The ecology and evolution of plant tolerance to herbivory

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How sessile plants defend themselves against attack from herbivores has been the subject of much investigation over the past century. Early observers noted that insect taxa tended to attack plants with similar tissue chemistries. Based on observations of the deterrent and protective properties of phytochemicals, Ehrlich and Raven[1] proposed that the defensive role of phytochemicals against herbivory resulted in the codiversification of plant and insect groups. In the past decade, researchers have increasingly focused on alternative defensive traits of plants against herbivores[2]. Tolerance, the ability of plants to regrow and/or reproduce after herbivory, could serve as such a defense. This ability has been investigated by agriculturists, who were stimulated by the need to estimate the economic costs of herbivory; however, plant tolerance to herbivory in natural populations has only recently received attention.

On average, terrestrial plants in natural communities sustain 18% damage in the field[3]. Individual plant species differ markedly in their ability to survive and reproduce after damage. Only 10% loss of leaf area significantly reduced fitness in *Piper arieianum* plants in the Costa Rican understory[4]; in contrast, wild radish plants (*Raphanus raphanistrum*) can experience 25% leaf area loss without any concomitant drop in seed set[5]. As for resistance to herbivore attack, we view tolerance to damage as a plant defense (Box 1). A term frequently used synonymously with tolerance is compensation, which refers to the degree of tolerance observed (Fig. 1). The degree of tolerance to herbivory is not necessarily directly related to plant fitness. For example, a plant that compensates completely for herbivore damage could still have lower overall

The tolerance of plants to herbivory reflects the degree to which a plant can regrow and reproduce after damage from herbivores. Autoecological factors, as well as the influence of competitors and mutualists, affect the level of plant tolerance. Recent work indicates that there is a heritable basis for tolerance and that it can evolve in natural plant populations. Although tolerance is probably not a strict alternative to plant resistance, there could be inter- and intraspecific tradeoffs between these defensive strategies.

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fitness than less tolerant genotypes with high fitness in both damaged and undamaged states (compare genotype F versus C, D and E in Fig. 1).

Mechanisms of plant tolerance to herbivore damage
Intrinsic factors

The basis of tolerance to herbivory varies greatly among plant species and often involves feedback loops among traits and events[6,7]. For example, removal of leaf tissue by herbivores decreases leaf area available for photosynthesis, but can also increase light levels to previously shaded portions of the canopy, thereby increasing photosynthetic capacity in remaining leaves[8]. There are five primary mechanisms involved in increased tolerance[6–22] (Table 1):

- Increased net photosynthetic rate after damage.
- High relative growth rates.
- Increased branching or tillering after release of apical dominance.
- Pre-existing high levels of carbon storage in roots for allocation to above-ground reproduction.
- Ability to shunt carbon stores from roots to shoots after damage.

The ability to tolerate herbivory is the result of diverse plant responses and life-histories. Consequently, exceptions to the patterns in Table 1, in terms of the mechanism involved and the direction of response, can be found in many cases. Reasons for these exceptions could arise from the differing scales at which tolerance is examined, as well as the kinds of herbivore damage received by plants. Studies of mechanism tend to take one of the three following approaches: comparisons of allocation patterns or physiology between damaged and undamaged individuals in species known to compensate for herbivory[8–10]; comparisons of
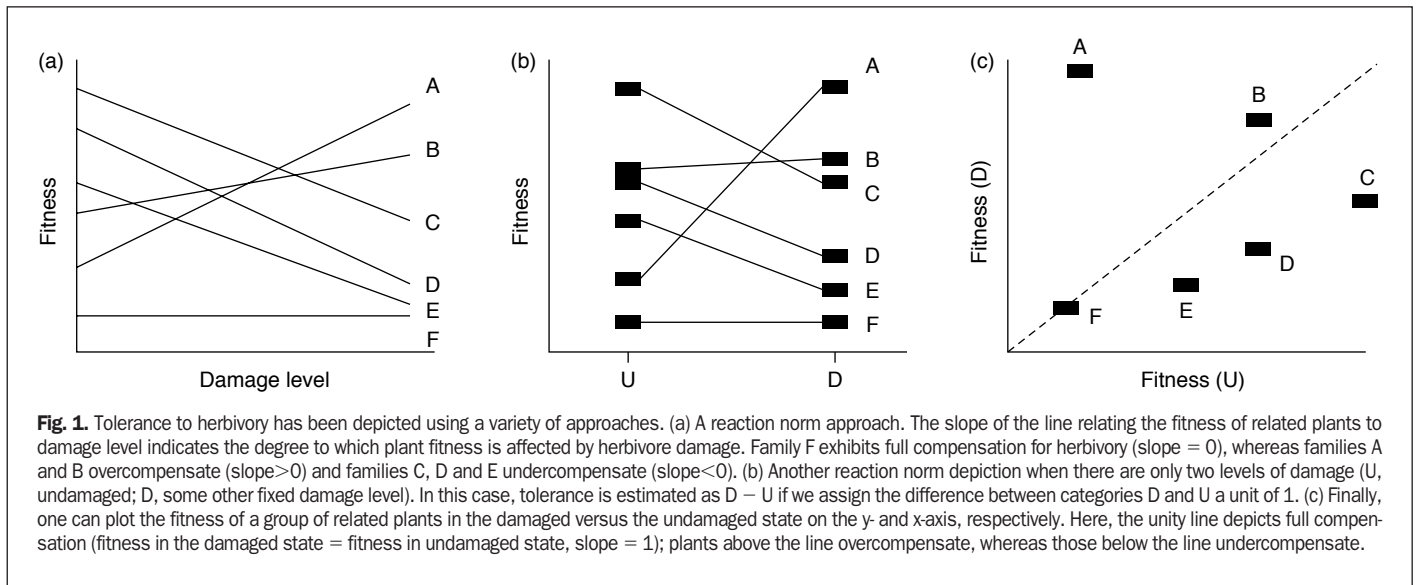

Box 1. Definitions of terms related to plant tolerance and defense against herbivory

Defense: any trait that confers a fitness benefit to the plant in the presence of herbivores[43]. A trait can be viewed as defensive even though defense is not its primary function. For example, the primary role of flavonoids, known deterrents of herbivores, might be to protect leaf tissues from UV damage.

Resistance: any plant trait that reduces the preference or performance of herbivores[43].

Tolerance: the degree to which plant fitness is affected by herbivore damage relative to fitness in the undamaged state. Tolerance can be estimated only from a group of related or cloned plants because the fitness of an individual plant cannot be examined in both damaged and undamaged states. When damage levels are continuous (e.g. in natural field situations), tolerance is measured as the slope of the line relating the fitness of plants to the level of damage. If damage is experimentally imposed at a single level, or if it is qualitative (such as loss, or not, of the apical meristem), then the definition of tolerance has traditionally been either the difference in fitness between related damaged (D) and undamaged (U) plants (D − U) or the proportional fitness of damaged individuals relative to undamaged ones (D ÷ U)[33] (Fig. 1).

Compensation: a term used to refer to the degree of tolerance exhibited by plants. If related damaged and undamaged plants have the same fitness, then that family has the ability to compensate fully for herbivory. If damaged plants have greater fitness than their undamaged relatives, then plants have **overcompensated** and if they have lower fitness, they have undercompensated for herbivory (Fig. 1).

Fig. 1. Tolerance to herbivory has been depicted using a variety of approaches. (a) A reaction norm approach. The slope of the line relating the fitness of related plants to damage level indicates the degree to which plant fitness is affected by herbivore damage. Family F exhibits full compensation for herbivory (slope = 0), whereas families A and B overcompensate (slope>0) and families C, D and E undercompensate (slope<0). (b) Another reaction norm depiction when there are only two levels of damage (U, undamaged; D, some other fixed damage level). In this case, tolerance is estimated as D − U if we assign the difference between categories D and U a unit of 1. (c) Finally, one can plot the fitness of a group of related plants in the damaged versus the undamaged state on the y- and x-axis, respectively. Here, the unity line depicts full compensation (fitness in the damaged state = fitness in undamaged state, slope = 1); plants above the line overcompensate, whereas those below the line undercompensate.

congeners that differ in their abilities to tolerate damage[16]; or comparisons among a suite of co-occurring species that differ in their degree of tolerance to herbivory[2,21]. Within-species comparisons provide information about how species might evolve to become more tolerant. Between-species, macroevolutionary comparisons cover a broader array of adaptations and suggest which attributes could be most closely tied to tolerance across more varied taxa.

The diverse mechanisms underlying tolerance to herbivory might also result from mode of action of the herbivore. For example, cotton plants (*Gossypium hirsutum*) that showed increased branching in response to bud removal[13], exhibited decreased axillary branching in response to attack by phloem-sucking aphids[20]; full compensation for damage was achieved for both damage types. Thus, feeding mode of the herbivore might influence which intrinsic traits are associated with increased tolerance even within a plant species.

Extrinsic influences on tolerance: abiotic and biotic factors

The plant's abiotic and biotic environment can also affect tolerance to herbivory. Maschinski and Whitham[23] originally proposed that plants should have the highest level of tolerance when they receive early season herbivory and are in environments free from competition with high light, nutrients and water availability. However, counterintuitively, nutrient availability has been found to be negatively associated with tolerance in several systems, especially when nutrient levels are high[24–26]. One explanation for this pattern might be that high nutrients generally reduce the root:shoot ratio[27], which in turn is associated with reduced tolerance (Table 1). The effect of water and light availability on tolerance has been little investigated, although it is generally assumed that these traits are positively associated with tolerance[23]. More factorial experiments are required to determine the relative importance of various environmental factors, and their interactions, in plant tolerance to herbivory.

Many studies support the notion that early season herbivory and low competition are positively associated with high tolerance (Table 2). Competition can reduce tolerance not only because competitors reduce soil resources, but also because the loss of apical dominance can be particularly detrimental in competitive environments where light is limiting[26]. Early season herbivory is generally easier to compensate for in established plants (Table 2), whereas immature and seedling plants can be poor tolerators of herbivory early in the season because the establishment phase is critical for survival.

The effects of plant mutualists on tolerance to herbivory is still relatively unknown. Pollinators, endophytic fungi, vesicular arbuscular mycorrhizal (VAM)

Table 1. Intrinsic mechanisms promoting tolerance to herbivory reported in recent studies (1993–present)

Attributes related to greater tolerance	Type of herbivory	Within or between taxon comparisons?	Refs
Increased leaf photosynthetic rate	Simulated	Within	9
	Simulated	Within	8
Increased (relative) shoot growth rate	Simulated	Within	9
	Simulated	Within	10
Increased branching or tillering	Stemborer[a]	Between	11
	Simulated	Within (female plants)	12
	Simulated	Within	13
	Simulated	Within	14
	Simulated	Between	15
Decreased branching or tillering	Simulated	Within (male plants)	12
	Aphids	Within	20
Later flowering time	Simulated	Within	14,15
Greater carbon storage in roots	Simulated	Within	10
	Simulated	Between	21
Greater root:shoot ratio	Simulated	Between	22
Increased percentage of fruit set	Simulated	Within	8
	Simulated	Between	16
Increased resource allocation from root to shoot	Simulated	Within	8
	Simulated	Between	21
Decreased leaf longevity	Simulated	Within	8

[a]Herbivory not imposed at random.

fungi and facilitating plants might all affect host tolerance. Pollinator limitation has been shown to reduce tolerance to herbivory in scarlet gilia (*Ipomopsis aggregata*)[28]. Tolerance to grazing was enhanced by hand pollination, which suggests that pollinators limit the seed set in grazed plants. Other mutualists also affect plant tolerance. Endophytic infection in grasses is often associated with the production of alkaloids and does not usually affect yield. Belesky and Fedders[29] found, however, that endophytic fungal infection interacted with defoliation to affect the ability of a plant to regrow. Furthermore, the direction of this effect (positive or negative) was dependent on plant genotype[29]. A VAM fungal infection in birdsfoot trefoil (*Lotus corniculatus*) was associated with decreased tolerance to artificial damage[30]; infected plants that were clipped transferred carbohydrates to undamaged neighbors[31]. These examples indicate that plant associates usually thought of as mutualists could become antagonists in different herbivore environments.

The evolution of tolerance

A growing consensus is that tolerance to herbivory, like resistance, is an evolving trait under selection from herbivores in natural plant populations. One popular approach has been to compare physiological and morphological attributes across species that differ in their ability to tolerate damage[2,7,11,16,22]. Although this method can be powerful, it requires much replication at the species level because species differ in attributes other than their ability to tolerate herbivore damage. In addition, the phylogenetic history of traits associated with tolerance must be considered; ideal comparisons are those made among species in which there have been multiple independent origins of increased tolerance. Despite these caveats, such interspecific comparisons are very useful for understanding macroevolutionary changes that might be associated with increased tolerance to herbivory.

A complementary approach has been to examine mechanisms involved in the evolution of tolerance through comparisons of conspecifics. One method has been to compare life histories and morphologies of populations with consistently different histories of attack from herbivores[14,15,32]. Lennartsson *et al.*[14,15] recently showed that overcompensation occurred only in historically grazed or mowed populations of field gentians (*Gentianella campestris*). Overcompensation was largely associated with changes in flowering phenology in these populations, as well as increased axillary branching. Common garden experiments, as in Lennartsson *et al.*'s study, or controlled breeding designs are especially valuable as they can separate environmental and genetic components of tolerance.

Tolerance can evolve by natural selection only if there is heritable variation that affects plant fitness. Such genetic variability is detected through a statistical interaction between genetically related plants (clones or families) and their (fitness) response to herbivory[33] (Table 3). Although many studies document physiological and morphological differences across species that differ in their tolerance to herbivory, few studies have measured physiological attributes when heritable intraspecific variation in tolerance has been found. Such measurements would provide us with a better understanding of tolerance mechanisms at the intraspecific level.

Costs of tolerance and the resistance–tolerance tradeoff

If heritable variation in tolerance exists within plant populations, why are plants not all maximally tolerant to herbivory? Selection for increased tolerance could be constrained by tradeoffs with other traits affecting fitness. Also, if allocation costs of maintaining mechanisms for regrowth are sufficiently great in environments where herbivores are scarce or unimportant, nontolerant plants could be favored. Both genotype by environment interactions arising from allocation costs and negative genetic correlations between tolerance and other fitness-affecting traits (such as resistance to herbivory) could slow or prevent fixation of alleles for maximal tolerance within populations.

Detecting costs of tolerance is not completely straightforward. The most intuitive approach is to examine the relationship between the fitness of undamaged plants and tolerance (i.e. plot the fitness of undamaged plants versus the fitness of damaged plants minus the fitness of undamaged

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Table 2. Extrinsic factors promoting tolerance to herbivory

Factor	Refs
Early timing of herbivory (mature plants)	17,23,46[a]
Late timing of herbivory (seedling plants)	47
High nutrient availability	23,24,28
Low nutrient availability	24–26
High water availability	23
High light availability	48[b]
Fewer plant competitors	23,26,48
VAM[c] plant mutualists	30
Endophyte infection (sometimes)	29

[a]But see Refs 15,23,24.
[b]But see Ref. 25.
[c]Vesicular arbuscular mycorrhizal fungi.

Table 3. Plant systems for which genetic variation in tolerance to herbivory has been reported

Plant species	Damage type	Fitness measure	Refs
Ipomea purpurea	Artificial (apical)	Capsule production	37
Cedrela odorata	Artificial (apical)	Apical dominance	49
Salix cordata	Artificial (folivory)	Growth	40
Quercus rubra	Caterpillar (folivory)	Survival and growth	41
Arabidopsis thaliana[a]	Natural herbivores (folivory)	Seed production	34
Brassica rapa	Artificial (folivory)	Seed production	38
Gentianella campestris[b]	Artificial (50% browse)	Fruit production	14,15
Crepis pulchra	Artificial (folivory)	Vegetative biomass	45
Festuca arundinacea	Artificial (folivory)	Elongation and mass	29
Lolium perenne[c]	Artificial (folivory)	Growth rate	50
Raphanus raphanistrum	Caterpillar (folivory)	Seed production	36
Medicago sativa	Livestock grazing	Shoot regrowth	32

[a]Herbivory treatments were not imposed randomly.
[b]Differences between plant populations measured in a common garden.
[c]All plants clipped, but main effect of genotype was still significant when initial mass was used as a covariate.
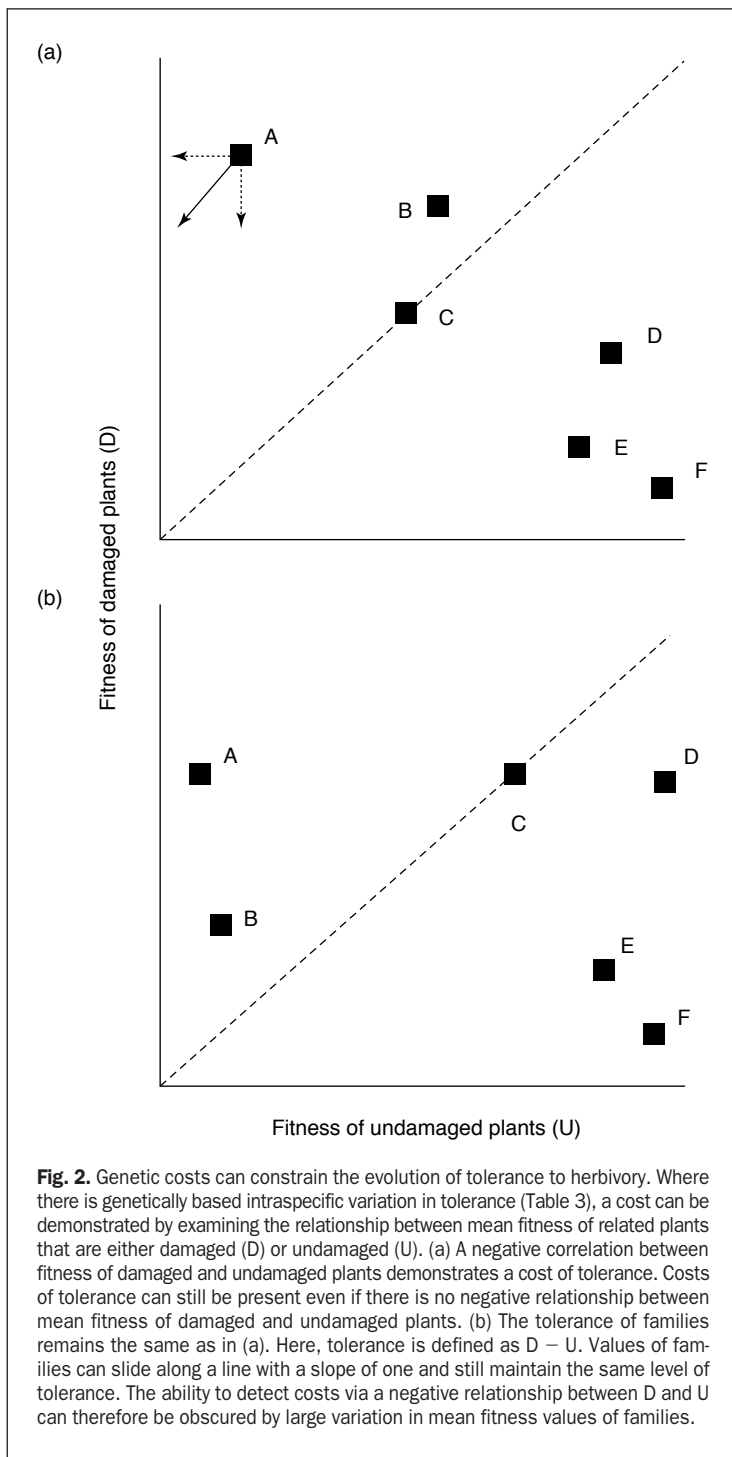
Fig. 2. Genetic costs can constrain the evolution of tolerance to herbivory. Where there is genetically based intraspecific variation in tolerance (Table 3), a cost can be demonstrated by examining the relationship between mean fitness of related plants that are either damaged (D) or undamaged (U). (a) A negative correlation between fitness of damaged and undamaged plants demonstrates a cost of tolerance. Costs of tolerance can still be present even if there is no negative relationship between mean fitness of damaged and undamaged plants. (b) The tolerance of families remains the same as in (a). Here, tolerance is defined as D − U. Values of families can slide along a line with a slope of one and still maintain the same level of tolerance. The ability to detect costs via a negative relationship between D and U can therefore be obscured by large variation in mean fitness values of families.

dependent and independent variables, but has its own set of problems. If fitness differences among families or genotypes are much greater than effects on fitness resulting from costs of tolerance, and if sample sizes of numbers of families are relatively small (as is often the case), then the detection of costs can be obscured by such variation (Fig. 2b). Thus, in these cases, we cannot necessarily interpret a positive relationship, or no relationship, as an absence of costs.

A similar approach to looking for tradeoffs or costs involved in tolerance employs the Hocking formulation of the mixed-model analysis of variance (MM-ANOVA)[33,35]. Because genetic variability in tolerance is detected through a statistical interaction between related plants and their fitness response to herbivory, its measurement would generally involve an MM-ANOVA where treatment (herbivory) would be a fixed effect and family would be a random effect. The Hocking formulation of the MM-ANOVA tests the family effect over the mean square of the interaction between family and treatment (as opposed to the traditional Scheffe formulation, which tests effects of family over the mean square error). The interpretation of a significant family effect using the Hocking formulation of the MM-ANOVA is that there is a significant genetic correlation in fitness across environments (damaged and undamaged states). The Hocking approach of detecting costs of tolerance has the advantage of superior power over the approach of simply regressing family fitness means in the damaged state versus the undamaged state[35]. A significant main effect of family with a negative correlation between how families perform across environments provides evidence for costs of tolerance. However, as with the regression technique already described, this approach does not resolve the problem of high among-family variance in fitness, which can obscure costs by making negative relationships difficult to detect.

Only two studies to date have tried to quantify a cost of plant tolerance to herbivory using these methods, and both have failed to demonstrate a negative relationship between fitness in the damaged and undamaged state[34,36]. In addition, we have depicted the data of Lennartsson *et al.*[14] (Fig. 3), and these show that there is a significant positive correlation between fitness of plants in clipped and unclipped states. Simms and Triplett[33] reported a negative genetic relationship between fitness in the damaged and undamaged state (evidence for costs of tolerance) in morning glory plants (*Ipomoea purpurea*), although this study examined tolerance to infection by a fungal pathogen, rather than herbivory.

Tradeoffs associated with tolerance have been examined as a negative genetic correlation between tolerance and other traits that affect fitness, such as resistance. Originally, van der Meijden *et al.*[2] proposed that tolerance and resistance could be alternative plant strategies to cope with herbivore damage because selection for resistance should favor plants that receive less attack by herbivores. Resistant plants will not experience selection for tolerance, largely because they receive minimal damage. Alternatively, if plant resistance mechanisms are relatively more costly, ineffective (as is the case for many specialized herbivores) or otherwise constrained, herbivory might result in selection for tolerance because resistance is not a viable strategy.

Results of intraspecific comparisons reveal that selection for resistance can result in a correlated negative response in tolerance[37,38], although the mechanisms behind this tradeoff are still unknown. At the simplest level, allocation to one function could divert resources away from others; however, this diversion should not be assumed.

plants). A negative relationship would indicate a cost of tolerance because more tolerant plants would be less fit in the undamaged state than less tolerant ones. A problem with this approach is that the fitness of undamaged plants appears both in the dependent and independent variables, and will therefore produce a negative relationship and the appearance of costs, even if fitness values are chosen at random. Consequently, the covariance between independent and dependent variables must be removed before one can examine the true slope of this relationship[34].

An alternative approach is to plot the mean fitness of damaged plants versus undamaged plants for a related group of plants[33]; a negative correlation between fitness of damaged and undamaged plants could provide evidence for a cost of tolerance (Fig. 2a). This approach avoids the problem of having fitness of undamaged plants in both the

Alternatively, if herbivores prefer more nutritionally complete or vigorous plants (Price's 'plant vigor hypothesis'[39]) and these plants, in turn, are also more tolerant to herbivory, then this preference would also produce a negative correlation between resistance and tolerance.

The generality of tradeoffs between resistance and tolerance is still unclear[34,40,41]. A lack of generality could arise from the diversity of mechanisms involved in both functions (Table 1), and/or because most studies have not rigorously tested for negative genetic correlations between these traits. Of the studies that have used controlled breeding designs to examine genetic correlations between these traits, two have supported[37,38] and one has refuted[34] the tolerance–resistance tradeoff.

There are several hypotheses that could explain why there might be no negative correlation between resistance and tolerance. A generally vigorous or well provisioned plant could have both high tolerance and high resistance. In addition, defensive chemicals could have other important functions aside from defense. For example, proteinase inhibitors (PIs), known anti-herbivore secondary metabolites, also function in the storage of plant proteins. High levels of PIs might result in higher levels of resistance against insects, as well as higher levels of protein storage, which could increase tolerance to herbivory. Both of these hypotheses would predict a positive relationship between tolerance and resistance, and such positive relationships have been reported[34].

Future directions in the investigation of tolerance

In their 1994 review, Rosenthal and Kotanen[42] concluded that studies of tolerance could benefit from the examination of resistance and tolerance in the same study and the inclusion of more non-grass plant species in studies of this phenomenon. The studies reviewed here have addressed many of these issues. However, the following four new areas could provide more information about the importance of tolerance and its evolution in natural populations.

Types of damage

Tolerance to herbivory is usually treated as a single trait. As for resistance, however, different kinds of herbivory have different effects on the response of the plant and its consequent fitness[5,43–45]. For example, we know cotton plants respond differently to aphid damage than to bud removal[13,20]. Similarly, simulated herbivory and natural herbivory evoke different responses in plants in terms of induction of phytochemicals and effects on fitness[43,44]. The vast majority of studies on tolerance consider damage from only a single type of herbivore, and usually damage is simulated (Tables 1 and 3). Simulated herbivory is usually a poor surrogate for real herbivory[43,44] (Fig. 4). Additionally, many studies of tolerance examine damage from grazing, which is likely to evoke different responses from herbivory by leaf- or root-feeding insects. A synthesis of known plant responses to these different kinds of damage could teach us more about mechanisms and costs of tolerance. The degree to which tolerance to one kind of damage provides cross-tolerance to others will also determine the strength and direction of selection for such traits.

Ascribing mechanism to differences in tolerance

Understanding the mechanisms of plant tolerance is important for predicting the consequences of tolerance for both natural and managed plants. Care must be taken, however, when we ascribe mechanism to underlying differences in tolerance among plant families or genotypes.
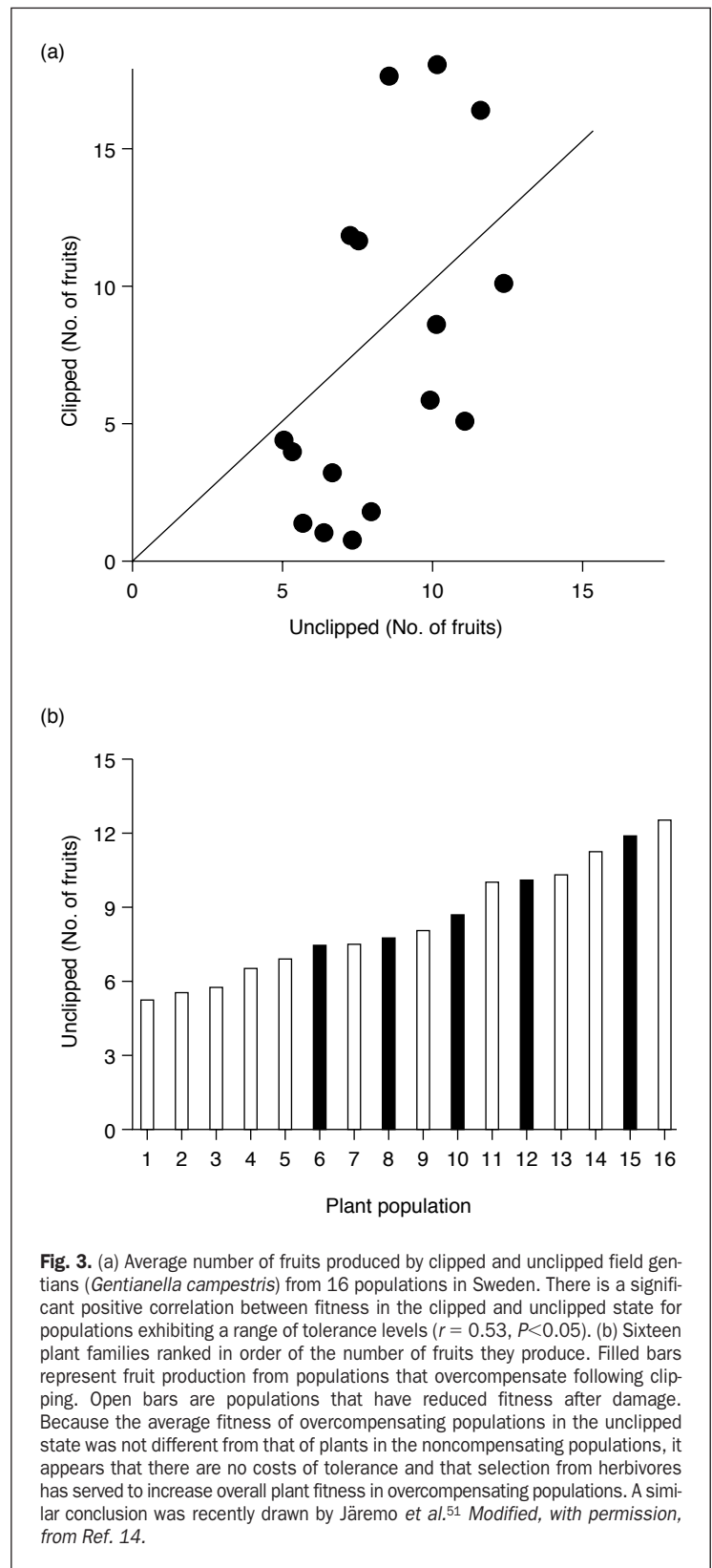

Fig. 3. (a) Average number of fruits produced by clipped and unclipped field gentians (*Gentianella campestris*) from 16 populations in Sweden. There is a significant positive correlation between fitness in the clipped and unclipped state for populations exhibiting a range of tolerance levels ($r = 0.53$, $P < 0.05$). (b) Sixteen plant families ranked in order of the number of fruits they produce. Filled bars represent fruit production from populations that overcompensate following clipping. Open bars are populations that have reduced fitness after damage. Because the average fitness of overcompensating populations in the unclipped state was not different from that of plants in the noncompensating populations, it appears that there are no costs of tolerance and that selection from herbivores has served to increase overall plant fitness in overcompensating populations. A similar conclusion was recently drawn by Järemo *et al.*[51] *Modified, with permission, from Ref. 14.*

For families that have incurred the same amount of leaf area removal, but exhibit different degrees of tolerance, the temptation is to attribute differences in fitness to costs associated with regrowth or other physiological mechanisms measured. But, differences in fitness could also arise from differences in the synthesis of phytochemicals induced after damage and their associated costs[43,44]. Simultaneous measurement of induced responses to herbivory as well as traits associated with regrowth (such as root:shoot ratio, leaf production and
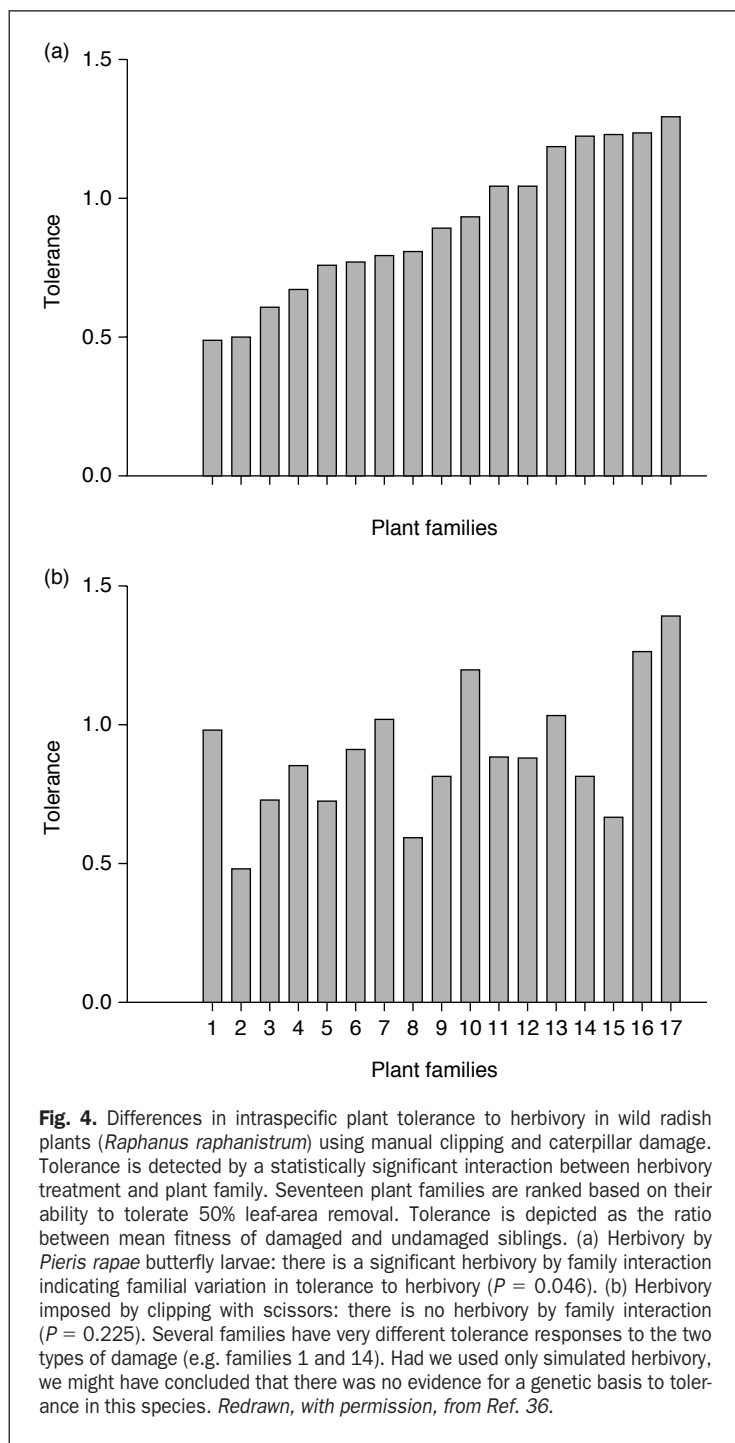
Fig. 4. Differences in intraspecific plant tolerance to herbivory in wild radish plants (*Raphanus raphanistrum*) using manual clipping and caterpillar damage. Tolerance is detected by a statistically significant interaction between herbivory treatment and plant family. Seventeen plant families are ranked based on their ability to tolerate 50% leaf-area removal. Tolerance is depicted as the ratio between mean fitness of damaged and undamaged siblings. (a) Herbivory by *Pieris rapae* butterfly larvae: there is a significant herbivory by family interaction indicating familial variation in tolerance to herbivory ($P = 0.046$). (b) Herbivory imposed by clipping with scissors: there is no herbivory by family interaction ($P = 0.225$). Several families have very different tolerance responses to the two types of damage (e.g. families 1 and 14). Had we used only simulated herbivory, we might have concluded that there was no evidence for a genetic basis to tolerance in this species. *Redrawn, with permission, from Ref. 36.*

photosynthetic rate) could allow greater insights into which processes are most important in determining tolerance to herbivore damage.

Measurements of plant fitness

In all but a few studies, seed production has been used as an estimate of total plant fitness. Number of seeds sired through pollen (male plant fitness) can be affected by damage as well as the number of seeds produced (female plant fitness)[46]. Leaf damage can affect pollen production, pollen quality and pollinator visitation[46]. Only Gronemeyer *et al.*[18] have examined simultaneously how plants compensate for damage in terms of both male and female plant fitness. They found overcompensation in both male and female plant fitness in scarlet gilia, which produced more than twice as many flowers on damaged than undamaged plants. Lehtilä and Strauss[5] examined lifetime pollen and

seed production in caterpillar-damaged versus undamaged wild-radish plants. Wild radish exhibited full compensation for herbivory in components of female fitness. However, pollen production per flower and petal size decreased significantly in damaged plants relative to undamaged plants. A full understanding of tolerance will occur only as we gain a better appreciation of how male and female plant fitness covary in damaged plants under field conditions.

Implications of the tolerance–resistance tradeoff in the measurement of impact of herbivores

A tradeoff between resistance and tolerance (although the evidence for such a tradeoff is mixed) has implications not only for the evolution of plant defense, but also for how the impact of herbivore damage on plant fitness is assessed. If resistant plants suffer less damage in the field and experience a greater decrement in fitness when they are damaged than tolerant plants (as would be required in such a tradeoff), then our estimate of the impact of herbivores on plant populations will vary depending on the proportions of resistant and tolerant genotypes in plant populations. Currently, to assess the effects of herbivores, we use a random sample of all plants from the population and impose herbivory or protection from herbivory at random. However, if resistant plants are naturally attacked infrequently (by nature of being resistant), then our imposition of damage at random could cause resistant (nontolerant) plants to be over-represented in our damaged sample (relative to what happens in the field). This bias will overestimate the effects of herbivores on plant fitness. Such problems will not be present if tolerance and resistance are uncorrelated traits, or if populations are composed primarily of either tolerant or resistant genotypes (i.e. not with a mixture of genotypes).

Conclusions: could herbivores act as selective agents to increase overall plant fitness?

The past five years have seen a plethora of papers addressing tolerance as a plant defense against herbivore damage. The emerging picture is that plants exhibit heritable variation for tolerance to herbivory. In contrast, there has been mixed support to date (but from only a few studies) for actual costs of tolerance, and the generality of the proposed tradeoff between resistance and tolerance is still unclear. As alternative but not mutually exclusive defenses to herbivory, plant resistance and plant tolerance might result in differing dynamics between plant and herbivore populations. The evolution of tolerance can promote an apparently mutualistic relationship between herbivores and their host plants. In the studies by Lennartsson *et al.*[14,15], not only did historically grazed gentians overcompensate, but the fitnesses of those plants in the ungrazed state were either greater than or not different from that of plants in the ungrazed, noncompensating populations (Fig. 3b). Thus, selection from herbivores could have served to increase overall plant fitness in these environments. For these cases, we might expect plant–herbivore relationships, and population dynamics, to remain more stable than for cases in which resistance serves as the plant defense. Tolerance does not impose selection on herbivores. In contrast, a 'coevolutionary arms race' of plant resistance and counterdefense by herbivores could cause greater long-term instability in the relationship between plant and herbivore taxa, and greater variation in population sizes as favorable defensive mutants in both taxa sweep through the populations.

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