

EVOLUTION OF MIXED STRATEGIES OF PLANT DEFENSE ALLOCATION AGAINST NATURAL ENEMIES

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Abstract.—In this study we present a simple optimization model for the evolution of defensive strategies (tolerance and resistance) of plants against their natural enemies. The model specifically evaluates the consequences of introducing variable costs and benefits of tolerance and resistance and nonlinear cost-and-benefit functions for tolerance and resistance. Incorporating these assumptions, the present model of plant defense predicts different evolutionary scenarios, not expected by previous work. Basically, the presence of an adaptive peak corresponding to intermediate levels of allocation to tolerance and resistance can arise when the shape parameter of the cost function is higher than the corresponding of the benefit function. The presence of two alternative peaks of maximum tolerance and maximum resistance occurs only when benefits of tolerance and resistance interact less than additive. Finally, the presence of one peak of maximum resistance or maximum tolerance depends on the relative values of the magnitude of costs for tolerance and resistance. An important outcome of our model is that under a plausible set of conditions, variable costs of tolerance and resistance can represent an important aspect involved in the maintenance of intermediate levels of tolerance and resistance, and in favoring adaptive divergence in plant defensive strategies among populations. The model offers a framework for future theoretical and empirical work toward understanding spatial variation in levels of allocation to different defensive strategies.

Key words.—Evolutionarily stable strategy, host-pathogen interaction, plant-herbivore interaction, resistance, tolerance.

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During the last decade, the understanding of plant-enemy interactions has benefited by the incorporation into models of a ubiquitous type of defense (i.e., tolerance). Tolerance has been defined as the ability of a plant genotype to reduce the negative effects of consumers (e.g., herbivores, pathogens) on plant fitness (Rosenthal and Kotanen 1994; Strauss and Agrawal 1999; Stowe et al. 2000; Fornoni et al. 2003a). Unlike resistance (i.e., the ability of a plant to reduce the attack of natural enemies), tolerance is not believed to negatively affect the success of herbivore or pathogen populations (Rosenthal and Kotanen 1994; Fay et al. 1996; Roy and Kirchner 2000; Tiffin 2000a; Restif and Koella 2003; but see Stinchcombe 2002). Consequently, the evolution of tolerance can limit antagonistic coevolution between plants and their enemies, whereas the evolution of resistance prolongs such coevolutionary outcome (Rausher 2001).

The joint evolution of plant tolerance and resistance to natural enemies has attracted substantial theoretical attention over the last decade (Rosenthal and Kotanen 1994; Fineblum and Rausher 1995; Strauss and Agrawal 1999; Mauricio 2000; Roy and Kirchner 2000; Stowe et al. 2000; Tiffin 2000a; Restif and Koella 2003, 2004; Fornoni et al. 2003a). Several experimental studies have tested some of the predictions made by these theoretical analyses (Simms and Triplett 1994; Fineblum and Rausher 1995; Mauricio et al. 1997; Stowe 1998; Agrawal et al. 1999; Tiffin and Rausher 1999; Fornoni and Núñez-Farfán 2000; Pilson 2000; Roy and Kirchner 2000; Stinchcombe 2002; Fornoni et al. 2003b, 2004; Valverde et al. 2003). Results of these empirical investigations often do not support theoretical expectations (Mauricio 2000; Bergelson et al. 2001; Fornoni et al. 2003a,

2004). For instance, previous models for the joint evolution of tolerance and resistance have suggested that they represent two alternative evolutionary strategies of defense (Fineblum and Rausher 1995; Mauricio et al. 1997; Roy and Kirchner 2000; Valverde et al. 2003). Specifically, these models predict a fitness landscape with two adaptive peaks, one corresponding to complete tolerance and the other to complete resistance. The expectation of mutual exclusivity arises from the assumption that costs of tolerance and resistance are increasing linear functions of resource allocation and having both strategies would be redundant. Thus, natural selection would not simultaneously favor an increase in tolerance and resistance (Simms and Triplett 1994).

Despite the reasonableness of this argument, there is little empirical evidence supporting the existence of two mutually exclusive peaks in the resistance-tolerance fitness landscape (e.g., Mauricio et al. 1997; Tiffin and Rausher 1999; Roy and Kirchner 2000; Fornoni et al. 2004). On the contrary, numerous studies have found the existence of intermediate levels of both tolerance and resistance in natural populations (Simms and Rausher 1987; Núñez-Farfán and Dirzo 1994; Fineblum and Rausher 1995; Mauricio et al. 1997; Tiffin and Rausher 1999; Fornoni and Núñez-Farfán 2000; Juenger and Bergelson 2000; Pilson 2000; Shonle and Bergelson 2000; Fornoni et al. 2003b). These results suggest that the maintenance of intermediate levels of both tolerance and resistance are favored by natural selection (Fornoni et al. 2003a) or represents a transient state toward a homogenous strategy of complete tolerance or resistance (Mauricio et al. 1997). Because the maintenance of intermediate levels of tolerance and resistance is at odds with published theoretical expectations,

we have explored additional models for the joint evolution of tolerance and resistance.

The predicted existence of two alternative peaks in the selective surface arises from specific assumptions that have been made about the nature of costs and benefits of tolerance and resistance. In addition, alteration of these assumptions in ways consistent with empirical information about the nature of costs and benefits leads to the prediction that intermediate levels of both tolerance and resistance may often be favored at evolutionary equilibrium (Restif and Koella 2004). This prediction, in turn, highlights the importance of incorporating nonadditivity when modeling the joint effect of multiple traits on fitness in trying to understand the dynamic of adaptive peaks in the evolution of populations (Whitlock et al. 1995; Fenster et al. 1997). Since the concepts of resistance and tolerance as well as the notion of mixed strategies of defense have also been applied to animal hosts (e.g., Hochberg 1997; Roy and Kirchner 2000; Restif and Koella 2003, 2004), the model presented below can be easily extended to predict animal responses to their natural enemies.

EMPIRICAL BACKGROUND

A substantial body of empirical evidence exists regarding the nature of cost-and-benefit functions of plant defensive characters. This information indicates that some assumptions made by previous models were not completely correct and suggests in some cases how those assumptions should be modified. Because this information motivates the way in which we relaxed these assumptions in our model, we first discuss the implications of this evidence.

The Shape of Cost-and-Benefit Functions

The scarcity of empirical evidence regarding the shape of cost-and-benefit functions has led previous models to assume that these functions are linear (Fineblum and Rausher 1995; Mauricio et al. 1997; Roy and Kirchner 2000; Tiffin 2000a; Weis and Hochberg 2000; but see Restif and Koella 2004). However, recent studies have revealed that nonlinear cost and benefit functions may be more common than previously expected (Skogsmyr and Fagerström 1992; Mauricio et al. 1997; Tiffin and Rausher 1999; Bergelson et al. 2001; Fornoni et al. 2003a). For instance, Skogsmyr and Fagerström (1992) showed that the cost function of resistance (estimated as reduced growth) can vary from being almost linear to being a concave upward function of resistance allocation. In a recent review, Bergelson et al. (2001) found costs and benefits of resistance to be commonly nonlinear. Although fewer studies have attempted to estimate the shape of the costs function for tolerance to herbivory, nonlinearity appears also to be the case for this type of cost (Mauricio et al. 1997; Pilson 2000). The evidence thus suggests that the consequences of nonlinearity of cost and benefit functions merit examination. We evaluated this by using a form of cost functions qualitatively similar to that presented by Skogsmyr and Fagerström (1992) for which a clear mechanistic basis was developed. In our case, we simplified the number of parameters associated with the form of the cost function while maintaining a similar shape to make the analysis tractable.

Relative Values of Maximum Costs of Tolerance and Resistance

A second simplifying assumption made in previous analyses is that the costs of maximal resistance and maximal tolerance are equal. However, several sources of evidence call into question the appropriateness of this assumption. First, the only empirical study that has estimated allocation costs of tolerance and resistance simultaneously revealed that these costs differ (Pilson 2000). Second, two studies have demonstrated experimentally that costs of resistance and tolerance are higher when resources are more limited (Bergelson 1994; Hochwender et al. 2000). Because tolerance and resistance are frequently genetically uncorrelated (Simms and Triplett 1994; Mauricio et al. 1997; Tiffin and Rausher 1999; de Jong and van der Meijden 2000; Stinchcombe 2002) and are thus controlled by different genes and physiological processes, it seems likely that their costs will be affected by different environmental resources. Moreover, since such resources are likely to vary independently, it is also likely that costs of tolerance and resistance will differ, and that the relative costs of these two types of defense will vary along environmental gradients (reviewed in Herms and Mattson 1992). By relaxing the assumption that costs of resistance and tolerance are equal, we are able to explore the consequences of environmental variation on the magnitude of costs of tolerance and resistance.

THE MODEL

The standard approach to modeling the evolution of defense is to assume that each additional unit of resource investment in defense increases both the benefits and costs of resistance and tolerance (Simms and Rausher 1987; Antonovics and Thrall 1994; Fineblum and Rausher 1995; Mauricio et al. 1997; Jokela et al. 2000; Roy and Kirchner 2000; Tiffin 2000a). For both resistance and tolerance there is ample experimental evidence supporting the expectation that resources devoted to defense reduce plant fitness in the absence of damage (Simms 1992; Tiffin and Rausher 1999; Pilson 2000; Stinchcombe 2002; Fornoni et al. 2004). Thus, costs of resistance and tolerance can be expressed in the same currency (resource allocation). This phenomenon is typically modeled by an equation of the form

$$W_i = W_0 + B(R_i, T_i) - C(R_i, T_i), \quad (1)$$

where W_i is the fitness of a plant of genotype i , W_0 corresponds to the fitness of a plant with no tolerance and no resistance, T_i and R_i are the amounts of resources allocated to tolerance and resistance, respectively, by genotype i , $B(R_i, T_i)$ is the increase in fitness associated with the benefits of resistance and tolerance, and $C(R_i, T_i)$ is the decrease in fitness due to costs of tolerance and resistance.

Equation (1) represents a two-dimensional fitness surface, where fitness is a function of allocation to tolerance and resistance. The shape of that surface will depend on the detailed form of the functions $B(R_i, T_i)$ and $C(R_i, T_i)$. Because the model developed by Mauricio et al. (1997) is representative of previous assumptions about the nature of these functions, and thus serves as a basis of comparison with our more

general model, we begin our analysis by describing their assumptions regarding these two functions.

First, unit costs of allocation to resistance or tolerance are assumed to be constant, that is, costs increase linearly with allocation to resistance or tolerance. This assumption is represented by the following linear relationships between costs and allocation for resistance and tolerance respectively, $C(\gamma_1 R_{\max}, 0) = \gamma_1 C(R_{\max}, 0)$, and $C(0, \gamma_2 T_{\max}) = \gamma_2 C(0, T_{\max})$. Here, R_{\max} and T_{\max} represent the lowest allocations to resistance and tolerance, respectively, that result in the maximum benefit, and γ_1 and γ_2 each vary between zero and one and represent the proportions of the maximal allocations realized. Although values of γ_1 and γ_2 greater than one are possible, such values would be characterized by no additional fitness benefit but by additional costs. Net fitness corresponding to such allocations would be lower than net fitness with allocations corresponding to R_{\max} and T_{\max} , and thus need not be considered.

Second, the interaction between costs of tolerance and resistance is assumed to be additive, $C(R, T) = C(R, 0) + C(0, T)$.

Third, benefits of tolerance and of resistance, when present alone, are assumed to increase linearly with allocation to tolerance or resistance. This assumption can be stated as $B(\gamma_1 R_{\max}, 0) = \gamma_1 B(R_{\max}, 0)$ for the benefit of resistance and $B(0, \gamma_2 T_{\max}) = \gamma_2 B(0, T_{\max})$ for the benefit of tolerance. This assumption indicates that benefits of resistance and tolerance increase linearly up to R_{\max} and T_{\max} , when maximum benefit is attained. Further allocation will show a diminishing fitness return. Hence, the model considers the parameter space for which any benefit of allocation to defense is expected.

Fourth, benefits and costs per unit allocation are assumed to be equal for resistance and tolerance. This assumption implies that $T_{\max} = R_{\max}$ and that the cost of tolerance are equal to the cost of resistance (i.e., $C_T = C_R$).

The fifth assumption is that the combined benefits of resistance and tolerance are less than additive. This assumption implies that, for an individual plant, being completely tolerant or resistant results in a greater benefit return than having a mixed strategy of partial tolerance and resistance. In Mauricio et al.'s (1997) model, a multiplicative interaction between benefits of resistance and tolerance was employed to produce this kind of subadditive relationship: $B(R, T) = B(\gamma_1 R_{\max}, \gamma_2 T_{\max}) = B_{\max}[1 - (1 - \gamma_1)(1 - \gamma_2)]$. Combining all these assumptions into equation (1) results in the following equation to estimate the expected fitness of a given genotype (W_i) as:

$$W_i = W_0 + B_{\max}[1 - (1 - \gamma_1)(1 - \gamma_2)] - C_{\max}(\gamma_1 + \gamma_2). \tag{2}$$

Equation (2) produces a fitness surface with two adaptive peaks, isolated by a valley of suboptimal combinations of partially resistant and tolerant genotypes. One of these peaks corresponds to the fitness of a completely resistant genotype and the other to the fitness of a completely tolerant genotype (Fig. 1).

ANALYSIS AND RESULTS

Two series of analyses were performed. The first series consisted in relaxing sequentially the first, third, fourth, and

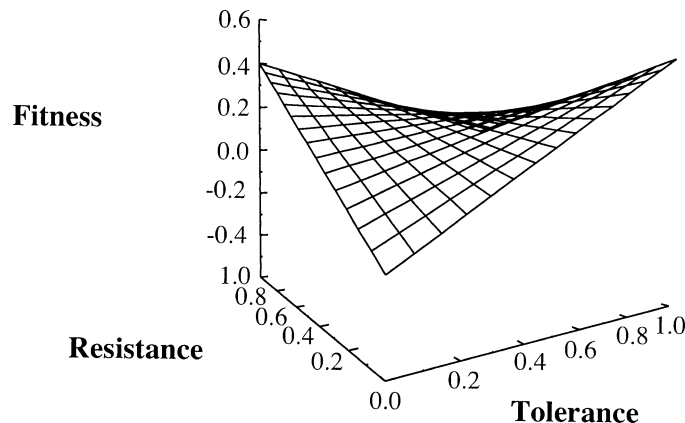


FIG. 1. Fitness surfaces for resistance (γ_1) and tolerance (γ_2) using equation (2). Values of the parameters are $W_0 = 0.1$, $B_{\max} = 1$, $C_{\max} = 0.7$.

fifth assumptions. For clarity each assumption was relaxed individually, leaving the other assumptions unchanged, to evaluate its specific effect on the adaptive surface. We assumed that costs of tolerance and resistance interact additively because there is no available evidence to suspect this condition is not satisfied in natural populations. The second series of analyses examined the effects of relaxing more than one assumption simultaneously to visualize their combined effect on the adaptive landscape.

Nonlinear functions for costs and benefits.—We let the cost functions for tolerance and resistance deviate from linearity by employing the following general expressions for the cost functions $C(\gamma_1 R_{\max}, 0) = \gamma_1^a C(R_{\max}, 0)$ and $C(0, \gamma_2 T_{\max}) = \gamma_2^a C(0, T_{\max})$, where a is a shape parameter that describes how costs of defense increase per unit allocation. For simplicity we assumed that a is the same for tolerance and resistance. Because we consider $0 \leq \gamma \leq 1$ to be the parameter space for which any benefit of allocation to defense can be obtained, when $a > 1$, marginal costs will increase more than linearly with allocation (concave-upward cost function). The condition where $a < 1$ was also evaluated.

The same approach was used to obtain nonlinear benefit functions for tolerance and resistance. In this case, the shape parameter is represented by b . General benefit functions for tolerance and resistance can thus be written as $B(\gamma_1 R_{\max}, 0) = \gamma_1^b B(R_{\max}, 0)$ and $B(0, \gamma_2 T_{\max}) = \gamma_2^b B(0, T_{\max})$. Again, we assumed for simplicity that b is the same for tolerance and resistance. Although for values of $b \leq 1$ this shape parameter has been interpreted as the effectiveness of defense (Fagerström et al. 1987; Simms and Rausher 1987; Jokela et al. 2000), we also evaluated the condition where $b > 1$. Introducing these assumptions into equation (2) yields:

$$W_i = W_0 + B_{\max}[1 - (1 - \gamma_1^b)(1 - \gamma_2^b)] - C_{\max}(\gamma_1^a + \gamma_2^a). \tag{3}$$

When maximal costs of tolerance and resistance, C_{\max} , decrease, maximum fitness increases, indicating that in those populations where costs of defense is low the fitness returns of defense will increase. Analytical examination of equation (3) indicates that the fitness function of tolerance and resis-

tance can be qualitatively different from that predicted by previous models, if the cost and benefit functions are nonlinear. To simplify the analysis, tolerance was considered fixed at intermediate levels. Setting the partial derivative of W_i with respect to resistance equal zero in equation (3), $\partial W(\gamma_1)/\partial \gamma_1 = 0$ and solving for γ_1 permit the determination of the value of resistance, (γ_1^*) that maximizes or minimizes fitness:

$$\gamma_1^* = \left[\frac{b(1 - \gamma_2^b)}{C_{\max} a} \right]^{1/a-b} \quad (4)$$

Determining the optimum level of resistance that maximizes fitness requires the examination of the existence and position of a maximum in the fitness function, $W(\gamma_1)$, for values of γ_1 between zero and one. The location of an optimum value of resistance (γ_1^*) between zero and one depends on the particular relationship between the parameters a and b .

Condition 1.—If $a > b$, the second derivative at γ_1^* is negative indicating the presence of a maximum in $W(\gamma_1)$ (Figs. 2A–C). Under this condition, an intermediate value of resistance will maximize fitness. For a given fixed value of tolerance, the value of γ_1^* corresponding to maximum fitness will depend on the magnitude of the positive difference between a and b (Figs. 2A–C). The pattern emerging from this analysis shows that when we increase the value of tolerance, optimum allocation to resistance decreases (Figs. 2A–C, Fig. 3). Another important result of this analysis is that for a given difference between the parameters a and b increasing tolerance produce a decrease in the optimum level of resistance (Figs. 2A–C, Fig. 3). When levels of tolerance are low ($\gamma_2 < 0.3$), the value of the parameter a needs to be at least 30% higher than b to satisfied the condition $0 < \gamma_1^* < 1$ for the optimum level of resistance. Our analyses indicated that the presence of an optimum value of resistance at intermediate values is robust either to variation in the level of tolerance, the magnitude of the relationship between the parameters a and b , and the variation in the maximum costs of defense, C_{\max} .

Condition 2.—If $a < b$, the second derivative at γ_1^* is always positive, indicating the presence of a minimum (Figs. 2D–F). Thus, either maximum ($\gamma_1 = 1$) or minimum ($\gamma_1 = 0$) values of resistance will maximize fitness (Fig. 3). However, the presence of two alternative peaks requires more restrictive conditions than that necessary to reach an optimum intermediate peak (see above). For instance, when levels of tolerance are relatively low ($\gamma_2 < 0.5$), maximum fitness will be attained at maximum resistance (Fig. 2D). Inversely, for $\gamma_2 > 0.5$, optimum fitness correspond to minimum values of resistance (Fig. 2F). Only for values of tolerance around 0.5, can maximum fitness be attained either through maximum or minimum resistance (Fig. 2E). The value of γ_1^* corresponding to minimum fitness will depend on the magnitude of the negative difference between a and b (Figs. 2D–F, Fig. 3). When $a < b$ it is satisfied the condition that $0 < \gamma_1^* < 1$.

Equation (4) cannot be solved when $a = b$, a condition without biological meaning. However, when $a \neq b$ and $0 < \gamma_1^* > 1$, maximum fitness will be attained close to $\gamma_1 = 0$ or $\gamma_1 = 1$ but not to both simultaneously. In particular, when $a, b < 1$, γ_1^* is always positive but it is found at very low values of resistance. Conversely, when $a, b > 1$, γ_1^* is found

for values of resistance higher than the possible maximum level of resistance. Under this condition γ_1^* is found out of the range where resistance has a biological meaning (i.e., $0 < \gamma_1^* < 1$), thus we interpret this scenario as a condition that favors maximum levels of resistance.

Numerical simulations also showed that while some parameter combinations do produce a fitness surface with two adaptive peaks, one corresponding to complete tolerance, the other to complete resistance (Fig. 4A), other parameter values of a and b yield fitness surfaces with only one adaptive peak corresponding to intermediate values of both tolerance and resistance (Fig. 4B). Overall, nonlinearity of the cost or benefit function of tolerance and resistance can alter the expectation that both strategies of defense function as mutually exclusive alternatives (Mauricio et al. 1997). The results of these analyses indicated that as long as the relationship between a and b is maintained, the consequences of varying the absolute values of a and b do not alter the qualitative predictions of the model. Given these results, subsequent analyses were carried out using values of a and b of 0.5, 1.0, and 2.0 as representative of the linear and nonlinear functions for costs and benefits.

Different maximal costs for tolerance and resistance.—We examined the effect of allowing maximal costs of tolerance and resistance to differ. We did this by incorporating separate maximal costs of resistance and tolerance, C_R and C_T , respectively, into equation (2) to yield

$$W_i = W_0 + B_{\max}[1 - (1 - \gamma_1)(1 - \gamma_2) - C_R\gamma_1 - C_T\gamma_2] \quad (5)$$

Equation (5) was numerically resolved 200 times for every combination of C_R and C_T values between 0.0 and 2.0 at 0.1 intervals, and letting $B_{\max} = 1$. Values of γ were the same as in previous analyses. Numerical exploration of the (C_R, C_T) space indicates that the conditions for the existence of two alternative adaptive peaks depend on the relative values of C_R and C_T with respect to B_{\max} (Fig. 5). For instance, when C_R and C_T are both less than B_{\max} , any combination of C_R and C_T results in an adaptive surface with two alternatives peaks (lower-left region in Fig. 5). When $C_R < B_{\max} < C_T$ one peak of maximum resistance is predicted (upper-left region in Fig. 5), whereas when $C_T < B_{\max} < C_R$ one peak of maximum tolerance is predicted (lower-right region in Fig. 5). As expected, having C_R and C_T higher than B_{\max} is maladaptive and neither tolerance nor resistance is favored (upper-right region in Fig. 5). These results indicate that increasing the maximum cost (or cost per unit allocation) of one type of defense lowers the height of the adaptive peak corresponding to that defense, until the peak disappears when the maximum cost exceeds the maximum benefit. As long as costs of tolerance and resistance are linear, the adaptive surface retains two peaks even if the relative costs of the two types of defense change.

Additive and greater than additive benefit interaction.—The interaction between benefits of resistance and tolerance had been considered previously to be less than additive. To relax this assumption and allow the possibility of additive or greater-than-additive benefits, we modeled the total benefit associated with resistance and tolerance as $B(R, T) = B_{\max}(\gamma_1$

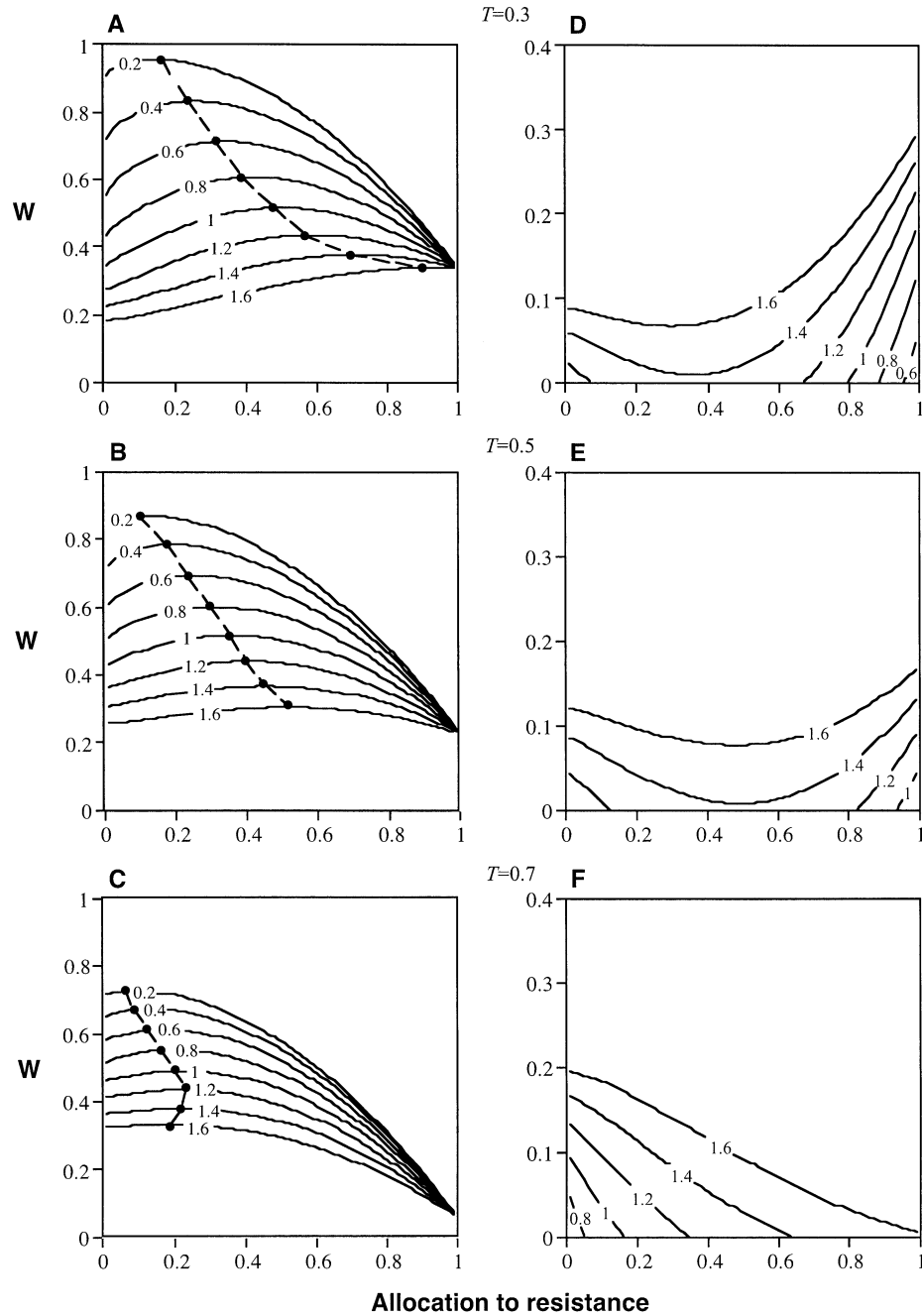


FIG. 2. Relationship between fitness (W) and resistance (γ_1) for different values of the shape parameter of the cost (a) and benefit (b) function using equation (3). (A–C) The value of a was fixed at 2.0 and the value of b varies from 0.2 to 1.6 representing the condition when $a > b$. (D–F) The value of b was fixed at 2.0 and the value of a varies from 0.2 to 1.6 representing the condition when $b > a$. Other parameter values were $W_0 = 0.1$, $B_{\max} = 1$, $C_{\max} = 0.7$. (A, D) $\gamma_2 = 0.3$; (B, E) $\gamma_2 = 0.5$; (C, F) $\gamma_2 = 0.7$. Connected filled circles in panels (A, B, C) indicate how the position of the maximum (evolutionarily stable strategy) in the fitness function corresponding to intermediate values of resistance changes with respect other parameters values (a , b , γ_2). T corresponds to the fixed level of tolerance for each pair of panels.

+ $\gamma_2 + k\gamma_1\gamma_2$), where $0 \geq k \geq 1$. The situation $k = 0$ corresponds to an additive interaction between tolerance and resistance benefits, while $k > 0$ corresponds to a synergistic (greater- than- additive) interaction. When $k < 0$ correspond to a less than additive interaction between benefits (Mauricio et al. 1997). A similar rationale was previously followed to evaluate the interaction between benefits of allocation of re-

sources to resistance against different species of natural enemies (Hougen-Eitzman and Rausher 1994). Substituting our modification into equation (2) yields:

$$W_i = W_0 + B_{\max}(\gamma_1 + \gamma_2 + k\gamma_1\gamma_2) - C_{\max}(\gamma_1 + \gamma_2). \quad (6)$$

When benefits are additive or more than additive (i.e., $k \geq 0$), the fitness surface has a single peak corresponding to a

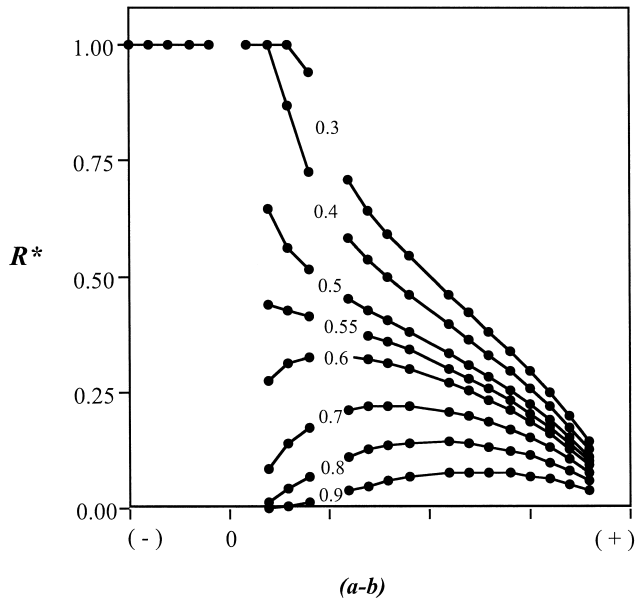


FIG. 3. Relationship between optimum resistance (γ_1^* ; i.e., R^*) and the magnitude of the differences between the shape parameters a and b for different values of tolerance. Numbers within the lines correspond to levels of tolerance. When tolerance increases, optimum levels of resistance decrease. Conversely, when tolerance is low, optimum resistance increases. When $a < b$, but a and $b > 1$, the optimum level of resistance is found at $\gamma_1 = 1$. When $a < b$, but a and $b < 1$, the optimum level of resistance is found at $\gamma_1 = 0$. Discontinuity in the lines correspond to the indetermination in the equation (4) produced when $a = b$. Simulations were for $W_0 = 0.1$, $B_{\max} = 1$, and $C_{\max} = 0.7$.

combination of maximum tolerance and resistance, as long as the maximum benefit, B_{\max} , exceeds the maximal costs, C_{\max} .

Relaxing multiple assumptions.—In the second series of analyses, the first, third, fourth, and fifth assumptions were relaxed simultaneously by incorporating equations (3), (5), and (6), into equation (2), yielding:

$$W_i = W_0 + B_{\max}(\gamma_1^b + \gamma_2^b + k\gamma_1^b\gamma_2^b) - C_R\gamma_1^a - C_T\gamma_2^a. \quad (7)$$

Equation (7) was evaluated numerically for each of the three types of benefit interaction (additive, $k = 0$; subadditive, $k < 0$; and greater than additive, $k > 0$), and for each pair of combination of values of a (i.e., 0.5, 1.0, 2.0) and b (i.e., 0.5, 1.0, 2.0), yielding a total of 27 combinations of parameter values. The result of each combination was evaluated for a range of values of C_R and C_T between 0.0 and 2.0 at 0.1 intervals, letting $B_{\max} = 1$ following the same rationale as for the evaluation of equation (5). Thus, every combination resulted in a C_R - C_T phase space produced by 200 adaptive surfaces. Numerical exploration of 5400 adaptive surfaces was conducted to determine the location of a maximum within the surface. This analysis indicated that three qualitatively different adaptive surfaces can occur depending on the type of benefit interaction, the relation between the shape parameters, and relative values of costs of tolerance and resistance (Table 1, Fig. 6).

First, adaptive surfaces with one peak of maximum tolerance or resistance occur depending on the relative values

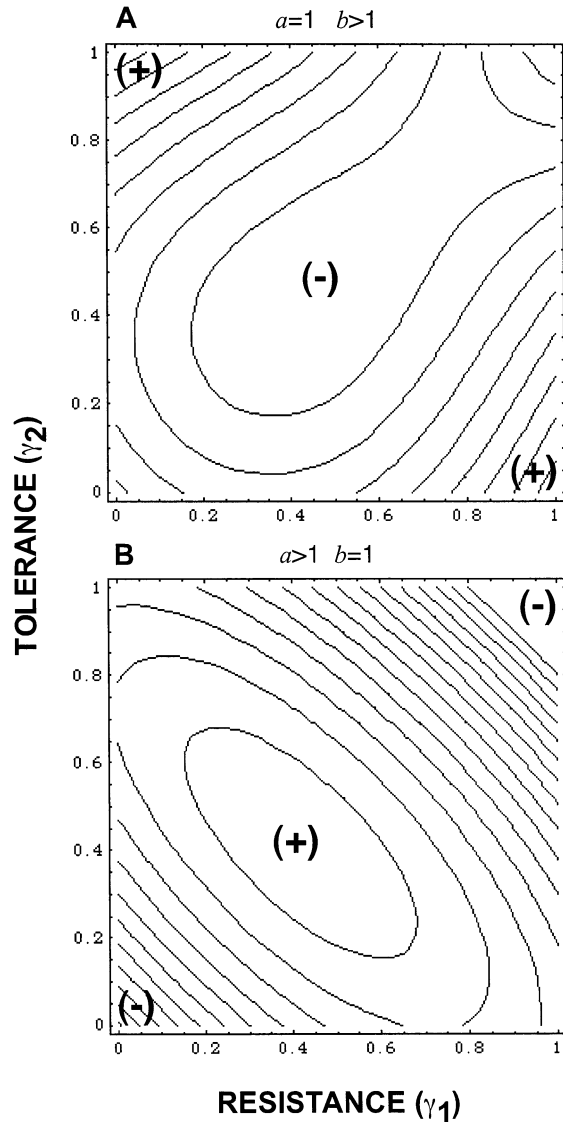


FIG. 4. Fitness surface produced using equation (3) for (A) $a = 1$ and $b = 2$, and (B) $a = 2$ and $b = 1$. The positive signs indicate the location of the adaptive peaks within the surface. The negative signs indicate the region of the lowest fitness values within the fitness surface. Values of the other parameters are $W_0 = 0.1$, $B_{\max} = 1$, $C_{\max} = 0.7$. Number of contours were adjusted to facilitate a clear visualization of the shape of the fitness surface.

of the corresponding cost for each strategy. When costs of tolerance are higher than those of resistance a peak of maximum or almost maximum resistance is expected (Figs. 6A–D). The reverse will occur when costs of resistance are higher than those of tolerance. Second, the presence of an adaptive surface with two alternative peaks of maximum tolerance and resistance occurs when benefits interact in a less-than-additive manner (Figs. 6A, B). The size of the area corresponding this type of adaptive surface in Figure 6B depends on the relative values of a and b . When the positive difference between a and b increases the opportunities for the existence of adaptive surfaces with two alternatives peaks is proportionately reduced. Conversely, as the magnitudes of a and b are less dissimilar, the area below B_{\max} will correspond to

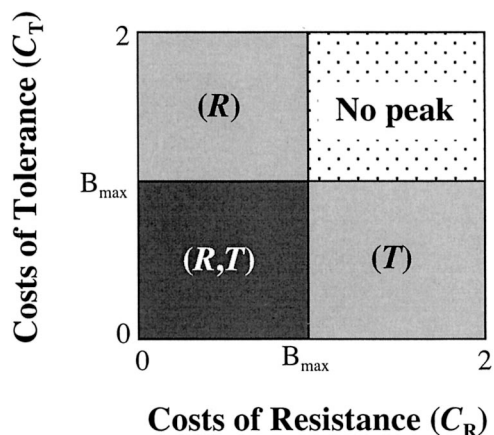


FIG. 5. Four regions in a (C_R, C_T) space with different implications for the evolution of tolerance and resistance. Letting $W_0 = 0.1$, $B_{max} = 1$, when $0 \geq C_R \leq 2$ and $0 \geq C_T \leq 2$, equation (5) predicts that the lower-left region corresponds to an evolutionary scenario with two alternative peaks of maximum tolerance and resistance (i.e., when $C_R, C_T < B_{max}$). The upper-left region corresponds to an evolutionary scenario with one optimum peak of maximum resistance (i.e., when $C_R < B_{max} < C_T$). The lower-right region corresponds to an evolutionary scenario with one optimum peak of maximum tolerance (i.e., when $C_T < B_{max} < C_R$). The upper-right region corresponds to an evolutionary scenario with no adaptive peak (i.e., when $C_T, C_R > B_{max}$).

an adaptive surface with two alternative peaks like that predicted in Figure 6A. Finally, the presence of adaptive surfaces with one peak corresponding to intermediate levels of tolerance and resistance are expected when the shape parameter of the cost function (i.e., a) is greater than the shape parameter of the benefit function (i.e., b ; Figs. 6B, D). Under this scenario an intermediate peak will represent a state of evolutionary equilibrium.

Within these combinations of cost-and-benefit functions whether the peak is biased toward more allocation to tolerance than resistance depends on the relative values of costs for both strategies. For example, when costs of tolerance are lower than those of resistance (i.e., $C_T < C_R$) the intermediate peak will be biased toward more allocation to tolerance than resistance (Fig. 6D). The reverse is expected when costs of resistance are lower than costs of tolerance.

DISCUSSION

Our results indicate that several different outcomes of the joint evolution of tolerance and resistance are possible de-

pending on the type of interaction between benefits of tolerance and resistance, the relative magnitudes of costs and the shapes of the cost and benefit functions. In particular, three generalizations can be drawn from our analysis.

First, for fitness surfaces to have two alternative peaks, the combined benefits of tolerance and resistance must be less than additive (i.e., $k < 0$). Mauricio et al. (1997) demonstrated that two peaks can occur if $k < 0$. Our analysis extends this result and demonstrate that two peaks cannot occur if $k > 0$. The general explanation for this result is that multiple peaks can arise only if resistance and tolerance provide redundant benefits, which is possible only if increasing one of these types of defense has little effect on fitness when the other provides substantial benefits. Three of four studies that have evaluated the joint pattern of selection on tolerance and resistance have found significant correlational selection between tolerance and resistance (Tiffin and Rausher 1999; Pilson 2000; Medel 2001). However, while the Tiffin and Rausher (1999) study supports the existence of an adaptive landscape with two adaptive peaks, the other two reported an adaptive surface with one intermediate peak of tolerance and resistance (Pilson 2000; Medel 2001). These studies indicate that benefits of tolerance and resistance can interact either subadditively or greater than additively. However, Mauricio et al. (1997) did not find significant correlational selection between tolerance and resistance and concluded that benefits interact additively. Provided the assumption of how benefits interact has a strong influence on the predictions of our model, additional data is needed before assuming a specific kind of interaction between benefits of tolerance and resistance. Yet, variation in the way benefits of tolerance and resistance interact may be the rule.

Second, in general, in cases in which there is one fitness peak corresponding to maximal or almost maximal resistance or to maximal or almost maximal tolerance depends on the relative costs of tolerance and resistance, that is, on the relative values of C_R and C_T . The former occurs when $C_R < C_T$, the latter when $C_R > C_T$. This result makes intuitive sense in that it indicates that selection will favor the cheaper of two redundant defenses (e.g., Hochberg 1997).

Previous models suggested that the evolution of tolerance and resistance within populations may be determined by the initial frequencies of tolerant and resistant genotypes (Mauricio et al. 1997; Roy and Kirchner 2000). This expectation depends on the existence of two peaks in the fitness surface, a condition that, according to our model, will arise only under certain conditions. Under a different scenario, the evolution-

TABLE 1. Results of simulations using equation (6) under different sets of parameter combinations. Asterisks indicate the occurrence of qualitatively different fitness surfaces.

Benefit interaction	Relationship between a and b	Type of fitness surfaces		
		One peak of max γ_1 or max γ_2	Two alternative peaks of max γ_1 and γ_2	One intermediate peak of partial levels of γ_1 and γ_2
$k < 0$	$a < b$	*	*	
	$a > b$	*	*	*
$k = 0$	$a < b$	*		
	$a > b$			*
$k > 0$	$a < b$	*		
	$a > b$			*

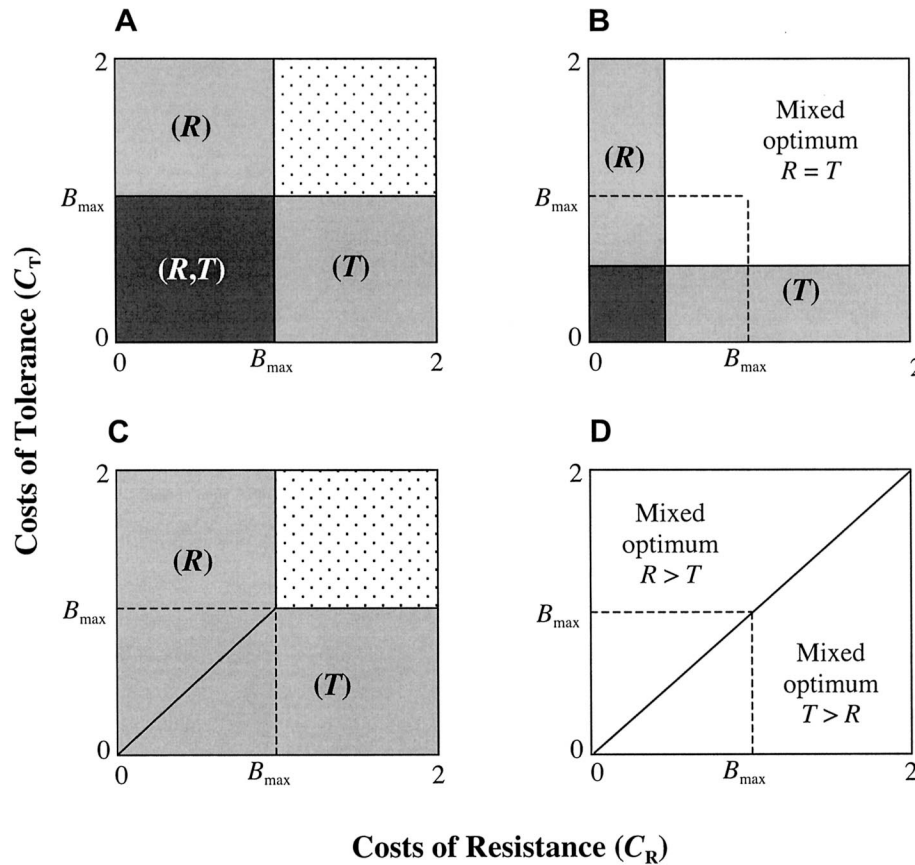


FIG. 6. Hypothetical evolutionary scenarios for the evolution of tolerance and resistance predicted by equation (7). (R) and (T) (gray regions) indicate that pure strategies of resistance or tolerance are favored, respectively. (R, T) (dark region) indicates the region in which two alternative peaks are present in the adaptive landscape, one corresponding to complete resistance, the other corresponding to complete tolerance. (A) C_R , C_T space when $a < b$ and $k < 0$. (B) C_R , C_T space when $a > b$, and $k < 0$. The white region (upper-right corner) corresponds to a mixed strategy of intermediate equivalent values of R and T (i.e., $\gamma_1 = \gamma_2$). The darkest region represents the area in which two alternative peaks of maximum R and T are expected. (C) C_R , C_T space when $a < b$ and $k \geq 0$ produce adaptive surface of only one peak corresponding to maximum T or R. (D) C_R , C_T space when $a > b$ and $k \geq 0$. The region above the diagonal line corresponds to a mixed strategy biased toward more allocation to R than T (i.e., $\gamma_1 > \gamma_2$). Below the diagonal line there is a region where a mixed strategy biased toward more allocation to T than R is expected (i.e., $\gamma_2 > \gamma_1$). For all panels, $W_0 = 0.1$, and $B_{max} = 1$.

any outcome will depend not on initial levels of tolerance and resistance, but on their relative costs. Furthermore, these results suggest that differences among populations in the relative magnitudes of tolerance and resistance may be caused by environmental differences that influence the relative magnitudes of the respective costs. Although several studies support the expectation that the expression of costs of defense probably increase under conditions of resource limitation (Herms and Mattson 1992; Bergelson 1994; Koricheva 2002; Stowe et al. 2000; Hochwender et al. 2000), studies that estimate the variation among populations in the magnitude of costs for tolerance and resistance are lacking (but see Pilson 2000; Stinchcombe 2002). In a study with one population of *Brassica rapa*, allocational costs of tolerance were found to be higher than those of resistance (Pilson 2000), supporting our expectation that for a given population costs of different defensive strategies probably differ. Recent data for *Datura stramonium* revealed that the variation among populations in the magnitude of costs of tolerance was consistent with the pattern of selection on tolerance (Fornoni et al. 2004). Finally, in *Ipomoea hederacea*, manipulation of the

presence of insect herbivores affected the pattern of selection acting on tolerance to deer herbivory, suggesting a change in the balance between costs and benefits of tolerance between environments (Stinchcombe and Rausher 2002). These findings support our expectation that costs of defensive strategies probably differ among environments and populations.

The phase-space panels of Figure 6 permit the visualization of the type of adaptive peak within the fitness surface of tolerance and resistance for independent variation in the costs of tolerance and resistance. Moving in any direction between two points within the panels may represent an environmental gradient expressed as variation in the costs of tolerance, resistance, or both. Along such gradients, investment in defense is expected to reach higher levels in areas of lower resource limitation (i.e., in areas of low C_R and C_T) compared to areas of higher resource limitation (i.e., in areas of high C_R and C_T). Similarly, for predator-prey systems, previous theoretical and empirical studies support our expectation that allocation to defense is expected to increase along productivity gradients (Hochberg and Holt 1995; Hochberg and van Baalen 1998). In our model, the evolutionary consequences of

the variation in the magnitude of costs may be reflected as a cline in which qualitative changes in the adaptive value of tolerance and resistance occur. Figure 6 indicates that, in general, when the cost of tolerance is sufficiently higher than that of resistance, the evolutionary equilibrium would be attained at higher levels of resistance. The reverse would be expected when the cost of tolerance is lower than the cost of resistance. Whether a steep or a gradual cline occurs will depend on how the environmental factors determining the costs of each defensive strategy change the position of the adaptive peak within the tolerance-resistance adaptive surface. For example, a gradient of variation in the costs of tolerance, resistance, or both that cross any combination of the different type of adaptive surfaces in Figures 6A, B, or C would result in a steep cline. Conversely, in Figure 6D, a gradient that connects two hypothetical sites corresponding to qualitatively different adaptive peaks would produce a gradual cline (i.e., a gradient that cross the diagonal).

Empirical evidence indicates that both steep and gradual clines can exist. For instance, steep clinal differentiation has been detected between related species that hybridize or single species that are exposed to contrasting selection imposed by abrupt environmental changes (Endler 1977; Epperson et al. 2001). Also, gradual clinal variation has been observed among closed related species or populations (Schoen 1982; Graves 1991; Stenøien et al. 2002; Silva-Montellano and Eguiarte 2003). Although an increasing number of studies have addressed the existence of selection mosaics in species interactions (Berenbaum and Zangerl 1998; Benkman 1999; Brodie et al. 2002; Thompson and Cunningham 2002), few studies have explored the existence of clinal variation in traits involved in species interactions (e.g., Nuismer et al. 2000; Schemske and Bradshaw 1999; Silva-Montellano and Eguiarte 2003). It remains to be determined how frequently environmental effects on the variation in the relative costs of tolerance and resistance actually contribute to adaptive variation among populations in defensive strategies (Fornoni et al. 2004).

A profitable approach to addressing this issue would be to determine how costs of tolerance and resistance change across specific resource-availability gradients. An important outcome from our model is that under a plausible set of assumptions, variable costs of tolerance and resistance can represent an important aspect involved in the maintenance of intermediate levels of tolerance and resistance, the occurrence of adaptive divergence in plant defensive strategies among populations, and in promoting the occurrence of a selection mosaic.

Finally, a mixed strategy generally can only occur when the shape parameter of the cost function is higher than that of the benefit functions (i.e., $a > b$), a conclusion obtained by a parallel theoretical study (Restif and Koella 2004). Recent studies for several plant species indicated that the shape of cost-and-benefit functions of tolerance and resistance are commonly nonlinear (Mauricio and Rausher 1997; Tiffin and Rausher 1999; Pilson 2000; Bergelson et al. 2001; Fornoni et al. 2004). However, the actual causes of nonlinearity of the costs and benefits function have been little explored. Based on the recognition that allocation to defense and other plant functions (growth and reproduction) involves the par-

tion of the same pool of limiting resources, a cost of defense is expected (Simms and Rausher 1987; Fagerström 1989). The amount of resource-overlapping between defense and other functions may increase not only with the amount or the type of specific resources devoted to defense but also by the extent of resource limitation (Skogsmyr and Fagerström 1992; Jokela et al. 2000). This argument has been proposed to sustain the presence of nonlinear cost functions (Fagerström 1989). More experimental data are needed for different types of defensive components and along gradients of resource availability to understand the effect of the environment on the shape of the cost-and-benefit function of defensive strategies.

Among species, differences in the shape of the cost function may be related to the type of defensive compounds (i.e., nitrogen- or carbon-based compounds). In contrast, within species, variation in the shape of the cost function may be more related to the extent of resource limitation present among populations. To the extent that these expectations are realized, our model predicts that a mixed defense strategy consisting of partial allocation to both resistance and tolerance should be more common than previously noted (Fineblum and Rausher 1995; de Jong and van der Meijden 2000; Jokela et al. 2000; but see Restif and Koella 2004). In addition, our result suggests that environmental effects on epistatic interactions between tolerance and resistance loci on fitness should be explored further.

To improve our understanding of spatial and temporal patterns of plant defense allocation, future empirical work should be directed toward the examination of the effect of the environment on the magnitude and shape of cost functions for different alternative plant strategies of defense.

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