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Fees or refuges: which is better for the sustainable management of insect resistance to transgenic *Bt* corn?

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The evolution of resistance in insect pests will imperil the efficiency of transgenic insect-resistant crops. The currently advised strategy to delay resistance evolution is to plant non-toxic crops (refuges) in close proximity to plants engineered to express the toxic protein of the bacterium *Bacillus thuringiensis* (*Bt*). We seek answers to the question of how to induce growers to plant non-toxic crops. A first strategy, applied in the United States, is to require *Bt* growers to plant non-*Bt* refuges and control their compliance with requirements. We suggest that an alternative strategy is to make *Bt* seed more expensive by instituting a user fee, and we compare both strategies by integrating economic processes into a spatially explicit, population genetics model. Our results indicate that although both strategies may allow the sustainable management of the common pool of *Bt*-susceptibility alleles in pest populations, for the European corn borer (*Ostrinia nubilalis*) one of the most serious pests in the US corn belt, the fee strategy is less efficient than refuge requirements.

Keywords: *Bacillus thuringiensis*;
European corn borer; resistance management;
common property resource; refuge policy;
economic model

1. INTRODUCTION

Genetically modified crops are currently grown over 81 million hectares worldwide. More than 20% of these crops are insect-resistant through the expression of insecticidal proteins of *Bacillus thuringiensis* (*Bt*). With a planted area of 11.2 million hectares, *Bt* corn is the major insect-resistant crop (James 2004). Preserving the efficiency of *Bt* corn requires delaying or preventing the evolution of resistance to *Bt* toxins in pest populations. The 'high-dose refuge' (HDR) strategy is the currently advised method for managing *Bt* resistance. Refuges are defined as non-*Bt* host plants sown in the vicinity of *Bt* crop fields (Gould 1998). The principle underlying the HDR strategy is that the mixing of pools of susceptible (preserved in the refuges) and resistant (selected in *Bt* crop fields) insects can delay resistance evolution, if *Bt* resistance is rare and functionally recessive (Alstad & Andow 1995). This theory has received experimental support (Gould 2000, 2003; Shelton *et al.* 2000; Tang *et al.* 2001). In this study, we address the problem of how to induce growers to plant non-*Bt* crops.

A first strategy is to require *Bt* growers to plant refuge fields. In the United States, the Environmental Protection Agency (EPA) specifies the minimum refuge size and maximum distance between refuges and *Bt* crops, and requires seed companies to promote compliance with these mandates among growers with the threat of rescinding the former's seed registration (USEPA 2001). The efficiency of this practice is, however, questionable (Dove 2001; Jaffe 2003; Bourguet *et al.* 2005). For instance, a survey revealed that almost 30% of corn growers could not accurately state the required size and location of their refuges (Dove 2001). Here we propose an alternative strategy to induce growers to plant less *Bt* crops: make *Bt* seed more expensive by instituting a user fee. The revenue from the fee could be used to improve *Bt* varieties or develop new pest control tools, hence benefiting all growers equally. The two strategies are hereafter called 'refuge strategy' and 'fee strategy'.

Non-compliance with requirements under the refuge strategy is a consequence of the pool of *Bt*-susceptibility alleles in mobile pest populations being a common property resource shared by *Bt* growers (Hueth & Regev 1974; Barnett & Gibson 1999; Bourguet *et al.* 2005). By planting *Bt* crops, each grower increases personal short-term benefits but favours the selection of resistant pests that can spread in the cultivated area, therefore potentially negatively affecting the long-term benefits of neighbouring *Bt* growers. Each grower is thus tempted to maximize their utilization of *Bt* crops (i.e. not to implement the mandatory refuge) before sharing the costs of resistance evolution with other growers. This temptation to overuse unmanaged common resources was first described by Garrett Hardin in the case of pasturelands left open to several herders and is called the *Tragedy of the Commons* (Hardin 1968).

From an economic perspective, the refuge strategy is a 'command-and-control' approach of common property resource management, because it imposes specific actions and technologies on all farmers, and is enforced through the control of farmer's compliance. It is generally argued that this approach is inferior to regulations relying on 'market-based' incentives such as Pigouvian fees or tradable environmental allowances, for two reasons (Baumol & Wallace 1988; Kolstad 2000). First, the command-and-control approach is more costly to implement,

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Table 1. Expected number of females per plant after migration and expected annual profit over the year of *Bt* crops introduction, depending on the geographical location of the field and the resistance management strategy. (For each field, the grower's choice that maximizes annual profit is given in bold. Model parameters are based on ECB populations in the US Corn Belt ($N=1800$).)

field location (km)	0	63	126	189	252	315	378	441	504	567	630
expected number of females per plant	0.19	0.18	0.16	0.15	0.14	0.13	0.11	0.1	0.09	0.07	0.06
expected profit ($ per ha)											
no regulation											
Cn field (untreated)	223	228	233	239	244	249	255	260	265	271	276
Cn field (treated)	252	253	254	255	256	257	258	259	261	262	263
Bt field	**278**	**278**	**278**	**278**	**278**	**278**	**278**	**278**	**278**	**278**	**278**
HDR strategy (20% treated refuge)											
Cn field (untreated)	223	228	233	239	244	249	255	260	265	271	**276**
Cn field (treated)	252	253	254	255	256	257	258	278	261	262	263
Bt field	**273**	**273**	**273**	**273**	**274**	**274**	**274**	**274**	**274**	**275**	275
fee strategy (20$ per ha fee)											
Cn field (untreated)	223	228	233	239	244	249	255	**260**	**265**	**271**	**276**
Cn field (treated)	252	253	254	255	256	257	**258**	259	261	262	263
Bt field	**258**	**258**	**258**	**258**	**258**	**258**	258	258	258	258	258

since it requires active monitoring to detect rule breakers. Moreover, some farmers might not comply when the risk of being detected or punishment in cases of non-compliance are too low. Second, contrary to the market-based approach, the command-and-control approach does not provide farmers with incentives to select efficient actions and technologies to preserve the resource.

Here we study whether the implementation of a fee on *Bt* seed is a sustainable alternative to the currently applied refuge strategy for managing the common pool of *Bt*-susceptibility alleles in pest populations. The management of *Bt* resistance alleles is of particular interest to the debate on command-and-control versus market-based regulation, because the state of the resource strongly depends on spatial components, such as refuge placement and pest dispersal (Caprio 2001; Ives & Andow 2002; Vacher *et al.* 2003; Cerda & Wright 2004). Recent bio-economical studies indeed show that the spatial functioning of the resource may have a major impact on optimal regulation instruments (Sanchirico & Wilen 1999, 2005; Janmaat 2005). Moreover, given the increasing popularity of market-based environmental instruments (Alper 1993; Dietz *et al.* 2003), it is crucial to predict their efficiency before they are actually applied to major agricultural pests targeted by *Bt*-transgenic crops.

2. MATERIAL AND METHODS

To compare the two strategies, we integrated economic processes into a spatially explicit model of population genetics composed of a chain of equal-sized crop fields interconnected by pest migration.

The population genetics model (based on Lenormand & Raymond 1998; Bourguet *et al.* 2000) assumes that resistance to *Bt* toxins is determined by a single diallelic locus. After hatching, larvae experience genotype-dependent mortality due to *Bt* toxicity and the fitness cost of resistance. They then experience genotype-independent mortality due to conventional pesticide application, density-dependent regulation and overwintering. The model assumes a linear mortality gradient reflecting winter temperatures along the chain of crop fields. Finally, adults emerge, migrate and reproduce. The distribution of dispersal distances follows a symmetric binomial distribution (Lenormand & Raymond 1998). Reproduction is panmictic at the field scale and each female adult gives rise to a fixed number of larvae. Crop yield is assumed to decrease with the number of larvae per plant after density-dependent regulation.

The economic model assumes that every year, each grower chooses the planting option that will maximize their profit the following year (table 1). Each grower is assumed to have one field. Under the refuge strategy, each grower decides whether to plant conventional crops or *Bt* crops with some refuge. A single chemical pesticide application is allowed on conventional crops. The chemical treatment of refuges is either imposed or forbidden. The model assumes a fixed proportion of growers who do not comply with refuge mandates. Cheaters are *Bt*-adopters for whom the difference between profit levels without and with the mandated refuge is the highest. Under the fee strategy, each grower chooses whether to plant conventional crops or costly *Bt* crops. The revenue from the fee on *Bt* seed is redistributed to all growers in a lump-sum way (i.e. that does not bias grower choice).

The model is run with a management strategy fixed through time. The sustainability of a management strategy is assessed over a given planning horizon (see Hurley *et al.* 2002; Linacre & Thompson 2004) based on three criteria: average frequency of the resistance allele, average conventional pesticide use and average cumulated profit made by growers.

Economic parameters are based on US corn crops (Hurley *et al.* 2002; Linacre & Thompson 2004) and biological parameters, when known, are based on published information (Caffrey & Worthley 1927; Labatte & Got 1991; Onstad & Gould 1998; Showers *et al.* 2001; Onstad *et al.* 2002) on the European corn borer (ECB), *Ostrinia nubilalis* (Hübner) (see table S1 in electronic supplementary material). Unknown parameters were varied over a realistic range of values to test for the sensitivity and robustness of our predictions (see table S2 in electronic supplementary material). In the following, we first consider an agrosystem at the scale of the corn belt. It is composed of $N=1800$ fields interconnected by migration. Each field is 30 acres (*ca* 0.35 km×0.35 km), which is the typical acreage of a field in the corn belt. Distance d between adjacent fields is taken as 0.35 km. The total length of the agrosystem is 630 km, or roughly the length of the state of Illinois. Then we consider a smaller agrosystem of only 10.5 km length, composed of $N=30$ fields. The scale of gene flow is increased relative to the scale of environmental heterogeneity by increasing pest dispersal distance, while keeping the slope of the environmental gradient constant.

3. RESULTS AND DISCUSSION

In agreement with previous studies (Hurley *et al.* 2002), we find that the refuge strategy permits the sustainable management of the common pool of *Bt*-susceptibility alleles in ECB populations at the scale of the corn belt (i.e. in an agrosystem of *ca* 600 km length). There is a refuge percentage that maximizes cumulated discounted profit, minimizes conventional

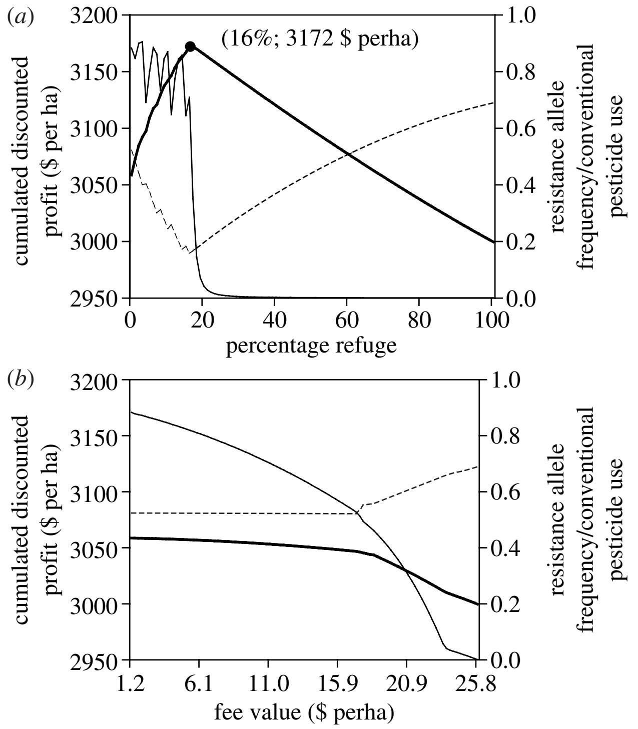

Figure 1. Cumulated discounted profit (thick plain line), resistance allele frequency (thin plain line) and conventional pesticide use (thin dotted line) at the end of the planning horizon. Model parameters are based on ECB populations in the US corn belt ($N=1800$). (*a*) Effect of per cent refuge under the assumption that compliance to refuge mandates is 100%. Conventional pesticide treatments are allowed in the refuge. (*b*) Effect of fee value. The range of values is chosen such that the cumulated discounted profit, the resistance allele frequency and conventional pesticide use are identical for (i) a 0% refuge and the minimal fee value and (ii) a 100% refuge and the maximal fee value.

pesticide use and maintains resistance alleles at low frequencies (figure 1*a*). Consistent with previous studies (Onstad & Gould 1998; Onstad *et al.* 2002), we find that the optimal percentage refuge is higher for refuges treated with conventional pesticides than for those untreated and depends on pest genetics, in particular the dominance level of resistance and the initial frequency of the resistance allele (see table S2 in electronic supplementary material). The optimal percentage refuge also varies with the level of compliance of refuge mandates (figure 2). Our results support the need for programmes aimed at reinforcing this level, by showing that growers' cumulated discounted profit increases with the level of compliance, whereas conventional pesticide use decreases (figure 2).

In contrast to the refuge strategy, no sustainable resistance management emerges under the fee strategy (figure 1*b*) for the corn belt. This is because the fee strategy leads to the spatial segregation of *Bt* and conventional crops (*Bt* crops are preferred by farmers experiencing high pest pressure in their fields), and ECB gene flow between the two crop types is not sufficiently high for conventional crops to serve as a refuge. Our numerical studies do, however, indicate that the fee strategy may constitute a sustainable pest management strategy when the agrosystem is smaller and more heterogeneous than is the case for the corn belt (i.e. an agrosystem of *ca* 10 km length). Under these conditions we find that the maximal profit under the fee strategy drastically increases with the geographical scale of gene flow in the agrosystem (table 2). Similarly, for a refuge strategy which has partially been complied with, an area covered with *Bt* crops emerges in the high pest pressure zone because of non-compliance and the maximal profit increases with the geographical scale of gene flow (table 2). In contrast, under a refuge strategy which has been fully complied with, refuges are evenly distributed within the *Bt* crop production area and profits vary little (table 2). Importantly, this latter result implies that the refuge strategy is more robust to variations in pest dispersal distance—a parameter that is often difficult to measure—when growers comply with refuge mandates. Hence, again, our results support the need for programmes aimed at reinforcing compliance to refuge mandates among *Bt* growers. Finally, we compared the maximal growers' cumulated discounted profit under the refuge and the fee strategies depending on the level of compliance to refuge mandates and pest dispersal distance. Low compliance to refuge mandates, high pest dispersal distance and pronounced environmental heterogeneity all favour the fee strategy (see figures S1 and S2 in electronic supplementary material), but overall, we find that the fee strategy rarely outperforms the refuge strategy.

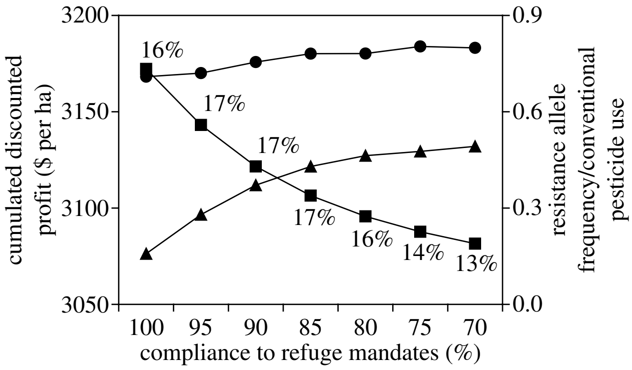

Figure 2. Maximal cumulated discounted profit (squares), resistance allele frequency (circles) and conventional pesticide use (triangles) at the end of the planning horizon as a function of the level of compliance to refuge mandates under the refuge strategy. Optimal refuge percentages are given above the profit line. Model parameters are adjusted to ECB populations in the US corn belt ($N=1800$).

4. CONCLUSION

Theoretical predictions derived from our bio-economical, simple model of corn production in the US corn belt indicate that there is no foundation for a fee on *Bt* seed as an alternative to the currently applied refuge strategy in the management of *Bt*-susceptibility alleles in ECB populations, even if market-based management strategies of common property resources are increasingly popular and tend to replace command-and-control environmental rules (Alper 1993; Dietz *et al.* 2003). Our results show that management strategies creating 'hot-spots' in the exploitation of the

Table 2. Impact of pest dispersal distance on the maximal cumulated discounted profit that can be obtained by growers, depending on the resistance management strategy. (Refuge percentage and fee value that maximize growers' cumulated discounted profit are indicated by italics. Model parameters are based on ECB populations in a small agrosystem ($N=30$).)

pest dispersal distance (km. gen$^{-1/2}$)	1	2	3	4	5	6	7
HDR strategy, full compliance							
profit ($ per ha)	3172	3172	3172	3172	3172	3173	3175
refuge percentage	*16*	*16*	*16*	*16*	*16*	*16*	*16*
HDR strategy, 70% compliance							
profit ($ per ha)	3071	3123	3152	3159	3162	3165	3167
refuge percentage	*8*	*55*	*37*	*32*	*30*	*29*	*29*
fee strategy							
profit ($ per ha)	3058	3085	3123	3161	3140	3144	3195
fee value ($ per ha)	*14.4*	*21.9*	*20*	*18.7*	*19.4*	*19*	*17.6*
no regulation							
profit ($ per ha)	3057	3052	3045	3041	3041	3046	3054

genetic resource, such as the fee strategy or the refuge strategy with imperfect compliance with refuge mandates have low sustainability because the state of the common-pool resource does not depend on *global* but rather on *local* exploitation rates. Therefore, we conclude that optimal policies for ECB management will require taking into account *local* pest pressure and specific agricultural practices.

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