

Economics Versus Alleles: Balancing Integrated Pest Management and Insect Resistance Management for Rotation-Resistant Western Corn Rootworm (Coleoptera: Chrysomelidae)

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J. Econ. Entomol. 96(6): 1872–1885 (2003)

ABSTRACT Western corn rootworm, *Diabrotica virgifera virgifera* LeConte, has overcome crop rotation in several areas of the central United States. We expanded a simple model of adult behavior and population genetics to explain how rotation resistance may have developed and to study ways to manage the western corn rootworm in a landscape of corn, soybean, and winter wheat where evolution of resistance may occur. We modeled six alternative management strategies over a 15-yr time horizon, as well as a strategy involving a 2-yr rotation of corn and soybean in 85% of the landscape, to investigate their effectiveness from both a biological and economic perspective. Generally, resistance to crop rotation evolves in fewer than 15 yr, and the rate of evolution increases as the level of rotated landscape (selection pressure) increases. When resistance is recessive, all six alternative strategies were effective at preventing evolution of rotation resistance. The two most successful strategies were the use of transgenic rotated corn in a 2-yr rotation and a 3-yr rotation of corn, soybean, and wheat with unattractive wheat (for oviposition) preceding corn. Results were most sensitive to increases in the initial allele frequency and modifications of the density-dependent survival function. Economically, three alternative strategies were robust solutions to the problem, if technology fees were not too high. Repellent soybean, attractive rotated corn, and transgenic rotated corn, all in 2-yr rotations, were economically valuable approaches. However, even the currently common 2-yr rotation was economical when resistance was recessive and the actual costs of resistance would not be paid until far in the future.

KEY WORDS *Diabrotica virgifera virgifera*, insect resistance management, crop rotation, modeling

FOR MANY YEARS, growers in the United States have managed the western corn rootworm, *Diabrotica virgifera virgifera* LeConte, by rotating corn, *Zea mays* L., with soybean, *Glycine max* (L.), or another nonhost crop. This univoltine beetle is the most serious insect pest of continuously grown corn in the United States (Levine and Oloumi-Sadeghi 1991). During late summer, eggs are normally laid in cornfields where they overwinter. The larvae, which emerge during spring, can survive only on the roots of corn and on a limited number of grasses (Levine and Oloumi-Sadeghi 1991). Since 1995, reports of serious larval injury to first-year corn in Illinois and Indiana have increased and growers who had successfully used crop rotation for corn rootworm management have suffered serious crop

losses (Levine et al. 2002). We hypothesize that the newly observed tendency of adults to move to non-corn areas from natal cornfields is the behavioral change that allows this insect to overcome management by crop rotation.

Recent investigations have shed some light on the population dynamics and behavior of the rotation-resistant phenotype. Where crop rotation has not been compromised (western Illinois), western corn rootworm adults have been observed in much greater densities in cornfields than in soybean fields, but where rotation is no longer as effective (east central Illinois), densities of adults, particularly females, are greater in soybean than in cornfields (O'Neal et al. 1999, Levine et al. 2002, Rondon and Gray 2003). Rondon and Gray (2003) trapped more female beetles in alfalfa, oat stubble, and soybean fields than in cornfields. Spencer et al. (1999) observed no attraction to or preference for soybean plants in a wind-tunnel experiment. Isard et al. (2000) observed cyclical changes in movement of adult beetles between adjacent corn and soybean fields during the day. Greater numbers of beetles moved into soybean after sunrise

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Table 1. Parameter values for the seven management strategies where the proportion of the landscape in continuous corn, rotated corn, soybeans and extra non-corn are Mc, Mr, S, and E, respectively

Allele expression	F, Relative fecundity	P, probability of moving to Mc	P, probability of moving to crop rotated with corn
2-yr rotation, 3-yr rotation, more continuous corn, transgenic rotated corn	1	$Mc / (Mc + Mr)$	0
X dominant	$(1 - \text{Fitcost} * (S + E))$	Mc	S
Y dominant			
Repellant soybeans			
X dominant	1	$Mc / (Mc + Mr)$	0
X dominant	$(1 - \text{Fitcost} * ((1 - Rsoy) * S + E + (Rsoy * S * E) / (Mc + Mr + E)))$	$Mc + (Rsoy * S * Mc) / (Mc + Mr + E)$	$(1 - Rsoy) * S$
Unattractive wheat stubble (E) in 3-yr rotation			
X dominant	1	$Mc / (Mc + Mr)$	0
X dominant	$(1 - \text{Fitcost} * ((1 - Ue) * E + S + (Ue * E * S) / (Mc + Mr + S)))$	$Mc + (Ue * E * Mc) / (Mc + Mr + S)$	$(1 - Ue) * E$
Y dominant			
More attractive rotated corn			
X dominant	1	$(1 - Ar)$	0
Y dominant	$(1 - \text{Fitcost} * ((1 - Ar) * (S + E) / (Mc + S + E)))$	$(1 - Ar) * Mc / (Mc + S + E)$	$(1 - Ar) * S / (Mc + S + E)$

Fitcost describes the fitness cost for beetles laying eggs in S and E (parameter from 0.00 to 1.00). Rsoy describes the repellency of soybean to polyphagous beetles (parameter from 0.00 to 1.00). Ar describes the attractiveness of rotated corn to all beetles (parameter from 0.00 to 1.00). Ue describes the unattractiveness of wheat to polyphagous beetles (parameter from 0.00 to 1.00).

and before sunset, but movement out of soybean was greater during the middle of the day.

In a 3-yr field study in eastern Illinois, Rondon (2002) observed no significant differences in percentages of gravid females in oat stubble, alfalfa, and soybean captured over the season, but percentages were lower in cornfields. From 1998 to 2000, Rondon observed increasing oviposition in noncorn habitat (soybean, alfalfa, and oat stubble). This trend resulted in her observing no significant differences between corn, soybean, and oat stubble in terms of egg laying by the western corn rootworm on a per liter or per hectare basis in 2000. Oviposition was significantly lower in alfalfa (Rondon 2002).

Onstad et al. (2001b) created a simple model of adult behavior and population genetics to explain how rotation resistance may have developed in a landscape with multiple crops. The model indicated that evolution may be caused by selection on a single gene for adult movement and that behavioral resistance only developed at high levels of rotation. In less diverse landscapes, crop rotation selected for the expansion of host preferences and polyphagy by adults. Diverse landscapes may delay resistance to crop rotation depending on the fitness costs and the nature of the genetic system.

In this article, we modified the Onstad et al. (2001b) model and used it to study ways to manage the western corn rootworm in a landscape of corn, soybean, and winter wheat. Our first goal was to find a robust solution for managing western corn rootworm in areas where evolution of resistance to crop rotation may occur in the future. In this scenario, there are uncertainties in resistance gene expression, in the timing of invasion by the rotation-resistant variant, and initial gene frequency. Long-term, possibly areawide strategies are the focus of attention for both integrated pest management (IPM) and insect resistance management (IRM). Our second goal was to determine the best strategy for managing western corn rootworm in areas where resistance to crop rotation is already a serious problem, and IRM is no longer feasible nor of primary concern. Our third goal was to use our results to emphasize the differences between IPM and IRM.

Materials and Methods

In this section, we describe the model and its analysis. First, we describe observations and literature that support the ecological model and the basic biological processes. Second, we describe the ecological equations. Third, we discuss our basic approach to the simulations. Fourth, we describe the alternative management strategies that we evaluated. Then, we explain the economic calculations.

Definitions of Alleles and Landscape Patches. In this population genetics model of *D. v. virgifera* in a landscape of corn and noncorn crops, we assumed an autosomal, single-locus, two-allele, diploid genetic system. In the normal monophagous phenotype the X allele is dominant and the Y allele is recessive ($X > y$). In the polyphagous phenotype the X allele is recessive

and the Y allele is dominant ($Y > x$). The landscape consists of four plant patches: corn grown every year (continuous cornfields), M_c ; a corn patch that follows a noncorn patch in a rotation (first-year cornfields), M_r ; and two noncorn patches, one of which soybean, S, typically precedes corn in a rotation, and the extra noncorn vegetation, E. We defined the X allele for no movement out of corn and the Y allele for the tendency to move to all patches.

Movement. The normal monophagous (XX) individuals move from the natal corn patch and distribute themselves (and their eggs) across the two corn patches according to their relative proportional areas (Table 1). Godfrey and Turpin (1983) observed equal proportions of adults in continuous and first-year (rotated) corn during the second half of the season in a region with slightly more first-year cornfields, indicating extensive dispersal out of continuous (natal) cornfields. We assumed that the polyphagous (YY) individuals move into all patches according to their proportional representation in the region. In the additive case, the heterozygotes (XY) are also polyphagous.

We use the terms polyphagy and monophagy to allow for easy identification of the phenotypes. The terms are not meant to emphasize feeding behavior over movement. We also do not want to confuse adult and larval feeding, because larvae only feed and survive on corn roots in the model.

Fecundity. We set the fecundity per individual to 220 viable eggs, which is half of the number per female, and ignore gender (Onstad et al. 2001a). Onstad et al. (2001b) had polyphagous beetles incur a fitness cost in reduced fecundity. This assumption was based on preliminary data suggesting that adult vigor was reduced significantly by feeding in soybean. However, recent work by Mabry (2002) indicates that as long as the beetles move around the landscape often enough to return to corn once every 2–3 d, then fecundity and longevity of beetles are not reduced. Other data collected over 3 yr (J.L.S., unpublished data) indicate that 5.5–8.3% of females caught in soybean fields have corn tissues in their guts, and 5.2–7.5% of the females are gravid. Smaller percentages of females captured in corn had soybean in their guts (0.3–1.3%) or contained mature eggs (1.3–3.0%). Mabry (2002) also concluded that the corn tissues that females eat for the first week or so after emergence are much more important for later reproduction than various crop tissues consumed during the oviposition period. Therefore, in our standard model, there is no fitness cost in fecundity for polyphagous individuals feeding in other crops. The offspring of polyphagous individuals are divided across the four patches according to their proportional areas. (Fitness is always reduced when oviposition occurs in crops not rotated to corn the next year.)

Survival. All larvae emerging from eggs in noncorn patches die. Offspring in continuous and rotated corn incur an overwintering mortality of 50% during the egg stage (Godfrey et al. 1995) and incur a density-dependent mortality during the larval stage. Onstad et al. (2001b) did not use density-dependent survival in

their model, but we now include the following function fit to the data of Gray and Tollefson (1988) by using Microsoft Excel (Microsoft 2002). The density-dependent survival of larvae per stage is $0.21 \times \exp(-0.058\text{EGG})$, where EGG is the density of eggs (in millions per hectare). When transformed using natural logarithms, the regression equation ($n = 12$, $r^2 = 0.82$) had an intercept not significantly different from zero ($P = 0.99$) and a slope significantly different from zero ($P < 0.001$). The maximum survival based on this function is 21%. We assumed that density-dependent mortality occurs after mortality due to overwintering and toxin exposure.

Model Equations. The number of eggs $L_{i,j}(t)$ of genotype i in patch j for year t as a function of the number of adults $N_{i,j}$ is

$$L_{i,j}(t + 1) = 220 \times \sum_{k=1}^3 P_{k,j} F_k [N_{k,c}(t) \sum_{m=1}^3 wQ_{m,c}(t) + N_{k,r}(t) \sum_{m=1}^3 wQ_{m,r}(t)] \quad [1]$$

P is the probability of moving to patch j for genotype k and F is the relative fecundity for genotype k (Table 1). The relative fecundity incorporates any fitness cost. Mated beetles carry offspring that have an expected frequency distribution dependent upon the frequencies of each genotype emerging in the natal patch. Therefore, Q is the frequency of genotype m in natal patch c or r (continuous or rotated corn) that can reproduce the particular offspring genotype i when mated with genotype k . Each weight, w , equals the Mendelian proportion of all offspring that are genotype i when genotypes m and k mate.

To calculate the number of older larvae and adults, we must calculate density-dependent survival. First, we calculated the total density of larvae TL in each kind of corn habitat in the landscape, f (where f is c or r), surviving the winter and toxicity, Q_{tox} , of either transgenic corn roots in rotated corn or soil insecticide in continuous corn. We assumed that all continuous corn is treated with an annual soil insecticide that has $Q_{tox} = 0.50$.

$$TL_f = \sum_{i=1}^3 L_{i,f}(t) \times 0.5 \times Q_{tox} \quad [2]$$

The numbers of older larvae or adults in the two corn habitats f are

$$N_{i,c}(t) = 0.5 \times Q_{tox} \times L_{i,c}(t) \times 0.21 \times \exp\{-0.058[TL_c/(100M_c \times 10^6)]\} \quad [3]$$

$$N_{i,r}(t) = 0.5 \times Q_{tox} \times L_{i,r}(t) \times 0.21 \times \exp\{-0.058[TL_r/(100M_r \times 10^6)]\} \quad [4]$$

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

Basic Simulations. The model is programmed in Visual Basic in Microsoft Excel (Microsoft 2002). The model has a time step of 1 yr and a time horizon of 15 yr with a spatial unit of 100 ha. The initial number of adults is 1 million per hectare of corn, which is one-half of the carrying capacity in corn for our model when simulating with 99% continuous corn. The 1 million per hectare is applied proportionally to the areas of continuous and rotated corn. The adults begin at Hardy-Weinberg equilibrium with an initial Y allele frequency of 10^{-4} . The rotation level, R, is the sum of the proportional areas of rotated corn and soybean, which are always equal in the model ($R = S + M_r$). In the basic simulation of a 2-yr rotation, the landscape is defined as $R = 0.85$, $E = 0.05$, and $M_c = 0.10$. Mutations do not occur after the start of the simulations. We studied three types of gene expression: X as dominant, additive, or recessive.

Alternative Management Strategies. Six management strategies with the potential to prevent or halt the evolution of rotation resistance were compared with the typical 2-yr rotation strategy. Each strategy was evaluated according to its effects on resistance allele frequency, 15-yr average larval densities, and the economic costs and benefits of each approach for the 100-ha farm.

Management strategies that retain the movement parameters of the 2-yr rotation strategy (Table 1, 3-yr rotation, more continuous corn and transgenic rotated corn) alter the proportions of the landscape in which rootworms will survive. The remaining three strategies attempt to influence the movement behavior of adults by either repelling or attracting beetles during oviposition (repellent soybean, 3-yr rotation with unattractive wheat and attractive rotated corn), thereby increasing the proportion of eggs laid in locations that will not be rotated to corn the following year.

First, we evaluated a 3-yr rotation with $S = M_r = E = 0.30$ with either S or E preceding M_r . The proportion of land planted to continuous corn is the same as the 2-yr rotation strategy, 0.10.

In the case of transgenic rotated corn, we used a value of 0.90 for mortality in transgenic rotated corn ($1 - Q_{tox}$), where Q_{tox} is the proportion of neonate larvae surviving in rotated corn (equations 2–4). This mortality is applied at the same time as overwintering survival and before density-dependent survival. We did not simulate the use of transgenic continuous corn.

In the case of planting more landscape to continuous corn, the initial $S = 0.425$ in a 2-yr rotation was changed to $S = 0.30$, with $S = M_r$. The amount of land planted to continuous corn is 0.35, and $E = 0.05$. This approach is not as likely to prevent the evolution of rotation resistance as a 3-yr rotation because the relative fitness of polyphagous beetles is not reduced as much.

We also considered the implementation of repellent soybean or attractive rotated corn either through breeding of new cultivars or by application of chemicals to each crop. We investigated a 2-yr rotation with a soybean cultivar that repels 90% of polyphagous phenotypes. The polyphagous beetles that are re-

pelled from soybean lay their eggs randomly throughout the rest of the landscape (Table 1). This strategy will increase the number of adults that lay eggs in continuous corn while decreasing the number that lay eggs in soybean.

The use of a rotated corn hybrid that attracts 90% of polyphagous and monophagous phenotypes will cause these beetles to lay more eggs in rotated corn than in other parts of the landscape (Table 1). With this strategy the number of beetles laying eggs in both continuous corn and soybean decreases.

The use of a 3-yr rotation with less attractive E attempts to prevent rotation resistance by affecting both the survival of larvae and the movement rates of adults. This strategy involves a 3-yr rotation where M_r is preceded by other noncorn vegetation, E (e.g., winter wheat). Only polyphagous individuals laying eggs in E will survive in rotated corn the following year. The initial $S = 0.425$ in a 2-yr rotation was reduced to 0.30 with $S = M_r = E$ and $M_c = 0.10$. We investigated a winter wheat crop (E) that repels 90% of polyphagous beetles. Polyphagous individuals that are repelled from wheat lay eggs randomly throughout the rest of the landscape (Table 1). This increases the proportion of beetles emerging in continuous corn while decreasing those emerging in rotated corn.

Sensitivity Analysis. In a sensitivity analysis, we studied five factors. First, we studied the influence of initial allele frequency on the results by raising the initial Y allele frequency to 0.001 or 0.01. Second, we evaluated the effects of a cost in fecundity due to feeding on noncorn tissues. We set the value of Fitcost in the functions for F (Table 1) to 0.5 or 1.0. Third, we simulated population dynamics with two versions of the density-dependent survival function used by Onstad et al. (2001a), $1/(1 + 2.42EGG^{0.7})$: one with no modification of the published version (maximum survival is 1.0) and another with this function's maximum survival capped at 0.40. Fourth, we changed the survival to insecticide toxicity in continuous corn to 0.65 and 0.35 for the larval stage.

In addition, for each strategy we tested whether the value of rotational level had a significant effect on results by running the simulations with $R = 0.75$ and $R = 0.95$. The landscape of the 2-yr rotation strategies is $M_c = 0.15$, $S = M_r = 0.375$ and $E = 0.10$ if $R = 0.75$, or $M_c = E = 0.025$ and $S = M_r = 0.475$ if $R = 0.95$. With the 3-yr rotation strategies and either level of rotation, M_c is the same as in the 2-yr rotation strategies and $S = M_r = E = (R + E [\text{in a 2-yr rotation}])/3$. The landscape of the more continuous corn strategy is $M_c = 0.3333$, $S = M_r = 0.2833$ and $E = 0.10$ if $R = 0.75$ or $M_c = 0.325 = S = M_r = 0.325$ and $E = 0.025$ if $R = 0.95$.

Yield Loss. The proportion of yield lost in habitat f is

$$LOSS_f = 0.251 [1 - \exp(-0.0089K_f^{0.589})], \quad [5]$$

where $K_f = TL_f/(100 M_f \times 10^4)$ is larvae per square meter 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. This

equation was derived using a sequence of linked models as follows.

Using field data from Gray and Steffey (1998), the regression model $LOSS = 0.128 RC + 0.192e$ was estimated, where RC is the root rating change, calculated as the root rating without a soil insecticide minus the root rating with a soil insecticide by using the scale of Hills and Peters (1971), and e has a standard normal distribution ($n = 330; r^2 = 0.144; F = 55.29; df = 1, 329; P < 0.0001$). By using the same data set, maximum likelihood was used to estimate a beta probability distribution for RC by using the ML procedure in TSP version 4.4 (TSP International 1997). The estimated mean and standard deviation were $0.3206(RR_{no} - 1) - 0.03785(RR_{no} - 1)^2$ and 0.09341, respectively; the minimum is set at zero and the maximum at RR_{no} , where RR_{no} is the root rating without a soil insecticide. All reported parameters were significant ($n = 330, P < 0.001$). Mitchell (1999) used field data of Riedell et al. (1996) to develop a beta probability distribution for RR_{no} with mean 6.0 [minus] 5.0(1.0 - exp(-0.0003795K)) and a quadratic spline for the standard deviation, a minimum of 1, and a maximum of 6, where K is larvae per square meter.

To derive the loss equation, Monte Carlo simulations were conducted by beginning with a larval population, and then drawing in sequence a random root rating without a soil insecticide, a random change in the root rating, and a random proportion of yield lost. The larval population was increased from 0 to 9,500 with a step size of 100. For each larval population, the algorithms of Press et al. (1992) were used to draw 20,000 random variables. The model was programmed in C++ by using Microsoft's Visual C++ compiler, version 6.0 (Microsoft 2000). The reported loss equation was estimated via maximum likelihood with the ML procedure in TSP version 4.4 (TSP International 1997) assuming a normal error. All reported parameters were significant ($P < 0.001$).

Economic Analysis. The economic analysis was based on calculation of returns for the 100-ha farm that includes corn, soybean, and wheat (extra vegetation). Returns (dollars per hectare) for the crop in habitat f in year t are as follows:

$$RETURN_{f,t} = PRICE_f \times Y_f \times (1.0 - LOSS_{f,t}) - COST_f \quad [6]$$

$PRICE_f$ 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. $LOSS_{f,t}$ is zero for soybean and wheat. For continuous and rotated corn, $LOSS_{f,t}$ depends in the larval population in year t according to the previously reported equation

Table 2 reports the prices, yields, and cost of production used for each crop. Prices are the approximate average of the marketing year average price from 1998 to 2001 (Illinois Agricultural Statistics Service 2002). Yields and costs were from Illinois crop budgets (Schnitkey 2001). The yield for continuous corn was set equal to the yield for rotated corn, because the

Table 2. Prices, yields, and costs of production for each crop

	Rotated corn	Continuous corn	Soybean	Wheat
Price (\$/ql)	7.88	7.88	17.46	8.27
Yield (ql/ha)	100.40	100.40	37.00	50.40
Variable cost (\$/ha)	442.13	464.36*	288.99	214.89
Return (\$/ha)	348.27	326.04	356.30	201.92

ql = quintals.

* Includes \$34.58/ha for cost of insecticide.

reported yield implicitly included yield loss due to corn rootworm and our economic analysis separately incorporated this yield loss. The variable cost for continuous corn included \$34.58/ha as the cost of applying a soil insecticide. No additional costs are assumed for transgenic corn, attractive corn, or repellent soybean. One type of transgenic corn has recently been approved for commercial sales, but the market price is not yet established. Similarly, attractive corn and repellent soybean are technically feasible, but these technologies have not been commercialized, so their costs are not yet established. As a result, the economic analysis calculated the cost at which each strategy was equal to any other strategy as described below.

The net present value per hectare for habitat f is the sum of the discounted annual returns:

$$NPV_f = \sum_{t=1}^{15} \beta(t) \times RETURN_{f,t} \quad [7]$$

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 grower cost of capital (Schnitkey 2001). The net present value per hectare of a strategy is then the sum of the net present value for each crop in the strategy, weighted by the proportion of the total landscape planted to each crop habitat for the strategy: $NPV = M_r \times NPV_{Mr} + M_c \times NPV_{Mc} + S \times NPV_S + E \times NPV_E$. The annualized net present value (ANPV) of each strategy is the fixed annual return for 15 yr that generates the same net present value:

$$ANPV = NPV/Z, \text{ where } Z = \sum_{t=1}^{15} \beta(t). \quad [8]$$

For the attractive corn, repellent soybean, and transgenic corn strategies, the annualized net present value with a constant annual cost T for the technology is $T \times Pr + ANPV_0$, where Pr is the proportion of the landscape to which the added cost applies and $ANPV_0$ is the annualized net present value with no added cost for the technology. For attractive rotated corn and transgenic rotated corn, $Pr = M_r$, and for repellent soybean, $Pr = S$. The annual cost for each technology that equates the annualized net present value for the attractive rotated corn, repellent soybean, or transgenic rotated corn strategies ($ANPV_a$) to the net present value of a base strategy ($ANPV_b$) is $T = (ANPV_b - ANPV_a)/Pr$.

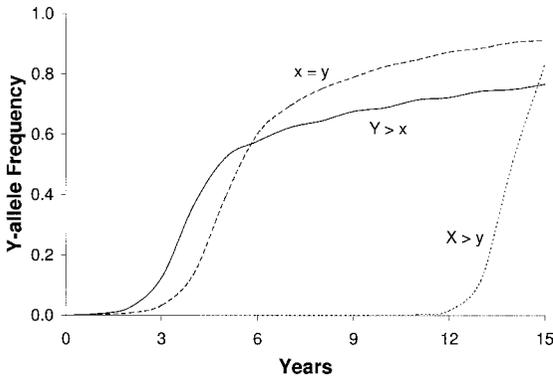


Fig. 1. Resistance allele frequencies over 15 yr with a 2-yr rotation ($R = 0.85$) and an initial Y allele frequency of 0.0001 with X dominant ($X > y$), X and Y additive ($x = y$), or Y dominant ($Y > x$).

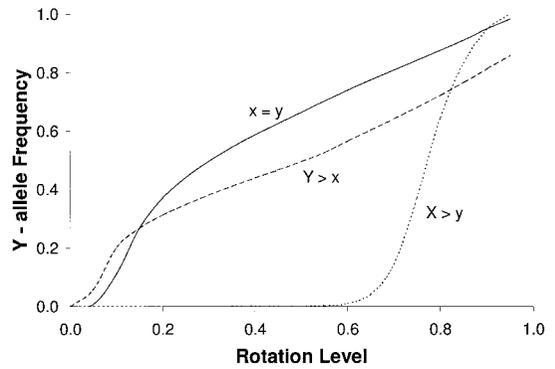


Fig. 2. Resistance allele frequency in year 15 as a function of the level of rotation, keeping E fixed at 0.05, with X dominant ($X > y$), X and Y additive ($x = y$), or Y dominant ($Y > x$).

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, we started with a 2-yr rotation with standard initial conditions and ran the simulations until the Y allele frequency reached 50%. Then, the management strategies were applied and the model was run for an additional 15 yr.

Results

Basic simulations of the 2-yr rotation strategy are shown in Figs. 1-3. Figure 1 shows how the Y allele frequency changes over 15 yr. The Y allele frequency reached 3% in years 13, 3, and 3 with a dominant X, additive, and dominant Y expression, respectively (Fig. 1). A dominant Y expression permits the Y allele frequency to increase the fastest, but after several years, the Y allele frequency is actually greater when expression of resistance is additive or recessive. The relative fitness of the heterozygotes ultimately determines the relative success of the Y allele. At $R = 0.85$ and a relative fitness of 0.475 for YY individuals, the heterozygotes have relative fitnesses of 0.085, 0.28 and 0.475, respectively, for X-dominant, additive and Y-dominant expression. Thus, the difference is greatest for dominant X and least for dominant Y, resulting in the X allele being successfully carried and passed on by heterozygotes to a greater extent when Y is dominant.

Figure 2 indicates how the level of rotation, R, influences the Y allele frequency after 15 yr. As R increases and M_c decreases, the Y allele frequency increases as expected. The scenario with the highest Y allele frequency depends on the value of R. For typical values of R for Illinois and Indiana, the additive expression produces very high Y allele frequencies, but recessive expression of resistance permits the highest Y allele frequencies when $R > 0.85$. (Results are similar when M_c is constant, R increases, and E decreases.) Figure 3 shows the influence of extra vege-

tation and indicates that the Y allele frequency declines as E increases. This supports the previous results of Onstad et al. (2001b).

Comparison of Resistance Allele Frequencies for Seven Strategies. We saw substantial differences in the time for rotation resistance to develop for our six alternative management strategies and a typical 2-yr rotation (Fig. 4). With a dominant X, all six alternative strategies were effective in slowing or preventing the evolution of resistance. The Y allele frequency reached 0.018 with the 3-yr rotation strategy and 0.01 with the more continuous corn strategy over the first 15 yr, whereas the other four strategies kept the Y allele frequency fixed at 0.0001. A 3-yr rotation or planting more land to continuous corn did not work well at preventing rotation resistance with either an additive or dominant Y gene expression (Fig. 4). The use of attractive rotated corn or repellant soybean was able to slow the evolution of rotation resistance with an additive expression, but not as well with a dominant Y (Fig. 4). The two most successful management strategies for preventing the evolution of resistance were the use of transgenic rotated corn and a 3-yr rotation

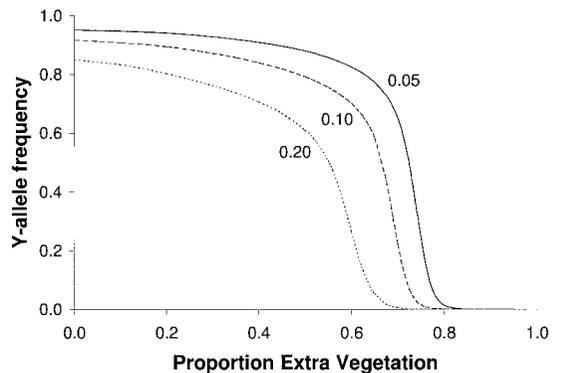


Fig. 3. Resistance allele frequency in year 15 produced with X and Y additive ($x = y$) as a function of the proportion of extra vegetation when continuous corn area $M_c = 0.05, 0.10, \text{ or } 0.20$.

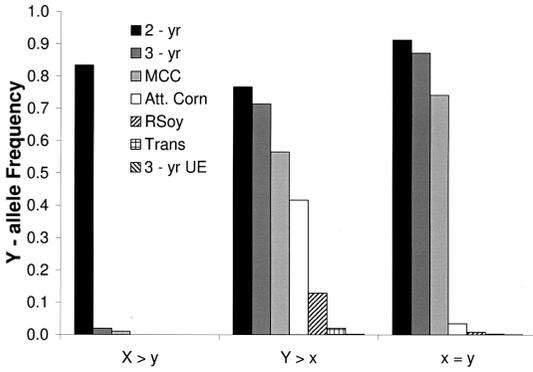


Fig. 4. Resistance allele frequency in year 15 for seven management strategies: 2-yr rotation (2-yr), 3-yr rotation (3-yr), more continuous corn (MCC), attractive rotated corn (Att. Corn), repellant soybean (RSoy), transgenic rotated corn (Trans), and a 3-yr rotation with unattractive E (3-yr UE), with three types of gene expression.

with unattractive wheat. Each of these strategies kept the Y allele frequency at low values (≤ 0.02) over 15 yr with each type of gene expression (Fig. 4).

If Y allele frequencies are higher than 0.0001 in an area before management is implemented, it may be difficult to prevent or counteract the evolution of rotation resistance. A 3-yr rotation with unattractive wheat was able to halt the evolution of resistance with either a dominant X or additive expression when implemented at an initial Y allele frequency of 0.01. At this frequency, the use of the transgenic rotated corn, more attractive rotated corn, or repellant soybean strategies were able to halt the evolution of rotation resistance only when the X allele was dominant. A 3-yr rotation with unattractive wheat was effective at preventing rotation resistance with any gene expression when implemented at an initial Y allele frequency of 0.001. At this frequency, transgenic rotated corn was able to halt evolution of rotation resistance with either a dominant X or additive expression but not with a dominant Y. Both repellant soybean and attractive corn were able to halt evolution of resistance only with a dominant X expression. Using a 3-yr rotation or planting more land to continuous corn was ineffective with all gene expressions at preventing resistance when implemented at Y allele frequencies of 0.01 or 0.001. These results indicate that most alternative management strategies will only have significant results at preventing rotation resistance when implemented at low Y allele frequencies (< 0.001).

Increased fitness costs had only slight effects on the evolution of rotation resistance. When we raised the fitness cost for polyphagous individuals to either 0.50 or 1.0 in a 2-yr rotation with $R = 0.85$, the Y allele frequency increased under all three gene expression scenarios, although slightly slower than with a fitness cost of zero. The resistance allele reached 3% in years 15, 4, and 3 and reached 50% in years 17, 6, and 6 for the dominant X, additive, and dominant Y scenarios, respectively. With a fitness cost of 1.0, the Y allele in

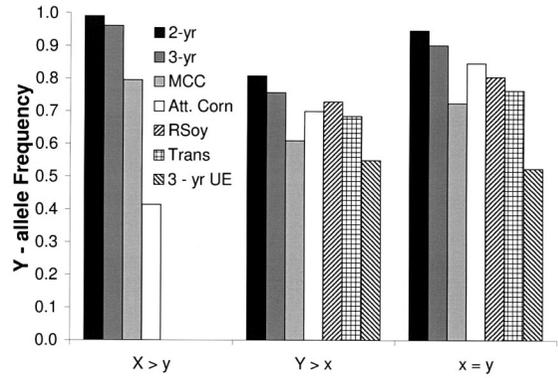


Fig. 5. Resistance allele frequency in year 15 for seven management strategies: 2-yr rotation (2-yr), 3-yr rotation (3-yr), more continuous corn (MCC), attractive rotated corn (Att. Corn), repellant soybean (RSoy), transgenic rotated corn (Trans), and a 3-yr rotation with unattractive E (3-yr UE), simulated with density-dependent survival function of Onstad et al. (2001) with maximum survival of 100%, with three types of gene expression.

a 2-yr rotation reached 3% in years 19, 4, and 4 and 50% in years 21, 7, and 7 for the dominant X, additive, and dominant Y scenarios, respectively. When we applied a fitness cost of 0.50 to polyphagous beetles with our alternative strategies, we saw slight reductions in the Y allele frequency for each of our strategies compared with a fitness cost of zero, but the results were similar. The two most effective strategies remained transgenic rotated corn and 3-yr rotation with unattractive wheat, while a 3-yr rotation and planting more land to continuous corn were still ineffective. With a fitness cost of 1.0, both the 3-yr rotation with unattractive wheat and transgenic rotated corn were able to reduce the Y allele frequency below 0.0001 in both the additive and dominant Y scenarios. The use of repellant soybean and attractive rotated corn were effective with an additive expression, but were still ineffective at preventing rotation resistance with a dominant Y. Even with a fitness cost of 1.0, the Y allele reached values $> 50\%$ with the 3-yr rotation and more continuous corn strategies with both an additive or dominant Y expression.

When we included the density-dependent survival function of Onstad et al. (2001a) in our model, with a maximum survival of 100%, the biological results were significantly different from those produced with our standard function. None of our six management alternatives were able to keep the Y allele frequency below 50% with either an additive or dominant Y expression over a 15-yr period (Fig. 5). With a dominant X, only a 3-yr rotation with unattractive wheat, repellant soybean and transgenic rotated corn were effective at preventing rotation resistance (Fig. 5).

When we limited density-dependent survival to a maximum of 40% in the function of Onstad et al. (2001a), the biological results were similar to using a maximum of 100% survival. A 3-yr rotation with unattractive wheat, repellant soybean, attractive rotated

corn and transgenic rotated corn were effective at preventing the evolution of rotation resistance with a dominant X expression. With an additive expression, the Y allele frequency was reduced greatly in these strategies (except for attractive rotated corn, 0.86 versus 0.79) compared with using a maximum 100% survival, but only a 3-yr rotation with unattractive wheat was able to keep the Y allele at significantly low values (<0.01). None of the six alternatives was effective at preventing rotation resistance with a dominant Y expression. The 3-yr rotation and more continuous corn strategies produced Y allele frequencies >0.60 for any expression.

When we changed insecticide survival to either 35 or 65% in continuous corn treated annually, the Y allele frequencies reached 3 and 50% in the same years as using 50% survival with a 2-yr rotation. With each of our six alternative strategies, the Y allele frequencies after 15 yr were 0–5% higher with 65% survival compared with 50% and 0–5% lower with 35% survival.

In a landscape with a rotation level of 0.75, biological results were similar to those produced with $R = 0.85$. With an additive expression, the 3-yr rotation with unattractive wheat, transgenic rotated corn, repellent soybean, and attractive rotated corn strategies all kept the Y allele frequencies < 0.005 over 15 yr. With a dominant Y expression, only a 3-yr rotation with unattractive wheat and transgenic rotated corn were effective at preventing the evolution of rotation resistance.

However, a landscape with a rotation level of 0.95 did have significantly different biological results. Increasing the rotation level to 0.95 substantially reduced the effectiveness of a 3-yr rotation, resulting in a Y allele frequency that reached 0.937 over 15 yr. With an additive expression, only a 3-yr rotation with unattractive E was effective at preventing evolution when the level of rotation was increased to 0.95. In contrast to a rotation level of 0.85, at $R = 0.95$ the use of attractive rotated corn, repellent soybean, and transgenic rotated corn were not effective, reaching Y allele frequencies >0.30 within 15 yr. Similarly, with a dominant Y expression and a rotation level of 0.95, only a 3-yr rotation with unattractive wheat was reasonably effective at preventing evolution (Y allele frequency reached 0.038). The use of transgenic rotated corn, effective at $R = 0.85$, was not effective at $R = 0.95$, reaching a Y allele frequency of 0.63.

Only when resistance is recessive (dominant X) do all six alternative management strategies prevent rotation resistance (Fig. 1). Therefore, we determined how different the landscapes and cultivars would have to be to prevent the Y allele frequency from reaching 3% after 15 yr with an additive or dominant expression of resistance. For the more continuous corn strategy, the proportion of land planted to continuous corn would have to exceed 0.882 and 0.91 for the additive and dominant scenarios, respectively. For a 3-yr rotation, the land planted to $M_r = S = E$ must be <0.034 and 0.019, respectively. For a 3-yr rotation with unattractive wheat (E), the repellency of E must exceed 0.775 and 0.849, respectively. For repellent soybean

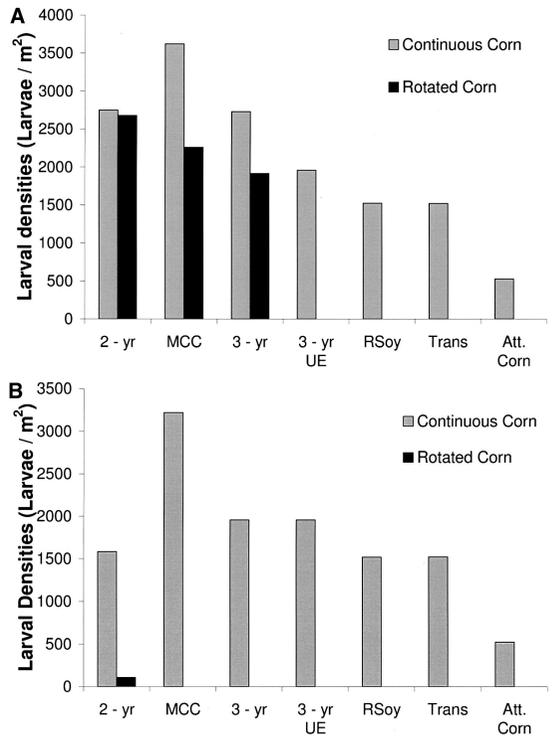


Fig. 6. Average larval densities in continuous and rotated corn for seven management strategies: 2-yr rotation (2-yr), more continuous corn (MCC), 3-yr rotation (3-yr), 3-yr rotation with unattractive E (3-yr UE), repellent soybean (RSoy), transgenic rotated corn (Trans), and attractive rotated corn (Att. Corn), with (a) X and Y additive ($x = y$) and (b) X dominant ($X > y$) over 15 yr after larvae have incurred overwintering and toxin mortality and before density-dependent survival is imposed under standard conditions.

crops, the repellency would have to exceed 0.869 and 0.925 for the additive and dominant scenarios, respectively. For attractive rotated corn, the attractiveness would have to exceed 0.902 and 0.99, respectively. For transgenic rotated corn, the mortality must exceed 0.845 and 0.895 for the additive and dominant scenarios, respectively, to prevent the Y allele from attaining 3%. Note that the mortality caused by transgenic corn is a consequence of the adoption levels (proportion of corn landscape) and the toxicity of the plant. The values described above for each of the six alternative strategies should provide guidelines for researchers interested in developing a new design or technology.

Comparison of Population Densities Simulated for Seven Strategies. To describe larval densities in continuous and rotated corn for each of our seven management strategies, we calculated the 15-yr average densities for larvae after they have incurred overwintering and toxin mortality under the standard conditions (Fig. 6). Larval density, not allele frequency, is the variable used in the economic analysis described below. With an additive expression, attractive rotated corn had much lower densities than any other strategy, followed by transgenic corn, repellent soybean,

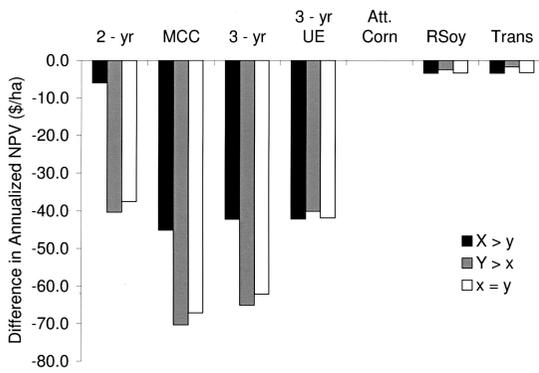


Fig. 7. Change in annualized net present value (dollars per hectare) of six management strategies: 2-yr rotation (2-yr), more continuous corn (MCC), 3-yr rotation (3-yr), 3-yr rotation with unattractive E (3-yr UE), repellant soybean (RSoy), transgenic rotated corn (Trans), and relative to attractive rotated corn (Att. Corn), the strategy with the greatest annualized net present value for each gene expression.

and a 3-yr rotation with unattractive wheat (Fig. 6a). These four strategies prevented larval populations from establishing in rotated corn, which led to reduced Y-allele frequencies over time compared with other strategies. The larval densities in the more continuous corn strategy were the highest of any management strategy, with a 2-yr rotation and a 3-yr rotation having slightly lower densities (Fig. 6a). The results with a dominant Y were similar to those for an additive expression.

With a dominant X, each of our six alternative management strategies was effective at preventing larval populations from establishing in rotated corn (Fig. 6b). Only a 2-yr rotation had larval populations >1 larva per square meter in rotated corn. Larval populations were reduced in continuous corn for both the two or 3-yr rotation strategies and planting more land to continuous corn, with reductions of 42, 28, and 11%, respectively, compared with the additive model (Fig. 6a and b). The other management strategies had similar larval densities in both continuous and rotated corn regardless of the gene expression.

Economic Analysis for Standard Model. Fig. 7 reports the change in the annualized net present value (dollars per hectare) for each management strategy relative to the strategy with the greatest annualized net present value for each gene expression. Reported payments are dollars per hectare of all cropland under the strategy (rotated and continuous corn, soybean, and winter wheat), not \$ per hectare of the crop denoting the strategy name. For each gene expression, the change is zero for attractive corn because it had the greatest annualized net present value for each gene expression: \$336.39, \$334.11, and \$336.00/ha for the dominant X, dominant Y, and additive expression cases, respectively. The transgenic rotated corn and repellant soybean strategies each have annualized net present values almost as large as for attractive corn, only \$1.76 to \$3.48/ha less for transgenic corn and

\$2.43 to \$3.48/ha less for repellant soybean, depending on the gene expression. These three strategies generate similar value for growers because they result in the lowest larval population densities (Fig. 6) and hence lowest yield losses.

The results in Fig. 7 do not include technology fees for transgenic corn, attractive corn, or repellant soybean. However, the technology fee that could be supported can be calculated, after adjusting for differences in the proportion of acres on which the costs are imposed. For example, with dominant X and no technology costs, the transgenic rotated corn strategy has an annualized net present value \$3.48/ha less than the attractive rotated corn strategy. If transgenic corn costs an additional \$24.70/ha, this reduces the annualized net present value of transgenic corn by $24.70 \times M_r = \$10.50$ /ha, where $M_r = 0.425$ (the proportion of the landscape in rotated corn and hence planted to transgenic corn). The total change in the annualized net present value is $10.50 + 3.48 = \$13.98$ /ha less than attractive rotated corn. Thus, if the cost of the attractive corn exceeds $13.98/M_r = 13.98/0.425 = \32.89 /ha, then the use of transgenic rotated corn is the preferred strategy according to this annualized net present value criterion.

According to the annualized net present value criterion, the worst strategies are more continuous corn and both 3-yr rotations (with or without unattractive extra vegetation). Because continuous corn and wheat generate lower returns than rotated corn and soybean, this result is not surprising. Growers in Illinois typically plant most of the landscape to a corn-soybean rotation because this practice generates the highest returns.

Interestingly, with a dominant X expression and no technology costs, the annualized net present value for the 2-yr rotation is only \$6.02/ha less than for attractive rotated corn. Thus, if X is truly dominant and the cost of attractive corn exceeds $6.02/0.425 = \$14.16$ /ha, then doing nothing about the rotation resistance problem is the preferred strategy according to the annualized net present value criterion. For repellant soybean and transgenic rotated corn, the annualized net present value difference is only \$2.54/ha. Thus, with dominant X, the 2-yr rotation is economically preferable to repellant soybean or transgenic rotated corn if the technology cost exceeds $2.54/0.425 = \$5.98$ /ha.

Economic Sensitivity Analysis for Biological Parameters. We compared economic results for the standard model, which has a maximum density-dependent larval survival of 21%, with those generated using the density-dependent survival function of Onstad et al. (2001a) with a maximum of 40 and 100% survival. As maximum survival increases from 21 to 40 to 100%, the annualized net present value (NPV) should decrease because more corn rootworm larvae survive to cause yield loss. The greatest effects are on the strategies with more corn and without corn rootworm control. As a result, the greatest effect is for the 2-yr rotation, 3-yr rotation, and more continuous corn strategies, where the decrease in annualized NPV exceeds \$10.00/ha. The least effect occurs for the 3-yr rotation

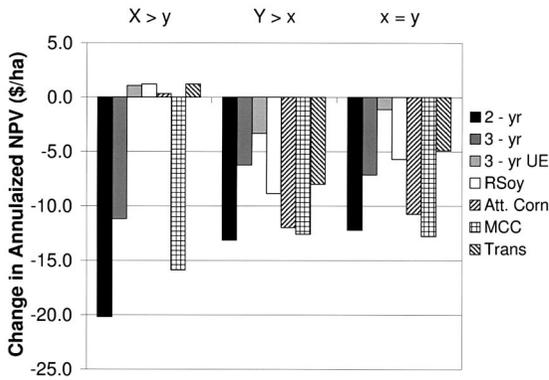


Fig. 8. Change in annualized NPV (dollars per hectare) for seven management strategies: 2-yr rotation (2-yr), planting more land to continuous corn (MCC), 3-yr rotation (3-yr), 3-yr rotation with unattractive E (3-yr UE), repellent soybean (RSoy), transgenic rotated corn (Trans), and attractive rotated corn (Att. Corn), with density-dependent survival function of Onstad et al. (2001a), with maximum survival of 100%, versus simulations by using the standard density-dependent function.

with unattractive wheat, transgenic rotated corn, and repellent soybean, where the decrease in NPV is generally $< \$5.00/\text{ha}$.

The effects of changing density-dependent larval survival are generally the same with a dominant Y or additive gene expression (Fig. 8). However, for strategies that are particularly effective at slowing the development of rotation resistance (repellent soybean, attractive, and transgenic rotated corn, and a 3-yr rotation with unattractive extra vegetation) when expression of X was dominant, there was a slight increase in annualized NPV for the 15-yr simulation period, but there was a slight decrease in annualized NPV when expression of Y was dominant. As expected, losses on rotated corn continuously increase over the 15 yr, but for these strategies, these losses remain too small to offset effects on continuous corn. Increased larval survival increases the time required for larval populations in the continuous corn portion of the landscape to stabilize. For these strategies, larval populations happen to be lower on continuous corn over many of the 15 yr when larval survival is higher. If the simulation period were extended, larval populations and losses on continuous corn would increase so that the annualized NPV would continue to decrease for these strategies when the maximum larval survival is increased.

Imposing a fitness cost on rotation-resistant individuals of 50 and 100% from the base assumption of no fitness cost had little effect on relative differences in the annualized NPV of the different strategies. Only when both rotation resistance and a significant larval population exist will the fitness cost have an economic impact, because otherwise it affects few corn rootworm larvae. As a result, as the fitness cost increases, the economic impact of resistance is diminished, because the annualized NPV of attractive rotated corn,

repellent soybean, and transgenic rotated corn decrease relative to the 2-yr rotation, the 3-yr rotation, and more continuous corn strategies.

Similarly, changing the larval soil insecticide survival rate had little impact because insecticides are only used on continuous corn in the model, which constitutes a small portion of the landscape. For example, decreasing the larval insecticide survival rate from 50 to 35% has the greatest impact on the annualized NPV for the more continuous corn case, which increased 1%.

We examined the effect of the rotation level (the proportion of the landscape in a corn-soybean rotation), by increasing the rotation level from 0.85 to 0.95. Because the corn-soybean rotation generates the greatest returns in the model, annualized NPV increases with the rotation level. The greatest effect is for repellent soybean and transgenic corn, where the annualized NPV increases $\approx \$15.00/\text{ha}$. These strategies keep the Y allele frequency and corn rootworm larval populations the lowest in rotated corn, and so generate the largest annualized NPV. Increasing the rotation level enhances these effects and generates more return for growers. However, the rotation level has the smallest effect for the more continuous corn and both 3-yr rotation strategies, because these have the least rotated corn. As a result, increasing the rotation level makes repellent soybean and transgenic corn even better relative to the other strategies. Decreasing the rotation level from 0.85 to 0.75 changed the annualized NPV for each strategy by essentially the same magnitude, but in the opposite direction.

Economic Sensitivity Analysis for Economic Parameters. The discount rate has little effect, except for the 2-yr rotation, the 3-yr rotation, and the more continuous corn strategies. Only in these cases do losses substantially rise toward the end of the 15-yr simulation period (losses are fairly constant for the other strategies). As the discount rate increases, growers put less weight on these losses. As a result, increasing the discount rate increases the annualized NPV of the 2-yr rotation, the 3-yr rotation, and the more continuous corn cases relative to the other cases. However, changing the discount rate from 7 to 15% increases the annualized NPV $< \$10.00/\text{ha}$. In addition, the discount rate has little effect if X is dominant. With a dominant X, though the Y allele frequency begins to increase, larval populations remain low and so do not create significant yield losses compared with the other gene expression cases. Changing the discount rate from 7 to 15% increases the annualized NPV $< \$2.00/\text{ha}$.

Net revenue for each crop relative to net revenues for the other crops are the important economic assumption, not the specific price, yield and cost assumptions. As a result, changes in potential revenue for each crop are used to examine the effect on economic results.

Increasing the net revenue for corn (both rotated and continuous) by 10% increases the annualized net returns for each strategy by at least $\$30/\text{ha}$ and up to $\$45/\text{ha}$. The largest increase occurs for strategies with more corn (e.g., more continuous corn) and the low-

est for the 3-yr rotation strategies that reduce corn acreage. The difference in annualized NPV increases by 10% for strategies with equal proportions of the landscape in corn. As a result, rankings of the strategies do not change—attractive corn still generates the greatest annualized NPV.

Increasing net revenue for soybean by 10% has a similar effect. The annualized NPV increases either \$27.42 or \$19.42/ha, depending on whether the strategy had either 42.5 or 30% of the landscape planted to soybean. Thus, the difference in annualized NPV increases by 10% for strategies with equal proportions of the landscape in soybean and again, rankings of the strategies do not change. Similarly, because wheat constitutes a small proportion of the landscape for all strategies, increasing its net revenue by 10% increases annualized NPV for all strategies only a little. The largest change (\$12.50/ha) is for both 3-yr rotation strategies, because they have the most wheat acreage. For the other strategies, the change is only \$2.08/ha. As a result, the rankings of the strategies do not change.

Increasing potential revenue from rotated corn relative to continuous corn is equivalent to increasing potential revenue for soybean—it increases the annualized NPV for all cases, but more for cases with more rotated corn. Similarly, increasing potential revenue from continuous corn relative to rotated corn is equivalent to increasing potential revenue from corn—it increases the annualized NPV for all cases, but more for cases with more continuous corn.

Economic Analysis for Severe Problem Areas. If management is implemented after the Y allele frequency has risen to >50%, four strategies are more profitable than a 2-yr rotation, as long as technology fees are not too high: transgenic rotated corn, repellent soybean, attractive rotated corn, and a 3-yr rotation with unattractive wheat. As expected, the strategies are not sensitive to the type of gene expression. Transgenic rotated corn has the greatest annualized net present value of any strategy: \$307.47 to \$313.62/ha (Fig. 9). The strategies with attractive rotated corn and repellent soybean each have similar annualized net present values, only \$0.54 to \$2.41/ha lower for repellent soybean and \$8.03 to \$8.99/ha lower for attractive rotated corn, depending on the type of gene expression. None of the seven management strategies were effective at halting the evolution of rotation resistance with any gene expression.

The annualized net present value of a 2-yr rotation was \$34.37 to \$38.06/ha less than for transgenic rotated corn, depending on gene expression (Fig. 9). Thus, transgenic corn is always preferred to a 2-yr rotation if the cost is $<34.37/0.425 = \$80.88/\text{ha}$. For repellent soybean, the annualized net present value was \$33.84 to \$36.27/ha higher than a 2-yr rotation and for attractive rotated corn the difference varied from \$26.34 to \$29.31/ha. Thus, repellent soybean and attractive rotated corn are preferred to a 2-yr rotation, with any type of gene expression, if the cost does not exceed $33.84/0.425 = \$79.61/\text{ha}$ and $26.34/0.425 = \$61.98/\text{ha}$, respectively.

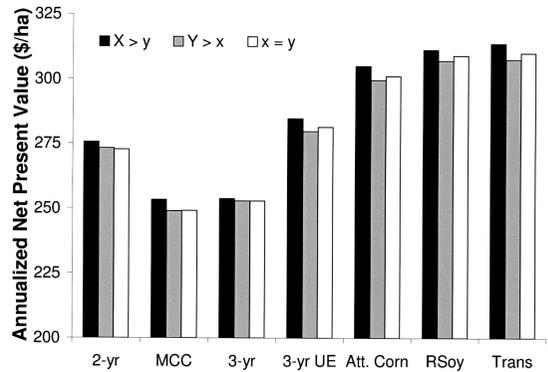


Fig. 9. Annualized NPV (dollars per hectare) for seven management strategies: 2-yr rotation (2-yr), more continuous corn (MCC), 3-yr rotation (3-yr), 3-yr rotation with unattractive E (3-yr UE), attractive rotated corn (Att. Corn), repellent soybean (RSoy), and transgenic rotated corn (Trans), simulated for 15 yr after the Y allele frequencies increased to >50% under standard conditions, with three types of gene expression.

Discussion

Western corn rootworm invaded east central Illinois between 1968 and 1970 (Metcalfe 1983), ≈ 16 yr before the first observation of resistance to crop rotation in Ford County, Illinois, during the 1980s (Onstad et al. 1999, 2003). In 1997, both Ford County and the adjacent Champaign County had $R = 0.96$, $M_c = 0.02$, and $E = 0.02$ (Illinois Agricultural Statistics Service 1998). Since the late 1960s, continuous corn has averaged from 2 to 9% ($M_c = 0.02$ – 0.09) in this area. Thus, according to our model, the landscapes certainly had enough corn–soybean rotation to have promoted the evolution of rotation resistance.

In the model, resistance to crop rotation generally evolves in <15 yr, and the rate of evolution increases as the level of rotation in the landscape (selection pressure) increases. When resistance is recessive, all six alternative management strategies were very effective in slowing or preventing the evolution of rotation resistance. The two most successful and robust management strategies for preventing the evolution of rotation resistance were the use of transgenic rotated corn and a 3-yr rotation with unattractive winter wheat. Each of these strategies kept the resistance allele frequency at low values (≤ 0.02) over 15 yr, regardless of gene expression.

Density-dependent survival had a significant effect on both the evolution and management of this pest. Previous work has demonstrated the importance of this process for the evolution of resistance by western corn rootworm to transgenic corn (Onstad et al. 2001a). Because we allowed survival to increase at lower densities, it became more difficult to prevent evolution of transgenic resistance and to manage the pest.

Economically, three alternative strategies were robust solutions to the IPM and IRM problems, if technology fees are not too high. Repellent soybean, at-

tractive rotated corn, and transgenic rotated corn, all in 2-yr rotations, were economically valuable approaches according to our net present value criterion. Thus, there are robust solutions for managing western corn rootworm and rotation resistance under the uncertainty of gene expression.

IPM takes grower returns into account, and so is greatly affected by the declining value of future profits and the rate of increase in resistance over time. The economic discount rate symbolizes the greater concern that growers, industry, and society place on the present value of a resource compared with the future value. However, the ecological 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 endpoints are achieved. However, growers 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.

For example, even the currently common 2-yr rotation was economical as an IRM strategy when resistance was recessive, and it took 14 yr for the resistance allele frequency to reach 50%. With expression of a dominant X allele, the 2-yr rotation strategy was economically preferred to repellent soybean or transgenic rotated corn strategies if the technology fee exceeds $2.54/0.425 = \$5.98/\text{ha}$. This result occurs because even though the frequency of the Y allele grows rapidly, population densities do not increase for several years. As a result, yield losses on rotated corn in excess of 1% do not occur until years 14 and 15, when losses are 4.2 and 11.7%, respectively. However, because these losses occur far in the future, they are substantially discounted by the net present value criterion, implying that growers concerned only with economic returns will prefer to do nothing about the evolution of rotation resistance. This result gives insight into the economic logic that underlies the evolution of rotation resistance among western corn rootworm.

It is difficult, if not practically impossible, to halt the evolution of rotation resistance once the resistance allele frequency reaches $\approx 1\%$. Thus, the uncertainty in the timing of invasion by the rotation-resistant variant and the initial resistance gene frequency make it more difficult to choose a good strategy. Furthermore, reductions in grower returns are not the only costs of resistance. If soil insecticide use will greatly increase as a result of rotation resistance, it may be desirable from a social perspective to subsidize growers in the present, so they have an incentive to change practices now and so delay the development of resistance in the future.

Our results also indicate that under our standard set of assumptions, several alternatives are superior to a typical 2-yr rotation with regard to rootworm IPM in areas where rotation resistance is a serious problem. This is not surprising. The maximum annualized technology fee of $\$81/\text{ha}$ for transgenic rotated corn that equalizes it with the typical 2-yr rotation is the maximum willingness to pay for the transgenic technology

relative to doing nothing. Because this exceeds current estimates of the cost of transgenic corn, transgenic technology is likely to be popular in these areas. Alston et al. (2003) found that in areas where the rotation-resistant variant was a problem, transgenic corn could increase grower returns $\approx \$64/\text{ha}$ over a soil insecticide just from the yield gain alone (Alston et al. 2003). Unless a third crop can be found that is less attractive for rootworm egg laying and economically competitive with corn and soybean, a 3-yr rotation does not seem to be a practical IPM solution in existing problem areas. Our analysis does not evaluate other potential strategies such as using soil insecticides in rotated corn nor using transgenic corn in continuous cornfields.

The application of these results is also 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. This simple genetic system was chosen because it is comparable with several natural systems described by Onstad et al. (2001b). Second, we assumed that all farms are the same in a homogeneous region or that areawide pest management is occurring. Third, we did not model resistance to transgenic corn or any other repellent or attractive crop. Changes in these assumptions could produce other outcomes.

In addition, we used a single economic criterion to compare strategies. Other economic criteria exist that take into account more than just grower 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 chemical insecticides in rotated corn because we believe that legislation such as the Food Quality Protection Act implies that such a solution is not socially or politically acceptable if other options exist (EPA 2003). It would be possible to develop an economic criterion that takes into account the social costs and benefits of insecticide use. We also ignored many of the issues surrounding transgenic crops and their economic impacts.

Several subjects deserve special attention in the future. Empirical studies should focus on determining the density-dependent survival of western corn rootworm at low densities. The model was sensitive to larval survival, so we need to know whether the maximum larval survival is 21%, 40%, or higher. The population genetics of the western corn rootworm by using a laboratory bioassay and standard crossing of individuals could also be performed. A future model should consider the evolution of resistance to both crop rotation and transgenic corn. Our current model could also be modified to consider alternative management strategies that involve other IPM approaches such as the use of economic thresholds for not only insecticide use but also for crop selection and planting (landscape design). This would allow the evaluation of dynamic strategies with tactics that can change on an annual basis. Too often system design and control are not considered simultaneously in IPM (Onstad 1985). Another model could also evaluate fitness cost

as a function of phenotype rather than as a phenotype-environment interaction.

We believe that our results emphasize the differences between IPM and IRM. Management recommendations and decisions by growers must be made even when we do not know how evolution will develop and when new phenotypes will invade our landscapes. IPM must address management concerns without being overwhelmed by these uncertainties and being overridden by IRM. In its best sense, IPM has accounted for both the ecological and economic factors of a problem. Too often in the past, evolutionary changes in pest populations have caused scientists to emphasize IRM over IPM, as if one gene and one risky tactic were more important than basic IPM. Perhaps this narrow focus on IRM makes sense when only one tactic is available. But some believe that IPM cannot be true IPM if it permits evolution of resistance. From this perspective, the extensive use of crop rotation, though very effective for many years, was not truly IPM. However, resistance by insects to highly effective IPM strategies is inevitable, but long-term success for IPM is not. Thus, we must constantly strive for better approaches that combine landscape design, host plant resistance, biological control, and other feasible tactics for pest management.

Acknowledgments

This project was funded by the Illinois Council on Food and Agricultural Research (C-FAR) through a Sentinel grant, the Illinois Soybean Program Operating Board (IS-POB), the USDA-ARS through the Corn Rootworm Area-wide Management Program via specific cooperative agreement number 58-5447-0-304, and several Hatch projects.

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Received for publication 16 May 2003; accepted 23 September 2003.
