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Natural selection and the joint evolution of tolerance and resistance as plant defenses

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Abstract. Plants can defend themselves against the damaging effects of herbivory in at least two ways. Resistant plants avoid or deter herbivores and are therefore fed upon less than susceptible plants. Tolerant plants are not eaten less than plants with little tolerance, but the effects of herbivore damage are not so detrimental to a tolerant plant as they are to a less tolerant plant. Biologists have suggested that these two strategies might represent two alternative and redundant defenses against herbivory since they appear to serve the same function for plants. I explore the relationship between resistance and tolerance, particularly with regards to how the joint evolution of these two traits will influence the evolution of plant defense. Although I briefly review some of the contributions of theory to the study of tolerance, I concentrate on an empirical, ecological genetic approach to the study of the evolution of these characters and the coevolution of tolerance and herbivores. In order to understand the evolution of any trait, we must understand the evolutionary forces acting on the trait. Specifically, we must understand how natural selection acts on tolerance. I review several studies that have specifically measured the form of selection acting on tolerance and tested the hypothesis that resistance and tolerance are alternative strategies. I also present a statistical analysis that does not support the hypothesis that herbivores are selective agents on tolerance. Finally, I consider a variety of constraints that possibly restrict the evolution of tolerance.

Key words: compensation, constraints, defense, herbivory, natural selection, resistance, tolerance, trade-offs

Introduction

The sky is blue, the oceans are deep and herbivory is bad. Universal scientific truths? Well, the sky is often not blue, some parts of the ocean are not so deep and herbivory may not always be so detrimental to plant fitness as biologists have always assumed. In the past 50 years, biologists have developed a framework for studying the interactions of plants and the animals that eat them (Ehrlich and Raven, 1964). Just as we begin to understand in some detail how plant resistance to herbivores evolves (Berenbaum, 1983; Mauricio and Rausher, 1997), we now face the exciting challenge of incorporating new ideas and results that show that plants may have alternative

strategies for tolerating herbivore attack. In this paper, I focus on trying to understand the evolutionary relationship between resistance and tolerance in plants and how natural selection might shape the joint evolution of these plant defenses.

Definitions

Although the study of plant–herbivore interactions is relatively young, we already have some ambiguity in the terms we researchers use. This may be evident, even within this issue. For my purposes, I will use terms as originally defined by Rausher (1992a): ‘a *resistance* trait is any plant character that influences the amount of damage a plant suffers,’ and *tolerance* is ‘the ability of plants to experience damage without a reduction in fitness’ (Crawley, 1983; McNaughton, 1983; Paige and Whitham, 1987). Rausher (1992a) reserved the term ‘defense’ for a trait that has evolved *because* of selection by herbivores, and therefore implies something about the ‘evolutionary *raison d’etre*’ of the trait. This is exactly parallel to the definitional distinction between a trait that is an adaptation (e.g., defense) and a trait that is adaptive (e.g., resistance) (see Futuyma, 1998, pp. 354–356). For this reason, I prefer the term ‘defense’ as the umbrella term, rather than resistance.

Resistance traits are some of the most striking features of plants, including thorns, spikes, hairs, and an endless variety of chemicals. We know that, at least in some cases, herbivores have been selecting plants to have greater levels of resistance (Berenbaum *et al.*, 1986; Simms and Rausher, 1989; Mauricio and Rausher, 1997; Shonle and Bergelson, 2000). This makes perfect sense to evolutionary ecologists: traits that protect a plant against being eaten should be favored by selection because herbivores can reduce the fitness of the plants on which they feed (Morrow and LaMarche, 1978; Marquis, 1984).

An alternative to preventing or deterring herbivores from finding and feeding on a plant is the evolution of a mechanism for reducing the detrimental effects of herbivore damage once the plant has been found and fed upon. This alternative strategy, ‘tolerance’, has long been recognized, particularly in agriculture (Painter, 1958). Unlike resistance, tolerance does not prevent herbivory, but allows the plant to compensate for damage that herbivores have already inflicted. If a plant can tolerate damage, herbivory will not always lead to a reduction in individual fitness (Owen and Wiegert, 1976; McNaughton, 1983; Paige and Whitham, 1987; Mauricio *et al.*, 1993).

Since both resistance and tolerance have the same function – to defend the plant against the detrimental effects of herbivore attack – several questions naturally arise: Do resistance and tolerance represent alternative defense ‘strategies?’ Are resistance and tolerance mutually exclusive? Are plants best defended when they can both resist and tolerate herbivore damage? How

will the evolution of resistance affect the evolution of tolerance? Unfortunately, empirical studies that integrate tolerance and resistance are still not common. Therefore, in this paper, I will take the opportunity to ask some speculative questions with the hope that rigorous answers will soon be provided. I will explore a variety of theoretical and empirical aspects of the relationship between tolerance and resistance, as well as provide some novel results from my own work on the joint evolution of tolerance and resistance.

Theoretical considerations

Theory drives and organizes empirical work in evolutionary ecology and there have been several theoretical approaches made to understanding the joint evolution of tolerance and resistance. The early, largely verbal, models of van der Meijden *et al.* (1988), Herms and Mattson (1992) and Belsky *et al.* (1993) established the biological underpinnings of later models. The quantitative genetic models of Fineblum and Rausher (1995), Mauricio *et al.* (1997), Tiffin and Rausher (1999) and Tiffin (2000) focused on understanding the genetic parameters under which both tolerance and resistance could be maintained, particularly the role of genetic correlations. Related models developed by Abrahamson and Weis (1997), Järemo *et al.* (1999), Roy and Kirchner (2000) and Tiffin (2000), make predictions regarding the form and magnitude of natural selection acting on tolerance and resistance traits.

Verbal models

Several workers have argued on theoretical grounds that resistance and tolerance should represent mutually exclusive adaptations to attack by herbivores. In other words, natural selection should favor either tolerance or resistance, but not both (van der Meijden *et al.*, 1988; Herms and Mattson, 1992; Belsky *et al.*, 1993). There are reasons to hypothesize that tolerance and resistance would be mutually exclusive. Complete resistance and complete tolerance seem to be redundant: a plant that is completely resistant would not benefit from being able to tolerate damage since it would never be attacked and a plant that could completely tolerate herbivore damage would not necessarily benefit from being resistance. The crux of this argument is based on the idea that complete tolerance and resistance have significant fitness costs and having both traits presumably incurs a total cost greater than having just one.

Several studies demonstrate that resistance traits can be negatively correlated with each other (Berenbaum *et al.*, 1986; Björkman and Anderson, 1990; but see Steward and Keeler, 1988; Mauricio, 1998) and at least one study shows

that redundant resistance characters can be mutually exclusive. Rehr *et al.* (1973) found that *Acacia* species possessed either cyanogenic glycosides or symbiotic ant-based defenses, but not both. However, since many plant species have evolved several distinct types of resistance characters, the trade-offs between resistance traits cannot be that common. For example, plants can produce two or more different classes of secondary compounds (e.g., Berenbaum, 1985; Hugentobler and Renwick, 1995), or both chemical and physical resistance traits (e.g., Mauricio, 1998). Although this pattern suggests that different types of resistance are not necessarily mutually exclusive, it is not known to what extent different types of resistance may have evolved in response to different sets of herbivores. Resistance traits are likely to be mutually exclusive only when they are directed toward the same set of herbivores and are thus completely redundant.

Models incorporating correlations

Under what genetic parameters are resistance and tolerance expected to be mutually exclusive? Fineblum and Rausher (1995) demonstrated theoretically that a specific kind of evolutionary cost, a negative genetic correlation between resistance and tolerance, can produce disruptive selection on both resistance and tolerance that leads to the evolution of either tolerance or resistance, but not both.

Even in the absence of such a correlation, it is plausible that the joint pattern of selection on tolerance and resistance could favor the evolution of one, but not both strategies. Mauricio *et al.* (1997) presented a model showing that fitness peaks at extreme defensive strategies (either complete tolerance and no resistance or complete resistance and no tolerance) could result from a combination of less-than-additive benefits of defense and additive costs of defense. These peaks arise because partial tolerance and partial resistance acting together are not as effective at reducing the detrimental effects of herbivores as complete tolerance or complete resistance alone. The fitness of genotypes possessing both complete resistance and complete tolerance is low relative to genotypes exhibiting either complete tolerance or complete resistance because genotypes with both complete resistance and complete resistance incur twice the cost, while obtaining the same benefit.

A model of Roy and Kirchner (2000) predicted that resistance and tolerance will be mutually redundant strategies as a consequence of the fact that the incidence and fitness consequences of herbivory (disease in their model) are negatively correlated.

In contrast to these models that predict tolerance and resistance to be mutually exclusive, Tiffin (2000) proposed a model that showed that resistance and

tolerance alleles could both be maintained at intermediate frequency, but only if the costs of tolerance and resistance are independent and unequal.

Models incorporating selection

Other models have generated predictions regarding the role of natural selection in the joint evolution of resistance and tolerance. Roy and Kirchner (2000) modeled specific interactions between disease and plants populations. In their model, plants that were resistant to the disease reduced the overall incidence of disease in the population (due to its effects on the transmission of the disease). This benefited both resistant and susceptible plants. Thus, as resistant hosts became more frequent, the overall incidence of disease in the population decreases, reducing the fitness advantage of being resistant. From the results of their model, Roy and Kirchner (2000) showed that the evolution of resistance acted as a negative feedback loop that converged to a polymorphic equilibrium. On the other hand, in the Roy and Kirchner (2000) model, tolerance prolonged the survival of infected plants and thus kept the disease in the population longer, increasing the risk of exposure to disease for both resistant and susceptible host plants. Thus, as tolerant plants became more prevalent, the overall incidence of infection increased, thereby increasing the fitness advantage of tolerant plants over non-tolerant hosts. This model suggested that the evolution of tolerance could be described as a positive feedback loop that leads to fixation of the tolerance trait in the population.

The initial model presented by Roy and Kirchner (2000) suggests that resistance and tolerance will be mutually exclusive (a conclusion supported by their review of empirical data). However, they offer several alternative interpretations of the pattern (including reasons why a spurious correlation between tolerance and resistance might be found). Roy and Kirchner (2000) also give examples of how resistance and tolerance could evolve as joint traits, meaning that a single trait could function in both resistance and tolerance capacities or that a resistance trait and tolerance trait could be genetically linked. Clearly, this is one way that resistance and tolerance could evolve together.

The models of Abrahamson and Weis (1997), Mauricio *et al.* (1997) and Järemo *et al.* (1999) assumed no trade-off between resistance and tolerance, but assumed that tolerance itself had significant fitness costs. These models predicted that selection on tolerance will always be directional, either favoring an increase or decrease in tolerance, depending on the level, timing, or predictability of herbivory. In addition, these models conclude that a trade-off between resistance and tolerance can arise as a result of this selection. Tiffin and Rausher (1999), on the other hand, demonstrated that selection on tolerance can be stabilizing when the costs of tolerance do not increase linearly with

tolerance. This form of selection would lead to an intermediate level of tolerance.

Theoretical conclusions

Thus far, then, theory has provided us with the following (in some cases, contradictory) hypotheses: (1) resistance and tolerance are mutually exclusive strategies, (2) disruptive selection should lead to either complete resistance or complete tolerance, but not both, (3) tolerance and resistance can both be maintained at intermediate frequencies, (4) resistance should be polymorphic, but tolerance should be fixed, (5) directional selection should be acting on tolerance, (6) stabilizing selection should be acting on resistance and tolerance and (7) at equilibrium, there should be no genetic variation for resistance or tolerance. Although theory can provide guidance in our studies of tolerance and resistance, rigorous and careful experiments are ultimately needed to test and refine the theory.

Empirical considerations

The measurement of resistance and tolerance

The measurement of resistance and tolerance traits provides an appropriate starting point for a discussion of an empirical approach to the study of these traits. There exist common approaches and drawbacks in attempts to measure resistance and tolerance.

When we think of resistance, we think of the physical traits that confer resistance, such as secondary chemicals, hairs or leaf toughness. Included in this definition of resistance is the ability of a plant to avoid being eaten by escaping herbivores in space and time (*sensu* 'apparency' of Feeny, 1976). In their landmark study, Simms and Rausher (1987) did not study any particular resistance character, but used an 'operational' definition of resistance. They reasoned that a plant that had been eaten by herbivores was not very resistant. Conversely, a plant that had no leaf damage was absolutely resistant. Using leaf damage, Simms and Rausher devised a scale of resistance – the more leaf damage a plant sustained, the less resistant the plant.

Although an operational definition of resistance integrates over all specific resistance traits and thus may be a preferable index of what is actually meant by resistance, this measure has some drawbacks (Mauricio, 1998). For example, plants that are, by chance, missed by herbivores will be scored as having high resistance whether or not they are actually palatable to herbivores or not. Likewise, plants that are repeatedly sampled by different individual herbivores

but rejected by each because the plant is highly unpalatable might have considerable damage and be scored as having low resistance. We assume, therefore, that there always exists a large enough population of herbivores so that all plants are being sampled and that the damage level reflects the actual 'resistance' level in the population. Interestingly, it is possible that our own experimental techniques might lead to situations where this is not the case. For example, some workers plant very large experimental monocultures in areas where the natural plant populations are not so large as in the experiment. Will the appropriate insect fauna be able to recruit to such an area quickly enough and in large enough populations to give an accurate operational measure of resistance? Do edge effects in the experimental plot influence the operational resistance status of an individual?

Herbivore damage and tolerance

Presently, tolerance is also defined by most researchers operationally, not on the basis of specific plant traits (but see Paige and Whitham, 1987; Fineblum and Rausher, 1995; Lennartsson *et al.*, 1997; Tiffin and Rausher, 1999; Juenger and Bergelson, 2000). Operationally, tolerance is inversely related to the degree to which fitness is reduced by herbivores. Because an individual plant cannot be both damaged and undamaged, it is not possible to estimate tolerance from measurement of a single plant. Instead, one estimates tolerance for a group of related individuals (ideally, individuals of an identical genotype, but often members of a sibship). For categorical measures of damage, tolerance can be defined as the difference in average fitness between individuals of the group attacked by herbivores and individuals not attacked (Fineblum and Rausher, 1995).

This measure of tolerance is not appropriate when all plants attacked do not experience the same level of damage. However, individual plants may experience different levels of damage because the sites in which they grow differ in local herbivore abundance. Therefore, tolerance can be considered a norm of reaction: each level of damage reflects a particular environment in which a plant grows, and the difference in fitness between plants experiencing a particular level of damage and the fitness of plants with no damage is a measure of tolerance for that level of damage (Abrahamson and Weis, 1997; Mauricio *et al.*, 1997). Because plant fitness is expected to decrease monotonically with increasing levels of damage, this norm of reaction can be modeled by a regression of fitness on damage (Simms and Triplett, 1994; Mauricio *et al.*, 1997). In particular, the slope of this regression is an index of tolerance: a shallow slope indicates low sensitivity to damage (high tolerance), while a steep slope indicates high sensitivity to damage (low tolerance). A positive slope indicates overcompensation.

The assumption that plant fitness decreases *monotonically* with increasing levels of damage seems reasonable. However, is a line the best description of the relationship between damage and fitness (see e.g., Huhta *et al.*, this issue)? Although Tiffin and Rausher (1999) found no evidence of non-linear effects of damage on fitness, one could imagine that relationship taking many forms (Fig. 1). Curves A, C and D in Figure 1 each show fitness decreasing monotonically with increasing damage, although only curve C changes linearly. Yet, the coefficient of linear regression line has often been used as a measure of tolerance. The relationship between damage and fitness may even be variable within an organism, depending, for example, on timing of damage (Lennartsson *et al.*, 1998). Clearly, an understanding of tolerance will require that we characterize the relationship between damage and fitness in a more detailed manner (Tiffin and Rausher, 1999; Tiffin and Inouye, 2000; Huhta *et al.*, this issue; Pilson, this issue).

Like resistance, an operational definition of tolerance integrates over all specific tolerance traits and thus may be a preferable index of what is actually

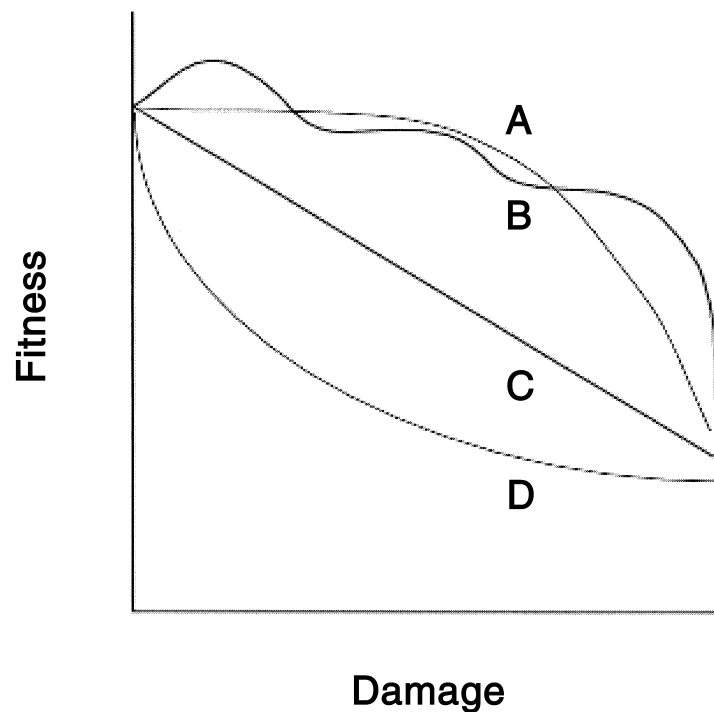


Figure 1. Possible relationships between plant fitness and damage by herbivores.

meant by tolerance. However, in order to more completely understand the mechanism and evolution of tolerance, researchers should begin to specifically identify particular tolerance traits (Paige and Whitham, 1987; Juenger and Bergelson, 2000). Yet, it will be important to demonstrate explicitly the relationship between the operational definition of tolerance and tolerance traits. For example, many researchers have demonstrated a relationship between secondary chemistry and damage in plants (a relationship which is not always negative). What is the relationship between relative growth rate, photosynthetic rate, hormone concentration, root weight and other putative tolerance traits and the operational definition of tolerance?

Coevolution of herbivores and tolerance

The identification of actual traits should lead to a better understanding of the evolution of tolerance. One of the lessons learned from the study of resistance is that resistance characters seem to have evolved in response to selective pressure of specific herbivores (Berenbaum, 1983; Mauricio and Rausher, 1997). Is this also the case for the evolution of specific tolerance traits? Do plants have suites of tolerance traits? Are different tolerance traits redundant? Will tolerance traits be genetically correlated with each other? Will certain tolerance traits have evolved in response to specific selective pressures exerted by particular groups of herbivores (e.g., compensatory photosynthesis to defoliators, release of lateral meristems to grazers)?

In the common morning glory, *Ipomoea purpurea*, there are at least two distinct forms of tolerance: tolerance to leaf damage and tolerance to apical meristem damage (Tiffin and Rausher, 1999). Thus, as in the case of resistance, different types of tolerance occur in the same plant. Different forms of tolerance do not appear to be mutually exclusive. However, we only expect tolerance traits to be mutually exclusive when they are directed at the same set of herbivores and are completely redundant (Tiffin and Rausher, 1999; Kotanen and Rosenthal, 2000). In the case of morning glories, the sets of herbivores that cause these different kinds of damage do appear to significantly overlap: grasshoppers, lepidopteran larvae and flea beetles cause both kinds of damage, although there are species of beetles that tend to eat leaves and avoid apical meristems (Tiffin and Rausher, 1999). Although this seems to indicate that we might expect the two forms of tolerance to be mutually exclusive, they do not seem to be.

Tiffin and Rausher (1999) measured the genetic correlation between the two forms of tolerance and found a significant positive genetic correlation. Therefore, if direct selection favored an increase in tolerance to folivory, indirect selection would cause tolerance to apical meristem damage to increase.

Such a genetic relationship would make it difficult to lose one, possibly redundant, form of tolerance without losing the other form as well.

Since tolerance should not directly reduce the fitness of herbivores, would we expect the same kind of coevolutionary dynamics as the interaction between resistance traits and herbivores? Will this coevolution be diffuse or pairwise? Rosenthal and Kotanen (1994) argued that tolerance may be more evolutionary stable than resistance because there should be no selection pressure for an herbivore to overcome tolerance. Thus an 'arms race' is unlikely to develop for tolerance as it might for resistance (Stahl *et al.*, 1999). Nevertheless, there may be feedback between tolerance and herbivore populations. In particular, a tolerant plant may be a better food source than a resistant plant and may lead to an increase in herbivore population size which, in turn, might lead to increased selection for tolerance and resistance (Roy and Kirchner, 2000).

Natural selection on tolerance

In order to understand the evolution of any trait, we must understand the evolutionary forces acting on the trait. Specifically, we must understand how natural selection acts on tolerance. Therefore, is tolerance under selection and what is the pattern of selection acting on tolerance? Mauricio *et al.* (1997) found no significant directional selection, but strong disruptive selection, acting on tolerance in their study of natural populations of the annual plant, *Arabidopsis thaliana*. Thus, it appears that there are two alternative stable evolutionary states in this set of field populations: (1) absence of tolerance and (2) complete tolerance or overcompensation. In addition, Tiffin and Rausher (1999) found neither significant directional nor stabilizing/disruptive selection acting on either tolerance to leaf damage or apical meristem damage in *I. purpurea* at the natural levels of herbivory their plants experienced.

Selection by herbivores on tolerance

We have direct evidence that herbivores are selective agents on resistance traits (Simms and Rausher, 1989; Mauricio and Rausher, 1997; Shonle and Bergelson, 2000). Is there any evidence that herbivores are the main selective agents on tolerance or tolerance traits? Could tolerance traits be under selection for other unknown functions? Using data from Mauricio *et al.* (1997), I performed a statistical analysis that specifically tested the hypothesis that herbivores are selective agents on tolerance. In this analysis, I tested whether the experimental removal of herbivores changed the pattern of selection on tolerance as measured by selection gradients (Lande and Arnold, 1983; Rausher, 1992b; Mauricio and Mojonner, 1997). If herbivores are agents of selection on

tolerance traits, we would expect that the pattern of selection (as measured by the selection gradients) would change when herbivores are experimentally removed (see Mauricio *et al.*, 1997 and legend of Table 1 for experimental details). In the case of tolerance, removal of herbivores caused no significant change in either directional selection or stabilizing/disruptive selection (the treatment by tolerance and the treatment by tolerance–tolerance interaction term in Tables 1A and B, respectively). Therefore, there is no evidence in this system that herbivores are acting as agents of selection on tolerance.

However, using a similar statistical analysis, Juenger and Bergelson (2000) found that selection gradients did significantly change when large mammalian browsers were excluded from field populations of the scarlet gilia, *Ipomopsis aggregata*. This finding provides direct evidence that two tolerance traits, phenology and branch production, are under direct selection by herbivores.

Evolution of tolerance and resistance

How will selection acting on tolerance affect the evolution of resistance? I will consider two approaches to this question. First, I will consider studies that

Table 1. Analysis of variance for relative fitness of *A. thaliana* grown in the field

Source of variation	df	Type III sums of squares	F	p
A. Analysis of directional selection				
Treatment	1	0.100	32.3	<0.0001
Tolerance	1	0.004	1.3	0.2622
Treatment × Tolerance	1	0.001	0.2	0.6389
Error	276	0.851	–	–
B. Analysis of stabilizing/disruptive selection				
Treatment	1	0.086	29.59	<0.0001
Tolerance	1	0.0005	0.16	0.6898
Tolerance ²	1	0.047	16.18	<0.0001
Treatment × Tolerance	1	0.00002	0.008	0.9283
Treatment × Tolerance ²	1	0.003	1.2	0.2746
Error	274	0.786	–	–

The treatments were plants exposed to the natural assemblage of herbivores or sprayed with pesticides. Tolerance is defined operationally as described in the text: the slope of the regression line of damage on fitness. All effects are fixed. A. Analysis of directional selection. Only linear terms are included because adding quadratic terms would result in biased estimates of directional selection gradients. Evidence for a role of herbivores as an agent of natural selection would be provided by a significant treatment (removal of herbivores) by tolerance interaction. B. Analysis of stabilizing/disruptive selection. Both linear and quadratic terms are included. Evidence for a role of herbivores as an agent of natural selection would be provided by a significant treatment (removal of herbivores) by tolerance² interaction.

have looked specifically at the joint pattern of selection on tolerance and resistance. Second, I will consider studies that measure constraints on the evolution of resistance and tolerance.

Joint pattern of selection on tolerance and resistance

Mauricio *et al.* (1997) analyzed the joint pattern of selection acting on tolerance and trichome density and glucosinolate concentration. The analysis revealed significant directional selection acting on the two resistance traits, but no significant directional selection on tolerance. Furthermore, they found no detectable disruptive selection on either glucosinolate concentration or trichome density and no significant two-way interactions (reflecting correlational selection) involving tolerance and these resistance characters. However, since they found strong disruptive selection acting on tolerance, they concluded that resistance and tolerance did not appear to be mutually exclusive defensive adaptations in *A. thaliana*. The pattern of selection on these characters seemed to favor the presence of both resistance and tolerance.

Although Tiffin and Rausher (1999) found no evidence of direct selection acting on either tolerance to leaf damage or apical meristem damage, they uncovered interesting patterns of correlational selection that would lead to the evolution of certain combinations of traits. In particular, Tiffin and Rausher (1999) found that, for leaf damage, selection favored genotypes with both high levels of resistance and tolerance. For damage to the apical meristem, however, selection favored genotypes with both low resistance and tolerance. Again, the joint pattern of selection on these defensive traits does not indicate that resistance and tolerance to the same kind of damage are mutually exclusive.

Fitness costs of tolerance

Many of the models that treat the evolution of resistance and tolerance make some assumptions about the presence and magnitude of the fitness cost of the trait. If there is some benefit to having a trait, one should expect the population to fix at some maximal level of that trait. However, it is commonly observed that plants do not contain the maximal amount of resistance or tolerance that one might predict from the amount of resources the plant has available. We know, for example, that most plants possess an intermediate level of resistance (Simms and Rausher, 1987). Therefore, it is widely assumed that resistance and tolerance must be costly to plants (Mauricio, 1998). If resistance and tolerance are costly, there should be some optimal level of resistance and tolerance that reflects a balance between the benefits of reducing herbivore damage or its

detrimental effects and the costs of diverting resources away from growth and reproduction (Simms and Rausher, 1987).

Costs have been envisioned as arising from several paths, but most biologists commonly refer to 'allocation' costs. Physiologically, an allocation cost is viewed as arising from internal competition for limiting resources. Evolutionarily, costs are envisioned as trade-offs between two characters, or antagonistic pleiotropy. An evolutionary trade-off exists between two characters if genetic change leading to an increase in the value of one character cannot occur without a decrease in the value of the other character. If both characters are of some benefit to the organism, then this negative genetic correlation will constrain evolutionary change because the benefit gained from selection to increase the value of one character will be counterbalanced by the cost of the correlated decrease in the value of the other character.

Several methods have been used to measure the fitness cost of tolerance. In the first method, we ask whether there is a genetic correlation between tolerance and fitness in the absence of herbivores. Tolerance can be determined as described above while fitness in the absence of herbivores must be determined by experimentally removing herbivores (Simms and Triplett, 1994; Fineblum and Rausher, 1995; Mauricio *et al.*, 1997). The rationale for this method follows that used in the measurement of costs of resistance: in the absence of herbivores, the benefits of tolerance are absent and only the costs are manifested (Simms and Rausher, 1987).

A second method of estimating costs of tolerance has the advantage that it uses only plants exposed to herbivory – no experimental manipulation is required (Mauricio *et al.*, 1997). In this method, fitness in the absence of herbivores is estimated by the intercept of a linear regression of fitness on damage. Cost of tolerance is then assayed by a regression of intercept on slope (Mauricio *et al.*, 1997; Tiffin and Rausher, 1999). One problem with this method is that even in the absence of a cost, slope and intercept are statistically correlated. Mauricio *et al.* (1997) describe a correction for this bias that allows the true cost of tolerance to be estimated.

Empirical investigations of costs have produced mixed results. Both Simms and Triplett (1994) and Tiffin and Rausher (1999) found evidence for fitness costs of tolerance. In contrast, Agrawal *et al.* (1999) found no evidence for a cost of tolerance in the wild radish, *Raphanus raphanistrum* and Fornoni and Núñez-Farfán (2000) found no evidence for a fitness cost of tolerance in jimsonweed, *Datura stramonium*. Finally, Mauricio *et al.* (1997) found no evidence for a linear cost of tolerance using either of the methods described above, but they did detect a highly significant quadratic relationship between tolerance and the fitness of plants in the absence of herbivores. For a range of tolerance, fitness decreased with increasing tolerance, suggesting a cost of tolerance in this range.

Trade-offs between tolerance and resistance

Another constraint on the joint evolution of tolerance and resistance is the degree to which there is a significant genetic correlation between tolerance and resistance within a species. The presence and strength of the genetic correlation will indicate whether these two traits will tend to evolve independently or jointly. Such a correlation can slow or accelerate the fixation of the traits in a population (Lande and Arnold, 1983; Via and Lande, 1995).

Like reports of the trade-offs between tolerance and fitness in the absence of herbivores, empirical studies on the trade-offs between tolerance and resistance have produced mixed results. Fineblum and Rausher (1995) provide evidence of a negative genetic correlation between tolerance of and resistance to apical meristem damage in the morning glory, *I. purpurea*. Similarly, Stowe (1998) demonstrated a negative genetic correlation between tolerance and glucosinolate content in the wild mustard, *Brassica rapa*.

In contrast, several empirical studies have failed to detect any genetic correlation between tolerance and resistance. In their study of tolerance to anthracnose fungus in *I. purpurea*, Simms and Triplett (1994) failed to detect a negative genetic relationship between tolerance and resistance. Mauricio *et al.* (1997) did not find a significant genetic correlation between tolerance and either trichome density or total glucosinolate concentration in *A. thaliana*. Finally, Tiffin and Rausher (1999) looked at resistance and tolerance to apical meristem damage in the same species of morning glory as Fineblum and Rausher (1995), and uncovered no significant genetic correlations between resistance and tolerance. Therefore, negative genetic covariances between tolerance and resistance may not constrain the evolution of these traits in all systems.

Conclusions

Does natural selection favor plants with either tolerance or resistance or both tolerance and resistance (or neither). It is clear that we do not yet have enough empirical evidence – either experimental or phenomenological – to determine how resistance and tolerance affect each other's evolution in a species or at a higher taxonomic level. The two studies that have most rigorously looked for evidence that tolerance and resistance are mutually exclusive (Mauricio *et al.*, 1997; Tiffin and Rausher, 1999) conclude that these two strategies can coexist in a species.

The assumption that many biologists start with is that tolerance and resistance are redundant – they do the same thing for the plant. But how do we determine if they are redundant? At some level, a plane, an automobile and a bicycle are redundant machines – each is capable of conveying us from point

A to B. Yet, each machine is most efficient at a different scale and in different circumstance. Are tolerance and resistance redundant only in the same gross way that a bicycle and plane are redundant? Have we discovered the scale and circumstances in which tolerance and resistance are the same or different?

Certainly, tolerance and resistance are sufficiently different that we expect them to evolve along different trajectories (Roy and Kirchner, 2000). We are now making efforts to understand the evolutionary processes that influence these trajectories and determine the equilibrium values of these traits.

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