

Economic Analysis of Dynamic Management Strategies Utilizing Transgenic Corn for Control of Western Corn Rootworm (Coleoptera: Chrysomelidae)

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ABSTRACT We studied management strategies for western corn rootworm, *Diabrotica virgifera virgifera* LeConte, using transgenic corn, *Zea mays* L., from both a biological and an economic perspective. In areas with and without populations adapted to a 2-yr rotation of corn and soybean (rotation-resistant), the standard management strategy was to plant 80% of a cornfield (rotated and continuous) to a transgenic cultivar each year. In each area, we also studied dynamic management strategies where the proportion of transgenic corn increased over time in a region. We also analyzed management strategies for a single field that is the first to adopt transgenic corn within a larger unmanaged region. In all areas, increasing the expression of the toxin in the plant increased economic returns. In areas without rotation-resistance, planting 80% transgenic corn in the continuous cornfield each year generated the greatest returns with a medium toxin dose or greater. In areas with alleles for rotation-resistance at low initial levels, a 2-yr rotation of nontransgenic corn and soybean, *Glycine max* (L.) Merr., may be the most economical strategy if resistance to crop rotation is recessive. If resistance to crop rotation is additive or dominant, planting transgenic corn in the rotated cornfield was the most effective strategy. In areas where rotation-resistance is already a severe problem, planting transgenic corn in the rotated cornfield each year was always the most economical strategy. In some cases the strategies that increased the proportion of transgenic corn in the region over time increased returns compared with the standard strategies. With these strategies the evolution of resistance to crop rotation occurred more rapidly but resistance to transgenic corn was delayed compared with the standard management strategy. In areas not managed by a regional norm, increasing the proportion of transgenic corn and increasing toxin dose in the managed field generally increased returns. In a sensitivity analysis, among the parameters investigated, only density-dependent survival affected the results.

KEY WORDS *Diabrotica virgifera virgifera*, modeling, transgenic corn, integrated pest management, insect resistance management

INSECTICIDAL CROPS PRODUCING TOXINS from *Bacillus thuringiensis* (Bt) have the potential to simplify pest problems while meeting integrated pest management (IPM) objectives (Roush 1997). In 2003, the first transgenic product effective against the western corn rootworm, *Diabrotica virgifera virgifera* LeConte, was commercialized and is being incorporated into management strategies for this pest. The western corn

rootworm has historically been managed with a combination of crop rotation and insecticides (Zhou et al. 2003). However, this pest has a history of developing resistance to these control tactics (Ball and Weekman 1962, 1963; Metcalf 1983; Meinke et al. 1998; Miota et al. 1998; Onstad et al. 1999, 2003b; Scharf et al. 1999). Given this history, transgenic corn, *Zea mays* L., must be managed carefully to maximize its effectiveness as a potentially very effective control tactic.

For managing a species such as the western corn rootworm that has historically been controlled with a variety of tactics, replacement of broad-spectrum insecticides by more specific methods such as transgenic corn may go a long way to simplifying pest management problems (Carrière et al. 2004a). Over-reliance on insecticides creates agricultural, environmental, and pest management problems (Walker et al. 1995) such as frequent evolution of insect resistance (Georghiou 1986) and environmental contamination

The ideas expressed in this paper may not represent those of the USDA.

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(Pimental et al. 1992; Matson et al. 1997). In Arizona, the introduction of Bt cotton for pink bollworm control led to important declines in the use of insecticides (Carrière et al. 2001, 2004a). The introduction of transgenic corn may have similar effects on management practices throughout the Corn Belt. To analyze the potential impacts of using transgenic crops, biologically rich simulation models (Guse et al. 2002, Onstad et al. 2002, Carrière et al. 2003, Storer 2003) in conjunction with spatially explicit empirical studies (Carrière et al. 2003, 2004b) are required to better understand how refuges should be deployed and managed (Carrière et al. 2004a), where refuges are areas not planted to a transgenic cultivar that maintain susceptible individuals that can disperse and mate with resistant individuals surviving in transgenic fields.

Simulation models have indicated that transgenic corn may be an effective management option for farmers in areas with rotation-resistant western corn rootworm phenotypes (Onstad et al. 2003a, Crowder and Onstad 2005, Crowder et al. 2005). Crowder and Onstad (2005) and Crowder et al. (2005) showed that transgenic corn, planted to 80% of rotated cornfields, could effectively prevent resistance to crop rotation from evolving in areas with 85% of the land in rotation between corn and soybean *Glycine max* (L.) Merr. Results also indicated that resistance to transgenic corn did not evolve with a management strategy of planting 80% transgenic corn in rotated cornfields.

Simulation models also have been used to evaluate the risk of resistance to transgenic corn in areas without rotation-resistant populations (Onstad et al. 2001a, Crowder and Onstad 2005, Crowder et al. 2005). In these areas, the gene expression of the allele for resistance to transgenic corn, R, is the most important factor affecting the evolution of resistance to transgenic corn. If R is recessive, resistance can be prevented with any toxin dose and refuges occupying 5–30% of continuous cornfields. If R is dominant, resistance may be difficult to prevent (Crowder and Onstad 2005, Crowder et al. 2005).

Onstad et al. (2003a) performed an economic analysis of management strategies with transgenic corn planted in rotated cornfields in areas with 85% of the landscape in rotation between corn and soybean. They assumed that transgenic corn killed 90% of all larvae and did not simulate the potential for resistance to transgenic corn or various doses of the transgenic toxin. In this article, we expand upon the analysis of Onstad et al. (2003a) and study the biological and economic implications of different strategies for using transgenic corn with a model that simulates evolution of resistance to both crop rotation and transgenic corn.

Long-term, possibly areawide, strategies are the focus of attention for both IPM and insect resistance management (IRM). Midgarden et al. (1997) showed that site-specific IPM, a strategy of spraying only areas that have densities above economic thresholds, slowed the development of insecticide resistance and conserved natural enemies of Colorado potato beetle. This type of IPM management strategy creates in-field refuges that slow the rate of evolution of resistance

(Midgarden et al. 1997). A similar result was observed by Peck and Ellner (1997), who showed that management strategies that reduce selection pressure in some areas have a beneficial effect on the regional level of resistance to a pesticide. In this article, we will attempt to determine whether deployment strategies for transgenic corn that lower the selection pressure for resistance to the transgenic crop also were effective at preventing resistance to crop rotation and maximizing economic returns.

Our goal was to determine the most effective strategy from both a biological and economic perspective for controlling western corn rootworm damage. We evaluate the impact of using transgenic corn with various toxin doses. We focus our analysis on three areas: areas with 100% continuous corn and no rotation-resistant phenotypes, areas where resistance to crop rotation may develop, and areas where rotation-resistance is already a serious problem and IRM is no longer feasible or of primary concern.

Materials and Methods

In this section, we describe the creation of the model and its analysis. First, we describe the functions used to create the model. All functions except for the economic analysis are the same as in the generational time-step model of Crowder and Onstad (2005), and the logic used to derive these functions is not discussed. Second, we describe the economic functions used in the model. Third, we describe the standard simulation conditions. Fourth, we describe the variations on the standard management strategies that were performed. Finally, we describe the sensitivity analyses that were performed.

Population Genetics. We assume this is an autosomal, two-locus, two-allele per locus, diploid genetic system. The allele for susceptibility to transgenic corn is S; the allele for resistance to transgenic corn is R. With regard to crop rotation, we defined the X allele for no movement out of corn and the Y allele for the tendency to move to all patches (Crowder and Onstad 2005). In a 3-yr field study in eastern Illinois, Rondon and Gray (2004) observed increased oviposition in noncorn habitat (soybean, alfalfa, and oat-stubble). This resulted in no significant differences in the numbers of western corn rootworm eggs laid in corn, soybean, and oat-stubble on a per liter or per hectare basis. These results support the assumption that rotation-resistant individuals disperse and oviposit into all patches in the landscape.

Despite a lack of empirical evidence on the population genetics of *D. virgifera virgifera*, this genetic system was chosen because it is comparable to several natural systems described by Onstad et al. (2001b), and has been previously used in models that simulated the development of resistance by western corn rootworm to crop rotation (Onstad et al. 2001b, 2003) and transgenic corn (Onstad et al. 2001a, Storer 2003).

Model Landscape. The region consists of 100 ha of cropland consisting of up to four crops and a maximum of six fields. The four crops are corn grown in the same

location each year (continuous corn), C_c ; corn that follows a soybean field in a 2-yr rotation of corn and soybean (rotated corn) C_r ; soybean, which precedes corn in a 2-yr rotation of corn and soybean, Soy; and the extra noncorn, Ex. A proportion of both corn patches can be planted to a transgenic cultivar in a block configuration. The proportion of the continuous and rotated cornfields that are planted to a transgenic cultivar is T_c and T_r , respectively. In cases where T_c or $T_r > 0$, we studied a refuge size occupying 20% of the field. In the model equations the abbreviations rc, rr, tc, and tr are used for the continuous corn refuge, rotated corn refuge, transgenic continuous corn, and transgenic rotated corn, respectively.

Movement and Oviposition. We set the fecundity per individual to 220 viable eggs, which is half of the number per female, and ignore gender (Onstad et al. 2003a). Normal (-XX) individuals move from the natal corn patch and distribute themselves (and their eggs) across all corn patches according to their relative proportional areas, where - indicates the alleles for susceptibility to transgenic corn. We assumed that rotation-resistant (-YY) individuals move into all patches according to their proportional representation in the region. In the additive case, 50% of the heterozygotes (-XY) distribute themselves and their eggs only into cornfields, whereas the others disperse into all fields.

Toxin Mortality. Toxin mortality incurred by larvae, Q_{tox} , is dependent on the dose of the toxin, the genotype of the individual at the locus for resistance to transgenic corn and the gene expression at this locus. We assume this mortality is applied at the same time as overwintering survival. We studied four doses of toxin (theoretical high, practical high, medium, and low) based on values used in Crowder and Onstad (2005), Crowder et al. (2005), and Onstad et al. (2001a).

Homozygous-resistant individuals, (RR-), always have 100% survival to the transgenic cultivar regardless of dose ($Q_{tox} = 0$). With R dominant, heterozygous (sR-) individuals also always have 100% survival to the transgenic crop. The survival of homozygous susceptible individuals (SS-), or heterozygotes with R recessive (Sr-), is 0, 0.001, 0.05, and 0.20 with a theoretical high, practical high, medium, and low toxin dose, respectively. With R partially recessive, survival of the heterozygotes, (sr-), is 0, 0.01, 0.50, and 0.60 with a theoretical high, practical high, medium, and low toxin dose, respectively. In cases where a proportion of both the continuous and rotated cornfields are planted to a transgenic cultivar, we assume that the dose used in each field is the same. The alleles for susceptibility to crop rotation (denoted by dashes), do not affect survival to the transgenic toxin.

Immature Survival. All larvae emerging from eggs in noncorn patches die. Offspring in continuous and rotated cornfields incur an overwintering mortality of 50% during the egg stage and incur density-dependent mortality during the larval stage (Onstad et al. 2001a, 2003a).

Individuals emerging in fields planted to a transgenic cultivar incur density-independent mortality, Q_{tox} , based on the dose of the toxin and the gene expression. The density-dependent survival of larvae per stage is $0.21 \times \exp(-0.058EGG)$, where EGG is the density of eggs (in millions per hectare) (Onstad et al. 2003a). The maximum larval survival based on this function is 21%. We assume that density-dependent mortality occurs after mortality due to overwintering and toxin exposure.

Model Equations. The number of eggs $E_{i,p}(t + 1)$ of genotype i in patch p for year $t + 1$ as a function of the number of adults $A_{i,p}$ in year t is as follows:

$$E_{i,p}(t + 1) = 220 \times \sum_{j=1}^9 \left\{ P_{j,p} \times \left[A_{j,rc}(t) \times \sum_{k=1}^9 wQ_{k,rc}(t) + A_{j,rr}(t) \times \sum_{k=1}^9 wQ_{k,rr}(t) + A_{j,tc}(t) \times \sum_{k=1}^9 wQ_{k,tc}(t) + A_{j,tr}(t) \times \sum_{k=1}^9 wQ_{k,tr}(t) \right] \right\} \quad [1]$$

P is the probability of genotype j (nine possible genotypes) moving to patch p . We assume that beetles mate randomly within the field of emergence and that the offspring will have an expected frequency distribution dependent upon the frequencies of each genotype emerging in the natal patch. Therefore, Q is the frequency of genotype k in natal patches rc, rr, tc, and tr that can reproduce the particular offspring genotype i when mated with genotype j . Each weight, w , equals the Mendelian proportion of all offspring that are genotype i when genotypes j and k mate.

To calculate the number of older larvae and adults, we calculated density dependent survival. First, we calculated the total density of larvae TL in each kind of corn habitat in the landscape, f (where $f = rc, rr, tc, \text{ or } tr$), surviving the winter and toxicity of transgenic corn roots ($1 - Q_{tox}$).

$$TL_f = \sum_{i=1}^9 E_{i,f}(t) \times 0.5 \times (1 - Q_{tox}) \quad [2]$$

The numbers of older larvae or adults in the four corn habitats f are as follows:

$$A_{i,rc}(t) = 0.5 \times E_{i,rc}(t) \times 0.21 \times \exp\{-0.058 \times [TL_{rc}/(100 \times (1 - T_c) \times C_c \times 10^6)]\} \quad [3]$$

$$A_{i,tc}(t) = 0.5 \times E_{i,tc}(t) \times (1 - Q_{tox}) \times 0.21 \times \exp\{-0.058 \times [TL_{i,tc}/(100 \times T_c \times C_c \times 10^6)]\} \quad [4]$$

$$A_{i,rr}(t) = 0.5 \times E_{i,rr}(t) \times 0.21 \times \exp\{-0.058 \times [TL_{i,rr}/(100 \times (1 - T_r) \times C_r \times 10^6)]\} \quad [5]$$

$$A_{i,tr}(t) = 0.5 \times E_{i,tr}(t) \times (1 - Q_{tox}) \times 0.21 \times \exp\{-0.058 \times [TL_{i,tr}/(100 \times T_r \times C_r \times 10^6)]\} \quad [6]$$

The number of adults emerging the next year is $A_{i,s}(t) = A_{i,e}(t) = 0$ in rotated soybean and in extra vegetation.

Male Dispersal. Previous models simulating resistance to transgenic corn have assumed that 25% of western corn rootworm males disperse out of the natal field before mating (Onstad et al. 2001a, Crowder and Onstad 2005, Crowder et al. 2005). To simulate this, we recalculated the genotype frequencies of males before mating in each field after dispersal. This was performed using our assumption that 50% of emerging adults are male. All females remain in the natal field to mate, whereas a proportion, PM, of the males move out of the natal field and into the other cornfields according to their proportional areas. The standard value for PM is 0.25. For example, the adjusted number of males in the continuous nontransgenic corn is as follows:

$$M_{i,rc}(t) = 0.5 \times M_{i,rc} \times (1 - PM) + 0.5 \times (M_{i,tc} + M_{i,rr} + M_{i,tr}) \times PM \times \left[P(f) / \sum_{k=1}^3 P(k) \right] \quad [7]$$

$M_{i,f}(t)$ is the adjusted number of males of genotype i in field f (rc, tc, rr, and tr), whereas $M_{i,f}(t)$ is the number of males of genotype i that emerged in field f . $P(f)$ is the proportion of land planted to field f that males are dispersing into and $P(k)$ is the proportion of land planted to each cornfield that is not the natal field f for individual $M_{i,f}(t)$. On the right-hand side of equation 7, the first product is the number of males that remain in field f . The other three products represent the number of males moving into f from the other cornfields.

The adjusted number of males after male dispersal is used to recalculate male genotype frequencies in each field before mating. In the model, these frequencies are calculated before equations 1–6 and are used in equation 1 to calculate eggs. However, we did not adjust population densities in any field due to male dispersal. The reason for this is a constraint of the model. Because the model does not simulate males and females separately, if population densities in each field are calculated after male movement there would be

deviation from a 1:1 sex ratio and our assumptions about fecundity per individual would not be valid.

Economic Analysis. Mitchell et al. (2004) compared two different pest-damage functions for western corn rootworm that predicted proportional yield loss as a function of measured root damage by corn rootworm larvae. They indicated that the results of an economic analysis using a damage function from a composed-error model were similar compared with the results of a conventional model unless the distribution of loss matters, such as when the analysis incorporates risk aversion (Mitchell et al. 2004). Because our analysis did not include risk aversion, we followed the conventional approach from Mitchell et al. (2004) and Onstad et al. (2003a) to calculate the proportion of yield lost due to rootworm damage. The proportion of yield lost in habitat f is as follows:

$$LOSS_{f,t} = 0.251 [1 - \exp(-0.0089K_{f,t}^{0.589})], \quad [8]$$

where $K_{f,t} = TL_{f,t}/(100C_f \times 10^4)$ is larvae per square meter in year t after mortality due to overwintering and toxin mortality. No loss occurs unless larvae are present. As the larval population increases, loss increases and asymptotically approaches the maximum of 0.251.

The economic analysis was based on calculation of returns for each cornfield in the region. In areas with rotation-resistant phenotypes and 85% rotated landscape, we did not include returns from soybean or extra vegetation in our analysis because the proportion of land planted to these patches never changed, and we wanted to focus on the returns for corn. Returns (dollars per hectare) for the crop in habitat f in year t are as follows:

$$RETURNS_{f,t} = PRICE_f \times Y_f \times (1.0 - LOSS_{f,t}) - COST_f \quad [9]$$

$PRICE_f$ is the price for crop f , Y_f is (pest-free) yield for crop f , $LOSS_{f,t}$ is the proportional yield loss for crop f in year t due to corn rootworm, and $COST_f$ is the variable cost of production for crop f .

For corn, a price of \$8.15/quintal (ql) was used, this is the approximate marketing year average price from 2000 to 2003 (Illinois Agricultural Statistics Service 2003). Yields and costs were from Illinois crop budgets (Schnitkey 2004). The variable costs for continuous and rotated corn are \$531 or \$519/ha, respectively. The yield for continuous corn, Y_{cc} , was set equal to the yield for rotated corn, Y_{rc} , 104 ql/ha, because the reported yield implicitly included yield loss due to corn rootworm and our economic analysis separately incorporated this yield loss. Therefore, returns for nontransgenic continuous or rotated corn are approximately \$317 or \$329/ha, respectively. We included a cost of \$37/ha for transgenic corn (\$15/acre). Although the price of transgenic corn may vary greatly depending on the quantity purchased and other factors, we believe this is a reasonable estimate of the price that may be charged for transgenic seed. The net present value per hectare for habitat f is the sum of the discounted annual returns:

$$NPV_f = \sum_{t=1}^{15} \beta(t) \times \text{RETURNS}_{f,t} \quad [10]$$

where $\beta(t) = 1/(1 + dr)^t$ and dr is the discount rate. A discount rate of 7% is used, because the Illinois budgets report this rate as the farmer cost of capital (Schmitkey 2004). The net present value (dollars per hectare) of a strategy is then the sum of the net present value for each corn crop in the strategy, weighted by the proportion of the total landscape planted to each crop habitat for the strategy: $NPV = C_r \times NPVC_r + C_c \times NPVC_c$. The annualized net present value (ANPV) of each strategy is the fixed annual return (dollars per hectare) for 15 yr that generates the same net present value:

$$ANPV = NPV/Z, \text{ where } Z = \sum_{t=1}^{15} \beta(t). \quad [11]$$

Simulation Conditions. The model is programmed in Visual Basic in Microsoft Excel 2002 (Microsoft 2002). The model has a time-step of 1 yr, a time horizon of 16 yr, and a spatial unit of 100 ha. The 16-yr time horizon includes the first year in which the model is initialized without transgenic corn plus an additional 15 yr. The initial number of adults is 50,000 per ha of corn, which is the value used in the model of Onstad et al. (2001a). The initial adults are distributed proportionally to the areas of continuous and rotated corn. The rotation level, RL , is the sum of the proportional areas of rotated corn and soybean, which are always equal in the model ($RL = \text{Soy} + C_r$). In the standard simulations of areas without rotation-resistant phenotypes, we set the initial R-allele frequency to 10^{-4} and the Y-allele frequency to 0 in a landscape with 100% continuous corn ($C_c = 1.0$). In the standard simulations of areas with rotation-resistance, the landscape is defined as $RL = 0.85$, $Ex = 0.05$, and $C_c = 0.10$. In these areas, the adults begin at Hardy-Weinberg equilibrium with initial R- and Y-allele frequencies of 10^{-4} .

In simulations without rotation-resistance, the standard management strategy was to plant 80% transgenic corn to the continuous cornfield each year. In the simulations of areas with rotation-resistance the standard management strategy was to plant 80% transgenic corn to the rotated cornfield each year. In these areas, we also performed simulations that represent a standard 2-yr rotation of nontransgenic corn and soybean. All reported R- and Y-allele frequencies are for the entire region simulated.

Dynamic Adoption. In addition to our standard management strategy, we studied a management strategy where the proportion of transgenic corn planted in the region increases over time, while the proportion of corn in the landscape remains constant. In simulations of areas without rotation-resistance, the proportion of the continuous cornfield planted to a transgenic cultivar increases over time; in simulations of areas with rotation-resistance, the proportion of the rotated cornfield planted to a transgenic cultivar in-

creases over time. In these simulations, the proportion of either the continuous or rotated cornfield (depending on simulated area) planted to a transgenic cultivar in the first year is 10%. We studied two strategies where the proportion of these fields planted to transgenic corn increased by an additional 5 or 10% each year until reaching a maximum value of 80%. These two strategies are referred to as the 5 and 10% dynamic adoption strategies. With the 5 or 10% dynamic adoption strategies, the proportion of the field planted to a transgenic cultivar reached 80% in year 15 or 8, respectively.

Simulations for Severe Problem Areas. We modified the simulation of our standard model to determine the best strategies for managing western corn rootworm in areas where rotation resistance is already a severe problem. For this new case, the landscape had $RL = 0.85$ and initial R- and Y-allele frequencies of 0.0001 and 0.5, respectively. For this case, we compared the standard management strategy of planting 80% transgenic corn in the rotated cornfield each year with the dynamic adoption and 2-yr rotation of nontransgenic corn and soybean management strategies. We did not perform a sensitivity analysis on simulations of severe problem areas.

Simulations of Areas Not Managed by the Regional Norm. We also attempted to determine the best strategies for managing western corn rootworm in areas not managed by a regional norm. This was meant to evaluate management options for a single farmer when they are the first to adopt transgenic corn within a larger region. To perform this analysis, we first simulated population densities over 15 yr in a 2,000-ha region consisting of 100% continuous corn and no transgenic corn (unmanaged). The simulated number of adults each year were recorded and used as potential immigrants into a smaller field within the region. We performed an analysis of either a 20- or 100-ha managed field contained within the larger 2,000-ha region. In these simulations, the number of adults that immigrate from the larger region into the smaller field or the number of adults that move out of the smaller field is proportional to the area of the smaller field. For example, if the field using transgenic corn is 20 ha, the proportion of adults each year dispersing in from the 2,000-ha region is 20/2,000 (1%), whereas the proportion of adults moving out of the field into the larger region is 1,980/2,000 (99%). If the field using transgenic corn is 100 ha, the proportion of adults dispersing in from the 2,000 region is 5%. To simplify these simulations, we assumed that adults moving out of the smaller field into the larger region did not affect population densities in the larger region. For each field size (20 or 100 ha), we simulated transgenic corn occupying 0, 20, 50, 80, and 95% of the field. We did not perform a sensitivity analysis on simulations of areas not managed by the regional norm.

This analysis also represents the lower end of the continuum of proportional areas planted with transgenic corn in landscapes without rotation-resistance. In our simulations of areas without rotation-resistance, the standard strategy was to plant 80% of the contin-

uous cornfield to a transgenic cultivar each year. In these simulations, the maximum proportion of the total landscape planted to a transgenic cultivar is $(0.95 \times 100 \text{ ha}) / (2,000 \text{ ha})$ or $\approx 5\%$.

Sensitivity Analysis. In a sensitivity analysis, we studied the influence of five factors on the economic results of the standard simulations. First, we varied the discount rate from the standard 7% to values of 1 and 15%. Second, we varied the price of corn by 10%. Third, we varied the variable costs for corn by 10%. Fourth, we varied the price of transgenic corn to \$24.7 and \$49.4/ha, or \$10 and \$20/acre, respectively.

We also simulated population dynamics with different versions of the density-dependent survival function. One was based on the model of Onstad et al. (2001a), $1 / (1 + 2.42EGG^{0.7})$, which has a maximum larval survival of 100%. One was based on the models in Crowder and Onstad (2005) and Crowder et al. (2005), $1 / (2.59 + 1.29EGG^{0.88})$, which has a maximum larval survival of 39%. We also tested the model without density-dependent mortality but with an added density-independent mortality based on field data collected by Hibbard et al. (2004). They revealed that density-independent establishment was between 2.5 and 5.7% when plants were sampled on the optimal date. For this model, we used the higher end of 5.0% for density-independent survival of larvae after overwintering and toxin mortality similar to Crowder and Onstad (2005) and Crowder et al. (2005).

Results

Biological Analysis of Areas without Rotation-Resistant Phenotypes. In general, in simulations of areas without rotation-resistant phenotypes, resistance to transgenic corn evolved more slowly with the dynamic adoption strategies compared with the standard strategy of planting 80% transgenic corn each season. With the dynamic adoption strategies, there is less selection for resistance to transgenic corn compared with the standard strategy. This is especially the case during the early years of the simulations, when the proportion of the region planted to a transgenic cultivar is relatively low. As the proportion of transgenic corn builds in the region, the rate of evolution of resistance to crop rotation increases.

In simulations of areas with 100% continuous corn and no rotation-resistant phenotypes, the R-allele frequency never exceeded 0.001 in 15 yr with R recessive or partially recessive with a theoretical or practical high dose and a 5 or 10% dynamic adoption strategy. These results were similar when compared with results of the standard simulations with 80% transgenic corn planted to the continuous cornfield each year, where the R-allele frequency did not exceed 0.0001 in 15 yr with R recessive or partially recessive and the high doses. Similarly, the R-allele frequency did not exceed 0.0001 in 15 yr with R recessive and a medium or low dose with either a 5 or 10% dynamic adoption strategy or the standard strategy.

With R partially recessive and a medium dose, the R-allele frequency exceeded 50% in year 8–9 with

either a 5 or 10% dynamic adoption strategy, compared with 6 yr with the standard management strategy of planting 80% transgenic corn in the continuous cornfield every year. With R partially recessive and a low dose, the R-allele frequency exceeded 50% in year 13 and 11 with a 5 and 10% dynamic adoption strategy, respectively, compared with 10 yr with the standard strategy.

With R dominant and a 5% dynamic adoption strategy, the R-allele frequency exceeded 50% in year 6, 6, 7, and 10 with a theoretical high, practical high, medium, and low dose, respectively (Fig. 1). With R dominant and a 10% dynamic adoption strategy, the R-allele frequency exceeded 50% in year 6, 6, 6, and 9 with a theoretical high, practical high, medium, and low dose, respectively. With the standard management strategy of planting 80% transgenic corn in the continuous cornfield each year, the R-allele frequency exceeded 50% in year 5 with a medium or greater dose and year 8 with a low dose and R dominant (Fig. 1).

Biological Analysis of Areas with Rotation-Resistant Phenotypes. In areas with rotation-resistant phenotypes, resistance to transgenic corn never evolved in 15 yr with any of the simulated management strategies. In general, resistance to crop rotation evolved more quickly with the dynamic adoption strategies compared with a strategy of planting transgenic corn each season. In years where transgenic corn is not planted in the region, the selection pressure for rotation-resistant phenotypes decreases, causing resistance to crop rotation to develop more rapidly.

In simulations of areas with 85% rotated landscape and rotation-resistant phenotypes, with the standard management strategy of planting 80% transgenic corn in the rotated cornfield each year, the Y-allele frequency never exceeded 0.03 and the R-allele frequency never exceeded 0.0001 in 15 yr with any toxin dose or allele expression for either trait. Likewise, the R-allele frequency never exceeded 0.0001 in 15 yr with any allele expression for either trait and toxin dose with a 5 or 10% dynamic adoption strategy. With a five or 10% dynamic adoption strategy and Y recessive, the Y-allele frequency never exceeded 0.0001 in 15 yr with any combination of R-allele expression or toxin dose.

Resistance to crop rotation did evolve with the dynamic adoption strategies and Y additive or dominant. With Y additive and a 5% dynamic adoption strategy, the Y-allele frequency exceeded 50% in year 14 with a medium or greater dose and year 13 with a low toxin dose with any R-allele expression. With Y additive and a 10% dynamic adoption strategy, the Y-allele frequency never exceeded 50% in 15 yr, reaching a maximum value of 0.06. With Y dominant and a 5% dynamic adoption strategy, the Y-allele frequency exceeded 50% in year 9 with any toxin dose and R-allele expression. With Y dominant and a 10% dynamic adoption strategy, the Y-allele frequency exceeded 50% in year 15 with a theoretical or practical high dose and in year 14 and 13 with a medium and low dose, respectively, with any R-allele expression.

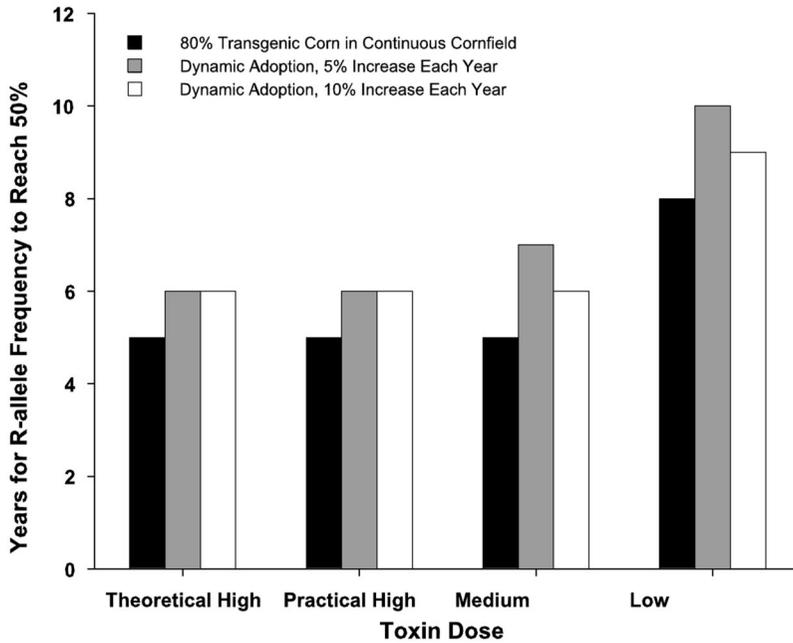


Fig. 1. Years for the allele for resistance to transgenic corn, R, to reach 50% in simulations with 100% continuous corn, four toxin doses, R dominant, and either the standard management strategy of planting 80% transgenic corn to the continuous field each year or the 5 or 10% dynamic adoption strategies.

Economic Analysis of Areas without Rotation-Resistant Phenotypes. In areas with 100% continuous corn and no rotation-resistant phenotypes, returns with the standard management strategy of planting 80% transgenic corn in the continuous cornfield each year differed depending on toxin dose and R-allele expression (Fig. 2). In all cases, returns were greatest with a theoretical or practical high toxin dose, whereas the medium and low doses generated lower returns. With R recessive, the annualized net present value was \$259/ha with a theoretical high dose. Returns decreased with lower toxin doses, by up to 40% with a low dose. With R partially recessive, the annualized net

present value with any dose did not differ from simulations with R recessive. With R dominant, returns decreased by 29% with a theoretical or practical high dose and 2–4% with a medium or low dose compared with the R recessive case.

Dynamic Adoption. Toxin dose determined the relative value of the dynamic adoption strategies. Implementing a 5 or 10% dynamic adoption strategy generated lower returns than the standard management strategy of planting 80% transgenic corn in the continuous cornfield each year with a medium or greater dose with any R-allele expression. With a theoretical or practical high toxin dose and a 5 or 10% dynamic adoption strategy, returns were ≈15 or 8% lower, respectively, compared with the standard strategy with R recessive or partially recessive and 2–5% lower with R dominant (Fig. 3a). With a medium dose and a 5 or 10% dynamic adoption strategy, returns were 6–10% less than the standard strategy. With a low toxin dose, the 5% dynamic adoption strategy generated greater returns than the 10% dynamic adoption strategy and the standard management strategy of planting 80% transgenic corn in the continuous cornfield each year with any R-allele expression (Fig. 3b). The greatest change occurred with R dominant, with the 5 or 10% dynamic adoption strategies generating returns 6 or 3% greater, respectively, than the standard strategy (Fig. 3b).

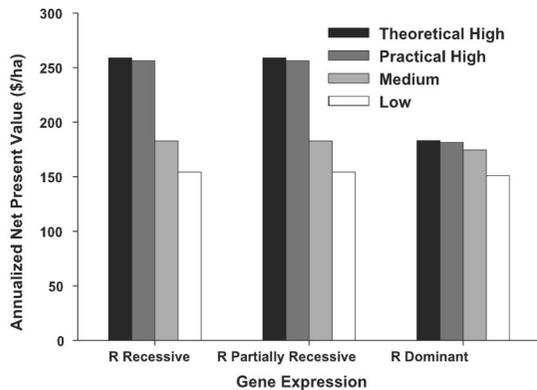


Fig. 2. Annualized net present value (dollars per hectare) of simulations with 100% continuous corn and 80% transgenic corn with three types of expression for the allele for resistance to transgenic corn, R, and four toxin doses.

Economic Analysis of Areas with Rotation-Resistant Phenotypes. In areas with rotation-resistant phenotypes and 85% rotated landscape, simulations of a 2-yr crop rotation without transgenic corn generated an annualized net present value of \$300, \$258, and

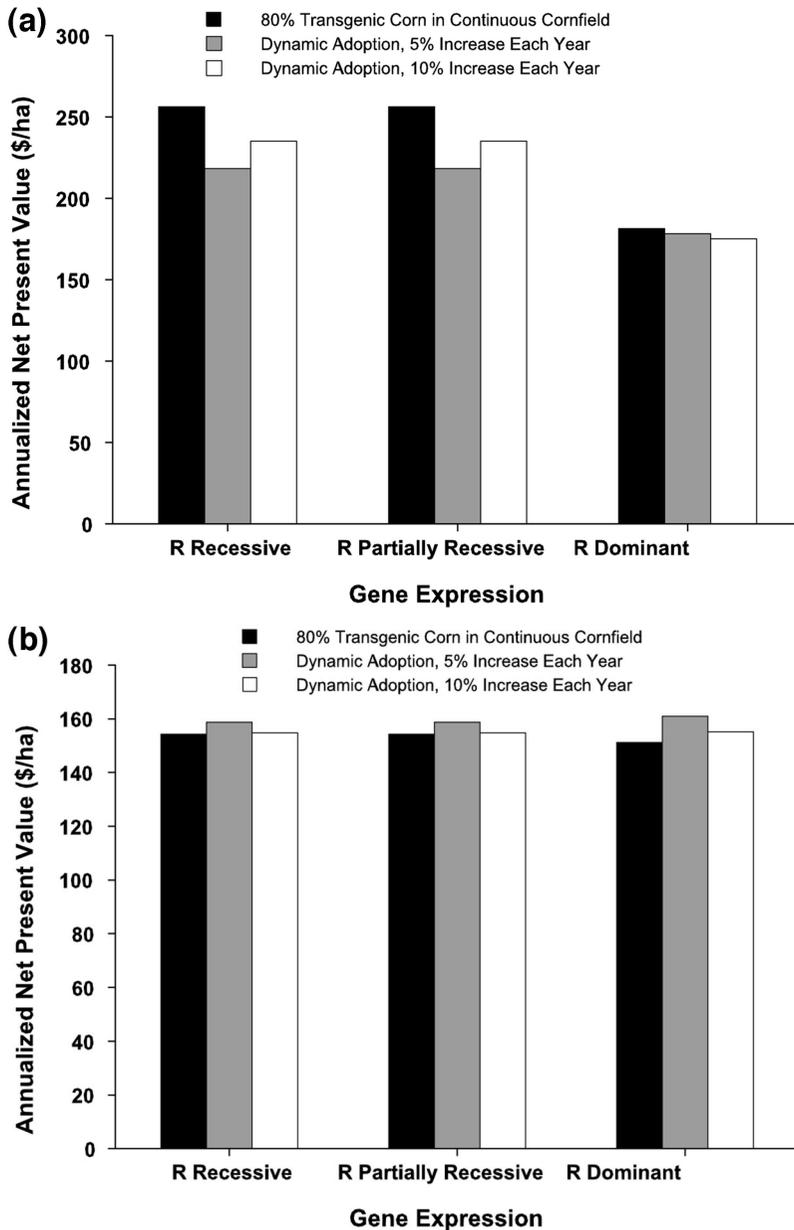


Fig. 3. Annualized net present value (dollars per hectare) of simulations with 100% continuous corn and three types of gene expression for the allele for resistance to transgenic corn, R, with the standard management strategy of planting 80% transgenic corn to the continuous field each year or the 5 or 10% dynamic adoption strategies with a practical high (a) or low toxin dose (b).

\$240/ha with Y recessive, additive, and dominant, respectively (Fig. 4). The highest returns occurred in the Y recessive case because the Y-allele frequency remained at 0.0001 over the course of the 15-yr simulation and damage to rotated cornfields was minimal.

In these areas, the standard management strategy of planting transgenic corn to 80% of the rotated cornfield resulted in similar returns regardless of gene expression for either trait. This differed from the 2-yr

rotation of nontransgenic corn and soybean, where returns decreased with Y additive or dominant compared with Y recessive (Fig. 4). Returns with the standard strategy were approximately \$277/ha with any combination of toxin dose and allele expression for either trait (Fig. 4). These returns represented an 8% decrease with Y recessive and a 7 and 13% increase with Y additive and dominant, respectively, compared with the 2-yr rotation of nontransgenic corn and soybean (Fig. 4). In each case, the highest returns oc-

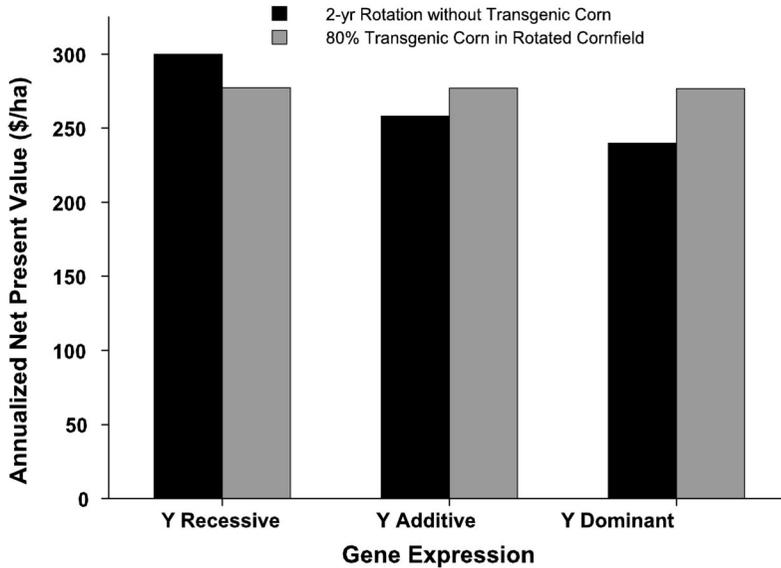


Fig. 4. Annualized net present value (dollars per hectare) of simulations with 85% rotation and three types of gene expression for the allele for resistance to crop rotation, Y, with a 2-yr rotation of nontransgenic corn and soybean or the standard management strategy of planting 80% transgenic corn to the rotated cornfield each year with a practical high toxin dose. Results were similar with the other three doses and are not shown.

occurred with a theoretical high dose and returns decreased as dose decreased. However, the difference between returns with a theoretical high dose and the lower doses was never $>0.9\%$. With any Y-allele expression or toxin dose, the expression of the R-allele did not affect returns by $>0.012\%$.

Dynamic Adoption. As Fig. 5 indicates, the standard management strategy of planting 80% transgenic corn in the rotated cornfield each year generated similar returns compared with the dynamic adoption strategies. Returns for the dynamic adoption strategies ranged from 8% less to up to 4% more than the standard strategy with any toxin dose and R-allele expression. With Y recessive, larval densities with the dynamic adoption strategies were 20–50% greater in the first 2 yr of simulations compared with the standard strategy with any dose but $<2\%$ different in subsequent years. Thus, returns were typically greater with the dynamic adoption strategies and Y recessive compared with the standard strategy because the gains from planting less transgenic corn outweighed losses due to larval damage (Fig. 5a and b). With Y dominant, larval densities were up to 100% greater in soybean with the dynamic adoption strategies compared with the standard strategy. Therefore, the dynamic adoption strategies typically generated slightly lower returns with Y dominant compared with the standard strategy (Fig. 5a and b).

Simulations of Severe Problem Areas. In simulations of areas with 85% rotation and an initial Y-allele frequency of 0.5, the Y-allele frequency increased toward 1.0 with any management strategy examined. With any management strategy simulated, the R-allele frequency never exceeded 0.0001 in 15 yr with any combination of gene expression or toxin dose. In these

areas, the annualized net present value of a 2-yr rotation of nontransgenic corn and soybean was approximately \$198/ha with any gene expression. The standard management strategy of planting 80% transgenic corn in the rotated cornfield each year generated returns 15–25% greater than a 2-yr rotation of nontransgenic corn and soybean with any toxin dose or gene expression. With any gene expression, the average annualized net present value was approximately \$263 with a theoretical high toxin dose. Returns decreased with the lower doses, up to a maximum of 12% with a low dose, but they were still greater than a 2-yr rotation of nontransgenic corn and soybean. In these problem areas the dynamic adoption strategies never generated returns as high as the standard management strategy of planting 80% transgenic corn in the rotated cornfield each year. With any allele expression or toxin dose, the 5 or 10% dynamic adoption strategies generated returns ≈ 12 or 7% lower, respectively, than the standard strategy. However, the dynamic adoption strategies did generate returns 5–19% greater compared with a 2-yr rotation of nontransgenic corn and soybean.

Simulations of Areas Not Managed by Regional Norm. We first simulated the 2,000-ha unmanaged region where the adults were used as potential immigrants into a smaller, managed field. In the unmanaged region, populations fluctuated considerably and never reached a carrying capacity. For example, in year 3 the population reached a density of ≈ 1.18 million adults per ha but fell to $\approx 15,000$ adults per ha in year 4, a 99% decrease. Similarly, populations in the unmanaged region reached a maximum density of ≈ 1.33 million adults/ha in year 10 but decreased to a minimum of 6,300 adults per ha in year 11. These fluctuations were

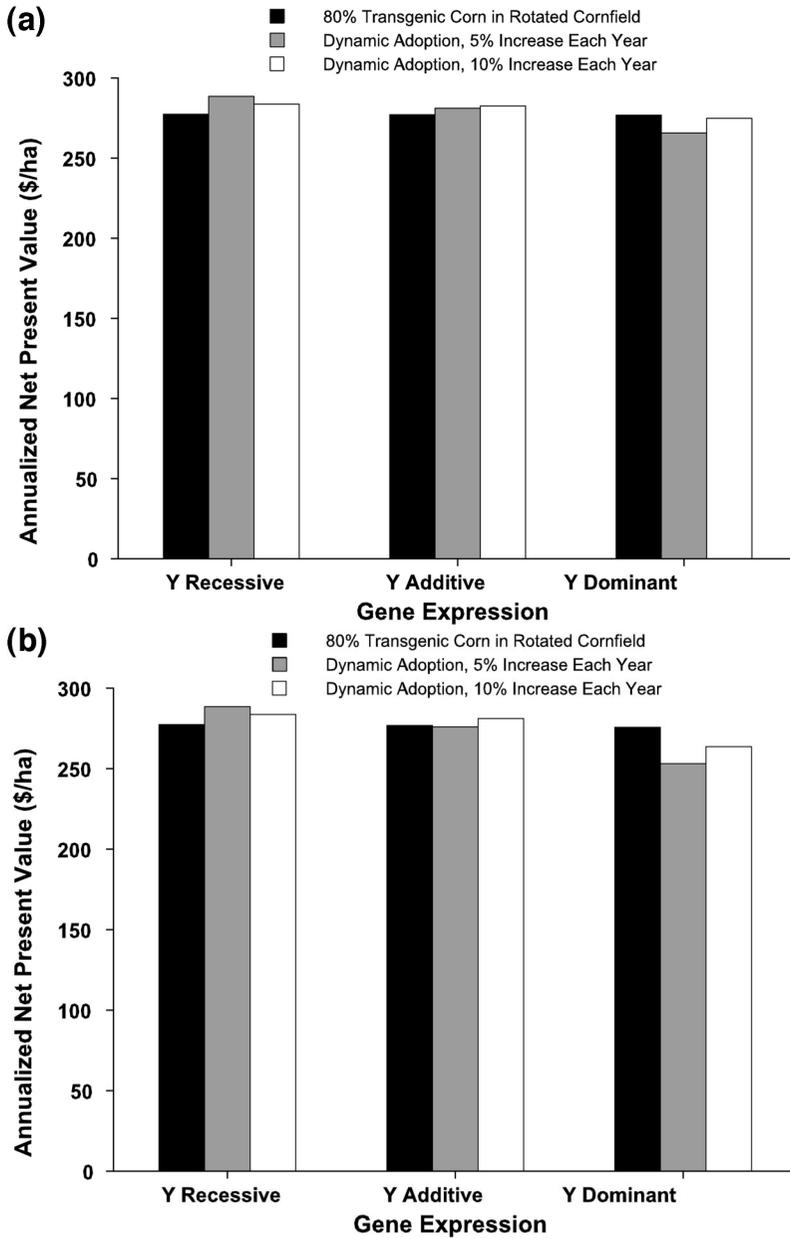


Fig. 5. Annualized net present value (dollars per hectare) of simulations with 85% rotation and three types of gene expression for the allele for resistance to crop rotation, Y, with the standard management strategy of planting 80% transgenic corn to the rotated field each year or the 5 or 10% dynamic adoption strategies with a practical high (a) or low toxin dose (b).

a result of density-dependent survival from year to year. The average number of adults each year in the unmanaged region over 15 yr was $\approx 481,000$ beetles per ha.

In simulations of a relatively small field that is the first to use transgenic corn in the larger region, increasing the proportion of transgenic corn in the field increased returns in most cases. In addition, greater toxin doses increased returns in these fields. In simulations of a 20- or 100-ha field of continuous corn with

a proportion of the landscape planted to a transgenic cultivar that is located within a 2,000-ha unmanaged region of continuous corn, planting 0% transgenic corn resulted in an annualized net present value of \$194/ha.

With a 20-ha managed field, increasing the proportion of transgenic corn in the region always increased returns over the no management strategy with any toxin dose (Fig. 6). Expression of the R-allele did not affect the returns with any toxin dose or refuge size.

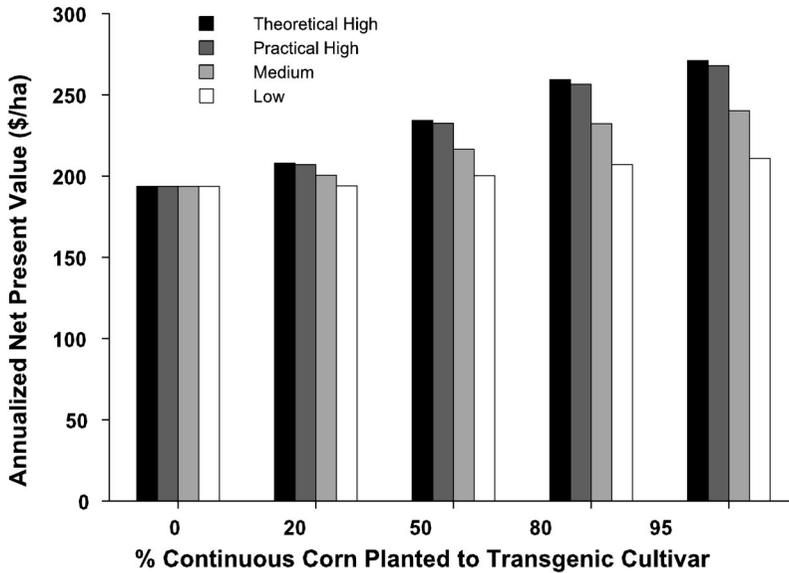


Fig. 6. Annualized net present value (dollars per hectare) of simulations of a 20-ha adjacent region with 100% continuous corn, four toxin doses, and varying proportion of the continuous cornfield planted to a transgenic cornfield. Toxin dose does not affect returns in simulations with 0% transgenic corn.

Returns were greatest with a theoretical high toxin and 95% transgenic corn in the continuous cornfield (\$271/ha). Returns decreased by up to 23% with 20% transgenic corn compared with 95% transgenic corn. Returns with the lower doses also decreased, up to a maximum of 22% with a low dose (Fig. 6). The differences between returns with each toxin dose increased as the refuge size increased (Fig. 6).

In simulations of a 100-ha managed field, increasing the proportion of transgenic corn from 20 to 95% in the region increased returns compared with no management in all cases with one exception. With a low dose, returns with 20% transgenic corn were 0.4% lower than returns with no management. The reason for this difference is that the savings from not planting transgenic corn with a low dose exceeded increased returns caused by decreasing larval damage by planting 20% transgenic corn. Returns were greatest with a theoretical high dose, with an annualized net present value of \$272/ha when the proportion of transgenic corn planted to the continuous cornfield was 95% with any R-allele expression. Returns decreased as dose decreased, up to a maximum of 19% with a low dose. Similar to simulations of a 20-ha managed field, the differences between returns with the theoretical high dose and the lower doses increased as the refuge size increased.

In the simulations of a 20- or 100-ha managed field, the R-allele frequency never exceeded 50% in 15 yr with any toxin dose, refuge size, or allele expression. The fastest evolution occurred with a theoretical or practical high dose and 95% transgenic corn, where the R-allele frequency reached 0.002 after 15 yr with R dominant with either a 20- or 100-ha managed field. With the lower doses the R-allele frequency never exceeded 0.001 within 15 yr.

Sensitivity Analysis of Areas without Rotation-Resistant Phenotypes. In a sensitivity analysis of areas with 100% continuous corn and no rotation-resistant phenotypes, changing the discount rate to one or 15% had little effect on the results, as the difference between the dynamic adoption strategies and the standard management strategy of planting 80% transgenic corn in the continuous cornfield each year relative to each other never changed by >3%. Changing the price of transgenic corn to \$24.7 or \$49.4/ha also had little effect on the results, as the difference between the various strategies relative to each other never changed by >3%.

Changes in the density-dependent survival functions did affect the results. Under standard conditions, the 5 or 10% dynamic adoption strategies never generated returns as high as the standard management strategy of planting 80% transgenic corn in the continuous cornfield each year with a medium or greater dose and any allele expression. This trend did not change with various density-dependent survival functions, although the differences between the dynamic adoption strategies and the standard management strategy increased. For example, with R recessive or partially recessive, returns with the 5% dynamic adoption strategy, a practical high dose, and a density-dependent function that allowed 100% maximum survival were 25 or 23% less, respectively, than the standard strategy. With the function that allowed 39% maximum survival or the density-independent function, returns were 23 or 50% less, respectively, than with the standard strategy. These results differed from the standard conditions where the 5% dynamic adoption strategy generated returns 15% less than the standard management strategy with R recessive or partially recessive. The results were similar with a

theoretical high or medium toxin dose or a 10% dynamic adoption strategy. The affect of density-dependence was not as great with a low dose, as the difference between the dynamic adoption strategies and the standard strategy never differed by >8% when comparing simulations run with different density-dependent functions.

With R dominant, a density dependence function that allowed 39 or 100% maximum survival did not affect the results, as the difference between the 5 or 10% dynamic adoption strategies compared with the standard management strategy of planting 80% transgenic corn in the continuous cornfield each year did not change by >3%. However, with the density-independent function and R dominant, the difference between the dynamic adoption strategies and the standard management strategy increased by 20–27% with a medium or greater dose.

Varying the price or variable costs of corn had the greatest effect on the returns of each strategy but never affected the best management strategy in any case. Because the amount of corn in the landscape was always 100%, changes in the price or variable costs of corn affected each strategy equally. The fluctuations in returns with any strategy were elastic due to fluctuations in price or variable costs. Increasing and decreasing the price of corn by 10% resulted in annualized net present values \approx 30–47% greater and 30–47% less, respectively, compared with the standard simulations. This indicated that returns had an elasticity of 3–4.7 due to changes in price. Increasing and decreasing the variable costs by 10% resulted in returns \approx 20–35% lower and 20–35% greater, respectively, compared with the standard simulations. This represented an elasticity of 2–3.5.

Sensitivity Analysis of Areas with Rotation-Resistant Phenotypes. Changing the discount rate, the price of transgenic corn, and density-dependent survival had little effect on the results, as the difference between the four different management strategies relative to each other never changed by >4%.

Varying the price and variable costs of corn had the greatest affect on returns generated with each strategy but never changed the best management strategy. Because the proportion of corn in the landscape never changed, changing the price or variable costs of corn affected each strategy equally. Fluctuations in returns were elastic due to fluctuations in price or variable costs. Increasing and decreasing the price of corn by 10% resulted in returns \approx 29% greater and 29% less, respectively, than the standard simulations, representing an elasticity of 2.9. Increasing and decreasing the variable costs of corn by 10% resulted in returns \approx 18% less and 18% greater, respectively, than the standard simulations, representing an elasticity of 1.8.

Discussion

In this article, we do not want to emphasize the exact annualized net present value of each management strategy but rather the differences between the various management strategies. In areas without ro-

tation-resistant phenotypes, both toxin dose and gene expression of the R-allele affected returns. In these areas, greater toxin doses resulted in increased returns in every case. Returns with the theoretical and practical high doses were similar, but decreased with the medium and low doses. Returns were similar with R recessive or partially recessive and the high doses, where resistance to the transgenic corn did not evolve, but decreased with R dominant. With the medium or low doses, returns were lower with R partially recessive or dominant compared with the R recessive case as resistance to transgenic corn did evolve.

In areas without rotation-resistant phenotypes, the most economical strategy for farmers may be to adopt transgenic corn as quickly as possible, especially if it is highly effective at controlling western corn rootworm (more than a low dose). In these areas, the dynamic adoption strategies never generated greater returns than the standard management strategy of planting 80% transgenic corn in the continuous cornfield each year with a medium or greater dose. With these doses and the dynamic adoption strategies, larval densities increased by up to 80% compared with the standard strategy. Increased densities, especially in the early years of the simulations, resulted in >20% yield lost in refuges and transgenic fields and decreased returns compared with the standard strategy, where yield loss never exceeded 20%.

These results are consistent with the theoretical findings of Laxminarayan and Simpson (2002) using a highly stylized model of Bt corn. They find that the pest population's intrinsic growth rate and the farmer's discount rate determine the optimal refuge and argue that empirically, the conditions can easily be met such that 0% refuge is economically optimal. In the context of our model, this would imply immediate adoption of Bt corn with 80% refuge would be economically superior to the two dynamic adoption strategies we examine when rotation resistant phenotypes are not present. However, Laxminarayan and Simpson (2002) do not examine optimal refuge strategies when the pest also can evolve resistance to another control method such as crop rotation.

With a low-dose corn hybrid planted in continuous cornfields, there were several cases where the dynamic adoption strategies increased returns over the standard management strategy. With a low dose, the percentage of yield lost in both refuge and transgenic fields increased >22% in most years with any R-allele expression and the standard strategy as larval densities in both fields were high, especially with R dominant. Densities were similar with the dynamic adoption strategies and returns increased in most cases compared with the standard strategy, as the economic gains from planting less transgenic corn exceeded losses due to larval damage.

This different result for a low dose is generally consistent with the finding of Secchi et al. (2001), who derive the economically optimal refuge for Bt corn for European corn borer when the farmer can choose a different level of refuge each year. They examine this economically optimal refuge time-path under heavy

and light suppression of the pest population by Bt corn, which are respectively comparable to the high and low dose modeled here. With light suppression (low dose), the optimal time path for refuge is centered around 60% refuge, as opposed to around 5% refuge for a high-dose product (Fig. 1 in Secchi et al. 2001). With a low dose, we find that a time-path beginning with 90% refuge and slowly decreasing to 20% superior to a constant time-path of 20%, whereas with higher doses, we find the opposite.

In areas with rotation-resistant phenotypes, if the rotation-resistant alleles are initially rare and recessive, planting transgenic corn is uneconomical. In this case, population densities remain low in rotated corn regardless of the type of management. Therefore, a 2-yr rotation of nontransgenic corn and soybean may be the most economical strategy if Y is recessive. In addition, the dynamic adoption strategies provided greater returns than the standard management strategy of planting 80% transgenic corn to the rotated cornfield each year in simulations of areas with rotation-resistant phenotypes with Y recessive. However, the results of Crowder and Onstad (2005) and Crowder et al. (2005) indicate that rotation-resistance is most likely not recessive based on comparisons between modeling work and field observations. If Y is additive or dominant, the most economical strategy for farmers may be to adopt transgenic corn as quickly as possible. With Y dominant, the dynamic adoption strategies were less effective than the standard management strategy. With Y recessive, the 5% dynamic adoption strategy provided greater returns than the 10% dynamic adoption strategy. In contrast, with Y dominant, the 10% dynamic adoption strategy provided greater returns. With Y recessive, larval populations in rotated corn are low and returns from planting less transgenic corn exceed losses from increased larval damage. With Y dominant, the opposite is true, as damage from increased larval populations in rotated corn exceed the gains from planting less transgenic corn throughout the region.

In areas where rotation-resistance is already a severe problem, planting 80% transgenic corn in the rotated cornfield each year was always the most economical management strategy. In these areas, IRM may no longer be feasible and IPM may be the only option. With any management strategy, the allele for resistance to crop rotation evolved from the initial value of 0.5 toward 1.0. In these severe problem areas, transgenic corn effectively reduces populations in rotated cornfields and was always more cost-effective than implementing a dynamic adoption strategy or a 2-yr rotation of nontransgenic corn and soybean.

Farmers who are the first to manage with transgenic corn in a region may benefit economically by increasing the proportion of their field planted to a transgenic cultivar. In all cases tested in this study, dispersal of susceptible insects from the surrounding region that is not managed with transgenic corn effectively prevents resistance to the transgenic cultivar from developing. If concerns about resistance are minimal, planting smaller refuges may be an effective way to increase

returns. Indeed, Hurley et al. (2002) lament that although the effect on the evolution of resistance when fields not managed with transgenic crops supply susceptible adults via dispersal has been studied, there is a general lack of economic assessments of optimal refuge when a farmer is the first to use transgenic crops in a region.

The biological analysis of the dynamic adoption strategies showed that such strategies can be useful or detrimental to IRM, depending on the resistance allele. The dynamic adoption strategies slowed the evolution of resistance to transgenic corn, especially in simulations with R dominant, compared with management strategies with 80% transgenic corn in either the continuous or rotated cornfield each year. With the dynamic adoption strategies, the selection pressure on susceptible phenotypes with regards to transgenic corn is not as intense, especially during the early years of the simulations, because the proportion of transgenic corn in the region is relatively low at the beginning of the 15-yr time horizon (10%) and builds over time. The result is delayed evolution to transgenic corn. However, the dynamic adoption strategies resulted in faster evolution of resistance to crop rotation compared with a strategy of planting 80% transgenic corn in the rotated cornfield each year. With the dynamic adoption strategies, there is relatively little control against rotation-resistant phenotypes in the early years of the simulations as the proportion of transgenic corn in the region is low. The result is increased survival of rotation-resistant individuals in rotated cornfields compared with the standard strategy and the evolution of resistance to crop rotation occurs more rapidly.

Changes in the density-dependent survival functions had the greatest impact on the results in areas without rotation-resistant phenotypes and 100% continuous corn, as the differences between the dynamic adoption and standard management strategies changed by up to 100%. Although changes in the density-dependent survival functions did not affect the most economical management strategy in these areas, allowing for increased larval survival decreased returns in every case.

The application of these results is limited by several assumptions in the model. First, we assumed that a very simple genetic system is responsible for evolution of the behavioral changes and rotation resistance. Second, we assumed that all farms are the same in a homogeneous region or that areawide pest management is occurring. Third, we assumed that plants expressing different toxin doses cost the same amount to produce. In addition, we used a single economic criterion to compare strategies. Other economic criteria exist that take into account more than just farmer earnings, such as the welfare of the agricultural sector, or society as a whole. For example, we did not consider a solution based on the application of insecticides in any cornfield. It would be possible to develop an economic criterion that takes into account the social costs and benefits of insecticide use. We also did not consider the use of a composed error-model similar to

Mitchell et al. (2004) to estimate yield loss due to pest infestations. Changes in these assumptions could have produced other outcomes.

We believe that our results emphasize some of the differences between IRM and IPM. IPM strategies focus on both farmer returns and resistance to management practices, and are affected by the declining value of future profits and the rate of increase in resistance over time. However, the focus with IRM is often on the distant future and the desire to achieve some biological end point, such as allele frequency or population density, regardless of when these end-points occur. However, farmers have little incentive to bear the costs of delaying resistance in the present when the actual costs of resistance will not be paid until far in the future.

In general, IPM and IRM have different goals, controlling pest damage to maximize returns versus maximizing years to resistance. However, other goals, such as environmental protection, are also the focus of IPM. In some instances, the strategies to pursue these goals coincide, in others they do not. For example, management strategies involving planting transgenic corn to rotated cornfields were effective at maximizing farmer returns in areas with rotation-resistant populations. In addition, this type of management prevented resistance to both crop rotation and transgenic corn from developing. In contrast, in areas without rotation-resistant phenotypes and with R dominant, the dynamic adoption strategies were effective at delaying resistance to transgenic corn, suggesting they may be useful from an IRM standpoint. However, the dynamic adoption strategies failed to delay resistance to crop rotation. In addition, these strategies generated lower returns than planting 80% transgenic corn each year, showing they were not effective from an IPM standpoint.

The clearest message for the pest management industry is that producing greater toxin doses may be beneficial from both an IRM and IPM standpoint. In every case, returns with the theoretical high and practical high doses were greater than with the medium or low doses. This was especially true in areas without rotation-resistant phenotypes. The greater doses were also the most effective at preventing resistance to transgenic corn with the standard management strategies. In addition, returns with the dynamic adoption strategies were always similar compared with the standard strategy with a medium or greater dose, but there was more uncertainty with a low dose. Therefore, if the pest management industry can achieve a high dose of toxin, farmers can plant 80% of their cornfields to a transgenic cultivar with confidence that this strategy will be beneficial both biologically and economically.

Too often in the past, evolutionary changes in pest populations have caused scientists to emphasize IRM over IPM. In addition, because of contractual agreements and regulatory requirements, farmers have been more willing to adopt IRM management practices compared with IPM. However, our results show that in many cases management strategies that focus on IPM are also beneficial from an IRM perspective.

Farmers must constantly strive to manage pests by using strategies that can be beneficial from both perspectives.

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References Cited

- Ball, H. J., and G. T. Weekman. 1962. Insecticide resistance in the adult western corn rootworm in Nebraska. *J. Econ. Entomol.* 55: 439–441.
- Ball, H. J., and G. T. Weekman. 1963. Differential resistance of corn rootworms to insecticides in Nebraska and adjoining states. *J. Econ. Entomol.* 56: 553–555.
- Carrière, Y., T. J. Dennehy, B. Petersen, S. Haller, C. Ellers-Kirk, L. Antilla, Y.-B. Liu, E. Willot, and B. E. Tabashnik. 2001. Large-scale management of insect resistance to transgenic cotton in Arizona: can transgenic insecticidal crops be sustained? *J. Econ. Entomol.* 94: 315–325.
- Carrière, Y., C. Ellers-Kirk, M. Sisterson, L. Antilla, M. Withlow, T. J. Dennehy, and B. E. Tabashnik. 2003. Long-term regional suppression of pink bollworm by Bt cotton. *Proc. Natl. Acad. Sci. U.S.A.* 100: 1519–1523.
- Carrière, Y., M. S. Sisterson, and B. E. Tabashnik. 2004a. Resistance management for sustainable use of *Bacillus thuringiensis* crops in integrated pest management, pp. 65–95. *In* A. R. Horowitz and I. Ishaaya [eds.], *Insect pest management: field and protected crops*. Springer, Berlin, Germany.
- Carrière, Y., P. Dutilleul, C. Ellers-Kirk, B. Pederson, S. Haller, L. Antilla, T. J. Dennehy, and B. E. Tabashnik. 2004b. Sources, sinks, and the zone of influence of refuges for managing insect resistance to Bt crops. *Ecol. Appl.* 14: 1615–1623.
- Crowder, D. W., and D. W. Onstad. 2005. Using a generational time-step model to simulate the dynamics of adaptation to transgenic corn and crop rotation by western corn rootworm (Coleoptera: Chrysomelidae). *J. Econ. Entomol.* 98: 518–533.
- Crowder, D. W., D. W. Onstad, M. E. Gray, C.M.F. Pierce, A. G. Hager, S. T. Ratcliffe, and K. L. Steffey. 2005. Analysis of the dynamics of adaptation to transgenic corn and crop rotation by western corn rootworm (Coleoptera: Chrysomelidae) using a daily time-step model. *J. Econ. Entomol.* 98: 534–551.
- Georgiou, G. P. 1986. The magnitude of the resistance problem, pp. 14–43. *In* National Academy of Sciences [ed.], *Pesticide resistance: strategies and tactics for management*. National Academy Press, Washington, DC.
- Guse, C. A., D. W. Onstad, L. L. Bushman, P. Porter, R. A. Higgins, P. E. Sloderbeck, G. B. Cronholm, and F. B. Peairs. 2002. Modeling the development of resistance by stalk-boring Lepidoptera (Crambidae) in areas with irrigated, transgenic corn. *Environ. Entomol.* 31: 676–685.
- Hibbard, B. E., M. L. Higdon, D. P. Duran, Y. M. Schweikert, and M. R. Ellersieck. 2004. Role of egg density on establishment and plant-to-plant movement by western corn rootworm larvae (Coleoptera: Chrysomelidae). *J. Econ. Entomol.* 97: 871–882.

- Hurley, T. M., S. Secchi, B. A. Babcock, and R. L. Hellmich. 2002. Managing the risk of European corn borer resistance to Bt corn. *Environ. Resour. Econ.* 22: 537–558.
- Illinois Agricultural Statistics Service. 2003. Illinois annual summary: field crops, pp. 21–22. Ill. Dept. Agric., Springfield, IL.
- Laxminarayan, R., and R. D. Simpson. 2002. Refuge strategies for managing pest resistance in transgenic agriculture. *Environ. Resour. Econ.* 22: 521–536.
- Matson, P. A., W. J. Parton, A. G. Power, and M. J. Swift. 1997. Agricultural intensification and ecosystem properties. *Science (Wash. DC)* 277: 504–509.
- Meinke, L. J., B. D. Siegfried, R. J. Wright, and L. D. Chandler. 1998. Adult susceptibility of Nebraska western corn rootworm (Coleoptera: Chrysomelidae) populations to selected insecticides. *J. Econ. Entomol.* 91: 594–600.
- Metcalf, R. L. 1983. Implications and prognosis of resistance to insecticides, pp. 703–733. In G. P. Georghiou and T. Saito [eds.], *Pest resistance to pesticides*. Plenum, New York.
- Microsoft. 2002. Microsoft Excel 2002. Microsoft, Seattle, WA.
- Midgarden, D., S. J. Fleischer, R. Weisz, and Z. Smilowitz. 1997. Site-specific integrated pest management impact on development of esfenvalerate resistance in Colorado potato beetle (Coleoptera: Chrysomelidae) and on densities of natural enemies. *J. Econ. Entomol.* 90: 855–867.
- Miota, F., M. E. Scharf, M. Ono, P. Marcon, L. J. Meinke, R. J. Wright, L. D. Chandler, and B. D. Siegfried. 1998. Mechanisms of methyl and ethyl parathion resistance in the western corn rootworm (Coleoptera: Chrysomelidae). *Pestic. Biochem. Physiol.* 61: 39–52.
- Mitchell, P. D., M. E. Gray, and K. L. Steffey. 2004. A composed-error model for estimating pest-damage functions and the impact of the western corn rootworm soybean variant in Illinois. *Am. J. Agric. Econ.* 86: 332–344.
- Onstad, D. W., M. G. Joselyn, S. A. Isard, E. Levine, J. L. Spencer, L. W. Bledsoe, C. R. Edwards, C. D. DiFonzo, and H. Willson. 1999. Modeling the spread of western corn rootworm (Coleoptera: Chrysomelidae) populations adapting to soybean-corn rotation. *Environ. Entomol.* 28: 188–194.
- Onstad, D. W., C. A. Guse, J. L. Spencer, E. Levine, and M. E. Gray. 2001a. Modeling the dynamics of adaptation to transgenic corn by western corn rootworm (Coleoptera: Chrysomelidae). *J. Econ. Entomol.* 94: 529–540.
- Onstad, D. W., J. L. Spencer, C. A. Guse, E. Levine, and S. A. Isard. 2001b. Modeling evolution of behavioral resistance by an insect to crop rotation. *Entomol. Exp. Appl.* 100: 195–201.
- Onstad, D. W., C. A. Guse, P. Porter, L. L. Bushman, R. A. Higgins, P. E. Sloderbeck, F. B. Peairs, and G. B. Gronholm. 2002. Modeling the development of resistance by stalk-boring lepidopteran insects (Crambidae) in areas with transgenic corn and frequent insecticide use. *J. Econ. Entomol.* 95: 1033–1043.
- Onstad, D. W., D. W. Crowder, P. D. Mitchell, C. A. Guse, J. L. Spencer, E. Levine, and M. E. Gray. 2003a. Economics versus alleles: balancing integrated pest management and insect resistance management for rotation-resistant western corn rootworm (Coleoptera: Chrysomelidae). *J. Econ. Entomol.* 96: 1872–1885.
- Onstad, D. W., D. W. Crowder, S. A. Isard, E. Levine, J. L. Spencer, M. O'Neal, S. Ratcliffe, M. E. Gray, L. W. Bledsoe, C. D. DiFonzo, B. Easley, and C. R. Edwards. 2003b. Does landscape diversity slow the spread of rotation-resistant western corn rootworm (Coleoptera: Chrysomelidae)? *Environ. Entomol.* 32: 992–1001.
- Peck, S. L., and S. P. Ellner. 1997. The effect of economic thresholds and life-history parameters on the evolution of pesticide resistance in a regional setting. *Am. Nat.* 149: 43–63.
- Pimental, D., H. Acquay, M. Biltonen, P. Rice, M. Silva, J. Nelson, V. Lipner, S. Giordano, A. Horowitz, and M. D'Amore. 1992. Environmental and economic costs of pesticide use. *Bioscience* 42: 750–760.
- Rondon, S. I., and M. E. Gray. 2004. Ovarian development and ovipositional preference of the western corn rootworm (Coleoptera: Chrysomelidae) variant in east central Illinois. *J. Econ. Entomol.* 97: 390–396.
- Roush, R. T. 1997. Managing resistance to transgenic crops, pp. 271–294. In N. Carozzi and M. Koziel [eds.], *Advances in insect control: the role of transgenic plants*. Taylor & Francis, London, United Kingdom.
- Scharf, M. E., L. J. Meinke, B. D. Siegfried, R. J. Wright, and L. D. Chandler. 1999. Carbaryl susceptibility, diagnostic concentration determination, and synergism for U.S. populations of western corn rootworm (Coleoptera: Chrysomelidae). *J. Econ. Entomol.* 92: 33–39.
- Schnitkey, G. 2004. Estimated cost of crop production in Illinois, 2004. Farm business management handbook FBM-0100. University of Illinois, Urbana-Champaign, IL.
- Secchi, S., T. M. Hurley, and R. L. Hellmich. 2001. Managing European corn borer resistance to Bt corn with dynamic refuges. Center for Agricultural and Rural Development, Iowa State University, Ames, IA. Working Paper 01-WP 287.
- Storer, N. P. 2003. A spatially explicit model simulating western corn rootworm (Coleoptera: Chrysomelidae) adaptation in insect-resistant maize. *J. Econ. Entomol.* 96: 1530–1547.
- Walker, K., J. Liebman, and W. Pease. 1995. Pesticide induced disruptions of agricultural ecosystems. California Policy Seminar Report. University of California, Berkeley.
- Zhou, X., M. E. Scharf, L. J. Meinke, L. D. Chandler, and B. D. Siegfried. 2003. Characterization of general esterases from methyl parathion-resistant and -susceptible populations of western corn rootworm (Coleoptera: Chrysomelidae). *J. Econ. Entomol.* 96: 1855–1863.

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