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# THE EVOLUTIONARY ECOLOGY OF TOLERANCE TO CONSUMER DAMAGE

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■ **Abstract** Recent theoretical studies suggest that the ability to tolerate consumer damage can be an important adaptive response by plants to selection imposed by consumers. Empirical studies have also found that tolerance is a common response to consumers among plants. Currently recognized mechanisms underlying tolerance include several general sets of traits: allocation patterns; plant architecture; and various other traits that may respond to consumer damage, e.g., photosynthetic rate. Theoretical studies suggest that tolerance to consumer damage may be favored under a range of conditions, even when the risk and intensity of damage varies. However, most of these models assume that the evolution of tolerance is constrained by internal resource allocation trade-offs. While there is some empirical evidence for such trade-offs, it is also clear that external constraints such as pollinator abundance or nutrient availability may also limit the evolution of tolerance. Current research also suggests that a full understanding of plant adaptation to consumers can only be achieved by investigating the joint evolution of tolerance and resistance. While tolerance to consumer damage has just recently received significant attention in the ecological literature, our understanding of it is rapidly increasing as its profound ecological and evolutionary implications become better appreciated.

## INTRODUCTION

Plant tissue damage caused by consumers is an important selective force molding plant phenotypes (3, 79, 92, 108, 109). Until recently, most studies of plant adaptation to consumers focused exclusively on the evolution of traits that prevent or reduce tissue damage, i.e. resistance (3, 36, 108, 109). However, consumers may also select for traits that allow plants to maintain fitness in the face of tissue loss (92, 108, 109, 127, 140, 153a). Plant genotypes that can sustain tissue loss with

little or no decrease in fitness relative to that in the undamaged state are termed tolerant of damage (108, 109). The term tolerance has also been used to describe the ability of plants to cope with other stresses (e.g. salinity, drought, heavy metals). In this paper, we drop the qualifier unless we are referring to an environmental stress other than consumer damage.

Among ecologists and evolutionary biologists, initial interest in tolerance was stimulated by several empirical studies reporting that consumer damage may increase, rather than decrease, plant productivity (89, 90, 103, 104). This remarkable observation was initially dismissed as the result of reallocation of below-ground resources to above-ground structures in perennial plants, which would eventually entail a net fitness decrement (13, 153a). However, when Paige & Whitham (107) discovered that grazed individuals of an Arizona population of *Ipomopsis aggregata* exhibited higher lifetime fitness than their ungrazed neighbors, the apparently paradoxical phenomenon of overcompensation could no longer be summarily dismissed.

Subsequent research stimulated by this seminal paper (107) focused largely on overcompensating tolerance. For example, considerable effort was devoted to determining whether other populations of *Ipomopsis* exhibit the same phenomenon (14, 15). Initially, these studies did not find overcompensating tolerance (14–16), leading to skepticism about the original result. Nevertheless, further work suggested that while overcompensating tolerance may be unusual in *Ipomopsis aggregata*, it does exist in some populations (47, 105, 106).

It is best to view overcompensating tolerance as one extreme along a continuum of plant responses to consumer damage (83). Even in populations for which the mean response to damage is incomplete tolerance, there is evidence that genetic variation in tolerance exists. Specifically, some families exhibit overcompensating tolerance, whereas others express incomplete tolerance (16, 56, 63, 137, 146). Moreover, recent studies comparing historically grazed and ungrazed plant populations indicate that repeatedly grazed populations can evolve overcompensating tolerance, even while other populations remain incompletely tolerant (74).

The ecological and evolutionary effects of tolerance differ from those of resistance in several important ways. For example, plant resistance traits may have a selective impact on herbivore traits, whereas tolerance will not (123). Further, evidence is mounting that a comprehensive theory of plant adaptation to consumption requires joint consideration of both resistance and tolerance traits (3, 38, 87, 137, 140, 146). Here, we synthesize recent literature concerning the evolutionary implications of tolerance to consumer damage and highlight numerous ecological and evolutionary questions therein.

## DEFINING TOLERANCE

While resistance was originally defined in the agricultural literature as an umbrella term including both tolerance and defense (26, 108, 109, 127, 138), we follow the convention often used in the ecological literature. They use defense as

the blanket term with resistance and tolerance as subcategories (3, 4, 37, 38, 64, but see 140). Thus, we consider defense as the umbrella term which includes both tolerance and resistance.

The distinction between tolerance and resistance was first described by agricultural scientists (26, 109, 108, 127), who determined that these composite traits are comprised of different sets of underlying characteristics, often controlled by different sets of genes (6, 19, 39, 44, 76, 88, 110, 116). As early as 1894, Cobb (26) distinguished between the ability to endure disease yet still "mature a far crop of grain" from the ability to resist disease attack. Painter (108) first described herbivore tolerant plants as those "surviving under levels of infestation that would kill or severely injure susceptible plants," but he subsequently expanded his definition to include a plant that "shows an ability to grow and reproduce itself or to repair injury ... in spite of supporting a population of herbivores approximately equal to that damaging a susceptible host" (109). In a review of tolerance to plant disease, Schafer (127) defined tolerance as "that capacity of a cultivar resulting in less yield or quality loss relative to disease severity or pathogen development when compared with other cultivars or crops." These definitions highlight the steps involved in measuring tolerance. First, individuals must be classified by their genetic relationships. Then, within each genetic class, fitness (or yield) must be measured at different levels of damage, disease, or pest population density. The fitness (or yield) responses of the individuals in a genetic class, across the damage, disease, or pest density gradient, is then an estimate of the tolerance of that group.

Thus, we can define tolerance as the reaction norm of fitness across a damage gradient, and it can be treated as a phenotypically plastic trait (137). As with other phenotypically plastic traits, tolerance to damage can be modeled by a mathematical function (129, 130, 154). The fitness function is probably modeled most accurately as a complex polynomial equation (3, 111, 112, 115, 146). For example, some potato varieties maintain yield at low damage levels (compensating tolerance), but experience decreasing yield with further increases in damage (incomplete tolerance) (95). Other varieties increase yield in response to damage (overcompensating tolerance), but undercompensate for heavier damage (95; also see 77, 78, 94, 133). However, for simplicity, a linear function is frequently used to describe tolerance (3, 56, 87, 137, 140, 146) and is often a good approximation (11).

The tolerance of a genotype can then be described by the linear function, $Y = a + bX$, where $Y$ indicates fitness and $X$ indicates damage level (Figure 1). The $Y$-intercept, $a$, denotes fitness when undamaged and describes the genotype's ability to tolerate all environmental stresses other than consumer damage. The mean height of the line, $\overline{Y}$, describes fitness averaged across all damage levels and is a measure of general vigor (42, 41, 43). Finally, the slope of the reaction norm, $b$, describes the change in fitness in response to consumer damage, or tolerance. A completely tolerant genotype has a flat reaction norm ($b = 0$) and experiences no fitness impact of damage. A negative slope ($b < 0$) indicates undercompensating tolerance; a positive slope ($b > 0$) describes overcompensating tolerance.

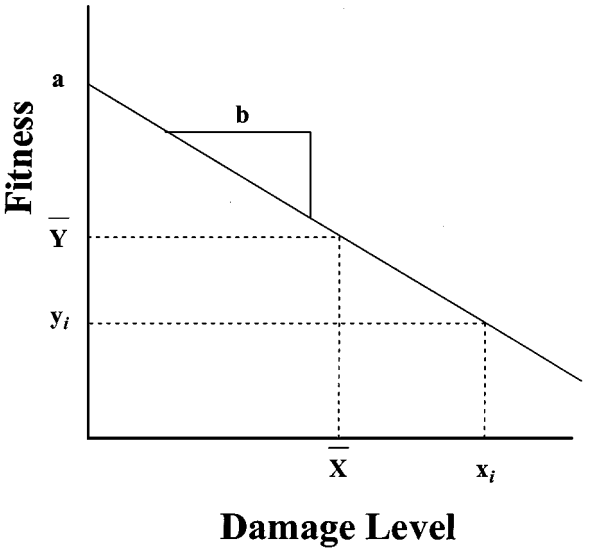


**Figure 1** Hypothetical fitness reaction norm of a genotype, obtained by regressing fitnesses of clonal replicates of the genotype on the damage level that each replicate sustained. The estimated slope, *b*, is an operational measure of tolerance to damage; the influence that damage has on fitness. The *y*-intercept, *a*, indicates the influence that other environmental variables have on fitness. This value can be obtained by extrapolation but is best measured on clonal replicates experimentally protected from damage. In this example, the slope is negative, indicating incomplete compensation for damage.

Some authors have defined tolerance to damage simply as the fitness of an individual at a particular level of damage (108, 109, 127). However, our model illustrates that defining tolerance in terms of fitness in a single damage environment fails to distinguish the effects of damage on fitness from those of other uncontrolled environmental factors. Therefore, defining tolerance as fitness at a definite level of damage (e.g. 108, 109, 127) obscures the action of traits that specifically allow plants to tolerate damage by consumers (see 56). To illustrate this with our simple model, we define fitness of a genotype *X* experiencing the *ith* level of damage as $Y_i$. This value is predicted by three factors: (i) the known level of damage, $X_i$, (ii) the slope of the genotype's fitness reaction norm to damage, *b*, and (iii) the genotype's fitness in the absence of damage, *a*. In the absence of damage, fitness is determined by the interaction of the genotype with all other environmental factors. Thus, the only component of the model that is not determined by the level of damage or the genotype's fitness response to damage is the intercept, which is determined by the genotype's fitness response to all other environmental variables. Further, the only way to determine whether a component trait contributes to tolerance of consumer damage rather than to tolerance of some other environmental stress is to measure how it affects fitness along a damage gradient.

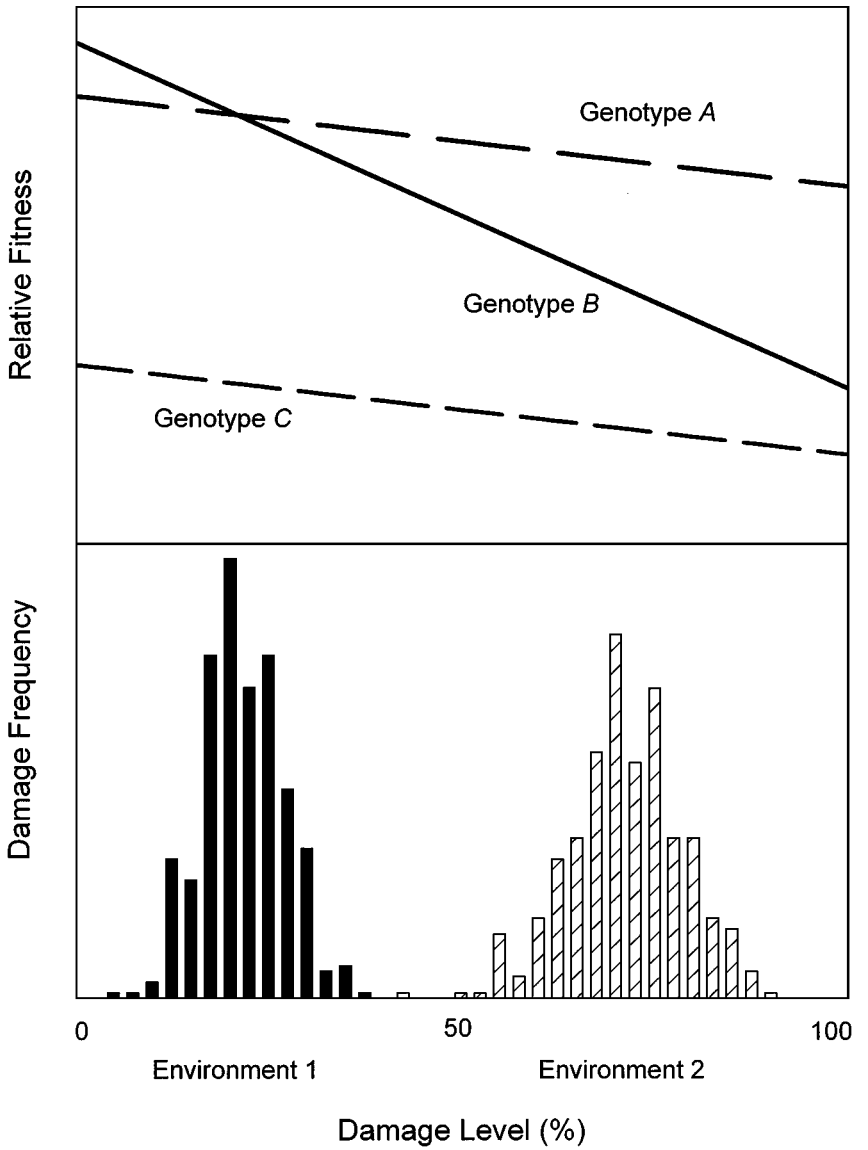


**Figure 2** Fitness reaction norms of three plant genotypes exposed to two environments that differ in mean levels of damage. In the upper panel, the relative fitnesses of the three genotypes are plotted against damage level; their tolerance phenotypes are indicated by their reaction norm slopes whereas the heights of their reaction norms indicate their general vigor in these environments. The lower panel indicates the relative frequencies of damage levels in each environment. Environment 1 has a lower mean level of damage than does environment 2.

It is also possible for genotypes to be highly tolerant of consumer damage (i.e. $b$ close to, or greater than, 0), but to have low general vigor ($\overline{Y}$). Thus, the relative contributions of general vigor versus tolerance to fitness of a species, variety, or genotype in any specific environment depends upon the range and frequencies of damage levels to which they may be exposed. The range of damage can also determine the detectability of fitness trade-offs (see below, artificial vs natural damage). These points are illustrated in Figure 2. In this figure, the mean damage level in environment 2 is relatively high and genotype A is always more fit than genotype B. Further, although genotype C is more tolerant than genotype B, genotype C always has the lowest fitness because it has low general vigor. Genotype A has the overall fitness advantage in environment 2 because it is always more vigorous than genotype C, as well as being both more tolerant and vigorous than genotype B. In this environment, selection should favor both increased tolerance and vigor, i.e. genotype A. However in environment 1, which has a lower average level of damage, the norms of reaction of genotypes A and B cross. Within this environment, genotypes A and B have approximately equal general vigor, but their crossing reaction norms reveal a cost of tolerance. Genotype A is more tolerant and therefore has higher fitness during times of moderate damage. But because of the cost of tolerance, genotype B is more fit during times of low damage. Both genotypes are more fit than genotype C, which still suffers from low general vigor. These hypothetical data demonstrate that distinguishing between general vigor and tolerance may be important in understanding the evolutionary response of plants to consumer-imposed selection.

The example in Figure 2 also illustrates the importance of knowing the probability distribution of different damage levels within plant populations (56, 140). When damage levels are uniformly high, as in environment 2, genotype A is always more fit than genotype B. However, in environment 1, in which plants tend to experience less damage, the relative fitnesses of A and B will depend critically on the frequency distribution of damage levels over time. An important question to answer, then, is how often these conditions occur (56, 140). Clearly, determining the frequency of damage environments that select for or against tolerance is essential for determining the evolutionary trajectory of plant-consumer interactions.

## OPERATIONALIZING THE TOLERANCE DEFINITION

While in theory the tolerance of an individual can be determined, in practice tolerance cannot be quantified as a property of an individual. Instead, it must be estimated as the property of a group (i.e. individuals of a species, variety, cultivar, population, or genotype). Thus, characterizing tolerance entails measuring the fitnesses of replicate individuals from the group that have experienced a range of damage levels. These individual values are then summarized statistically to estimate the tolerance of the group. Recent empirical studies have employed

variants of this method to evaluate genetic variance for tolerance to both artificial and natural damage (56, 87, 135, 137, 140, 146). Despite the seeming simplicity of this protocol, however, there are many potential pitfalls involved in measuring tolerance.

## Natural versus Artificial Damage

While it has been argued that to completely characterize the tolerance function, all damage levels should be investigated (3), others have argued that a focus on natural damage is more effective when estimating tolerance (145). Thus, controversy exists over whether tolerance should be evaluated using natural variation in damage or experimentally imposed damage levels (56, 140, 145). This controversy is composed of several issues that should be considered individually. The first issue involves statistical biases. Natural levels of damage are determined by a multiplicity of environmental and genetic factors that may also directly influence plant fitness. These confounding factors may create a bias if natural damage is used to estimate tolerance (56, 140, 146). For example, natural damage levels undoubtedly reflect individual variation in resistance. If resistance is costly, then individuals with less damage (i.e. more resistance) may exhibit lower fitness, thereby creating a downward bias in the estimate of tolerance (140).

Concerns about confounding factors have prompted several investigators to impose controlled levels of damage that can be randomly assigned among individuals (e.g. 56, 140). However, the use of artificial damage entails its own problems (145). Recent studies clearly indicate that the nature of plant resistance traits induced in response to tissue damage can be strongly influenced by the identity of the causal agent (4, 10a, 88a). While the mechanisms by which different responses are induced are not always clear (10b), it seems ever more likely that the same unit of damage might impose different fitness effects, depending upon its causal agent.

Even when damage is imposed using natural agents, achieving controlled levels of damage often requires some artificiality. For example, insects may be confined to small cages attached to individual leaves (4, 72a). Such constraints will alter the dispersion, timing, and duration of damage. Several studies now suggest that these factors influence the fitness impact of damage (79a, 85). These concerns have led some investigators to argue that the biases caused by natural damage are relatively less important than the loss of precision caused by using artificial damage to estimate tolerance (145).

## Difficulty Estimating Fitness

In most organisms, it is virtually impossible to measure *total* fitness. In many plants, however, it is even more complicated. Fitness is determined not only by the number of offspring produced by an individual, but also by the number of offspring it sired, and the survival and fecundity of offspring. Thus, estimates of tolerance may depend on which fitness components are considered.

Most empirical studies have estimated tolerance using female components of fitness (e.g. seed production: 49, 50, 87, 137, 140, 146). However, damage may also impact male fitness components (40, 47, 93, 141, 143). For example, foliar damage can alter attractiveness to pollinators (141, 143) and thus reduce a plant's success at siring seeds. Mechanisms that mitigate the impact of damage on female fitness components may differ from those that reduce the impact on male fitness. Indeed, tolerance measured via the female fitness components might even be achieved by shifting resources from male to female reproductive structures (50, 156a). However, if siring seeds consumes less resources than filling seeds, tolerance may be achieved by shifting resources from female to male reproduction. Thus, a better measure of tolerance would consider both female and male components of fitness (47, 140).

Even when growth and/or reproduction of damaged individuals appear equivalent to that of undamaged plants, subtle fitness trade-offs may cause new tissues (i.e. leaves) or replacement progeny to differ in quality (i.e. seed viability, seedling survivorship, and/or seed output). When damaged individuals produce the same number of offspring, yet of lower quality, tolerance may be overestimated. For example, *Pastinaca sativa* appeared tolerant to *Depressaria pastinacella* caterpillars because damaged plants produced the same number of seeds as undamaged plants. However, seeds from damaged and undamaged plants were not always equally large or viable (50). Consumer damage may also affect flowering phenology (50). Depending on the length of the growing season, changes in phenology may affect seed quality or threaten the possibility of reproduction altogether (63, 146). Biotic factors such as pollinator availability may also constrain phenology and limit tolerance via reproductive delay (62). Such constraints may not always be manifested. For example, although seeds produced by browsed *Ipomopsis aggregata* are produced later in the growing season, existing studies have shown that delayed seed maturation does not reduce germination or subsequent growth of progeny (107). Of course, this outcome may vary with the date of first frost.

## Difficulty Measuring Damage

Finally, when consumer damage is difficult to quantify, resistance and tolerance may appear indistinguishable. It is particularly difficult to quantify systemic damage, such as that imposed by sap feeders or systemic diseases (see 125). Agricultural scientists have developed some methods to deal with these types of problems (76, 110, 138). For example, rather than measuring leaf area damaged, they use the biomass gain of the consumer or its population growth as an estimate of resistance. Thus, plants that produce less consumer biomass are considered more resistant. Further, regression methods have been used to distinguish between tolerance and resistance in crop varieties, and may be usefully applied to natural populations (76, 110, 138). This is done by regressing plant fitness on damage level, or consumer biomass. The intersection of a line marking the mean damage level and the

regression line then forms four quadrants that indicate different combinations of tolerance and resistance.

## MECHANISMS OF TOLERANCE

Attempts to predict the evolution of tolerance will benefit from a more detailed understanding of the genetic mechanisms controlling plant responses to damage. Despite extensive efforts devoted to elucidating how increases in defense are selected for by consumer feeding, there is still only cursory understanding of these processes (3, 4, 27, 36, 56, 80, 87, 125, 140, 141). Total fitness represents a lifetime integration of phenotypic interactions with the ever-changing environment. Thus, mechanisms underlying the fitness response to damage (tolerance) are likely to be far more complex than those underlying resistance. Consequently, current understanding of the fundamental mechanisms of tolerance resides at a very gross level (147).

Traits currently known to provide tolerance to damage are involved in two general roles: one, resource reallocation; and two, plant architecture. Clearly, replacing tissue or progeny lost to consumers involves allocation of mobile resources (49, 50). Yet, even when resources are adequate, tolerance may be limited by the number of available meristems (45). Further, patterns of vascular architecture can restrict the flow of resources among plant parts (157), limiting the use of existing resources to tolerate tissue loss (81).

### Resource Allocation Patterns

Resource allocation patterns prior to and/or following damage may contribute to tolerance. Patterns of resource allocation are characterized by (*a*) relative allocation to storage, growth, or reproductive organs, (*b*) qualitative aspects of the organs (e.g. thick vs thin leaves, storage vs feeder roots), and (*c*) the timing of allocation.

Allocation decisions prior to damage may condition tolerance. In *Asclepias syriaca*, for example, genotypes that stored more resources in rhizomes were more tolerant of losing leaf area to consumers (56).

Changes in allocation following damage may also influence tolerance. In undamaged individuals, source-sink relationships direct resource allocation among organs (157), with the relative strength of sinks determining which will accumulate more resources (54). Consumer damage often removes sinks and/or sources, thereby altering source-sink relationships and modifying allocation patterns (147). The existence of sinks is determined by hormones, and the way that allocation patterns shift in response to damage are under hormonal control as well. Consequently, tolerance may depend in part on hormonal control of meristem release and differentiation. For example, removal of the apical meristem in *Ipomopsis aggregata* releases lateral meristems, which would otherwise remain dormant (105–107).

The branches formed from these lateral meristems together can produce as many, or even more, seeds as the lost apical shoot (105, 107).

Damage-induced changes in hormonal meristem control may also alter allocation to sexual functions. For example, in undamaged wild parsnip (*Pastinaca sativa*) (49, 50), early inflorescences are composed mainly of hermaphroditic flowers, which will become sinks if they set seed, whereas later maturing inflorescences produce mostly male flowers. However, floral damage on early inflorescences alters sex expression of later maturing inflorescences, allowing them to produce more hermaphroditic flowers. As a consequence, damaged plants produce as many seeds as undamaged plants (although, as described earlier, seeds produced on the later maturing inflorescences are smaller than those that would have been borne on the earlier maturing inflorescences).

Tolerance may also depend on qualitative differences among plant modules made or modified following damage (5, 30, 97, 126, 155). Much of the research concerning physiological changes has focused on changes in photosynthetic rates, which often increase in damaged leaves and/or in neighboring undamaged leaves (90a). The pathways to increased photosynthetic rates are numerous. For example, photosynthetic rates of *Phaseolus vulgaris* increased after herbivory because the remaining leaves had higher levels of RUBISCO (155). In contrast, in *Agropyron* species, increased photosynthetic rates were due to delays in leaf senescence (97). Further, *Solidago* leaves produced following damage showed higher photosynthetic rates than leaves on control plants because they had both high specific leaf area and delayed senescence (90a). Future experimentation should take into account how both the pattern of damage within a leaf (90b) and within the plant canopy (90a) may influence photosynthetic rates. However, the question of whether increased photosynthetic rates are of sufficient magnitude or duration to compensate for lost tissue is still open.

The timing of allocation to growth, storage, and reproduction can also be critical to tolerance. In *Isomeris arborea*, floral damage by a pollen-feeding beetle occurs during the first half of the flowering season (68, 69). Some genotypes achieved tolerance by prolonging flowering in response to damage, allowing them to set seed after the beetles stopped feeding. This example highlights how tolerance may depend critically on the degree of overlap in plant and consumer phenology. It also illustrates the close relationship between resistance and tolerance. Genotypes of *I. arborea* that delay flowering until after the beetle has pupated are generally described as resistant (escape in time). In contrast, genotypes that flower while the beetles are active, but then reallocate resources to flowering post-damage are termed tolerant, yet they can only be tolerant if they escape damage in the second half of the season, i.e. are resistant.

## Plant Architecture

As described above, allocation patterns contribute to plant architecture (45). In turn, plant architecture influences resistance (80, 82) and may affect plant tolerance in

several different ways (81). First, architecture may influence tolerance through its impact on resource capture. For example, wild tomatoes are more tolerant than their domesticated kin, largely because the canopy structure of wild tomatoes allows them to better exploit increased light availability following damage (159).

The number and distribution of meristems can also influence tolerance (20, 81, 100). For example, the extent of growth following damage may depend on the number and distribution of meristems surviving damage, the pattern of meristem release from dormancy, and the number of new meristems produced after damage. Plants may be tolerant by having more meristems prior to damage. For example, two wild relatives of maize have a greater number of tillers than the domesticated species and are more tolerant of stem borer damage (124). Palms provide a classic example of meristem limitation of tolerance. Because they lack basal adventitious shoots, palms are completely intolerant of meristem herbivory. Damage to the single meristem kills the tree (31).

Sectoriality imposed by vascular architecture may be another important constraint on tolerance to damage (81, 156, 157). Since plants are modular in their construction, resource movement among modules is not completely independent (156, 157). Vascular piping does not connect every plant part to all other parts, and resources from distant modules may be unavailable for allocation to sites of localized damage. Two factors may limit the ability of plants to respond to localized damage (81, 157). First, plants may be unable to respond to damage if sources cannot detect the demand from distant sinks (156, 156a, 157). Second, inadequate vascular connections may impede resource transfer to distant locations, thereby hampering the ability to tolerate consumer damage (81, 157). In many cases, plant resources appear sufficient to compensate for localized leaf area loss, but vascular constraints on resource allocation limit compensatory growth, leading to localized decreases in growth and reproduction (81). Further, vascular constraints on reallocation responses can also decrease overall plant fitness (79, 85, 86). In some plants, it appears that new vascular connections form after damage (134). It seems reasonable that genotypes better able to form such connections would be more tolerant, yet this idea remains unexplored.

Although increased vascular integration may improve plant tolerance to foliar damage (131), it might also increase resources available to internal feeding consumers such as systemic pathogens and xylem- or phloem-feeding herbivores. Consequently, selection on vascular architecture by one consumer guild might be opposed by selection imposed by other consumer guilds. For example, stem-boring and sucking consumers may have a smaller fitness impact on clonal plants because their feeding is restricted to a particular ramet (124). However, individual ramets may sacrifice tolerance to leaf chewers by giving up the ability to share resources (7, 131). Because so little is known about the effects of plant architecture on tolerance to damage, future studies are needed to test these predictions. Further comparative and experimental studies examining plant architecture effects on tolerance may be a promising avenue for investigation.

## EVOLUTION OF TOLERANCE

A large body of theory (1, 60, 61, 96, 136, 148, 150, 149, 151) has been developed to elucidate the conditions under which overcompensating tolerance may evolve. These models all make specific assumptions about how patterns of resource allocation constrain fitness under different consumption regimes. Consequently, in our review below, we refer to them as *reallocation models*. More recent theoretical work has addressed tolerance that is not necessarily overcompensating (3, 125, 146). These models also consider the *joint evolution of tolerance and resistance*. Below, we summarize the predictions and evaluate the assumptions of both types of models.

### Models

***Reallocation Models*** Several models were designed to investigate the implications of internal resource trade-offs for the evolution of overcompensating tolerance to meristem damage. As a group, they explore how the pattern of meristem removal, both within and among growing seasons, influences the evolution of tolerance (1, 60, 61, 96, 132, 136, 150, 149, 151). Some models examine the effects of individual selection (96, 148, 150), whereas others explore selection among lineages (61, 136).

### Individual Selection

Simple mathematical models invoking individual selection suggest that overcompensating tolerance can evolve when the chance of being damaged is greater than the chance of escaping (148, 150, 152). When the probability of being damaged is greater than 50%, individual fitness is maximized by withholding investment in reproduction until after damage (150, 151). In contrast, when there is less than a 50% probability of being damaged, individual fitness is maximized by committing all resources to reproduction prior to damage, leaving none available for reallocation (63, 151, 152).

These models assume that meristem-removal occurs randomly among individuals, individuals are damaged only once, and damage occurs at the same life stage every generation. Thus, damage is the environmental cue that indicates that it is safe to allocate stored reserves to reproduction. However, plants that rely on environmental cues for their allocation decisions may allocate resources suboptimally (33, 63). Further, plants that delay reproduction regardless of damage can invade a population of overcompensating individuals unless damage is universal (84, 144). Thus, individuals that allocate resources to reproduction late in the season, i.e. after the danger of damage, will be more fit than those that wait until damage occurs (61, 63). This highlights the important influence of allocation patterns on the evolution of tolerance.

These simple allocation models seem unrealistic because they predict the evolution of incomplete tolerance only when all allocation strategies are equally

fit, i.e. in the limited case when being damaged or undamaged are equally likely (150). Further, their assumptions about the pattern and timing of damage are quite restrictive and maybe unrealistic (79a, 85). Relaxing these assumptions produces predictions that appear more realistic. For example, tolerance can evolve if consumers preferentially damage larger individuals that have invested more of their total resource pool into growth or reproduction rather than storage (150). Further, as consumers become choosier (i.e. express stronger preference for larger individuals), the amount that plants should invest in growth/reproduction prior to damage decreases, relaxing the conditions for the evolution of overcompensating tolerance. However, introducing a trade-off between active and future meristem production favors intermediate allocation strategies (148), which leads to incomplete tolerance. Such a trade-off can be included in the model by assuming a cost of currently active buds versus maintaining dormant buds. This added cost increases the intensity and risk of damage needed to favor bud dormancy, thereby restricting the conditions under which tolerance in any form can evolve.

Other assumptions have been explored in a series of models developed by Tuomi and colleagues. They first (148) relaxed the assumption that heavy damage is required to activate dormant meristems. This model predicts that a high probability of experiencing a single grazing episode favors meristems that are activated by small amounts of damage. Next, they relaxed the twin assumptions that plants experience only a short window of vulnerability prior to flowering and never suffer secondary damage (96). By incorporating repeated grazing events within a season, they found that optimal meristem reactivity to damage declined with increases in the number of grazing events, grazing risk, or intensity of damage. Thus, when a population is likely to experience multiple grazing events, grazers must remove a relatively large proportion of active meristems from an individual before its dormant buds are stimulated to grow. However, the model also predicts that repeated within-season grazing events relax the conditions that favor tolerance. Specifically, as the number of grazing events increases, overcompensating tolerance may evolve at lower risks of and levels of damage than when damage occurs only once during a growing season (96).

## Does Overcompensating Tolerance Equal Plant-Consumer Mutualism?

Several authors have suggested that plants with overcompensating tolerance have evolved a mutualistic relationship with consumers (for review, see 13, 90, 84, 153a). However, theory makes clear that simply observing overcompensation in response to artificial damage (or even to natural damage that is heavier than normal) is not sufficient evidence with which to conclude that plants have evolved a mutualistic relationship with consumers. A mutualism requires that the two parties perform better when acting in concert than when separate (17a). However, models that predict evolution of overcompensation in the presence of consumers usually predict higher fitness in populations that are never damaged (84). Moreover,

even when selection does not explicitly favor overcompensating tolerance, plants that have evolved incomplete compensation may exhibit overcompensation after experiencing heavier than typical meristem loss (96). This phenomenon arises because adaptation to repeated grazing creates a hump-shaped fitness function in which a small number of intense grazing episodes can produce startlingly large overcompensation. These theoretical outcomes challenge the notion that plants expressing overcompensating tolerance participate in a mutualism with consumers.

***Lineage Selection*** Selection among lineages may act directly on the reaction norm of phenotypically plastic traits that are expressed only once per lifetime. In this case, the optimal norm of reaction is found in the lineage with the greatest among-generation geometric mean fitness (113, 132). Models incorporating this form of selection predict that tolerance can evolve under less restricted conditions than needed under individual selection (61, 136). For example, they predict evolution of overcompensating tolerance under lower probabilities of within-season damage without requiring that damage be size-dependent (136). Neither do such models require that the risk of damage be predictable among growing seasons (61).

One such lineage selection model explored how variation in the timing and probability of damage among growing seasons affects selection on the relationship between tolerance and flowering time (61). This model found that less predictable damage favors plants that avoid damage by flowering early, i.e. escape in time, but are less tolerant. Damage that is more predictable favors plants that achieve tolerance by delaying investment of resources in reproduction until late in the season.

***Models of the Joint Evolution of Tolerance and Resistance*** Because resistance and tolerance may both evolve in response to the same selection pressure, i.e. consumer damage, their evolution is most appropriately considered jointly (3, 27, 38, 87, 125, 140, 144, 146, 153). Van der Meijden et al (153) first considered the possibility that tolerance and resistance might be negatively genetically correlated and therefore evolve antagonistically. A negative correlation could arise from pleiotropic effects of genes involved in an allocation trade-off between resistance and tolerance or could arise from linkage disequilibrium produced by correlated selection on these traits (37, 71, 137, 140, 153). Correlated selection occurs because as resistance increases, damage declines. Thus, the fitness advantage of tolerance declines with increasing resistance. Likewise, because the fitness decrement due to damage declines as tolerance increases, the fitness advantage of resistance decreases as tolerance increases (3, 38, 125, 144, 153).

The first mathematical model to examine the joint evolution of resistance and tolerance was developed by Fineblum & Rausher (38). Like van der Meijden et al (153), these authors assumed a trade-off between resistance and tolerance. Their model predicts two fitness peaks: one fixed for high resistance with no tolerance, the other for high tolerance but no resistance. However, the model does not consider

the strongly divergent effects that resistance and tolerance may have on consumer populations, which could feed back as very different selection regimes on the two traits.

Like the models discussed above, this model assumes that changes in plant damage are independent of both plant and consumer traits. Such an assumption may be unrealistic. Of course, plants may evolve increased defense, which may include phenological traits allowing them to escape damage. Similarly, consumers may evolve the ability to overcome plant resistance, to detect, and/or find suitable host plants. Consumers may also evolve phenological changes that allow them to use a previously unavailable host (36, 59). Further, evolution of consumers in response to unrelated selective factors might change levels of plant damage. For example, damage may increase as consumers escape regulation by natural enemies through the evolution of resistance to these enemies (17). Finally, consumer populations may exhibit numerical responses to the frequency of resistant or tolerant plant genotypes, causing changes in the fitness consequences of possessing such traits. Many aspects of this complexity have yet to be incorporated into theoretical treatments of tolerance evolution. The models reviewed below (3, 125, 144) begin the challenging task of integrating some of these ideas into our understanding of the evolution of plant-consumer interactions.

Feedback among resistance and tolerance alleles has recently been addressed by three models (3, 125, 144). These models assume that consumer fitness declines as resistant genotypes increase in frequency, which then decreases damage, and thereby, the fitness advantage of resistance. This negative feedback between resistance alleles and selection imposed on them prevents fixation of alleles conferring complete resistance (3, 125, 144). Instead, plant populations remain polymorphic for resistance (125, 144), a classic prediction of antagonistic optimality models, which are reviewed by Burdon (23).

In contrast to resistance, tolerance alleles do not reduce consumer fitness or population size (3, 125). Thus, the possibility of damage remains the same or increases as tolerance alleles increase in frequency. This positive feedback allows the benefits of tolerance alleles, and thus selection for such alleles, to increase with their frequency, ultimately resulting in their fixation (125, 144). Further, as the level of tolerance conferred by an allele increases, its probability of becoming fixed also increases (125). Similarly, alleles coding for resistance through avoidance of damage should also become fixed within a population, so long as the consumer is not truly monophagous (144). As with tolerance, this outcome is based on the premise that avoidance alleles have no impact on consumer fitness. However, generalist and specialist consumers may create different selection pressures on plant populations (140, 144), resulting in the maintenance of both tolerant and resistant genotypes within plant populations. For example, some phytochemicals may defend against generalists but attract specialists, which use them as feeding or oviposition cues (32, 48, 57, 101, 117). This may create a situation in which generalists select for increased chemical resistance, whereas specialists that are attracted to these compounds may select for increased tolerance. Thus, whether

tolerance becomes fixed within a population may depend in part on the composition of the consumer community (140, 144).

The evolutionary dynamics of tolerance and resistance alleles are slightly different if the genes are linked (125, 144). Consider, for example, a tolerance mutation linked to a resistance gene. When the benefit of tolerance is greater than that of resistance, tolerance will invade the population and increase to fixation. If the cost of tolerance is greater than that of resistance, however, tolerant and susceptible alleles will instead achieve a stable polymorphism.

## EVALUATION OF MODEL ASSUMPTIONS

### Selection Factors

Models investigating the evolution of tolerance share several key assumptions. Primary among these is the assumption that tolerance evolves in response to consumer damage (37, 38, 146, 147). Several lines of evidence support the validity of this assumption (87, 146). For example, wild plants which probably experience more intense damage from consumers than do domesticated plants, which are protected by pesticides, are more tolerant of damage (124, 159).

However, several authors contend that rather than being a specific adaptation to consumer damage, tolerance of damage is a by-product of selection for the ability to tolerate other environmental stresses (1, 2, 153). Thus, an alternative explanation for the wild–domestic comparison is that wild plants have evolved tolerance to competition because they experience relatively more intense competition than do their domesticated kin. This idea may stem from definitions of tolerance that tie the ability to outgrow damage primarily to intrinsic growth rate (24, 27, 51). However, rather than being directly associated with intrinsic growth rate, tolerance may also depend on traits associated with plant architecture and internal resource allocation. Further, if tolerance of damage were the by-product of selection for tolerance of competition, then these two traits would be positively correlated genetically. Instead, tolerance and competitive ability may be negatively correlated, each constraining the evolution of the other. For example, the most damage-tolerant genotypes of the common milkweed, *Asclepias syrica*, allocate more resources to root tissue than do less tolerant genotypes (56), possibly sacrificing their ability to compete for light.

The best evidence that tolerance to damage has evolved in response to selection by consumers comes from studies comparing multiple populations with divergent grazing histories. In several of these studies, individuals originating from predictably grazed (35) or more frequently damaged (114) populations exhibit greater levels of tolerance. A particularly compelling study compared managed and unmanaged populations of field gentian, *Gentianella campestris* (74). Some populations have been either mown or grazed every year for at least 100 years (and possibly 1000 years), whereas unmanaged populations growing along roadsides or (more recently) in electric power line clearings, have not experienced

such consistent damage. Individuals from managed populations exhibited greater tolerance to damage than those from unmanaged populations (74).

## Safe Storage of Resources

Another implicit assumption of reallocation models is that plants can store resources/meristems in a manner that makes them unavailable to consumers. For example, if the probability of foliar damage is high and there is a relatively low risk of root damage, plants can defend resources (through avoidance) by allocating them to roots. Plants that do so may be more tolerant because these resources are available for subsequent reallocation following foliar damage (56). Thus, the best tolerance strategy may be to resist damage to tissues that contribute most significantly to fitness (95a), as predicted by *optimal defense theory* (67, 162). For example, in acorns the apical area adjacent to the developing embryo is highly resistant to consumers due to the level of tannins (139). Thus, consumer damage is concentrated in the basal portion of acorns (139). This allocation to resistance increases the probability that the embryo will survive, and thus tolerate, consumer damage to the acorn. In cases where tolerance is achieved by allocating resources to highly resistant plant organs (e.g. 95a), then tolerance and resistance may be positively genetically correlated. This expectation contrasts with the trade-off between these two traits generally predicted from theory (38, 136a, 153).

## Herbivory Limits Plant Fitness

Another unstated assumption in tolerance theory is that plant fitness is limited solely by consumers. However, individual fitness is often limited by processes independent of damage. Such factors may restrict the expression of the phenotypic variation in tolerance among genotypes, thereby constraining the evolutionary response to damage.

Abiotic conditions may alter the phenotypic expression of tolerance (8, 21, 40, 46, 52, 56, 58, 98, 99). For example, while *Brassica napus* plants grown at field capacity (well watered) were more fit overall, they were less tolerant of damage than those grown under drought conditions (98). This observation suggests that water stress may limit the expression of genetic variance in tolerance. Further, in *Asclepias syriaca*, genetic variation in the ability to tolerate damage was greater under high compared to low nutrient conditions (56).

Biotic factors other than damage may also limit fitness and thereby limit the expression of variation in tolerance. For example, under pollen-limiting conditions, pollinator availability can influence the expression of tolerance (62). Pollinator availability significantly affected the ability of *Ipomopsis aggregata* individuals to tolerate damage (62). Damaged individuals produced more flowers than undamaged individuals, but exhibited little tolerance in terms of seed production. Hand-pollination greatly increases tolerance as measured by seed production. Such a population could evolve greater tolerance to damage by losing its dependence on

pollinators, i.e. evolving selfing. Evolving selfing would remove pollen limitation and restore the dependence of fitness on damage. Selfing would also provide tolerance to the detrimental effects of folivory on pollinator attraction (90c, 141, 143).

### Semelparous Reproduction

Most existing models of the evolution of tolerance assume semelparous reproduction (but see 125). Specifically, resources are acquired and stored until maturity, at which time all available resources are committed to reproduction and the plant subsequently dies. However, tolerance is also expressed by iteroparous plant species (for a review, see 147). Because damage in one growing season can have an impact on survivorship and reproduction through many reproductive seasons (34, 122), iteroparity adds significant complexity to both modeling and measuring tolerance. Tackling this added complexity is an important challenge for future theoretical and empirical studies.

## CONSTRAINTS ON THE EVOLUTION OF TOLERANCE

### Allocation Trade-off

The most prominent assumption of evolutionary models is that tolerance is costly (37, 38, 125, 137, 140, 144), although in some cases these models require vanishingly small costs (125). As discussed earlier, tolerance can be described as the reaction norm of fitness across a damage gradient, which can be treated as a phenotypically plastic trait (137). Schlicting (130) and Scheiner (129) provide general insights into the evolution of phenotypically plastic traits. It is important to note, however, that methods for detecting costs of most phenotypically plastic traits (33) may not be applicable to examining costs of tolerance. This is because tolerance has been defined as the reaction norm of fitness, rather than that of a specific trait.

While a cost of tolerance may be manifested in various forms, reallocation models assume that tolerant individuals store resources in some form that is available for allocation only after damage. Thus, plants that withhold allocation of resources to growth or reproduction until after damage will be more tolerant of damage but will be less fit in the absence of damage. This assumption has rarely been explicitly tested (but see 35, 56).

Because an allocation trade-off dictates that the optimal allocation pattern in an environment with natural damage differs from that in an environment without damage, its existence might be inferred from a negative fitness correlation across damage environments (41, 42, 56, 137). However, a negative fitness correlation across damage environments could also be caused by a cost of resistance (136a). Thus, a better method for detecting an allocation trade-off is to examine the genetic

correlation between the slope (tolerance) and the intercept (fitness in the absence of damage) of the fitness reaction norm. If the slope and the intercept are estimated from measurements made on the same individuals, however, the two variables are not independent (87, 146). This problem can be circumvented in two ways. First, fitness in the absence of damage can be measured on a different set of replicates than that used to measure tolerance (87, 137). Using this method, Simms & Triplett (137) found a trade-off in *Ipomea purpurea* between tolerance to damage imposed by a fungal pathogen and fitness in the absence of the pathogen. It is also possible to apply a statistical correction to deal with the lack of independence between the slope and intercept of the reaction norm in response to damage (87, 146). One of the two studies that have used this statistical correction has detected a cost of tolerance (87, 146).

A cost of tolerance can also be detected by comparing the levels of tolerance exhibited by ancestral populations that are subjected to damage with those descendent populations protected from damage. If tolerance is costly, it is likely to be lost in populations not experiencing damage because its costs will no longer be offset by the fitness benefit it provides in the presence of damage. For example, domesticated populations of agricultural species, which are commonly protected from consumers by pesticides, typically express lower levels of tolerance than do their wild ancestors (124, 159), suggesting that tolerance declined due to its fitness cost. However, domestication is a complex process, and this decline in tolerance may be due to selection on other correlated traits. In a more natural example, recently established Pacific Coast populations of *Spartina alterniflora* exhibit less tolerance than their Atlantic Coast ancestors (28). While this decline in tolerance might be due to genetic drift during the founding of new populations, it suggests that tolerance is lost in the absence of damage. This is further supported by comparisons among introduced Pacific Coast populations in habitats differing in herbivory. Populations in which herbivores are present are more tolerant (28); however, which Pacific Coast populations are ancestral or derived is unknown. Thus, determining if tolerance is costly in this case requires more investigation. While these cases suggest that tolerance is costly (28, 124, 159), whether the costs of tolerance are due to allocation trade-offs or trade-offs with other traits is unknown.

## Tolerance and Resistance Trade-off

Models of the joint evolution of tolerance and resistance have either assumed (38) or predicted (3, 125, 144) a trade-off between these traits. Some studies have detected a negative correlation between resistance and tolerance across species (125, 153), and others have found evidence within populations for a negative genetic correlation between tolerance and constitutive resistance (38, 140, 146). Tolerance may also be negatively correlated with induced resistance. For example, induction of glucosinolates in *Raphanus raphanistrum* decreases the ability of individuals to tolerate damage by consumers (4).

Two genetic mechanisms may cause a negative correlation between resistance and tolerance: (*a*) antagonistic pleiotropy, caused by the same sets of genes affecting both traits, and (*b*) linkage disequilibrium, caused by correlational selection (71) favoring individuals that possess one or the other trait, but not both (37, 137, 140). Selection experiments can be used to disentangle these two mechanisms. In one such experiment, selection for increasing resistance produced a decrease in tolerance in *Brassica rapa* (140), suggesting that this trade-off was due to antagonistic pleiotropy rather than linkage disequilibrium.

Trade-offs between tolerance and resistance may not be universal, however (87). For example, across species of *Zea*, constitutive resistance to a stem borer was positively correlated with tolerance of its damage (124). Similarly, many crop varieties are both resistant and tolerant (76, 102, 110, 138).

If tolerance and resistance are negatively correlated genetically, then selection may maintain both traits at intermediate levels (140). For example, in *Brassica rapa*, the fitnesses of undamaged, highly defended individuals are statistically indistinguishable from those of damaged, poorly defended individuals (140). In contrast to some recent theoretical predictions (38), this empirical result suggests that, highly defended, poorly tolerant individuals can coexist with poorly defended, highly tolerant individuals.

## Ontogenetic Trade-offs

Another common assumption of tolerance evolution models is that the expression of tolerance does not differ among growth stages. However, growth stages may vary in tolerance (19, 160). For example, young seedlings of the woody shrub *Prosopis glandulosa* tolerate damage better than do older seedlings (160). Although unexamined, ontogenetic variation in allocation to above- and below-ground tissues may explain observed age differences in tolerance in this species. Thus, depending on when selection occurs, ontogenetic changes in the expression of tolerance may significantly influence its evolution. Specifically, the evolution of tolerance may be constrained if selection operates in opposite directions at different ontogenetic stages, if selection acts only at specific stages, or if there are genetic correlations among stage-specific levels of tolerance.

Similar to "safe storage," plants may invest more resources to resist consumers at certain life stages that contribute most to fitness (67, 162) and thus be able to tolerate damage. Life history theory and empirical evidence suggest that the life stage with the greatest probability of mortality should be the most defended (118–120). The fact that juvenile plants often allocate more resources to resistance than do older plants (12, 18, 22, 72, 128) has been used to argue that plants defend tissues in an optimal manner (162). This hypothesis depends upon the assumption that juveniles have the highest mortality, which appears to be a common observation (9a, 9b, 25b, 27a, 64a). This suggests that greater understanding of the evolution of plant responses to damage requires further exploration of the timing of consumer damage relative to plant life history stages.

### Architectural Constraints

Storing meristems in case of damage may entail a cost to immediate growth and reproduction (132). Further, maintaining meristems in a quiescent state may also involve costs associated with the synthesis and transport of growth inhibitors. These costs, due to meristem storage, are similar in concept to allocation costs associated with storing resources (carbohydrates, proteins, nutrients) (45, 156, 156a, 157; see below) in protected or unavailable organs that can later be reallocated to replace tissues lost to consumer attack. These potential costs vis-à-vis growth and reproduction may constrain the evolution of tolerance.

Vascular architecture, and the degree to which it limits flow of resources within and among plant parts (79a, 85, 86, 156, 157), may also constrain a plant's ability to tolerate tissue loss. Marquis (80, 81) predicted that individuals with more vascular connections among plant parts would show less impact of spatially restricted damage. He suggested that this is due to the greater possibility of resources to flow from undamaged to damaged portions of the plant. Currently, however, we are lacking the empirical studies concerning the range of phenotypes available among plant species and genotypes upon which selection might act. Thus, evaluation of this hypothesis may be premature.

However, a response to selection for more resource communication among plant parts might be constrained by the opposing selective effects of different consumer guilds. Increased vascular connections, allowing greater resource movement from undamaged to damaged portions of plants, which may contribute to tolerance of foliar damage, may simultaneously increase the potential resource base available to phloem- and xylem-tapping consumers. This constraint should apply to plants with multiple ramets (e.g. tillering grasses), as well as to nonclonal species.

## ECOLOGICAL IMPLICATIONS OF TOLERANCE

Once a plant responds to tissue loss, its value as a food resource and habitable environment may change (4, 64). These changes may influence the community of plant consumers, as well as that of the natural enemies of those consumers (65). While plant responses to damage, such as the production of new tissues, may affect consumers either positively or negatively (29, 53, 64, 121, 161, Hochwender and Fritz, unpublish. data), traits contributing directly to tolerance are generally thought to have no negative impact on consumer population size (3). In fact, they may actually allow consumer populations to increase (125). However, tolerance may also be accompanied by induced resistance (4), which may negatively affect consumer populations.

The best-studied examples of the effects of plant tolerance on consumers are found in studies of the effect of vertebrate consumers on later abundances of insect consumers (29, 53, 121; Hochwender & Fritz, unpublished data). Most research has found that insect abundance typically increases on plants following

natural browsing or clipping (29, 52, 53, 121, Hochwender & Fritz, unpublished data). Changes in plant chemical or physical traits following damage may also affect higher trophic levels. For example, if consumer populations increase due to tolerance, this provides a larger resource for their predators and parasitoids. This increase in resources, i.e. herbivore population size, may also result in increased population densities at higher trophic levels (65). However, not all species in the consumer community increase in response to prior damage (29, 53, 56). Thus, plant tolerance may change not only the structure of the consumer community, but also that of the predators and parasitoids.

Consumers can have profound effects on the structure of plant communities in which they feed, altering both succession (10, 23a, 73, 75, 91) and regional differences in plant diversity (25a). Such changes are commonly attributed to the combined effects of host preference by consumers (i.e., interspecific differences in plant resistance) and interspecific differences in the competitive and colonizing ability of plants (52, 99a). However, differential plant tolerance among species may also influence community structure (9). One study, specifically designed to differentiate between the relative importance of plant tolerance and resistance for explaining consumer impacts on plant communities (9), suggests that the effects of consumers on plant community composition are more influenced by plant resistance than tolerance to damage. That is, replaced species were as tolerant or more tolerant than those that were replacing them. Thus, it appeared that levels of damage due to plant resistance were causing the species replacement. However, it is still too early to make general conclusions concerning the effects of tolerance on plant diversity.

## CONCLUSION

Since Ehrlich & Raven's (36) seminal paper describing coevolution between consumers and their host plants, our knowledge of the evolutionary responses of plants to damage has dramatically increased. With the incorporation of tolerance as a possible response to consumer-imposed selection, we have begun to form a more comprehensive understanding of the evolution of plant-consumer interactions. While significant advances concerning the evolution of tolerance have been made, important questions still need to be answered, including the following:

- What are the specific traits underlying tolerance to damage?
- Are there mechanistic distinctions between resistance and tolerance?
- How does consumer-imposed selection differ between generalist and specialist consumers?
- Is tolerance evolution constrained by environmental variation?
- What implications does perenniality have for the measurement and evolution of tolerance?

- What role does ontogenetic constraints play in the evolution of tolerance?
- Are costs of tolerance a general phenomenon?
- What influence does plant tolerance have on higher trophic levels?
- What is the role of plant tolerance in structuring biotic communities?

These questions point to promising areas of future research. Further, when we have answers to them, our understanding of the evolution of plant-consumer interactions will be greatly enhanced.

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