



## Dynamics of insect resistance in Bt-corn

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### Abstract

The development of genetically modified Bt-corn, incorporating various toxin genes from *Bacillus thuringiensis* that act as a chemical defense against insect pests, such as the European Corn Borer, provides farmers with a new pest management option. However, the emergence of insect resistance is a threat to the continued use of Bt-corn. The United States Environment Protection Agency (US EPA) has developed planting strategies, for preventing insect resistance by planting a mixture of Bt- and non-Bt-corn. Decisions about the exact proportion of Bt- and non-Bt-corn are based on complex spatially explicit mathematical models using detailed biological assumptions about the population genetics and life history of the European Corn Borer. We develop an alternative simpler model for the spread of resistance based on the logistic growth model, which we believe has utility in situations where it is impossible or impractical to estimate the different life history and genetics parameters required by more detailed models. We use our model to investigate the US EPA's planting rules for Bt-corn and find that short-term economic behavior is likely to lead to these rules not being followed. Our results add weight to existing work on this problem. We also investigate the economics of planting Bt-corn in markets where consumers do and do not differentiate between the modes of production for the corn. We find that Bt-corn appears to be economic in markets that do not differentiate and uneconomic in markets where consumers do differentiate.

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### 1. Introduction

Insect pests of agricultural crops are a major problem. In the United States, 33% of all crops are lost to disease, weeds, and insects. Since the 1940s, crop losses due to insects have risen from about 7 to 13% (May and Dodson, 1986). The reason for this problem has been our inability to manage the emergence of insect resistance to pesticides. With the advent of genetically modified crops, we have another opportunity to

manage a new technology in a way that prevents the emergence of insect resistance.

Arguably the most important agricultural crop is corn. Corn is projected to become the highest volume agricultural product, exceeding the production of rice, as consumers in developing countries demand higher quality diets with more meat and dairy products. Most of the increase in meat production to supply these markets will come from increases in corn production, with the corn being used to feed additional livestock (Islam, 1995; Pinstrup-Andersen et al., 1999). Anticipating this trend, biotechnology companies have developed strains of genetically modified corn, incorporating various toxin genes from *Bacillus thuringiensis*

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that act as a chemical defense against the European Corn Borer (ECB).

The ECB is a major pest of corn crops and can be responsible for significant crop losses if the density of the borers reaches one borer per corn plant. At such densities a yield reduction of about 5% may be expected (Wilson, 1989; Edwards et al., 2001). With the introduction of genetically modified Bt-corn, a new management option exists for farmers who have traditionally either timed their plantings of corn or used insecticides to protect their crops. Early larval stages of the ECB tend to be foliage feeders while later stages bore deep into the plant stalk or ear. Once larvae bore into the stalks they cannot be treated with insecticides. Therefore, management has relied on detecting ECB infestations in a vulnerable stage of their life cycle, either as eggs or early larval stages, by field sampling of the corn crop (Wilson, 1989; Edwards et al., 2001). With the advent of Bt-corn, this intensive management may no longer be required. However, with insect populations constantly exposed to the toxin proteins the risk of resistance is likely to increase.

The emergence of resistance in ECB is a threat to the sustained use of Bt-corn and various suggestions have been made about how best to manage this problem<sup>1</sup> (United States Environment Protection Agency (US EPA), 2000). In the United States, for example, the Environment Protection Agency (EPA) has required that in areas planted with Bt-corn, at least 20% of the area should be planted with non-Bt-corn as a way to manage the emergence of insect resistance. While concern has been expressed about this approach (e.g. US EPA, 2000; Losey et al., 2001), some bioeconomic modeling support this kind of strategy (e.g. Onstad and Guse, 1999). Work in this area is usually based on modeling the spread of resistance genes. This requires detailed biological information about the genetics controlling resistance<sup>2</sup> and estimates of fitness parameters of the different genotypes, which in many cases may not be available or may be difficult and time consuming to obtain. For example, Peck et al. (1999), Caprio (2001), and Storer et al. (2003) use spatially explicit stochastic simulation models with various assumptions, in-

cluding: insect population age structure, movement of larvae and adults, and development time.

Here, we propose an alternative dynamical systems model for the spread of insect resistance based on the logistic growth model (Laxminarayan and Simpson, 2000). For simplicity, we ignore correlation effects and assume that total borer numbers are constant from year to year. The evolution of our simple model is then determined by the rate of spread of resistant insects. We then use our model to investigate the impact of insect resistance on the economic value of various planting strategies for Bt- and non-Bt-corn, including the above-mentioned EPA 20% rule. While such economic analysis is not new (e.g. Onstad and Guse, 1999; Hurley et al., 2001; Hyde and Martin, 2001), we believe that our simple alternative model can provide valuable and meaningful insights into the dynamics affecting the value of Bt-corn planting strategies.

We stress that the model presented here is simplistic and that some of the assumptions, both biological and economic, are almost certainly not universally valid. Further discussion of these assumptions is postponed to the final section where future work, including more complex and realistic stochastic generations of our model are outlined.

## 2. Methods

### 2.1. Model

We assume that the emergence of insect resistance in the presence of Bt-corn can be modeled by a logistic growth curve. That is, if  $p_t$  denotes the proportion of Bt-resistant borers in the population at time  $t$ , then  $p_{t+1}$  is given by:

$$p_{t+1} = \begin{cases} p_t + rp_t(1 - p_t), & \text{with Bt-corn} \\ (1 - s)p_t, & \text{with no Bt-corn} \end{cases} \quad (1)$$

where  $r$  is the rate of increase in the proportion of resistant borers in the presence of Bt toxin (resistance growth rate) and  $s$  is the rate of decrease in the proportion of resistant borers in the absence of Bt toxin.

For simplicity, we consider here the deterministic form of the model where planting strategies are predetermined and  $r$  and  $s$  are constants. We take unit time step to represent 1 “year” (or one planting cycle) so that for a given  $r$  and  $s$  and initial value  $p_0$ , the

<sup>1</sup> For a general discussion of approaches to insect resistance management, see Gould (1988) or Georghiou (1993).

<sup>2</sup> For a detailed discussion of the genetic basis for insect resistance, see Heckel et al. (1997).

proportion of Bt-resistant borers in any given year is determined by iterating Eq. (1).

Having determined  $p_t$  ( $t = 1, 2, 3, \dots$ ), it follows that the number of resistant borers per plant is given by

$$\lambda_t = p_t B_t \tag{2}$$

where  $B_t$  is the total number of borers per plant in year  $t$ . It follows that the number of non-resistant borers or susceptible borers per plant in year  $t$  is

$$\lambda'_t = (1 - p_t) B_t \tag{3}$$

In the remainder of this paper, we will take  $B_t$  to be a constant. While this is unrealistic, it nevertheless serves to illustrate out main points concerning the economic value of various planting strategies. We consider in particular the following four strategies:

- (1) plant only Bt-corn;
- (2) plant only non-Bt-corn and do not use insecticide;
- (3) plant a mixture of Bt- and non-Bt-corn and do not use insecticide; and
- (4) plant non-Bt-corn and use insecticide.

Strategy 1 represents pure GM farming, strategy 2 insecticide-free farming, strategy 3 is the EPA recommend strategy for the planting of Bt-corn, and strategy 4 represents current farming practice pre-Bt-corn.

If  $L$  is the yield lost per corn borer per plant, then the yield per hectare from a field of Bt-corn (strategy 1) can be written as

$$Y_t^{(1)} = M(1 - L(\lambda_t + (1 - q)\lambda'_t)) \tag{4}$$

where  $M$  is the expected yield per hectare in the absence of borers and  $q$  is the effective mortality of susceptible borers due to the Bt toxin produced by Bt-corn.

The yield from a field of non-Bt-corn when no insecticide is applied (strategy 2) is given by

$$Y_t^{(2)} = M(1 - L(\lambda_t + \lambda'_t)) = M(1 - LB_t) \tag{5}$$

The yield for mixtures of Bt-corn and non-Bt-corn (strategy 3) is given by

$$Y_t^{(3)} = \alpha Y_t^{(1)} + \beta Y_t^{(2)} \quad (\alpha + \beta = 1) \tag{6}$$

where  $\alpha$  is the proportion of Bt-corn and  $\beta$  is the proportion of non-Bt-corn.

The yield from a field of non-Bt-corn when insecticide is applied (strategy 4) is given by

$$Y_t^{(4)} = M(1 - L(\lambda_t + (1 - q')\lambda'_t)) \tag{7}$$

where  $q'$  is the effective mortality due to the Bt toxin insecticide on susceptible borers and we have assumed that the insecticide has no effect on resistant borers.

When comparing the four different strategies, we consider the profit per hectare in year  $t$ , given for strategy  $i = 1, 2, 3, 4$  by

$$Pr_t^{(i)} = Y_t^{(i)} P_t^{(i)} - C_t^{(i)} \tag{8}$$

where the yields  $Y_t^{(i)}$  are given by Eqs. (4)–(7),  $P_t^{(i)}$  denotes the market price for the corn produced under strategy  $i$  and  $C_t^{(i)}$  denotes the total costs in producing the corn under strategy  $i$  in year  $t$ .

Given prices and costs, we then calculate the net present value for each strategy over a time horizon of  $N$  years, defined by

$$NPV^{(i)} = \sum_{t=0}^{N-1} Pr_t^{(i)} (1 + y_t)^{-(t+1)} \tag{9}$$

where  $y_t$  is the rate of interest used for discounting in year  $t$ .

In the following, we assume that

$$C_t^{(1)} = C_t + T_t \tag{10}$$

where  $C_t$  is the cost of production in year  $t$  and  $T_t$  is the technology cost of using Bt-corn.

For the insecticide-free strategy 2, we assume that the cost of production is that associated with current production practice

$$C_t^{(2)} = C_t \tag{11}$$

For the mixed strategy 3, we assume

$$C_t^{(3)} = C_t + \alpha T_t \tag{12}$$

i.e. that the production costs are the same as for the pure Bt-corn strategy 1 and that the technology costs are in proportion to the use of Bt-corn. For strategy 4, we assume that

$$C_t^{(4)} = C_t + I_t \tag{13}$$

where  $I_t$  is the cost of insecticide.

In general, we assume that prices satisfy the following relationship

$$P_t^{(1)} = P_t^{(3)} \leq P_t^{(4)} \leq P_t^{(2)} \tag{14}$$

Equality occurs in markets where consumers do not differentiate between the methods of corn production,

such as the animal feed markets. The inequalities occur in markets where consumers differentiate between the methods of corn production and embody the assumed consumer preferences for insecticide-free foods, over non-GM foods, followed by GM foods. We further assume that any individual farmer cannot influence the market price for corn or the prices of inputs (i.e. the farmer is a price taker) and that the  $P_t^{(i)}$ 's can be regarded as constants.

In order to illustrate the impact of the dynamical behavior of the model on the economic value of the various planting strategies, we take constant values for the prices and costs in Eqs. (8)–(13).

### 3. Results

In deriving our results, we used parameter values in Table 1 to construct several scenarios for our four strategies. In particular, the growth rate parameter  $r$  was determined numerically to give 50% of the population as resistant over 5-, 10-, and 20-year periods. For simplicity, we refer to these periods as “times to resistance”. We also assume certain price margins for the different methods of production as given in Table 1.

In Fig. 1 we present the NPV's for two market prices over horizons of 25 years for times to resistance of 5, 10, and 20 years, respectively. For a market

Table 1  
Model parameters values, description, and source information

Parameter	Value	Description	Source
$M$	9500 kg/ha	The expected yield per hectare in the absence of borers	Monsanto (2000), USDA (2001b)
$P_t^{(1)}$	US\$ 0.09/kg	The projected market price of Bt-corn (strategy 1)	Monsanto (2000), USDA (2001a)
$P_t^{(2)}$	$=P_t^{(1)}, =1.05P_t^{(1)}$	The projected market price of non-Bt-corn no insecticide (strategy 2)	In some markets consumers are indifferent between insecticide-free and GM production and in other markets consumers differentiate and pay a premium for insecticide-free produce
$P_t^{(3)}$	$P_t^{(3)} = P_t^{(1)}$	The projected market price of a mix of Bt and non-Bt-corn (strategy 3)	No price difference since GM and non-GM grain is mixed
$P_t^{(4)}$	$=P_t^{(1)}, =1.025P_t^{(1)}$	The projected market price of non-Bt-corn using insecticide (strategy 3)	In some markets consumers are indifferent between non-GM and GM production and in other markets consumers differentiate and pay a premium for non-GM produce
$T_t$	US\$ 24.70/ha	The technology cost associated with using Bt-corn	Onstad and Guse (1999)
$I_t$	US\$ 24.70/ha	The technology cost associated with using Bt insecticide spray	Assume that approximately the same cost applies for Bt insecticide use as Bt-corn use
$C_t$	US\$ 800/ha	The cost of production	Foreman (2001)
$q$	0.96	The effective mortality from the use of Bt-corn on the ECB	Monsanto (2000)
$q'$	0.50	The effective mortality from the use of Bt insecticide spray on the ECB	Hyde and Martin (2001)
$L$	0.05	Effective yield lost per ECB	Monsanto (2000), Hyde and Martin (2001), Monsanto (2001)
$B_t$	1.19	Number of borers per plant	Steffey and Gray (1999)
$r$	Calculated	Resistance growth rate is calculated numerically to give 50% of the population as resistant over 5, 10, and 20 years	May and Dodson (1986)
$s$	0	Rate of decline in resistance	Onstad and Gould (1998)
$y_t$	10.00%	The interest rate used for discounting	N/A
$\alpha$	0.80	If the proportion of the area planted with Bt-corn is 20%, then only 80% of the technology fee is assumed payable	N/A
$p_0$	0.001	Initial proportion of the population that is resistant	Onstad and Gould (1998)

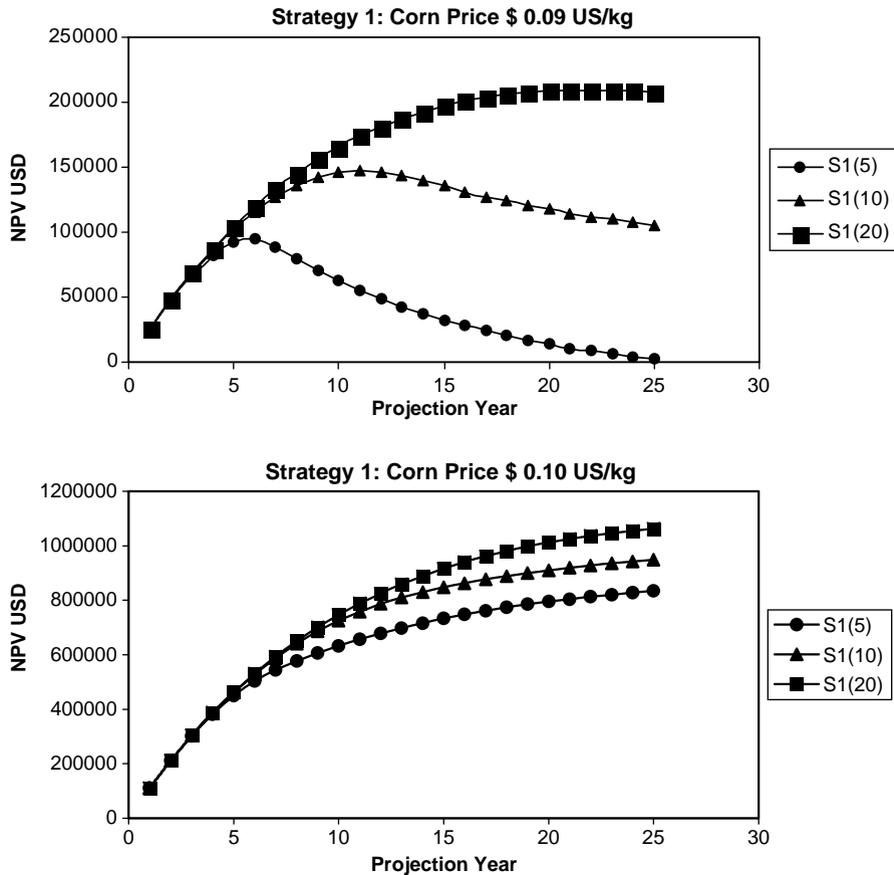


Fig. 1. Strategy 1 under two different market prices for Bt-corn for 5, 10, and 20 years to resistance. In the top graph, maximum behavior is observed because the market price for corn is low enough that when resistance occurs the cost of the technology fee results in a loss to the farmer. Monotone increasing behavior is observed in the bottom graph because the market value of the corn production always exceeds production costs, including the technology fee.

price of US\$ 0.09/kg the NPV of profits for strategy 1 exhibited maxima for different times to resistance. This occurs because, as resistance is achieved, losses result from paying the technology fee. In reality of course, farmers would stop paying the technology fee if this occurred thus rendering the model essentially invalid beyond this point. At a price of US\$ 0.10/kg the NPV of profits exhibited monotone increasing behavior arising from the fact that in this case the price of Bt-corn always exceeded the production costs, including the technology fee.

Two types of consumer preferences were investigated. Firstly, consumers were assumed to be indifferent between the technologies used to produce the corn. Such a situation may occur in the grain markets

for animal feed. In this case, comparing all four strategies using a market price of US\$ 0.09, the top graph (Fig. 2) shows planting Bt-corn with insect resistance emerging over 5 years and the bottom graph shows planting Bt-corn with insect resistance emerging over 10 years. Planting Bt-corn, strategy 1, has the highest NPV over the first 6 years with resistance emerging over 5 years [S1(5)] and over 12 years with resistance emerging over 10 years [S1(10)]. After strategy 1, the US EPA's mixed planting strategy, strategy 2, has the highest NPV (Fig. 2).

Finally, all four strategies were compared assuming consumers differentiated between the technologies used to produce the corn. In this case, insecticide-free farming, strategy 2 [S2(5%)] has the highest NPV, as-

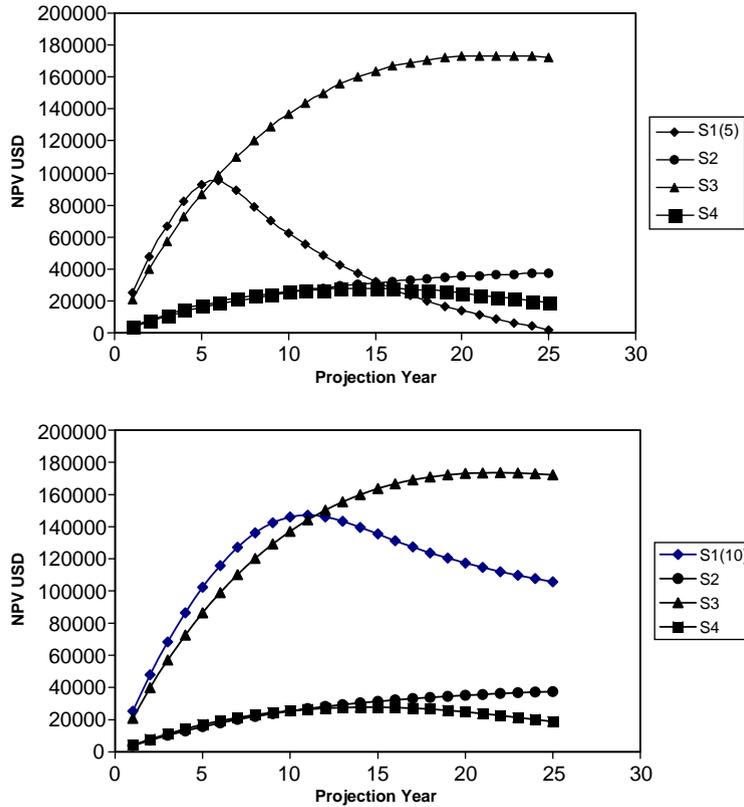


Fig. 2. All four strategies are compared at the same market price of US\$ 0.09. The top graph shows planting Bt-corn with insect resistance emerging over 5 years, S1(5) and the bottom graph shows planting Bt-corn with insect resistance emerging over 10 years, S1(10).

suming a 5.0% premium for insecticide-free produce. Current farming practice, strategy 4 [S4(2.5%)] has the next highest NPV assuming a 2.5% premium for non-Bt-corn (Fig. 3).

Alternate yearly plantings of Bt- and non-Bt-corn were investigated. The Bt-corn planting strategy with resistance emerging over 10 years, S1(10), was compared to alternate yearly planting of Bt- and

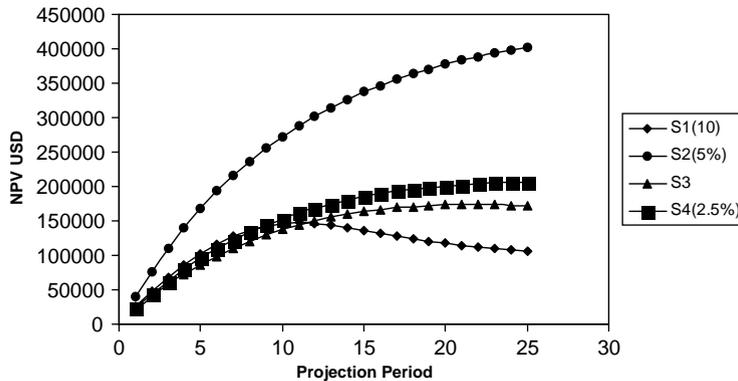


Fig. 3. All four strategies are compared with insecticide-free farming, S2(5%), assumed to earn a premium of 5.0% and non-Bt farming, S4(2.5%) assumed to earn a premium of 2.5%.

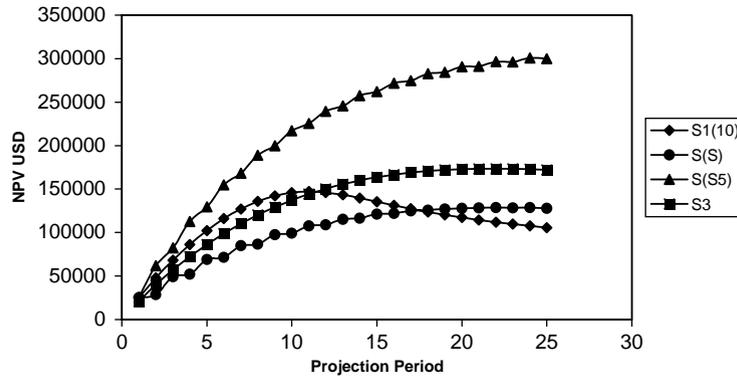


Fig. 4. The Bt-corn planting strategy with resistance over 10 years, S1(10), is compared to alternate yearly planting of Bt- and non-Bt-corn with and without a price advantage for the non-Bt plantings, S(S5) and S(S). In both cases the resistance growth rate is the same as in the Bt-corn planting strategy. These temporal planting strategies are compared with the EPA mixed strategy (S3).

non-Bt-corn with and without a price advantage for the non-Bt plantings [S(S5) and S(S)]. In both cases the resistance growth rate was the same as in the Bt-corn planting strategy. These temporal planting strategies are compared with the EPA mixed strategy (S3). Provided a price premium exists in the years when non-Bt-corn is planted, then this is the strategy with the highest NPV (Fig. 4). However, the success of this strategy depends on the level of contamination resulting from volunteer plants. If a premium cannot be charged in the years of planting non-Bt-corn, then this strategy produces a lower NPV than the Bt-corn planting strategy.

#### 4. Discussion

Analysis of our simple deterministic logistic model suggests that the primary factor in the decision to plant Bt-corn is the market price consumers are willing to pay for non-Bt-corn. Even a small premium (5%) for insecticide-free corn can make a significant difference to the NPV of profits. This advantage does not exist in markets that do not discriminate on price.

For markets unwilling to pay a premium the US EPA's resistance management plan appears economically viable over terms in excess of 10 years. To this extent, our work supports the work of Onstad and Guse (1999). However, it seems unlikely that farmers will plant 20% of their fields with non-Bt-corn when they have to wait 10 years for this to be the strategy with the

highest NPV. Additionally, for such a planting strategy to be effective, cooperation is required on a regional scale. The incentives would then be high for individual farmers to ignore the US EPA's requirements. Taken together, these factors suggest that the US EPA's required planting strategy would not be followed.

Temporal planting strategies appear to offer an alternative management approach but the success depends on farmers being able to obtain a price premium in the years when non-Bt-corn is planted. This may be problematic because volunteer plants are likely to contaminate production in the years non-Bt-corn is planted.

An important and implicit assumption of our simple model is that we take account of the spatial nature of the environment through the resistance growth rate parameter  $r$ . This implies that  $r$  is related to the area planted with Bt-corn. An explicit spatial analysis like those of Peck et al. (1999), Caprio (2001), and Storer et al. (2003) is possible by using our model to describe the emergence of insect resistance in the subpopulations of a meta-population model (Tilman et al., 1997), with resistance emerging in the subpopulations occurring on Bt-corn habitat patches. However, detailed understanding of insect dispersal behavior between patches is required for this approach. Such data are likely to be lacking for some of the species we may be interested in. We therefore believe that the spatially explicit approaches taken by Peck et al. (1999), Caprio (2001), and Storer et al. (2003) offer valuable insights in data rich environments, but have less utility in data poor environments where we believe that

the simple approach we have taken may offer useful insights in situations where biologists are prepared to put upper and lower bounds on the time to resistance.

We stress again that the version of our model considered here is deterministic and contains many simplifying assumptions. In particular, we assumed constant values for various parameters, such as total borer numbers, mortality and resistance growth rates, prices and costs. In constructing particular scenarios, we also made some assumptions that may not be universally valid such as price differentials and derived resistance to related insecticides. More realistically, like the models used by Caprio and others, our model parameters should be considered as random variables and stochastic simulations should replace the deterministic iterations considered here. These and other generalizations of our model are currently under investigation.

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