ECOLOGICAL EFFECTS OF TRANSGENIC CROPS AND THE ESCAPE OF TRANSGENES INTO WILD POPULATIONS

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Key Words   genetically engineered crop, GM crop

■ **Abstract**   Ecological risks associated with the release of transgenic crops include nontarget effects of the crop and the escape of transgenes into wild populations. Nontarget effects can be of two sorts: (*a*) unintended negative effects on species that do not reduce yield and (*b*) greater persistence of the crop in feral populations. Conventional agricultural methods, such as herbicide and pesticide application, have large and well-documented nontarget effects. To the extent that transgenes have more specific target effects, transgenic crops may have fewer nontarget effects. The escape of transgenes into wild populations, via hybridization and introgression, could lead to increased weediness or to the invasion of new habitats by the wild population. In addition, native species with which the wild plant interacts (including herbivores, pathogens, and other plant species in the community) could be negatively affected by "transgenic-wild" plants. Conventional crop alleles have facilitated the evolution of increased weediness in several wild populations. Thus, some transgenes that allow plants to tolerate biotic and abiotic stress (e.g., insect resistance, drought tolerance) could have similar effects.

INTRODUCTION

Tomato with delayed ripening and canola with altered oil content were, in 1994, the first commercially released transgenic crops in the United States. In the past ten years, the number of hectares planted with crops containing genetic material derived from unrelated species has increased dramatically. Worldwide in 2003 transgenic crops were planted on more than 67.7 million hectares (James 2003). The United States accounted for 63% of this total, growing transgenic crops on 42.8 million hectares. Other large producers are Argentina, Canada, Brazil, China, and South Africa, and together with the United States, these countries plant about 99% of all transgenic crops worldwide. In the United States in 2003, 40% of the corn, 81% of the soybeans, and 73% of the cotton was transgenic, and these crops together account for the vast majority of transgenic plantings. Other transgenic

crops planted in the United States in 2003 include canola, squash, and papaya (James 2003).

Although more than 40 crop phenotypes have been approved for commercial release in the United States (ISB 2004a), herbicide tolerance (in soybean, cotton, corn, and canola) and insect resistance [conferred by toxin genes derived from *Bacillus thuringiensis* (*Bt*) in cotton and corn] account for nearly all the transgenic hectareage in this country (James 2003). Transgenic virus-resistant squash and papaya are also currently planted, but together they are planted on only a few thousand hectares (although more than half of U.S. papaya crop consists of transgenic varieties) (Gianessi et al. 2002). Other crops that have been approved for commercial sale, but that have been withdrawn from the market or are rarely adopted by farmers, include *Bt* potatoes, *Bt* and herbicide-tolerant sweet corn, herbicide-tolerant sugar beets, canola with altered seed oil content, and tomatoes with various quality traits.

Three types of potential risks are associated with the commercial release of transgenic crops: food safety, agronomic, and ecological. Food safety risks include, for example, the potential for allergenicity and decreased food quality of transgenic crops relative to their nontransgenic progenitors. Food safety issues have been reviewed by Kaeppler (2000), the Royal Society (2002), GM Science Review Panel (2003, 2004), Kok & Kuiper (2003), and Thomson (2003). Agronomic risks include crop-to-crop gene flow and the evolution of insecticide resistance in insect pests and herbicide resistance in weeds. These issues have been reviewed by Tabashnik (1994), Gould (1998), Shelton et al. (2000), Tabashnik et al. (2003), Martinez-Ghersa et al. (2003), and Mellon & Rissler (2004). The focus of this review is the potential for ecological risks resulting from the commercial release of transgenic crops. Over the past several years, ecological risks have been discussed at considerable length in the literature [Tiedje et al. 1989; Rissler & Mellon 1996; Snow & Moran-Palma 1997; Wolfenbarger & Phifer 2000; Dale et al. 2002; Letourneau & Burrows 2002; National Resource Council (NRC) 2000, 2002a; GM Science Review Panel 2003, 2004; Snow et al. 2004]. Also, many websites provide a wealth of information on transgenic crops. A particularly useful site is maintained by Information Systems for Biotechnology (ISB) at Virginia Tech University (www.isb.vt.edu); links to other sites can be found at the ISB site.

Ecological risks can be divided into two types. First, nontarget effects of transgenic crops occur when the expression of a transgene in a crop has negative effects on nontarget species. For example, corn engineered to express a *Bt* toxin gene will have intended negative effects on lepidopteran pests, but it may also have unintended direct or indirect effects on native nonpest species. Nontarget effects could also occur if the crop becomes more persistent in nonagricultural habitats. Second, transgenes might escape into wild populations through the hybridization of crop plants with their wild relatives. Transgenes that increase to high frequency in wild populations might affect seed production, population size, or habitat use in the wild species. In addition, transgenes for insect resistance that establish in wild populations could have negative effects on native herbivores as well as on

species with which the native herbivores interact. Horizontal gene transfer, via recombination, from transgenic plants to viruses or bacteria is also possible.

NONTARGET EFFECTS OF GENETICALLY MODIFIED CROPS

The many hypothesized nontarget effects of transgenic crops fall into two general categories. First, nontarget species could be affected, either directly or indirectly, by the transgenic product. For example, the abundance of nonpest herbivores, predators and parasitoids of target species, or pollinators might be reduced on transgenic crops. Similarly, the soil microbial community might be altered under transgenic plants. Second, a transgene that alters the habitat requirements of a crop plant could allow cultivation of crops or persistence of feral plants in previously unsuitable habitats. This could lead to a reduction in the quantity or quality of native habitat.

Species Effects of Transgenic Crops

DIRECT EFFECTS ON NONTARGET HERBIVORES   Researchers estimate that insect herbivory reduces crop yields by 30–40% worldwide (Oerke et al. 1994). In response, insecticides, traditionally bred insect resistance, and now transgenic resistance are used to reduce yield losses. Each of these management tools may have unintended effects on nontarget species. For example, effects of insecticides have been well documented (Benbrook 1996). By contrast, little work has evaluated nontarget effects of traditionally bred resistance. To the extent that transgenic resistance is specific to a particular group of pests (e.g., *Bt*s), effects on nontarget herbivores of transgenic crops might be less common.

A direct effect on nontarget species occurs when the transgenic trait in the crop negatively affects herbivores that do not reduce crop yield. These nontarget species generally feed on the crop, but they may also feed on plants in and adjacent to the crop field. Several studies have examined the direct effects of transgenic plants or artificial diet with transgenic protein on nontarget herbivores (see Poppy 2000 for review), although it is not clear that all these species would naturally feed on transgenic crops (see Supplemental Table 1 and nontarget entries in Supplemental Table 3: Follow the Supplemental Material link from the Annual Reviews home page at http://www.annualreviews.org). Most of these experiments evaluated the effect of a *Bt* toxin on a nonlepidopteran herbivore, and most studies found no effect. Just four studies evaluated the effects of transgenes other than *Bt*, and in all four a negative effect was found. Without knowing more about patterns of host use in these nontarget herbivores or about the effects of conventional management practices on nontarget species, it is difficult to evaluate the ecological importance of these results.

Less commonly, a transgenic plant could directly affect herbivores feeding on adjacent plants. Perhaps the best-known example is the case of *Bt* corn pollen

and the monarch butterfly. Losey et al. (1999) reported that monarch larvae fed milkweed leaves dusted with *Bt* corn pollen in the laboratory had decreased survival. The logical conclusion of this work was that if milkweed plants adjacent to *Bt* corn frequently accumulate large amounts of *Bt* pollen, and if such plants constitute a large proportion of the milkweed available to monarchs, then monarch populations would be negatively affected. Since the original Losey et al. (1999) study, and an additional study by Jesse & Obrycki (2000), a huge effort has been made to evaluate the risk to monarchs presented by *Bt* corn. In particular, a research consortium funded by the U.S. Department of Agriculture (USDA) and an industry group completed several studies on different aspects of the monarch-milkweed-*Bt*-corn interaction and found the risk to be negligible (Sears et al. 2001, Wraight et al. 2000, Hellmich et al. 2001, Oberhauser et al. 2001, Pleasants et al. 2001, Stanley-Horn et al. 2001). Although high concentrations of *Bt* corn pollen clearly have negative effects on monarch larvae, only a very small proportion of milkweed plants accumulate any *Bt* pollen, let alone pollen in sufficient concentration to have negative effects (see Obrycki et al. 2001 for review). Few other cases of potential nontarget effects on adjacent plants have been examined (Wraight et al. 2000, Zangerl et al. 2001).

EFFECTS ON POLLINATORS   The effect of transgenic pollen on foraging, learning, and life history characteristics of honeybees and bumblebees has been evaluated in several laboratory studies (Supplemental Table 2). The general conclusion from this work is that proteinase inhibitors have negative effects on bees, but that *Bt* does not (Supplemental Table 2; and for review, Malone & Pham-Delegue 2001). However, interpretation of these results is difficult because the concentrations of transgenic product used in these laboratory tests, often with artificial diet, may be greater than typically encountered in the field, and the importance of nontransgenic varieties and other species in the diet is unknown.

EFFECTS ON THE THIRD TROPHIC LEVEL   Natural enemies of crop pests can greatly affect pest abundance and are often used in integrated pest management programs (Bellows & Hassell 1999). Conversely, broad-spectrum insecticides generally reduce natural enemy abundance (Croft 1990). Thus, a potential advantage of transgenic crops is that relatively specific resistance to particular insect pests might leave natural enemies unaffected. However, Groot & Dicke (2002) argue that little is known about how changes in herbivore abundance or quality might affect the food web.

A variety of studies have evaluated effects of transgenic crops on the natural enemies of crop-feeding herbivores (Supplemental Table 3; see also Schuler et al. 1999 for review). In these studies, all combinations of effects have been found. The prey species can be either affected or unaffected by eating the transgenic product. In turn, predators can be either affected or unaffected by eating prey that have eaten transgenic product. It appears that effects on the predator (third-trophic-level effects) are most likely when the prey species is affected by eating the transgenic crop (or transgenic product in an artificial diet). This result contrasts

with the suggestion by Groot & Dicke (2002) that unaffected prey may not modify the transgenic product, which retains its toxicity to the predator. Thus, although direct toxicity is sometimes observed (e.g., Hilbeck et al. 1998), this effect may be uncommon.

In addition to effects of the transgenic product or prey quality on predator performance, reductions in prey abundance may also lead to a reduction in predator abundance in transgenic fields. For example, a specialist predator of Colorado potato beetle was less abundant in transgenic potato fields, presumably because its prey was also less abundant (Riddick et al. 1998). By contrast, the abundance of a generalist predator (that feeds on herbivores not targeted by *Bt* potato, as well as on Colorado potato beetle) was not affected by transgenic potato (Riddick et al. 1998). Similarly, in other field studies (Hoffmann et al. 1992, Pilcher et al. 1997, Orr & Landis 1997), the densities of predators were generally not reduced in transgenic fields.

EFFECTS ON THE SOIL COMMUNITY: MICROORGANISMS AND MACROFAUNA   The composition and activity of the soil microbial community are profoundly affected by the plant community (through both root exudates and litter quality and quantity), as well as by characteristics of the soil, climate, and, in agricultural communities, management practices. For example, plant species, and even crop variety, can have very large effects on rhizosphere microbial communities (Kourtev et al. 2003; Wardle 2002, Chapter 3). It is against this backdrop of natural variation that researchers must evaluate the potential effect of transgenic crop varieties. Studies of the effects of transgenic crops on the soil microbial community are summarized in Supplemental Table 4. Kowalchuk et al. (2003) have reviewed these effects and conclude that changes induced by transgenic plants are generally small relative to the effects of plant community and ecosystem properties. Similarly, transgenic varieties generally do not have negative effects on soil macrofauna (Supplemental Table 5).

Transgenic crops could affect the soil community in one of two ways. First, transgenic products could exude from roots and directly affect soil organisms; this possibility has been evaluated in a number of studies (e.g., Saxena et al. 1999, Saxena & Stotsky 2001). Second, transgenic crops could affect plant tissue quality (e.g., lignin or cellulose content) (Escher et al. 2000; Hopkins et al. 2001; for review, see Halpin & Boerjan 2003) and therefore affect tissue decomposition rates. Effects on tissue quality are most likely to have important ecological consequences (Kowalchuk et al. 2003). However, because links between microbial community structure and functional consequences (such as C and N cycling) are only poorly understood (Wardle 2002), these effects are difficult to evaluate.

Habitat Effects of Transgenic Crops

TRANSGENIC CROPS MAY BECOME FERAL   If a cultivar contains a transgene that enhances the fitness of crop plants in weedy environments, the crop might become

feral or might persist longer in feral populations. The potential for increased weediness in feral crops has been discussed widely (Snow & Moran-Palma 1997, Rissler & Mellon 1996, Warwick et al. 1999, Marvier 2001) but has received relatively little empirical attention. Parker & Kareiva (1996) and Bullock (1999) advocate the use of population matrix models to evaluate this risk. This approach involves gathering demographic data on nontransgenic varieties of crops in appropriate habitats (such as fields and roadsides), using these data to construct projection matrices, then performing elasticity analyses to determine which demographic transitions have the largest effects on λ, the annual rate of population increase. By comparing the transitions affected by particular transgenes with the transitions important for population growth, the potential weediness of a transgenic variety can be evaluated.

Few studies have taken such an explicitly demographic approach to evaluate the potential for transgenic crops to persist in feral populations. Parker & Kareiva (1996) found that transgenic oil-modified canola varieties had λ's that were not significantly different from those of nontransgenic isolines. Crawley et al. (1993, 2001) found no differences in persistence between transgenic herbicide-tolerant and nontransgenic varieties of oilseed rape, maize, beet, or potato. However, because the varieties used in Crawley et al.'s experiments were herbicide tolerant, and persistence was evaluated in the absence of herbicide, these results are not especially informative. It seems more likely that resistance to insects, pathogens, or other environmental stresses will enhance persistence in feral populations. For example, oilseed rape persists on road verges in France (Pessel et al. 2001), and time to extinction of feral populations might increase if plants contained transgenic insect resistance or drought tolerance.

REDUCTION IN WEED OR PEST POPULATIONS MAY NEGATIVELY AFFECT SPECIES USING AGRICULTURAL HABITATS   Crop yields can be substantially reduced by insects, other pests, and weeds. To maintain yield, farmers spray herbicides and pesticides, cultivate fields, alter planting times, and plant conventionally bred varieties that are resistant to pests or are tolerant of herbicides. This intensification of farm management practices has led to a reduction in farmland biodiversity, including reductions in weed, invertebrate, and bird populations (reviewed in Champion et al. 2003). Transgenic crops represent a further intensification of agriculture, and the effects of this technology on remaining farmland biodiversity are of some concern. For example, Watkinson et al. (2000) modeled the effect of herbicide-resistant transgenic sugar beet on weed biodiversity and bird populations using farmland in Great Britain. Depending on the particular management practices considered, their model predicts large decreases in weed biodiversity. Because insects feed on these weeds, and some farmland birds depend on these insects, decreased weed biodiversity and abundance results in decreased bird populations.

In response to this concern, the Farm Scale Evaluations (FSE) were initiated in Great Britain in 2000. These studies involve transgenic and conventional varieties of four crops, each planted in a split-field design at 60–70 sites across Great

Britain (Firbank et al. 2003, Squire et al. 2003, Champion et al. 2003). The transgenic crops included in this study are glyphosate-resistant sugar beet, glufosinate-resistant field corn, and glufosinate-resistant spring- and winter-sown oilseed rape (canola); results for winter-sown rape are not yet published. Dicot and monocot weed populations, including seedbank populations (Heard et al. 2003a,b); above- and below-ground invertebrate biodiversity, including pollinators (Brooks et al. 2003, Haughton et al. 2003); and higher-trophic-level effects (Hawes et al. 2003) were monitored over the following three years in the fields and at field margins (Roy et al. 2003). The larger objective of this work is to determine if genetically modified crops (and the management practices associated with these crops) affect farmland biodiversity differently than the management practices associated with conventional agriculture.

Data presented in papers published in 2003 (cited in the previous paragraph) suggest that transgenic varieties of sugar beet and spring-sown oilseed rape have reduced above- and below-ground (seedbank) populations of weeds, and reduced weed populations have led to generally reduced insect populations. In contrast, transgenic corn had higher weed and weed seedbank densities and generally higher insect populations than did the conventional corn fields. This is presumably because atrazine, the conventional herbicide used in corn, was more effective than glufosinate. A detailed interpretation of the FSE results and an in-depth review of other studies examining effects of transgenic herbicide-resistant crops is found in Squire et al. (2003), and Andow (2003) provides a succinct graphical summary of the results published to date. Similarly, in a comparison of transgenic and conventional soybeans, Buckelew et al. (2000) reported that weed management systems that allowed more weeds to persist supported larger insect populations.

The FSE results have been interpreted by some as evidence that transgenic herbicide-resistant beet and oilseed rape are bad for the environment, whereas transgenic herbicide-resistant maize is good for the environment (for discussion, see Dewar et al. 2004). However, another interpretation might be that transgenic varieties with improved weed control will allow higher yields and thus permit the return of marginal agricultural land to natural vegetation. In addition, application of generally less toxic herbicides (e.g., glyphosate) may be environmentally beneficial. Thus, the negative effects of transgenic crops on farmland biodiversity must be weighed against the potential benefits associated with increased yield and decreased herbicide use.

ADDITIONAL LAND MAY BE PLACED IN CULTIVATION   Transgenes that affect agronomic properties (e.g., salt tolerance, Zhang et al. 2001; water stress, Hsieh et al. 2002; low soil iron availability, Takahashi et al. 2001) could allow cultivation of currently marginal land that is nonetheless good native habitat. Conversely, through irrigation farmland often becomes too saline to sustain economically viable crops (Ghassemi et al. 1995), and transgenic salt tolerance could allow this land to remain in cultivation. These effects are currently hypothetical and have received little consideration.

MECHANISMS AND RISK OF ESCAPE OF TRANSGENES INTO WILD POPULATIONS

There are two mechanisms through which transgenes could move into wild populations: horizontal gene transfer and hybridization. Each of these mechanisms is discussed below.

Horizontal Gene Transfer

VIRUSES   Transgenic virus resistance in crops released thus far has been achieved by insertion of a viral coat protein, and there is concern that recombination between infecting viruses and the transgene could result in new virus genotypes with altered host range, transmissibility, or virulence. Accumulating evidence suggests that virus/transgene recombination is likely, although most (but not all; see Aaziz & Tepfer 1999) studies have been done in laboratory conditions favoring recombination (for review, see Hammond et al. 1999, Rubio et al. 1999, Power 2002, Tepfer 2002). As discussed by Hammond et al. (1999), the ecological risks of such recombination must be evaluated against the effects of natural recombination between viruses in mixed infections, which presumably occurs at similar rates. Because such recombination can have large effects on the population biology of viruses, and in fact is responsible for much viral evolution (Roossinck 1997), the potential ecological consequences (e.g., on the effects of virus infection in wild plants) deserve further attention (Tepfer 2002, Power 2002).

Another risk associated with virus coat proteins in transgenic crops is the possibility that viral RNA will be encapsidated with transgenic coat protein. Transencapsidation is known to occur in natural mixed infections, and it can alter the transmissibility of a virus. However, because the viral genome is unaltered, this effect does not persist, and for this reason ecological risks associated with transencapsidation are thought to be low (Hammond et al. 1999). Finally, increased disease severity may occur if there are synergistic interactions between invading viruses, and by extension, potentially between invading viruses and transgenic viral genes (Tepfer 2002, Power 2002).

SOIL BACTERIA   Horizontal gene transfer could also occur by natural transformation, a process through which DNA that is free in the environment can be stably integrated into the genome of competent bacteria (Nielsen et al. 1998, Bertolla & Simonet 1999). Although natural transformation is probably rare in nature (Nielsen et al. 1998, Gebhard & Smalla 1999, Nielsen et al. 2001), it is generally observed at low frequency in favorable experimental conditions (Schlüter et al. 1995; Nielsen et al. 1997, 2000a,b; Kay et al. 2002).

Hybridization with Wild Relatives

The ecological risks associated with the movement of transgenes into wild populations via hybridization must be evaluated by sequentially addressing three

questions: (*a*) Is the transgenic variety of the cultivated plant sexually compatible with wild relatives? If the crop has no compatible wild relatives, then no crop genes can move into wild populations, and there is no risk of transgene escape. However, if the crop does have compatible relatives, the next question is, (*b*) Will the transgene increase in frequency in the wild population (either by demographic swamping or by natural selection)? If the transgene is not expected to increase in frequency, then the ecological risks of transgene escape are minimal. Finally, if the transgene increases the fitness of the wild relative, and therefore the transgene is expected to increase in frequency in wild populations by natural selection, the third question is, (*c*) What are the ecological consequences of the escape of the transgene into a wild population? We address the first two questions in the next two sections. In the Consequences of the Escape of Transgenes into Wild Populations section below, we discuss the third question.

IS THE TRANSGENIC VARIETY OF THE CULTIVATED PLANT SEXUALLY COMPATIBLE WITH WILD RELATIVES?   All crop species were derived from one (or more) wild species, and most crops are planted sympatrically with compatible wild relatives somewhere in the world (Ellstrand 2003, Ellstrand et al. 1999). In addition, although the fertility of F1 crop-wild hybrids varies dramatically, both among crops and among crosses within crops, frequently fertility is restored in F2, BC1, and later generations. For example, in sunflower, F1 crop-wild hybrids have fertilities ranging from 1% to 100% of wild fertility, depending on the cross (Snow et al. 1998, Cummings et al. 2002), and the frequency of cultivar-specific alleles drops in later generations (Cummings et al. 2002). However, several studies have demonstrated that cultivar alleles persist in wild and weedy sunflower populations (Arias & Rieseberg 1994, Linder et al. 1998, Whitton et al. 1997). In fact, hybridization with wild relatives has been documented for 22 of the 25 most important crop species (by worldwide area planted) (Ellstrand 2003, and see Eastham & Sweet 2002), and it is likely that crop genes have introgressed into these wild populations. In addition to the overwhelming empirical evidence of gene flow between crops and their wild relatives (e.g., Warwick et al. 2003), theoretical models also suggest that introgression of transgenes is likely (e.g., Meagher et al. 2003, Thompson et al. 2003).

Because it is generally expected that crops will hybridize with their wild relatives, a variety of genetic methods of reducing the probability of introgression are under consideration and development (reviewed in Daniell 2002, NRC 2004). These include placing transgenes on chromosomes or chromosome segments that are less likely to introgress into wild populations (e.g., Rieseberg et al. 1999, 2000), closely linking transgenes with genes for domestication traits that are expected to have low fitness in wild populations, and controlling the viability or fertility of hybrid offspring using gene use–restriction technology.

Another way to reduce the risk of crop-wild hybridization is to restrict transgenic crops to areas where wild relatives do not occur. For example, wild relatives of corn and soybeans are not native to the United States, and thus, in this country,

transgenes from these crops cannot move into wild relatives. Similarly, in the United States transgenic cotton is restricted to areas where wild relatives of cotton do not grow naturally (Mendelsohn et al. 2003). By contrast, transgenic virus-resistant squash (*Cucurbito pepo*) is planted within the native range of wild squash, also *Cucurbito pepo* (Wilson 1993). Although cultivated alleles have been found in wild populations (Kirkpatrick & Wilson 1988, Decker-Walters et al. 2002), little is known about either the importance of viruses in wild populations (Spencer & Snow 2001) or the frequency of hybridization between cultivated and wild squash.

Because humans move seeds around the globe, both intentionally and accidentally, restricting transgenic crops to areas outside the native range will only temporarily delay the movement of transgenes into wild relatives. For example, even though cultivation of transgenic corn has been prohibited in Mexico since 1998, transgenic material has been found in land races of maize in remote mountainous regions of Oaxaca (Quist & Chapela 2001, 2002; and see Biotech InfoNet 2002, Mann 2002). The ecological effect of a *Bt* gene that introgresses into the land races will clearly depend on the importance of lepidopteran herbivores in these populations, which is unknown. If pleiotropic effects of the *Bt* gene are weak or absent, and if linkage to other cultivar-derived traits is reduced by recombination, the *Bt* gene will only increase in frequency in the land races if it leads to the reduction of lepidopteran damage and, therefore, to an increase in seed production. Moreover, even if selection favoring the *Bt* gene in land races is strong, genetic diversity in the land races will be reduced only at loci tightly linked to the *Bt* gene itself (Maynard Smith & Haigh 1974). Thus, overall genetic diversity in the land races (and in other wild populations into which transgenes introgress) is unlikely to be affected by the escape of transgenes. In fact, at least initially, genetic diversity in wild populations hybridizing with crops may be increased (Ellstrand 2003, table 9.1).

WILL THE TRANSGENE INCREASE IN FREQUENCY IN THE WILD POPULATION?   In contrast to the huge literature evaluating the potential for hybridization between transgenic crops and their wild relatives, there are few studies that have attempted to evaluate the fitness effects of transgenes once they have entered wild populations (Letourneau et al. 2003). Moreover, many authors seem to assume that if hybridization is rare (or can be made less common by the use of appropriate genetic technologies), then the consequences of hybridization do not need to be considered (e.g., Stewart et al. 2003). Similarly, many authors have suggested that if crop-wild hybrids have low fitness, the probability of introgression of a transgene into the wild population is low. This assertion is contradicted by theoretical work (Barton 1986) indicating that the rate of introgression of an allele from one population to another through hybrids can be very rapid even if the selective advantage is small, as well as by the frequent occurrence of transgressive hybrids (Rieseberg et al. 2003). In addition, Rieseberg & Wendel (1993) have documented the importance of introgression in the evolution of plant populations. Thus, evaluating the conditions under which transgenes will increase in frequency in wild populations is crucial.

A transgene could increase in frequency by either demographic swamping or by natural selection. Demographic swamping occurs with continual migration from a large source population (e.g., a crop) into a smaller recipient population (e.g., a wild relative). In a theoretical model, Haygood et al. (2003) found that with continual migration, as would occur when the crop is continuously planted, crop alleles can rapidly become fixed in wild populations, even when they are deleterious. In particular, alleles that reduce fitness can be fixed if the migration rate exceeds the selection coefficient, and when this occurs demographic swamping can lead to reduced population size and possibly local extinction. These effects (see also Huxel 1999, Wolf et al. 2001, Ferdy & Austerlitz 2002) could lead to extinction by hybridization (e.g., Levin et al. 1996, Rhymer & Simberloff 1996) and to wild populations that are endangered because of hybridization with crops (Ellstrand 2003, table 9.4).

If, instead, the effects of natural selection are expected to be more important than the effects of migration, then we must evaluate the fitness effects of the transgene in wild plants. The appropriate way to evaluate these effects is to compare the fitness of transgenic plants with the fitness of plants of the same genetic background but without the transgene. From this sort of experiment it is possible to estimate s, the selection coefficient, which quantifies the strength of selection either favoring or not favoring genotypes that include the transgene (Hartl & Clark 1997). Statistically significant selection favoring transgenic plants implies that the transgene will increase in frequency in wild populations. Moreover, if the phenotype of transgenic plants is the phenotype predicted by the transgene (e.g., lepidopteran resistance in the case of a *Bt* gene), then increased (or decreased) fitness of transgenic plants can more confidently be ascribed to the transgene, rather than to an idiosyncratic position effect. Ideally, these experiments should be done in more than one environment and year, so that the results can be more easily generalized. In addition, if the benefit of the transgene is predicted to vary across environments (e.g., because the environments vary in herbivore pressure) then the strength of selection favoring the transgene should vary as well.

If the transgene is of no benefit (or is always costly) to the wild plant, genetic drift (or purifying selection) will determine its fate in the wild population. For example, transgenes controlling traits such as ease of harvest, fruit ripening, and product shelf life, as well as newer generation traits such as pharmaceutical or industrial chemical production, are likely to be neutral or costly in wild populations. Similarly, although weeds with transgenic herbicide resistance may be more difficult to control with herbicides, these genes are likely to be neutral or costly in wild populations that are not sprayed (Snow et al. 1999, Gueritaine et al. 2002, Zhang et al. 2003).

In contrast to costly or neutral characters, transgenes for characters such as insect or pathogen resistance and drought tolerance may benefit wild populations, and therefore may increase in frequency in wild populations by natural selection. For example, damage by herbivores is generally detrimental to plant fitness in wild populations (e.g., Marquis 1992, Crawley 1997, Letourneau et al. 2002), and similarly viruses and fungal pathogens also commonly reduce fitness of wild plants

(e.g., Burdon 1987, Jarosz & Davelos 1995, Maskell et al. 1999). These results suggest that transgenic herbivore and pathogen resistance would be favored by natural selection in many wild relatives of crop plants. The evolutionary dynamics of each of these traits will be determined by the balance between the benefit of the trait (in the presence of the selective agent, such as herbivores) and the cost of the trait (the reduction in fitness of transgenic individuals in the absence of the selective agent) (Simms & Rausher 1987).

Only one study has evaluated the fitness effects of a transgene in a wild genetic background in an ecologically relevant environment. In field-planted BC1 and BC3 *Helianthus annuus* with a *Bt* transgene, lepidopteran damage was reduced to near zero, and seed production was increased 15–55% (relative to plants without the transgene), depending on the year and field site (Snow et al. 2003, Pilson et al. 2004). Because lepidopteran damage is known to reduce fitness in wild *Helianthus annuus* populations (Pilson 2000, Pilson & Decker 2002), this result is not surprising. Moreover, when BC1 plants were grown in the greenhouse (in the absence of herbivores), there was neither a benefit nor a cost of the transgene (Snow et al. 2003). These results suggest that, if a *Bt* gene were to escape into wild sunflower populations, it would increase in frequency by natural selection, and the rate of increase would vary in space and time as a function of the abundance of lepidopteran herbivores.

A few additional studies have evaluated effects of transgenes in F1 or BC plants. In a cage experiment replicated in three states in the United States, Burke & Rieseberg (2003) experimentally inoculated BC3 sunflower segregating for a transgene conferring resistance to white mold. They found that both the effect of the transgene on infection frequency and the effect of infection on seed production depended on the location of the experiment. Furthermore, because the transgene had no effect on infection in locations where the pathogen had large effects on fitness, in this experiment the transgene provided no fitness benefit. Fuchs & Gonsalves (1997, 1999) found that transgenic virus-resistant F1 and BC1 squash inoculated with virus do not display symptoms and do produce fruit. BC1 and BC2 *Brassica rapa* plants (with a *Bt* gene introgressed from *Brassica napus*) produced more reproductive biomass than nontransgenic plants when inoculated with high, but not low, densities of diamondback moth larvae (Mason et al. 2003). Furthermore, in the absence of moth larvae there was no effect of the *Bt* gene on plant growth, indicating that the *Bt* gene is not costly to the plant (Mason et al. 2003). However, interpreting these studies is difficult because the incidences of naturally occurring white mold in wild sunflower populations, virus in wild squash populations, and diamondback moth in weedy *B. rapa* populations are not reported.

Because it is known that conventionally bred crop alleles have introgressed into wild populations, one way to evaluate the potential effects of transgenes in these populations is by examining the effects of these conventional alleles. Ellstrand (2003) documents 16 cases in which crop-wild hybridization has led either to the evolution of a new taxon (Ellstrand 2003, table 9.2) or to a wild population with changed ecological properties (Ellstrand 2003, table 9.3). In most of these cases

the newly derived taxon or population is weedier than its wild parent. Clearly, crop alleles can sometimes enhance weediness in wild plants, but whether transgenes are more likely than conventional alleles to have this effect is an open question. Genes that affect environmental tolerances (e.g., resistance to biotic and abiotic stress) would seem the most likely candidates.

Genetic and ecological models provide another way to evaluate the potential effects of transgene movement into wild populations. Muir & Howard (1999, 2001, 2002; Howard et al. 2004) have developed and parameterized a model for transgenic fish that is now being modified for application to plant populations (ISB 2004b). Their original model predicts that a transgene that increases growth rate and adult size can (paradoxically) cause the extinction of wild populations. Extinction occurs because the transgene has opposite effects on different components of fitness, and this phenomenon has been called the Trojan gene hypothesis. Specifically, larger fish (with the transgene) get most of the matings, but because their transgenic offspring have lower viability, few survive to maturity, and population size declines. Evaluating the effects of a transgene on various components of fitness in plant populations is clearly of value (e.g., to measure λ; see Parker & Kareiva 1996, Bullock 1999). However, for plants it is not clear how frequently transgenes might have such different effects on mating success and offspring viability.

CONSEQUENCES OF THE ESCAPE OF TRANSGENES INTO WILD POPULATIONS

Although the movement of a transgene into a wild population, and its subsequent increase in frequency, are necessary, they are not sufficient to predict the environmental consequences of transgene escape. Specifically, these processes are only important to the extent that they lead to the alteration of existing ecological interactions between the wild plant and its biotic and abiotic environment. Thus, it is necessary to answer the third question raised above: What are the ecological consequences of the escape of the transgene into a wild population? A transgene that increases in frequency by natural selection in a wild population does so, by definition, because it increases survival or fecundity, and one ecological risk is the effect of increased individual fitness on population size, dynamics, and habitat use in the wild plant. In addition, transgenes that confer resistance to herbivores and pathogens will have direct effects on native species using the wild plant as a host. Clearly, these questions must be the crux of any ecological risk assessment. However, very little work has been done in these areas.

Population Dynamics and Habitat Use in the Wild Relative

A much discussed potential consequence of the escape of transgenes into wild populations is that transgenic-wild plants will become weedier (Darmency 1994, Snow & Moran-Palma 1997, Warwick et al. 1999). The size of transgenic-wild

populations could increase in the wild plant's original habitat, or broader environmental tolerances could allow transgenic-wild plants to invade previously unsuitable habitat. These risks are difficult to evaluate because little is known about factors controlling population size or range in plants, or about characteristics of invading species and the receiving community that allow invasion (Hoffmann & Blows 1994, Lonsdale 1999, Kolar & Lodge 2001, Gerlach & Rice 2003).

INCREASE IN POPULATION SIZE   A transgenic-wild population could increase in size if either fecundity (e.g., Snow et al. 2003) or competitive ability (e.g., Damgaard & Jenson 2002) increase as a result of expressing the transgene, and if population size was previously limited by characters affected by the transgene. However, this possibility is difficult to evaluate because little is known about factors controlling population size in natural plant populations. However, changes in fecundity can have large effects on population growth rate (λ; Silvertown et al. 1993), suggesting that transgenes that increase fecundity could lead to increases in population size. Fecundity in sunflowers is limited by herbivory (Pilson 2000), and experimental sunflower populations in western Nebraska appear to be seed-limited, suggesting that a reduction in herbivory would lead to larger populations. In contrast, in similar populations in eastern Kansas population size is affected more by density-dependent processes (such as competition for resources) than by seed production (D. Pilson, H. Alexander, J. Moody-Weis, A. Snow, manuscript in preparation). Seed production by individual thistle plants and thistle populations can be limited by insect herbivory (Louda & Potvin 1995, Guretzky & Louda 1997). Weedy roadway populations of oilseed rape were seed-limited at the landscape scale (Crawley & Brown 1995). Small experimental populations of *Arabidopsis thaliana* were not seed-limited (Bergelson 1994).

Within a community, a likely consequence of an increase in population size of one species is the decrease in size of others. For example, in experimental plots in which goldenrod plants were sprayed with insecticide, goldenrod abundance increased while the abundance of other species decreased (Carson & Root 1999, 2000). This effect was attributed to increased competitive ability when plants were not subject to insect attack. These results suggest that if insect-resistant transgenic-wild plants (or plants with any character that increases competitive ability) are present, the abundance of other species could decline. Changes in community structure in natural habitats are thus one potential consequence of the incorporation of transgenes into wild populations.

INVASION OF PREVIOUSLY UNSUITABLE HABITAT   In addition to increased population size in their original habitat, transgenic-wild plants might also be able to invade previously unsuitable habitats. For example, one reason introduced plants are believed to become invasive is that they have escaped from their natural enemies (Mack et al. 2000, Sakai et al. 2001, NRC 2002b, Louda et al. 2003, Mitchell & Power 2003, Callaway et al. 2004). Escape from natural enemies might allow invasion directly, or reduced natural enemy attack might free resources and thus allow the evolution of increased competitive ability (Blossey & Nötzold 1995; but

see Willis et al. 1999, 2000). In addition, hybridization has been shown to provide the genetic variation necessary for the evolution of invasiveness in many taxa (Ellstrand & Schierenbeck 2000), and transgressive segregation is common in crop and wild populations (Rieseberg et al. 2003). Taken together these considerations suggest that crop-wild hybrids could facilitate the evolution of broader habitat tolerances, and perhaps invasiveness, in wild populations.

Insect and Pathogen Community Structure

If transgenes for resistance to herbivores or pathogens increase to high frequency in wild populations, there will be immediate, and negative, effects on those native species that were responsible for selection to increase the frequency of the transgene in the first place. If these species are specialists, their populations could decline dramatically, perhaps resulting in local extinction. By contrast, if these species have additional host plants, the effect of the transgene will depend on how important the transgenic-wild plant is in the diet of the herbivore or pathogen. For example, although many moths feed on more than one *Helianthus* sp., *Helianthus annuus* is the most important host for many lepidopteran herbivores (Charlet et al. 1992, 1997). This fact suggests that if a *Bt* gene were to enter wild *H. annuus* populations (Snow et al. 2003, Pilson et al. 2004), the abundance of *H. annuus*–feeding lepidopterans would decrease. Furthermore, because one of the most common moths feeding on *H. annuus* has negative competitive effects on a seed midge and a seed weevil, reduction in lepidopteran abundance could result in increased seed midge and seed weevil populations (M. Paulsen & D. Pilson, manuscript in preparation). Effects at the next trophic level might include increased abundance of seed midge and seed weevil parasitoids and decreased abundance of lepidopteran parasitoids. Community-level consequences of the removal of a few species are likely to be quite complex and unpredictable (Denno et al. 1995, Polis & Strong 1996, Dunne et al. 2002, Groot & Dicke 2002).

Changes in community structure that occur because of transgenic-wild plants will not be static. Specifically, transgenic herbivore or pathogen resistance will impose strong selection on the affected species to evolve counter-resistance, similar to the selection pressure imposed by conventional insecticides. Crop pests have evolved resistance to virtually all chemical insecticides applied to crops (NRC 1986), and thus there is every reason to expect that herbivores in natural systems will evolve resistance to transgenic pesticides. The speed with which this happens will depend on the strength of selection on the transgenic host, the presence of alternative hosts, and pre-existing variation for resistance.

CURRENT TRANSGENES VERSUS TRANSGENES OF THE FUTURE

Most of our discussion has focused on transgenic traits that are likely to enhance the fitness or environmental tolerances of wild plants (e.g., insect and pathogen resistance, drought tolerance), because these traits are most likely to affect natural

plant and animal populations. Furthermore, much of our discussion of insect resistance has focused on *Bt* crops because these have been released commercially and extensively evaluated (Shelton et al. 2002, Mendelsohn 2003). In the future, crops with other types of insect resistance are likely (Schuler et al. 1999, Moar 2003), as are crops with transgenic resistance to pathogens and nematodes (Atkinson et al. 2003). The sorts of ecological risks discussed here will likely be relevant to these newer transgenic products as well. By contrast, the next generation of transgenic products will probably also include plants with enhanced product quality (e.g., increased yield, altered ripening time or nutritional content, reduced lignin content in trees), as well as plants producing industrial and pharmaceutical chemicals (Dunwell 1999, Fischer & Emans 2000, Jaworski & Cahoon 2003, Ma et al. 2003, Sinclair et al. 2004). Although some of these genes could present very large agronomic or food safety risks, they seem less likely to have important ecological effects. This is because these traits are less likely to increase the fitness of wild plants and so are less likely to increase in frequency in wild populations.

POTENTIAL BENEFITS OF TRANSGENIC CROPS

Although the focus of this review is the ecological risks associated with the commercial release of transgenic crops, it is important to recognize that there may be ecological benefits as well (Wolfenbarger & Phifer 2000; Hails 2000). One potential benefit is a reduction in pesticide and herbicide use. For example, in the United States insecticide use has decreased on corn and cotton since the release of *Bt* varieties of these crops (Benbrook 2003). Similarly, in China planting *Bt* cotton has resulted in dramatic reductions in pesticide use (with both environmental and human health benefits) and increased yields (Pray et al. 2002). In addition, the use of *Bt* crops, rather than broad spectrum insecticides, could allow larger populations of beneficial insects and nonpest herbivores to persist in crop fields. However, herbicide use on herbicide-tolerant crops, especially soybean, has increased since the release of transgenic varieties, although this increase has largely been the result of increases in relatively benign herbicides such as glyphosate (Benbrook 2003). Another potential benefit of transgenic herbicide-tolerant crops is an increase in no-till or other conservation tillage practices, which lead to reduced soil erosion and run-off to streams, reduced fuel use (Fawcett & Towery 2003), and increased sequestration of atmospheric carbon. Evaluating the ecological benefits of transgenic crops is not straightforward, and no comprehensive reviews have been published.

CONCLUSIONS

We draw three general conclusions. First, transgenes that affect plant response to biotic and abiotic stress (e.g., insect and pathogen attack, drought and salt tolerance) are more likely to have negative ecological effects than are transgenes

for traits affecting product quality or industrial and pharmaceutical chemical production. Second, escape of transgenes into wild populations, via hybridization and introgression, is more likely to result in negative ecological effects than are nontarget effects of the transgenic crop itself. The escape of transgenes into wild populations could lead to increased weediness or the invasion of new habitats by the wild population. In addition, native species with which the wild plant interacts (including herbivores, pathogens, and other plant species in the community) could be negatively affected by transgenic-wild plants. Conventional crop alleles have allowed the evolution of increased weediness in several wild populations. Thus, there is reason to believe that some transgenes (e.g., for insect resistance, drought tolerance) could have similar effects. Finally, there are relatively few data available with which to evaluate the potential for increased weediness in wild relatives of crop plants. A better understanding of factors controlling population size, dynamics, and range limits in weedy plants is necessary before a full ecological risk assessment can be made.

ACKNOWLEDGMENTS

The *Annual Review of Ecology, Evolution, and Systematics* is online at
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