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Evolutionary concepts

Can tolerance traits impose selection on herbivores?

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Abstract. Plant tolerance reduces the fitness consequences of herbivore and natural enemy damage, while resistance reduces the amount of damage suffered. In contrast to resistance, tolerance is often assumed to not affect herbivore performance and evolution. Evidence from the literature, however, suggests that it is possible for plant tolerance to affect herbivore performance and evolution, and potentially plant–herbivore coevolution. First, for cases when genetic correlations between resistance and tolerance are due to pleiotropy, the genes and loci for tolerance and resistance are the same, and as such both traits will affect herbivore performance directly. Second, it is possible that the physiological basis and mechanisms of plant tolerance – for example, changes in plant physiology and resource allocation – directly alter herbivore fitness characters. In this paper, I review the evidence for these potential effects of plant tolerance on herbivore performance, and suggest straightforward experiments to evaluate these possibilities. More generally, I propose that this untested assumption is constraining our view of plant–herbivore coevolution.

Key words: coevolution, genetic correlations, herbivory, plant defense, resistance, tolerance, tolerance mechanisms

Introduction

A major challenge in evolutionary ecology is to describe the evolutionary response of plants to damage by herbivores. Evolutionary responses to damage include resistance traits, which minimize the amount of damage a plant experiences (e.g., Rausher and Simms, 1989), and tolerance traits, which minimize the fitness consequences of damage (Painter, 1958; for a thorough overview of recent tolerance studies, see Evolutionary Ecology **14**, 283–570). Since resistance traits often deter feeding by herbivores, they are expected to produce reciprocal selection on herbivores and lead to coevolution (Janzen 1980). In contrast, tolerance is often thought to have no effect on herbivores, leading many investigators to assert that tolerance will not directly impose reciprocal selection on herbivores or lead to coevolution (e.g., Rosenthal and Kotanen, 1994; Strauss and Agrawal, 1999; Juenger and Lennartsson, 2000;

Stowe *et al.*, 2000; Tiffin 2000a). The prevalence of this assertion probably stems, in part, from the realization that tolerance traits may not lend themselves to clear predictions about plant–herbivore coevolution, especially in comparison to the arms race scenario envisioned for resistance traits.

In this paper, I argue that the notion that tolerance does not alter herbivore performance or evolution is an untested assumption. Based upon data available in the literature, it appears *possible* that tolerance could affect herbivore performance, and conceivably could lead to coevolution. As such, determining the effects, if any, of plant tolerance on herbivore evolution remains a largely unexplored area of evolutionary ecology, both theoretically and empirically. My purpose here is not to raise a semantic discussion about what is *defined* as resistance or tolerance, but rather to illustrate how a series of untested assumptions are altering and potentially constraining our view of plant–herbivore coevolution.

In the sections below, I first provide operational definitions for resistance and tolerance, in part because imprecise definitions of these characters are likely to obscure whether tolerance could indeed impose selection on herbivores. I then review two possible mechanisms by which tolerance could affect herbivore performance and evolution, the existing evidence in the literature for each of these possibilities, and conclude with some suggestions for future experimental tests of my hypothesis.

Operational definitions

Tolerance is often defined operationally as the slope of a regression of fitness on damage for a group of related individuals (Simms and Triplett, 1994; Mauricio *et al.*, 1997; Tiffin and Rausher, 1999). This approach essentially defines tolerance as a reaction norm of fitness along a gradient of herbivory (Abrahamson and Weis, 1997). For cases where damage is a discrete variable (e.g., meristem damage is present or absent) or is imposed by the investigator, tolerance is often defined as the difference in fitness of between damaged and undamaged plants (e.g., Simms and Triplett, 1994; Tiffin and Rausher, 1999). Tolerance traits or tolerance mechanisms, therefore, have been defined as traits that increase plant fitness once a plant has been damaged (Juenger and Bergelson, 2000; Juenger *et al.*, 2000; Tiffin, 2000b). As noted by these authors, however, this definition need not imply that these traits evolved specifically to minimize the fitness effects of herbivore damage.

Resistance traits reduce the amount of damage a plant suffers. Resistance to leaf damage is often estimated in the field as the complement of the proportion of leaf tissue consumed by herbivores, or 1 minus % damage (e.g., Rausher and Simms, 1989). Alternatively, one can measure the density or frequency of specific traits that are thought to deter or minimize feeding such as thorns (Gomez and Zamora, 2000), trichomes (Mauricio and Rausher, 1997), or egg mimics (Gilbert, 1973). If the latter approach is taken, however, then one must also demonstrate that a negative correlation exists between the putative resistance trait and the amount of damage a plant suffers (e.g., Mauricio and Rausher, 1997).

Many authors also include under the term 'resistance' or 'antibiosis resistance' traits that minimize herbivore performance, such as glucosinolates, alkaloids, and other secondary chemicals (reviewed by Bernays and Chapman, 1994). Antibiosis resistance traits can be measured indirectly by using measures of herbivore performance as a bioassay, often without direct knowledge of the plant chemistry or traits that are producing resistance (reviewed by Karban, 1992). Using herbivore fitness components as a measure of plant resistance, however, can be misleading because these observations are not always perfectly correlated with the amount of damage suffered by an individual plant (Simms, 1992). For example, compounds that inhibit digestion by insect herbivores can decrease herbivore growth rates and performance, but also increase the amount of tissue they consume (Moran and Hamilton, 1980). For this reason, throughout the remainder of this article I restrict my use of the term 'resistance' to traits that reduce the amount of damage incurred – either by deterring feeding or by decreasing herbivore performance.

Effects of tolerance on herbivore performance

Correlations between tolerance and resistance

One potential mechanism by which tolerance to herbivore damage can affect herbivore performance and evolution is through a genetic correlation between tolerance and resistance – a point undoubtedly recognized by those authors who have argued that tolerance traits will not directly affect herbivore performance (e.g., Rosenthal and Kotanen, 1994; Strauss and Agrawal, 1999; Juenger and Lennartsson, 2000; Stowe *et al.*, 2000; Tiffin 2000a). However, depending on the mechanism underlying a genetic correlation between resistance and tolerance, it is still possible that tolerance traits could *directly* affect herbivore evolution. For example, if a genetic correlation between resistance and tolerance was due to pleiotropy, the same traits that produce tolerance *necessarily* produce resistance (cf. Roy and Kirchner, 2000), and it would be impossible for the evolution of tolerance to not have effects on herbivore evolution. If this were to be the case, the genes and loci that produce tolerance and resistance may be identical, and as such it is unavoidable that both resistance and tolerance will directly impose selection on herbivores.

By contrast, if the genetic correlation between resistance and tolerance were due to linkage disequilibrium, then the effects of tolerance on herbivore performance would be indirect, or mediated by correlated resistance traits. In these cases it is likely that any decay of linkage disequilibrium between resistance and tolerance would have the effect of reducing the indirect effects of tolerance has on herbivore performance through correlated resistance traits. Obviously, determining the genetic mechanism that produces a genetic correlation is a challenging endeavor. Nevertheless, assuming that tolerance cannot directly affect herbivore performance and evolution does not address the problem.

The consequences of genetic correlations between resistance and tolerance for the evolution of these plant traits is straightforward (e.g., Falconer and Mackay, 1996) – for instance, if resistance and tolerance are negatively correlated, selection for increased tolerance will result in a correlated decrease in resistance, and perhaps a relaxation of selection on herbivores. In like fashion, if tolerance and resistance are positively correlated, selection for increased tolerance will result in correlated increase in resistance, possibly intensifying the pattern of selection on insect herbivores. However, despite its theoretical and empirical importance, research addressing how the joint evolution of resistance and tolerance *affects herbivore evolution* is lacking.

Several empirical studies have assessed whether tolerance and resistance are genetically correlated, and it still remains unclear how often significant genetic correlations between these traits exist. For example, Simms and Triplett (1994), Mauricio *et al.* (1997), Tiffin and Rausher (1999), and Stinchcombe and Rausher (2002) all failed to detect significant genetic correlations between tolerance and resistance, as measured in the field. These data clearly suggest that genetic correlations between tolerance and resistance are not universal. In contrast, Fineblum and Rausher (1995), Stowe (1998), and Pilson (2000) have reported significant genetic correlations between resistance and tolerance. At minimum, the existing data on genetic correlations between tolerance and resistance suggest that before declaring that the evolution of tolerance will not affect herbivore performance, one must first determine that tolerance and resistance are indeed genetically uncorrelated.

Direct effects of tolerance on herbivore performance

A second potential mechanism by which tolerance traits might affect herbivore performance and evolution is if the biological processes and mechanisms that allow a plant to minimize the fitness consequences of damage (i.e., tolerance traits) also affect herbivore performance. If this is the case, it is possible for tolerance traits to impose selection on herbivores. To illustrate this, in the following examples I show how a proposed physiological mechanism that allows a plant to tolerate damage could also alter herbivore performance without affecting the amount of leaf tissue lost to herbivores (i.e., resistance), thus *potentially* leading to reciprocal selection on herbivores and eventually co-evolution. Because the exact nature of many tolerance mechanisms is unclear (e.g., Tiffin, 2000b), many of my examples are hypothetical. I focus on how tolerance traits could affect insect herbivores, although the principles may apply to vertebrate herbivores as well.

Many proposed tolerance mechanisms involve changes in plant physiology or resource allocation (reviewed by Rosenthal and Kotanen, 1994; Strauss and Agrawal, 1999; Tiffin, 2000b). Changes in plant chemistry and resource allocation have the potential to alter plant quality or quantity for herbivores. Changes in plant quality and quantity have been shown in other contexts to reduce a variety of insect fitness characters, including survival, development rate, fecundity, pupal mass, or size at adulthood (e.g., Tallamy and Raupp, 1991; Karban, 1992; Morris, 1997). If the physiological responses to damage that provide tolerance also affect plant quality or the quantity of resources available to herbivores, it is possible that these mechanisms could also affect herbivore performance and fitness components without affecting consumption.

If the mechanism by which tolerance is achieved does not affect total leaf tissue consumption, tolerance could directly impose selection on insect herbivores. While data directly bearing on this issue is lacking, circumstantial evidence indicates that these effects are certainly possible. For example, consider the possibility that tolerance is achieved by reallocating nutrients from roots or leaves to reproductive structures. Nutrient-poor tissue commonly slows the growth and development of insect herbivores (e.g., Scriber and Slansky, 1981; Slansky and Wheeler, 1992; Bezemer and Jones, 1998). Thus, tolerance could potentially impose selection on insect herbivores to accelerate their development or to increase their digestive efficiency without altering the amount of tissue consumed.

Other types of observations suggest that the mechanisms that produce tolerance can also have a mixture of positive and negative effects on herbivores. A common response to herbivore damage is regrowth or activation of dormant meristems (e.g., Doak, 1991; Bergelson *et al.*, 1996; Juenger *et al.*, 2000). While regrowth may allow the plant to replace a portion of the leaf tissue originally lost to herbivores, it is also creates a new food source for herbivores of altered quality and quantity. For instance, many plants tolerate mammalian herbivory by the regrowth of tissue. There are several documented cases that demonstrate that feeding on regrowth tissue has positive effects on insect herbivore performance (e.g., Danell and Huss-Danell, 1985; Hjalten and Price, 1996; Roininen *et al.*, 1997; Martinsen *et al.*, 1998). Thus, in this example, the physiological response that allows a plant to tolerate herbivory imposed by mammals (regrowth) will likely have the effect of altering the pattern of selection on herbivorous insects. Moreover, feeding on regrowth can also have negative effects on herbivore performance (e.g., Brown and Weis, 1995). In either case, there is the potential for the mechanism that provides tolerance to change the pattern of selection on insect herbivores, and affect herbivore evolution.

If tolerance traits can impose selection on herbivores, it is not clear whether the patterns of selection imposed by plant tolerance traits and plant resistance traits would be qualitatively or quantitatively similar. One might expect that resistance traits that directly minimize tissue loss are likely to have more severe effects on herbivore fitness than tolerance traits that might affect herbivore fitness as 'side-effects' of their function as tolerance traits, but this is also fundamentally an empirical question.

Conclusions

The possibilities described above can be evaluated using relatively simple experiments. An obvious place to start is to measure performance characters of insect herbivores when reared on host-plant genotypes that are known to differ in their tolerance to herbivory. If the mechanisms that provide tolerance to herbivory do not affect herbivore performance, there should be no correlation between the levels of host plant tolerance and herbivore performance. If herbivore performance and host plant tolerance are correlated, however, then this indicates that the mechanisms that provide tolerance are affecting herbivore performance and could thus lead to coevolution. However, distinguishing whether it is tolerance *per se* or a correlated resistance trait that is negatively affecting herbivore performance requires great care. If the effects of tolerance on herbivore performance are due to a correlated resistance trait, then one would expect a significant correlation between tolerance and the amount of leaf damage. If this is the case, the effects of tolerance on herbivore evolution are likely to be indirect and mediated by correlated resistance traits. If tolerance and the amount of tissue consumed are uncorrelated, then tolerance can impose selection on herbivores independent of the effects of resistance.

Whether or not these scenarios occur in the field is an unanswered empirical question, but under a biologically reasonable set of assumptions they are certainly *possible*. Moreover, if tolerance does affect herbivore performance and evolution, theoretical models of the evolutionary and ecological consequences of tolerance and resistance that assume the opposite (e.g., Roy and Kirchner, 2000; Tiffin, 2000a) could potentially be misleading. The consequences of plant tolerance on herbivore evolution remains a theoretically and empirically unexplored question.

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