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The Ecological Risks and Benefits of Genetically Engineered Plants

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Discussions of the environmental risks and benefits of adopting genetically engineered organisms are highly polarized between pro- and anti-biotechnology groups, but the current state of our knowledge is frequently overlooked in this debate. A review of existing scientific literature reveals that key experiments on both the environmental risks and benefits are lacking. The complexity of ecological systems presents considerable challenges for experiments to assess the risks and benefits and inevitable uncertainties of genetically engineered plants. Collectively, existing studies emphasize that these can vary spatially, temporally, and according to the trait and cultivar modified.

Ecologists and other scientists have long expressed concerns about the potential impacts of releasing genetically engineered organisms (GEOs) into the environment (*1*), while others emphasize their potential environmental benefits. The broad implications of national and international regulations underscore the policy and research communities' need for current scientific information and for awareness of where informational gaps occur. Here, we synthesize available empirical, published information, primarily from academic, peer-reviewed journals, on the potential environmental risks and benefits of genetically engineered plants. Our focus reflects a current emphasis on crop plants, but developments of genetically engineered fish, trees, and microbes may alter perspectives.

Potential Risks

Risk of invasiveness. The release of GEOs highlights the general difficulty in predicting the occurrence and extent of long-term environmental effects when nonnative organisms are introduced into ecosystems. Nonindigenous species have been introduced into the United States intentionally and unintentionally for centuries; an estimated 50,000 species in the United States are not native (*2*). While many nonindigenous species are regarded as harmless or beneficial, other introduced species, commonly referred to as invasive species, have spread widely in their nonnative ecosystems and caused unintended degradation of natural ecosystem functions and structure (*2*, *3*). Invasive species are also expensive, costing the United States an estimated $137 billion annually in direct and indirect effects, and control or prevention measures (*2*). Indeed, invasive species have been categorized as one of the three most pressing environmental problems, in addition to global climate change and habitat loss (*4*).

Genetic modifications, through traditional breeding or genetic engineering, of crop or other species can potentially create changes that enhance an organism's ability to become an invasive species. Although genetic engineering transfers only short sequences of DNA relative to a plant's entire genome, the resulting phenotype, which includes the transgenic trait and possibly accompanying changes in traits, can produce an organism novel to the existing network of ecological relationships. Potential ecological impacts through invasiveness depend on existing opportunities for unintended establishment, persistence, and gene flow of an introduced organism; each of these, in turn, depends on various components of survival and reproduction of an organism or its hybrids (Fig. 1). Few introduced organisms become invasive, yet an issue for the management of all introduced organisms, including GEOs, is how to identify those modifications that may lead to or augment invasive characteristics.

For GEOs, one approach has compared the likelihood that transgenic organisms or their hybrids would persist outside of cultivation compared to nontransgenic controls. Two experiments on oilseed rape suggest that self-sustaining populations were unlikely under these experimental conditions (*5*–*7*) (Table 1). In contrast, some evidence indicates that under experimental conditions transgenic crops can hybridize with closely related species or subspecies (Table 1), a prerequisite for gene introgression. Such results are not surprising. Natural hybridization occurs between 12 of the world's 13 most important food crops, including wheat, rice, maize, soybean, barley, and cotton seed, as well as numerous other crop species, and some wild relatives (*8*, *9*). Large areas of cultivation may increase the opportunity for range overlap with compatible relatives; therefore, the probability that crop genes, newly introduced through genetic engineering or through other, more traditional techniques, will introgress into wild relatives may increase as particular cultivars are more widely adopted. Genetic modifications could change the propensity of outcrossing (*10*), although this has not been reported in the one crop species studied (*11*).

Ecological impacts of pollen transfer, a reproductive mechanism through which introgression might occur, depend on whether hybrids survive and reproduce. Equivocal rates of survival or reproduction between transgenics and controls suggest, but do not indicate, the opportunity for introgression of transgenes into natural populations (*12*–*17*), depending on subsequent gene flow and selective pressures. Not all studies support these conclusions (*18*), and ecological consequences in nonagricultural habitats and ecosystems largely remain unstudied.

No published studies have examined whether introgression of transgenes or its potential ecological consequences have occurred in natural populations; however, past experience with crop plants suggests that negative effects are possible. For seven species (wheat, rice, soybean, sorghum, millet, beans, and sunflower seeds) of the world's top 13 crops, hybridization with wild relatives has contributed to the evolution of some weed species (*8*). In some cases, high levels of introgression from cultivated or introduced relatives have eliminated genetic diversity and the genetic uniqueness of native species, effectively contributing to their extinction (*8*, *19*, *20*).

The complex nature of biological invasions means that simple comparisons of fecundity and survival will not adequately predict invasiveness. Variation in the competitive environment and timing of introductions

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can confound predictions (*21*, *22*). Unknown factors cause unexplained time lags that occur between the establishment of an introduced species and the subsequent expansion of its population and range (*23*). These represent key challenges for assessing the risk of invasiveness. A thorough understanding of factors, such as viral infections, insect predators, competition, or human-mediated controls, that limit reproduction will highlight how transgenic traits affect the reproductive ability of GEOs and their wild relatives in different ways so that we may consider what, if any, ecological impacts might arise from any differences.

Direct nontarget effects on beneficial and native organisms. Plants engineered to produce proteins with pesticidal properties, such as *Bacillus thuringiensis* (Bt) toxin, may have both direct and indirect effects on populations of nontarget species. One group of toxins from Bt primarily targets Lepidoptera (butterflies and moths, such as the European corn borer), and another mostly affects beetles (Coleoptera) (*24*). Effects on nonpest species in these groups could vary widely owing to differences in sensitivity among species and concentration of Bt toxin produced by tissue or by transgenic lines (*25*, *26*).

Laboratory experiments suggest that adverse effects may occur when monarch butterfly larvae ingest Bt corn pollen on host plants (*25*, *27*). How broadly these results apply to natural populations is not known because neither study addressed the rate at which larvae encounter the toxin, a necessary component for assessing risks. How these potential risks compare with those of chemical pest control remains critical to understanding the net effect of Bt crops on nontarget populations. In contrast, other studies show no direct effect of transgenic Bt crops on nontarget organisms for particular life history or reproductive traits measured (*26*, *28*, *29*).

Some genetically engineered crops affect soil ecosystems (*30*–*34*), but the long-term significance of any of these changes is unclear. At least two consequences could potentially occur from reported alterations of soil ecosystems—decrease of plant decomposition rates and of carbon and nitrogen levels, which could affect soil fertility (*35*). Similarly, declining species diversity of soil microorganisms, in some cases, can cause lower community diversity and productivity above ground (*36*).

Indirect effects. GEOs may have indirect impacts on populations of species that depend on the pests controlled for survival or reproduction. Population models suggest that more effective control of weeds by using herbicide-tolerant crops could lead to lower food availability for seed specialists (*37*). Effective control of the Colorado potato beetle in transgenic fields probably explains the decrease in a predatory specialist on it (*38*). In contrast, population estimates of predatory insects were similar in plots of Bt and nontransgenic corn (*39*).

Pesticidal proteins produced by GEOs may have effects indirectly through bioaccumulation, if exposure occurs when predators consume prey items that contain pesticidal proteins. When Bt spores are sprayed to control insects, the toxins they contain rapidly decline in abundance and toxicity (*24*), leaving little opportunity for bioaccumulation. In accordance, some studies conducted with Bt crops indicate no effects on survivorship or reproduction of predatory insects that eat prey items that have ingested genetically engineered Bt plant tissue (*40*–*42*) (Table 2). In contrast, other studies suggest that the opportunity for bioaccumulation may occur (*43*, *44*) (Table 2). Like most studies on direct effects, field exposure levels to the toxin and toxin-laden prey are unknown. Therefore, with the data available from published, peer-reviewed literature, extrapolation of these results to natural ecosystems cannot yet be made.

The rate of persistence of pesticidal proteins may affect the probability of nontarget effects. In neutral soil pH, bioassays revealed a rapid decline in the biological activity of Bt toxin from transgenic cotton and transgenic corn (*45*, *46*), and at 120 days, the soil inhibited larval growth by 17 to 23% of its starting biological activity (*46*). Similarly, varying rates of persistence of Bt toxin from transgenic plant tissue, from 0 to 35%, remained detectable through soil extractions after 140 days (*47*). In soil, high microbial activity degrades Bt toxin, but active toxin readily binds to soil particles, an association that inhibits biodegradation (*24*). Purified, active Bt toxin persisted in certain soil types for at least 234 days, the longest duration studied (*48*), and high clay content and low soil pH increased the persistence (*24*). Information on how prevalent these conditions are within agricultural systems and nearby ecosystems will reveal the extent to which these data indicate a risk.

Laboratory results suggest the possibility that Bt toxin may contact soil ecosystems by way of exudate from Bt corn plant roots (*49*), but results under field conditions have not been reported. Any ecological consequences of the presence and persistence of Bt toxin in soils have not been published, and empirical studies addressing these consequences will provide much-needed information to evaluate the possibility of long-term effects on nontarget organisms and how these compare to risks when chemical pest control is used.

New viral diseases. Viruses with new biological characteristics could potentially arise in transgenic viral-resistant plants through recombination and heteroencapsidation (*50*). New viral strains can evolve through recombination between closely related strains, and transference of transgenic sequences can occur under laboratory conditions (*51*, *52*). However, we lack empirical evidence to understand the likelihood of this transference under natural circumstances. As occurs in other plant viruses, closely related viruses can exchange coat proteins (CPs). Under laboratory conditions, CPs produced by transgenic virus-resistant plants encapsidated a related virus that subsequently altered its transmissibility (*53*). Again, we lack empirical data to understand the prevalence of these events under more natural conditions. The modified, encapsulated virus cannot produce the new CPs because its genome does not contain those genes; therefore, new viral

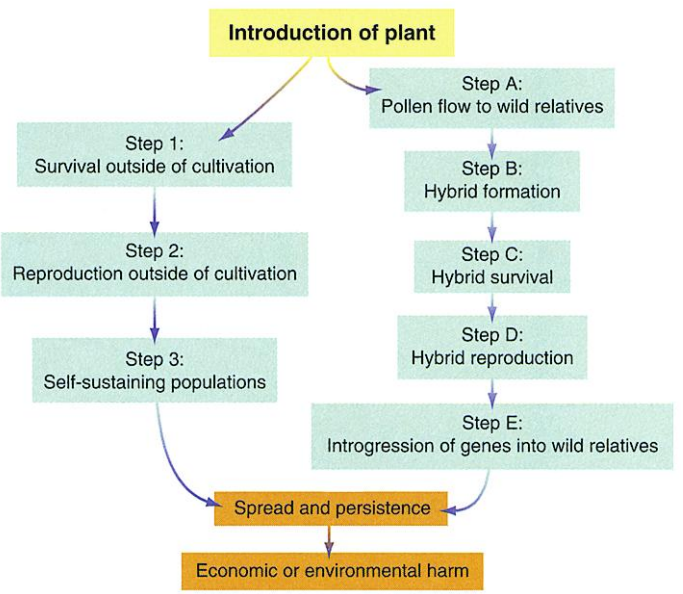

Fig. 1. The flow chart illustrates two main pathways (self-sustaining populations or introgression of genes) for how an introduced organism, such as a GEO, or its genes could have negative impacts on natural ecosystems. These stepwise factors are necessary for an invasion, but not sufficient to cause one.

strains created through heteroencapsidation are not propagated (*50*). Strategies to reduce the biological risk of heteroencapsidation and accompanying changes in transmissibility are under investigation (*54*.).

Variability and unexpected results. Ecosystems are complex, and not every risk associated with the release of new organisms, including transgenics, can be identified, much less considered. Unknown risks may surface as the frequency and scale of the introduction increases (*55*). Because some consequences, such as the probability of gene flow, are a function of the spatial scale of the introduction (*56*), limited field experiments do not always sufficiently mimic future reality prior to widespread planting. Ecological relationships include many cascading and higher order interactions that are intrinsically difficult to test and evaluate for significance at limited temporal and spatial scales. At larger spatial scales, there is a greater possibility for contact with sensitive species or habitats or for landscape-level changes because at larger scales more ecosystems could be altered (*57*).

Environmental and cultivar variability complicates the task of assessing risk. Transgenic organisms, such as genetically engineered crops, released into the environment will potentially interact with a diversity of habitats in time and in space, and the potential risks from a single type of transgenic organism may vary accordingly. For example, among cultivated and natural populations, gene flow can occur regularly or not at all, and substantial variation in risks from gene flow may arise from variation among cultivars, from factors such as distance from the source population, or from the size and density of the source population relative to recipient populations. Risk assessments will need to be especially sensitive to temporal and spatial factors.

Potential Benefits

Reduced environmental impacts from pesticides. As regulations are considered, the potential risks of GEOs should be evaluated and compared to possible environmental benefits, as well as to risks from conventional and other agricultural practices, such as organic farming. Insect-resistant and herbicide-tolerant transgenic crops may decrease the use of environmentally harmful chemicals to control pests. In 1998, 8.2 million fewer pounds of active pesticide ingredient (3.5%) were used on corn, cotton, and soybeans than in 1997 and corresponded to an increase in the adoption of genetically engineered crops (*58*). Annual variation in agrochemical use can depend on multiple factors, including pest problems, weather, and cropping patterns (*59*), besides adoption of genetically engineered crops. Statistical models controlling for additional factors influencing pesticide use estimated that the total volume of pesticides used

Table 1. Published studies on the survival and reproduction of transgenic crops and their hybrids are often used as evidence for or against the likelihood of invasiveness. Studies on oilseed rape, a crop with wild relatives close to agricultural settings, dominate the literature. UH, uncultivated habitats; AP, agricultural plot; AF, agricultural field; FE, field experiments; GH, greenhouses. Steps refer back to Fig. 1.

Crop	Transgenic trait(s)	Potential invasive characteristic examined	Habitat studied	Conclusion	Ref.
Oilseed rape (*Brassica napus*)	Two lines used: 1. Glufosinate tolerance 2. Kanamycin resistance	Persistence in natural habitats	12 UH	Step 1 unlikely	(*5*)
Oilseed rape	Same as above	Seed survival overwinter	12 UH	Step 1 unlikely.	(*7*)
Oilseed rape	Three lines used: 1. Male sterility, glufosinate tolerance, and kanamycin resistance 2. Fertility restorer, glufosinate tolerance, and kanamycin resistance 3. Hybrid between #1 and #2	Yield densities used to assess intraspecific competition and interspecific competition with *Sinapsis alba*	AP	No enhanced risk of step 1; likelihood of step 1 not addressed	(*6*)
Oilseed rape	Glufosinate tolerance	Intraspecific gene flow: hybrid formation	AP	Step A, B possible. No enhanced risk.	(*15*)
Oilseed rape	Glufosinate tolerance, kanamycin resistance, and male fertility restorer	Gene flow with *B. rapa*: Hybrid reproductive characteristics	FE, GH	Step D possible; no enhanced risk; no information on steps A to C.	(*17*)
Oilseed rape	High stearate	Seed survivorship	AF	Step 1 possible	(*12*)
Oilseed rape	1. High laureate 2. High stearate 3. High laureate × *B. rapa* hybrid	Seed germination; seedling vigor	AF	Step 1, steps B, C possible; no information on step A	(*12*)
Oilseed rape	Glufosinate tolerance	Gene flow with *B. campestris* (=*rapa*)	FE	Steps A to D possible	(*13*)
Oilseed rape	Glufosinate tolerance	Gene flow with wild mustard (*S. arvensis*)	FP, GH	Steps A, B unlikely	(*18*)
Potato (*Solanum tuberosum*)	Phosphoresence and kanamycin resistance	Gene flow with *S. tuberosum*		Steps A, B possible	(*16*)
Sugar beet (*Beta vulgaris*)	Glufosinate tolerance	Overwinter survival; hybrid survival	FP	Step 1, Step C possible; no enhanced risk.	(*14*)

on corn, cotton, and soybeans in 1998 decreased 2.5 million pounds (1%) owing to the adoption of genetically engineered crops (*58*). More dramatic decreases are reported for the number of acre-treatments (number of acres times number of treatments per pesticide), a measure that does not incorporate the volume of pesticide used.

In 1998 the area treated with chemicals traditionally used to combat the European corn borer (ECB) was 7% less than in 1995, according to United States Department of Agriculture (USDA) survey data compiled by the National Center for Food and Agricultural Policy. Their unpublished, but widely cited, report estimated that adoption of a new chemical accounted for a 2% reduction, leaving a 5% reduction (4 million acres) unexplained (*60*). The report attributed one-half (2 million acres) of the unexplained reduction in acreage treated with agrochemicals to the adoption of Bt corn (18% of total acreage in 1998 versus 0% in 1995), a figure cited in various media articles. The assumptions used to arrive at this figure are not described, making the conclusion tenuous. Furthermore, as indicated in the report, ECB infestation rates were up to 20 times lower in 1998 than in 1995, raising the possibility that significant declines in acres sprayed would have been observed even in the absence of Bt corn planting (*60*).

Comparisons of herbicide use on soybeans in 1995, when glyphosate-tolerant soybeans were not available, and in 1998, when they were, revealed that on average more herbicides were applied in 1998 but in fewer applications (*61*). The increase in herbicide usage is primarily due to a 7.3 times (SE = ±0.6, range 2.2 to 25.9) increase in pounds of glyphosate used per acre and smaller increases in 7 other herbicides, accompanied by declines in 16 other herbicides (*62*).

The trend between 1997 and 1998 suggests that adoption of genetically engineered crops has resulted in an overall reduction of agrochemical use, but some transgenic crops, such as glyphosate-tolerant soybeans, have not. Carefully designed experiments are needed to ascertain what effect individual transgenic crops have on agrochemical use, independent of other important variables, and the toxicity of the chemicals used needs to be assessed. For example, are environmentally friendly chemicals replacing more potentially harmful ones, or are we using a greater amount of chemicals with comparable toxicity?

Soil conservation. Herbicide-tolerant crops may lead to environmental benefits by facilitating a shift to conservation tillage practices. Specifically, these crops may allow farmers to eliminate preemergent herbicides that are incorporated into the soil and rely on postemergent herbicides, such as glyphosate. The shift to postemergent control of weeds may promote no-till and conservation tillage practices that can decrease soil erosion and water loss and increase soil organic matter (*63*). Studies are needed to address whether soils are improving as a result of crops genetically engineered for herbicide tolerance.

Increased yield. If genetically engineered crops increase yields, some suggest that environmental benefits will include the preservation of natural habitats because less land may be developed for agriculture. Evidence indicates that transgenic crops in the United States have increased yields somewhat, but like the data reported on pesticide use, other factors may account for differences or the lack of differences between transgenic and conventional crops (*60*, *64*). However, the potential environmental benefits of genetically engineered crops through increased yield may be greatest in developing countries where agricultural output may stand for the most improvement.

Phytoremediation. Some genetic modifi-

Table 2. Summary of studies addressing whether transgenic plant tissue could harm nontarget organisms through direct ingestion or indirectly by ingesting prey that have fed on transgenic plants. L, laboratory; F, field GNA, *Galanthus nivalis* agglutin.

Study species, (type of study)	Source of toxin	Effect observed	Ref.
Monarch butterfly (*Danaus plexippus*), (L)	Bt corn pollen	56% survival on Bt pollen (event 176), 100% on non-Bt pollen and no pollen; larvae on Bt pollen dusted leaves consumed less than controls.	(*27*)
Monarch butterfly, (L)	Bt corn pollen	Larvae fed leaves with naturally deposited Bt pollen (event Bt11) had 20% mortality vs. 0 and 3% for controls. In laboratory, highest mortality for Bt pollen from event 176 and for larvae exposed when <12 hours old. Surviving larvae developed normally into adults.	(*25*)
Black swallowtail butterfly (*Papilio polyxenes*), (F, L)	Bt corn pollen, event 810 and event 176	No relation in the field between pollen deposition (event 810) and larval weight or morality. In laboratory, no effect of event 810 on larval survivorship. 20% survivorship when fed leaves with high amounts of Bt pollen from event 176.	(*26*)
Eulophus phennicornis, (L)	Live prey (*Lacanobia oleracea*) fed dried GNA* potato leaves	No effect on egg number, female size, development time; longevity not measured.	(*40*)
Green lacewing (*Chrysoperla carnea*), (L)	Live prey (*S. littoralis* and *O. nubilalis*) fed Bt corn	62% mortality (+Bt) vs. 37% (-Bt) for entire immature life stage.	(*44*)
2-spot ladybird beetle (*Adalia bipunctata*), (L)	Aphids colonizing transgenic GNA* potato plants	Negative effects on fecundity, egg viability, and adult longevity.	(*43*)
Convergent lady beetle (*Hippodamia convergens*), (L)	Aphids colonizing Bt potato plants	No effect on development time, pupal weight, fecundity, or female offspring longevity.	(*42*)
Soil microorganisms	GNA* potatoes	Some transient differences in the rhizosphere microbial community; no significant effect on development of a subsequent crop.	(*32*)
Soil microorganisms	Glyphosate-tolerant canola	Less diverse bacterial community of rhizosphere and differences in community structure compared with two nontransgenic canola.	(*33*, *34*)

*GNA crops are not commercialized, but the *gna* gene has been proposed as a means of protecting plants against aphids and other Homopterans.

cations of plants or microorganisms may provide in situ remediation of polluted soils, sediments, surface waters, and aquifers. Transgenic plants can increase removal of toxic heavy metals from polluted soils and waters and sequester these into plant tissue available for harvest (*65–67*), or can transform pollutants into less toxic forms (*68*). Environmental remediation through transgenic plants has not yet been used widely, so net environmental benefits have not been measured.

Sustainability of GEOs: Implications for Risks and Benefits

For any crops with insecticidal properties, viral resistance, or herbicide tolerance, the continued effectiveness or sustainability of these traits is intricately connected to the evolution of resistance. Transgenic crops that continuously express an insecticidal protein may lead to an increase of insects resistant to the toxin. The diamondback moth (*Plutella xylostella*) has developed resistance to Bt toxins sprayed in the field, and at least 10 species of moths, 2 species of beetles, and 4 species of flies have developed resistance under laboratory exposure to Bt toxins (*69*). The evolution of resistance will, at the least, eliminate the benefits associated with a particular genetically modified crop, and at the most, resistance will have negative ecological consequences, if it results in using harsher pesticides or more applications of pesticides.

Currently, insect resistance management advises a strategy that combines a high-dose exposure to toxin interspersed with planting refuges, areas without the transgenic crop, to minimize the spread of resistance in a population (*70*). Evidence indicates that a properly implemented refuge strategy can slow the rate of resistance evolution (*71–73*) but does not prevent it. Refuges of susceptible individuals are intentionally maintained to mate with resistant individuals and produce offspring vulnerable to high doses of insecticide. Gene flow between these two groups depends on random mating between resistant and susceptible individuals, dispersal before mating, and synchrony of breeding between resistant and susceptible individuals. These conditions are sometimes met, but not always (*74–77*).

The continued effectiveness of particular herbicide-tolerant transgenic crops is also uncertain. Herbicide-tolerant weeds may evolve through the transfer of herbicide-tolerant traits by way of gene flow from transgenic plants, or as a consequence of the increased use of a restricted number of herbicides. Glyphosate, considered an environmentally friendly herbicide, was used widely for 15 to 20 years without the evolution of weed resistance to the herbicide; however, glyphosate tolerance is now known in rigid ryegrass (*Lolium rigidum*), a pernicious grass weed. If glyphosate resistance spreads, there is the concern that more toxic alternatives may replace glyphosate.

Conclusions

1) Neither the risks nor the benefits of GEOs are certain or universal. Both may vary spatially and temporally on a case-by-case basis. Comparisons among transgenic, conventional, and other agricultural practices, such as organic farming, will elucidate the relative risks and benefits of adopting GEOs.

2) Our capacity to predict ecological impacts of introduced species, including GEOs, is imprecise, and data used for assessing potential ecological impacts have limitations. Our inability to accurately predict ecological consequences, especially long-term, higher-order interactions, increases the uncertainty associated with a risk assessment and may require modifications in our risk management strategies.

3) Additional or unidentified benefits and risks may exist that published data do not yet address.

4) Two aspects of genetic modification may warrant special consideration for assessing risks. First, the quantity of modification and modified products may differ from those available through traditional breeding programs. As more economically useful and health-related genes are identified and isolated, it appears that the variety of GEOs will increase dramatically. This increase may collectively represent an environmental risk, given the limitations of predicting negative effects. Second, the quality of modifications and modified products may also differ from those available through selective breeding. Traditional breeding is limited by the available genetic variability in the target organism or its relatives. The great potential, as well as risk, of genetic engineering is that it removes those limits, providing a greater range of possibilities for transferring desired phenotypes into organisms.

5) Evaluation of potential environmental benefits, still in its infancy, will allow risk managers and decision-makers to balance these against the extent and irreversibility of any ecological change. How we document the benefits is critical. In particular, we should incorporate relative environmental toxicity into analyses of changes in pesticide use and quantify the impacts of herbicide-tolerant crops on soil conservation.

6) Measures that prevent transfer of genes that may negatively impact wild populations and that slow the evolution of resistance to the transgenes can minimize some of the possible ecological risks and can prolong the possible benefits associated with genetically engineered plants.

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