

Planting Transgenic Insecticidal Corn Based on Economic Thresholds: Consequences for Integrated Pest Management and Insect Resistance Management

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ABSTRACT A simulation model of the western corn rootworm, *Diabrotica virgifera virgifera* LeConte, was used to investigate whether sampling and economic thresholds can improve integrated pest management (IPM) and insect resistance management (IRM) when transgenic insecticidal crops are used for insect pest management. When transgenic corn killed at least 80% of susceptible larvae, the calculated economic threshold increased linearly as the proportion of susceptible beetles surviving the toxin increased. The use of economic thresholds slightly slowed the evolution of resistance to transgenic insecticidal crops. In areas with or without rotation-resistant western corn rootworm phenotypes, the use of sampling and economic thresholds generated similar returns compared with strategies of planting transgenic corn, *Zea mays* L., every season. Because transgenic crops are extremely effective, farmers may be inclined to plant transgenic crops every season rather than implementing costly and time-consuming sampling protocols.

KEY WORDS economic thresholds, sampling, transgenic crops, western corn rootworm, IPM

Economic thresholds, or the level of pest infestation at which the application of a pesticide may be economically justified, are integral parts of integrated pest management (IPM) programs (Stern et al. 1959). Economic thresholds tie life-history parameters of pest insects to the timing of pesticide applications (Peck and Ellner 1997). The typical densities of a pest population, the amplitude of its fluctuations, and the pest's destructiveness all influence the value of sampling a population (Onstad 1987). In many cases, sampling and economic thresholds are not economically worthwhile (Poston et al. 1983, Onstad 1987). Nyrop et al. (1986) showed that costs of sampling or uncertainty because of sampling error can affect the value of using economic thresholds.

The use of sampling and economic thresholds has been used in insect resistance management (IRM) and IPM (Tabashnik et al. 1992, Midgarden et al. 1997, Peck and Ellner 1997). Simulation modeling has been used to examine the interaction between sampling with economic thresholds and population dynamics of pest insects (Tabashnik 1986, Hardmann 1989, Rosenheim and Tabashnik 1990, Follett et al. 1993, Argentine et al. 1994, Peck and Ellner 1997, Caprio 1998).

We used a simulation model to investigate whether economic thresholds can be used to improve IPM and IRM when transgenic insecticidal corn is used for insect pest management. We sought to determine how sampling and economic thresholds can make IPM more efficient and IRM more effective when farmers are deciding whether to plant transgenic crops. We explored the use of economic thresholds that determine the planting of transgenic insecticidal crops in a traditional manner without the use of a spatial refuge as well as strategies that use economic thresholds to determine the planting of transgenic crops along with spatial refuges. These results may be of interest to the United States Environmental Protection Agency (USEPA) because they evaluate the potential usefulness of a prescriptive deployment of transgenic insecticidal crops.

Our evaluation was based on a case study using a model of the western corn rootworm, *Diabrotica virgifera virgifera* LeConte. We compared sampling strategies using economic thresholds with management strategies of planting transgenic corn every season. We evaluated the impact of using sampling and economic thresholds on the evolution of resistance to both crop rotation and transgenic corn. We determined how different toxin doses affected economic thresholds.

Materials and Methods

In this section, we described the creation of the model and its analysis. First, we described the eco-

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logical functions used to create the model. All functions used to develop the model were the same as in Crowder et al. (2005a), and the logic used to derive these functions was not discussed. We described the economic functions used in the model, the techniques used to calculate economic thresholds, the standard simulation conditions, and the sensitivity analyses that were performed on the model.

Population Genetics. We used a simple population genetics model of *D. virgifera virgifera* to explain the development of resistance to both crop rotation and transgenic corn. We assumed an autosomal, two-locus, two-allele per locus, diploid genetic system. The allele for susceptibility to transgenic corn was S; the allele for resistance to transgenic corn was R. The allele for no movement out of corn was X (susceptible to crop rotation), and the allele for movement to all crop fields was Y (resistant to crop rotation).

Model Landscape. The region consisted of 100 ha of cropland with up to four crops and a maximum of six fields. The four crops were corn planted in the same location each year, continuous corn, C_c ; corn that followed soybean, *Glycine max* (L.) Merr., in a 2-yr rotation, rotated corn, C_r ; soybean, which preceded corn in a 2-yr rotation, Soy; and the extra noncorn, Ex. T_c and T_r were the proportion of the continuous and rotated cornfields planted to a transgenic cultivar in a block configuration. In cases where refuges were used along with transgenic crops, the refuge occupied 20% of the field. In the model equations, the abbreviations rc, rr, tc, and tr were used for the continuous corn refuge, rotated corn refuge, transgenic continuous corn, and transgenic rotated corn, respectively.

Oviposition and Movement of Females. The fecundity per individual was 220 viable eggs (Onstad et al. 2003). Individuals that did not disperse out of corn ($-XX$) moved from the natal cornfield and distributed themselves (and their eggs) across all cornfields according to their relative proportional areas, where $-$ indicates the alleles for susceptibility to transgenic corn. Rotation-resistant ($-YY$) individuals moved into all fields and laid eggs according to their proportional representation in the region. In the additive case, 50% of the heterozygotes ($-XY$) distributed themselves and their eggs only into cornfields, whereas the others dispersed into all fields.

Toxin Mortality. Density-independent toxin mortality incurred by larvae emerging in fields planted to a transgenic cultivar, 'Qtox', depended on toxin dose, the genotype for resistance to transgenic corn, and gene expression. This mortality was applied at the same time as overwintering survival. We simulated three toxin doses based on values used in the model of Onstad et al. (2001).

Homozygous resistant individuals, (RR-), always had 100% survival to the transgenic cultivar regardless of dose ($Q_{tox} = 0$). With R dominant, heterozygous (sR-) individuals also always had 100% survival to the transgenic crop. The survival of homozygous susceptible individuals (SS-), or heterozygotes (Sr-) with R recessive, was 0.001, 0.05, and 0.20 with a

high, medium, and low toxin dose, respectively. With R partially recessive, survival of the heterozygotes, (sr-), was 0.01, 0.50, and 0.60 with a high, medium, and low toxin dose, respectively.

Immature Survival. All larvae emerging from eggs in noncornfields died. Overwintering mortality of eggs was 50% (Godfrey et al. 1995). Density-dependent survival of larvae was $0.21 \times \exp(-0.058EGG)$, where EGG is the density of eggs (in millions per hectare) (Onstad et al. 2003). The maximum larval survival based on this function was 21%. Density-dependent mortality occurred after mortality from overwintering and the toxin.

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

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

P is the probability of genotype j (nine possible genotypes) moving to field f. Beetles mated randomly within the field of emergence and their offspring had an expected frequency distribution dependent upon the frequencies of each genotype emerging in the natal field. Therefore, Q is the frequency of genotype k in fields rc, rr, tc, or tr that reproduced the particular offspring genotype i when mated with genotype j. Each weight, w, equals the Mendelian proportion of offspring that are genotype i when genotypes j and k mated.

In the model, the number of eggs was used to calculate the total density of larvae in each cornfield after overwintering and toxicity because of transgenic corn (Crowder et al. 2005a, equation 2). Then, the total density of larvae was used to calculate the number of adults in each cornfield after density-dependent mortality (Crowder et al. 2005a, equations 3–6). No adults emerged in rotated soybean or extra vegetation fields.

Male Dispersal. A proportion, PM, of males moved out of the natal field before mating, whereas all females remained in the natal field to mate (Onstad et al. 2001, Crowder and Onstad 2005, Crowder et al. 2005b). The standard value for PM was 0.25. This was calculated using our assumption that 50% of emerging adults are male. For example, the adjusted number of males in the continuous nontransgenic corn was as follows:

$$M_{i,rc}(t) = 0.5 \times A_{i,rc} \times (1 - PM) + 0.5 \times (A_{i,tc} + A_{i,rr} + A_{i,tr}) \times PM \times [P(f) / \sum_{k=1}^3 P(k)] \quad [2]$$

$M_{i,f}(t)$ is the adjusted number of males of genotype i in field f (rc, tc, rr, and tr), whereas $A_{i,f}(t)$ is the number of adults of genotype i that emerged in field f . $P(f)$ is the proportion of land planted to field f that males dispersed into and $P(k)$ is the proportion of land planted to each cornfield that was not the natal field f for individual $A_{i,f}(t)$. On the right-hand side of equation 2, the first product is the number of males that remained in field f and the other three products represent males moving into field f from the other cornfields. [Note that our older equation in Crowder and Onstad (2005) and Crowder et al. (2005a) used M rather than A on the right-hand side of the equation; this was a mistake in symbolism but not calculation.]

The adjusted number of males in each field after male dispersal was used to recalculate genotype k (male) frequencies before mating, Q in equation 1. We did not adjust population densities in any field for the purposes of calculating fecundity, only genotype frequency, because adult density was the primary variable representing ovipositing females.

Economic Analysis. The proportion of yield lost in cornfield f was (Onstad et al. 2003, Crowder et al. 2005a):

$$LOSS_f = 0.251 [1 - \exp(-0.0089K_f^{0.589})] \quad [3]$$

where $K_f = TL_f / (100C_f \times 10^4)$ is larvae per square meter after mortality due to overwintering and toxin mortality, and C_f is the proportion of landscape planted to field f .

The economic analysis was based on calculation of returns for all cornfields in the region. Returns (dollars per hectare) for crop c in year t were as follows:

$$RETURNS_{c,t} = PRICE_c \times Y_c \times (1.0 - LOSS_{c,t}) - COST_c \quad [4]$$

$PRICE_c$ is the price for crop c , Y_c is (pest-free) yield for crop c , $LOSS_{c,t}$ is the proportional yield loss for crop c in year t due to corn rootworm, and $COST_c$ is the variable cost of production for crop c .

For corn, a price of \$8.16/ql was used (3.94 ql per bushel corn), the approximate marketing year average price from 2000 to 2003 (Illinois Agricultural Statistics Service 2003). The variable costs for continuous and rotated corn were \$531 or \$519/ha, respectively (Schnitkey 2004). The pest-free yield for continuous and rotated corn was 104 ql/ha (Schnitkey 2004). Transgenic corn cost \$37/ha (Crowder et al. 2005a). The net present value per hectare for cornfield f was the sum of the discounted annual returns:

$$NPV_f = \sum_{t=1}^{15} \beta(t) \times RETURNS_{f,t} \quad [5]$$

where $\beta(t) = 1 / (1 + dr)^t$ and dr is the discount rate. A discount rate of 7% was used (Schnitkey 2004). The net present value per hectare of a strategy was 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 cornfield for the strategy: $NPV = C_r \times NPVC_r + C_c \times NPVC_c$. The annualized net present value (ANPV) of each strategy was the fixed annual return for 15 yr that generated the same net present value:

$$ANPV = NPV / Z, \text{ where } Z = \sum_{t=1}^{15} \beta(t). \quad [6]$$

Economic Thresholds and Sampling. We studied management strategies where sampling in cornfields was used along with economic thresholds to determine the amount of land planted to transgenic corn. This approach was similar to Foster et al. (1986), who used sampling and economic thresholds to determine the use of soil insecticides for *D. virgifera virgifera*. The economic thresholds calculated with the model should not be confused with economic injury levels; they were simply used to determine the use of transgenic corn from season to season. In areas without rotation-resistant phenotypes, we studied the use of transgenic corn in continuous cornfields with and without the use of spatial refuges. Although planting transgenic corn without the use of a refuge is not currently approved by the USEPA because of their focus on a high dose/refuge strategy for IRM, we wanted to determine whether sampling could be an effective management strategy in areas with 100% transgenic corn. In areas with rotation-resistant phenotypes, we only studied the use of transgenic corn in rotated cornfields based on results from Crowder and Onstad (2005).

Field scouting for corn rootworms should begin after 90% cumulative emergence (Nowatski et al. 2002). We adjusted the overall number of beetles simulated in cornfields to represent the period of peak emergence. In the daily time-step model of Crowder et al. (2005b), 90% cumulative emergence of western corn rootworm beetles occurred by 31 July, at which point $\approx 50\%$ of the total emerging beetles were still alive. Therefore, we used 50% of the adult populations simulated in our model for each generation to represent the population sampled during the peak period of emergence, when farmers would typically sample for *D. virgifera virgifera* (Foster et al. 1986).

We calculated economic thresholds for each toxin dose based on adult populations in 1 yr. In this analysis, we ignored genetics and assumed all individuals were susceptible to the transgenic toxin (SS-). We calculated the economic threshold for each toxin dose by determining the adult population level at which the costs of planting transgenic corn in 100% of the corn-

fields the following season equaled the benefits of planting transgenic corn. Onstad (1987) observed that in some situations it is necessary to sample a noninjurious stage of an insect to make control decisions for the injurious stage. This is the case in our analysis, because we used adult population densities to make decisions about the use of transgenic corn to control the larval stage. If the number of adults per hectare in corn at the economic threshold is EC , the number of larvae per hectare in field f , EL_f , that will survive overwintering and toxin mortality the following season was as follows:

$$EL_{NT} = 2 \times EC \times 220 \times 0.5,$$

for fields without transgenic corn

$$EL_T = 2 \times EC \times 220 \times 0.5 \times (1 - Q_{tox}),$$

for transgenic fields [7]

where $2 \times EC$ is the total number of adults during the year based on a sampled density of EC , 220 is the number of eggs laid per adult, and 0.5 is overwintering mortality. We then calculated the loss in both a transgenic and nontransgenic field by using our loss equation economic thresholds for each dose were calculated by equating cost and benefit:

$$37 = 8.16 \times 103.6 \times (LOSS_{NT} - LOSS_T) \quad [8]$$

where \$37/ha is the variable (extra) cost of producing transgenic corn and 8.16×103.6 is the price multiplied by the maximum yield for all corn. Results are presented as both beetles per hectare and beetles per plant, assuming a typical cornfield in Illinois has 74,100 plants per hectare.

In the model, because all adults dispersed into corn based on the proportional area of each field regardless of genotype, simulated adult densities in each hectare of cornfield were the same. Therefore, adult densities from any cornfield were compared with the economic threshold each year to determine the use of transgenic corn. In our analysis, we did not include costs for sampling because we wanted to let the analysis show how much sampling would be worth to a farmer. We did not attempt to account for variability and risk because of uncertainty in sampling (Nyrop et al. 1986).

Simulation Conditions. The model was programmed in Visual Basic in Microsoft Excel 2002 (Microsoft 2002). The model had a time step of 1 yr, a time horizon of 16 yr, and a spatial unit of 100 ha. The 16-yr time horizon included the first year in which the model is initialized without transgenic corn plus an additional 15 yr. The initial number of adults was 50,000 per hectare of corn, distributed proportionally to the areas of continuous and rotated corn. The rotation level, RL , was the sum of the proportional areas of rotated corn and soybean, which were equal in the model ($RL = Soy + C_r$).

In the standard simulations of areas without rotation-resistant phenotypes, the initial R-allele frequency was 10^{-4} and the Y-allele frequency was 0 in a landscape with 100% continuous corn ($C_c = 1.0$).

When sampling was used along with refuges, if adult densities exceed the economic threshold in a certain year then transgenic corn was planted to 80% of the continuous cornfield the following season, and 0% was planted if densities did not exceed the threshold. When sampling was used without refuges, and adult densities exceeded the economic threshold in a certain year, then transgenic corn was planted to 100% of the continuous cornfield the following season. Henceforth, these two strategies were referred to as sampling with and without refuges, respectively. In these simulations we compared the sampling strategies with the standard management strategy of planting 80% transgenic corn to the continuous cornfield every year (20% refuge) as well as a strategy of planting 100% transgenic corn every season (0% refuge).

In the standard simulations of areas with rotation resistance, the landscape was defined as $RL = 0.85$, $Ex = 0.05$, and $C_c = 0.10$. In these areas, the genotypes of adults began at Hardy-Weinberg equilibrium with initial R- and Y-allele frequencies of 10^{-4} . We only simulated the R partially recessive case with three types of gene expression for the Y-allele based on Crowder and Onstad (2005). When sampling was used, if adult population densities from sampling exceeded the economic threshold, transgenic corn was planted to 80% of the rotated cornfield the next year. We compared the sampling management strategies with a standard strategy of planting 80% transgenic corn to the rotated cornfield each year. We also performed simulations without transgenic corn to represent a 2-yr rotation between nontransgenic corn and soybean.

In the biological analysis, we emphasized changes in the R- and Y-allele frequencies over the 15-yr time horizon after the first year when the model was initialized. Time to resistance was the number of years for the resistance allele frequencies to increase from the initial value to 0.5. In some cases, we also presented the frequencies of the resistance alleles if they did not exceed 0.5 within 15 yr.

Simulations for Severe Problem Areas. We sought to determine the best strategies for managing western corn rootworm in areas where rotation resistance is already a severe problem. The landscape had $RL = 0.85$ and initial R- and Y-allele frequencies of 10^{-4} and 0.5, respectively. We compared the sampling management strategies with the standard strategy of planting 80% transgenic corn in the rotated cornfield each year and with a 2-yr rotation of nontransgenic corn and soybean.

Sensitivity Analysis. In a sensitivity analysis we studied the influence of two factors on the economic results of the standard simulations. First, we varied the economic thresholds by 10 or 20%. We also simulated population dynamics with different versions of the density-dependent survival function, one based on the model of Onstad et al. (2001), $1/(1 + 2.42EGG^{0.7})$, which has a maximum larval survival of 100%, and another based on the models of Crowder and Onstad (2005) and Crowder et al. (2005b),

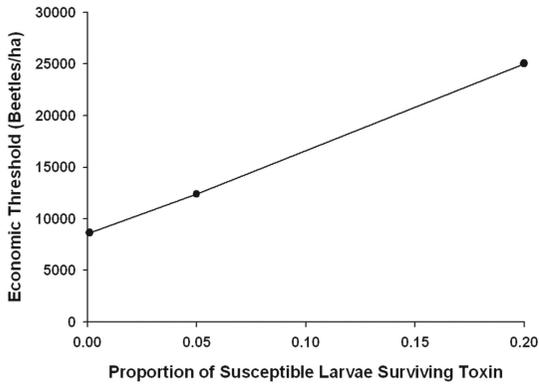


Fig. 1. Calculated economic thresholds with varying survival of susceptible larvae to toxicity of transgenic corn.

$1 / (2.59 + 1.29EGG^{0.88})$, which has a maximum larval survival of 39%.

Results

Calculation of Economic Thresholds. The calculated economic threshold increased as toxin dose decreased (Fig. 1). The economic threshold was 8,634 beetles per hectare (0.12 beetles per plant) with a high dose and increased linearly to 25,038 beetles per hectare (0.34 beetles per plant) with a low dose. These values represent the mean number of adults per hectare in cornfields after 90% emergence, assuming that all individuals are susceptible (SS-). We simulated the model without insecticides and found a carrying capacity of ≈1 million individuals per hectare, so the economic thresholds for using transgenic corn were 1–3% of the carrying capacity.

Biological Analysis of Areas without Rotation-Resistant Phenotypes. In areas without rotation-resistant phenotypes, sampling with refuges resulted in the slowest evolution of resistance (Table 1). However,

the R-allele frequency after 15 yr was at most 3% lower when comparing management strategies involving sampling with refuges to planting 80% transgenic corn each season. Similarly, planting 100% transgenic corn every season or sampling without refuges resulted in a similar rate of evolution of resistance to transgenic corn with a medium or low dose. In these simulations, the time to resistance was at most 1 yr faster compared with the management strategies involving refuges every year. However, with a high toxin dose, resistance evolved faster with planting 100% transgenic corn every season or sampling without refuges compared with the strategies using refuges every season (Table 1).

Biological Analysis of Areas with Rotation-Resistant Phenotypes. Sampling and using economic thresholds increased the rate of resistance to crop rotation in areas with rotation-resistant phenotypes in one case. However, sampling did not affect resistance to transgenic corn compared with planting transgenic corn every season, because the R-allele frequency never exceeded 0.0001 within 15 yr with any strategy.

With any strategy simulated, the Y-allele frequency never exceeded 50% within 15 yr. There were no differences between the sampling strategies and the standard strategy of planting 80% transgenic corn in the rotated cornfield each year except in one case. With a low dose and Y dominant, resistance to crop rotation evolved slightly more rapidly with sampling compared with the standard strategy, as the Y-allele frequency reached 0.08 in yr 15 compared with 0.04. In all other cases, the Y-allele frequency with any strategy never increased above 0.02 within 15 yr.

Economic Analysis of Areas without Rotation-Resistant Phenotypes. The optimal management strategy from an economic perspective in areas without rotation-resistant phenotypes depended on toxin dose and gene expression. Increasing toxin dose increased returns (Table 2). Sampling was not effective with R recessive because resistance to transgenic corn never evolved, and the most economical strategy was to

Table 1. Year in which the allele for resistance to transgenic corn, R, reached 50% along with the R-allele frequency in year 15 with three toxin doses, three types of gene expression for R, and four management strategies

Toxin dose	Management strategy			
	Tc = 80% each season	Sampling with refuges	Tc = 100% each season	Sampling without refuges
R recessive				
High	>15 (0.0001)	>15 (0.0001)	15 (0.59)	>15 (0.0003)
Medium	>15 (0.0001)	>15 (0.0001)	>15 (0.0001)	>15 (0.0001)
Low	>15 (0.0001)	>15 (0.0001)	>15 (0.0001)	>15 (0.0001)
R partially recessive				
High	>15 (0.0005)	>15 (0.0005)	4 (1.00)	8 (1.00)
Medium	6 (1.00)	6 (0.99)	5 (0.99)	5 (0.99)
Low	10 (0.95)	10 (0.93)	9 (0.97)	10 (0.95)
R dominant				
High	5 (0.91)	5 (0.90)	2 (0.93)	3 (0.92)
Medium	5 (0.90)	5 (0.89)	4 (0.92)	4 (0.91)
Low	8 (0.85)	5 (0.83)	7 (0.88)	8 (0.85)

Management strategies included 1) planting 80% transgenic corn to the continuous cornfield each season; 2) planting transgenic corn based on sampling and economic thresholds along with 20% refuge; 3) planting 100% transgenic corn to the continuous cornfield each season; and 4) planting transgenic corn based on sampling and economic thresholds without refuges. The landscape simulated consisted of 100% continuous corn and no rotation-resistant phenotypes.

Table 2. Annualized net present value (dollars per hectare) with three toxin doses, three types of gene expression for the allele for resistance to transgenic corn, R, and four management strategies

Toxin dose	Management strategy			
	Tc = 80% each season	Sampling with refuges	Tc = 100% each season	Sampling without refuges
R recessive				
High	256	256 (15)	275	259 (7)
Medium	222	222 (15)	256	256 (15)
Low	163	163 (15)	166	159 (14)
R partially recessive				
High	256	256 (15)	236	230 (9)
Medium	183	185 (14)	190	198 (13)
Low	154	154 (15)	156	149 (14)
R dominant				
High	181	184 (14)	182	188 (13)
Medium	175	176 (14)	176	179 (14)
Low	151	151 (15)	163	152 (13)

Management strategies included 1) planting 80% transgenic corn to the continuous cornfield each season; 2) planting transgenic corn based on sampling and economic thresholds along with 20% refuge each season; 3) planting 100% transgenic corn to the continuous cornfield each season; and 4) planting transgenic corn based on sampling and economic thresholds without refuges. The landscape simulated consisted of 100% continuous corn and no rotation-resistant phenotypes. For the sampling strategies, the number of years transgenic corn was planted in the region is shown in parentheses.

plant transgenic corn every season. Sampling was more effective with R dominant season because resistance to transgenic corn evolved relatively quickly and yield loss was high regardless of the type of management. In all cases, the differences between the sampling strategies and planting transgenic corn every season were small (Table 2).

With R recessive, planting 100% of the region to transgenic corn every season was always the most economical strategy with any toxin dose (Table 2). With this strategy and any dose, returns were 2–13% greater than returns with a strategy of planting 80% transgenic corn to the continuous cornfield every season or sampling with refuges. Planting 100% of the region to transgenic corn every season generated returns 0–6% greater than sampling without refuges with any dose (Table 2).

With R recessive and a high or medium dose, sampling without refuges produced greater returns than sampling with refuges or planting 80% transgenic corn to the continuous cornfield each season (Table 2). With a low dose, sampling with refuges or planting 80% transgenic corn each season produced returns 3% greater than sampling without refuges. Sampling with refuges was never more effective than planting 80% transgenic corn in the continuous cornfield each year, because populations exceeded the economic thresholds each year, and transgenic corn was always planted.

The most effect management strategy with R partially recessive depended on toxin dose (Table 2). With a high dose, the most effective management strategy was either to plant 80% transgenic corn in the continuous cornfield each season or sampling with

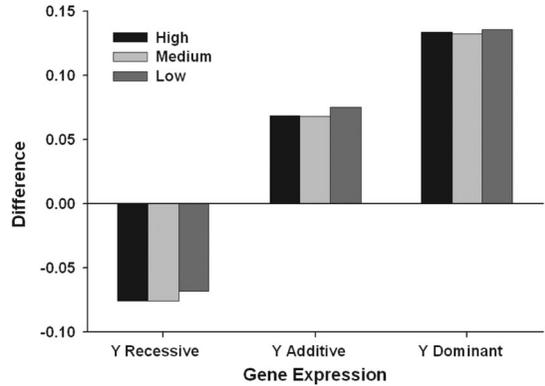


Fig. 2. Difference (proportion) in annualized net present value (dollars per hectare) between sampling strategies and a 2-yr rotation of nontransgenic corn and soybean in a landscape with rotation-resistant phenotypes and $RL = 0.85$ with three types of gene expression for the allele for resistance to crop rotation, Y, and three toxin doses.

refuges, generating returns 8–10% greater than the other strategies. With a medium dose, sampling without refuges was the most effective management strategy, generating returns 4–8% greater than the other three strategies. With a low dose, planting 100% of the region to transgenic corn every season was the most effective strategy, generating returns 1–4% greater than the other three strategies (Table 2).

With R dominant and a high or medium dose, sampling without refuges produced the greatest economic returns, 2–4% greater than any other strategy. With R dominant and a low dose, planting 100% transgenic corn to the region every season produced the greatest returns, $\approx 7\%$ greater than returns with any other strategy (Table 2).

Economic Analysis of Areas with Rotation-Resistant Phenotypes

In areas with rotation-resistant phenotypes, sampling did not affect returns with a high or medium toxin dose. Sampling only increased returns with a low toxin dose.

With any expression of the Y-allele, sampling provided the same returns as the standard management strategy of planting 80% transgenic corn in the rotated cornfield each year with a high or medium dose, because populations never fell below 25,000 beetles per hectare (0.3 beetles per plant) and transgenic corn was planted every season. With a low dose, sampling with an economic threshold provided returns 0.6–0.8% greater than the standard strategy with any Y-allele expression. With any toxin dose, returns with sampling were 7–8% lower than a 2-yr rotation of nontransgenic corn and soybean with Y recessive and 7–14% greater with Y additive or dominant (Fig. 2).

Sensitivity Analysis of Areas without Rotation-Resistant Phenotypes. In our sensitivity analysis of areas without rotation resistance, neither factor studied had a large affect on the results. Changing the economic

thresholds by 10 or 20% never changed the differences between the strategies by $>1\%$. Changing the maximum density-dependent survival of larvae to 39 or 100% did not affect the returns of the sampling strategies compared with the management strategies of planting 80 or 100% transgenic corn in the continuous cornfield each year, because the differences between the strategies did not change by $>5\%$ compared with the standard simulations.

Sensitivity Analysis of Areas with Rotation-Resistant Phenotypes. Similar to areas without rotation-resistant phenotypes, changing the economic thresholds or density-dependent survival had small effects on the results. Changing the economic thresholds by 10 or 20% never changed the differences between the strategies by $>1\%$. In general, changing the density-dependent survival did not affect the returns of the sampling strategies compared with the standard strategy of planting 80% transgenic corn in the rotated cornfield each year, because the differences between the strategies never changed by $>5\%$ compared with the standard simulations.

Simulations of Severe Problem Areas. In areas where resistance to crop rotation was already a severe problem, planting transgenic corn every season was always the most beneficial management strategy. In these areas, the Y-allele frequency approached 1.0 within 15 yr with any management strategy. Sampling with an economic threshold generated returns 0–1% less than the standard management strategy of planting 80% transgenic corn in the rotated cornfield each season with any simulated conditions. These returns were $\approx 15\text{--}25\%$ greater than returns with a 2-yr rotation of nontransgenic corn and soybean.

Discussion

In this article, we do not want to emphasize actual returns or economic thresholds from our simulations but rather differences between the strategies. Planting transgenic insecticidal corn based on sampling and economic thresholds did not generally increase returns compared with planting transgenic corn every season. Large adult densities in refuges and subsequent dispersal into transgenic fields caused populations to exceed the economic thresholds in almost every year. This resulted in minimal differences between the sampling strategies and the strategies of planting transgenic corn each season, because transgenic corn was planted nearly every season even when sampling was used.

Results showed that the use of sampling and economic thresholds can slightly slow the evolution of resistance to transgenic insecticidal corn, similar to results of Peck and Ellner (1997) and Caprio (1998), because selection did not occur in years when transgenic corn was not planted. Sampling strategies increased the rate of evolution of resistance to crop rotation, because rotation-resistant phenotypes had increased survival in rotated fields and the frequency of the alleles for resistance to crop rotation increased in years without transgenic crops.

In areas with initially rare rotation-resistant phenotypes, returns with sampling were never $>1\%$ greater than returns with the standard strategy of planting 80% transgenic corn in the rotated cornfield every year. Thus, if sampling costs are above 1% of the net returns for a farmer, then sampling would be less profitable than the standard strategy. Sampling was never effective in areas where rotation resistance is already a severe problem. Therefore, planting transgenic corn every season may not only be the most economical but also the safest strategy for risk-averse farmers to ensure maximum returns in areas with rotation-resistant phenotypes.

In areas without rotation-resistant phenotypes, using sampling along with refuges never increased returns by $>1\%$ over the standard strategy of planting 80% transgenic corn in the continuous cornfield every season. A similar result was obtained by Foster et al. (1986), who showed the most economical strategy for corn rootworms is not to scout and treat continuous corn each season with a soil insecticide. In these areas, the most economical strategy depended on toxin dose and gene expression of the R-allele. With a low dose or R recessive, planting 100% of the region to transgenic crops provided the greatest returns. There were several cases with a high or medium dose where planting 100% of the region to transgenic crops or sampling without refuges increased returns compared with management strategies involving refuges.

In addition, in areas without rotation-resistant phenotypes, the refuge strategy did not delay the evolution of resistance to transgenic corn by >1 yr compared with planting 100% transgenic corn every season with a medium or low dose. Thus, if the dose achieved by the chemical or seed industry is medium or low, mandating that farmers plant at least 20% of their fields to refuges may decrease their economic returns and may not significantly decrease the rate of evolution of resistance. Currently the transgenic hybrid used for corn rootworm is most similar to the low dose simulated with our model (Vaughn et al. 2005). However, when the dose was high, evolution of resistance to transgenic corn occurred faster when no refuges were used compared with refuge strategies. This supports the high dose/refuge strategy for deploying transgenic crops.

We compared our results with those of Crowder et al. (2005a) who analyzed dynamic management practices involving transgenic corn for western corn rootworm. The results in this article supported the results of Crowder et al. (2005a) that in areas without rotation-resistant phenotypes that the most economical strategy for farmers may be to adopt transgenic corn as quickly as possible. In these areas, increasing the proportion of the region planted to transgenic corn over time (Crowder et al. 2005a) or sampling with refuges never increased returns by $>1\%$ compared with planting transgenic corn every season. A similar result was found in areas with rotation-resistant phenotypes. In these areas, slowly incorporating transgenic corn over time into a region (Crowder et al. 2005a) or sampling with economic thresholds never

increased returns by >2% compared with planting 80% of rotated cornfields to transgenic corn every season.

Gray and Luckmann (1994) suggested that if corn rootworm populations exceeded 0.75 and 0.5 beetle per plant in continuous and rotated corn, respectively, then farmers should apply a rootworm soil insecticide the following year. In a 3-yr field study of continuous cornfields in Nebraska, Stamm et al. (1985) showed that an IPM approach using an economic threshold of 0.75 or one beetle per plant was reliable in predicting future populations 90 or 80% of the time, respectively. Our results suggest that the economic thresholds for using transgenic corn, which represent 90% of the emergent population if all adults are susceptible, may be lower than the thresholds recommended by Gray and Steffey (1999) and used by Stamm et al. (1985). This is because transgenic corn is much more effective than typical soil insecticides and costs about the same.

The application of these results are 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 did not include costs of sampling or uncertainty because of sampling error, unlike Nyrop et al. (1986). Changes in these assumptions could have produced other outcomes.

Our results emphasize that sampling and using economic thresholds for transgenic crops did not generally increase returns over strategies of planting transgenic crops every season in some cases. With the added uncertainty pertaining to gene expression and initial allele frequency, farmers may be inclined to plant transgenic corn every season rather than sampling to perform dynamic management with transgenic corn. Results support the validity of the high dose/refuge strategy, although alternatives may be effective and valuable under some conditions. These results may be applicable to other pest insects beside the western corn rootworm that are managed using transgenic insecticidal crops.

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