Outcrossing among crops and feral descendents - geneflow

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Rationale Crops and wild plants have lived side by side and exchanged genes since the beginning of agriculture. Oilseed rape typifies these exchanges, having arisen from two wild species and being now a crop and a feral weed at the same time. Oilseed rape is also an outcrossing species: its crop and feral forms exchange genes freely, and they both cross at very low frequency with several wild arable plants (Fig. 1). The fields and feral populations form a shifting patchwork that changes spatially over time as crops are sown and harvested and as feral populations arise and die. The crop and ferals provide an interesting case study of evolution in fragmented and dynamic populations, but they have also brought to wider attention the issues of crop purity and integrity of habitat, specially following applications by seed companies to grow GM oilseed rape and other GM crops in Europe. Debate has intensified during the present Farm Scale Evaluations of herbicide-resistant GM crops. Particular issues are -

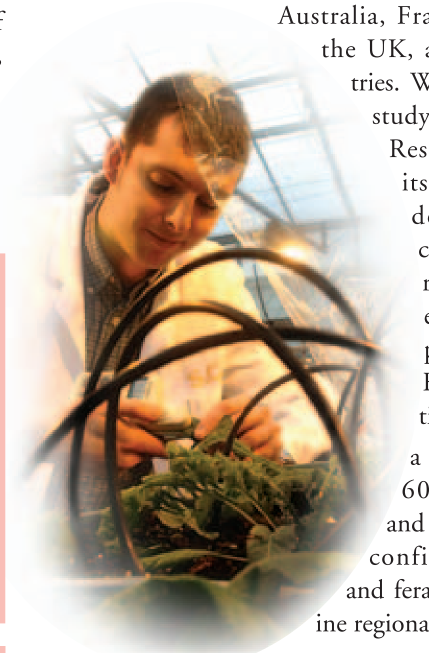
Figure 1 A field of oilseed rape contained the sown crop, probably feral descendents of previous crops grown in the same field, and occasionally a wild relative such as the Raphanus raphanistrum (white flowers) shown here.

impurities in crop yield might result from outcrossing between nearby fields and feral populations left by an earlier crop

feral populations might become more competitive than species in the existing arable seedbank, and so change the composition of the seedbank assemblage, especially if they acquire GM traits such as herbicide resistance

Various authorities have set, or are considering, thresholds for GM impurities should GM crops be commercially grown. Quantitative and predictive approaches to geneflow and population dynamics are therefore sought.

Methods of study Research on geneflow and GM impact assessment is well networked internationally. Major projects are underway in North America, Australia, France, Germany and the UK, among other countries. Within this subject of study, the Scottish Crop Research Institute and its collaborators have developed a major capability in geneflow research with an emphasis on regional processes (Table 1). Facilities and expertise include -



a study area of around 600 km^2 in Tayside and Angus in which the configurations of fields and ferals are used to examine regional dynamics

a range of molecular diagnostic techniques for detecting and estimating geneflow and paternity

techniques using male sterile 'bait' plants for estimating distance and frequency of geneflow from fields into the surrounding region (1 to10 km)

the study of physiological traits (e.g. induced dormancy) that differentiate crop varieties and encourage persistence

an extensive network of sites in the UK for tracking the population dynamics of feral weeds in the seedbank and their effect on the arable plant community,

predictive models of geneflow and persistence of

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Factors affecting cross-pollination between fields of different male fertility. (Development of advanced diagnostic and statistical methods for estimating and managing whole-field average cross pollination.) DEFRA. 2003-06. Consortium: SCRI, IACR, CEH, CSL, NIAB, ADAS. Contact: Geoff Squire, Scottish Crop Research Institute g.squire@scri.sari.ac.uk

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Modelling the persistence and population dynamics of feral (volunteer) oilseed rape in relation to field management. DEFRA. 1999-2003. Contact: g.squire@scri.sari.ac.uk.

Experimental and mathematical study of regional-scale geneflow in oilseed rape. DEFRA. 1998-2001. Contact: Gavin Ramsay g.ramsay@scri.sari.ac.uk

Investigation of feral oilseed rape populations. (Definitive study of the origin and persistence of feral populations.) DEFRA. 1993-96. Contact: g.squire@scri.sari.ac.uk

Table 1. Research projects on geneflow in Scotland

crop-derived feral seed (relevant to management of GM residues)

advanced diagnostic and statistical sampling techniques for estimating whole-field average cross-pollination between fields, including GM crop fields

Work in the large study area is a particular strength of the programme. It provides a natural environment in which processes can be scaled between plant and landscape (Fig. 2).

Persistence and role of ferals Feral populations are established both in fields and along waysides and waste ground when seed from a crop drops to the soil during harvest or is moved around by farm machinery and vehicles. The populations decline rapidly during their first two years, but then persist as a residual at a typical density of 100 m^{-2}. Oilseed rape is one of very few species to have entered the arable seedbank community in this way in the 20th century. It is now a widespread weed of middle to low rank in abundance. Factors that have caused its appearance are seed shatter at or before harvest, then inducible dormancy if conditions at the soil surface do not promote germination. Commercial varieties differ greatly in the fraction of seed that can be induced into dormancy by factors such as low temperature or dryness. The trait is largely unobserved in conditions used for standard testing of uniformity in crop varieties.

Given that ferals commonly persist for more than five years, and that oilseed rape appears as a ‘break’ crop in a cereal rotation every two to four years, oilseed rape fields commonly consist of the sown crop and an assortment of ferals of different origin. This has caused little concern when the sown crop and ferals are of the same general oil type (e.g. both are food-quality varieties). If the ferals were of GM origin, and the sown crop not, then GM seed would be present in the harvested seed, though no GM-derived protein would be in the oil processed from the seed. Our understanding of the evidence on biosafety is that GM traits such as herbicide tolerance are neither more harmful nor beneficial to human or animal health than non-GM varieties. However, the presence or degree of GM impurity in harvested yield is an issue for many people. As a guide to management, therefore, mathematical models of GM feral persistence in the seedbank and in harvested yield have been constructed, based on research by SCRI and other groups, notably Peter Lutman and colleagues at Rothamsted Research. The models will be used to define forms of

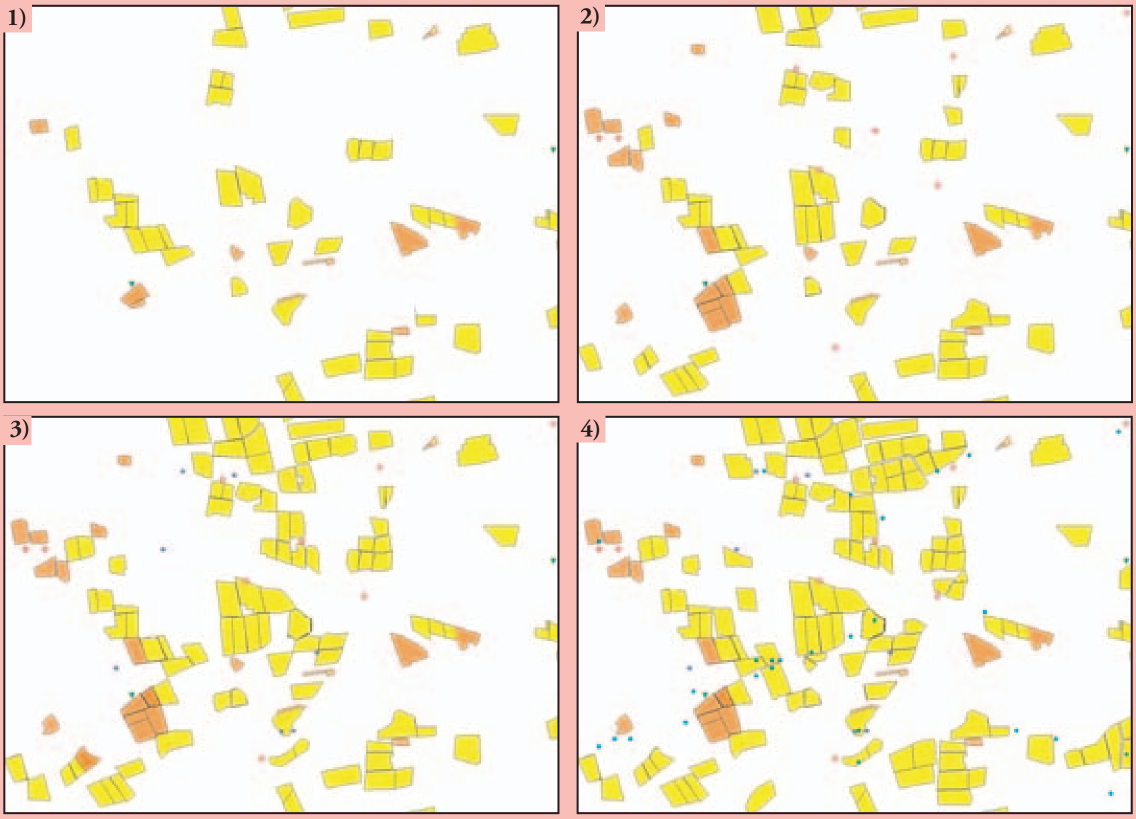

Figure 2 A 5 x 7 km section of the study area, showing the cumulative area over four years (1, 2, 3, 4) occupied by winter (yellow) and spring (orange) oilseed rape and the occurrence of wayside feral populations (symbols) first observed in each of the four years. By the 4th year, oilseed rape had been grown in much of the arable land in the section

field management that would keep impurities arising through ferals below specified thresholds. At present, a level of impurity of less than 1% is feasible provided the most rigorous field management is applied. Impurities also arise through geneflow between fields however.

Geneflow between and from crops Research in the early 1990s at SCRI found that geneflow in oilseed rape was more extensive than was previously believed. Subsequent models of regional geneflow over several kilometers suggested cross-pollination at a receptor field or population should depend on the arrangement of donor fields in the landscape; moreover, the proportion of crossing from a particular type or variety of crop should depend on the proportion of this type among all donor fields.

A regional scale experiment was therefore put in place to test this hypothesis. A combination of male sterile bait plants (which are only fertilised by pollen from external sources), male fertile plants and molecular diagnostic techniques was used by Gavin Ramsay, Caroline Thompson and colleagues to measure geneflow from normal commercial fields and a field that had unique markers. This experiment demonstrated that insects were important vectors (the previous model has incorporated only wind-borne pollen), that after declining very steeply over 50 m from a field-edge, geneflow continued at low frequency for several kilometres; and that cross-pollination from different types of donor field was indeed in proportion to their area and configuration. From this research, and complementary studies by Jeremy Sweet and colleagues at the National Institute of Agricultural Botany (NIAB), workers in France and more recently in Australia, whole field cross-pollination was estimated to be typically less than 0.1%, i.e. 1 seed in one thousand set on the plants in a field would be from a pollen source outside the field.

How the values are influenced by local context is highly uncertain, however. Therefore work is now in progress to measure outcrossing from fields in Scotland which are sown with the GM herbicide-tolerant crops of oilseed rape used in the Farm Scale

Evaluations (Fig. 3). The easily detectable markers in these crops should allow more accurate estimates off cross-pollination at low frequency than had been possible before. For wider applications, a consortium led by SCRI is developing advanced, high throughput diagnostic techniques for measuring geneflow at low frequency among non-GM fields. Together these studies will also quantify the pollination efficiency of insects, such as bumble bees, hive bees and pollen beetles that contribute to crossing, quantify the spatial patterns of crossing in fields, and develop the sampling protocols necessary to estimate whole-field crossing accurately.

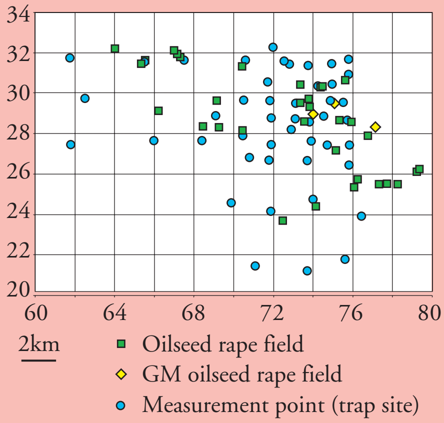

Figure 3 Plan of experimental study area in 2002, showing oilseed rape crops (green), GM oilseed rape crops in the Farm Scale Evaluations (yellow) and stations for measurement of geneflow and pollinators (dots).

Impact on habitat integrity At present, feral oilseed rape is less abundant than the main cruciferous weeds such as charlock (*Sinapis arvensis*) but more frequent than most of the wild and feral relatives with which it might potentially cross (albeit at very low frequency). Very substantial records now exist on the 'position' of feral oilseed rape in the arable plant community. It has not risen to dominance in weed populations despite the high seed drop that occurs at each harvest, nor has it invaded semi-natural habitats around farmland. Even in field management regimes that allowed many other species to increase in population, feral oilseed rape has remained a small component of the seedbank. It might be abundant enough to cause impurities in harvested yield, but not enough to cause even moderate shifts in the seedbank community. Whether it will increase or die out is uncertain, however. Other weed species have risen or declined over time, but the weed community has remained a resilient assemblage, admitting new species only occasionally. It is very unlikely therefore that a single new weed species could cause major disruption to the habitat.

Concerns that feral oilseed rape possessing GM herbicide-tolerance traits would increase in abundance to the point of having major effects on the habitat are also unfounded. Herbicide tolerance confers no advantage, at least in the absence of use of the herbicide to which it is tolerant. Herbicide tolerant ferals would increase (or decrease more slowly) if the herbicide was used with later crops of oilseed rape. Many other options exist to control such GM feral plants, and again, no major disruption of the habitat is likely to be caused by the plants themselves.

Conclusions. Geneflow in oilseed rape occurs at low frequency over several km, mediated by a range of insect vectors and wind-borne pollen.

geneflow is a regional process depending on the configuration of fields in a locality

best current estimates indicate cross pollination between nearby fields is 1 in 1000 or less; the values might be much higher to fields of partial male fertility (as in some modern varieties) or from fields to small feral populations

ferals persist in the arable seedbank and can contribute more (i.e. 1 in a 100) to impurities in crops than does geneflow by pollen movement from other crops

impurities cannot be prevented in the harvested yield of outcrossing crops or crops that give rise to feral populations, but could be reduced to around 1% by rigorous field management and regional segregation of crop types

herbicide-tolerant feral populations should have no selective advantage except where the specific herbicide is used

geneflow and feral persistence in oilseed rape makes an interesting 'model' for studying the links between physiological process and regional meta-population, but the ecological risk of ferals, herbicide tolerant or otherwise, is presently small.

Present effort is directed in two topics, including basic science and potential practical applications (Table 1). The first is to obtain more certain estimates of geneflow to small populations of feral plants and its impact on their evolution: oilseed rape is again used as a 'model' system for an outcrossing species. The second topic is to refine diagnostic techniques for detecting geneflow between fields, and then to develop high throughput methodologies for assessing the level of impurity in crop yields.

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