Over the past 20 years, it has become possible to isolate genes from microbes, plants, and animals and to insert them into a range of plant species. During the next two decades, it is likely that genetically engineered crops will become widespread in agriculture. This presents new opportunities for making plants resistant to pests and diseases, better able to withstand stressful environments, and capable of producing better quality products. As with most significant advances in biological science, questions are raised about the consequences of these developments to life and the environment.

One of the principal queries about the widespread use of genetically engineered crops is the likelihood and possible consequences of the introduced genes (transgenes) being transferred by cross-pollination to wild populations of plants. What would happen, for instance, if a transgene conferring resistance to a herbicide or to an important pest became established in a wild plant population?

The aim in this short review is to discuss the likelihood of gene transfer and its possible consequences and what procedures are being adopted to evaluate novel transgenic plants before they are used for widespread cultivation.

**OPPORTUNITIES FROM GENETIC ENGINEERING**

Since the discovery of enzymes capable of cutting and rejoining DNA at specific base sequences, it has become possible to isolate genes and DNA sequences that regulate gene activity from a range of organisms. Genes that control an array of plant processes are being inserted into crop plants, and it has been demonstrated that plants can produce specialized substances of pharmaceutical value (Fig. 1). In addition to the genes already available, modern methods of gene isolation (e.g. by chromosome walking or transposon gene tagging) will in the future make it possible to modify plants in ways difficult to envision at present.

Genes have been manipulated by humankind for thousands of years through the deliberate selection and propagation of useful plants. The genetic basis of crop improvement gradually became understood following the rediscovery in 1900 of Mendel’s experiments. Since that time, plant breeding has made a significant contribution to improving crop production; the abundance of food, at least in developed countries, testifies to this. How then is modern genetic engineering different from conventional plant breeding?

In conventional breeding, new combinations of genes are obtained by sexual hybridization. Cross-pollination is carried out within the crop species or occasionally between the crop and a related species. Although this is a very effective method of creating a wide range of genetic variability, it is constrained by sexual incompatibility. Only those genes contained in species that are sexually compatible with the crop species are available to the plant breeder. The advantage of genetic engineering is that it allows genes to be introduced into crops from many and varied kinds of organisms, and genes can also be synthesized in the laboratory.

Even with traditionally bred crop varieties, there has always been the opportunity for cross-pollination with sexually compatible wild species in nature. But because it is now possible to insert genes into crops that were previously inaccessible to the plant breeder, it is feasible that the transfer of engineered genes from crop species to their wild relatives may have consequences different from those of traditional crop breeding.

**LIKELIHOOD OF GENE TRANSFER TO WILD SPECIES**

The extent of gene transfer to wild populations depends on various factors: the crop plant and wild species must be sexually compatible, they must be growing in the same location, they should flower at the same time, and they should have a means of transporting pollen from one to the other. The first two, sexual compatibility and distance over which cross-pollination will occur, are particularly important and will be discussed further.

Wild species have been the source of many genes used in crop improvement, so there is information about the degree of sexual compatibility between crop species and their wild relatives. Potato (*Solanum tuberosum*) will cross-pollinate with wild diploid solanaceous species found at its place of origin in South America, but there is no evidence of cross-hybridization under field conditions with its relatives *S. nigrum* and *S. dulcamara* (5), which are common weeds of potato crops in Europe. In contrast, sugar beet will cross under field conditions with wild sea beets, and oilseed rape (*Brassica napus*) with *B. adpressa* (for other examples, see Fig. 1). When there is poor sexual compatibility between a crop and its wild relatives, breeders may resort to ovary and embryo culture to obtain hybrids. By this means it is possible to obtain hybrids between *B. napus* and the common weed species *Sinapis arvensis* (charlock), but gene transfer in nature is unlikely (8).

There is good evidence of coevolution of crop plants and certain wild species that have become important weeds of crops. Although coevolution can occur from genetic variabil-

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ity existing within the weed population, for example in *Echinochloa crusgalli* (barnyard grass), which is sexually incompatible with *Oryza sativa* (rice), in other instances there is evidence of genetic exchange between crop and weed. Hybridization between *O. sativa* and *O. perennis* under field conditions is reported to have produced *O. perennis* populations with reduced seed shattering, weak seed dormancy, and more synchronous germination (2), characteristics that would make them less likely to survive in wild habitats.

Although there is information in the literature on sexual compatibility between crop plants and related weed species, much of this is from controlled-hand pollination. More data are required to determine the extent of gene flow under field conditions, along with assessments of the competitiveness and fertility of those hybrids.

Studies to estimate pollination distance have been important in the past to determine the isolation distance necessary for the multiplication of genetically pure seed stocks of plant varieties. Distances of 200 to 400 m are commonly used; however, it is reported that cultivated radish can cross-pollinate with wild radish (both *Raphanus sativus* L.) over a distance of 1000 m (6). Transgenic plants generally contain convenient markers to estimate the distance of pollen movement and pollination, and data from a potato field trial using kanamycin resistance as a marker show 24% cross-pollination between adjacent potato plants (leaves touching), 0.017% at 10 m, and no evidence of cross-pollination at 20 m (5). Gene dispersal data from typical field test plots with transgenic plants are limited at present, and measurements of pollination distance could usefully be built into the field assessment programs currently being approved.

In addition to isolating crops by distance, other strategies are used to genetically isolate transgenic plants, including removal of flowers from the transgenic plants, removal of sexually compatible species, adjustment of flowering time, and planting a surrounding buffer crop of nontransgenic plants of the same species (4).

Assessments of the frequency of pollination at various distances are important to determine isolation distances for the early evaluation of novel transgenic plants, but exhaustive assessments of the probability of rare pollination events are unjustified. With any field release of a transgenic plant it is never possible to guarantee that a pollen grain will not fertilize another plant at great distance. In cases where a crop is known to hybridize with a wild species in the same

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**Figure 1.** Schematic representation of potential gene transfer from domesticated crops to wild species.
geographic area, the focus of any risk assessment should be on the consequences of potential hybridization.

CONSEQUENCES OF GENE TRANSFER TO WILD SPECIES

Rhododendron was introduced into Britain as an ornamental plant for gardens and is now considered by many ecologists to be a plant pest of semi-natural vegetation. Spartina anglica is a valuable species for reducing soil erosion but also causes problems by blocking waterways and harbors. This species was formed from a hybrid that arose a century ago between the native British S. maritima and the introduced American S. alterniflora (12, for other examples see ref. 11). These examples, where whole organisms are introduced into new habitats, are sometimes used to illustrate what might happen from the widespread use of transgenic crops. Either the modified crops themselves, or wild species that receive the engineered genes by cross-pollination, may become plant pests.

Although these examples are not directly analogous to the introduction of one or a few genes into crops to modify them in specific ways, they illustrate what can happen when plants are released that have a substantial selective advantage. A careful assessment needs to be made for each type of novel transgenic plant to determine the consequences of the introduced gene on seed output, seed longevity, seed dormancy, seed dispersal, tolerance or plasticity to a range of environments, vegetative reproduction, and competitive ability (1). Assessment of these characters is relevant both in the modified crop plant and in any wild relative the transgene might transfer to, some of which might be weed species.

Studies using transgenic crop plants containing herbicide resistance genes, insecticidal genes, and marker genes are already under way to compare the growth characteristics of some of the currently available transgenic crop plants with their nontransgenic counterparts in various habitats (3).

RISK ASSESSMENT OF NOVEL TRANSGENIC PLANTS

It is generally acknowledged by scientists involved in genetic engineering that the field release of these modified plants should be regulated. It is accepted that because it is now possible to introduce genes that were inaccessible through traditional plant breeding, a risk assessment should be undertaken for each novel class of genetically engineered plant. An important part of that assessment is to determine what the consequences would be if engineered genes were transferred to wild populations.

The transfer of herbicide resistance to wild species may allow plants of that species to proliferate in the presence of the herbicide. Because herbicides are unlikely to be used on natural plant populations, this is not likely to create a problem. But if the resistant wild species happens to be a weed of that crop, this could make weed control difficult, especially if no suitable alternative control measures are available.

Careful consideration needs to be given to the consequences of introducing various herbicide resistance genes into different varieties of a crop species. This could give the opportunity, under appropriate selective conditions, for a weed species to become resistant to several herbicides.

The transfer of pest and disease resistance, or resistance to environmental stress, might also give a wild population a selective advantage in some circumstances. Although there have been many conventionally bred varieties used in agriculture with similar classes of resistance characteristics, the introduction of genes from a considerably larger gene pool means that the choice of genes, and the mechanisms by which they modify plant phenotype, can be very different. There have now been over 500 field releases of genetically engineered crops, with no untoward consequences. However, as more is learned about how plant processes are controlled, new opportunities for modifying plants will emerge. It is important, therefore, that risk assessment be carried out case by case, and be based on a sound knowledge of the distance pollen can travel to give cross-pollination, the extent of cross-pollination between crops and their wild relatives, and the competitiveness of those recipient species in different habitats.

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LITERATURE CITED