Parasitoids may Determine Plant Fitness—A Mathematical Model Based on Experimental Data

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The present paper deals with the problem of enhancement of plant fitness due to parasitization of herbivores. The experimental evidence for such situations is reviewed. Two mathematical models, plant–herbivore (two trophic) and plant–herbivore–parasitoid (three trophic) are considered to analyse the experimental observations. The effect of environmental fluctuation in the tritrophic system is also observed and optimum values of the inaccessible parameters involved in the system are estimated for purposes of biological control.

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1. Introduction

The role of induced plant defences against herbivores is currently receiving much attention from both fundamental and applied ecologists. These defences, which are activated or increased in response to herbivory, may be grouped into two categories, direct and indirect defences. Induced direct defences can be mediated by toxins, repellents, digestibility reducers, spines and thorns, and have been reported since 1970 for more than 100 plant species within 34 families (Karban & Baldwin, 1997). A few studies on direct plant defences have shown that herbivore-induced chemical changes enhances plant fitness under field conditions (e.g. Baldwin, 1999; Agrawal & Karban, 1999; Agrawal, 1998, 1999).

Indirect defences involve the participation of a third-trophic level, the natural enemies of the herbivores. One example of indirect defence is the attraction of ants by plants with domita and/or food and it has been well documented that this may reduce herbivory and enhance plant fitness (e.g. Janzen, 1966; McKey, 1988; Oliveira, 1997). It has also been suggested that herbivore-induced emissions of plant volatiles serve to attract predators and parasitoids of herbivores (Vet & Dicke, 1992; Turlings & Benrey, 1998). This form of signalling by plants has been reported since 1980 for more than 20 plant species in 13 families (for review, see Dicke, 1999). However, evidence that plants benefit from the attraction of natural enemies by induced volatiles has been lacking and several authors have stressed the need for such evidence, particularly for the attraction of parasitoids (Faeth, 1994; van der Meijden & Klinkhamer, 2000; Hare, 2001). Currently, only three studies present experimental evidence showing increases in fitness (seed production) by herbivore-infested plants as a result of the action of parasitoids (see below). In this paper, we analyse these experimental findings using two

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mathematical models of population dynamics in which we consider a plant–herbivore system (two trophic), and a plant–herbivore–parasitoid system (three trophic). In the two-trophic system, we have observed that plant seed production can decrease considerably due to the introduction of a herbivore, while in the three-trophic system we have observed that a parasitoid may act as a stabilizing agent in a plant–herbivore system. In this latter model, we have also incorporated a periodic disturbance in the herbivore population and have calculated an optimal level of parasitoid growth for which the plants fitness increases, by using a technique developed by Sarkar *et al.* (2001).

2. Experimental Evidence for Parasitoids Enhancing Plant Fitness

It is generally recognized that parasitoids can be an important mortality factor of herbivores, and that this may reduce the overall negative impact of herbivores on plants. The successful use of parasitoids as biological control agents against herbivorous pests attests to the fact that they can have a positive impact on plant performance. This is usually seen in the context of parasitoids suppressing the population density of the pests, and thus affecting the degree of subsequent plant infestation. However, individual plants may also directly benefit from the action of a parasitoid if parasitization of herbivores leads to a significant reduction of their lifetime consumption. To date,

three studies have presented conclusive evidence that parasitoids can enhance plant fitness by affecting the consumption rate of their hosts.

Gomez & Zamora (1994) demonstrated a top–down effect by chalcid parasitoids that attack a seed weevil (*Ceutorhynchus sp.*) on a woody crucifer *Hormathophylla spinosa*. In exclusion experiments in the field, they found that in the presence of the parasitoids, plants that were attacked by the weevil produced more seeds per fruit than weevil-infested plants without parasitoids. The parasitoids reduced weevil-inflicted seed damage to such an extent that the plants produced on average 173% more seeds as compared to plants with unparasitized larvae (Table 1).

Van Loon *et al.* (2000) studied a tritrophic system comprising *Arabidopsis thaliana* (Brassicaceae), *Pieris rapae* (Lepidoptera: Pieridae) caterpillars that specialize in brassicaceous plants and the parasitoid *Cotesia rubecula* (Hymenoptera: Braconidae). In a greenhouse experiment, individual *A. thaliana* plants were either (a) left undamaged, (b) subjected to feeding damage by an unparasitized *P. rapae* larvae, (c) subjected to feeding by a parasitized *P. rapae* larvae, or (d) mechanically damaged. As a result of parasitization, consumption of leaf tissue by *P. rapae* decreased dramatically, resulting in as much as 250% more seeds produced by plants with parasitized larvae.

In a similar study, we found that young maize plants infested by a single larva of the noctuid

TABLE 1

Seed production by plants (mean $\pm$ S.E) that were subjected to feeding by unparasitized and parasitized herbivores

Tritrophic system		Control (undamaged) plants	Damaged by "healthy" herbivores	Damaged by parasitized herbivores	Decrease due to herbivore	Increase due to parasite
H. spinosa–Ceutorhynchus sp.– 3 chalcid parasitoids*		1.28 ± 0.03	0.15 ± 0.02	0.41 ± 0.09	88%	173%
A. thaliana–Pieris rapae–	(a)	4257 ± 294	876 ± 101	3066 ± 208	79%	250%
Cotesia rubecula†	(b)	6065 ± 571	1665 ± 174	4569 ± 608	73%	175%
Z. mays–Spodoptera littoralis– *Cotesia marginiventris‡*		597 ± 67	362 ± 10	535 ± 53	39%	48%

*Gómez & Zamora (1994), seeds per fruit.
†van Loon *et al.* (2000), seeds per plant; (a) *A. thaliana* ecotype 1, (b) *A. thaliana* ecotype 2.
‡Fritzsche-Hoballah & Turlings (2001), seeds per plant.

moth *Spodoptera littoralis* will produce about 48% more seeds at maturity, if the larva is parasitized by the braconid *Cotesia marginiventris* (Fritzsche-Hoballah & Turlings, 2001). The results of these studies, which are summarized in Table 1, all show the considerable potential of parasitoids to increase the fitness of individual plants.

We are now in a position to formulate the above experimental observations in terms of mathematical modelling.

3. The Mathematical Model for the Plant–Herbivore System

Let x be the density of plant biomass and y denotes the density of the herbivore at time t. In the absence of herbivore, the plant population grows in a logistic manner with an intrinsic rate of increase r and environmental carrying capacity K. Let us also assume that the rate at which the plant population is eaten by the herbivore is proportional to the product of the two population sizes and is denoted by α. Let us also assume that s denotes the death rate of herbivores and β is the conversion factor of herbivores. From the above assumptions, we can now write down the following well-known basic mathematical model of the plant–herbivore dynamical system:

$$\frac{dx}{dt} = rx\left(1 - \frac{x}{K}\right) - \alpha xy,$$

$$\frac{dy}{dt} = -sy + \beta xy, \tag{1}$$

where r, s, α, β, K are all positive constants.

The possible steady states of eqn (1) are $E_0 : (0, 0)$, $E_1 : (K, 0)$, $E_* : (x_*, y_*)$ where $x_* = s/\beta$, $y_* = r/\alpha(1 - s/\beta K)$.

The positive equilibrium E_* exists if $\beta K > s$.

Let us now compare these mathematical results with those of experimental observations. In experiments, we observed that the yield of a plant decreases due to herbivore attack. First we study this behaviour in terms of the size of the equilibrium values. The size of the positive equilibrium (plant) is K when there is no herbivore (equilibrium E_1), and in the presence of the herbivore, the size of the positive equilibrium is $E_* (x_*, y_*)$. Now comparing these two equilibria for the plant population, we find that $K - s/\beta > 0$ (condition for the existence of E_*). This shows that the yield of plant production decreases with the introduction of the unparasitized herbivore (see Table 1).

The local stability properties of the system around equilibrium points are well known, for example see Maynard Smith (1974). We are just mentioning the main results. System (1) around E_0 is unstable (saddle), and the existence of E_* implies that system (1) around E_1 is also unstable (saddle). The population will exhibit a monotonic decline to equilibrium if $rs > 4\beta K(\beta K - s)$, or it will oscillate either side of the equilibrium with decreasing amplitude if $rs < 4\beta K(\beta K - s)$. The stability results of the system also support the experimental findings.

In the next section, we introduce parasitoids in the plant–herbivore system and show that parasitism has a stabilizing effect on the system.

4. The Mathematical Model for the Plant–Herbivore–Parasite System

Let z denotes the density of the parasite population at time t. Let us assume that the number of attacks per unit time per herbivore is proportional to the density of the parasite population, and the transmission parameter is denoted by γ. Let the rate of increase of the parasite population be denoted by δ, and the death rate of the parasite population by μ. With the above assumptions, the model eqn (1) can be reformulated as

$$\frac{dx}{dt} = rx\left(1 - \frac{x}{K}\right) - \alpha xy,$$

$$\frac{dy}{dt} = -sy + \beta xy - \gamma yz,$$

$$\frac{dz}{dt} = \delta yz - \mu z. \tag{2}$$

The possible steady states of eqn (2) are $E'_0 : (0, 0, 0)$, $E'_1 : (K, 0, 0)$, $E'_2 : (s/\beta, r/\alpha(1 - s/\beta K), 0)$, $E'_* : (x'_*, y'_*, z'_*)$ where $x'_* = K(1 - \alpha\mu/\delta r)$, $y'_* = \mu/\delta$, $z'_* = 1/\gamma(-s + \beta K(1 - \alpha\mu/\delta r))$. The positive equilibrium E'_* exists if $\delta > \alpha\mu\beta K/r(\beta K - s)$.

Here, we also compare the size of the equilibrium (plant) in a way similar to that in the previous section. The size of the plant population for the plant–herbivore system is s/β and for the tritrophic system is $K(1 - \alpha\mu/\delta r)$. Comparing these two values, we obtain $K(1 - \alpha\mu/\delta r) - s/\beta > 0$ (for the existence of the positive equilibrium E'_*). This result shows that parasitization of the herbivore by the parasitoids increases plant fitness, as indicated by the experimental results (see Table 1).

By computing the variational matrices around the equilibria of system (2), it can be easily shown that E'_0 is always unstable (saddle), and the existence of E'_2 implies that E'_1 is also unstable (saddle). It is also to be noted here that if the parasite death rate μ has a lower threshold value given by $\delta r/\alpha(1 - s/\beta K)$, then system (2) around E'_2 will exhibit monotonic or oscillating decline to the equilibrium value. The parasite population will tend to extinction, i.e. the tritrophic system will behave as two-trophic system. On the other hand, if $\mu < \delta r/\alpha(1 - s/\beta K)$ then the three-trophic system will persist.

The characteristic equation of system (2) around E'_* is given by

$$p_3\lambda^3 + p_2\lambda^2 + p_1\lambda + p_0 = 0, \qquad (3)$$

where $p_3 = 1, p_2 = rx'_*/K, p_1 = \gamma\delta y'_* z'_* + \alpha\beta x'_* y'_*$ and $p_0 = (\gamma\delta r/K)x'_* y'_* z'_*$.

By using Routh–Hurwitz criteria, it can be easily shown that system (2) around E'_* is locally asymptotically stable and the role of parasitism in the tritrophic system is clear.

Environmental disturbances always exist in nature. We are now ready to consider the tritrophic model in which the growth rate of the herbivore is not constant, but is able to fluctuate. We have already shown that for the tritrophic system a lower threshold value (δ) is required for stability. In the next section, we shall estimate the optimal value of δ for the tritrophic system to persist under environmental fluctuation.

5. The Mathematical Model for the Plant–Herbivore–Parasite System with Environmental Fluctuation

By introducing environmental periodicity in the form of additive periodic fluctuation on the herbivore, we shall investigate the dynamical behaviour of system (2). The behaviour of this system in a periodic environment will be considered within the framework of the following model:

$$\frac{dx}{dt} = rx\left(1 - \frac{x}{K}\right) - \alpha xy,$$

$$\frac{dy}{dt} = -sy + \beta xy - \gamma yz + \eta(t)y,$$

$$\frac{dz}{dt} = \delta yz - \mu z, \qquad (4)$$

where $\eta(t) = a\cos\lambda_1 t + b\sin\lambda_1 t, (-\infty < t < \infty)$ is the periodic fluctuation and a, b, λ_1 are real constants. Substituting $X = \log x, Y = \log y, Z = \log z$ and using the transformation $u = X - X^*, v = Y - Y^*, w = Z - Z^*$, respectively, we rewrite the linearized system as

$$\frac{du}{dt} = -\frac{rx^*}{K}u - \alpha y^* v,$$

$$\frac{dv}{dt} = \eta(t) + \beta x^* u - \gamma z^* w,$$

$$\frac{dw}{dt} = \delta y^* v, \qquad (5)$$

where (x^*, y^*, z^*) is the positive equilibrium of system (4) without fluctuation (from now on we shall use (x^*, y^*, z^*) in place of (x'_*, y'_*, z'_*)).

By eliminating u, v, w, respectively, from (5) we get

$$\frac{d^3u}{dt^3} + A\frac{d^2u}{dt^2} + B\frac{du}{dt} + Cu = F_1(t),$$

$$\frac{d^3v}{dt^3} + A\frac{d^2v}{dt^2} + B\frac{dv}{dt} + Cv = F_2(t),$$

$$\frac{d^3w}{dt^3} + A\frac{d^2w}{dt^2} + B\frac{dw}{dt} + Cw = F_3(t), \qquad (6)$$

where $A = \alpha y^* - \beta x^*, B = -\alpha\beta x^* y^*, C = -(r\delta\gamma/K)x^* y^* z^*$ and $F_1(t) = -(rx^*/K)(d\eta/dt), F_2(t) = d^2\eta/dt^2 + \alpha y^*(d\eta/dt), F_3(t) = -(r\delta x^* y^*/K)\eta$.

In order to find the solutions of the above equations we use the approach of Hoel *et al.* (1993); the solutions are given by

$$u(t) = u(0)\phi_1(t) + u'(0)\phi_2(t) + u''(0)\phi_3(t) + \eta_1(t),$$

$$v(t) = v(0)\phi_1(t) + v'(0)\phi_2(t) + v''(0)\phi_3(t) + \eta_2(t),$$

$$w(t) = w(0)\phi_1(t) + w'(0)\phi_2(t) + w''(0)\phi_3(t) + \eta_3(t),$$

$$\tag{7}$$

where $\phi_i(t) = e^{r_i t}$, $(i = 1, 2, 3)$ and

$$r_1(t) = p + q - \frac{A}{3} \quad \text{when} \quad G^2 + 4H^3 > 0$$

$$= 2p - \frac{A}{3} \quad \text{when} \quad G^2 + 4H^3 = 0$$

$$= 2r'^{(1/3)}\cos\frac{\theta'}{3} - \frac{A}{3} \quad \text{when} \quad G^2 + 4H^3 < 0.$$

$$r_2(t) = -\frac{1}{2}(p + q) + \frac{\sqrt{3}}{2}(p - q)i - \frac{A}{3}$$

$$\text{when} \quad G^2 + 4H^3 > 0$$

$$= -p - \frac{A}{3} \quad \text{when} \quad G^2 + 4H^3 = 0$$

$$= 2r'^{(1/3)}\cos\frac{\theta' + 2\pi}{3} - \frac{A}{3}$$

$$\text{when} \quad G^2 + 4H^3 < 0.$$

$$r_3(t) = -\frac{1}{2}(p + q) - \frac{\sqrt{3}}{2}(p - q)i - \frac{A}{3}$$

$$\text{when} \quad G^2 + 4H^3 > 0$$

$$= -p - \frac{A}{3} \quad \text{when} \quad G^2 + 4H^3 = 0$$

$$= 2r'^{(1/3)}\cos\frac{\theta' + 4\pi}{3} - \frac{A}{3}$$

$$\text{when} \quad G^2 + 4H^3 < 0$$

with $G = (9C - 3AB + 2A^2)/9$, $H = (3B - A^2)/9$, $p^3 = \frac{1}{2}(-G + \sqrt{G^2 + 4H^3})$, $q^3 = \frac{1}{2}(-G - \sqrt{G^2 + 4H^3})$, $r' = \sqrt{a'^2 + b'^2}$, $a' = r'\cos\theta'$, $b' = r'\sin\theta'$, $a' = -G/2$, $b' = -(i/2)\sqrt{G^2 + 4H^3}$ and $u(0) = \log(x(0)/x^*)$, $v(0) = \log(y(0)/y^*)$, $w(0) = \log(z(0)/z^*)$, $u'(0) = r(1 - x(0)/K) - \alpha y(0)$, $v'(0) = -s + \beta x(0) - \gamma z(0)$, $w'(0) = \delta y(0) - \mu$, $u''(0) = 1/x(0)[r - 2rx(0)/K - \alpha y(0)] - [r(1 - x(0)/K - \alpha y(0)]^2$, $v''(0) = 1/y(0)[-s + \beta x(0) - \gamma z(0)] - [-s + \beta x(0) - \gamma z(0)]^2$, $w''(0) = 1/z(0)[\delta y(0) - \mu] - [\delta y(0) - \mu]^2$, $\eta_1(t) = -rx^*/K(a\cos\lambda_1 t + b\sin\lambda_1 t)$, $\eta_2(t) = (a\alpha y^* + b\lambda_1)\cos\lambda_1 t + (b\alpha y^* - a\lambda_1)\sin\lambda_1 t$, $\eta_3(t) = -r\delta x^* y^*/\lambda_1(a\sin\lambda_1 t - b\cos\lambda_1 t)$.

Now, without periodic fluctuation eqns (7) take the following form:

$$u(t) = u(0)\phi_1(t) + u'(0)\phi_2(t) + u''(0)\phi_3(t),$$

$$v(t) = v(0)\phi_1(t) + v'(0)\phi_2(t) + v''(0)\phi_3(t),$$

$$w(t) = w(0)\phi_1(t) + w'(0)\phi_2(t) + w''(0)\phi_3(t). \tag{8}$$

In this case, $\langle u(t)\rangle = u(0)\langle\phi_1(t)\rangle + u'(0)\langle\phi_2(t)\rangle + u''(0)\langle\phi_3(t)\rangle$ and for $t \to \infty$, $\langle\phi_i(t)\rangle \to 0$, $(i = 1, 2, 3)$. Then $\langle x(t)\rangle = x^*$ and similarly $\langle y(t)\rangle = y^*$ and $\langle z(t)\rangle = z^*$ but the variances σ_x^2, σ_y^2, σ_z^2 are all zero. This result shows that the persistence condition implies the stability of the system.

We are now in a position to see the effect of periodic fluctuation on the system. Recently, Sarkar *et al.* (2001) developed a method to estimate the optimal values of the parameters and the safe region for an eco-epidemiological model of Tilapia and Pelican populations proposed by Chattopadhyay & Bairagi (2001). Here we shall use their method by generalizing it to the tritrophic system.

From the Central Limit Theorem, we have a pre-assigned small value $\varepsilon_0 > 0$ for which $\lim_{t\to\infty}\text{Prob}(|x - x^*| < \varepsilon_0) = 1$ (since $\sigma_x = 0$) and similarly $\lim_{t\to\infty}\text{Prob}(|y - y^*| < \varepsilon_0) = 1$ (since $\sigma_y = 0$), $\lim_{t\to\infty}\text{Prob}(|z - z^*| < \varepsilon_0) = 1$ (since $\sigma_z = 0$). Hence, the distribution of the x-population, y-population and z-population will lie within the tolerance intervals $(x^* - \varepsilon_0, x^* + \varepsilon_0)$, $(y^* - \varepsilon_0, y^* + \varepsilon_0)$ and $(z^* - \varepsilon_0, z^* + \varepsilon_0)$, respectively.

With the introduction of periodic fluctuation in the system, the solutions of eqn (6) can be obtained as

$$x(t) = x^* \exp[u(0)\phi_1(t) + u'(0)\phi_2(t)$$
$$+ u''(0)\phi_3(t) + \eta_1(t)],$$

$$y(t) = y^* \exp[v(0)\phi_1(t) + v'(0)\phi_2(t)$$
$$+ v''(0)\phi_3(t) + \eta_2(t)],$$

$$z(t) = z^* \exp[w(0)\phi_1(t) + w'(0)\phi_2(t)$$
$$+ w''(0)\phi_3(t) + \eta_3(t)]. \qquad (9)$$

For $t \to \infty$, we have $\langle x(t) \rangle = x^*$, $\langle y(t) \rangle = y^*$, $\langle z(t) \rangle = z^*$. But the variances are different from zero and given by $\sigma_x^2 = 2rbx^{*3}/\pi\lambda_1 K$, $\sigma_y^2 = 2y^{*2}(b\alpha y^* - a\lambda_1)/\pi\lambda_1$ and $\sigma_z^2 = 2ra\delta x^* y^* z^{*2}/\pi\lambda_1^2$. Now for a different choice of system parameters when σ_x^2 is greater than ε_0 and similarly when σ_y^2 and σ_z^2 are also greater than ε_0, all the populations will deviate from the tolerance level and the system will become unstable around the positive equilibrium. It is well known that the population will remain stable if the variances about the equilibrium level are minimum (May, 1973) i.e. the probabilities that the populations will lie within the tolerance level described previously are maximum.

In terms of system parameters, the deviations from the mean of three populations x, y and z are, respectively, given by

$$\sigma_x^2 = \frac{2rbK^2}{\pi\lambda_1}\left(1 - \frac{\alpha\mu}{\delta r}\right)^3,$$

$$\sigma_y^2 = \frac{2b\alpha\mu^3}{\pi\lambda_1\delta^3} - \frac{2\alpha\mu^2}{\pi\delta^2},$$

$$\sigma_z^2 = \frac{2arK\mu}{\pi\lambda_1^2\gamma^2}\left(1 - \frac{\alpha\mu}{\delta r}\right)\left(-s + \beta K - \frac{\alpha\mu\beta K}{\delta r}\right)^2. \qquad (10)$$

Our aim is now to estimate the inaccessible parameters, to minimize the deviations so that the tritrophic system will attain an ecological stable situation in spite of environmental fluctuation. In our tritrophic system, the inaccessible parameters are α, β, γ and δ. Here we are looking for control of the growth terms of herbivore and parasitoid; for this we need to estimate the critical values of β and δ. Now differentiating σ_z^2 partially with respect to β and δ, respectively, and equating to zero, we obtain the following set of equations:

$$\beta = \frac{rs\delta}{K(\delta r - \alpha\mu)}, \quad \delta = \frac{3\alpha\mu\beta K}{r(3\beta K - s)}. \qquad (11)$$

Solving for these, we find $\beta_c = s(r - 3K)/3K(r - 1)$. We note here that the estimated value of β depends only on r, s and K (i.e. in terms of the accessible parameters of the system). Substituting this critical value of β in the second equation of (11), we obtain $\delta_c = \alpha\mu(3K - r)/r(3K - 1)$. This is a useful result in the sense that in a real field observation, if one can estimate the critical value for the growth rate of the herbivore (β_c) by this method, one can easily estimate the critical value for the growth rate of parasitoids (δ_c); this may be useful for biological control.

6. Conclusion

The role of parasitoids and other natural enemies in controlling herbivore populations and their impact on plant performance has long been considered important for the structure of plant communities (Hairston *et al.*, 1960; Price *et al.*, 1980; Price, 1987; Bernays & Graham, 1988). Parasitization, however, is usually not considered to have an immediate impact on plant performance. Several recent studies show that parasitization of herbivores may reduce the feeding rate by these herbivores to such an extent that it increases seed production in plants that carry the herbivores (Gomez & Zamora, 1994; van Loon *et al.*, 2000; Fritzsche-Hoballah & Turlings, 2001). This will obviously not be the case for all parasitoids, as many will not reduce feeding, and in some cases they cause their host to actually feed more (Rahman, 1970; Parker & Pinnell, 1973; Byers *et al.*, 1993). However, it appears that all species of solitary parasitoids of Lepidoptera reduce food consumption in their host (van Loon *et al.*, 2000). Thus, even if the parasitoid larvae do not kill their hosts immediately, their effect

on host development can directly benefit plant fitness.

With the help of mathematical modelling, we have studied the dynamics of a two-trophic (plant–herbivore) and a three-trophic (plant–herbivore–parasitoid) system, using parameter values that fall within the range of the reviewed studies. The two-trophic model shows that the yield of plants decreases due to herbivore attack, whereas the introduction of parasitoids has a stabilizing effect on the system. We have also observed that a lower threshold value (depending on the population growth of the parasitoid) is required for stability in the tritrophic system, despite the simplified assumptions of our models. More biological realism, e.g. a functional response of the herbivore and of the prey, a delayed effect of endoparasites on herbivores, or a parasitoid specificity (Berryman, 1992; Tuomi *et al.*, 1994; Holt & Hochberg, 1998; Weis & Hochberg, 2000), will be more appropriate and might require additional parameters as well as more experimental informations. At this point, difficulties will arise both from mathematical and experimental sides. An estimation of inaccessible parameters will then require some more details of experimental findings which is not available at present.

The use of a mathematical model allows us to identify key parameters that determine the dynamics of the biological systems. In the context of biological control, the crucial parameter is δ, the growth rate of the parasitoid. With the classical tritrophic approach, we found a lower threshold for δ for the three-species system to persist. Such an inequality can be useful in the case of failure of the biological control. From this lower threshold, one can see that a decrease in α, the 'predation' rate of the herbivore, will increase the likelihood of persistence of the system. This may be achieved with more resistant varieties of maize. In the ideal, noise-free environment depicted by our model, δ has no upper bound. However, it may not be the case in a fluctuating environment, and large values of δ may generate an overexploitation of the parasite, leading to the extinction of the herbivore from the system, and ultimately of the parasite if no alternative hosts are available. Such a situation may be undesirable because the crop will then be more vulnerable to immigrant herbivores. To overcome this situation, the inaccessible parameters are estimated under the assumptions that their values are such as to maximize the probability of persistence of the system. In our case, the growth rate of the herbivore (β) can be found from the estimation of the accessible parameters r, s and K (e.g. McCallum, 2000). Once β is known, the population growth rate of the parasitoid (δ) may be computed and used to estimate the number of parasitoids needed to successfully control the herbivores. To validate models like ours, plant–herbivore–parasitoid interactions and their population dynamics need to be studied under realistic field situations.

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