Transgenic Insecticidal Corn: Beyond Insecticidal Toxicity to Ecological Complexity

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Many researchers have hailed transgenic insecticidal crops—plants modified to produce insecticidal proteins derived from genes of the bacterium *Bacillus thuringiensis* (Bt)—as the most important technological advancement in insect pest management since the development of synthetic insecticides (Vaeck et al. 1987, Koziel et al. 1993, Perlak et al. 1990, 1993). At least 18 transgenic insecticidal crops have been field-tested in the United States, and three (corn, cotton, and potato) have been widely planted (Andow and Hutchison 1998, Federici 1998, Gould 1998, USDA 1999). But as the commercial availability of these crops has grown, so too has controversy over how to assess and manage the risks posed by this method of pest control.

The widespread planting of millions of hectares of transgenic crops with high levels of insecticidal proteins raises concerns that pest populations might develop resistance to Bt toxins and that food webs might be disrupted (Gould 1998, McGaughey et al. 1998, Marvier 2001). Indeed, the US Environmental Protection Agency (EPA) requires industry to maintain populations of susceptible (nonresistant) insect pests to slow development of resistant populations. Nor are concerns limited to the United States: Anxiety over the safety of food and products derived from transgenic crops have created tensions among international trading partners (Balter 1997, Butler and Reichhardt 1999, Masood 1999).

In this article we focus on transgenic insecticidal corn (Bt corn) developed for selected lepidopteran species that feed on above-ground portions of the corn plant. Over 2.8 million hectares of Bt corn were planted in the United States in 1998, limited only by seed availability (Andow and Hutchison 1998); an estimated 9.7 million hectares of Bt corn were planted in 1999. Thus, although acreage declined to approximately 6.2 million hectares in 2000, Bt corn is now the most common management tactic for the European corn borer, *Ostrinia nubilalis*, throughout the corn-growing regions of the United States.

The potential benefits of transgenic insecticidal corn include savings in resources devoted to scouting for pest insects, reduced applications of broad-spectrum insecticides, increased or protected yields due to season-long control of *O. nubilalis* (Rice and Pilcher 1998), protection of stored corn from lepidopteran insect pests (Giles et al. 2000), and lower mycotoxin levels due to a reduction in fungal plant pathogens associated with *O. nubilalis* feeding (Munkvold et al. 1997, 1999).

> ANALYSIS OF TRANSGENIC INSECTICIDAL CORN DEVELOPED FOR LEPIDOPTERAN PESTS REVEALS THAT THE POTENTIAL BENEFITS OF CROP GENETIC ENGINEERING FOR INSECT PEST MANAGEMENT MAY NOT OUTWEIGH THE POTENTIAL ECOLOGICAL AND ECONOMIC RISKS

Balanced against these potential benefits are possible drawbacks. Such disadvantages of genetically modified crops can, in general, be grouped into three categories: (1) selection for resistance among populations of the target pest, (2) exchange of genetic material between the transgenic crop and related plant species, and (3) Bt crops' impact on nontarget species. The potential for *O. nubilalis* to develop resistance to toxins in Bt corn has been discussed in several publications (Gould 1998, McGaughey et al. 1998, Huang et al. 1999). Although the transfer of genetic material between Bt corn and its wild relatives can be a concern (Snow and Palma 1997, Bergelson

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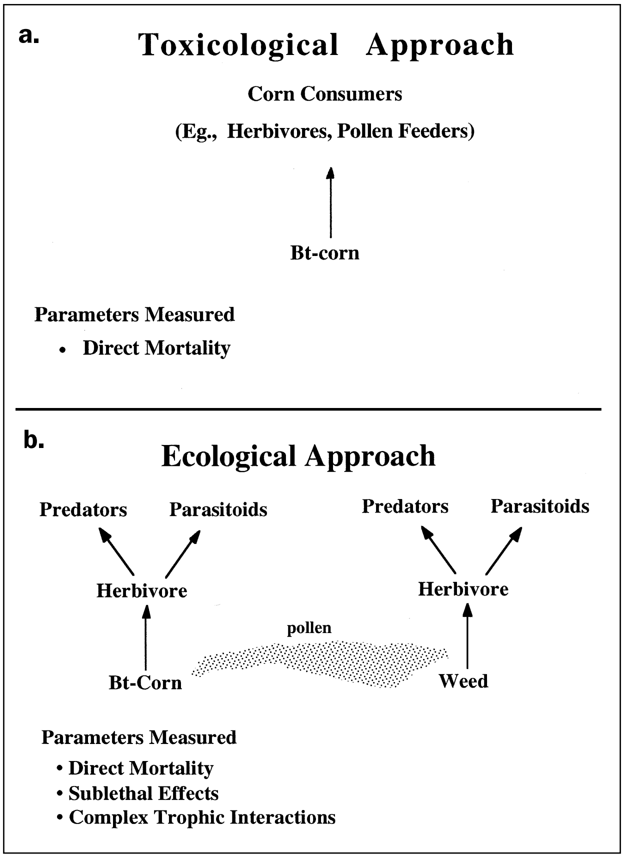

Figure 1. (a) Assessment of the risks from Bt corn based solely on toxicological studies that examine direct effects of Bt toxins on potential nontarget organisms. (b) A broader ecological assessment of nontarget effects of Bt corn based on the dispersal of transgenic corn pollen and potential trophic-level effects on natural enemies.

et al. 1998, Traynor and Westwood 1999), the potential for that transfer is limited to Mexico and Central America, where the wild species are located (Galinat 1988).

The impact of Bt corn on nontarget species

We focus in this article on the potential negative effects of Bt corn on nontarget species—specifically, the impact on arthropods and microorganisms associated with corn. Recent studies documenting negative impacts indicate that nontarget effects may be subtle and complex, and thus may be overlooked in the risk assessment conducted during the registration process for governmental approval of this transgenic crop (Figure 1a). Indeed, we examined the Web sites of EPA and APHIS (Animal Plant Health Inspection Service, US Department of Agriculture) and found no indication that potential ecological interactions had been analyzed during the registration process for transgenic corn. In this article we discuss those ecological effects on several trophic levels within and outside cornfields. Among species that were not explicitly considered in the registration process but that may be adversely affected by Bt corn pollen is the monarch butterfly (*Danaus plexippus*), which we use as a case study in this article.

Predators and parasitoids

Because research has shown that microbial insecticide formulations of Bt have some negative effects on natural enemy species (Croft 1990, Laird et al. 1990, Glare and O'Callaghan 2000), it is important to determine the impact of Bt corn on populations of insect predators and parasitoids in the corn ecosystem. Numerous insect species attack the European corn borer in North America, including several predatory species with relatively broad host ranges and insect parasitoids that are specific to *O. nubilalis* (Steffey et al. 1999). Transgenic corn affects natural enemies in several ways: The enemy species may feed directly on corn tissues (e.g., pollen) or on hosts that have fed on corn, or host populations may be reduced (Hoy et al. 1998). Data submitted for governmental registration of transgenic crops appear to focus primarily on direct feeding on corn tissues (USEPA 1999).

Because several species of insects that attack the corn borer also feed on corn pollen, researchers have examined the effects of corn pollen on these species (Table 1). Direct consumption of transgenic corn pollen by immature stages of three predatory species commonly found in cornfields did not affect development or survival (Pilcher et al. 1997a). The mortality rate of nymphal stages of the predator *Orius majusculus* was much the same when fed a thrips species reared on Bt corn as when the thrips were fed on non-Bt corn (Zwahlen et al. 2000). However, increased mortality of lacewing (*Chrysoperla carnea*) larvae was observed when the larvae fed on an artificial diet containing Bt toxin or preyed on corn borers or other lepidopteran larvae that had fed on transgenic corn (Hilbeck et al. 1998a, 1998b, 1999). Indirect negative effects on predators have not been documented in the field; sampling from transgenic cornfields has not shown declines in predator abundance (Orr and Landis 1997, Pilcher 1999). In one field study, higher numbers of predators were observed in Bt cornfields (Table 1).

The potential trophic-level effects of Bt corn on vertebrate predators also need to be considered in an ecological assessment of this biotechnology (Figure 1b), because bats and birds are known to prey on larvae and adults of several lepidopteran corn pests. Feeding Bt toxin directly to bobwhite quail for 14 days produced no evident effect on the quail (USEPA 1999). We are not aware of any studies that have considered the indirect effects on bird populations resulting from declines in *O. nubilalis* densities after use of transgenic corn. However, if Lepidoptera and their predators and parasitoids are significantly reduced in Bt cornfields and adjacent margins, we might expect the insect prey available for birds, rodents, and amphibians to decrease (see Watkinson et al. 2000 for a simulation of the potential effects of herbicide-tolerant crops on seed-eating birds). When Bt sprays were purposely used to reduce caterpillar abundance in a forest, fewer black-throated blue warbler nests were observed in sprayed areas (Rodenhouse and Holmes 1992). In one of the four years in

Table 1. Interactions between natural enemies and transgenic insecticidal corn (Bt corn).

Species and insect predator	Location of study (L = Lab; F = Field)	Effect (– = negative; + = positive; 0 = no effect)	Aspect of natural enemy showing an effect	Reference
Neuroptera: Chrysopidae				
Chrysoperla carnea	F	0	Number of adults	Pilcher 1999
	L	0	Larval development and survival on transgenic pollen	Pilcher et al. 1997a
	L	–	Larval survival on transgenic pollen or prey exposed to Bt toxins	Hilbeck et al 1998a, 1988b, 1999
	L	0	Larval development and survival on aphid prey reared on Bt corn	Lozzia et al. 1998
Coleoptera: Coccinelllidae				
Coleomegilla maculata	F	0	Number of adults and larvae	Orr and Landis 1997
	F	0, +	Greater number of adults	Pilcher 1999
	L	0	Larval development and survival on transgenic pollen	Pilcher et al. 1997a
Cycloneda munda	F	0	Number of adults	Pilcher 1999
Hippodamia convergens	F	0	Number of adults	Pilcher 1999
Hemiptera: Anthocoridae				
Orius insidiosus	F	0	Numbers of adults and nymphs	Orr and Landis 1997
	F	–, +	Number of adults	Pilcher 1999
	L	0	Nymphal survival and development on transgenic pollen	Pilcher et al. 1997a
Orius majusculus	L	0	Nymphal survival and development on thrips prey reared on Bt corn	Zwahlen et al. 2000
Insect Parasitoids				
Hymenoptera: Braconidae				
Macrocentris cingulum (formerly *M. grandii*)	F	–	30%–60% reduction in adults in transgenic fields	Pilcher 1999
	F	0	Parasitism of larval hosts on nontransgenic plants within transgenic plots	Orr and Landis 1997
Hymenoptera: Ichneumonidae				
Erioborus terebrans	F	0	Parasitism of larval hosts on nontransgenic plants within transgenic plots	Orr and Landis 1997

which observations were made, the lack of caterpillar prey led to a reduction in nesting, which is turn lowered breeding activity below that needed to balance annual mortality.

In a two-year field study, Pilcher (1999) found abundance of the parasitoid species *Macrocentris cingulum* (formerly *Macrocentris grandii*), which is specific to corn borer larvae, to be lower in Bt cornfields in Iowa than in non-Bt fields (Table 1), as might be expected because of significant reductions in larval hosts in Bt corn. We predict that the abundance of a second parasitoid species, *Erioborus terebrans*, will also decline in transgenic fields because of the lack of corn borer hosts, even though findings from one field study indicated that transgenic corn had no effect on *E. terebrans* parasitism (Orr and Landis 1997). In this field study relatively small nontransgenic plots were planted within transgenic plots, and *O. nubilalis* larval hosts were parasitized on the nontransgenic plants. It is possible that Bt corn will show an effect on *E. terebrans* parasitism only in a field study conducted on a larger scale.

Long-term field studies are needed to determine whether the widespread planting of transgenic corn creates an "ecological desert" with relatively few hosts for natural enemies. This type of ecological pattern has been observed following the overuse of insecticides or regional planting of highly resistant crop varieties (Gould 1991, 1998). The interactions among natural enemy and pest populations will probably occur within a mosaic of transgenic and nontransgenic cornfields because of the regulatory requirement that susceptible corn borer populations be maintained in nontransgenic corn refugia. If corn borer densities are significantly suppressed by the use of transgenic corn, it might follow that significant reductions in natural enemy densities will occur also, which could influence the rate of development of resistant pest populations (Gould et al. 1991, Johnson et al. 1997). Natural enemies now account for a high level of mortality of the corn borer (Phoofolo and Obrycki n.d.). If this level of mortality were lowered and corn borer populations developed resistance, the result could be higher densities of the corn borer. Thus, the negative impact on natural enemies raises the possibility that overuse of transgenic corn could lead to the types of resurgence and secondary-pest outbreaks that are associated with misuse of synthetic broad-spectrum insecticides.

Insect herbivores

The foundation for regulation of transgenic Bt crops is based on a history of relatively safe use of Bt sprays (Laird et al. 1990, Miller 1998, Glare and O'Callaghan 2000). The rapid breakdown of Bt toxins in the environment reduces the effects on nontarget organisms, although studies of the ecological interactions of Bt insecticide sprays have documented some effects on nontarget organisms. For example, *Tyria jacobaeae*, a beneficial lepidopteran introduced into North America for biological control of the weed tansy ragwort, has been found in laboratory bioassays to have increased mortality of fourth and fifth instars after feeding on tansy ragwort leaves dipped in Bt (James et al. 1993). Bt sprays can affect nontarget Lepidoptera for up to 30 days after spraying (Johnson et al. 1995), and Bt drift effects have been observed up to 3000 meters from a spray site (Whaley et al. 1998). Furthermore, a reduction in lepidopteran species richness was found 2 years after forest plots were sprayed with Bt (Miller 1990).

Many species of Lepidoptera, both target and nontarget, are likely to be directly susceptible to the Bt toxins produced by transgenic corn hybrids. Because herbivores that feed on corn plant tissue within the cornfield are considered target pests, we consider nontarget herbivores to be those species that may contact corn pollen on weedy plant species within fields or on plants outside of fields. The lepidopteran species most likely to be affected by Bt corn pollen can be determined by examining their distribution and phenology (Losey et al. 2001).

Plant communities within range of corn pollen dispersal will, to a large degree, determine which herbivore (and therefore natural enemy) species are most likely to be present and subject to the effects of Bt corn pollen. An initial list of nontarget lepidopteran species can be generated by cross-referencing the species of plants likely to be found near corn with the species of Lepidoptera that feed on these and related plant species. Because many plant species in and around cornfields are considered to be weeds, the makeup of these plant communities is fairly well known. Unfortunately, what knowledge is lacking for most of the plants associated with corn is the proportion of their total distribution that is composed of field edges and the species composition of the lepidopteran fauna. Specialist herbivores that feed on plants that grow exclusively near corn would be of particular interest. These herbivore species may be more likely to be affected by Bt corn pollen than are herbivores that feed on plants growing in several habitats in addition to cornfield margins.

Once it has been determined which lepidopteran species feed on plants within the shadow of corn pollen, the next step is to determine which subset of those lepidopteran species are feeding in the larval stage during the period that corn pollen is shed. Individual cornfields shed pollen for 8 to 10 days between late June and mid-August (the period varies with corn hybrid and latitude). Thus, to encounter corn pollen, larvae must be feeding during or after this period, while the corn pollen is still on the host plant. Unfortunately, we do not know how long pollen remains on plants adjacent to cornfields or how long the Bt toxin remains active within corn pollen.

The final step in predicting which lepidopteran species are likely to be affected is to determine the relative susceptibility of each species to Bt toxins expressed in transgenic corn pollen. Although the toxin in Bt corn is active against several lepidopteran families, variation in susceptibility has been observed (Pilcher et al. 1997b, Williams et al. 1997, 1998, Wraight et al. 2000). It may be possible to link susceptibility and phylogeny to allow prediction of susceptibility of a given lepidopteran species. Integrating distribution, phenology, and susceptibility permits a ranking of the risk to specific lepidopteran species. Species at particularly high risk could then be identified for further testing.

Case study: The monarch butterfly

The monarch butterfly, *Danaus plexippus*, is widely distributed in North America, producing up to five generations in the United States and Canada (Brower 1996). Several factors may make the risk to monarch butterflies from Bt corn pollen higher than risks to other nontarget lepidopteran species. Monarchs migrate annually in spring and summer from overwintering sites in Mexico to breeding areas across eastern North America (Brower 1996). Fifty percent of the overwintering adults in Mexico originate from the central United States, the major corn-growing area in North America (Wassenaar and Hobson 1998).

The common milkweed, *Asclepias syriaca*, is a secondary successional plant that frequently occurs in and around the edges of cornfields (Bhowmik 1994, Yenish et al. 1997, Hartzler and Buhler 2000); it is the primary host plant of monarch butterflies in the northern United States and southern Canada (Malcolm et al. 1989), and monarch larvae feed exclusively on milkweed leaves (Malcolm et al. 1993). Monarch females oviposit on milkweeds throughout the summer; the egg laying that gives rise to the fall migratory generation occurs from approximately 20 July to 5 August in the northern half of the corn belt. Corn anthesis, in which pollen is dispersed at least 60 meters by the wind (Raynor et al. 1972), coincides with this time period over large areas of the Midwest. Thus, the monarch, milkweeds, and Bt-corn pollen overlap spatially and temporally in the central United States.

A recent study has shown that monarch larvae reared for 96 hours in the laboratory on milkweed leaves dusted with pollen from Bt corn suffered significantly higher mortality (44%) within 96 hours than did larvae reared on leaves dusted with untransformed corn pollen or leaves without pollen (Losey et al. 1999). In addition, larvae that were fed leaves dusted with pollen from Bt corn consumed significantly less foliage per larva and grew significantly slower. In field studies, transgenic corn pollen was naturally deposited on *A. syriaca* leaves within and adjacent to a transgenic cornfield (Jesse and Obrycki 2001). The levels of pollen deposition were highest on plants within the cornfield and lowest 10 meters from the field edge.

Leaf samples taken from within and at the edge of the cornfield were used to assess mortality of first-instar *D. plexippus*. Within 48 hours, mortality was 20% for those instars exposed to Bt-corn pollen, compared with 0% for those not exposed to Bt-corn pollen and 3% for controls not exposed to any pollen (Jesse and Obrycki 2001). Mortality (at 120 hours) of *D. plexippus* larvae exposed to 135 pollen grains/cm^2 of transgenic pollen for 48 hours ranged from 60% to 70% (Jesse and Obrycki 2001). No sublethal effects were observed in adult *D. plexippus* reared from larvae that survived 48 hours of exposure to three concentrations of Bt corn pollen (Jesse and Obrycki 2001).

Based on these laboratory and field results, it appears that pollen from Bt corn may pose a risk to monarch populations. Monarchs may also be negatively affected by the use of transgenic corn and soybeans that are resistant to the herbicides Roundup and Liberty. If these herbicides are used to kill weeds in these transgenic crops, then the abundance of milkweed, which supports monarch populations in agricultural fields, will decline (Taylor et al. 2000).

Pollinators

An assessment of the impact of each Bt-corn hybrid on pollinators is required for EPA registration (USEPA 1999). Although the toxins expressed in Bt-corn pollen are specific for Lepidoptera, several studies raise questions about Bt effects on pollinators, that is, domesticated and wild bees. Documentation for the EPA registration shows that pollen from Bt corn has no effect on survival of either larval or adult domesticated bees (USEPA 1999). However, some unexpected effects of transgenic plants on domesticated bees have been reported. For example, one preparation of Bt (var. *tenebrionis*), reported to be specific for Coleoptera, caused significant mortality in domesticated bees (Vandenberg 1990). Another study indicated that proteins (other than Bt) produced in transgenic rapeseed pollen and targeted for Coleoptera and Lepidoptera interfered with learning by domesticated bees (Picard-Nioi et al. 1997). These studies raise concerns about the precision of genetic transformations and the unintended side effects of genetic transfers. In addition, although wild bees provide a substantial amount of the pollination in many systems, they apparently were not tested for registration of Bt corn. We are not aware of any studies that have examined the impact of Bt pollen on wild bees.

Decomposers

According to the EPA, the insecticidal toxin (CryIA[b]) found in one type of transgenic corn caused significant mortality and reduced reproduction in the soil-dwelling collembolan *Folsomia candida* (USEPA 1999). An earlier study, however, had shown no effects on *F. candida* from feeding on transgenic cotton leaves, which contained the same insecticidal protein as in the corn (Yu et al. 1997). The higher dose in the corn appears to have caused the adverse effects.

Despite its own finding of an adverse effect on a nontarget species, the EPA has concluded that there is a 200-fold "safety factor" in the levels of toxin present in the field (USEPA 1999). The meaning of this EPA safety factor is not entirely clear, though perhaps it signifies that the concentration of Bt toxin in corn residue or soil is less than 1/200th of the concentration needed to kill Collembola. In addition, because no buildup of cornstalk residues has been observed after use of soil insecticides in cornfields, which presumably would have a negative effect on Collembola, "an observable deleterious effect on the soil ecosystem is not expected to result from the growing of CryIA(b)-endotoxin-containing corn plants" (USEPA 1999). This conclusion may need to be rethought: Considering the seasonal life cycle of Collembola, there are potentially important differences between the use of soil insecticides at planting and the occurrence of transgenic Bt toxins in roots (Saxena et al. 1999), pollen deposition, and stalk residues at harvest.

Microorganisms

We found no consideration of the interactions between transgenic corn and plant pathogens or beneficial insect pathogens in the EPA registration documentation for Bt-corn hybrids (USEPA 1999). An ecological approach to evaluating the effects of Bt corn would, we believe, greatly enhance the effectiveness of the registration process in assessing the potential nontarget effects of this new technology.

Transgenic insecticidal corn reduces the incidence of plant pathogens that infect corn following attack by *O. nubilalis* (Munkvold et al. 1997). These plant pathogens also produce mycotoxins, which may be harmful to humans and livestock; levels of these compounds also were reduced in transgenic corn (Munkvold et al. 1999). Reductions in mycotoxin levels were observed when both Bt- and non-Bt-corn hybrids were artificially infested with high densities of corn borer larvae. In two of three field seasons, however, no differences in mycotoxin levels were observed when relatively low densities of naturally occurring *O. nubilalis* larvae infested the Bt and non-Bt plots (Munkvold et al. 1999)

Two insect pathogen species infecting *O. nubilalis* in North America are *Nosema pyrausta*, a microsporidum, and *Beauveria bassiana*, an entomopathogenic fungus (Steffey et al. 1999). *Nosema pyrausta* appears to be specific to the corn borer, so we would expect declines in corn borer densities to affect its prevalence. In contrast, the fungus *B. bassiana* may not be adversely affected by transgenic corn because it attacks a wide range of insects and forms a symbiotic relationship with the corn plant (Bing and Lewis 1991).

Risk mitigation for Bt-corn pollen

We suggest three strategies for reducing risks for nontarget species associated with pollen from Bt corn. The simplest strategy would be to use only those Bt-corn hybrids that do not express the Bt toxin in the pollen. Expression in pollen is controlled by a single gene promoter (Fearing et al. 1997), and there are commercial hybrids that do not express detectable levels of Bt toxins in pollen (Andow and Hutchison 1998; USEPA 1999). The drawback of this strategy is that Bt-corn hybrids lacking Bt toxin in the pollen may not be as effective against first-instar *O. nubilalis*, which feed on corn pollen before feeding on plant tissues. This lower efficacy may present problems for resistance-management programs that are based on high mortality of target populations (Ostlie et al. 1997).

An alternative solution would be to create buffer zones of non-Bt corn around Bt cornfields (Rice 1999). Very little corn pollen travels more than three or four rows from the original plant (Louette 1997). A buffer zone of at least four rows would serve to trap most transgenic pollen. Some 20% to 30% of the corn a grower plants should be nontransgenic, so that it may serve as a refuge in resistance management (Ostlie et al. 1997), which in turn might be used as a buffer zone for Bt pollen collection. The size and shape of the areas of non-Bt corn would have to be designed carefully to ensure that they effectively serve both purposes.

Simply not planting transgenic corn hybrids, a third option, would eliminate the potential risks to nontarget species that this biotechnology poses.

Conclusions and recommendations

Unlike the use of transgenic potatoes and cotton, the use of transgenic corn will not significantly reduce insecticide use in most of the corn-growing areas of the Midwest. During the past 5 years, the percentage of field corn treated with insecticides in the United States has remained at approximately 30%, despite a significant increase in the hectares of Bt corn planted (Figure 2). From 1995 to 1998, about 1% to 2% of the corn grown in Iowa—where over 4 million hectares of corn are grown annually—was treated with insecticides for *O. nubilalis* (Figure 3). A survey of veteran corn farmers in Iowa and Minnesota—the average farming career was 21 years—showed that 70% had never used insecticides for the first generation of the corn borer, and 82.7% had never treated for the second generation (Rice and Ostlie 1997). Approximately 5% had used insecticides three or more times in 21 years to manage the corn borer.

Despite the relatively low use of insecticides during the 1990s for corn borer suppression, between 20% and 30% of the corn planted in the United States in 1998 and 1999 was transgenic (Fernandez-Cornejo and McBride 2000), suggesting that the Bt plantings are not being used as a replacement for insecticides but in addition to them. A core concept of integrated pest management is to use a management tactic only when pest populations exceed a threshold level. It seems, then, that the hectares planted in Bt corn represent a change in approach from management of *O. nubilalis* to a prophylactic strategy.

Because population densities of the European corn borer are unpredictable, the economic benefits of using transgenic corn are not assured (Rice and Pilcher 1998, Hyde et al. 1999, Archer et al. 2000). Comparisons of yields from transgenic and genetically similar nontransgenic corn hybrids grown in replicated plots in 14 to 16 locations in Iowa (Farnham and Pilcher 1998, Rice 1998) showed that only 34% of the transgenic lines produced significantly higher yields in 1997. In locations

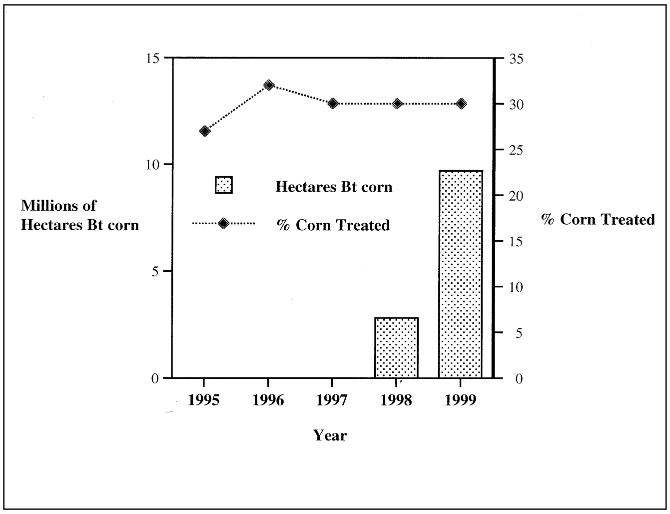

Figure 2. The percentage of field corn treated with insecticides and the number of hectares of transgenic Bt corn planted in the United States from 1995 to 1999. Insecticide data from USDA Agricultural Chemical Usage, National Agricultural Statistics Service for Field Corn. (1 May 2001; **usda.mannlib.cornell.edu/reports/nassr/other/pcu-bb/**)

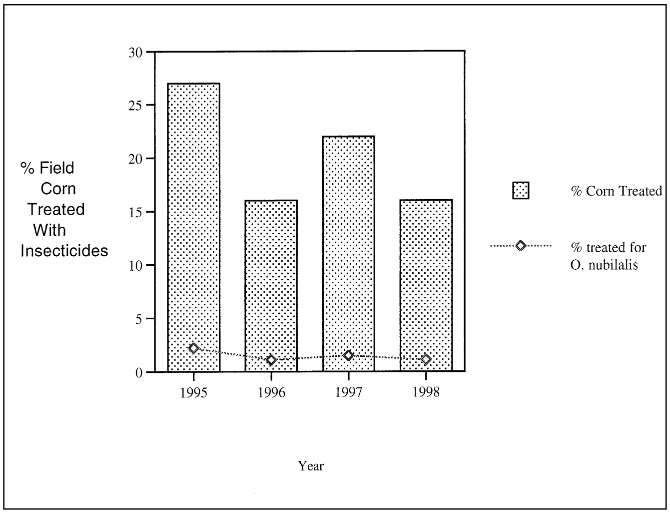

Figure 3. Percentage of field corn treated with insecticides in Iowa, 1995 to 1998. Data from Howard Holden, Iowa Agricultural Statistics, and Rich Pope, Iowa State University Extension Service. In 1995, 2.2% of the field corn in Iowa was treated with broad-spectrum insecticides for the European corn (Wintersteen and Hartzler 1997). In this report, 31.3% of the corn acres in Iowa were treated with insecticides (Wintersteen and Hartzler 1997), similar to the 27% recorded by the Iowa Department of Agriculture Statistics. We calculated that about 7% of the treated acres of field corn were sprayed with broad-spectrum insecticides for the corn borer. Using this 7% value, we estimated the acres treated for the corn borer for 1996 to 1998. It is quite likely that the percentage of acres treated for the corn borer in 1995 did not vary significantly from that found for 1996 to 1998.

where corn borer damage was highest in nontransgenic lines, 50% to 58% of the transgenic hybrids produced significantly higher yields. In 1998, when corn-borer densities were generally lower than usual in Iowa, 12% of transgenic lines produced significantly higher yields.

Further analysis of these comparative data shows a weak relationship ($r^2 = 0.13$) between the amount of insect damage and increased yields in the Bt corn in 1997 and no relationship in 1998. Analysis of a second data set collected for the USDA National Agricultural Statistics Survey in 1998 showed no economic benefit of transgenic insecticidal corn in Iowa (Duffy and Ernst 1999), probably because of differences in the amount of fertilizer applied to the Bt and non-Bt fields. Previous assessments of Bt corn have indicated that the economic benefits of this technology are highly dependent on the population densities of the corn borer and the market value of field corn (Rice and Pilcher 1998). From 1997 to 1999, corn borer densities were generally low in Iowa and the value of field corn had declined. Thus, in these 3 years the economic benefits of Bt corn were not consistently demonstrated.

Given the limited benefits for insect management and the documented ecological effects of transgenic insecticidal corn on nontarget species, we conclude that this biotechnology has a limited role in management of lepidopteran pests in corn. The use of transgenic crops has been promoted as safer for humans and the environment than use of broad-spectrum insecticides (Pimentel and Raven 2000). However, most field corn in the US corn belt is not treated for above-ground insect pests, and most corn hybrids already have substantial resistance to corn borers (Barry and Darrah 1991).

The approach taken in the registration of transgenic corn and in its current use in pest management has been narrowly focused on insecticidal toxicity, but we believe that a more comprehensive approach is required (see, e.g., Stern et al. 1959, Lewis et al. 1997), one that considers the ecological complexity of agroecosystems (Figure 1b). We have outlined in this article the potential benefits and ecological risks of the use of Bt corn. These potential risks are not thoroughly addressed in the US governmental registration process, an oversight that should be attended to.

The widespread and unquestioned acceptance of Bt corn by the agricultural research, regulatory, and educational communities is similar to the rapid adoption and deployment of synthetic insecticides in the early 1950s. During that time ecologically based management programs suffered, and predicted adverse ecological and environmental effects were generally ignored, resulting in limited management options for farmers as targeted species developed resistance and nontarget predator and parasitoid species declined. We are not advocating the elimination of Bt corn, nor do we discount the potential benefits of biotechnology for agriculture. We do argue, however, that a balanced examination of Bt corn suggests ways to improve the regulatory process and to incorporate this technology into an integrated control framework, and we caution against the acceptance of yet another silver bullet for pest management.

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