

Modeling the invasion of recessive Bt-resistant insects: An impact on transgenic plants

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Received 25 November 2003; received in revised form 13 May 2004; accepted 14 June 2004

Abstract

There is a growing public concern on ecological and evolutionary consequence of the use of genetically modified organisms. We study the impact of Bt-resistant pests on genetically modified Bt crops. We develop and analyse a conceptual reaction–diffusion model of the Bt crop–Bt-susceptible insects–Bt-resistant insects to simulate the invasion of Bt-resistant insects. We show by means of computer simulations that there is a key parameter, which we define as the growth number that characterizes the insects' fitness. We also show that the Bt-resistant insect invasion can lead to inhomogeneity in plant and insect spatial distributions. The plant biomass is found to be essentially dependent on the duration of the Bt-resistant insect reproduction period. There are two types of this dependence. One of them exhibits, respectively, higher plant biomass in comparison with another. The ambiguity in the response of the Bt crop–Bt-susceptible insects system to the invasion of Bt-resistant insects can lead to serious complications in attempts to regulate the dynamics of the system.

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Keywords: Invasion; Transgenic plants; Bt-resistant pests

1. Introduction

There is a growing interest in mechanisms of pest resistance against genetically modified insecticidal pest-resistant crops due to considerable ecological and/or economical concerns (Dale et al., 2002; Mellon and Rissler, 1998). Transgenic crops (Bt crops) express *Bacillus thuringiensis* genes which produce insecticidal proteins (Bt toxins) and, by doing so, provide pest control in agricultural practice (Groot and Dicke, 2002). Such a control is an important component of durable

crop-protection programs (Armstrong et al., 1995; Benedict et al., 1996; Lewis et al., 1998).

Whenever pests are exposed to pesticides, selection occurs for alleles that confer resistance to those pesticides. Since the work by Comins (1977), where the development of insecticide resistance was considered theoretically, a lot of field and laboratory observations of resistance of insects to Bt toxins have been reported (Alstad and Andow, 1995; Chaufaux et al., 1997; Gould, 1998; Huang et al., 1999; Luttrell et al., 1999; Perez and Shelton, 1997; Tabashnik, 1994; Tabashnik et al., 2000). Widespread and long-term planting of Bt crops makes pest resistance more probable because it increases pest exposure to Bt toxins in time and in space. Unlike the Bt toxins in sprays which are degraded by sunlight in hours or days, the Bt toxins in Bt protected crops are produced throughout a season. As a result, Bt

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crops planted on millions of hectares (Dale et al., 2002) vastly increase the area over which pests are exposed to Bt toxins and the probability of appearance and expansion of Bt-resistant insects.

The appearance and expansion of insecticide resistance in an agricultural ecosystem depends on a set of biological and ecological factors. Computer simulations can reveal key factors and integrate them in order to evaluate an environmental impact of the Bt-resistant insect invasion. Mechanisms of pest evolutionary adaptation to a pest-resistant crop have been the subject of much investigation (Gould, 1998; Hillier and Birch, 2002a, b; Onstad and Gould, 1998; Onstad et al., 2002; Storer et al., 2003a, b). In the proposed model we will consider spatio-temporal dynamics of an agricultural ecosystem consisting of transgenic Bt plants, insects susceptible to Bt toxins, and adapted, Bt-resistant insects carrying a recessive mutation enabling them to grow on Bt plants. We show that the invasion of the Bt-resistant insects can lead to spatially inhomogeneous distributions of plants and insects. Spatially averaged plant biomass is shown to be strongly and ambiguously dependent on the duration of the Bt-resistant insect reproduction period.

2. Model

Conceptual minimal models are an appropriate tool for searching and understanding basic mechanisms of pattern formation and nonlinear system dynamics (Hiller and Birch, 2002a, b; Kolmogorov et al., 1937; Levin and Segel, 1976; Lotka, 1925; Medvinsky et al., 2002; Turing, 1952; Volterra, 1926). Following this approach, we develop the 1D three-component model where at any point X and time τ the dynamics of Bt plant and insect biomass are given by the differential equations

$$\frac{\partial P}{\partial \tau} = rP \left(1 - \frac{P}{K} \right) - \frac{C_1 P}{C_2 + P} (I_s + I_r) - \left[\frac{1}{4} \eta_s(P) I_s^2 + \frac{1}{4} \eta_r(P) I_r^2 + \frac{1}{2} \eta_s(P) I_s I_r \right]_{\tau \in [nT, nT + \varepsilon T]}, \quad (1)$$

$$\frac{\partial I_s}{\partial \tau} = \frac{k_s C_1 P}{C_2 + P} I_s - \mu I_s + \delta_s \left[\frac{1}{4} \eta_s(P) I_s^2 + \frac{1}{2} \eta_s(P) I_s I_r \right]_{\tau \in [nT, nT + \varepsilon T]} + D \frac{\partial^2 I_s}{\partial X^2}, \quad (2)$$

$$\frac{\partial I_r}{\partial \tau} = \frac{k_r C_1 P}{C_2 + P} I_r - \mu I_r + \delta_r \left[\frac{1}{4} \eta_r(P) I_r^2 \right]_{\tau \in [nT, nT + \varepsilon T]} + D \frac{\partial^2 I_r}{\partial X^2}. \quad (3)$$

Eqs. (1)–(3) describe the spatio-temporal dynamics of plant $P(X, \tau)$, susceptible insect $I_s(X, \tau)$ and resistant insect $I_r(X, \tau)$ biomass, correspondingly. The parameters r and K denote the intrinsic growth rate and the carrying capacity of the plant population; μ is the combined per unit mass insect respiration and mortality rates. The constants C_1 and C_2 parameterize the saturating functional responses. D is the insect diffusion coefficient. The terms that are in the square brackets “work” only throughout the reproduction period of an εT length. The introduction of these terms takes into account the common assumption that Bt-resistant mutant alleles are usually recessive (see Hillier and Birch, 2002a for more details). This implies that mating of susceptible and resistant insects should yield Bt-susceptible offsprings. The functions $\eta_s(P)$ and $\eta_r(P)$ are the effective fecundity rates of the susceptible and Bt-resistant pests, respectively; the terms involving these functions of the plant biomass P account for both insect reproduction and maturation of insects’ offsprings. We allow for the fact that Bt plants selectively affect larvae (Rajamohan et al., 1998), that is embodied in the form of the function $\eta_s(P)$; namely, we suppose that the effective fecundity rate falls as soon as P is more than a critical value P_{cr}

$$\eta_s(P) = \eta_s^0 P \exp\left(-\frac{\lambda P}{K}\right), \quad (4)$$

where η_s^0 and λ are constants, and $\lambda > 1$; $P_{cr} = K/\lambda$. In contrast to $\eta_s(P)$, the effective fecundity rate $\eta_r(P)$ of Bt-resistant insects does not tend to decrease with increase in the Bt plant biomass, and we suppose that

$$\eta_r(P) = \eta_r^0 P, \quad (5)$$

where η_r^0 is a constant. The parameters k_s and k_r in Eqs. (2) and (3) are yield coefficients of, respectively, susceptible and resistant insects to the plants; δ_s and δ_r are the yield coefficients of susceptible and resistant larvae, correspondingly. Our model also accounts for Bt plants being periodically sowed. This implies that

$$P = P_0 \quad \text{at } \tau = nT, \quad \text{where } n = 0, 1, 2, \dots \quad (6)$$

In other words, we define the start of a growing season as the beginning of the reproduction period of εT length (Eqs. (1)–(3)). We set $T = 150$ days, which roughly corresponds to the length of a normal growing season (Storer et al., 2003a).

For later convenience, the model (1)–(6) is simplified by introducing dimensionless variables

$$p = \frac{P}{K}; \quad i_s = \frac{I_s}{K}; \quad i_r = \frac{I_r}{K}; \quad t = \frac{A\tau}{T}; \quad x = X \sqrt{\frac{A}{DT}}.$$

As a result, from Eqs. (1)–(6) we obtain

$$\begin{aligned} \frac{\partial p}{\partial t} = & \alpha p(1-p) - \frac{\beta p}{\gamma+p} (i_s + i_r) \\ & - [\omega_s(p)i_s^2 + \omega_r(p)i_r^2 \\ & + 2\omega_s(p)i_s i_r]_{t \in [nA, nA+\varepsilon A]}, \end{aligned} \quad (7)$$

$$\begin{aligned} \frac{\partial i_s}{\partial t} = & \frac{k_s \beta p}{\gamma+p} i_s - v i_s + \delta_s [\omega_s(p)i_s^2 \\ & + 2\omega_s(p)i_s i_r]_{t \in [nA, nA+\varepsilon A]} + \frac{\partial^2 i_s}{\partial x^2}, \end{aligned} \quad (8)$$

$$\begin{aligned} \frac{\partial i_r}{\partial t} = & \frac{k_r \beta p}{\gamma+p} i_r - v i_r \\ & + \delta_r [\omega_r(p)i_r^2]_{t \in [nA, nA+\varepsilon A]} + \frac{\partial^2 i_r}{\partial x^2}, \end{aligned} \quad (9)$$

$$\omega_s(p) = \omega_s^0 p \exp(-\lambda p), \quad (10)$$

$$\omega_r(p) = \omega_r^0 p, \quad (11)$$

$$p = p_0 \text{ at } t = nA, \text{ where } n = 0, 1, 2, \dots \quad (12)$$

where $\alpha = rT/A$, $\beta = C_1 T/A$, $\gamma = C_2/K$, $v = \mu T/A$, $\omega_s = (T/4A)\eta_s K$, $\omega_r = (T/4A)\eta_r K$, $\omega_s^0 = \eta_s^0 K$, $\omega_r^0 = \eta_r^0 K$. Putting $A = T$, we obtain that numerically $t = \tau$, $x = X\sqrt{1/D}$, $\alpha = r$, $\beta = C_1$, $\gamma = C_2/K$, $v = \mu$, $\omega_s = \frac{1}{4}\eta_s K$, $\omega_r = \frac{1}{4}\eta_r K$.

To complete the mathematical description, the model (7)–(12) must be provided with boundary and initial conditions. Here, we use Neumann zero-flux boundary conditions. Plants and susceptible insects are supposed to be homogeneously distributed in space at $t = 0$, while Bt-resistant insects are initially (at $t = 0$) concentrated in a small region at the center of the whole domain.

To investigate the spatio-temporal dynamics of the system, Eqs. (7)–(9) together with Eqs. (10)–(12) were solved numerically by an explicit finite difference scheme. The mesh step sizes $\Delta x = 1$ and $\Delta t = 0.001$ were chosen in such a way to ensure that the results obtained were invariant under variations of the steps which confirmed the accuracy of the simulations.

3. Main results

A key parameter of the insect fitness: The study of the after-effects of invasion of Bt-resistant insects is a main objective of this work. Because of this, it was important to reveal a key parameter (or parameters) of the model (7)–(12) that could characterize the Bt-resistant pest’s fitness, or, in other words, the possibility of Bt-resistant insects surviving and impacting the plant biomass. Computer simulations allow us to reveal such a parameter. We call it “the growth number”. It is defined

in the following way:

$$Gr = \frac{k\beta}{\gamma+1} - v. \quad (13)$$

The invasion of Bt-resistant insects leads to spatial inhomogeneity in plant and insect spatial distribution: Fig. 1 shows the area (shaded) in the Gr -space that corresponds to the survival of the Bt-resistant insects and their successful invasion of the plants–susceptible insects system. One can see that this area is situated in the right half-space where the Bt-resistant insect growth number $Gr_r > 0$; the condition for survival and expansion of the Bt-resistant insects is the inequality $Gr_r > Gr_s$. As this takes place, Bt-susceptible pests are displaced by Bt-resistant ones.

The invasion of Bt-resistant insects is accompanied by formation of inhomogeneities in spatial distributions of plant and insect biomass. Fig. 2 demonstrates the formation and dynamics of the spatial structures in plant and Bt-resistant insect populations (here $Gr_r = 0.2$ and $Gr_s = 0.07$). One can see that a small patch of Bt-resistant insects gives rise to two population waves of the resistant insects propagating on either side of the center of the domain. Then, these waves transform into the set of peaks, which are gradually extending over the whole domain (Fig. 2, the left column). The shape and location of these peaks are not constant and change in time. Spatial distributions of the plants are in a good correspondence with the insect distributions: the plant biomass is higher where and when the insect biomass is lower, and *vice versa* (Fig. 2). This is an evident consequence of consumption of the plant biomass by insects.

The dynamics of transgenic plant biomass depends dramatically on the duration of the insect reproductive period: To characterize an impact of the Bt-resistant

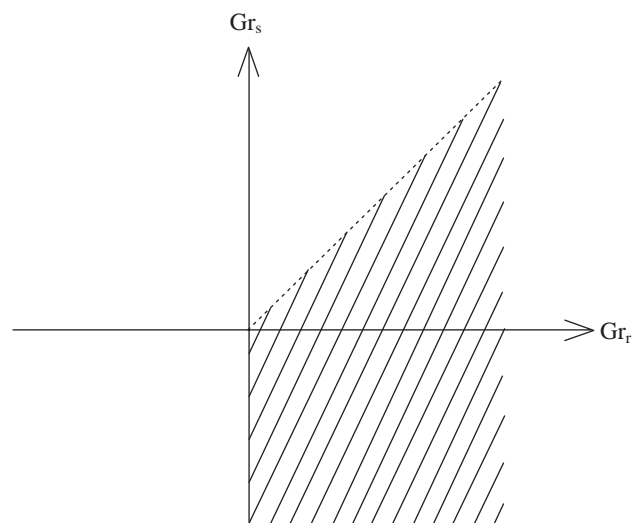


Fig. 1. The growth number (Gr_r, Gr_s) space. The area of survival of Bt-resistant insects is shaded.

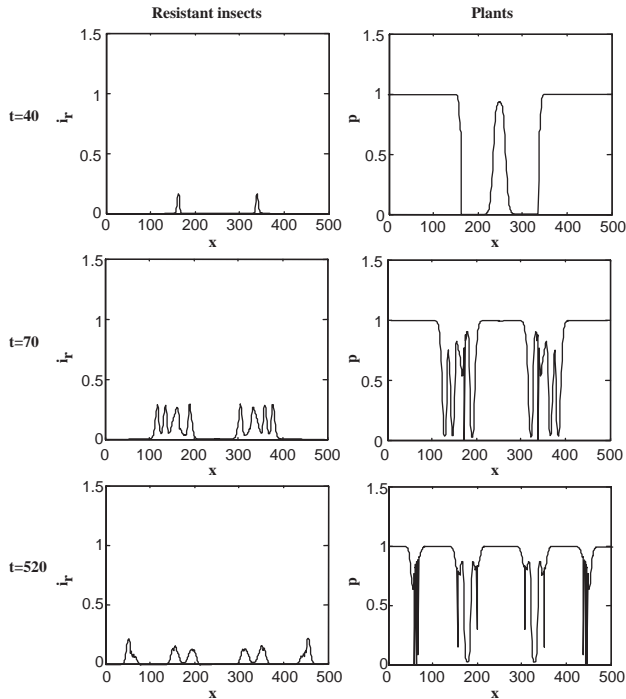


Fig. 2. Bt-resistant insect (the left column) and Bt plant (the right column) spatial patterns resulting from the invasion of the Bt-resistant insects. The calculations are carried out at the following set of model parameters: $\alpha = 1$; $\beta = 1.5$; $\gamma = 0.1$; $\nu = 0.75$; $k_r = 0.7$; $k_s = 0.6$; $A = 150$; $n = 10$; $\varepsilon A = 40$; $\delta = 1$; $\omega_s^0 = 40$; $\omega_r^0 = 20$; $\lambda = 10$.

insects on the plants, we calculate the averaged plant biomass

$$\langle p \rangle = \frac{1}{t} \int_0^t \int_0^L p(x, t') dx dt', \quad t = nA, \quad (14)$$

in the area of the Gr -space where $Gr_r > Gr_s$ (Fig. 1).

Our simulations revealed that in contrast to the pests' fitness, the $\langle p \rangle$ value given by Eq. (14) depends on the whole set of the model parameters rather than on the only growth number (Eq. (13)).

It turned out that invasion of Bt-resistant insects can affect the plant biomass in two different ways. Fig. 3 demonstrates two types (A and B) of the dependence of the averaged plant biomass on such a biologically significant parameter as the duration of the insect reproduction period εA (see Eqs. (7)–(9)). In this case, $Gr_r^{(A)}$ and $Gr_r^{(B)}$ are very close to each other ($Gr_r^{(A)} \approx 0.2077$; $Gr_r^{(B)} \approx 0.2115$), but values of the parameters k_r , k_s and ν are essentially distinct for each of the curves A and B (Fig. 3). One can see that the curve A is characterized by higher values of the plant biomass in comparison with the curve B.

The distinction between these two types of the dependence of $\langle p \rangle$ on the duration of the insect reproduction period becomes even more prominent when $Gr_r^{(A)}$ differs essentially from $Gr_r^{(B)}$ (Fig. 4). In this case, both the curves A and B remain very close to each

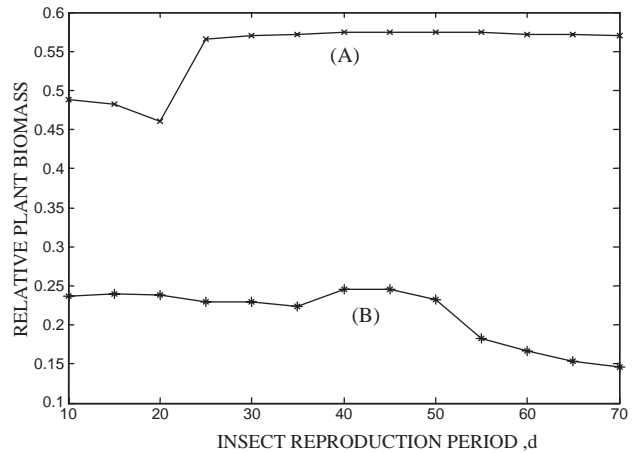


Fig. 3. Two types of the dependence of the relative plant biomass $\langle p \rangle / \langle p \rangle_{max}$ on the insect reproduction period; $\langle p \rangle_{max}$ is the maximum value of $\langle p \rangle$. Curve A: $\gamma = 0.3$; $\nu = 0.6$; $k_s = 0.6$ (other parameters are as in Fig. 2). Curve B: $\gamma = 0.3$; $\nu = 0.1$; $k_s = 0.17$. Here $Gr_s^{(A)} = 0.09$, $Gr_s^{(B)} = 0.1$. The values of the growth numbers $Gr_r^{(A)}$ and $Gr_r^{(B)}$ are very close to each other (see the text).

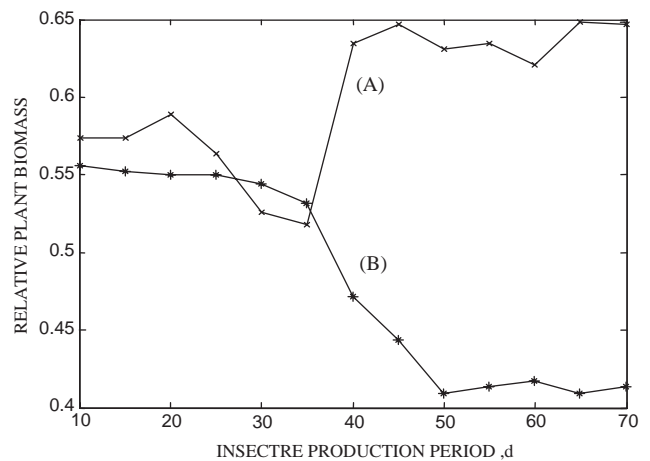


Fig. 4. Two types of the dependence of the relative plant biomass $\langle p \rangle / \langle p \rangle_{max}$ on the insect reproduction period in the case when $Gr_r^{(A)} \neq Gr_r^{(B)}$; $\langle p \rangle_{max}$ is the maximum value of $\langle p \rangle$. Curve A: the values of the model parameters are the same as in Fig. 2. Curve B: $\gamma = 0.3$; $\nu = 0.2$; $k_r = 0.25$; $k_s = 0.22$. Here $Gr_s^{(A)} = 0.07$, $Gr_r^{(A)} = 0.2$, $Gr_s^{(B)} = 0.05$, $Gr_r^{(B)} = 0.09$.

other so long as the duration of the insect reproduction period is less than a critical value (35 days in Fig. 4). But, as soon as the duration of the reproductive period is over the critical value the averaged plant biomass value bifurcates: it can either increase sharply (curve A; Fig. 4) or decrease drastically (curve B; Fig. 4).

The question arises: what are those features of the plant biomass dynamics responsible for the jump of the $\langle p \rangle$ values up or down?

Let us compare the changes in spatially averaged plant and Bt-resistant insect biomass during one season (150 days) for each of the curves (A and B) shown in

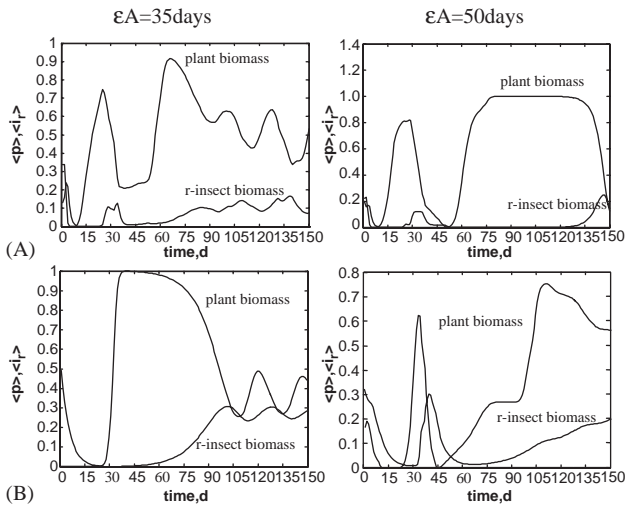


Fig. 5. Changes of plant and Bt-resistant insect (*r*-insect) biomass during one season under different values of the insect reproductive period εA before and after the jumps of the $\langle p \rangle$ values shown in Fig. 4; $\langle i_r \rangle(t) = \int_0^t \int_0^L i_r(x, t') dx dt'$.

Fig. 4 before and just after the jumps of the $\langle p \rangle$ values. Before bifurcation (at $\varepsilon A = 35$), the dynamics of both Bt plant and Bt-resistant insect (*r*-insect) biomass was characterized by temporal oscillations which lasted a comparatively long time (Fig. 5, the left column). After the bifurcation shown in Fig. 4, at the beginning of the season, the plant biomass underwent fast oscillations followed by oscillations of *r*-insect biomass. As a result, the insect biomass fell to a very low level (Fig. 5, the right column). Then it began to grow. But the growth rate was much slower for the regime A in comparison with the regime B. This leads to the persistence of higher values of the plant biomass typical of the regime A (Fig. 5, the right column).

The parameter space of the model (7)–(12) is high dimensional. This circumstance does not allow us to carry out a comprehensive analysis of the parameter domains, which correspond to each of the regimes (A or B). Nevertheless, a rough idea of the structure of the parameter space can be inferred from projection of the parameter space onto a 2D sub-space of some vitally important parameters. Fig. 6 gives us an insight into a projection of the whole model parameter space onto the plane of the parameters k_r and v (see Eqs. (8) and (9)). The non-shaded area in the upper left corner corresponds to the set of parameters where growth numbers of both Bt susceptible and resistant insects are negative (Fig. 6), and the insects became extinct in a few years. One can see that A regime (Fig. 5) appears for parameters k_r and v exceed some critical values. For k_r values which lie within the range between around 0.35 and 0.6, the growth of the parameter v can be followed by an inverse transition from A to B regime (Fig. 6).

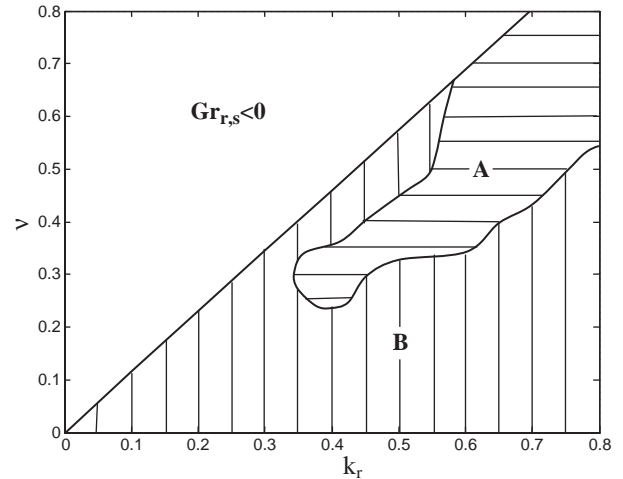


Fig. 6. The border between A and B regimes in the (k_r, v) parameter space. The calculations are carried out at the following set of model parameters: $\alpha = 1$; $\beta = 1.5$; $\gamma = 0.3$; $A = 150$; $k_s = k_r - 0.1$; $n = 10$; $\delta = 1$; $\omega_s^0 = 40$; $\omega_r^0 = 20$; $\lambda = 10$.

4. Concluding remarks

This study has identified key parameters, the growth numbers Gr_s and Gr_r , which determine either, or not recessive Bt-resistant insects can invade a field sowed with a Bt crop. The results obtained imply that thorough measurements of the constants C_1 and C_2 , which parameterize the saturating functional responses (Eqs. (1)–(3)), the parameters k_s and k_r , which are yield coefficients of, respectively, susceptible and resistant insects to the plants, the crop carrying capacity K (Eq. (1)) and the insect mortality rate μ (Eqs. (2) and (3)) to calculate the growth numbers Gr_s and Gr_r , could allow us to make an estimate of invasibility for a given transgenic crop sowed in a given geographical region. Such measurements would be of particular interest in order to check the validity of the growth numbers in agricultural practice and for invasion risk assessment. To our knowledge such measurements have not been yet carried out.

Since the growth numbers (Eq. (13)) depend on uncertain values of input parameters, the model output should not be interpreted as predictive of the fitness of a given insect population, but must be interpreted within the context of possible scenarios of population dynamics. Such an approach is typical of conceptual mathematical modeling (Medvinsky et al., 2002). It goes back to the classic paper by Turing (1952), where it has been shown that the nonlinear interaction of at least two agents with considerably different diffusion coefficients can give rise to spatial structures. Segel and Jackson (1972) were the first to apply Turing’s idea to ecology, having considered the dissipative instability in the predator–prey interaction of phytoplankton and

herbivorous copepods with higher herbivore motility. Here, we demonstrate that insect and plant spatial structures can be a result of the invasion of Bt-resistant insects (Fig. 2). The condition for the invasion is $Gr_r > Gr_s$ (Fig. 1).

The invasion of Bt-resistant insects into the model Bt plant–Bt-susceptible insect system and the replacement of Bt-susceptible insects by Bt-resistant ones, which took place in our simulations, was followed by an essential (up to 35%) decrease of the plant biomass (p). The numerical value of this decrease depends on the parameters of the model (7)–(12). One of essential parameters affecting the changes in the plant biomass is the duration of the insect reproduction period. We show that the plant biomass can undergo a jump up (regime A) or down (regime B) (Fig. 5) if the duration of the insect reproduction period exceeds a critical value (around 1 month). In the parameter space (Fig. 6), there is a border separating these two regimes.

The results obtained imply that the response of the system Bt plants—Bt-susceptible insects to the invasion of Bt-resistant insects can be non-unique which could cause serious complications in attempts to regulate the dynamics of the system. Indeed, even slight changes in the system parameters due to environmental factors (temperature, moisture, etc.) can lead to dramatic changes in the plant biomass resulting in its growth or decline (if the system parameters lie in the vicinity of the border between regime A and regime B). With this awareness of the parameter sensitivities, we can better understand what are those strategies, which could allow us to prevent the invasion of Bt-resistant insects or to ensure a minimum crop waste if the invasion occurred.

Acknowledgements

We are thankful to the anonymous referee for helpful suggestions.

This work was partially supported by NSF and the University of California Agricultural Experiment Station. Extensive discussion with Norm Ellstrand and his group is very beneficial for us on this subject. Norm Ellstrand and Aaron Jenks commented on the early draft of this manuscript.

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