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Managing European Corn Borer Resistance to Bt Corn with Dynamic Refuges

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Abstract

Genetically engineered Bt (*Bacillus thuringiensis*) corn provides farmers with a new tool for controlling the European corn borer (ECB). The high efficacy and potential rapid adoption of Bt corn has raised concerns that the ECB will develop resistance to Bt. The Environmental Protection Agency has responded to these concerns by requiring farmers to plant refuge corn. Current refuge requirements are based on models that do not consider the value of dynamically varying refuge in response to increased scarcity and diminished control over time or the importance of backstop technologies currently being developed. The purpose of this paper is to evaluate dynamically optimal refuge requirements with the arrival of alternative backstop technologies and to compare the results to an optimal static refuge policy. The results show that a dynamically optimal refuge requirement only provides modest benefits above a static optimum. The results also show how the type of backstop technology and characteristics of ECB population dynamics affect the optimal refuge requirement.

Key words: Bt corn, optimal control, pesticide resistance.

Introduction

Bt corn is corn that is genetically engineered to produce a protein found in the soil bacterium *Bacillus thuringiensis* (Bt). The protein is toxic when consumed by lepidopteran insects such as the European corn borer (ECB), a pest that is estimated to cost U.S. farmers over \$1 billion annually in yield loss and control costs (Mason et al.). The high efficacy and full season control provided by Bt corn has resulted in its rapid adoption by farmers. Between 1996 and 2001, Bt corn acreage in the United States increased from less than 1 percent to over 20 percent (USDA-NASS). In 1999, for counties in Illinois, Iowa, Minnesota, North Dakota, and South Dakota, more than 50 percent of corn planted was Bt corn.¹ The rapid adoption of Bt corn raises concerns that the ECB will develop resistance to it. The Environmental Protection Agency (EPA) has responded to these concerns by requiring farmers to plant refuge corn (EPA 1998a). Refuges slow the proliferation of resistance by allowing susceptible pests to thrive and mate with resistant ones (EPA 1998a).

Previous studies provide the rationale for the EPA's resistance management requirement. Pests are a detrimental renewable resource because they propagate and damage crops (Hueth and Regev; Regev, Gutierrez, and Feder; Regev, Shalit, and Gutierrez). Pest susceptibility (the converse of resistance) is a valuable resource because susceptible pests are controllable (Hueth and Regev; Regev, Shalit, and Gutierrez). The use of pesticides reduces the biological capital of susceptibility as it increases resistance through natural selection, thereby making pests less controllable in the future. The ECB is a mobile pest that farmers will treat as common property (Clark and Carlson). Thus, farmers are unlikely to privately manage resistance.

Early literature characterized the dynamic optimal dose of pesticides for managing resistance. Recent literature explores the value of static refuges (e.g., Alstad and Andow 1995; Roush and Osmond; Gould; Onstad and Gould 1998a,b; Hurley et al. 1999, 2001; and Livingston, Carlson, and Fackler). The purpose of this paper is to (i) extend the literature on resistance management using refuge to consider the type of dynamic optimum used to characterize pesticide dose, (ii) explore the sensitivity of a dynamic

optimum to the population characteristics of the ECB, and (iii) consider the sensitivity of a dynamic optimum to the introduction of new technology that depends on the existing technology.

Varying pesticide dose is not feasible with Bt corn because the pesticide is in the plant. Still, it is possible to vary exposure to Bt by varying the size of refuge. Previous results suggest that varying refuge size in response to scarcity and diminishing control will more effectively manage resistance, but it is not clear how much a dynamic refuge improves resistance management when compared to the static refuges recently evaluated in the literature.

Commercialized varieties of Bt corn rely on one of three toxins.² Many new varieties under development rely on more than one toxin. Resistance is thought to evolve more slowly when pests must overcome multiple toxins. Therefore, the introduction of multiple toxins into Bt corn may make less refuge optimal; how much less depends on the characteristics of the new technology, and this has not been explored within a bioeconomic context.

Models of resistance management for Bt corn often find that ECB populations are reduced substantially because of the high efficacy of Bt corn. Therefore, even when resistance develops, it may take years for populations to recover to economically important levels. Entomologists express concern with this type of result because they believe the ECB is more buoyant than predicted by models. The dynamics of the pest population biology, and in particular the recovery rate of the ECB after resistance occurs, affect agricultural productivity and resistance management benefits (see Hurley, Babcock, and Hellmich).

The results show that varying refuge improves resistance management by accounting for increased scarcity and diminished control over time. These opposing effects make it optimal to require less refuge when Bt corn is first introduced, more refuge once the ECB is better controlled and resistance starts to emerge, and less refuge as the arrival of a new technology nears. The improvement offered by an optimal dynamic refuge is modest when compared to an optimal static refuge. The characteristics of the ECB population and new technology are the main determinants of the optimal resistance management strategy. If the backstop technology adds only a new toxin, and still incorporates the toxin

used in the old technology, resistance management is more valuable than when two new toxins are introduced. Therefore, if the first-best policy is not to exhaust susceptibility before the new technology arrives, more refuge is optimal in the case of a backstop dependent on the old technology. If the ECB quickly recovers to economically important levels after resistance, refuge is a low-fixed–high-marginal cost input and is not typically optimal to exhaust susceptibility. Alternatively, if the ECB is slow to recover to economically important levels after resistance, refuge is a high-fixed–low-marginal cost input and is optimal to exhaust susceptibility.

Conceptual Model

Following Alstad and Andow 1995; Roush and Osmond; Gould; and Onstad and Gould (1998a,b), we consider a simplified production region with a single crop and pest. The region is closed to migration. While there is a single crop, there are two different varieties. The first is a toxic Bt variety. The second is a non-toxic refuge variety. The proportion of the refuge planted in season t is denoted by $1 \geq f_t \geq 0$. The proportion of resistant pests in season t is $1 \geq R_t \geq 0$ and the number of pests is $N_t \geq 0$. The variable Π_t is the value of agricultural production, which determines the value of pests and pest susceptibility in season t , while Ω_T is the salvage value of pests and pest susceptibility for all $t \geq T$, the season when a new technology is introduced.

The proportion of refuge and resistant pests determines how many susceptible pests are available to mate with resistant pests. The change in resistance from one season to the next is

$$R_{t+1} = r(f_t, R_t) + R_t. \tag{1}$$

Equation (1) assumes that the size of the pest population does not affect the evolution of resistance, which is common for biological models of resistance management. With more refuge, fewer pests are exposed to Bt. This slows down the evolution of resistance so that r_f is negative.³ Common biological models also imply that, all else equal, increasing resistance today increases resistance tomorrow: $r_R > 0$. Assuming susceptibility is nonrenewable implies $R_{t+1} \geq R_t$.

Surviving pests reproduce, while the effectiveness of Bt depends on pest exposure and resistance. The change in the population of pests from one season to the next is

$$N_{t+1} = n(\mathbf{f}_t, N_t, R_t) + N_t. \quad (2)$$

Planting more refuge decreases exposure to Bt, and it increases the rate of survival of the pests, so that n_f is positive. Pest populations may increase or decrease over time depending on whether the population is below or above carrying capacity. However, when pests are actively managed, as in agricultural systems, populations are maintained below carrying capacity, and n_N is positive. Increasing resistance decreases the effectiveness of Bt; therefore, n_R is positive.

We assume the value of pests and pest susceptibility is determined exclusively by the value of agricultural production:⁴

$$\Pi_t = \mathbf{p}(\mathbf{f}_t, N_t, R_t). \quad (3)$$

Because pest control for the Bt variety is better than for the refuge variety, increasing the proportion of refuge tends to decrease production, $\mathbf{p}_f < 0$, by decreasing the amount of crop protected. Increasing pests increases yield loss, which will also decrease production, $\mathbf{p}_N < 0$. Increasing resistance increases survival rates and reduces control, which will decrease production, $\mathbf{p}_R < 0$.

We assume the salvage value of pests and resistance is determined by the value of agricultural production in the seasons following $T - 1$:

$$\Omega_T = \mathbf{w}(N_T, R_T). \quad (4)$$

More pests will reduce future production such that the salvage value will be decreasing in the size of the pest population, $\mathbf{w}_N < 0$. Greater susceptibility will improve future production, but only if new technology relies on susceptibility to the original toxin for control. For example, if the new technology supplements original toxins with novel toxins, remaining susceptibility will influence the effectiveness and durability of the new technology. Alternatively, if novel toxins replace original toxins, remaining susceptibility

will not affect future production provided new technology is better than existing technology.⁵ Therefore, the salvage value will be non-increasing in resistance, $\mathbf{w}_R \leq 0$.

Given initial values for pests and resistance, N_0 and R_0 , the optimal dynamic time path for refuge, maximizes

$$\sum_{t=0}^{T-1} \mathbf{d}^t \Pi_t + \Omega_T = \sum_{t=0}^{T-1} \mathbf{d}^t \mathbf{p}(\mathbf{f}_t, N_t, R_t) + \mathbf{d}^T \mathbf{w}(N_T, R_T), \quad (5)$$

subject to $1 \geq \mathbf{f}_t \geq 0$ and equations (1) and (2) for $t = 0, \dots, T-1$ where \mathbf{d} is the discount factor. Because the new technology considered is better than the existing technology, it is optimal to introduce it immediately; then attention can focus on the fixed-time, free-state solution.

For an interior solution, the current value Hamiltonian is

$$\tilde{H} = \Pi_t(\mathbf{f}_t, N_t, R_t) + \mathbf{d} \mathbf{l}_{t+1} n(\mathbf{f}_t, N_t, R_t) + \mathbf{d} \mathbf{m}_{t+1} r(\mathbf{f}_t, R_t). \quad (6)$$

Note that the first Lagrange multiplier, \mathbf{l}_{t+1} , reflects the shadow value of pests, while the second, \mathbf{m}_{t+1} , reflects the shadow value of pest resistance. First-order conditions are

$$\frac{\partial \tilde{H}}{\partial \mathbf{f}_t} = \frac{\partial \Pi}{\partial \mathbf{f}_t} + \mathbf{d} \mathbf{l}_{t+1} \frac{\partial n}{\partial \mathbf{f}_t} + \mathbf{d} \mathbf{m}_{t+1} \frac{\partial r}{\partial \mathbf{f}_t} = 0, \quad \text{for } t = 0, \dots, T-1, \quad (7)$$

$$\mathbf{d} \mathbf{l}_{t+1} - \mathbf{l}_t = -\frac{\partial \tilde{H}}{\partial N_t} = -\frac{\partial \Pi}{\partial N_t} - \mathbf{d} \mathbf{l}_{t+1} \frac{\partial n}{\partial N_t}, \quad \text{for } t = 0, \dots, T-1, \quad (8)$$

$$\mathbf{d} \mathbf{m}_{t+1} - \mathbf{m}_t = -\frac{\partial \tilde{H}}{\partial R_t} = -\frac{\partial \Pi}{\partial R_t} - \mathbf{d} \mathbf{l}_{t+1} \frac{\partial n}{\partial R_t} - \mathbf{d} \mathbf{m}_{t+1} \frac{\partial r}{\partial R_t}, \quad \text{for } t = 0, \dots, T-1, \quad (9)$$

$$N_{t+1} - N_t = \frac{\partial \tilde{H}}{\partial (\mathbf{d} \mathbf{l}_{t+1})} = n(\mathbf{f}_t, N_t, R_t), \quad \text{for } t = 0, \dots, T-1, \quad (10)$$

$$R_{t+1} - R_t = \frac{\partial \tilde{H}}{\partial (\mathbf{d} \mathbf{m}_{t+1})} = r(\mathbf{f}_t, R_t), \quad \text{for } t = 0, \dots, T-1, \quad (11)$$

$$\mathbf{l}_T = \frac{\partial \Omega}{\partial N_T}, \quad (12)$$

and

$$\mathbf{m}_T = \frac{\partial \Omega}{\partial R_T}. \quad (13)$$

To understand the factors determining the optimal refuge, it is useful to first evaluate shadow values of pests and resistance. Combining equations (8) and (12) recursively yields the shadow value of pests:

$$\mathbf{l}_t = \sum_{k=t}^{T-1} \mathbf{d}^{k-t} \frac{\partial \Pi_k}{\partial N_t} + \mathbf{d}^{T-t} \frac{\partial \Omega_T}{\partial N_t}. \quad (14)$$

Assuming $\partial \Pi_t / \partial N_t < 0$, $\partial N_{t+1} / \partial N_t > 0$, and $\partial \Omega_T / \partial N_T < 0$ for $t = 0, \dots, T-1$ implies the shadow value of pests in season t is negative, $\mathbf{l}_t < 0$. Combining equations (9) and (13) recursively yields the shadow value of resistance:

$$\mathbf{m}_t = \sum_{k=t}^{T-1} \left\{ \mathbf{d}^{k-t} \frac{\partial \Pi_k}{\partial R_t} + \mathbf{d}^{k-t+1} \frac{\partial N_{k+1}}{\partial R_t} \mathbf{l}_{k+1} \right\} + \mathbf{d}^{T-t} \frac{\partial \Omega_T}{\partial R_t}. \quad (15)$$

Assuming $\partial \Pi_t / \partial R_t < 0$, $\partial R_{t+1} / \partial R_t > 0$, $\partial N_{t+1} / \partial R_t > 0$, $\mathbf{l}_t < 0$, and $\partial \Omega_T / \partial R_T < 0$ for $t = 0, \dots, T-1$ implies the shadow value of resistance in season t is also negative, $\mathbf{m}_t < 0$.

These results are intuitively appealing as pests and resistance serve to reduce production.

The marginal condition in equation (7) can now be written as

$$-\frac{\partial \Pi_t}{\partial \mathbf{f}_t} - \mathbf{d} \mathbf{l}_{t+1} \frac{\partial N_t}{\partial \mathbf{f}_t} = \mathbf{d} \mathbf{m}_{t+1} \frac{\partial R_t}{\partial \mathbf{f}_t}, \quad \text{for } t = 0, \dots, T-1. \quad (16)$$

The left-hand side of equation (16) reflects the marginal cost of increasing refuge. The first expression represents direct cost; the second represents indirect cost. The direct cost of increasing refuge is a decrease in current production because less of the crop is protected. The indirect cost represents the reduction in future production. Increasing refuge increases pest survival, which means there will be more pests to contend with in

the future. Equation (14) details the negative impact of increasing pest survival today on future production, that is, the shadow value of the pest population at each point in time.

The right-hand side of equation (16) captures the marginal benefit of increasing refuge. Increasing refuge decreases resistance. Equation (15) shows that there are two components to this indirect benefit. First, decreasing resistance improves control,

reducing crop losses and increasing production: $\sum_{k=t}^{T-1} \mathbf{d}^{k-t} (\partial \Pi_k / \partial R_t) + \mathbf{d}^{T-t} (\partial \Omega_T / \partial R_t)$.

Second, improved control has the cascading effect of lowering future pest pressure

further, reducing crop loss and increasing production: $\sum_{k=t}^{T-1} \mathbf{d}^{k-t+1} (\partial N_{k+1} / \partial R_t) \mathbf{l}_{k+1}$.

The optimal proportion of refuge in season t equates the marginal direct and indirect costs of having less of the crop protected by Bt to the indirect benefit of improved control in the future for the protected crop. Analytically characterizing the optimal dynamic path is difficult. From equations (14) and (15), the time paths of the co-state variables are

$$\mathbf{d} \mathbf{l}_{t+1} - \mathbf{l}_t = -\frac{\partial \Pi_t}{\partial N_t} - \mathbf{d}^{T-t} \frac{\partial \Omega_T}{\partial N_{t+1}} \frac{\partial n(\mathbf{f}_t, N_t, R_t)}{\partial N_t}, \quad (17)$$

and

$$\mathbf{d} \mathbf{m}_{t+1} - \mathbf{m}_t = -\frac{\partial \Pi_t}{\partial R_t} - \mathbf{d} \frac{\partial N_{t+1}}{\partial R_t} \mathbf{l}_{t+1} - \mathbf{d}^{T-t} \frac{\partial \Omega_T}{\partial R_{t+1}} \frac{\partial r(\mathbf{f}_t, N_t, R_t)}{\partial R_t}, \quad (18)$$

which are ambiguous. However, if we abstract from the effect of the backstop and assume the new technology is independent of the existing technology for simplicity, the change in the current shadow value of pests and resistance over time is positive at the optimum, which means the absolute value of pests and resistance is decreasing. If the absolute shadow value of pests decreases over time, all else equal, the marginal cost of increasing refuge in equation (16) falls, suggesting that more refuge is optimal. On the other hand, if the absolute shadow value of resistance decreases over time, all else equal, the marginal benefit of increasing refuge in equation (16) falls, suggesting that less refuge is optimal. Due to these opposing effects, it is not possible to analytically characterize the

optimal time path for refuge without more restrictive assumptions on the evolution of pests and resistance even without including the impact of the backstop technology.

An Application

Even with a rather parsimonious model, it is not possible to characterize analytically the optimal path of refuge because increasing refuge leaves more of the crop unprotected and increases future pest pressure, but it also slows resistance, improving future control on protected crop and decreasing future pest pressure. Ultimately, the question of which of these effects dominates is an empirical one. We explore this question by evaluating the optimal path of refuge for a typical continuous corn region in the North Central United States assuming Bt corn is planted to control the ECB.

The ECB is a mobile diploid⁶ pest whose reproduction produces as many as four generations a season. Southern, warmer climates experience three to four generations, while more temperate northern climates face one to two generations. A bivoltine (two-generation) population is typical for most of the North Central United States. (Mason et al.).⁷

The development of resistance is a function of natural selection caused by the use of Bt. Bt corn currently uses a single toxin. Resistance to this toxin is assumed to be conferred by a single allele that is not sex linked. Thus, an allele can be either resistant (r) or susceptible (s). Each parent contributes an allele, so the offspring's gene, the combination of alleles contributed by its parents, will be determined as shown in Table 1. The frequency with which parents are homozygote resistant (rr), heterozygote (rs), or homozygote susceptible (ss) determines the probabilities of the offspring's genotype. Bt corn produces a high dose of toxin and is believed to kill all the ss and almost all the rs pests throughout the season. The evolution of resistance depends on the initial frequency of resistant alleles and on the genotypic survival rates, which in turn depend on whether the crop is Bt or refuge.

The backstop technology we model uses two toxins and therefore affects two genes, a and b . We discuss two possible scenarios. In the first, one of the toxins is the original toxin. In the second, two new toxins are introduced. This allows us to quantify the effect of a positive value of susceptibility to the original toxin in the salvage function. We

TABLE 1. Possible offspring genotypes given mother's and father's genotypes

	Father	<i>rr</i>		<i>rs</i>		<i>ss</i>	
Mother	Alleles	<i>r</i>	<i>r</i>	<i>r</i>	<i>s</i>	<i>s</i>	<i>s</i>
<i>rr</i>	<i>r</i>	<i>rr</i>	<i>rr</i>	<i>rr</i>	<i>rs</i>	<i>rs</i>	<i>rs</i>
	<i>r</i>	<i>rr</i>	<i>rr</i>	<i>rr</i>	<i>rs</i>	<i>rs</i>	<i>rs</i>
<i>rs</i>	<i>r</i>	<i>rr</i>	<i>rr</i>	<i>rr</i>	<i>rs</i>	<i>rs</i>	<i>rs</i>
	<i>s</i>	<i>rs</i>	<i>rs</i>	<i>rs</i>	<i>ss</i>	<i>ss</i>	<i>ss</i>
<i>ss</i>	<i>s</i>	<i>rs</i>	<i>rs</i>	<i>rs</i>	<i>ss</i>	<i>ss</i>	<i>ss</i>
	<i>s</i>	<i>rs</i>	<i>rs</i>	<i>rs</i>	<i>ss</i>	<i>ss</i>	<i>ss</i>

define $\mathbf{r}_g = [r^{rr}_g, r^{rs}_g, r^{ss}_g]$ as the survival rate of resistant and susceptible homozygotes and heterozygotes for gene $g = a, b$ and crop i where $i = 0$ for the Bt and 1 for the refuge crop. Following Hurley, Babcock, and Hellmich, we assume $\mathbf{r}_{a0} = \mathbf{r}_{b0} = [1.0, 0.0, 0.02]$ and $\mathbf{r}_{a1} = \mathbf{r}_{b1} = [1.0, 1.0, 1.0]$. This implies that the two toxins are equally effective in the elimination of pests. Hurley, Babcock, and Hellmich consider a single gene model and assume that the initial frequency of resistant alleles is 3.2×10^{-4} . We assume that the initial frequency of resistant alleles is the same for both genes and equal to 3.2×10^{-4} .

A gamete represents the combination of alleles a parent contributes to its offspring for each gene. With a single gene there are two possible gametes: r and s . With two genes, there are four possible gametes: $r|r$, $r|s$, $s|r$, and $s|s$. Therefore, we define R_g as a 1×4 vector of the proportion of each type of gamete at the beginning of generation g : $[R^{r|r}_g, R^{r|s}_g, R^{s|r}_g, R^{s|s}_g]$. The initial gamete proportions are $R_0 = [1.0 \times 10^{-7}, 3.2 \times 10^{-4}, 3.2 \times 10^{-4}, 0.9993]$. The initial gamete proportions at T when two new toxins are introduced are $R_T = [1.0 \times 10^{-7}, 3.2 \times 10^{-4}, 3.2 \times 10^{-4}, 0.9993]$. When a new toxin is added to supplement an existing toxin, R_T will depend on how much resistance remains for the first toxin. The dynamics of resistance with two genes are detailed in Appendix A.

To capture the change in ECB from one generation to the next, we adopt the modified logistic growth model,

$$N_{g+1} = \mathbf{b}_{0g} + \mathbf{b}_{1g} \mathbf{r}_g N_g + \mathbf{b}_{2g} (\mathbf{r}_g N_g)^2 + \mathbf{r}_g N_g, \quad (19)$$

used by Hurley, Babcock, and Hellmich, where \mathbf{b}_{0g} , \mathbf{b}_{1g} , and \mathbf{b}_{2g} are parameters to estimate, \mathbf{r}_g is the survival rate of the ECB in generation g , and N_g is the number of pests

at the beginning of generation g . Note $r_g N_g$ reflects the number of pests that survive in generation g . The traditional logistic growth model is modified with b_{0g} , which, when positive, eliminates the possibility of eradicating the ECB. The reason for the choice of this growth function is that Hurley, Babcock, and Hellmich show that the high efficacy of Bt corn results in near eradication or heavy suppression of ECB with a conventional logistic growth function. Many entomologists express skepticism about such a result; therefore, the modified growth function is used to test the sensitivity of results to the degree of pest suppression.

We define the current value of agricultural production between period T_1 and T_2 as the average annualized net revenues per acre for Bt and refuge corn:

$$\Pi(T_1, T_2) = \frac{\sum_{t=T_1}^{T_2} d^{t-T_1} \left\{ (1-f_t) [pY(1-D_t^0) - C^0] + f_t [pY(1-D_t^1) - C^1] \right\}}{\sum_{t=T_1}^{T_2} d^{t-T_1}} \quad (20)$$

where Y is equal to the pest-free yield, p is equal to the real price of corn, D_t^i is the proportion of pest-free yield lost to the ECB on crop i in season t , and C^i is the cost of production for crop i . The proportion of yield loss is defined explicitly as $D_t^i = \text{Min}[1.0, r_{2t+1}N_{2t+1}d^2 + r_{2t}N_{2t}d^1]$, where d^1 and d^2 are the constant yield loss per pest for first- and second-generation ECB.

Using equation (20), we define the value function as $\Pi_t = \Pi(0, T-1)$ and the salvage value as

$$\Omega_T = (1/1-d) \text{Max}_{f_t} \left\{ \Pi(T, T') \mid 1.0 \geq f_t = f_T \geq 0.0, N_{t+1} = n(f_t, N_t, R_t) + N_t, \text{ and } R_{t+1} = r(f_t, R_t) + R_t \forall t \in [T, T'] \right\}$$

Thus, the value function reflects the annualized present value of production between the initial season and season $T-1$. The salvage value reflects the value of a stream of income equal to the annualized value of the new technology for $T'-T$ years when an optimal static refuge is used to manage resistance. Our salvage value assumes a new technology arrives every $T'-T$ season to restore the efficacy of pest control as resistance develops to the current pest control technology. We use an optimal static refuge to calculate

the salvage value of the new technology to reduce the computational burden of solving the model and because our results suggest that an optimal static refuge provides a good approximation to the optimal dynamic refuge.

Having parametrically specified the evolution of resistance, the ECB population dynamics, the value function, and the salvage function, we now choose benchmark parameters. Table 2 presents the benchmark configuration for all but the population dynamics. Table 3 presents estimated parameters for two alternative population models.

National Agricultural Statistical Service (NASS) and Economic Research Service (ERS) data provide values for the real price, pest-free yield, and production cost of refuge corn (USDA-NASS). The real price of corn, \$2.35, is the monthly average from 1991 to 1996 deflated to 1992.⁸ The average Iowa yield from 1991 to 1996 was about 123 bushels per acre. Assuming an average annual ECB yield loss of 6.4 percent (Calvin) implies that the pest-free yield is 130 bushels per acre. Excluding returns to management, the average production cost, \$185, comes from 1995 ERS corn budgets deflated to 1992 prices. The interest rate used for discounting is 4 percent.

The pest-free yield and production cost of Bt corn is the same as refuge. We are unaware of studies showing a significant difference in Bt and conventional corn yields in the absence of the ECB. While farmers typically pay a \$7 to \$10 per acre technology fee for Bt seed, this premium does not reflect an increase in the marginal cost of growing Bt corn from a social perspective. Once Bt is introduced into corn, the cost of producing Bt and conventional corn seed stock is essentially identical. Given that research and development costs for Bt corn are sunk, the technology fee reflects an economic rent for using Bt technology.

Hurley, Babcock, and Hellmich consider two specifications for the population model and find very different results. We explore the same two specifications. The first assumes that population growth follows a logistic curve with no intercept: $b_{0g} = 0$. In this case, in the absence of pest resistance, eradication is possible. When pest resistance develops, heavy ECB suppression results instead of eradication. The second specification estimates a positive intercept for the growth curve: $b_{0g} > 0$. Therefore, eradication is not possible even with susceptible pests, while when resistance has developed, ECB suppression is light. The biological difference between heavy and light suppression is the amount of

TABLE 2. Benchmark parameter values

Parameter	Existing Technology	New Technology
Economic Parameters		
Years	15	15
Discount rate	$1/(1+0.04)$	$1/(1+0.04)$
Price of corn (\$/bushel)	\$2.35	\$2.35
Pest-free yield (bushels/acre)	130	130
Production cost (\$/acre)	\$185	\$185
First generation constant marginal yield loss (pests/plant)	0.055	0.055
Second generation constant marginal yield loss (pests/plant)	0.028	0.028
Biological Parameters		
Initial pest population (pests/plant)	0.23	N_{15}
Recombination factor	0.5	0.5
Initial gamete proportions (r_0')	$\begin{bmatrix} 1.0 \times 10^{-7} \\ 3.2 \times 10^{-4} \\ 3.2 \times 10^{-4} \\ 0.9993 \end{bmatrix}$	R_{15}
Gene a		
Refuge survival rates for all genotypes	1.00	1.00
Survival rate of resistant homozygotes on Bt corn	1.00	1.00
Survival rate of susceptible homozygotes on Bt corn	0.00	0.00
Survival rate of heterozygotes on Bt corn	0.02	0.02
Gene b		
Refuge survival rates for all genotypes	1.00	1.00
Survival rate of resistant homozygotes on Bt corn	1.00	1.00
Survival rate of susceptible homozygotes on Bt corn	1.00	0.00
Survival rate of heterozygotes on Bt corn	1.00	0.02

TABLE 3. European corn borer population model parameters

Parameters	First Generation		Second Generation	
	Heavy Suppression	Light Suppression	Heavy Suppression	Light Suppression
Constant	0.000	0.028	0.00	0.26
Previous population	-0.757	-0.802	7.76	5.96
Previous population squared	-0.053	-0.040	-10.30	-8.13
Equilibrium population without Bt corn (pest/plant)	0.248	0.227	1.54	1.43
Calibration factor	1.01		0.97	

Note: Population parameters are adopted from Hurley, Babcock, and Hellmich.

time it takes low ECB populations to return to carrying capacity. This amount of time is longer with heavy suppression.

Hurley, Babcock, and Hellmich estimate different parameters for first- and second-generation ECB using data reported in Calvin. These parameter estimates are given in Table 3. The calibration factors that are also reported assure that the steady-state ECB population is comparable across specifications when no pest control is used.

The constant marginal damage rates for first- and second-generation ECBs, 0.055 and 0.028, are taken from Ostlie, Hutchison, and Hellmich. Combined with the equilibrium populations, the implied average annual yield loss is 5.3 percent, which is 20 percent lower than the 6.4 percent reported in Calvin.

The final parameter to specify is the length of the planning horizon for assessing the benefits and costs of resistance management. A fifteen-year planning horizon is used to conform to the 1998 EPA scientific advisory and International Life Sciences and Health and Environmental Sciences Institute (ILSI/HESI) panel reports (EPA 1998b; ILSI/HESI).

The model is implemented in C++ and solved using numerical optimization routines adopted from Press et al. It is important to note that the biological processes used to characterize resistance do not guarantee the satisfaction of second-order sufficiency conditions for a global optimum. Therefore, there is no guarantee that a numerical

solution is globally optimal. Assuring a global optimum is computationally infeasible, so we use a range of starting values with the optimization routine to increase the robustness of the results.

Results

An analytical characterization of the optimal dynamic path for refuge is generally not possible. Increasing refuge has both a negative and positive impact. The negative impact is a reduction in current production and increased ECB pressure in the future. The positive impact is the preservation of ECB susceptibility that affords better control and reduced ECB pressure in the future. Adding more structure and solving the model with parameter values found in the literature allows us to explore which of these countervailing effects tends to dominate and when.

Our results focus on four scenarios. We consider two alternative population models. The first assumes that ECB suppression is light, while the second assumes that suppression is heavy. We also consider two distinct salvage functions. The first assumes that resistance to the new technology is independent of the current technology because two novel toxins replace the existing toxin and there is no cross-resistance. The second assumes that resistance to the new technology is dependent on the current technology because the original toxin is supplemented with a novel toxin. It is important to note that while resistance to the new technology will be either dependent or independent, the value of the new technology always depends on the old one, as the number of ECBs when the new technology arrives depends on how the old technology is used. Combining the alternative population models with the alternative salvage functions yields the four scenarios.

Before interpreting the results, it is useful to summarize the optimal dynamic path for refuge, resistance, and ECB for each scenario, while highlighting important similarities and differences. Figure 1 reports the optimal dynamic refuge. The first interesting result is the consistent pattern for all scenarios. In the initial period, the optimal refuge is relatively low. It increases sharply in the second period, before a series of more moderate increases. Eventually, the optimal refuge begins to decrease, typically at an increasing rate. While this pattern is similar for all scenarios, there are notable differences. The

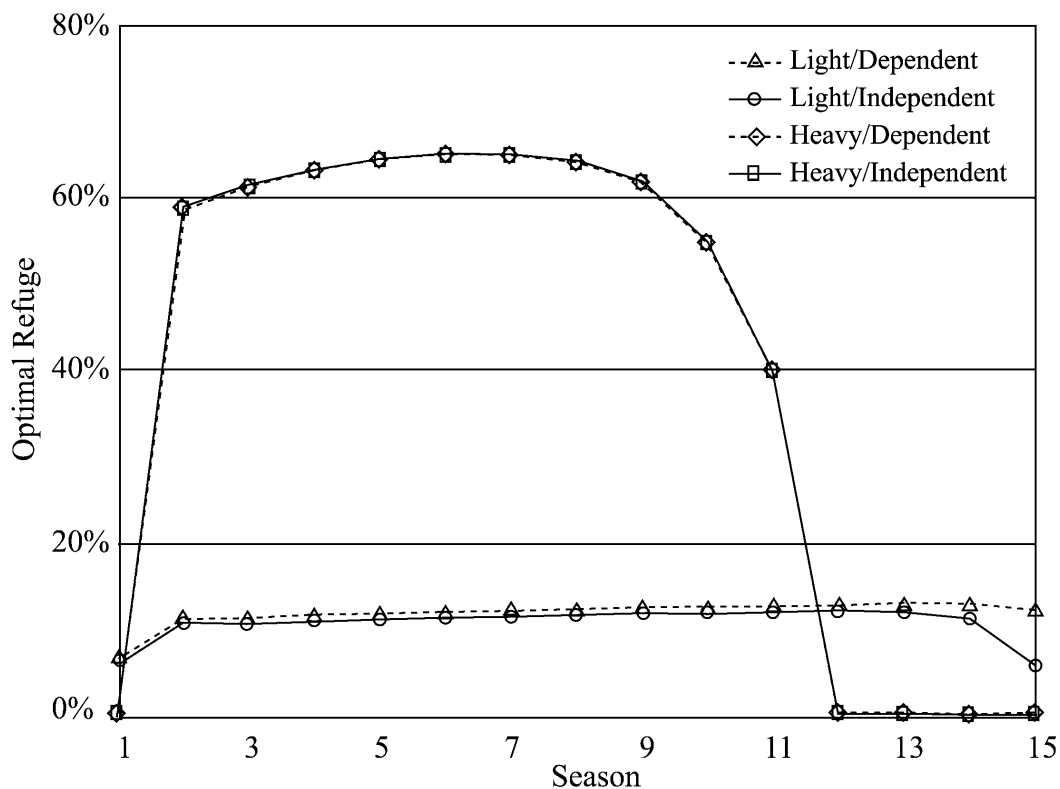


FIGURE 1. Optimal dynamic refuge

pattern is more exaggerated with heavy suppression. With heavy suppression, the optimal refuge does not depend on whether the new technology is independent or dependent. When suppression is light, on the other hand, it is optimal to have more refuge if the new technology is dependent. This difference becomes more pronounced as the introduction of the new technology nears.

Figure 2 illustrates how the characteristics of the optimal time path for resistance differ substantially depending on whether suppression is light or heavy. When suppression is light, the optimal resistance for the original toxin increases at an increasing rate. The rate of increase is faster when resistance to the new technology is independent. But even when the new technology is independent, it is not optimal to fully exhaust susceptibility. On the other hand, when suppression is heavy, the optimal evolution of resistance is sigmoidal. Initially, resistance increases at an increasing rate. Later, it increases at a decreasing rate until susceptibility is fully exhausted. With heavy

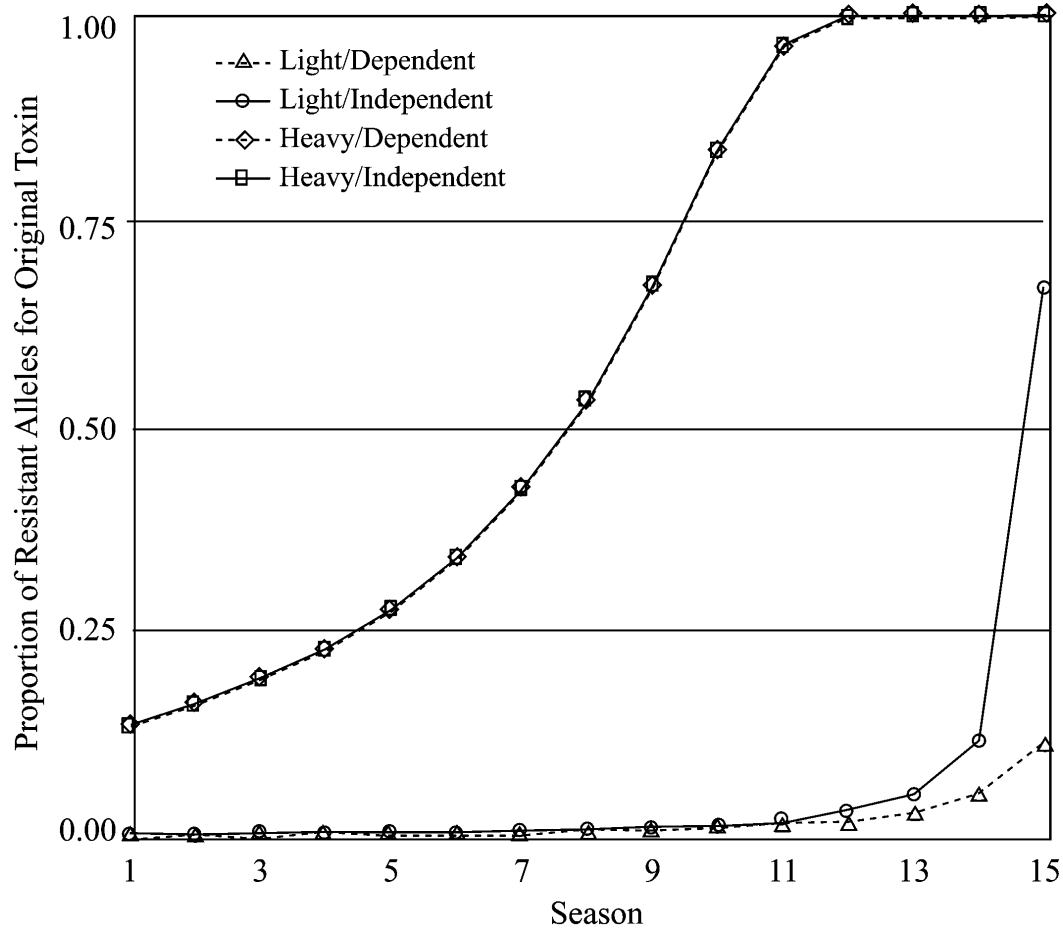


FIGURE 2. Optimal dynamic resistance

suppression, the evolution of resistance is not affected by whether resistance to the new technology is dependent or independent.

As with the optimal dynamic refuge, the optimal dynamic ECB population (Figure 3) for each scenario follows a similar pattern. The population rapidly declines in the first two periods. It then levels off and begins to increase. The increase is more pronounced as the introduction of the new technology nears. Despite these similarities, there are several notable differences. First, populations are substantially lower (by two to three orders of magnitude) with heavy suppression. Also, with heavy suppression, it takes longer for the population to recover, and the type of new technology does not matter. When suppression is light, the population immediately begins to recover and the

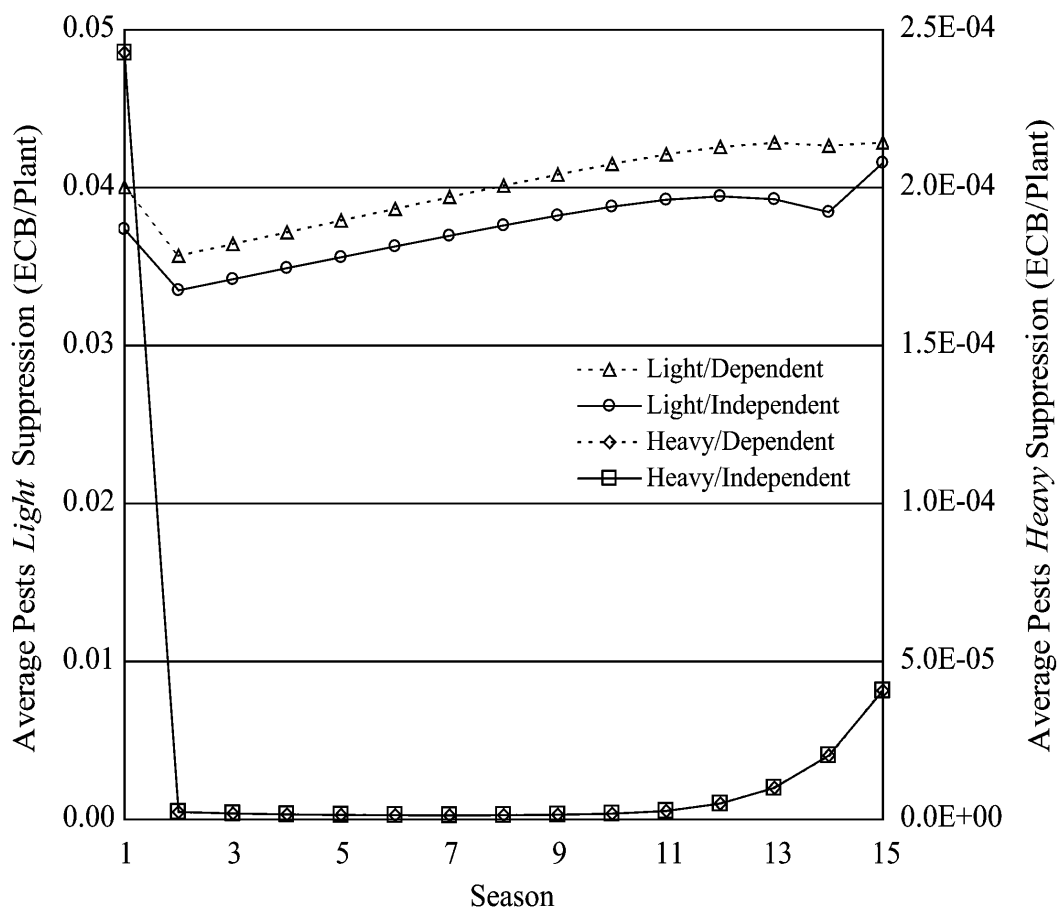


FIGURE 3. Optimal dynamic pest population

type of new technology does matter. The optimal population is always lower when the new technology is independent.

Equation (16) provides the intuition for understanding the general pattern of the optimal dynamic refuge in Figure 1. Increasing refuge reduces the current value of production and tends to increase pest pressure in the future, but it also increases susceptibility, which allows for better control and reduces future pest pressure. Because the starting value for ECB is the carrying capacity, the initial level of ECB pressure is high and the marginal cost of refuge in terms of reduced yield is high relative to the marginal benefit of managing resistance. Figure 3 shows that the initial emphasis on control reduces the ECB population substantially. Once there are few pests left to control, the marginal cost of refuge decreases relative to the marginal benefit of managing resistance, and more refuge is optimal. As the pest population begins to recover, the

marginal cost of refuge increases once again. Additionally, as the arrival of the new technology nears, the value of susceptibility diminishes, particularly when the new technology is independent. With the marginal cost of refuge increasing and the marginal benefit of refuge declining, less refuge is again optimal.

Resistance management has different characteristics according to the resilience of the pest population. Susceptibility is more valuable with light than with heavy suppression. Figure 4 illustrates why by showing how fast the pest population recovers to carrying capacity after a reduction by four orders of magnitude. It takes three years for the population to exceed one ECB per plant and seven years to return to carrying capacity with light suppression. With heavy suppression, it takes fourteen years to exceed one ECB per plant and twenty years to return to carrying capacity. Therefore, with light

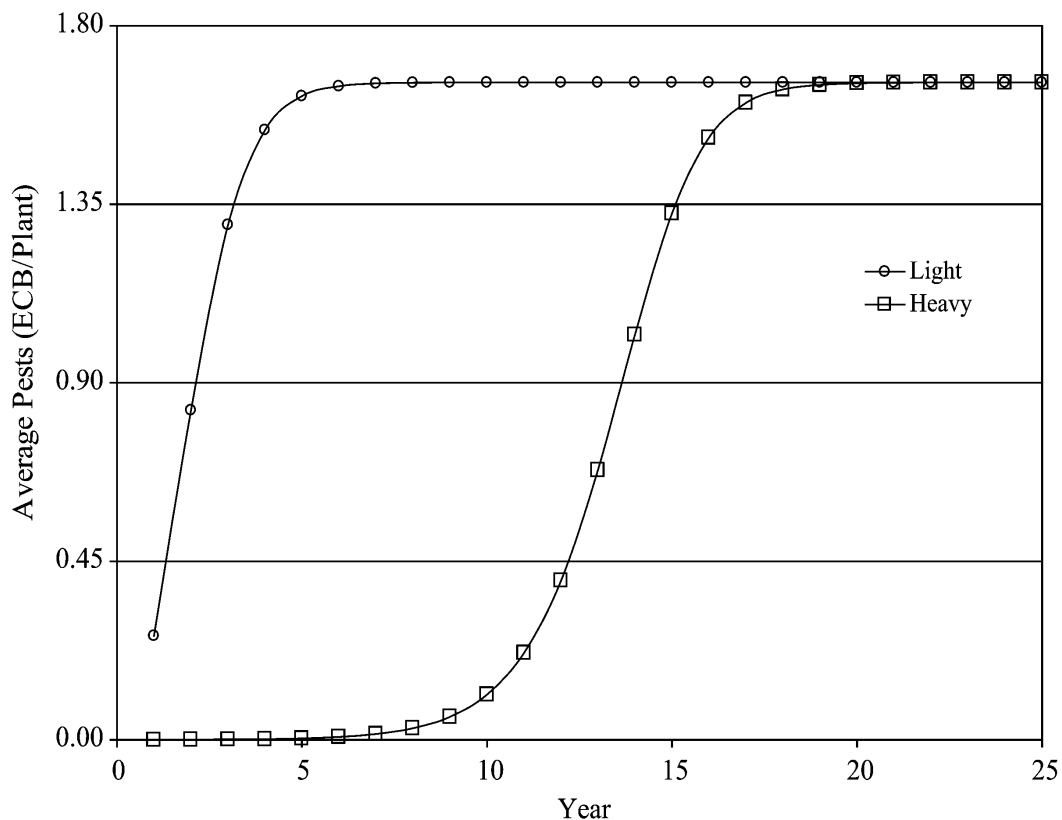


FIGURE 4. Comparison of the recovery rate of pests for light and heavy suppression models

suppression, economically important levels of pest population can return in just three years after the evolution of resistance, while it takes over ten years with heavy suppression.

Hurley, Babcock, and Hellmich argue that when suppression is heavy, refuge is a high-fixed–low-marginal cost input. The situation is reversed when suppression is light: refuge is a low-fixed–high-marginal cost input. Therefore, when suppression is heavy, it is optimal to do no resistance management or to carry out intensive resistance management depending on whether there are a large number of ECBs to control. When suppression is light, the best strategy is to do some resistance management all of the time, but not as much as when suppression is heavy because there will always be more ECBs to control and a higher marginal cost. The results in Figure 1 are described well by this argument.

Figure 2 shows it is optimal to exhaust susceptibility with heavy suppression, even when the new technology is dependent.⁹ When suppression is heavy, the dependence of the new technology on the current toxin does not matter because it is not optimal to maintain susceptibility until the new technology arrives. Since the ECB can be brought to near extinction, it is optimal to do so by exhausting susceptibility regardless of the characteristics of the backstop.

Conversely, it is not optimal to fully exhaust susceptibility when suppression is light, even if the technology is independent.¹⁰ This result is justified by the biological constraints on exhaustion and the fact that the value of susceptibility is linked inextricably to controlling the ECB. Because of the biological processes governing the evolution of resistance, planting no refuge right before the introduction of the new technology does not necessarily exhaust susceptibility. To fully exhaust susceptibility, less refuge must be planted over a period of time. Planting less refuge over time imposes an implicit cost because resistance evolves sooner, thereby increasing pest pressure and reducing the value of production. When the cost of resistance is high, it is not optimal to fully exhaust susceptibility by planting less refuge over time. This extraction cost is higher when there are multiple generations of a pest in a season because any resistance that develops during the first generation reduces control in subsequent generations, and it is not possible to offset increased resistance by adjusting refuge during the season.

Therefore, it is optimal to plant refuge even in the season before the introduction of a new technology. Sensitivity analysis shows that with a single generation of pests per season, it is not optimal to plant refuge in the season before the introduction of an independent new technology, but it still may not be optimal to exhaust susceptibility because of the implicit extraction cost.¹¹

Figure 1 shows that over time, the proportion of refuge that maximizes the long-run value of production changes in response to changes in the value of susceptibility and ECB control. Therefore, holding the proportion of refuge static over time will reduce the value of production. To understand the cost of using a second-best static refuge for resistance management, Table 4 reports the annualized net present value of production for the optimal dynamic refuge, optimal static refuge, and for the case where Bt corn is never introduced. It also reports the optimal size of a static refuge.

Table 4 shows that the annualized value of Bt corn in all our scenarios is about \$7.00 an acre, which represent just over a 6 percent increase in the value of production. What is more interesting is the difference in the value of production between the optimal dynamic and static refuge for all four scenarios. With light suppression, the dynamic refuge increases the annualized value of production by about \$0.01 an acre when compared to the optimal static refuge regardless of whether the new technology is dependent or independent. This difference represents less than 0.1 percent of the value of production and less than 0.25 percent of the value of Bt corn. With heavy suppression, the difference is essentially zero.

TABLE 4. Dynamic versus static optima

Salvage Function	Suppression	Dynamic Optimum	Static Optimum		Without Bt Corn
		Value of Production	Value of Production	Refuge	Value of Production
		<i>\$/Acre</i>		<i>Percent</i>	<i>\$/Acre</i>
Independent	Light	\$120.34	\$120.33	10.6	\$113.36
	Heavy	\$120.50	\$120.50	0.2	\$113.36
Dependent	Light	\$120.32	\$120.31	11.5	\$113.36
	Heavy	\$120.50	\$120.50	0.2	\$113.36

Optimally varying refuge over time provides few benefits when compared to a second-best static refuge regardless of whether suppression is heavy or light or whether the new technology is dependent or independent of the current technology. This result is due to the effectiveness with which Bt corn controls the ECB. When suppression is heavy, the effectiveness of Bt corn allows the immediate and near eradication of the ECB. This is accomplished by planting almost no refuge in the first year. After that, how much refuge is planted has a little effect on the value of production because the ECB is not able to reestablish itself and cause appreciable damage before the new technology arrives. When suppression is light, planting a modicum of refuge until the new technology arrives maintains resistance to levels that are low enough for Bt corn to still provide greater than 98 percent control. Comparing the optimal dynamic and static refuge reveals there is little difference in the two strategies, with the exception of the initial period and the period right before the introduction of the new technology. This and the high level of control (greater than 98 percent) explain the small difference in the value of production.

Conclusions

Bt corn is a valuable new tool for controlling the European corn borer. However, this value will be diminished if the European corn borer develops resistance to Bt. Therefore, the Environmental Protection Agency has mandated insect resistance management guidelines based on farmers planting a proportion of their corn acreage to refuge—corn that does not use Bt for pest control. Refuge slows the proliferation of resistance by making more susceptible ECBs available to mate with resistance ECBs. So far, models used to guide EPA policy have focused on static recommendations and have not considered how the introduction of new technologies affects the value of resistance management. We explore how varying refuge optimally over time can increase the value of resistance management. We also consider how refuge requirements should account for pest population dynamics and the introduction of new technologies.

The results of our analysis show that varying refuge does improve the benefits of resistance management by accounting for the increased scarcity and diminished control

as resistance develops. These opposing effects make it optimal to require less refuge when Bt corn is first introduced, more refuge once pests are better controlled and resistance starts to emerge, and less refuge as the introduction of a new technology nears. However, the improvement offered by optimally varying refuge is modest when compared to an optimal static refuge.

The population dynamics of the ECB are an important determinant of the optimal refuge. If the ECB population recovers rapidly once resistance emerges, refuge is a low-fixed-high-marginal cost input. Some resistance management will always be optimal, but too much will not provide adequate pest control. If the ECB population recovers slowly once resistance emerges, refuge is a high-fixed-low-marginal cost input. No resistance management will be optimal when there is a high pest population to control. Alternatively, intensive resistance management is optimal when there are few ECBs to control.

We find that the affect of introducing a new technology on the optimal refuge depends on the population dynamics of the ECB. If the ECB recovers slowly, it is optimal to fully exhaust pest susceptibility regardless of the type of new technology being introduced. If the ECB recovers rapidly, the type of technology introduced impacts the optimal refuge. If the new technology depends on susceptibility to the old, relatively more refuge should be planted over time. When the ECB is buoyant, it is not typically optimal to exhaust susceptibility regardless of the backstop, because the evolution of resistance is biologically constrained and the value of susceptibility is linked inextricably to the value of pest control. These two factors impose an implicit extraction cost that tends to exceed the value of exhaustion.

The results of this analysis have policy and research implications. Recent survey data suggests farmers have been confused by the changes in refuge recommendations that took place before the EPA mandated resistance management for Bt corn in 2000.¹² This data indicates that there is an implicit cost associated with varying the size of refuge that could be avoided with a static policy. In light of these potential costs and the modest increase in the value of agricultural production provided by optimally varying refuge in response to scarcity and diminished control, a static policy that avoids these costs may be preferable.

Understanding the population dynamics of the ECB is important for resistance management, yet we are unaware of research currently underway to fill this gap in knowledge. Given the lack of information on the dynamics of ECB populations and other important parameters (e.g., the initial resistance frequency and the dominance of resistance), if new information reveals that current assumptions are unfounded, adjustments to refuge in response to this new information could be valuable. How and when refuge requirements should adjust to new information is an important question for future research.

The optimal dynamic refuge we explore assumes there is perfect control of the amount of refuge planted, but this is not the case. The EPA mandates refuge requirements, and growers choose whether or not to meet or exceed those requirements. Our model suggests that Bt corn may substantially reduce ECB populations. If growers pay extra to plant Bt corn, there may be substantial incentives to discontinue use after a few seasons. The rapid adoption of Bt corn slowed in 2000. There are several explanations for this result, one of which is the low number of ECBs experienced across much of the Midwest since the 1997 growing season. Grower adoption and de-adoption of Bt corn and compliance with refuge requirements will have a substantial impact on the efficacy of EPA policy. New models integrating the complexities of pest biology and human behavior will provide the EPA with more reliable information and improve resistance management policy.

Our model focuses on optimizing agricultural productivity, while ignoring conventional pesticides. In the region we model, conventional pesticides are seldom used because of high cost and poor efficacy. There are, however, regions where conventional pesticides are more important. In these regions, the EPA is also concerned about reducing the use of these pesticides because it believes they are more hazardous to the environment and to human health. Therefore, a useful extension of the model could include an evaluation of conventional pesticides and the objective of reducing their use.

Appendix A

Quantity R_g is a 1×4 vector of the proportion of each type of gamete at the beginning of generation g : $[R_g^{r|r}, R_g^{r|s}, R_g^{s|r}, R_g^{s|s}]$. The notation $\mathbf{r}_{ig} = [r_{ig}^{rr}, r_{ig}^{rs}, r_{ig}^{rs}, r_{ig}^{ss}]$ is the survival rate of resistant and susceptible homozygotes and heterozygotes for gene g on crop i where $i = 0$ for the Bt crop and $= 1$ for the refuge crop. It is also useful to define

$$\mathbf{P}_{ig} = (R_g \text{ ' } R_g) \times \begin{bmatrix} \mathbf{r}_{ig}^{rr} \mathbf{r}_{ig}^{rr} & \mathbf{r}_{ig}^{rr} \mathbf{r}_{ig}^{rs} & \mathbf{r}_{ig}^{rs} \mathbf{r}_{ig}^{rr} & \mathbf{r}_{ig}^{rs} \mathbf{r}_{ig}^{rs} \\ \mathbf{r}_{ig}^{rr} \mathbf{r}_{ig}^{rs} & \mathbf{r}_{ig}^{rr} \mathbf{r}_{ig}^{ss} & \mathbf{r}_{ig}^{rs} \mathbf{r}_{ig}^{rs} & \mathbf{r}_{ig}^{rs} \mathbf{r}_{ig}^{ss} \\ \mathbf{r}_{ig}^{rs} \mathbf{r}_{ig}^{rr} & \mathbf{r}_{ig}^{rs} \mathbf{r}_{ig}^{rs} & \mathbf{r}_{ig}^{ss} \mathbf{r}_{ig}^{rr} & \mathbf{r}_{ig}^{ss} \mathbf{r}_{ig}^{rs} \\ \mathbf{r}_{ig}^{rs} \mathbf{r}_{ig}^{rs} & \mathbf{r}_{ig}^{rs} \mathbf{r}_{ig}^{ss} & \mathbf{r}_{ig}^{ss} \mathbf{r}_{ig}^{rs} & \mathbf{r}_{ig}^{ss} \mathbf{r}_{ig}^{ss} \end{bmatrix} \quad (\text{A.1})$$

where \times indicates multiplication by element. The net survival rate on the i th crop in generation g is $\mathbf{r}_{ig} = I_4 \text{ ' } \mathbf{P}_{ig} I_4$ where I_4 is a 1×4 identity vector. The net survival rate in generation g and season t is $\mathbf{r}_g = (1 - \mathbf{f}_t) \mathbf{r}_{ig} + \mathbf{f}_t \mathbf{r}_{ig}$. Let $\mathbf{P}_g = [(1 - \mathbf{f}_t) \mathbf{r}_{0g} \mathbf{P}_{0g} + \mathbf{f}_t \mathbf{r}_{1g} \mathbf{P}_{1g}] / \mathbf{r}_g$. Extending the Hardy-Weinberg model with random mating (see Hartl), the evolution of resistance is characterized as

$$R_{g+1}^{x|y} = P^{x|y \ x|y}_g + P^{x|y \ x|y'}_g + P^{x|y \ x|y}_g + 0.5P^{x \ |y' \ x|y}_g + 0.5P^{x|y' \ x|y}_g \quad (\text{A.2})$$

for all $x, x', y,$ and $y' \in \{r, s\}$, $x \neq x'$, and $y \neq y'$ where $P^{z \ z'}_g$ represents the z row and z' column of \mathbf{P}_g .

Endnotes

1. This information was provided by the Agricultural Biotechnology Stewardship Technical Committee and compiled by Fulfillment Systems, Inc., 1999. The data is available from the authors upon request.
2. Two of the toxins, Cry 1ab and Cry 1ac, have the same mode of action and are considered the same. The toxin with a different mode of action, Cry 9c, has been removed from the market due to regulatory concerns.
3. The subscripts denote partial derivatives.
4. This objective is common among economic models of resistance management but differs from entomological models of resistance management.
5. This assumes that there is no cross-resistance between the original and novel toxins.
6. A diploid organism carries in the nucleus of each cell two sets of chromosomes, one from each parent.
7. In some areas, farmers can face two different strains of European corn borer. For instance, a farmer may face both a univoltine and bivoltine population. While not considered here, the model can be readily extended to such scenarios.
8. Depending on the rate of adoption of Bt corn and the refuge size, there could be supply-side price effects that are not included here.
9. Sensitivity analysis (available upon request) indicates that this result is robust even if the delay in the new technology is substantially shorter or the discount rate is much lower.
10. Sensitivity analysis (available upon request) shows that this result is robust for much larger discount rates and if the new technology is delayed much longer. However, with a long enough delay and a high enough discount rate, it does become optimal to exhaust susceptibility even when suppression is light (e.g., 50 years and a 20 percent interest rate).
11. This sensitivity analysis is available upon request.
12. Survey results provided by the Agricultural Biotechnology Stewardship Technical Committee and compiled by Marketing Horizons, Inc., in 2000 show that 26 percent of respondents thought that a minimum of a 5-15 percent refuge was mandated by the EPA, while 39 percent indicated they did not know the minimum amount of mandated refuge. A summary of survey results is available from the authors upon request.

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