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Bacillus thuringiensis resistance management: experiences from the USA

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Abstract

The role of the US Environmental Protection Agency (EPA) in the regulation of Bt crops is discussed with an emphasis on resistance management. A stochastic bioeconomic simulation model is presented to show how previous analyses of insectresistance management (IRM) policy can be improved by including the effect of farmer adoption and compliance behaviour on the evolution of Bt resistance. An example shows that the traditional assumptions of full adoption and compliance overestimate the risk of Bt resistance. However, since adoption and compliance behaviour have countervailing effects on the evolution of resistance, the result should be interpreted with caution until better information is available on farmer adoption and compliance behaviour.

Keywords: *Bt* corn; *Bt* cotton; resistance management; bio-economic; simulation; plant-incorporated protectants

Introduction

Bt crops are engineered with genetic material from the soil bacterium *Bacillus thuringiensis*. This genetic material instructs plants to produce proteins that are toxic when consumed by certain insect pests. *Bt* crops commercialized in the United States (US) include varieties of corn, cotton and potato that control agricultural pests such as the European corn borer, corn rootworm, tobacco budworm, pink bollworm and Colorado potato beatle. In 2002, 24% of nearly 78.8 million acres of corn and 35% of nearly 14.3 million acres of cotton were planted with *Bt* varieties (NASS 2002). While *Bt* corn and cotton adoption has been rapid, Monsanto removed *Bt* potatoes from the market in 2001 because consumer concerns led companies like McDonald's, Burger King, McCain's and Pringles not to buy them (Brammer, Dixon and Ambrose 2003).

The US Environmental Protection Agency (EPA) is responsible for registering pesticides for commercial use in the U.S. While the EPA does not require companies to register the genetic material in herbicide-tolerant crops like Roundup Ready® soybean, it does require companies to register the genetic material in *Bt* crops, which it refers to as plant-incorporated protectants (PIPs). The EPA requires the registration of PIPs because they enable the plant to produce a pesticide. Alternatively, herbicide-tolerant crops do not produce a pesticide. They are treated with a pesticide that is independently registered by the EPA.

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Companies registering Bt PIPs with the EPA are required to develop and implement an approved insect-resistance management (IRM) plan, which is contrary to requirements for other pesticides. The EPA has more requirements for Bt PIPs because it wants to promote the sustainable use of what it believes are reduced-risk pesticides (EPA 1998). The potential for Bt-resistant insects to evolve is established in the literature (e.g. Tabashnik 1994; Bauer 1995; McGaughey and Beeman 1988; Gahan, Gould and Heckel 2001; Morin et al. 2003) and poses a threat to the sustainable use of Bt. With effective IRM, the EPA believes it can conserve the efficacy of Bt in order to accomplish greater reductions in human and environmental exposure to more hazardous conventional pesticides.

EPA approved IRM plans are currently based on a high-dose refuge strategy. For a high-dose, the crop is engineered to produce enough toxins to kill all but the most resistant insects (resistant homozygotes). For refuge, farmers are required to plant some crop with a non-*Bt* variety. Refuge slows the evolution of resistance by allowing *Bt*-susceptible insects (heterozygotes and susceptible homozygotes) to thrive and mate with *Bt*-resistant ones. With a high-dose, the majority of progeny are *Bt*-susceptible. The potential for delaying resistance using a high-dose refuge strategy has been demonstrated with simulation models (e.g. Alstad and Andow 1995; Roush and Osmond 1997; Caprio 1998; Gould 1998; Onstad and Gould 1998b; Peck, Gould and Ellner 1999) and experimentally (e.g. Liu and Tabashnik 1997; Tang et al. 2001).

Debate surrounding what constitutes an acceptable IRM plan has centred around three factors: (i) refuge size, (ii) refuge configuration, and (iii) refuge treatment with non-*Bt* insecticides. The proportion of refuge plays a role in determining how fast resistance evolves because it determines the proportion of pests exposed to *Bt*. Refuge configuration, where the refuge is planted in relation to the *Bt* crop, plays a role because it influences the degree to which susceptible pests mate with resistant ones. Treating refuge with non-*Bt* insecticides may speed the evolution of resistance because fewer susceptible pests survive to mate with resistant ones. However, requiring farmers to leave part of their crop unprotected may discourage the adoption of *Bt* crops and encourage the use of more hazardous pesticides.

Early economic models of IRM (e.g. Hueth and Regev 1974; Taylor and Headley 1975; Regev, Gutierrez and Feder 1976; Regev, Shalit and Gutierrez 1983; Gorddard, Pannell and Hertzler 1995) framed the problem as a joint renewable-/nonrenewable-resource problem. It is a renewable-resource problem because pests can rapidly re-establish their populations in the absence of pesticides. It is a nonrenewable-resource problem because pest susceptibility (the converse of resistance) tends to regenerate slowly in the absence of pesticides. Another key feature of the problem is that the marginal productivity of a pesticide depends on the level of resistance. This literature shows how a farmer's long-run economic returns can improve by optimally varying pesticide application rates over time in response to pest abundance and the scarcity of pest susceptibility. Laxminarayan and Simpson (2002) extends this work to *Bt* crops relaxing the assumption that pest susceptibility is nonrenewable. This literature provides additional justification for EPA policy. Since farmers treat pests as common property (Clark and Carlson 1990), they are unlikely to manage pest resistance optimally.

Entomologists and simulation models dominate the IRM literature directly related to EPA policy. The majority of this literature focuses on characterizing how fast resistance evolves under alternative assumptions regarding IRM policy and pest and crop biology (Alstad and Andow 1995; Roush and Osmond 1997; Caprio 1998; Gould 1998; Onstad and Gould 1998b; 1998a; Peck, Gould and Ellner 1999; Caprio 2001;

Onstad et al. 2001; Andow and Ives 2002; Ives and Andow 2002). Others also explore the effect of IRM on agricultural productivity and pesticide use (Onstad and Guse 1999; Hurley, Babcock and Hellmich 2001; Hurley et al. 2002). The strength of these models is their attention to insect behaviour and the biological processes that govern resistance. A notable weakness is the lack of attention given to how farmer behaviour influences the risk of resistance. Two particularly relevant factors are *Bt* crop adoption rates and farmer compliance with IRM guidelines. Both these factors are important because they influence the proportion of pests exposed to *Bt*. One reason for a lack of attention to farmer behaviour is the lead role entomologists have played in the formulation of EPA guidelines. Another is a lack of information on farmer adoption and compliance behaviour.

The purpose of this paper is to demonstrate how ignoring adoption and compliance behaviour can result in an inaccurate assessment of the efficacy of IRM policy. To accomplish this goal, the model developed in Hurley et al. (2002) is extended to include a behavioural model of partial adoption and compliance. Adoption increases with the expected benefits of Bt crops, while compliance decreases with the size of refuge and expected benefits of Bt crops. Results for partial adoption and compliance are compared with full adoption and compliance.

Model

US EPA (1998, p. 1) expresses the agency's objectives for IRM: "pesticide resistance management is likely to benefit the American public by reducing the total pesticide burden on the environment, and by reducing the overall human and environmental exposure to pesticides". It also illuminates the important trade-offs and constraints that concern the EPA: "It is desire of the EPA that this focus on pesticide resistance management not overly burden the regulated community, jeopardize the registration of reduced risk pesticides, or exclude conventional pesticides or other control practices which can contribute to the further adoption of integrated pest management (IPM)".

Most entomological IRM models focus on quantifying the rate of resistance evolution and do not quantify the effect of IRM on the use of conventional pesticides, the burden to the regulated community or the incentive for industry to develop new reduced-risk pesticides. The models also do not consider the role of IPM. Economic models focus on optimizing the benefits of IRM to farmers, but not on the effect of IRM on environmental loadings of conventional pesticides or incentives for industry to develop new reduced-risk pesticides. IPM is seldom considered. Hurley et al. (2001; 2002) are exceptions who look at agricultural productivity and conventional pesticide use as well as resistance. Still, the models do not distinguish between the burden to the regulated community and incentives for industry to develop new reduced-risk pesticides. All of these models assume full adoption and compliance.

Following Hurley et al. (2002), consider a simplified production region with a single crop and pest. The region is divided between two crop varieties. The first, denoted by i = 0, is a conventional variety that also serves as refuge. The second, denoted by i = 1, is a *Bt* variety that is toxic when consumed by susceptible pests. Let $1.0 \ge \phi_t \ge 0.0$ be the proportion of conventional acreage planted in season t. The pest reproduces with G generations per season where g denotes the generation in season t. Let $1.0 \ge u_{tg}^{i} \ge 0.0$ be the proportion of crop i that receives a conventional pesticide application in season t and generation g. The model allows conventional pesticide

treatments on Bt acreage because if Bt fails due to resistance, farmers may turn to conventional pesticides for supplemental control.

The number of pests per plant emerging to damage crops and reproduce is $n_{tg} \ge 0.0$. Pest populations are random due to environmental events such as storms, though not independent from past populations due to reproduction:

(1)
$$n_{tg} \sim \begin{cases} N_g(n_{tg-1}^s), & \text{for } g > 1 \\ N_g(n_{t-1G}^s), & \text{for } g = 1 \end{cases}$$

where n_{tg}^{s} is the number of pests that escape control and survive to damage crops and reproduce, and $N_{g}(\cdot)$ is a conditional distribution function.

The Hardy-Weinberg model characterizes resistance, assuming it is conferred by a single allele that is not sex-linked. There are two types of alleles: resistant and susceptible. The proportion of resistant alleles is $1.0 \ge r_{tg} \ge 0$. Each pest has two alleles, one from its mother and one from its father, and can be one of three genotypes: resistant homozygote – with two resistant alleles; heterozygote – with one resistant allele; or susceptible homozygote – with no resistant alleles. The Hardy-Weinberg model implies the proportion of each genotype is

(2) $\eta_{tg} = [r_{tg}^2, 2 r_{tg}(1 - r_{tg}), (1 - r_{tg})^2]$

corresponding to resistant homozygotes, heterozygotes, and susceptible homozygotes.

The Hardy-Weinberg model assumes no selection pressure – survival rates are the same for all genotypes. *Bt* crops select for resistant pests. Let σ_g^{i} be a 1×3 vector of genotypic survival rates for pests on crop i in generation g with elements corresponding to resistant homozygotes, heterozygotes and susceptible homozygotes. The survival rate of all genotypes treated with conventional pesticides is σ_g^{i} . The vector of genotypic survival rates for each crop is then $\rho_{tg}^{i} = \sigma_g^{i} + \iota_{tg}^{i}(\sigma_g^{i}\sigma_g^{i} - \sigma_g^{i})$, implying the number of pests that survive to damage crop i and reproduce is $n_{tg}^{S_{i}} = \rho_{tg}^{i} \cdot \eta_{tg}^{i} n_{tg}$. The vector of genotypic survival rates for the region is $\rho_{tg} = \rho_{tg}^{1} + \phi_t (\rho_{tg}^{0} - \rho_{tg}^{1})$, implying the number of pests that survive to reproduce is $n_{tg}^{S_{i}} = \rho_{tg} \eta_{tg} n_{tg}$.

Since each surviving pest contributes two alleles, resistant homozygotes contribute two resistant alleles and heterozygotes contribute one resistant allele, the proportion of resistant alleles in the subsequent generation is

(3)
$$r_{tg} = \begin{cases} \frac{\rho_{tg-1}M\eta_{tg-1}}{\rho_{tg-1}\cdot\eta_{tg-1}}, & \text{for } g > 1\\ \frac{\rho_{t-1G}M\eta_{t-1G}}{\rho_{t-1G}\cdot\eta_{t-1G}}, & \text{for } g = 1 \end{cases}$$

where M is the 3×3 diagonal matrix [1.0, 0.5, 0.0].

Equations (1) – (3) and the initial conditions $n_{01} = N_0$ and $r_{01} = R_0$ describe a dynamic stochastic biological system, which is controlled by the parameters for the proportion of conventional acreage, ϕ_t for t =0,...,T, and conventional pesticide use, u_{tg}^{i} for t = 0,...,T, g = 1,...,G, and i = 0, 1. The performance of this system under alternative IRM plans is compared using measures of the risk of resistance, conventional pesticide use, production value to farmers and production value to industry.

The probability that the proportion of resistant alleles exceeds 0.5 within T years measures the risk of resistance to *Bt*:

$$\Theta = \Pr(r_{1T} \ge 0.5)$$

where the probability is defined over the random distribution of pests for t = 0,..,T and g = 1,..,G. The expected number of conventional pesticide applications measures conventional pesticide use:

(5)
$$\Gamma = \mathsf{E}_{\mathsf{n}} \left[\sum_{t=0}^{\mathsf{T}-1} \sum_{g=1}^{\mathsf{G}} \frac{\phi_t \iota_{tg}^0 + (1-\phi_t) \iota_{tg}^1}{\mathsf{T}} \right]$$

where E_n is the expectation operator defined over the random distribution of pests for t = 0,..,T and g = 1,..,G. The expected annualized net present production value to farmers is a measure of value of the *Bt* crop to the regulated community:

(6)
$$\Pi_{F} = \mathsf{E}_{\mathsf{n}} \left[\frac{\sum_{t=0}^{I-1} \delta^{t} (\phi_{t} \pi_{t}^{0} + (1 - \phi_{t}) \pi_{t}^{1})}{\sum_{t=0}^{T-1} \delta^{t}} \right]$$

where π_t^i is the annual production value to farmers in season t for variety i, $\delta = 1 / (1 + r)$ is the discount rate and r is the real rate of interest. The annual production value for variety i is

(7)
$$\pi_{t}^{i} = P_{t}^{i}Y_{t}^{i} \left[1 - D(n_{t1}^{S^{i}}, ..., n_{tG}^{S^{i}}) - FC_{t}^{i} - \sum_{g=1}^{G} \iota_{tg}^{i}VC_{tg}^{i} \right]$$

where Y_t^i bushels/acre and P_t^i \$/bushel are the pest-free yields and crop prices; FC_t^i \$/acre is the production cost for items such as seed, fertilizer and labour that are exclusive of the cost of a conventional pesticide application; VC_{tg}^i \$/acre is the cost of a conventional pesticide application; VC_{tg}^i \$/acre is the cost of a conventional pesticide application; and $D_t^i(n_{t1}^{S_{i1}},...,n_{tG}^{S_{i0}})$ is the seasonal proportion of yield lost to pests. The expected annualized net present value of farmer payments to industry for the use of the *Bt* variety is another measure of the production value of *Bt* crops to the regulated community as well as a measure of incentives to develop new reduced-risk pesticides:

(8)
$$\Pi_{1} = \mathsf{E}_{\mathsf{n}} \left| \frac{\sum_{t=0}^{\mathsf{T}-1} \delta^{t} (1-\phi_{t}) \mathsf{TF}_{t}}{\sum_{t=0}^{\mathsf{T}-1} \delta^{t}} \right|$$

where TF_t is technology fee paid by farmers for the right to use the *Bt* variety.

Equations (4)-(6) and (8) are conditional on values assigned to the generations of pest per season, genotypic survival rates, survival rates for conventional pesticides, number of time periods, prices, pest-free yields, production costs, technology fee, discount rate, initial pest population and initial proportion of resistance. While reasonable values are available for many parameters, others are not known for certain. Typically, this uncertainty is addressed using sensitivity analysis for reasonable variations in parameter values. However, with suitable data, this uncertainty can be captured more directly using estimated distributions for the parameters. Let E_{UP} be the expectation operator defined over the distribution of uncertain parameters. Combined with equations (1)-(3) and (7), $E_{UP}[\Theta]$, $E_{UP}[\Gamma]$, $E_{UP}[\Pi_F]$, and $E_{UP}[\Pi_I]$ can be compared for alternative IRM policies to assess how well each meets the EPA's objectives.

Analyses of EPA policy alternatives have focused on the proportion of refuge assuming full adoption and compliance. These analyses hold ϕ_t constant over time assuming it is equal to the EPA's mandated proportion of refuge, ϕ . The adoption rate of a *Bt* variety in season t will depend on the expected return of conventional and *Bt* varieties: $\alpha_t = \alpha[EF(\pi_t 0), EF(\pi_t 1)]$ where $EF(\pi_t 0)$ and $EF(\pi_t 1)$ is the expected return for the conventional and Bt variety in season t. Adoption of Bt varieties of corn and cotton is far from full even after seven years in the field (NASS 2002). Furthermore, Carrière et al. (2003) found that Bt cotton leads to the regional suppression of the pink bollworm, a result predicted by many simulation models. The regional suppression of pests by Bt crops serves to reduce the value of these crops to farmers over time and puts downward pressure on adoption. Both of these factors reduce the proportion of the pest population exposed to Bt and the risk of resistance.

Becker (1968) argues that compliance costs play an important role in determining compliance rates, suggesting compliance with IRM will depend on the required proportion of refuge and expected return of conventional and *Bt* varieties: $\varphi_t = \varphi[EF(\pi_t 0), EF(\pi_t 1), \phi]$. Agricultural Biotechnology Stewardship Technical Committee (2002) found that 13% of *Bt*-corn farmers surveyed in the Midwestern US did not plant at least 20% refuge as required by the EPA. In the Southern US, where the EPA requires 50% refuge and pest pressure is more severe, 23% of *Bt*-corn farmers reported not planting enough refuge. These results provide anecdotal evidence against full compliance. They also suggest compliance rates are lower for higher refuge requirements and more severe pest pressure.

Given these behavioural adoption and compliance functions, the proportion of conventional variety planted in season t can be written as

(9) $\phi_t = (1 - \alpha_t) + \alpha_t \phi_t \phi.$

To the extent that *Bt* varieties are not fully adopted, previous analyses tend to underestimate the proportion of conventional acreage. To the extent that farmers violate refuge-size requirements, previous analyses tend to overestimate the proportion of conventional acreage.

Model implementation

Partial adoption and compliance have countervailing effects on the proportion of conventional variety planted and the evolution of resistance. Complex interactions between the biological processes governing resistance and economic incentives governing farmer and industry behaviour make the model generally intractable. Therefore, simulation provides a useful tool for understanding how partial adoption and compliance influence the efficacy of IRM policy. As an example, simulation results are constructed for European corn borer (ECB) *Bt* corn, based on parameter values that are consistent with corn production in the North-Central US.

Table 1 summarizes a variety of the parameter values used for this example. With the exception of the technology fee paid for *Bt* corn, these parameters come from Hurley et al. (2002). Other information not provide in Table 1 includes the distribution of random pests (N_g(·)), initial frequency of resistance (R₀), heterozygote survival rate on *Bt* corn (σ_{RS}), frequency of conventional pesticide applications (t_{tg}^{i}), *Bt*-corn adoption rates (α_t), compliance rates (ϕ_t), and expectations for the benefit of conventional and Bt corn (E_F(π_t^0), E_F(π_t^1)).

The log-normal distribution of random pest populations is also taken from Hurley et al. (2002). The mean of this distribution for first and second generation ECB are - $3.52 + 1.81n_{t-1,2}^{S} - 0.39n_{t-1,2}^{S}^{2}$ and $-1.59 + 9.47n_{t-1}^{S} - 11.31n_{t-1}^{S}^{2}$ (ECB/Plant). The standard deviation for first and second generation ECB is 0.96 and 1.11 (ECB/Plant). The distributions were estimated using field data from the North-Central US and imply an intergenerational dependence in random ECB populations that can result in

the type of regional suppression reported by Carrière et al. (2003). The distributions also imply that population growth is naturally limited.

The initial frequency of resistant alleles and heterozygote survival rate on *Bt* corn are key parameters that are not known for certain. Hurley et al. (2002) use Bayesian methods to estimate a joint distribution for these parameters based on field data. This distribution is used for calculating the expectation E_{UP} . The mean and standard deviation of the initial frequency of resistance is 1.1×10^{-3} and 1.1×10^{-3} . The mean and standard deviation of the heterozygote survival rate on *Bt* corn is 0.026 and 0.027. The correlation is -0.49.

Conventional pesticide applications are simulated based on an IPM economic threshold. Following Mason et al. (1996), the threshold used in the model for first and

second generation ECB are
$$\frac{VC_{t1}^{i}}{0.055P_{t}^{i}Y_{t}^{i}\sigma_{1}^{i}\eta_{t1}(1-\sigma_{1}^{\iota})} \text{ and } \frac{VC_{t2}^{i}}{0.028P_{t}^{i}Y_{t}^{i}\sigma_{2}^{i}\eta_{t2}(1-\sigma_{2}^{\iota})}.$$

When ECB populations exceed the threshold, conventional pesticides are applied. The thresholds imply that conventional pesticides are used only when the within-season value of an application exceeds the cost.

Table 1. Simulation parameter values

Parameter	Values
Biological parameters	
Pest generation	G = 2
Genotypic survival rates	$\sigma_{\rm g}^{0} = [1.0, 1.0, 1.0], \sigma_{\rm g}^{1} = [1.0, \sigma_{\rm RS}, 0.0]$
Conventional pesticide survival rate	$\sigma_1^{1} = 0.20, \sigma_2^{1} = 0.33$
Initial pest population (pests/plant)	$N_0 = 0.12$
Economic parameters	
Planning horizon (years)	T = 15
Interest rate	r = 0.04
Price of corn (\$/bushel)	$P_t^i = 2.35
Pest-free yield (bushels/acre)	$Y_t^{i} = 130$
Fixed production costs (\$/acre)	$FC_t^0 = $185.00, FC_t^1 = 193.00
Variable production costs (\$/acre)	$VC_t^0 = $14.00, VC_t^1 = 14.00
<i>Bt</i> -corn technology fee (\$/acre)	$TF_{t} = \$8.00$
Yield loss (bushels/acre)	$D_{t}^{i}(n_{t1}^{S_{i}}, n_{t2}^{S_{i}}) = Min\{0.055 n_{t1}^{S_{i}} + 0.028 n_{t2}^{S_{i}}, 1.0\}$

There continues to be a lack of the farm-level data necessary to estimate how adoption and compliance are influenced by the expected production value of Bt corn, the size of refuge, and other factors. To illustrate the need for this type of information, exponential adoption and compliance functions are employed. The functions are based on the increase in production value to farmers for switching from conventional to Bt corn. The compliance rate also depends on the required refuge size. Specifically, $\alpha_t =$

 $\frac{103.0 \frac{\mathsf{E}_{\mathsf{F}}(\pi_{\mathsf{t}}^{0}) - \mathsf{E}_{\mathsf{F}}(\pi_{\mathsf{t}}^{0})}{\mathsf{E}_{\mathsf{F}}(\pi_{\mathsf{t}}^{0})} - 2.9}$ and $\varphi_{\mathsf{t}} = \mathbf{e}$ of farmers adopt *Bt* corn even when there is no expected increase in production value due to a risk or convenience benefit. Adoption reaches 90% when *Bt* corn is expected to increase the production value by 5%. This adoption equation does not account for the typical technology-adoption cycle, so it tends to over-predict observed adoption trends. The compliance equation assumes that 13% of farmers will not plant a required 20% refuge and 23% will not plant a required 50% refuge when the expected increase in the production value is 5%. These results are roughly consistent with anecdotal evidence (Agricultural Biotechnology Stewardship Technical Committee)

2002). The expectation for the production value of conventional and Bt corn is the

five-year moving average of the past production value: $E_F(\pi_t^i) = \sum_{\tau=t-5}^{t-1} \frac{\pi_{\tau}^i}{5}$.

The model is implemented in C^{++} using algorithms in Press, Teukolsky and Vetterling (1992). Monte-Carlo techniques are used to evaluate expectations of the distribution of pest and uncertain parameters.

Results

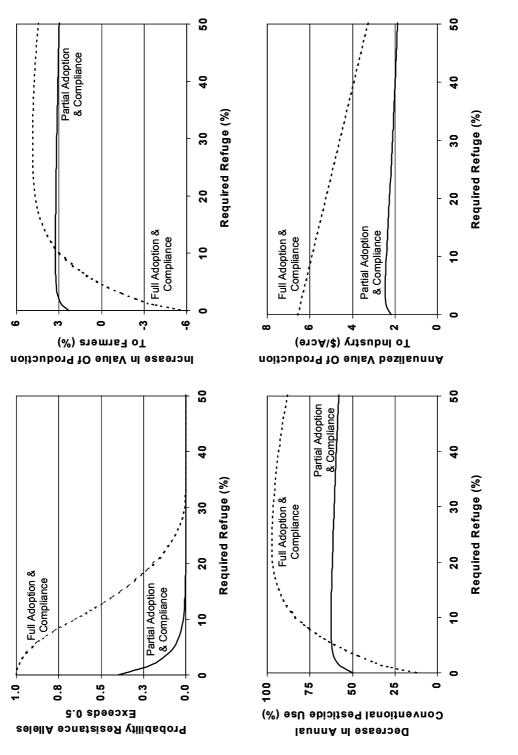
Comparing the stylized model of full adoption and compliance ($\phi_t = \phi$) to partial adoption and compliance ($\phi_t = (1 - \alpha_t) + \alpha_t \phi_t \phi$) illustrates the important role human behaviour plays in influencing the efficacy of IRM policy. Figure 1 shows this comparison for the probability that the proportion of resistant alleles exceeds 0.5 in 15 years (risk of resistance), expected percentage decrease in conventional pesticide use (environmental benefit), expected percentage increase in the production value to farmers (farmer benefit), and annualized production value to industry (industry benefit) for refuge requirements ranging from 0 to 50%.

The full model predicts a higher risk of resistance and larger industry benefits than the partial model. For the environmental and farmer benefit, the full model predicts lower values than the partial model for low refuge requirements and higher values for high refuge requirements.

Both models indicate that the risk of resistance falls with an increase in the refuge requirement. However, sensitivity analysis shows that the risk of resistance in the partial model can inrease with the refuge requirement when compliance rates are more sensitive to the cost of compliance. For example, the risk of resistance can be reduced to less than 5% with a refuge requirement of at least 26% in the full model and 7% in the partial model.

Both models show there are limited environmental and farmer benefits to requiring additional refuge. The full and partial models predict environmental benefits are maximized with a 23 and 9% refuge requirement, while farmer benefits are maximized with a 28 and 10% refuge requirement. What is in the interest of the environment is in the interest of farmers. Farmer and environmental benefits move similarly with changes in the refuge requirement because the more farmers can take advantage of Bt corn to increase their production value the less they rely on conventional pesticides. Adding human behaviour makes this result more pronounced. A disturbing result in the full model that demonstrates the weakness of the underlying assumptions is a decrease in the production value to farmers when the required refuge is small. Why would farmers ever plant Bt corn if it reduced their production value?

The full and partial models produce somewhat conflicting results for industry benefits. The full model predicts no industry benefit from refuge requirements (the industry benefit is maximized with no refuge requirement), while the partial model predicts limited benefits (the industry benefit is maximized with a 4% refuge requirement). The full model assumes farmers must plant Bt corn even if it is not in their interest, so the industry has a captive market. Maximizing the amount of Bt corn or minimizing the amount of refuge maximizes the industry benefit from this captive market. For the more plausible assumptions of the partial model, farmers choose not to plant Bt corn if it is not in their interest. Therefore, if industry wants to sell more Bt corn it must ensure its product remains both effective and necessary. Two factors work against the effectiveness and necessity of Bt corn. First, as resistance increases





the product becomes less effective. Since refuge slows the evolution of resistance, it provides an important industry benefit by maintaining the efficacy of Bt. Second, regional suppression of ECB reduces the necessity of Bt corn, as well as other pesticides. Planting refuge reduces suppression and increases the long-run need for Bt corn to the benefit of industry. Interestingly, industry never strongly opposed having refuge requirements. Instead, they argued about how much refuge was necessary. Anecdotally, Monsanto's original voluntary IRM plan required farmers to plant 5 percent refuge for Bt corn and cotton.

Most of the entomological literature has relied on the risk of resistance to gauge the efficacy of IRM policy. Figure 1 shows why the risk of resistance may not be a good measure of IRM success given the EPA's stated objectives. While the benefits of increasing the required refuge on the risk of resistance appear unlimited, the benefits to the environment, farmers and industry are. The risk of resistance is only positively correlated with specific measures of EPA objectives for relatively low refuge requirements.

Conclusions

The EPA has determined that IRM for Bt crops is in the interest of the American public because it will reduce the use of more hazardous conventional pesticides. To develop IRM guidelines, the EPA has relied heavily on simulation models due to the novelty of Bt PIPs. Entomologists have taken a lead role in the developing IRM models to inform policy. These models focus on the insect behaviour and the biological processes governing resistance. A shortcoming is a lack of attention to human behaviour. Of particular importance is farmer adoption and compliance behaviour. Another shortcoming is their focus on the risk of resistance, without explicit consideration of the effect of IRM on conventional pesticide use, and the production value of Bt crops to farmers and industry, which are factors that relate more directly to the EPA's stated IRM objectives.

The purpose of this paper was to demonstrate how ignoring adoption and compliance behaviour can result in an inaccurate assessment of the efficacy of IRM policy. An example shows that the traditional assumptions of full adoption and compliance may over-estimate the risk of resistance. However, since adoption and compliance behaviour have countervailing effects, the result is sensitive to underlying assumptions of human behaviour that are not precisely specified at this time. The example also shows the risk of resistance can be a poor gauge of the success of alternative IRM policies.

Farmer adoption and compliance behaviour will play a key role in determining the successes and failures of IRM policy. To assure more successes than failures, farmlevel data on adoption and compliance would be useful, so farmer behaviour can be more accurately specified. Another important issue not addressed by any IRM model is industry behaviour. Industry behaviour is important because it sets the price farmers pay for *Bt* crops and is required by the EPA to enforce IRM guidelines. In the present example, the price of the technology is held constant over time and industry enforcement of IRM guidelines is ignored. Since the introduction of ECB *Bt* corn, the price has fallen from around \$10/acre to about \$5/acre. In 2003, the industry instituted a new IRM-compliance assurance programme that includes on-farm monitoring and sanctions for non-compliant farmers. New data and models exploring industry pricing and enforcement behaviour under alternative IRM policies would provide additional insights into how to regulate *Bt* crops more effectively. Adaptive models of IRM are also starting to emerge (Andow and Ives 2002). With better surveillance techniques for monitoring the evolution of resistance, adaptive IRM policies become attractive because much of the information necessary to develop an effective policy can only be learned from commercial release and close scrutiny of *Bt* crops in the field.

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