Concepts

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THE BENEFITS OF INDUCED DEFENSES AGAINST HERBIVORES

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Abstract. Previous explanations for the evolution of induced resistance of plants to herbivory emphasized arguments based on saving costs when allocations to defense were not needed; these models met with limited empirical support. We offer a novel explanation based on induced resistance providing increased variability in defense. As long as maximal levels of defense are constrained, variability will increase the effectiveness of a given level of investment in defense. We show that variability can decrease herbivore performance if herbivore performance is a concave function of the level of resistance. In particular, if herbivores can choose among different plants and plant tissues, then variability created by induced resistance may benefit plants under attack and hence may be favored by selection. The key assumptions of this model are broadly supported by empirical data from many plant–herbivore systems.

Key words: defenses, variability; induced responses to herbivory; modeling; plant–herbivore interactions; variability, constitutive vs. induced.

For many plants, resistance to herbivory can be an induced trait, changing following damage, as well as a constitutive or constant trait (Fowler and Lawton 1985, Karban and Myers 1989, Tallamy and Raupp 1991, Karban and Baldwin 1997). Since resistance to herbivory is assumed to benefit plants, a question that has puzzled workers is why resistance is expressed facultatively and variably. One possibility is that resistance has allocation costs for plants: individuals that express resistance only when it is needed are able to reduce costs by allocating resources to growth and reproduction when they are not under attack (Feeny 1976, McKey 1979, Rhoades 1979, Fagerstrom et al. 1987, Clark and Harvell 1992). This hypothesis, involving saving allocation costs, is intuitive, and has dominated the thinking about the evolution of induced resistance by both theoreticians and empiricists. Unfortunately, most workers who have looked for costs of induced resistance by expressing resistance in environments that lacked herbivores have failed to demonstrate any costs (Brown 1988, Simms 1992, Karban 1993, Mole 1994; but see Baldwin et al. [1990] for an example in which induced resistance was found to be costly). This has led to various explanations (Simms 1992, Karban 1993, Mole 1994), including: (1) costs of resistance exist but they are too small or too difficult to detect, (2) costs exist but they will only be detectable in competitive environments, or (3) costs existed when resistance traits first spread in plant populations, but more recently they have been minimized by selection.

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Here we suggest an explanation for the prevalence of variable induced resistance that is unique because it is based on its effectiveness rather than simply its low allocation cost. In particular, we propose that plants with resistance phenotypes that vary as the result of induction are selectively favored because herbivores experience reduced performance when faced with variability and will thus choose to avoid such plants. By definition, induced responses create variability in the food encountered by herbivores. For example, some plants respond very little to herbivory and others produce high levels of toxins. Induced plant responses, especially different responses in different plant tissues and in tissues at different stages of development, will produce variability within individual plants (Baldwin and Karb 1995, Zangerl and Rutledge 1996). Induced responses can create temporal variability, exemplified

by damaged plants that became more variable than undamaged controls (e.g., van Dam and Vrieling 1994, Stout et al. 1996). Induced responses can also create spatial variability, exemplified by changes that are localized to particular tissues that receive damage (e.g., Tuomi et al. 1988, Jones et al. 1993). Induced responses are not the only source of variability in resistance phenotypes. Indeed, plants are constitutively variable as well. For example, different plant tissues have different nutrients and different secondary chemicals providing constitutive variability in space, and plant development provides constitutive variability in time. Constitutive variability may provide many of the same benefits that we describe for induced variability. However, induction may be favored as an additional source of variablity, particularly as a rapid response and particularly to those plants and plant parts that are under attack by herbivores. We use a simple model to illustrate how such increased variation may reduce herbivore performance and benefit plants.

Our hypothesis is based on herbivore performance on diets that include chemicals (which we call ''toxins'') produced by the plant in response to herbivory. Our use of the term ''toxin'' is an oversimplification because in reality a chemical's toxic effects on an herbivore depend upon the chemical and physical environments of the plant and herbivore. Nonetheless, the notion that some plant chemicals will lead to reduced herbivore performance provides a useful model. We assume that the benefit $B(t)$ that an herbivore receives from feeding on a plant producing a level of toxin t is a declining function of the level of the toxin, as in Fig. 1. If the level of toxin is sufficiently low, then benefits to herbivores are not reduced, and if the level of toxin is sufficiently high the herbivore dies (zero benefit). Our key assumption is that the benefit function for herbivores with respect to levels of toxin is concave (Fig. 1). This assumption is satisfied for many well-studied plant–herbivore systems including hornworm larvae fed nicotine (Parr and Thurston 1972), four caterpillar species fed diterpene acids of sunflower (Elliger et al. 1976), cabbage looper larvae fed esters from crown vetch (Byers et al. 1976), and tobacco budworm caterpillars fed any of several allelochemicals from cotton (Jenkins et al. 1983). These studies measured insect survival, growth, and pupal mass, each of which reflects fitness components of the herbivores.

The key result of our model is that a plant that produces a variable level of toxin (an inducible strategy) will always provide lower levels of benefit to herbivores than a plant that produces the mean level constitutively. This result is true whenever the benefit function is concave (as in Fig. 1); this outcome is sometimes called ''Jensen's inequality'' (DeGroot 1970). We can generalize the result in Fig. 1 by assuming that a plant produces toxin level t with frequency $f(t)$ in response to herbivory. This interpretation of $f(t)$ is quite general. It can range from a single plant producing differing levels of toxins in different leaves or at different times to populations of many individuals each of which has homogeneous levels of toxins. In either case, when an herbivore attacks a plant (or plant tissue), or when it moves to another plant individual, the levels of toxins it will encounter are uncertain. This model favors variability, regardless of whether it is constitutive or induced.

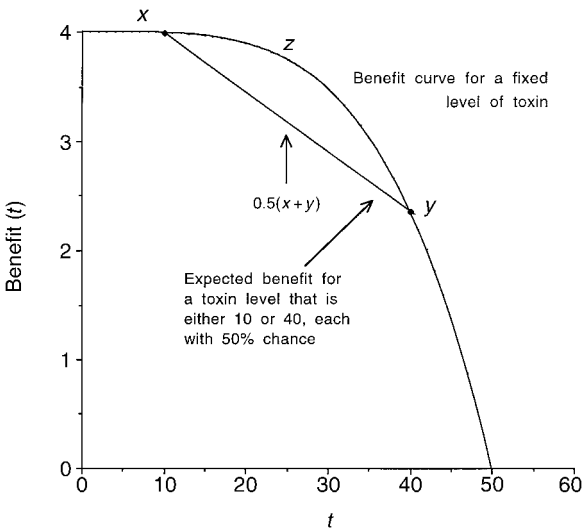

FIG. 1. We assume that the benefit $B(t)$ an herbivore accrues from feeding on a plant is a decreasing function of the toxin t produced by the plant. (For the computation here, we used $B(t) = \max(0, 4[1-(t/50)^4])$ so that $t = 50$ is a fatal level of toxin.) A plant that produces a variable level of toxin will lead to consistently lower levels of benefit than a plant that produces the mean level. For example, imagine a plant that produces 10 units of toxin with probability 0.5 and 40 units of toxin with probability 0.5. This corresponds to a variable plant (or plant tissue) that produces 10 units of toxin half the time and 40 units the other half. The corresponding benefits are x and y and the average benefit is $0.5(x + y)$. The benefit z associated with the average level of toxin, 25 units, is larger than this average benefit (top arrow in Fig. 1). Thus, herbivores will have reduced success on plants that vary in their levels of defense compared to those with the same mean levels of toxin but less variability. If herbivore behavior reflects performance, an herbivore will prefer to feed on a plant that produces the constant level of toxin.

Real plants are heterogeneous and present a distribution of toxin levels, rather than a single mean level, to herbivores. Under these circumstances, we compute the expected level of benefit as $\int_0^\infty \text{Benefit}(t)f(t)\,dt$. For example, assume that the frequency distribution of toxin is normally distributed with mean $\bar{t}$ and variance σ^2. Three expected benefit curves are shown in Fig. 2, for $\bar{t}$ equal to 10%, 30%, or 50% of the fatal level of toxin. From this figure, we note that increasing the mean levels of toxin leads to decreased benefit. More interestingly, also note that for a fixed mean level of toxin, the expected benefit decreases as the value of

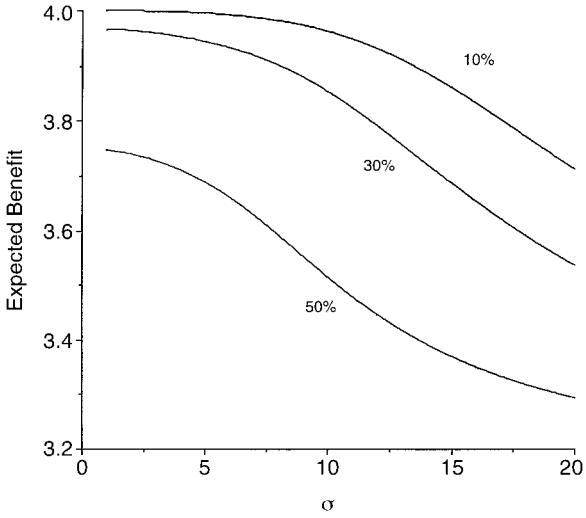

FIG. 2. Expected benefits accrued by an herbivore from feeding on a plant (see Fig. 1) as a function of the square root of the variance. Plants are heterogeneous and produce levels of toxins described by frequency distributions rather than single values. We assume that the level of toxin is normally distributed, with mean equal to 10%, 30%, or 50% of the fatal level and variance σ^2. Under these conditions, benefits to herbivores decrease as the variance in toxin level increases.

σ increases. In other words, increased variability results in reduced herbivore performance.

Although higher toxin levels reduce benefits to herbivores, plants may be constrained to have less than maximal levels of toxins for many reasons other than allocation costs: toxins may cause autotoxicity (e.g., Kuc 1987, Baldwin and Callahan 1993), high levels of a toxin may make the plant more vulnerable to certain enemies but more susceptible to others (e.g., Raffa and Berryman 1987, Tallamy and McCloud 1991), and consistently high levels may make counteradaptation by herbivores more likely (e.g., Whitham 1983, Gershenzon and Croteau 1991). Thus our model relies on costs of defense in the broad sense (constraints other than allocation costs) that favor sub-maximal levels of toxins, and it does not require there to be a resource-based trade-off between defense and plant growth or reproduction. The advantages of variability may intensify selection for induced defenses because investment in a variable defense is more effective than an equal investment in a constant defense.

This model shows how variability caused by induction could reduce herbivore performance. Thus, we predict that, given a choice, an herbivore will seek plants that have lower variability, even if the mean level of toxin is the same. In addition, we predict that herbivore benefit functions will not be convex with respect to plant toxins; such a case could be a disaster for the plant. Given that herbivores respond to plant quality (Bryant 1981, Edwards et al. 1991, Price 1991, Waldbauer and Friedman 1991, Slansky 1993, Stockhoff 1993*a*), it is likely that natural selection will favor the production of spatial and temporal variation in toxin levels. In our model, then, variability caused by induction reduces benefits to herbivores and concurrently increases the benefit-to-cost ratio for the plant relative to a constitutive strategy. We implicitly assume that costs (allocation or otherwise) to the plant of having chemical toxins do not also increase in a convex fashion as the level of toxin increases; such a convex cost would minimize the benefits of variability to the plant. At present, this assumption seems justified since few experimental studies have demonstrated any evidence for fitness costs of toxins.

Induced responses increase the level of variability that herbivores face among and between plants. The negative effect of variability to the herbivore in our model resulted simply from the concave benefit function. Many other mechanisms could cause plant variability to reduce herbivore performance further. Herbivores may be unable to compensate for changes in nutrition or secondary plant metabolites (Stockhoff 1993*b*). Many of the enzymatic systems that herbivores employ to detoxify plant chemicals are inducible, so that varying the level of plant secondary chemicals may present herbivores with foods that do not correspond well with their existing enzymatic capabilities (Lindroth 1991). Herbivores may habituate to high levels of plant secondary metabolites as long as levels are increased in small increments, but larger shifts can result in poisoning (Brattsten et al. 1983). Where physiological compensation does not occur, learning may enable some herbivores to avoid less nutritious parts of their habitats; changing plant phenotypes may lessen their ability to use this learned information (Jones and Ramnani 1985). In addition, over longer time frames herbivores may be less able to adapt to their hosts if plants change phenotypes, since selection will not be directional (Whitham 1983, Gershenzon and Croteau 1991).

In summary, if herbivore performance is a concave function of the level of chemical resistance and is reflected in herbivore behavior, then induced resistance in plants may be favored by selection because it provides variability. We have presented a graphical model that illustrates how this may occur. Variability in the defenses encountered by herbivores can reduce their benefits in ecological time by any of several mechanisms. This model emphasizes the potential benefits of variability rather than of cost-saving arguments. In other words, given that a plant is going to deploy a certain level of toxin, how can it maximize the effectiveness of that deployment? Our thinking was stimulated by the observation that induced responses were often variable in nature and by the scarcity of evidence that induced responses had allocation costs. This model describes a potential benefit of variability whether or not

resistance is also costly. Until now, estimates of potential benefits have recieved little consideration; a true understanding of facultative resistance may require new approaches, including more consideration of its benefits.

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