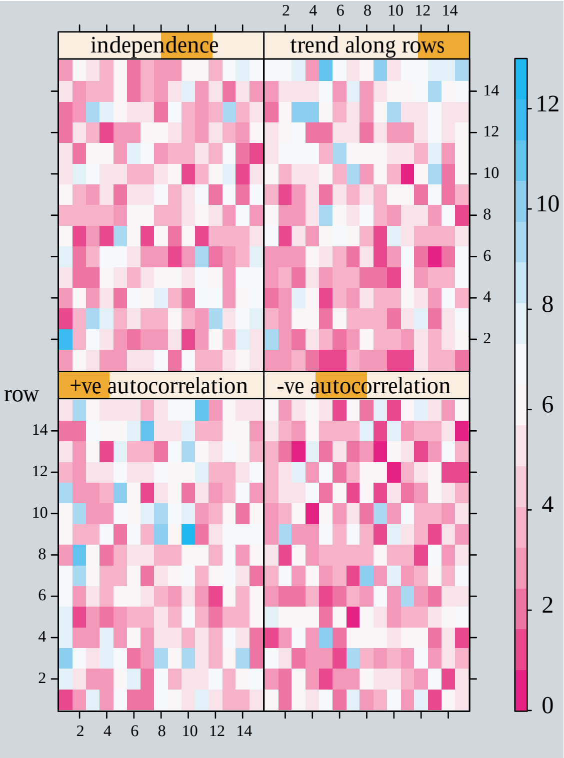


Figure 3 Four computer-simulated patterns to show different types of spatial arrangement between pink and blue 'organisms', the abundance of which is indicated by intensity of colour[9]. Text gives explanation.

pink at the top and more blue at the bottom. The two graphs at the bottom show different forms of distribution where the colours and intensities are not independent: deep pink squares are commonly adjacent on the right, rarely adjacent on the left. Similar patterns occur in nature and tell us something of the underlying processes. It is not easy, however, to establish by eye that the four patterns are different, and in particular, independence (top left) looks very similar to positive autocorrelation (bottom left). There is a clear need, therefore, to demonstrate and quantify spatial pattern and its change over time using such advanced statistics. These methods are now being applied to vegetation and will find many uses in population dynamics and gene flow.

Imposing pattern experimentally A further, complementary step is to study the way artificial patterns affect interactions between plants. Much previous work in cropped land has examined plants in fairly uniform arrangements. Experiments on crops typically vary the density (number of stems per square metre) but keep plants regularly spaced. This is not how weeds and other wild populations become arranged. Rather, invading individuals find themselves within complex existing structures of different size, density and shape. Trial designs that simulate more variable states are needed for this purpose.

As examples, three planting patterns are shown in Figure 4. Each represents a feral or weedy patch having the same number of plants but a different degree of aggregation. From left to right, the pattern gets more aggregated, with more open space, more crowding, and more internal ‘edge’. The basic pattern is a Sierpinski triangle, whose various forms allow precise computation of inter-plant distance and plant neighbourhood. Comparing a number of designs like this enables us to look at both competition and gene exchange over a wide range of plant neighbourhood in a (relatively) very small space. The design illustrated was used in 1998 to examine the exchanges that might occur if a new cultivar of oilseed rape (pink squares) invaded an existing patch (blue squares). The more aggregated patterns caused greater size inequality among the individuals. Also, molecular detection techniques showed that up to 60% of the pink progeny contained genetic information from the blue, suggesting that the type in low number was diluted by the dominant type. In this experiment, the types were two different conventional varieties, but the technique can be adapted to investigate the influx of new types of crop. This is fairly fundamental science that will help our understanding of applied work on the spread of genes among feral crop plants. Research using these imposed patterns provides a link to understanding the real happenings in nature.

Mathematics for scaling-up and management

When a gene is modified by conventional or GM technology, it causes certain changes in the properties of the plant. However, many questions about that gene are asked of its effects at the much larger scales of the plant community or landscape. Will it alter the use of pesticides or the diversity of arable flora and fauna? Is there some state in the regional distribution of vegetation fragments that gives rise to rapid invasion and gene flow, and can land management act to prevent this state occurring? Do things happen at the landscape scale that are simply not evident from research on small scale trials? Very often, the full information required to answer such questions is not available. Pieces of the picture exist but not the whole. Research funding is limited, so where should the effort go?

At SCRI, we are developing advanced mathematical techniques both to link disparate sets of information and to form hypotheses to aid our experiments. The sequence goes like this: certain patterns (in species

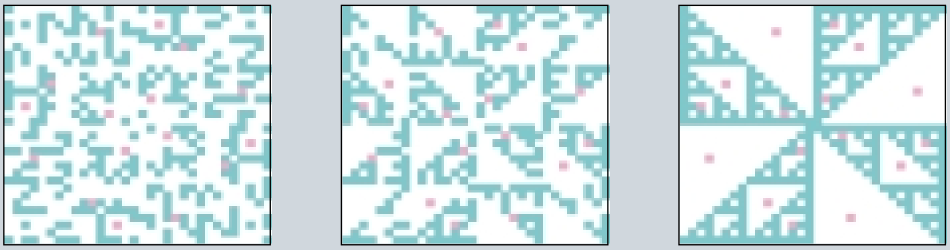


Figure 4 An experimental design based on a Sierpinski triangle, used as a planting pattern to study gene flow and competition among two plant types (identified by colours). The number of plants in the patch remains the same but the degree of aggregation increases from left to right.

abundance, spatial distribution, etc.) in a vegetation type have been detected in the field. The origins of these are uncertain so they cannot be managed. If the community is not probed, its functioning will be obscure; if it is disturbed, it might show untypical effects. As an intermediate step to gain further knowledge, a limited number of plants are removed and their physiology and genetic diversity investigated. Next, simulated communities can be set up (as above) in imposed patterns. But despite all this, there is still uncertainty. Mathematical models are therefore used to reconstruct the community from all the knowledge there is about it. The point of modelling is that it predicts something about some feature of the community that can then be tested with minimal interference back in the field. The process of modelling and experiment is cyclical.

In the most advanced models, individuals interact through physiological processes over a spatially and temporally variable resource (simulating nutrients). Change over time shows a succession from plants that seed rapidly (typical invaders) to plants that retain resource. In this way, models show how the interactions between individuals affect the evolution of patches, and how invasions might occur and be checked. Research is moving rapidly towards simulating the effect of introducing new botanical characteristics (including those of GM plants) to the modelled community. Other forms of modelling work at the scale of the landscape to examine how genes might move between fragments or from crops to feral plants and weeds[10, 11].

Questions answered on conservation and ecological risk

Conservation of fragmented populations The spread of urban land and intensive agriculture and forestry during the past two centuries has caused wild places to decline in area. Many wild plants now exist in fragmented habitats or patches sometimes separated by long distances. Modern approaches to conservation demand that such habitat is at least maintained and where feasible increased. However, the conflict of different interests means that questions are often asked of the importance of a plant or a group of plants. For instance, how much of the diversity of a species will be removed if a certain habitat is destroyed or how much habitat needs to be conserved if the diversity is to be maintained? The techniques described are now being used to answer these practical questions. A local and a more exotic example illustrate the potential.

The wild raspberry (*Rubus idaeus*) grows throughout Europe, including the raspberry-growing areas of Scotland where it is important to the economy. The wild and cultivated raspberry can cross-pollinate and exchange genes. Questions arise about the diversity of the wild populations, whether the cultivated raspberry is eroding the diversity of these populations, and whether the wild populations contain genes and character traits that might be useful in breeding for, say, pest resistance or hardiness to cold? One obvious difference between the two forms is that the wild are generally spiny while the cultivated have smooth stems. A search for smooth stems in wild populations[10] suggested there was little escape from plantations to the wild. However, spininess is not a neutral character, in that spine-free escapes might be more likely to get eaten than spiny ones. Accordingly, a combination of DNA-based[7] and physiological methods were used to explore the diversity of wild populations compared to the widely used commercial clones.

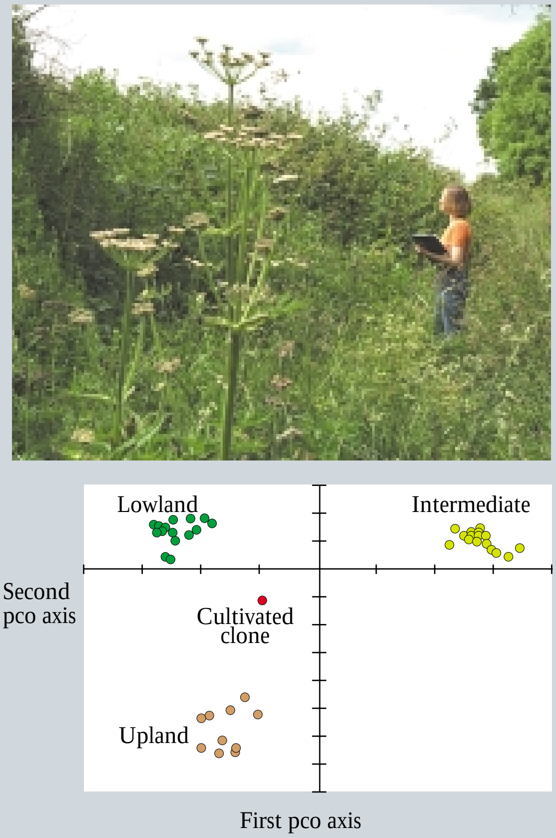


Figure 5 Statistical analysis of genetic marker data (RAPD, Fig.1) of wild raspberry individuals collected from upland, lowland and intermediate sites; distance between symbols (individuals) is a measure of genetic dissimilarity and clumping shows genetic differentiation between sites. None of the populations is similar to the cultivated clone. Photograph shows a lowland population.

The results showed evidence of great diversity in the wild populations compared with the cultivated clones. The study is not complete, but results so far indicate there is not much gene exchange between the wild and cultivated forms. Are there areas of greater diversity? The most diverse forms occurred in the Angus Glens, but even wild populations near the Tay estuary were quite different from the cultivated clones (Fig. 5). If the upland populations were erased, then certainly much of the diversity in form and genotype would be lost. They have an important ecological role, providing cover and food, but we do not yet know whether these wild populations contain genes and characters that would benefit the soft fruit industry. A collection of wild raspberry has now been established at SCRI, for the purposes of study and conservation.

The second example is a dispersed population of the tropical hardwood mahogany, *Sweitania humilis*, where the remaining trees occupy isolated patches in the landscape. Pollination occurs by means of an insect. Questions were asked whether isolated single trees or small groups were genetically cut off from the rest and how their conservation should be managed. They might, for instance, contain important genes and characters but not be able to contribute these to the larger patches, some of which lay several kilometers distant. A DNA marker technique was developed[11] which enabled the genetic material carried in pollen from each individual tree to be identified. If a DNA marker from one tree appeared in the seedlings produced by another tree, then clearly, genes had moved with pollen from one to the other. The results showed there was extensive gene flow between patches and that isolated trees were still contributing to and receiving genes from the larger patches (Fig. 6). Keeping the isolated trees was therefore important for conservation of the species in that area. Much is being learnt from this work and that on wild raspberry, about the kinds of fragmentation pattern that encourage genetic exchange and diversity.

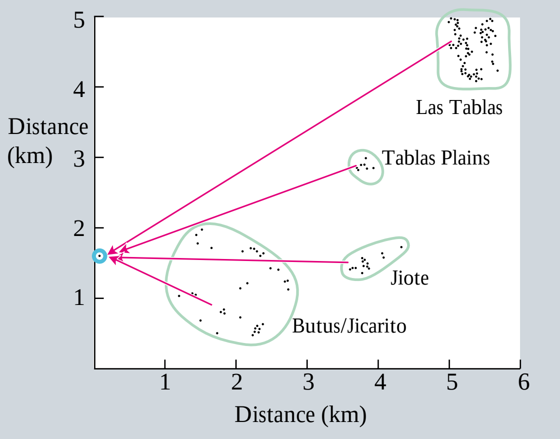


Figure 6 Gene flow to an isolated tree of the mahogany, *Sweitania humilis*, from fragmented patches up to 5 km away (using microsatellites, Fig. 1)[11].

Risk assessment and GM Crops Since 1993, work at SCRI on the assessment of ecological risk has concentrated on oilseed rape. A number of important questions were asked by government concerning the distance travelled by pollen and genes, the persistence of feral populations, the contact between ferals and crops and the general likelihood and extent of gene

Figure 7 Feral oilseed rape population (large plants left) growing adjacent to a crop field in 1998, and DNA fingerprints (ISSRs, Fig. 1) of two varieties, Rafal (grown 1987) and Inca (grown 1998), and of a selection of the feral progeny in 1998 showing the Rafal fingerprint and Rafal-Inca hybrids.

flow across an agricultural region. One outstanding question was settled in 1998, and that was whether a feral descended from one crop type could hybridise in a subsequent year with a new crop cultivar. It was previously shown that the predominant DNA fingerprint in a persistent feral population was equated with a source crop last sown in autumn 1986. Other genetic types, possibly other varieties and hybrids were present also in the population. However, corroboration of gene flow was obtained by showing that an adjacent oilseed rape crop, flowering in 1998, hybridised with the feral descendants of the original cultivar (Fig. 7).

Moreover, the integration of data and theories through mathematics enabled a finer definition of the problem at the scale of the landscape. The question that modelling addressed was whether earlier measurements from single fields near SCRI could be scaled up to predict gene flow in a landscape of tens or hundreds of kilometres. Different sets of data were combined with a physical model of pollen dispersion to give the first regional scale model of gene flow, which predicted (contrary to much current thinking at the time) that most feral populations could receive genes from several fields and that the regional aggregation pattern of the fields determined how much each population would receive from a hypothetical GM field. Fields and ferals were therefore ‘regionally coupled’[12, 13].

This prediction of course, required verification. Accordingly, male sterile bait plants, which do not produce their own pollen and which act as biological pollen detectors, were dispersed around the countryside during the oilseed rape flowering season in 1998. Any seed set on these plants indicates pollination by other plants. This large-scale approach in an agricultural landscape was a radical departure from previous methods. It confirmed that pollen indeed travelled long distances, that bees were important vectors between crops and ferals, and crucially (by taking advantage of the presence of a commercial GM trial in Tayside), that the spatial arrangement of GM and non-GM fields determined the balance of GM genes in the progeny of the bait plants[14, 15]. Because the bait plants do not produce their own pollen, uncertainty remains in the true magnitude of gene exchange and establishment of hybrids at distance from a source field. Research is continuing to examine the relative ability of self and foreign pollen to fertilise flowers and, in effect, to calibrate the data using bait plants.

The progression of research on the ecological effects of oilseed rape [6, 12-16] would not have been possible without the contribution of many disciplines. The main findings can be summarised as:

- pollen moves over at least 4 kilometers;
- the pollen is still alive at these distances and can pollinate flowers;
- it can be carried by both wind and insects;
- many feral populations die out quickly but others persist in fields and around agricultural land for at least 10 years and probably longer;
- feral populations can receive genes from crops of oilseed rape.

The implication is, that by these means, genes from GM crops will likely enter feral oilseed rape populations and persist there for several years. However, the ferals are unlikely to dominate the arable community. For example, feral oilseed rape occurred at all three sites in Figure 2, but did not take particular advantage of the new niches as did many other weed species.

The need to explain complex and uncertain information
The public increasingly want to be informed and reassured about risk and hazard. Scientists must find ways of getting the message over, despite the various grades of certainty in the data. Some conclusions can be stated with absolute certainty and these are the easiest to transmit. The statements on oilseed rape bulleted above are all-or-nothing statements. They are very useful for giving government departments and the informed public the “worst case scenario”. Even though quantities are included (4 kilometres, 10 years), none of the statements gives a measure of how much will occur or how likely each event is to happen.

Others conclusions have to be qualified by some expression of uncertainty. Moving to the question of how much pollination or gene flow there was at such and such a distance, there is no certain answer. The result depends on many factors: local weather, the lie of the land, the number and behaviour of insect pollinators, the size of the source field, the size of the sink population, and the arrangement of surrounding fields. The answer to a question of this type is therefore much less straightforward but can be given scientifically by means of graphs and cautiously worded arguments stating statistical probabilities. In order to address this problem, a research area is developing at the Institute specifically on modelling and interpreting uncertain information[17].

Admittedly, this advanced uncertainty-modelling is unlikely to enable the non-scientist to grasp the risks and hazards. Other forms of wording are needed. Few of us can cope with too many categories; perhaps no more than three, such as certain to happen, likely to happen and unlikely to happen. Examples of certain to happen are given above. That genes will move from GM oilseed rape crops to some relatives is likely to happen. Take again the scare of 'superweeds': the notion that herbicide tolerance will spread from GM crops to arable weed species and create new weeds that are very difficult to control. The weight of evidence is that (although such hybrids are likely to happen), GM superweeds are unlikely to arise in the UK for the following reasons: (a) the wild relatives in question are not particularly aggressive or competitive as weeds, (b) having herbicide tolerance will not alter this aggressiveness unless the particular herbicide is used, (c) other herbicides or weed control practices could be used to control them, (d) other highly aggressive weeds are more likely to dominate in any case.

The implications for agricultural systems The movement of seed and pollen will have to be measured and managed much more in the future than it has been. This will be so whether GM crops are grown commercially or not. Crop products are becoming more specialised and there is an increasing general need for purity. Large sections of the public are insisting that agriculture protects and enhances the habitat and the wider environment.

In principle, and as shown above, detection of gene flow from a GM or other specialised crop into a conventional crop is straightforward. The novel gene can be detected in seeds, or seedlings grown from them, by PCR-based methods. However, when GM pollen from an extraneous source is competing with a much larger concentration of pollen from within the conventional crop itself, the proportion of seeds acquiring the novel gene may be very small. Thus, although PCR-based methods are extremely sensitive, there will be a lower limit below which gene flow will not be detected in practice.

The detectability of gene flow has acquired considerable political importance in the context of food labelling, because consumers are demanding that food derived from GM crops be labelled as such, so that they can choose whether to buy it or not. In a crop such as sweet corn, gene flow from a nearby GM maize crop could result in a few kernels on an otherwise non-GM cob being GM. A scientific question is: at what level is such "contamination" detectable? But there is also a political question: what level is acceptable? The Soil Association, representing organic farmers, wishes there to be a zero tolerance of GM gene flow into organic crops, but this is probably impracticable. A draft EC Regulation proposes a 1% tolerance level for the adventitious presence of GM-derived material in any food ingredient from a non-GM source, for labelling purposes.

In a crop such as sugar beet, in which the yield is vegetative, the product will be unaffected by gene flow into the crop itself, but gene flow in the previous generation into the seed crop may be relevant. Moreover, with a product such as refined sugar, which contains neither nucleic acid nor protein from the source plant, there is no analytical way in which to determine whether it is derived from a GM crop, a non-GM crop, or whether gene flow has occurred in the crop. The consumer's "right to know" may be satisfied only by an elaborate and costly system of traceability.

An interesting sidelight on gene flow occurs when the companies that have developed GM crops try to enforce their prohibition on farmers saving seed from them. Companies will have to counter the defence that the seed were saved from a conventional crop, which had acquired the novel gene by natural gene flow.

Managing geneflow Such issues highlight the fact that gene flow will increasingly be a factor that has to be monitored and managed in daily agricultural practice. Isolation distances that cause detectable or acceptable gene exchange might need to be revised as our understanding of regional processes increases. Much greater co-ordination of planting between farms is likely, as happens already in certain parts of the UK[18], both to reduce genetic exchanges and to manipulate seasonal habitat. New agronomy should result in greater diversity within and around the crop if cultivar mixtures are more widely grown and refuges more widely introduced for natural predators of insect pests. Whatever new technology comes in (GM or otherwise), its effects on the existing biodiversity have to be assessed, and land husbandry altered accordingly.

In 1999, a new wave of research began at SCRI to tackle these issues. One thrust is through mathematical modelling which allows the prediction of the risk of introducing a specified genetic type without necessarily deploying GM crops. Models to understand how to suppress herbicide-tolerant feral crop plants and to prevent antifeedant genes harming non-target organisms are in this category. At some stage in the procedure of risk assessment, models and small trials are not enough. Given initial appraisal of safety, farm-scale trials are required to confirm or examine ecological processes or possible emergent properties. The farm-scale evaluation of the effect of GM herbicide-tolerant crops on arable diversity is of this type. These government-funded trials, carried out by a consortium comprising ITE, IACR and SCRI, will lead to new definitions of arable ecosystems in the UK. They are, moreover, an example of 'open' research in a highly contentious area.

Fitting the cultivar to the system. There is ample scope also for the plant breeding industry to concentrate more on properties that discourage feral descendants from persisting and spreading. For instance, the proportion of secondary dormancy (which encourages overwintering of feral populations) differs greatly between oilseed rape cultivars. This secondary dormancy occurs mainly when the imbibing seed is exposed to low temperature or water stress, so is less likely to occur when seed is sown as a crop than when it falls from feral plants. For crops such as oilseed rape, potato and sugar beet that leave ferals, breeding should consider the ecological as well as the agronomic properties of its new cultivars. The deployment of 'terminator' technology and engineered sterility, assuming they can be made to work reliably, is contentious and requires further ecological appraisal. Research is just beginning in some highly relevant topics, while greater effort is appropriate in some other areas.

Future questions – new science The concerns over GM crops have brought to attention the need for science to understand agricultural systems, not only the crop varieties or the specific genetic modification. Land has more than one purpose and science must help management optimise several functions rather than maximise one. Yet behind the intensity of the GM debate, two factors are repeatedly implicated. The first concerns the impartiality of the science and the scientists that are carrying out ecological risk assessment. While science must work with industry, it has to retain a degree of independence through public funding. Otherwise, people will not believe its findings on these issues. The second is that the information required to answer the most pressing questions of recent times is seldom immediately available. Too much 'firefighting' research is put in place in an attempt to provide the answers. The solution is a much sounder infrastructure for studying the flow of individuals, species and genetic information across the countryside.

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