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Managing European Corn Borer Resistance to Bt Corn with Dynamic Refuges

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Abstract

We develop a dynamic bioeconomic model of temporally optimal dynamic refuge recommendations for resistance management when a backstop technology arrives at a known date. The impact of the characteristics of the backstop on the use of the current technology, and the difference between static and dynamic refuges are examined.

Introduction

Bt corn is genetically engineered to produce one of many proteins found in the soil bacterium *Bacillus thuringiensis* (Bt). The protein is toxic when consumed by lepidopterous insects such as the European Corn borer (ECB), a significant pest estimated to cost U.S. corn 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 rapid and widespread adoption. Between 1996 and 2000, the percentage of corn acreage planted to Bt in the U.S. increased from practically zero to about 25 percent. In some cases, market penetration has been even higher. For example, in 1999, many counties in Illinois, Iowa, Minnesota, North Dakota, and South Dakota had more than 50 percent of corn planted to Bt varieties. The rapid widespread adoption of Bt corn raises concerns that the ECB may soon develop resistance. The Environmental Protection Agency (U.S. EPA, 1998a) has responded to these concerns by requiring farmers to plant a proportion of their acreage to refuge corn. Refuge slows the proliferation of resistance by allowing ECB that are susceptible to Bt to thrive and mate with resistant ECB emerging from Bt corn (EPA, 1998).

Previous studies provide rationale for the EPA's decision to require resistance management. Pests are a detrimental renewable resource because they propagate and damage crops (Hueth and Regev, Regev, Gutierrez, and Feder, and Regev, Shalit, and Gutierrez). Pest susceptibility (the converse of resistance) is a valuable resource because susceptible pests are controllable (Hueth and Regev, and Regev, Shalit, and Gutierrez). Capturing the value of susceptibility however increases resistance through natural selection, making pests less controllable in the future. Thus, there is a dynamic trade off in the use of pesticides.

The early literature characterized the dynamic optimal dose of pesticides for managing resistance. More recent literature explores the value of temporally static refuges for managing resistance (e.g. Alstad and Andow; Roush and Osmond; Gould; Onstad and Gould, 1998 a and b; Hurley *et al.*, 1999 and 2001; and Livingston *et al.*). The purpose of this paper is to (i) extend the literature on resistance management using refuge

to consider the type of dynamic optimum previously used to characterize pesticide dose and (ii) consider the sensitivity of this dynamic optimum to the introduction of a new technology that depend on the current technology.

Varying pesticide dose is optimal for managing resistance because the scarcity of susceptibility increases and the value of control decreases as resistance develops over time. While varying pesticide dose is not feasible with Bt corn because the pesticide is embedded in the crop, it is possible to vary pest exposure by varying the size of refuge. While previous results suggest varying refuge size will lead to more effective resistance management, it is not clear how much a dynamic refuge policy would improve the value of resistance management when compared to the type of static refuges currently evaluated in the literature.

All commercialized varieties of Bt corn rely on one of three toxins¹. However, the new varieties of Bt corn that are under development are likely to rely on more than one toxin. Resistance is thought to evolve slower when pests must overcome multiple toxins. Therefore, the introduction of multiple toxin varieties, may makes less refuge optimal. How much less is unclear and depends on the characteristics of the new technology.

The results of our analysis show that varying refuge does improve the benefits of resistance management by accounting for the increasing scarcity and decreasing value of control as resistance develops. These countervailing effects typically make it optimal to require less refuge when Bt corn is first introduced, more refuge once the pest is under control and resistance starts to emerge, and less refuge as the arrival of a new technology nears. However, the improvement offered by the optimal dynamic refuge is typically modest when compared to the optimal static refuge. Therefore, if there are additional costs associated with varying refuge requirements from year to year, a static policy could in fact be superior to a dynamic policy.

We also find that the characteristics of the new technology effect optimal resistance management. If the new technology simply supplements the existing technology by adding a second new toxin, maintaining susceptibility to original toxin has more value, such that it is optimal to require more refuge over time.

Alternatively, when the new technology replaces the existing technology with two new toxins, the value of susceptibility to the original toxin is diminished and it is optimal to plant less refuge over time.

Conceptual Model

Following Alstad and Andow, Roush and Osmond, Gould, Onstad and Gould (1998 a and 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 Bt variety that is toxic to pests. The second is a non-toxic refuge variety. The proportion of the refuge planted in season t is denoted by $1 \geq \phi_t \geq 0$. The proportion of resistant pests in season t is $1 \geq R_t \geq 0$ and the number of pests is $N_t \geq 0$. 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 will be available to mate with resistant pest. The change in susceptibility from one season to the next is:

$$(1) \quad R_{t+1} = r(\phi_t, R_t) + R_t.$$

Equation (1) assumes that size of the pest population does not effect the evolution of resistance, which is typical of genetic models used to evaluate resistance management. With more refuge, fewer pests are exposed to Bt slowing the evolution of resistance such that, if we denote derivatives with subscripts, r_ϕ is typically negative. Genetic models also typically imply that with all else equal increasing resistance today will increase resistance tomorrow: $r_R > 0$. Assuming susceptibility is nonrenewable implies $R_{t+1} \geq R_t$.

Surviving pest propagate, 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 :

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

¹ In 2001, only one of these toxins will likely be available due to various regulatory and market forces.

Planting more refuge decreases pest exposure to Bt increasing the rate of survival such that n_ϕ 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 such that n_N is positive. Increasing resistance decreases the effectiveness of Bt such that n_R is also positive. We assume the value of pests and pest susceptibility is determined by the value of agricultural production:

$$(3) \quad \Pi_t = \pi(\phi_t, N_t, R_t).$$

Since pest control on the Bt variety is better than on the refuge variety, increasing the proportion of refuge tends to decrease the value of agricultural production, $\pi_\phi < 0$, by decreasing the proportion of the crop that is protected against pests. Increasing pests increases yield loss, which will also decrease the value of agricultural production, $\pi_N < 0$. Increasing resistance increases survival rates and reduces pest control, which will decrease the value of agricultural production, $\pi_R < 0$.

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

$$(4) \quad \Omega_T = \omega(N_T, R_T).$$

More pests will reduce the value of future agricultural production such that the salvage value will be decreasing in pests, $\omega_N < 0$. Greater susceptibility will improve the value of future agricultural production, but only if new technology still relies on that susceptibility to the original toxin for control. For example, if the new technology adds novel toxins to the original toxins, remaining susceptibility will influence the effectiveness and durability of the new technology. Alternatively, if novel toxins completely replace the original toxins, remaining susceptibility

will have no impact on the future value of agricultural production provided that the new technology is better than the existing technology.² Therefore, the salvage value will tend to be non-increasing in resistance, $\omega_R \leq 0$.

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

$$(5) \quad \sum_{t=0}^{T-1} \delta^t \Pi_t + \Omega_T = \sum_{t=0}^{T-1} \delta^t \pi(\phi_t, N_t, R_t) + \delta^T \omega(N_T, R_T),$$

subject to $1 \geq \phi_t \geq 0$ and equations (2) and (1) for $t=0, \dots, T-1$ where δ is the discount factor. Since the new technology we consider will be strictly better than the existing technology, it is optimal to introduce it immediately. Therefore, we focus our attention on the fixed time, free state solution.

For an interior solution, the current value Hamiltonian is

$$(6) \quad \tilde{H} = \Pi_t(\phi_t, N_t, R_t) + \delta \lambda_{t+1} n(\phi_t, N_t, R_t) + \delta \mu_{t+1} r(\phi_t, R_t).$$

Note that the first Lagrange multiplier, λ_{t+1} , reflects the shadow value of pests, while the second, μ_{t+1} , reflects the shadow value of pest resistance. First order conditions are

$$(7) \quad \frac{\partial \tilde{H}}{\partial \phi_t} = \frac{\partial \Pi}{\partial \phi_t} + \delta \lambda_{t+1} \frac{\partial n}{\partial \phi_t} + \delta \mu_{t+1} \frac{\partial r}{\partial \phi_t} = 0, \quad \text{for } t = 0, \dots, T-1,$$

$$(8) \quad \delta \lambda_{t+1} - \lambda_t = -\frac{\partial \tilde{H}}{\partial N_t} = -\frac{\partial \Pi}{\partial N_t} - \delta \lambda_{t+1} \frac{\partial n}{\partial N_t}, \quad \text{for } t = 0, \dots, T-1,$$

$$(9) \quad \delta \mu_{t+1} - \mu_t = -\frac{\partial \tilde{H}}{\partial R_t} = -\frac{\partial \Pi}{\partial R_t} - \delta \lambda_{t+1} \frac{\partial n}{\partial R_t} - \delta \mu_{t+1} \frac{\partial r}{\partial R_t}, \quad \text{for } t = 0, \dots, T-1,$$

$$(10) \quad N_{t+1} - N_t = \frac{\partial \tilde{H}}{\partial (\delta \lambda_{t+1})} = n(\phi_t, N_t, R_t), \quad \text{for } t = 0, \dots, T-1,$$

$$(11) \quad R_{t+1} - R_t = \frac{\partial \tilde{H}}{\partial (\delta \mu_{t+1})} = r(\phi_t, R_t), \quad \text{for } t = 0, \dots, T-1,$$

$$(12) \quad \lambda_T = \frac{\partial \Omega}{\partial N_T}, \text{ and}$$

²Assuming that there is no cross-resistance between the original and novel toxins.

$$(13) \quad \mu_T = \frac{\partial \Omega}{\partial R_T}.$$

To understand the factors that determine the optimal proportion of refuge, it is useful to begin by evaluating the shadow value of pests and pest resistance. Combining equations (8) and (12) recursively yields the shadow value of pests:

$$(14) \quad \lambda_t = \sum_{k=t}^{T-1} \delta^{k-t} \frac{\partial \Pi_k}{\partial N_t} + \delta^{T-t} \frac{\partial \Omega_T}{\partial N_t}.$$

Assuming $\frac{\partial \Pi_t}{\partial N_t} < 0$, $\frac{\partial N_{t+1}}{\partial N_t} > 0$, and $\frac{\partial \Omega_T}{\partial N_T} < 0$, implies the shadow value of pests in season t

is negative, $\lambda_t < 0$. Combining equations (9) and (13) recursively yields the shadow value of resistance:

$$(15) \quad \mu_t = \sum_{k=t}^{T-1} \left\{ \delta^{k-t} \frac{\partial \Pi_k}{\partial R_t} + \delta^{k-t+1} \frac{\partial N_{k+1}}{\partial R_t} \lambda_{k+1} \right\} + \delta^{T-t} \frac{\partial \Omega_T}{\partial R_t}.$$

Assuming $\frac{\partial \Pi_t}{\partial R_t} < 0$, $\frac{\partial R_{t+1}}{\partial R_t} > 0$, $\frac{\partial N_{t+1}}{\partial R_t} > 0$, $\lambda_t < 0$, and $\frac{\partial \Omega_T}{\partial R_T} < 0$ for $t = 0, \dots, T-1$,

implies the shadow value of pest resistance in season t is also negative, $\mu_t < 0$. These results are intuitively appealing since both pests and pest resistance reduce the value of agricultural production.

Equation (7) can now be rewritten in terms of the marginal costs and benefits of increasing refuge in season t :

$$(16) \quad -\frac{\partial \Pi_t}{\partial \phi_t} - \delta \lambda_{t+1} \frac{\partial N_t}{\partial \phi_t} = \delta \mu_{t+1} \frac{\partial R_t}{\partial \phi_t}, \quad \text{for } t = 0, \dots, T-1.$$

The left-hand-side of equation (16) reflects the marginal costs of increasing refuge. The first expression represents direct costs, while the second represents indirect costs. The direct costs of increasing refuge are a decrease in the current value of production because less of the crop is protected from pests. The indirect costs represent the reduction in the future value of agricultural production. Increasing refuge increases pest survival today, 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 the future value of 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 benefits of increasing refuge. Increasing refuge decreases resistance. Equation (15) shows that there are two important components to the indirect benefits of decreasing resistance. First, decreasing resistance improves control of pests reducing crop losses and increases the value of production: $\sum_{k=t}^{T-1} \delta^{k-t} \frac{\partial \Pi_k}{\partial R_t} + \delta^{T-t} \frac{\partial \Omega_T}{\partial R_t}$. Second, improved pest control also has the cascading effect of lowering future pest pressure further reducing crop loss and increasing the value of

production: $\sum_{k=t}^{T-1} \delta^{k-t+1} \frac{\partial N_{k+1}}{\partial R_t} \lambda_{k+1}$.

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 benefits of improved control in the future on the proportion of crop protected by Bt. Analytically characterizing the optimal dynamic path is particularly difficult. From equations (14) and (15), the time path of the costate variables is:

$$(17) \quad \delta \lambda_{t+1} - \lambda_t = -\frac{\partial \Pi_t}{\partial N_t} - \delta^{T-t} \frac{\partial \Omega_T}{\partial N_{t+1}} \frac{\partial n(\phi_t, N_t, R_t)}{\partial N_t}, \text{ and}$$

$$(18) \quad \delta \mu_{t+1} - \mu_t = -\frac{\partial \Pi_t}{\partial R_t} - \delta \frac{\partial N_{t+1}}{\partial R_t} \lambda_{t+1} - \delta^{T-t} \frac{\partial \Omega_T}{\partial R_{t+1}} \frac{\partial r(\phi_t, N_t, R_t)}{\partial R_t},$$

which are both generally ambiguous. However, assuming that the new technology is independent of the existing technology for a moment, the change in the current shadow value of pest and pest resistance over time is positive at the optimum, which means the absolute value of pests and pest 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) would fall, suggesting more refuge is optimal. Alternatively, if the absolute shadow value of pests resistance decreases over time, all else equal, the marginal benefit of increasing refuge in equation (16) would fall

suggesting less refuge is optimal. Due to these two countervailing effects, it is not possible to analytically characterize the optimal time path for refuge without more restrictive assumptions on the evolution of pests and pest resistance even with a new technology that does not depend on these factors.

An Application

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

The ECB is a mobile diploid that reproduces sexually with 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 U.S. (Mason et al.).³

The development of resistance is a function of the natural selection caused by the use of Bt. Bt corn currently uses a single toxin only. Resistance to this toxin is assumed to be conferred by a single allele that is not sex linked. Thus, an allele can either be resistant (r) or susceptible (s). Each parent contributes an allele, and the frequency at which parents are homozygote resistant (rr), heterozygote (rs) or homozygote susceptible (ss) will determine the probabilities of the offspring's genotype. Bt corn produces a high dose 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.

³ 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.

The backstop technology we model uses two stacked 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 define $\rho_{\gamma i} = [\rho_{\gamma i}^r, \rho_{\gamma i}^{ss}, \rho_{\gamma i}^{s}]$ as the survival rate of resistant and susceptible homozygotes and heterozygotes for gene $\gamma = a, b$ and crop i where $i = 0$ for the Bt and 1 for the refuge crop. Following Hurley, Babcock, and Hellmich, we assume $\rho_{a0} = \rho_{b0} = [1.0, 0.0, 0.02]$ and $\rho_{a1} = \rho_{b1} = [1.0, 1.0, 1.0]$. 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: 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 : $[R_g^r, R_g^{rs}, R_g^{sr}, R_g^s]$, the initial gamete proportion vector is $R_0 = [1.0 \times 10^{-7}, 3.2 \times 10^{-4}, 3.2 \times 10^{-4}, 0.9993]$. The initial gamete proportion vector at T when two new toxins are introduced is $R_T = [1.0 \times 10^{-7}, 3.2 \times 10^{-4}, 3.2 \times 10^{-4}, 0.9993]$. 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 the evolution of resistance are detailed in Appendix I.

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

$$(19) \quad N_{g+1} = \beta_{0g} + \beta_{1g} \rho_g N_g + \beta_{2g} (\rho_g N_g)^2 + \rho_g N_g,$$

used by Hurley, Babcock, and Hellmich. Note that $\rho_g N_g$ is the number of pests that survive in generation g . The traditional logistic growth model is modified with β_{0g} , which eliminates the possibility of eradicating the ECB.

With a conventional logistic growth function, Hurley, Babcock, and Hellmich show that the high efficacy of Bt corn results in near eradication or *Heavy* suppression of the pest. Many entomologists expressed skepticism with

such a result, so the modified growth function was estimated and used to test the sensitivity of the results to the degree of pest suppression. 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 pest population growth follows a logistic curve with no intercept: $\beta_0 = 0$. In this case, eradication is possible without pest resistance. With pest resistance, *Heavy* ECB suppression results instead of eradication. The second specification estimates a positive intercept for the growth curve: $\beta_0 > 0$. Therefore, eradication is not possible even without resistance. With resistance, ECB suppression is *Light*. The biological difference between *Heavy* and *Light* suppression is the amount of time it takes the pest to reach carrying capacity from low populations.

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:

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

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 the i th crop. The proportion of yield loss is defined more explicitly as $D_t^i = \text{Min}[1.0, \rho_{2t+1}N_{2t+1}d^2 + \rho_{2t}N_{2t}d^1]$ where d^1 and d^2 are the constant proportion of yield loss per pest for first and second generation ECB in a season t .

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

$$\Omega_T = \frac{1}{1 - \delta} \text{Max}_{\phi_T} \left\{ \Pi(T, T') \mid 1.0 \geq \phi_t = \phi_T \geq 0.0, N_{t+1} = n(\phi_t, N_t, R_t) + N_t, \right.$$

and $R_{t+1} = r(\phi_t, R_t) + R_t \quad \forall t \in [T, T'] \}$. Thus, the value function reflects the annualized 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 over $T' - T$ years when an optimal static refuge is

used to manage resistance. Our salvage value assumes new technologies will arrive every $T' - T$ seasons 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 substantially reduce the computational cost of solving the model. Furthermore, this simplification is likely to have a negligible effect on our solution.

Having parametrically specified the evolution of resistance, the ECB population dynamics, the value function, and the salvage function, benchmark parameters are now chosen. Table 1 presents the benchmark configuration for all but the population dynamics. Table 2 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. The real price of corn, \$2.35, is the monthly average from 1991 to 1996 deflated to 1992.⁴ 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 discount rate is four percent.

The pest-free yield and production cost of Bt corn is the same as refuge for the benchmark simulation. 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. The difference in the marginal production cost between Bt and Non-Bt seed is the result of more rigorous quality control for Bt seed. Assuming the difference in production costs is negligible focuses attention on the resistance management benefits of refuge.

Hurley, Babcock, and Hellmich estimate different parameters for the first and second generation of ECB in a season using data reported in Calvin. These parameter estimates are reproduced in Table 2. The

⁴ Depending on the rate of adoption of Bt corn, there could be supply-side price effects that are not treated and depend on refuge size.

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 ECB, 0.055 and 0.028, are taken from Ostlie et al. 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 assumptions made by the 1998 EPA scientific advisory and ILSI/HESI panel reports (U.S. EPA, 1998b and ILSI/HESI).

The model is implemented using C++ and solved using standard numerical optimization routines adopted from Press et al. It is important to note that the biological processes commonly used to characterize pest resistance do not allow the satisfaction of second-order sufficiency conditions. There is no guarantee that the optimum identified is necessarily global. Assuring a global optimum is computationally impractical. However, exploring a wide range of starting values for the numerical optimization routines bolsters our confidence in the results.

Results

The analytical characterization of the optimal dynamic path for refuge is generally not possible. Increasing refuge has both a negative impact, the reduction in current production and the increased pest pressure in the future, and a positive one, the preservation of pest susceptibility that allows for better control and tends to reduce pest pressure in the future. Adding additional 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 the two alternative population models. The first assumes that pest suppression is *Light*. The second assumes that suppression is *Heavy*. We also consider two distinct salvage functions. The first assumes that pest 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 pest resistance to the new technology is *Dependent* on the current technology because a single novel toxin is added to the original toxin. Combining the two alternative population models with the two alternative salvage functions yields the different scenarios.

Before interpreting the results, it is useful to first summarize the optimal dynamic time path for refuge, resistance, and pests for each scenario, while highlighting important similarities and differences. Figure 1 reports the optimal dynamic proportion of refuge. The first interesting result apparent in Figure 1 is the consistent pattern across all four scenarios. In the initial period, the optimal refuge is relatively low. It tends to increase 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 four cases, there are also several notable differences. First, the pattern is more exaggerated with *Heavy* suppression. Second, when suppression is *Light*, it is optimal to have more refuge if the new technology is *Dependent* on the current technology. This difference becomes more pronounced as the introduction of the new technology nears. On the other hand, with *Heavy* suppression, the optimal refuge does not depend on whether the new technology is *Independent* or *Dependent* of the current technology.

The general characteristics of the optimal time path for resistance differ substantially depending on whether the suppression is *Light* or *Heavy* (Figure 2). When suppression is *Light*, the optimal proportion of resistant alleles for the original toxin increases at an increasing rate. The rate of increase is faster when pest resistance to the new technology is *Independent* of the current technology. But, even when pest resistance to the new technology is independent of the current technology it is not optimal to fully exhaust susceptibility. When suppression is *Heavy*, the evolution of resistance is sigmoidal. Initially, it increases at an increasing rate. Later it increases at a decreasing rate until susceptibility is fully exhausted. With *Heavy* suppression, the evolution of resistance is not affected by whether pest resistance to the new technology is *Dependent* or *Independent* of the current technology.

As with the optimal dynamic refuge, the optimal dynamic pest 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 tends to be more pronounced as the introduction of the new technology nears. Despite these similarities there are several notable differences. First, populations are substantially lower (two to three orders of magnitude) with *Heavy* suppression. Also, it takes longer for the population to begin increasing and the type of new technology does not matter when suppression is *Heavy*. When suppression is *Light*, the population immediately begins to increase and the type of new technology does matter. The optimal population is always lower when the new technology is *Independent* of the current technology.

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 pest susceptibility, which allows for better control and tends to reduce pest pressure in the future. Since the starting value for the pest population is the carrying capacity, the initial level of pest pressure is high and the marginal costs of refuge in terms of reduced yield are also high relative to the marginal benefits. Figure 3 shows that the initial emphasis on control reduces pests substantially. Once there are fewer pests to control, the marginal costs of refuge – the level of pest damage – decrease sharply relative to the marginal benefits and more refuge is optimal. As the pests begin to recover, the marginal costs of refuge increases. Additionally, as the arrival of the new technology nears, the value of susceptibility begins to diminish, particularly when the new technology is *Independent* of the current technology. With the marginal costs of refuge increasing and the marginal benefits of refuge declining, less refuge is again optimal.

Figure 1 indicates that when suppression is *Heavy* the optimal dynamic path of refuge is to start at zero in the first season and then to increase markedly. The optimal refuge stays high, above 60 percent, until the 9th season, and then decreases. This path reflects essentially a bang-bang solution to the control problem. The pest population is almost wiped out in the first season, and remains extremely low for the following 8 years (see

Figure 3). Refuge levels are high in this interval because the benefits of refuge in terms of resistance far outweigh the costs: yield loss is close to zero, since the pest population is so low. The refuge starts decreasing after the 9th year as the pests become more substantial again.

Note that in the case of *Heavy* suppression susceptibility is in effect a less valuable resource than in the case of *Light* suppression because the pest population has less buoyancy, so an increase in resistance has lower costs in terms of reduced control in the future. Resistance management, therefore, has different characteristics according to the resilience of the pest population. Hurley, Babcock, and Hellmich argue that when suppression is *Heavy*, resistance management is a high fixed cost- low marginal cost activity. The situation is reversed when suppression is *Light*: resistance management has a low fixed cost and a high marginal cost. Therefore, when suppression is *Heavy*, it is optimal either to do no resistance management by planting virtually no refuge or to do a lot of resistance management by planting a lot of refuge. 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 the marginal costs tend to be higher. The results in Figure 1 are well described by this argument.

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 pest control. Therefore, holding the proportion of refuge constant over time will reduce the value of production. To better understand the costs of using a second best optimal static refuge for resistance management, Table 3 reports the annualized net present value of production for the optimal dynamic refuge, optimal static refuge, and when Bt corn is never introduced. It also reports the optimal size of a static refuge.

Table 3 shows that the annualized value of Bt corn in all our scenarios is about \$7.00 an acre, which represent just over a six 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 increase 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 represent 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 practically zero.

Optimally varying refuge over time provides few benefits when compared to a second best static refuge regardless of whether suppression is *Heavy* or *Light* and the new technology is *Dependent* or *Independent* of the current technology. This result is due to the effectiveness with which Bt corn controls the European corn borer, though the optimal strategy varies depending on whether suppression is *Heavy* or *Light*.

When suppression is *Heavy*, it is optimal to nearly eradicate the pest immediately. 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 pest 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 below levels that still typically afford greater than 98 percent control. Comparing the optimal dynamic to the optimal static refuge reveals there is really very little difference in the two, with the exception of the initial period and the period right before the introduction of the new technology. With such a small difference and greater than 98 percent control, a small difference in the value of production is to be expected.

In terms of the effects of the characteristics of the backstop technology, when suppression is *Heavy*, the dependence of the new technology on the current toxin does not matter because it is inefficient to maintain susceptibility until the new technology arrives. Since the pest population can be brought down almost to extinction, it is optimal to do so irrespective of the characteristics of the backstop technology. However, the optimal policy does depend on the backstop when suppression is *Light*. In this case, if the new technology is *Dependent* on the current technology, it is optimal to have more refuge, since the value of susceptibility is positive when the new technology arrives.

With *Light* suppression, when the new technology is *Independent*, Figure 2 indicates that it is not optimal to fully exhaust susceptibility.⁵ This result is justified by the biological constraints on the exhaustion of susceptibility and the fact that the value of susceptibility is inextricably linked to controlling pests. Planting no refuge right before the introduction of the new technology will not necessarily exhaust susceptibility because of the biological processes governing the evolution of resistance. Therefore, to fully exhaust susceptibility, less refuge must typically 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 pest in a season because any resistance that develops during the first generation reduces control in the subsequent generations and it is not possible to offset this resistance by adjusting refuge during the a season. Therefore, it is optimal to plant refuge even in the season before the introduction of the new technology. Sensitivity analysis shows that when there is a single generation of pests in a season, it is not optimal to plant refuge in the season before the introduction of the new technology, but it may still not be optimal to fully exhaust susceptibility because of the implicit cost of extraction.⁶

Figure 2 shows that it is optimal to exhaust susceptibility with *Heavy* suppression even when the new technology is *Dependent*.⁷ Full exhaustion with *Heavy* suppression and a new technology that is *Dependent* on the current technology is consistent with a bang-bang solution of the control problem, as in this case the pest population is somewhat similar to a classical nonrenewable resource. It is useful to contrast the *Heavy* suppression results with the *Light* suppression ones, when it is not optimal to exhaust susceptibility. In particular, it is instructive to look at how well pests rebound from extremely low levels once susceptibility is exhausted. For example, suppose we are able to use Bt corn to reduce the initial population by four orders of magnitude to

⁵ Sensitivity analysis (available on 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 becomes optimal to exhaust susceptibility even with *Light* suppression .

⁶ This sensitivity analysis is available on request.

2.3×10^4 , a result that the model indicates is within the realm of possibility when suppression is *Heavy* or *Light*.

Figure 4 shows how fast the population returns to its carrying capacity assuming susceptibility is fully exhausted.

Note that the average number of pests per plant in year 1 for the *Light* suppression case is very close to the intercept term for the second generation. This indicates that the difference between the *Heavy* and *Light* suppression case is due to the intercept term, which drives the recovery of the population. When suppression is *Light* it takes 12 years before the population returns to carrying capacity, but only 3 years before average population exceed one pest per plant. When suppression is *Heavy*, it takes 14 years for the population to exceed one pest per plant and over 25 years before the population returns to carrying capacity. In fact, in the first four years there is almost no noticeable increase in the pest population when suppression is *Heavy*. Since the population recovers so slowly with *Heavy* suppression, there is no need to preserve some susceptibility to combat resurgent pests once the introduction of the new technology approaches. Alternatively, with *Light* suppression, preserving some susceptibility allows a more resilient pest to be pushed back year after year, until the new technology arrives.

Conclusions

Bt corn is a potentially valuable new tool for controlling the European corn borer. This value may be substantially diminished if ECB resistance to Bt rapidly emerges. The Environmental Protection Agency (EPA) 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 ECB available to mate with resistance ECB. 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

⁷ Sensitivity analysis (available on request) indicates that this result is robust even if the delay in the new technology is substantially shorter or the discount rate is much less.

of resistance management. We also consider how refuge requirements should account for 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 increasing scarcity and the decreasing value of control as resistance develops. These countervailing effects often make it optimal to require less refuge when Bt corn is first introduced, more refuge once the pest is under control 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. Our analysis has abstracted from the presence of a technology fee, since, as we noted before, such a fee would simply be a transfer. In a decentralized world, though, farmers' behavior is likely to be influenced by the presence of such a fee.

We also find that the affect of the introduction of a new technology on the optimal dynamic refuge depends crucially of the population dynamics of the pest. If it is possible to substantially suppress the pest over long periods of time, it is optimal to fully exhaust pest susceptibility regardless of the type of new technology being introduced. If it is not possible to suppress the pest, the type of technology being introduced does impact the optimal dynamic refuge. If the new technology depends on susceptibility, relatively more refuge should be planted over time. When the pest population is buoyant, it is typically not optimal to fully exhaust susceptibility regardless of the backstop, because the evolution of resistance is biologically constrained and the value of susceptibility is inextricably linked to the value of pest control.

The results of this analysis have several implications for both policy and research. The benefit of optimally varying refuge in response to the increased scarcity of susceptibility and decreased control benefits of Bt corn is likely to be small because of the high efficacy of Bt corn. Therefore, actively managing resistance based on changes in scarcity and control makes little sense if there are any costs associated with varying refuge, such as grower understanding and acceptance. The optimal strategy for managing resistance is very sensitive to

the population dynamics of the pest. If heavy suppression is feasible and the value of production is the primary objective, eradication type strategies that use little or no refuge until there is substantial resistance and a measurable loss of control will tend to be optimal. If heavy suppression is not possible, then a relatively consistent source of refuge tends to be optimal until a new technology is introduced.

While optimally varying refuge in response to decreasing scarcity and control does not appear to be particularly valuable for managing resistance to Bt corn, the sensitivity of our results to population dynamics and the fact that these dynamics are not well understood suggests that optimally varying refuge in response to new information on unknown or uncertain factors will be valuable. Thus, new models that determine how to optimally vary refuge in response to new information would be useful.

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 sets 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 continue to have to pay a technology fee for planting Bt corn, there may be substantial incentives for them to discontinue the use of Bt corn after just a few seasons. The rapid increase in adoption of Bt corn stopped abruptly in 2000. There are many reasons for this to have occurred and one of those reasons is that ECB populations across much of the Midwest have been particularly low in recent years. Grower adoption and de-adoption of Bt corn and compliance with refuge requirements is likely have a substantial impact on the efficacy of EPA policy. Thus, models that integrate the complexities of pest biology and human behavior could provide the EPA with more reliable information and improve the design of resistance management policy.

Appendix I

R_g is a 1×4 vector of the proportion of each type of gamete at the beginning of generation g : $[R_g^{rr}, R_g^{rs}, R_g^{sr}, R_g^{ss}]$, while $\rho_{\gamma i} = [\rho_{\gamma i}^{rr}, \rho_{\gamma i}^{ss}, \rho_{\gamma i}^{rs}]$ is the survival rate of resistant and susceptible homozygotes and heterozygotes for gene γ on crop i where $i = 0$ for the Bt crop and 1 for the refuge crop. It is also useful to define

$$(21) \quad P_{ig} = (R_g' R_g) \times \begin{bmatrix} \rho_{ai}^{rr} \rho_{bi}^{rr} & \rho_{ai}^{rr} \rho_{bi}^{rs} & \rho_{ai}^{rs} \rho_{bi}^{rr} & \rho_{ai}^{rs} \rho_{bi}^{rs} \\ \rho_{ai}^{rr} \rho_{bi}^{rs} & \rho_{ai}^{rr} \rho_{bi}^{ss} & \rho_{ai}^{rs} \rho_{bi}^{rs} & \rho_{ai}^{rs} \rho_{bi}^{ss} \\ \rho_{ai}^{rs} \rho_{bi}^{rr} & \rho_{ai}^{rs} \rho_{bi}^{rs} & \rho_{ai}^{ss} \rho_{bi}^{rr} & \rho_{ai}^{ss} \rho_{bi}^{rs} \\ \rho_{ai}^{rs} \rho_{bi}^{rs} & \rho_{ai}^{rs} \rho_{bi}^{ss} & \rho_{ai}^{ss} \rho_{bi}^{rs} & \rho_{ai}^{ss} \rho_{bi}^{ss} \end{bmatrix}$$

where $\times$ indicates multiplication by element. The net survival rate on the i th crop in generation g is $\rho_{ig} = I_4' P_{ig} I_4$ where I_4 is a 1×4 identity vector. The net survival rate in generation g and season t is $\rho_g = (1 - \phi_t) \rho_{ig} + \phi_t \rho_{ig}$. Let $P_g = [(1 - \phi_t) \rho_{0g} P_{0g} + \phi_t \rho_{1g} P_{1g}] / \rho_g$. Extending the Hardy-Weinberg model with random mating (see Hartl, 1988), the evolution of resistance is characterized as:

$$(22) \quad R_{g+1}^{x|y} = P_{g}^{x|y|x|y} + P_{g}^{x|y|x|y'} + P_{g}^{x|y|x'|y} + 0.5 P_{g}^{x'|y'|x|y} + 0.5 P_{g}^{x|y'|x'|y}$$

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

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Table 1: Benchmark parameter values.

<i>Economic Parameters</i>	Parameter	Existing Technology	New Technology
	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
	1st Generation Constant Marginal Yield Loss (Pests/Plant)	0.055	0.055
	2nd Generation Constant Marginal Yield Loss (Pests/Plant)	0.028	0.028
<i>Biological Parameters</i>			
	Initial Pest Population (Pests/Plant)	0.23	N_{15}
	Recombination Factor	0.5	0.5
	Initial Gamete Proportions (R_0')	$\begin{bmatrix} 1.0 \times 10^{-7} \\ 3.2 \times 10^{-4} \\ 3.2 \times 10^{-4} \\ 0.9993 \end{bmatrix}$	$\begin{bmatrix} 1.0 \times 10^{-7} \\ 3.2 \times 10^{-4} \\ 3.2 \times 10^{-4} \\ 0.9993 \end{bmatrix}$
<i>Gene a</i>			
	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
<i>Gene b</i>			
	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 2: European Corn Borer population model parameters.^a

	First Generation		Second Generation	
Parameters	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
Eq. Pop. w/out Bt Corn (Pest/Plant)	0.248	0.227	1.54	1.43
Calibration Factor	1.01		0.97	

^a Population parameters adopted from Hurley, Babcock, and Hellmich.

Table 3:

		Dynamic Optimum	Static Optimum	Without Bt Corn	
Salvage Function	Suppression	Value of Production	Value of Production	Refuge	Value of Production
		\$/Acre	Percent	\$/Acre	\$/Acre
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

Figure 1: Optimal dynamic refuge.

Figure 2: Optimal dynamic resistance.

Figure 3: Optimal dynamic pest population.

Figure 4: Recovery of pests from low populations with susceptibility .