

# Defense and Tolerance: Is the Distinction between these Two Plant Strategies Useful?

Kirk A. Stowe

Interdisciplinary Studies, Beacon College, Leesburg, FL, 34748 USA

**Abstract** Resistance to herbivores has typically been divided into two categories: defense and tolerance. However, defense and tolerance may not be distinct traits. In this opinion paper, I will argue that the distinction between these two categories of resistance may inhibit our understanding of how these traits might evolve. That is, they may evolve in conjunction and those traits that confer defense may also confer tolerance to herbivores. A number of examples are given to support this argument

**Keywords** Resistance, Defense, Tolerance

Plants possess a multitude of traits that allow them to contend with consumers. These traits include leaf physical and chemical characteristics, phenology, and/or resource storage[1, 2, 3, 4, 5, 6, 7, 8, 9]. Further, these traits appear to be adaptations to those consumers[3].

Originally, these traits were grouped under the umbrella term, resistance[10, 11, 12]. This term included both defense and tolerance as subsets[10, 11, 12, 13, 14]. While defense has more recently been used as the inclusive term, with resistance and tolerance as subcategories[15, 16, 17, 18], in this paper I will follow the former view, i.e., I will interpret defense and tolerance as types of resistance[14]. Defense traits are those that decrease the probability of damage to the plant[5, 10, 11]. In contrast, tolerance traits do not decrease damage, instead they decrease the fitness impact of the incurred damage and in some instances may increase fitness[10, 11, 12, 13, 14, 18, 19].

While defense and tolerance should both evolve in response to selection imposed by consumer damage, the evolution of either of these groups of traits may depend on the phenotypic expression of the other[14, 20, 21, 22]. That is, there will be correlated selection[23] between defensive and tolerance traits. Since defended individuals receive low levels of damage, they should undergo weaker selection for tolerance. In contrast, tolerant individuals would not undergo selection for increased defense[21]. Such patterns of selection should result in a negative genetic correlation, or a trade-off between defense and tolerance traits[13, 14, 20, 22, 24]. However, a trade-off between tolerance and defense traits may also be directly due to the pattern of resource allocation within a plant[13, 25]; but see reference[26].

Thus, defense and tolerance have often been considered different anti-herbivore strategies[9, 14, 17, 19, 20, 27, 28, 29], but I will argue that this may not always be the case.

While in theory, these two groups of traits can be considered alternative, distinguishable strategies for coping with consumer damage[9, 13, 16, 17, 19, 20, 29, 30, 31], in practice, defense and tolerance traits may not always be distinguishable. As discussed above, their phenotypic expression and evolution may not be independent[9, 14, 21, 29]. Thus, it can be argued that the distinction between 'defense' and 'tolerance' may be an artificial construct and biologically unimportant. In this commentary, I will illustrate several cases where defense may actually contribute to tolerance, which may limit our ability to distinguish between these two strategies. Thus, examining tolerance without considering defense may potentially lead to inaccurate interpretations of how plant resistance against consumers evolves[9, 13, 14, 25, 29].

Tolerance models have often assumed that stored resources are packaged in a manner that is inaccessible to consumers, i.e., stored resources that escape damage and as such are defended which can then be reallocated to growth and/or reproduction following damage (for rev. see[14]). Reallocation of 'defended' resources then allows individuals to tolerate consumer damage. Thus, characteristics that appear to confer tolerance may actually be contingent on defensive traits which allow plants to store resources in a manner such that they escape damage (i.e., defended).

Some examples of this are demonstrated in scarlet gilia, *Ipomopsis aggregata*[6, 32, 33, 34, 35, 36, 37], the common milkweed, *Asclepias syriaca*[38], goldenrod *Solidago altissima*[39], and *Arabidopsis thaliana*[40]. In *Ipomopsis*, individuals withhold differentiation of meristems, i.e., in a defended form, into reproductive branches until the apical meristem has been removed by consumers. As a result

\* Corresponding author:

kstowe@beaconcollege.edu (Kirk A. Stowe)

Published online at <http://journal.sapub.org/ijmb>

Copyright © 2013 Scientific & Academic Publishing. All Rights Reserved

*Ipomopsis* can often tolerate and in some case overcompensate for this type of damage [6, 32, 33, 34, 35, 36, 37]. Similarly, *Arabidopsis* and *Solidago* exhibit this type of tolerance to apical meristem damage, by defending their axillary meristems from damage [39, 40]. However, release of axillary meristems is not typically a response to foliar damage and may not depend on reallocation of resources following damage.

Another pattern of resource storage in a defended manner such that they escape foliar damage resulting in tolerance is seen in *Asclepias*. The ability of *Asclepias* to tolerate foliar damage depends on allocation of resources to below-ground tissue at the expense of above ground growth [38]. Consequently, allocating resources to tissue inaccessible to foliar consumers seems to provide tolerance to foliar damage in this species. Thus, when the allocation of resources stored in a defended form provides a viable means of tolerating consumer damage, the distinction between defense and tolerance becomes blurred. However, the relationship in this species may result in a cascade if the herbivores evolve to attack both the store/defended resources as well as the non-stored resources. This may result in a non-defended/non-tolerance individual.

Optimal defense theory posits that plants should allocate resources to the defense of those plant parts that are most valuable [41]. Thus, if plants tend to allocate resources optimally to defense, discriminating between defense and tolerance may also be problematic because consumers may actively avoid damaging plant structures that are highly defended. For example, if one genotype/species allocates more resources to chemical/physical/escape defensive traits of more valuable tissues (i.e., investment in is defense optimal; sensu [41]) than another genotype/species, then the first genotype/species may receive the same amount of measurable damage, yet incur less fitness decrement, i.e., more tolerant. As a result the first genotype/species would be more 'tolerant,' simply because its most valuable organs were more defended than those of the other. Thus, the level of tolerance expressed by an individual may depend on its allocation to defense of specific plant parts. An example of this is exhibited by the allocation patterns of resources to defense in acorns by oak trees. In the apical area of an acorn, adjacent to the developing embryo, tannins occur in much higher quantities than in other parts of the acorn [7]. This results in consumers damaging only the basal portion of the acorn, while avoiding the apical portion of acorns which include the embryo and some stored resources allowing the acorn to germinate. Another example of this idea comes from *Pastinaca sativa* [42]. In this species, most of the defensive chemicals, furanocoumarins, are concentrated in the seeds [42]. This encourages herbivores to damage leaves rather than seeds, allowing plants of this species to tolerate damage. Thus, genotypes/species that provision their offspring with resources in areas that are defended against consumer damage will produce more offspring and appear to be more tolerant of the experienced damage than those genotypes/species that do not invest in this form of defense. Both of

these patterns of allocation to defense allows the plants to tolerate consumer damage, obscuring the distinction between the two types of traits.

Defense may also contribute to the phenotypic expression of tolerance when plants tissues are defended when they are most vulnerable to consumers and/or most intolerant of damage [31]. For example in *Nasturtium officinale*, levels of glucosinolates (defensive chemicals) are highest in fresh foliage. However, when leaves begin senescing, i.e., less valuable, glucosinolate concentration decreases rapidly [43]. As such, consumers are less likely to attack fresh foliage, but readily consume senescing tissues. Investing in glucosinolates in this manner may allow *Nasturtium* to tolerate consumer damage. That is, consumers are only causing damage to foliage that can be tolerated by the plant. An example of nonuniform distribution of defense is demonstrated by *Arabidopsis thaliana*; glucosinolates, are concentrated in the leaf midvein and the leaf periphery causing the generalist herbivore, *Helicoverpa armigera*, to feed almost exclusively on the inner lamina [44]. This pattern of damage may indeed confer tolerance in this species. Similarly, new leaves, the most valuable leaf tissue, of tropical plant species are typically more defended than older leaves [27]. This may be due to the fact that plants might be better able to tolerate consumer damage to older leaves than to new leaves as in *Nasturtium*.

The timing of the allocation of resources to defense may significantly affect the expression of tolerance [31, 45, 46]. This may be especially true when tolerance depends on timing of damage. For example, when plants cannot tolerate early damage, those species/genotypes that allocate resources to defense early may be more tolerant of later damage. However, if both groups received equivalent levels of damage at the same time, different conclusions may be drawn. As such, it has been argued that in order to determine the true relationship between damage and fitness, tolerance must be divorced from defense by imposing equal amounts of damage and at the same time [13, 16, 38, 47, 48]. However, artificial damage may also obscure our estimates of tolerance and/or defense in natural populations [47, 48]. Thus, when tolerance and defense traits are closely intertwined we may not be able to disentangle the traits that contribute independently to them.

Moreover, induced defense may also be intimately involved in the phenotypic expression of tolerance. For example, changes in levels of defense in response to consumer damage may result in a dispersion of damage throughout a plant's canopy. This dispersed damage may have much less of an impact on an individual's fitness than concentrated damage [49, 50]. Thus, dispersed damage may allow individuals to better tolerate consumer damage [47, 50]. Therefore, when we consider induced defense, the line between tolerance and defense becomes less distinct.

Clearly, our current concept of defense and tolerance as two distinct types of traits [10, 11, 12, 19, 20, 29, 52] may not fully capture the complexity of the interactions between plants and their natural enemies [14, 18, 26]. While tolerance

may not actually contribute to the expression of defense, it is clear that both constitutive and induced levels of defense contribute to an individual's ability to tolerate damage [7, 13, 38, 43, 47, 50], resulting in selection for traits that confer both tolerance and defense. Therefore, the idea typically espoused that defense and tolerance are alternative plant strategies to contend with consumers may be misleading [14]. Thus, an accurate understanding of the ecology and evolution of plant-consumer interactions may be hampered by this false dichotomy between defense and tolerance and both of these groups of trait should be considered together in order to better understand the evolution of plant-consumer interactions.

## ACKNOWLEDGEMENTS

I would like to thank Cris Hochwender, Tom Juenger, and Ellen Simms for many discussions that helped clarify my ideas concerning the distinction and/or similarity between tolerance and defensive traits. Lisa Gershwin, Cris Hochwender, and Gretchen LeBuhn also provided valuable comments on this manuscript. This manuscript was greatly improved due to comments from two anonymous reviewers. This work was supported by a National Research Council Fellowship (Ford Foundation) to K.A.S., DEB-9815550 and DEB-9527900 to E.L.S.

## REFERENCES

- [1] Feeney, P.P. 1976. Plant apparency and chemical defense. *Rec. Adv. Phytochem.* 10: 1-40.
- [2] Rhoades, D.F. and R. Cates. 1976. Towards a general theory of plant antiherbivore chemistry. *Rec. Adv. Phytochem.* 10: 168-213.
- [3] Marquis, R.J. 1992a. The selective impact of herbivores. In *Plant Resistance to Herbivores and Pathogens*. (eds) R.S. Fritz and E.L. Simms. University of Chicago Press, Chicago, IL.
- [4] Aide, T.M. 1991. Synchronous leaf production and herbivory in juveniles of *Gustavia superba*. *Oecologia* 88: 511-514.
- [5] Aide, T.M. 1992. Dry season leaf production – An escape from herbivory. *Biotropica* 24: 532-5[16].
- [6] Paige, K.N. 1992. Overcompensation in response to mammalian herbivory from mutualistic to antagonistic interactions. *Ecology* 73: 2076-2085.
- [7] Steele, M., T. Knowles, K. Bridle, and E.L. Simms. 1993. Tannins and partial consumption of acorns: Implications for dispersal of oaks by seed predators. *Am. Midl. Nat.* 130: 229-238.
- [8] Tuomi, J., P. Nilsson, and M. Åström. 1994. Plant compensatory responses: bud dormancy as an adaptation to herbivory. *Ecology* 75:1429-36
- [9] Tiffin, P. 2000. Are tolerance, avoidance, and antibiosis evolutionarily and ecologically equivalent responses of plants to herbivores? *Am. Nat.* 155: 128-138.
- [10] Painter, R.H. 1951. *Insect resistance in crop plants*. Macmillan, New York, NY.
- [11] Painter, R.H. 1958. Resistance of plants to insects. *Ann. Rev. Entomol.* 3: 267-290.
- [12] Smith, C.M. 1991. *Plant resistance to insects: A fundamental approach*. J. Wiley and Sons, New York, NY.
- [13] Stowe, K.A. 1998. Experimental evolution of resistance in *Brassica rapa*: Correlated responses of tolerance in lines selected for glucosinolate content. *Evolution* 52: 703-712.
- [14] Stowe, K.A., R.J. Marquis, C.G. Hochwender, and E.L. Simms. 2000. The evolutionary ecology of tolerance to consumer damage. *Ann. Rev. Ecol. Syst.* 31: 565-595.
- [15] Rausher, M.D. 2001. Co-evolution and plant resistance to natural enemies. *Nature* 411:857-864.
- [16] Abrahamson, W. and A. Weis. 1997. *Evolutionary ecology across three trophic levels: Goldenrods, gallmakers, and natural enemies*. Princeton University Press, Princeton, NJ.
- [17] Strauss, S.Y. and A. Agrawal. 1999. The ecology and evolution of tolerance to herbivory. *Trends Ecol. Evol.* 14: 179-185.
- [18] Nuñez-Farfan, J., J. Fornoni, and P.L. Valverde. 2007. The evolution of resistance and tolerance to herbivores. *Ann. Rev. Ecol. Evol. Syst.* 38: 541-560.
- [19] Van der Meijden, E., M. Wijn, and H. Verkaar. 1998. Defence and regrowth, alternative plant strategies in the struggle against herbivores. *Oikos* 51: 355-361.
- [20] Mauricio, R., M.D. Rausher, and D.S. Burdick. 1997. Variation in the defense strategies of plants: Are resistance and tolerance mutually exclusive? *Ecology* 78: 1301-1311.
- [21] Weinig, C., J.R. Stinchcombe, and J. Schmitt. 2003. Evolutionary genetics of resistance and tolerance to natural herbivory in *Arabidopsis thaliana*. *Evolution* 57: 1270-1280.
- [22] Leimu, R., J. Koricheva, and S. Larsson. 2006. A meta-analysis of tradeoffs between plant tolerance and resistance to herbivores: Combining the evidence from ecological and agricultural studies. *Oikos* 112: 1-9.
- [23] Lande, R. and S. Arnold. 1983. The measurement of selection on correlated characters. *Evolution* [16]: 1210-1226.
- [24] Fornoni, J., J. Nuñez-Farfan, P.L. Valverde, and M.D. Rausher. 2004. Evolution of mixed strategies of plant defense allocation against natural enemies. *Evolution* 58: 1685-1695.
- [25] Simms, E.L., and J. Triplett. 1994. Costs and benefits of plant responses to disease: Resistance and tolerance. *Evolution* 48: 1973-1985.
- [26] Restif, O. and J.C. Koella. 2004. Concurrent evolution of resistance and tolerance. *Am. Nat.* 164: 90-102.
- [27] Coley, P.D. 1983a. Herbivory and defensive characteristics of tree species in a lowland tropical rainforest. *Ecol. Mon.* 53: 209-234.
- [28] Fineblum, W.L. and M.D. Rausher. 1995. Tradeoff between resistance and tolerance to herbivore damage in a morning

- glory. *Nature* 377: 517-520.
- [29] Roy, B., and J. Kirchner. 2000. Evolutionary dynamics of pathogen resistance and tolerance. *Evolution* 54: 51-63.
- [30] Roosa, L., J. Koricheva, and S. Larsson. 2006. Combining evidence from ecological and agricultural studies, *Oikos* 112: 1-9.
- [31] Barton, K.E. and J. Koricheva. 2010. The ontogeny of plant defense and herbivory: Characterizing general patterns using meta-analysis. *Am. Nat.* 175: 481-493.
- [32] Paige, K.N. and T.G. Whitham. 1987. Overcompensation in response to mammalian herbivory: The advantage of being eaten. *Am. Nat.* 129: 407-416.
- [33] Bergelson, J. and M.J. Crawley. 1992a. The effects of grazers on the performance of individuals and populations of scarlet gilia, *Ipomopsis aggregata*. *Oecologia* 90: 435-444.
- [34] Bergelson, J. and M.J. Crawley. 1992b. Herbivory and *Ipomopsis aggregata*: The disadvantages of being eaten. *Am. Nat.* 139: 870-882.
- [35] Paige, K.N. 1999. Regrowth following ungulate herbivory in *Ipomopsis aggregata*: Geographic evidence for overcompensation. *Oecologia* 118: 316-326.
- [36] Bergelson, J., T. Juenger, and M.J. Crawley. 1996. Regrowth following herbivory in *Ipomopsis aggregata*: Compensation but not overcompensation. *Am. Nat.* 148: 744-755.
- [37] Juenger, T.J. and J. Bergelson. 2000. The evolution of compensation to herbivory in scarlet gilia, *Ipomopsis aggregata*: Herbivore-imposed natural selection and the quantitative genetics of tolerance. *Evolution* 54: 79-92.
- [38] Hochwender, C.G., R.J. Marquis, and K.A. Stowe. 2000. The potential for and constraints on the evolution of compensatory ability in *Asclepias syriaca*. *Oecologia* 122: 361-370.
- [39] Wise, MJ and WG Abrahamson. 2008. Applying the limiting resource model to plant tolerance to apical meristem damage. *Am. Nat.* 172: 635-647.
- [40] Banta, J.A., Martin H.H. Stevens, and Massimo Pigliucci. 2010. A comprehensive test of the 'limiting resources' framework applied to plant tolerance to apical meristem damage. *Oikos* 119: 359-369.
- [41] Zangerl, A. and F. Bazzaz. 1992. Theory and pattern in plant defense allocation. In *Plant Resistance to Herbivores and Pathogens*. (eds) R.S. Fritz and E.L. Simms. University of Chicago Press, Chicago, IL.
- [42] Berenbaum, M.R., A.R. Zangerl, and J.K. Nitao. 1986. Constraints on chemical coevolution: Wild parsnips and the parsnip webworm. *Evolution* 40: 1215-1228.
- [43] Newman, R.M., C.W. Kerfoot, and Z. Hanscom III. 1996. Watercress allelochemical defends high-nitrogen foliage against consumption: Effects on freshwater invertebrates. *Ecology* 77: 2321-2323.
- [44] Shroff, R., F. Veraga, A. Mack, A. Svatos, and J. Gershenson. 2008. Nonuniform distribution of glucosinolates in *Arabidopsis thaliana* leaves has important consequences for plant defense. *PNAS* 105: 6196-6201.
- [45] Boege, K. 2005. Herbivore attack in *Casuarina nitida* influenced by plant ontogenetic variation in foliage quality and architecture. *Oecologia* 143: 117-125.
- [46] Boege, K. and R. J. Marquis. 2006. Plant quality and predation risk mediate by plant ontogeny: Consequences for herbivores and plants. *Oikos* 115: 559-572.
- [47] Lehtila, K. 2003. Precision of herbivore tolerance experiments with imposed and natural damage. *Evolution* 57: 677-680.
- [48] Tiffin, P. and B. Inouye. 2000. Measuring tolerance to herbivory: Accuracy and precision of estimates using natural and artificial damage. *Evolution* 54: 1024-1029.
- [49] Marquis, R.J. 1992b. A bite is a bite? Constraints on response to folivory in *Piper arieianum* (Piperaceae). *Ecology* 73: 143-152.
- [50] Mauricio, R., M. Bowers, and F. Bazzaz. 1993. Pattern of leaf damage effects fitness of the annual plant *Raphanus sativa* (Brassicaceae). *Ecology* 78: 2066-2071.
- [51] Tiffin, P. and M.D. Rausher. 1999. Genetic constraints and selection acting on tolerance to herbivory in the common morning glory *Ipomoea purpurea*. *Am. Nat.* 154: 700-716.