

Commentary

Evolution of mixed strategies of plant defense against herbivores

Plants have evolved an impressive diversity of defenses to protect themselves from a correspondingly diverse assemblage of herbivores. These defenses include toxic chemicals, trichomes, tough leaves, resins, volatiles that recruit extra defenders such as parasitoids, and compensatory growth following damage, to name a few. Understanding the mechanisms that plants use to defend themselves, and the ecological drivers of plant defense evolution, have been major research problems for over a century (Fraenkel, 1959; Hartmann, 2008; Agrawal, 2011). While many studies still focus on pairwise plant–herbivore interactions, it is becoming increasingly clear that the ecological diversity of herbivore communities is an important factor shaping the evolution of plant defense strategies (Fox, 1981; Lankau & Strauss, 2008). In this issue of *New Phytologist*, Carmona & Fornoni (pp. 574–583) report on a field experiment in which they test whether patterns of natural selection on the two principal plant defense strategies – resistance (i.e. traits that reduce damage) and tolerance (i.e. traits that reduce the fitness impacts of a given amount of damage) – depend on the complexity of herbivore communities. They show that this ecological complexity selects for mixed resistance–tolerance strategies, contrary to a long-standing prediction that resistance and tolerance are mutually exclusive defenses (van der Meijden *et al.*, 1988). This result highlights the importance of understanding ecological context and complexity when studying evolution of traits mediating species interactions, and it provides unique insight into the evolutionary ecology of plant defenses.

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A brief history of research on plant defense evolution

Early research on plant defenses focused on the evolution of resistance traits, with a primary focus on chemical resistance and a

secondary focus on physical resistance traits. The direction of research was strongly influenced by Fraenkel’s (1959) compelling arguments that the main function of secondary metabolites is to defend plants against herbivores. Ehrlich & Raven (1964) built upon these ideas and advanced interest in plant defense evolution with their concept of co-evolution, which proposed ongoing reciprocal selection and adaptation between plant chemical defenses and insect counter-defenses. These ideas continue to pervade modern thinking on the evolution of plant resistance, but we also now recognize that plant defense evolution is more complex than originally imagined (Agrawal, 2011).

An alternative defensive strategy involves the evolution of traits that allow plants to tolerate herbivory (Rosenthal & Kotanen, 1994). This involves any trait that reduces the fitness impacts of damage, such as increased photosynthesis following herbivory, compensatory growth, architecture of axillary buds, and carbon storage organs (Stowe *et al.*, 2000). However, our understanding of the joint evolution of tolerance and resistance is still limited (Núñez-Farfán *et al.*, 2007). An early hypothesis proposed a trade-off between tolerance and resistance leading to fixation of one or the other defense strategy (van der Meijden *et al.*, 1988). The rationale for this argument was based on the premise that highly resistant plants receive little damage and therefore receive no benefit from tolerance. Likewise, plants that are perfectly tolerant accrue few benefits from resistance. This idea gained traction with the publication of empirical data and theoretical models that supported the predicted tradeoff (Fineblum & Rausher, 1995; Stowe *et al.*, 2000).

Despite the appealingly simple logic of a tradeoff between resistance and tolerance, many natural populations comprise intermediate levels of both strategies (Núñez-Farfán *et al.*, 2007). Moreover, a meta-analysis of empirical studies finds no consistent tradeoff between resistance and tolerance (Leimu & Koricheva, 2006a). In light of such data, theoretical research on plant defense evolution has derived conditions for the evolution of mixed resistance–tolerance strategies (Núñez-Farfán *et al.*, 2007). Despite these advances, empirical tests of the evolutionary processes that lead to mixed strategies remain scarce.

Empirical evidence for the evolution of mixed resistance–tolerance strategies

Carmona & Fornoni present the best evidence to date that herbivores select for mixed resistance–tolerance defense strategies in natural plant populations. They conducted a large ecological genetics field experiment to test how herbivore community composition on *Datura stramonium* (Solanaceae) selects for tolerance and resistance by two leaf-feeding beetles. One beetle feeds on a wide diversity of plants in the Solanaceae, while the other is a specialist of *Datura*. They manipulated the presence/absence of

these beetles on plants and measured plant fitness, resistance to each beetle species (quantified as -1% leaf herbivory), and tolerance (proportional reduction in fitness due to herbivory). Using quantitative genetics methods they estimated directional and quadratic selection on resistance and tolerance and generated fitness landscapes based on these measures (Fig. 1a).

Their results show that herbivore community composition dramatically affects selection on resistance and tolerance. Specifically, the specialist beetle imposed directional selection for increased tolerance but no selection on resistance. By contrast, the generalist beetle imposed stabilizing selection on resistance and no selection on tolerance. When both herbivores were present, the population's fitness optimum was situated at intermediate

resistance and high tolerance. Previous work in this system showed similar patterns: resistance was selected for in a location dominated by generalist grasshoppers while tolerance was favored in a location with more specialized herbivores (Fornoni *et al.*, 2004). These results provide empirical evidence that different selective pressures imposed by multiple consumers are important in driving adaptive evolution of mixed resistance–tolerance defense strategies. These processes are likely general given that plants are typically attacked by ecologically and taxonomically diverse herbivore communities (Agrawal, 2011).

A conceptual framework for studying plant defense evolution

Extending from these results we propose a simple framework in which the ecological context of selection by herbivores leads to predictions on the joint evolution of resistance and tolerance (Fig. 1). We start by outlining combinations of resistance and tolerance that are expected to be adaptive only in specific ecological contexts (textured pink region of Fig. 1b). The evolution of low resistance and tolerance (zone 1, Fig. 1b) is expected to evolve in environments with little or no herbivory, assuming defense has some cost. Plants were likely only completely free of herbivory before the occurrence of plant feeding arthropods over 400 million years ago (Labandeira, 2007). However, some extant plants do experience consistently low herbivory in harsh abiotic landscapes or on recently colonized islands. Studies do indeed show evolution of decreased resistance and tolerance in environments with decreased herbivory (Lennartsson *et al.*, 1997; Zangerl & Berenbaum, 2005).

The evolution of high resistance and low tolerance (zone 2, Fig. 1b) could occur following mutations of large effect that allow plants to escape their herbivores (Ehrlich & Raven, 1964). This should select for decreased tolerance, assuming tolerance is costly, leading to the predicted evolutionary tradeoff between resistance and tolerance (van der Meijden *et al.*, 1988; Fineblum & Rausher, 1995). Based on the vast diversity of toxic chemicals and other defensive traits found in plants, such events have certainly occurred but they likely offer only a brief respite from attack before herbivores evolve counter-defenses.

Evolution of high tolerance and low resistance (zone 3, Fig. 1b) could, in theory, be adaptive in two specific scenarios. First, selection imposed by a small number of specialized herbivores that evolve to circumvent and even benefit from resistance traits could select for high tolerance and low resistance as an evolutionary stable strategy (van der Meijden *et al.*, 1988). Carmona & Fornoni's study partially supports this prediction in that the *Datura* specialist only imposed selection for high tolerance. Similarly, on milkweeds (*Asclepias*), a specialized herbivore community has driven the evolution of increased tolerance and decreased resistance over macro-evolutionary time (Agrawal & Fishbein, 2008). Second, the evolution of high tolerance and low resistance could also be adaptive if greater tolerance confers a competitive advantage in plant communities consistently damaged and maintained by generalist grazing herbivores (e.g. grasslands, McNaughton, 1979). However, in all the cases cited earlier plants still possess potent chemical and physical resistance traits, suggesting that these

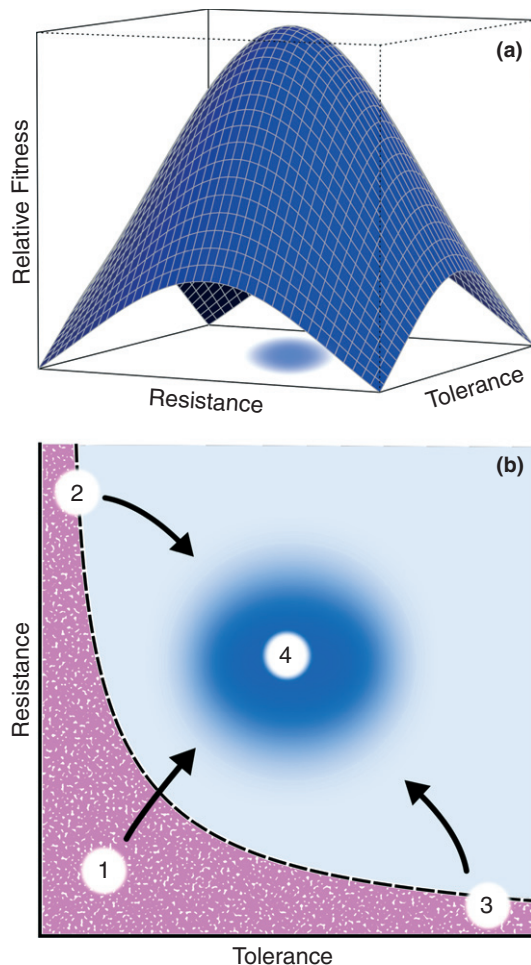


Fig. 1 Selection and evolution of mixed resistance–tolerance plant defense strategies. (a) Hypothetical fitness landscape showing stabilizing selection on both resistance and tolerance within a population. The adaptive peak is shown as a blue dot at intermediate values of resistance and tolerance. (b) A surface showing hypothetical positions of adaptive peaks for resistance and tolerance. The textured pink area represents adaptive zones that occur only under specific ecological scenarios (see text for discussion of zones 1–3), and the dark blue circle (zone 4) represents the expected adaptive space for most plants attacked by ecologically diverse herbivore communities. The arrows represent the evolutionary trajectories of populations away from simple defensive strategies once they are subject to selection by ecologically diverse herbivore communities.

simple theories are incorrect. Evolution towards very low resistance is unlikely in most systems because a loss of resistance will inevitably result in damage from new herbivore species that were previously deterred (Kessler *et al.*, 2004). The role of resistance by deterrence is underappreciated in plant defense evolution but it may help to explain why the existing diversity of herbivores makes an evolutionary strategy of no resistance unlikely.

The common theme in all scenarios discussed thus far is that ecological diversity in herbivore communities drives the evolution of intermediate to high levels of resistance and tolerance (zone 4, Fig. 1b). In addition to the mechanisms already described, herbivore diversity can select for mixed strategies of defense because herbivores as a rule exhibit relatively weak to no correlation in their response to variation in plant resistance (Leimu & Koricheva, 2006b). Thus, no one strategy will be effective against all herbivores in the community. For example, some herbivores select for resistance traits and others for tolerance traits, as described by Carmona & Fornoni. Given the abundance of mechanisms by which herbivore diversity can promote mixed strategies of defense, a simple testable prediction is that the ecological diversity of herbivore communities should be positively correlated with the diversity of both resistance and tolerance defensive mechanisms.

It should be noted that these simple predictions are complementary to many of the leading theories of plant defense evolution. Resource availability in the environment (Coley *et al.*, 1985), tradeoffs in allocation to growth and defense (Herms & Mattson, 1992), and variation in plant sex (Núñez-Farfán *et al.*, 2007), may all constrain or promote selection on resistance or tolerance. However, herbivore community complexity is still expected to cause evolution of mixed defensive strategies.

Trait diversity and mixed plant defenses

An important limitation of our paper is that we have oversimplified our discussion of resistance and tolerance. In reality, both resistance and tolerance are a function of many biochemical, physiological, morphological, and phenological traits, which may be specialized to different herbivores or play other roles in addition to defense against herbivores. Therefore, the evolution of resistance and tolerance to herbivores will be shaped and constrained by ecological interactions with other plant parasites, mutualists, competitors, and abiotic factors (Stowe *et al.*, 2000; Lankau & Strauss, 2008). While unraveling this complexity is a monumental task it opens up a plethora of possible hypotheses and mechanisms explaining the adaptive evolution of mixed strategies of defense.

Nash E. Turley*, **Ryan M. Godfrey** and **Marc T. J. Johnson**

Department of Biology, University of Toronto at Mississauga,
Mississauga, ON, L5L 1C6, Canada

(*Author for correspondence: tel +1 905 828 5231;
email nash@nashturley.org)

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Key words: co-evolution, defense syndrome, herbivory, plant–insect interactions, resistance, secondary chemistry, tolerance.