

# Future directions in the study of induced plant responses to herbivory

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## Abstract

This paper reviews current progress and makes recommendations for future studies of induced plant responses to herbivory in three research areas: the role of induction in structuring herbivore communities, costs associated with the expression of induced responses, and theory and data on the macro-evolution of induced responses. It is argued that although mechanistic approaches will be important for progress, it is also critical to maintain a holistic approach, including a consideration of field environments, multi-species interactions, and patterns over ecological and evolutionary time.

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## Introduction

Induced plant responses to herbivory that reduce the preference or performance of subsequently feeding herbivores are a paradigm of plant defense (Karban & Baldwin, 1997). Originally formulated as a potential novel mechanism of pest control in agriculture (Green & Ryan, 1972) and insect herbivore population regulation (Haukioja & Hakala, 1975), studies of induced responses have grown in number and depth, addressing major concepts in ecology and evolutionary biology. This paper highlights three major avenues of current and future directions in the study of induced plant responses: their impact on herbivore communities, the costs associated with their expression, and their macro-evolution. Indeed, although the perspectives presented are primarily ecological and evolutionary in nature, mechanistic tools will certainly be useful for progress. Nonetheless, throughout the paper it is argued that a focus on questions and hypothesis testing, coupled with field observations, is critical to any scientific exploration of induced responses.

### Induced responses and the community structure of insects

Early ecologists believed that competition for resources was the most important factor structuring communities. However, a seminal paper by Hairston et al. (1960) suggested that herbivores, in particular, were not subject to strong competition. Hairston et al. elegantly argued that herbivore populations were controlled by higher trophic levels (predators

and parasitoids), and thus were not limited by resources (plants). Though there was some strong opposition to this view (Murdoch, 1966), the fact that herbivores rarely outstrip nature's greenery was used as evidence for Hairston et al.'s logic, and the argument nearly became dogma following reviews and experiments in the 1970s (Lawton & Strong, 1981; Strong et al., 1984). Not until non-food competition was considered (Karban, 1986), and induced plant responses were widely accepted (Karban & Myers, 1989), did competition among herbivores again receive consideration as an organizing factor (Denno et al., 1995), and thus the paradigm began to shift.

The fact that quite a small amount of herbivory can induce plant responses, which then strongly influences insects' host choice, growth, and rates of attack by predators and parasitoids, suggests that herbivores may indeed be competing strongly, even when plant resources are not physically limiting. Here I broadly define 'competition' as any negative impact of one species on another that shares a common resource. Because induced responses are typically systemic throughout the plant, the influences of herbivory on one plant part may influence herbivores on different plant parts (e.g., Moran & Whitham, 1990). Similarly, the pronounced seasonal phenology of insect herbivores (e.g., Kause et al., 2001), even in tropical areas, allows for herbivores to interact through the host-plant without coming into contact. Thus, neither extensive consumption, nor spatial or temporal overlap is required for herbivory to strongly impact other herbivores that share host-plants.

Plant responses induced by herbivores may have direct consequences for herbivores or indirect consequences

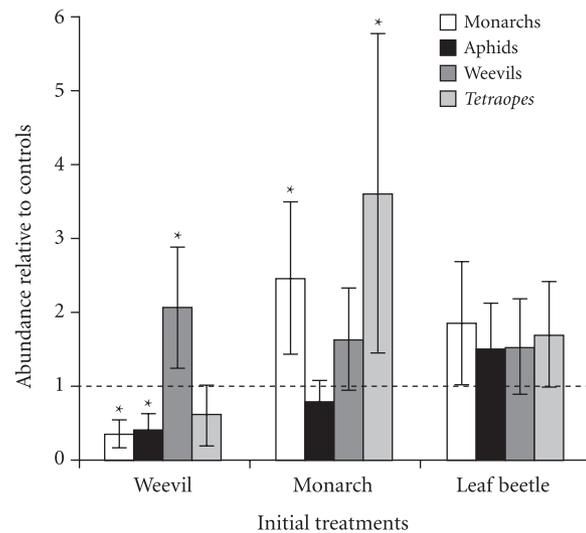
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mediated via changes in the community of carnivores (i.e., indirect defense) (Karban & Baldwin, 1997). In particular, the volatile responses of plants to herbivory can have a strong effect on tritrophic interactions. Recent studies have documented the impact of particular chemical constituents of induced plant responses (James, 2003; James & Price, 2004), and the full blend of volatile compounds (Bernasconi Ockroy et al., 2001) on the carnivore community.

The additional discovery of specificity in induced responses, namely the differential response of plants to attack by different herbivores and the differential response of arthropods to the plant phenotype, provides a mechanism for induced responses to shape arthropod community structure (De Moraes et al., 1998; Stout et al., 1998; Agrawal & Karban, 2000; Agrawal, 2000b; Van Zandt & Agrawal, 2004a,b). Because herbivores, omnivores, predators, and parasitoids all show variation in their responses to plant induction (i.e., some respond positively, some negatively, and some not at all), the influence of induction on the community can be both potent and complex. Thus, in addition to competition, facilitation and similar effects on other trophic levels will contribute to the community structure. Although only a few studies have implicated induced responses to herbivory per se in shaping arthropod community structure (i.e., more than a few arthropod species) (Wold & Marquis, 1997; Thaler, 1999; Bernasconi Ockroy et al., 2001; Thaler et al., 2001; Van Zandt & Agrawal, 2004b), future studies are likely to further reveal its importance. The challenge is to conduct repeated censuses of arthropod colonists, and to weed-out the relative importance of induced responses and other factors contributing to the effects of herbivory on arthropod communities (Figure 1).

In an excellent study, González-Megías & Gómez (2003) demonstrated strong effects of a herbivorous beetle on the diversity and relative abundance of several guilds of herbivorous and predatory arthropods on *Hormathophylla spinosa*. Nonetheless, induced responses per se were not implicated in that study. The use of elicitors (e.g., Thaler et al., 2001) and genetically modified plants (e.g., Kessler et al., 2004) will certainly aid in this regard. For example, field applications of jasmonic acid to tomato plants has been shown to induce defensive proteins and negatively impact several herbivores (aphids, thrips, caterpillars, and beetles) in three feeding guilds. In addition, genetically modified wild tobacco plants that exhibited normal levels of constitutive resistance, but lacked inducibility, harbored a greater abundance of two herbivores which are typically rare on tobacco. Thus, induced responses can clearly structure herbivore communities, irrespective of leaf damage.

Nonetheless, given that leaf loss and induction are typically coupled in nature (i.e., herbivory), it is important to study their relative impacts on herbivore community



**Figure 1** Specificity in induced plant responses influenced the abundance of four specialist herbivores on milkweed (data from Van Zandt & Agrawal, 2004b). In this field experiment, plants were initially treated with herbivory by weevils, monarch larvae, or leaf beetle adults. Following imposition of the treatments, the abundances of naturally colonizing herbivores were monitored weekly for several weeks. Results reported are from Poisson logistic regression analyses; significant effects compared to controls (value 1 reference dashed line) are indicated with an asterisk. The effects reported for weevil induction were long lasting throughout the season, whereas interaction cascades generated the effects of induction by monarchs (Van Zandt & Agrawal, 2004b).

structure. I propose a quantitative extension of the 'keystone species' concept (Paine, 1966; Power et al., 1996), termed the 'keystone herbivore concept' (González-Megías & Gómez, 2003). Extending the quantitative framework outlined by Power et al. (1996), a keystone herbivore species is one which has a disproportionately large impact on the arthropod community given the percentage damage it imposes on a plant. By this definition, the absolute value of the community importance of a herbivore must be greater than '1', when defined as follows:

$$\text{Community importance} = (t_n - t_d) / (t_n \times p_i),$$

where  $t_n$  is the measure of the intact arthropod community (species richness, diversity, biomass, etc.),  $t_d$  is the measure of the arthropod community where the  $i$ th herbivore species has been deleted, and  $p_i$  is the proportional plant damage (or biomass lost) when the  $i$ th herbivore species is on control plants.

For example, if the presence of a herbivore species reduces arthropod species richness on a plant from 15 to 10 species, and the herbivore imposes 10% leaf loss, then the community

importance is 3.3, that is  $[(15 - 10)/(15 \times 0.1)]$ . This result can be interpreted as the herbivore species having a greater than threefold higher impact on the arthropod community than would normally be predicted by damage alone. When the presence of a keystone herbivore increases arthropod community variables, the community importance will be a negative value less than  $-1$ . In Power et al.'s (1996) formulation of community importance, a species' biomass (not damage imposed) is the metric against which community effects are standardized. This may be appropriate for keystone herbivores as well, especially in the case where herbivores are not removing plant tissues that are easily assessed (e.g., phloem feeders).

It should be noted that not all keystone herbivores will have caused effects on the arthropod community via induced plant responses. Direct effects of the presence of herbivores or indirect effects of resources provided (i.e., honeydew from homopterans) may also result in keystone herbivore status (Wimp & Whitham, 2001). Nonetheless, keystone herbivore status is suggestive of some ecological interaction that can then be further addressed. This is especially the case since herbivory by some species reduces plant leaf area (known to be important in arthropod community structure (Strong et al., 1984)) and causes induced responses, suggesting that the keystone species concept may be particularly useful in providing a null expectation for the effects of herbivory on arthropod communities.

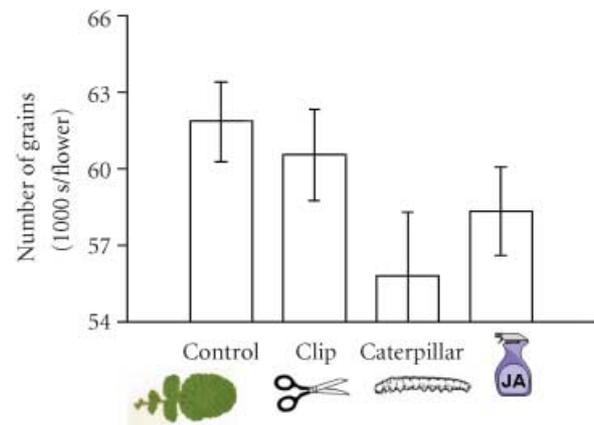
If a herbivore species influences the structure of the arthropod community via induced plant responses, some of the effects may be due to long-lasting impacts of induced responses, while others may be attributed to cascades of indirect interactions (Van Zandt & Agrawal, 2004b). In the first case, herbivory-induced changes in the plant's defensive phenotype may persist throughout the season and affect several herbivore species. Conversely, effects of induced responses may affect the densities or traits of a subset of the arthropod community, and these changes in intermediate species may affect other arthropods. Although statistical techniques are available to partially address these divergent mechanisms (Van Zandt & Agrawal, 2004b; Viswanathan & Thaler, 2005), they have rarely been employed, and the relative impact of long-lasting effects and interaction cascades remains largely untested.

#### Costs and trade-offs associated with induced responses

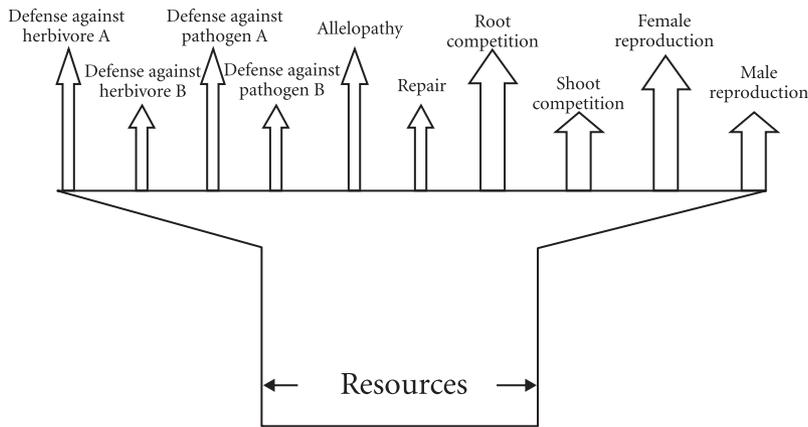
The currently accepted view on the micro-evolution of induced plant responses to herbivory has been that induction evolved as a cost saving strategy. That is, given the costly nature of plant allocation to defense, plant fitness could be enhanced by only allocating to defense in the presence of herbivory. From the perspective of producing defenses, no matter what their molecular structure, there

must be an energetic cost. Measuring this cost has frequently been attempted by comparing the performance of undamaged control plants with induced plants, both in the absence of herbivory. Although some studies have quite successfully detected costs by tracing plant acquisition and allocation of limiting nutrients to defense away from reproduction (Baldwin & Hamilton, 2000), many others have not (Brown, 1988; Karban, 1993; Gianoli & Niemeyer, 1997; Agrawal & Karban, 1999). One limitation in the detection of costs is that most studies only measure components of female fitness. Given that most plant species must outcross, 50% of fitness is through male function: seeds sired by pollen grains. A single study to date has estimated the costs of induced responses both in terms of female and male fitness components, and detected costs only in male traits (Figure 2).

Even if considering both female and male fitness components, allocation to defense may not be easily detectable



**Figure 2** Costs of induced plant responses to herbivory in pollen production of wild radish (means  $\pm$  SE; there were 70 replicates per group) (adapted from Agrawal et al., 1999). This experiment controlled for leaf area removal in a factorial design employing plants both with and without leaf tissue removal, and plants with and without induced responses: controls, 50% leaf area removed by clipping with scissors, jasmonic acid application, or 50% leaf area removed by caterpillars. Although elicitors of induced plant defenses (and other techniques such as genetic transformation) provide an exciting opportunity to answer ecological and evolutionary questions, it is important to include real herbivory treatments when using elicitors, so as to calibrate the manipulation and be sure that real herbivory has the same effect. Our approach was powerful because the effects of induced responses and leaf tissue loss were uncoupled. From a statistical standpoint, the factorial analysis has superior power compared to non-crossed designs, and has the ability to detect interactions between leaf area removal and induction. In this case, there was a significant reduction in pollen production caused by induction ( $P = 0.019$ ), but not of leaf tissue removal or an interaction between the two. No such cost was detected in terms of seed production or pollen size.



**Figure 3** Ecological costs of induced plant responses to herbivory depicted as trade-offs through various ecological functions (redrawn from Karban & Baldwin, 1997).

(Karbon & Baldwin, 1997; Agrawal & Karban, 1999). Zavala et al. (2004) have argued and demonstrated that an approach combining genetic modification and artificial elicitation of plants can facilitate the detection of costs, especially in competitive environments. Continued frustration among evolutionary ecologists on the lack of detecting the costs of induced responses, though in part due to methodological limitations, is very likely due to the fact that the detection of costs is dependent on a diversity of environments (Agrawal & Karban, 1999; Heil, 2002). Costs can take many forms, and here I define ecological costs as those that are only detectable under certain conditions, some of which may include the biotic environment (i.e., the presence of other species in the community). Ecological costs may be much more difficult for selection to minimize compared to allocation costs (Strauss et al., 2002). Below I use Karban & Baldwin's (1997) broad framework (Figure 3) for discussing the emerging picture on detecting the ecological costs of induced responses. Future studies should compare the relative magnitude of allocation (or energetic) costs of induction to the ecological costs.

Specificity in induced responses provides an important mechanism for ecological costs. For example, a cost may be present when induced responses make plants more resistant to some herbivores, but more susceptible to others. The classic work of Carroll & Hoffman (1980) demonstrated such a double-edged effect of induction for two beetles on *Cucurbita moschata*. Although the chemical mechanisms proposed for the ecological cost were not correct (McCloud et al., 1995), the important finding of the trade-off between resistance and susceptibility still stands. Additional examples of this phenomenon abound in other plant–herbivore systems (Landau et al., 1994; Alados et al., 1996; Agrawal et al., 1999; Agrawal & Sherriffs, 2001). The further discovery that plant responses to herbivores may make plants more susceptible to pathogens (and vice versa) suggests that an

ecological cost may only be detected in the presence of diseases (Preston et al., 1999; Thaler et al., 1999). In addition to herbivores and pathogens, other interactions or abiotic environmental effects may also decrease the detection of costs of induced responses (Agrawal & Karban, 1999). For example, from a tri-trophic perspective, plant responses to herbivory that increase attractiveness to predators and parasitoids may be co-opted by herbivores and used as host-finding cues (Dicke, 2000).

Competition may limit resource availability for plants and in turn this may exacerbate the costs of induced responses (van Dam & Baldwin, 1998; Agrawal, 2000a). Even when competing plants do not take resources directly away from a focal plant, plant responses to competition may impose costs (Cipollini, 2004). Especially for non-rosette plants (i.e., those with apical dominance and elongating internodes), the shade-avoidance response has been classically studied as an adaptive response to light competition (Morgan & Smith, 1981; Schmitt et al., 1995; Dudley & Schmitt, 1996). The shade-avoidance response is conceptually similar to herbivore-induced responses in that it is environmentally triggered, with specific cues and receptors in the plant, and is produced following the initiation of a phytohormonal cascade (Table 1). Recent models and evidence suggests that plant responses to herbivores and light competition may present a trade-off (Cipollini, 2004; Kurashige & Agrawal, 2005), which may be due to phytohormonal interactions or simply opposing trait values when plants are challenged by competitors vs. herbivores. For example, we recently reported that *Chenopodium album* had reduced resistance to herbivory, and somewhat impaired induced resistance when grown in shade compared to full sunlight (Figure 4). Available plants with genetically altered phytochromes and jasmonate signaling could be prime mechanistic tools available to address the relationship between plant responses to competition and herbivory.

**Table 1** Two classically studied plant responses to environmental threats of herbivory and light competition: induced responses to attack and the shade-avoidance response. These responses are produced hierarchically by the environment, specific signals, receptors in the plant, and hormonal cascades. Trade-offs in these responses have recently been suggested from models and data

| Herbivory             | Competition        |
|-----------------------|--------------------|
| Induced responses     | Shade avoidance    |
| Herbivore damage      | In the shade       |
| Insect specific cues  | Red: far red light |
| Perception/receptors? | Phytochromes       |
| Jasmonate, etc.       | Auxins, etc.       |

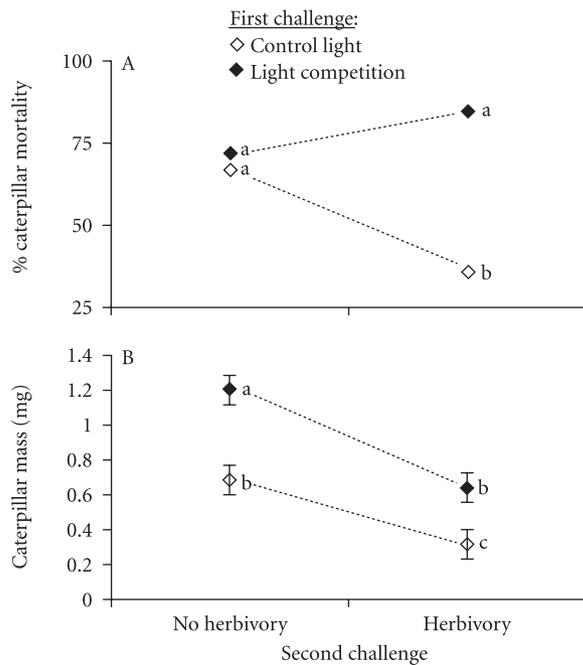
The trade-off between defense and competitive resource acquisition is likely to be quite general in both animals and plants. In animals, responses to competition frequently result in increased foraging activity, which increases prey

susceptibility to predators (McPeck, 1996; Relyea, 2002). In plants, increased resource capture associated with neighbor-shade typically results in increased leaf nitrogen content, thinner leaves, fewer trichomes, and reduced toughness compared to plants in full sunlight (Young & Smith, 1980; Morgan & Smith, 1981; Jansen & Stamp, 1997). All of these traits are likely to make plants more susceptible to herbivory. At the same time, both animals and plants subject to the threat of predation tend to be less competitive. Animals frequently reduce their foraging activity, while plants simply have a reduced leaf area, which leads to reduced light capture and photosynthesis. In summary, a strong trade-off can be expected between responses to competitors and predators/herbivores due to effects on limited resources, hormonal interactions, and the trait values associated with these responses.

**Phylogenetic patterns of induced responses**

Why do we need a phylogenetic approach to study the induced plant responses to herbivory? Of course, there are descriptive questions about the big picture of the macro-evolution of induced responses. Is constitutive resistance ancestral? How many times has induction evolved? Are there plant traits, habitat characteristics, or ecological correlates associated with the evolution of induction? Is the evolution of induced responses associated with changes in the macro-evolutionary rates of diversification (including extinction and speciation)? In addition to these important questions, a phylogenetic approach provides a critical control in any investigation of comparative ecology. Whenever ecologists want to compare species, phylogeny is an important issue because closely related species are not typically considered independent, and thus may confound comparative analyses (Felsenstein, 1985). Comparing the biology of species in a phylogenetic context allows for an assessment of the relative importance of evolutionary history and ecological selection in generating phenotypic patterns across species. If the same traits (say, induced plant responses) have arisen several times during the diversification of a group of taxa, this suggests a convergent solution to ecological selection. If induction has arisen only once, even if widespread among related species, the patterns of phenotypic evolution are more likely to have been constrained by evolutionary history (Webb et al., 2002).

Theory loosely predicts that: (1) constitutive defense is ancestral, (2) induction evolved as a cost saving strategy, (3) induction was favored by environments with variable herbivores, and (4) costs of plasticity per se are small, given its evolution over constitutive defense (Adler & Karban, 1994; Karban & Baldwin, 1997; Thaler & Karban, 1997; Karban & Nagasaka, 2004). Presumably, high costs of constitutive defenses were avoided when plasticity in defense



**Figure 4** The effect of a sequential set of challenges for *Chenopodium album* (light environment followed by herbivory) on induced resistance to herbivory. The stem-elongation response to shade attenuated induced resistance to herbivores in terms of: (A) herbivore (*Spodoptera exigua*) mortality, but not in terms of (B) growth of the survivors (adapted from Kurashige & Agrawal, 2005). Different letters represent significant differences at P < 0.05 using ANOVA contrasts. Although shade did not affect proportionally induced resistance in terms of herbivore growth (B), it still increased plant quality for herbivores, making the resistance in shaded plants with herbivory not different from overall controls (undamaged plants in full sunlight).

was favored by selection. In this case, the costs of plasticity per se (i.e., the cost of the ability to be plastic) are assumed to be low because plasticity is assumed to be favored over constitutive defense (i.e., costs of plasticity are smaller than costs of constitutive defense) (Cipollini, 1998; Agrawal et al., 2002). An alternative scenario proposed by Karban & Baldwin (1997) was that the ancestral state was undefended, rather than constitutively defended. Here, costs of plasticity are predicted to be higher, because plastic defense was favored as an initial defensive strategy, not as a less costly alternative to constitutive defense.

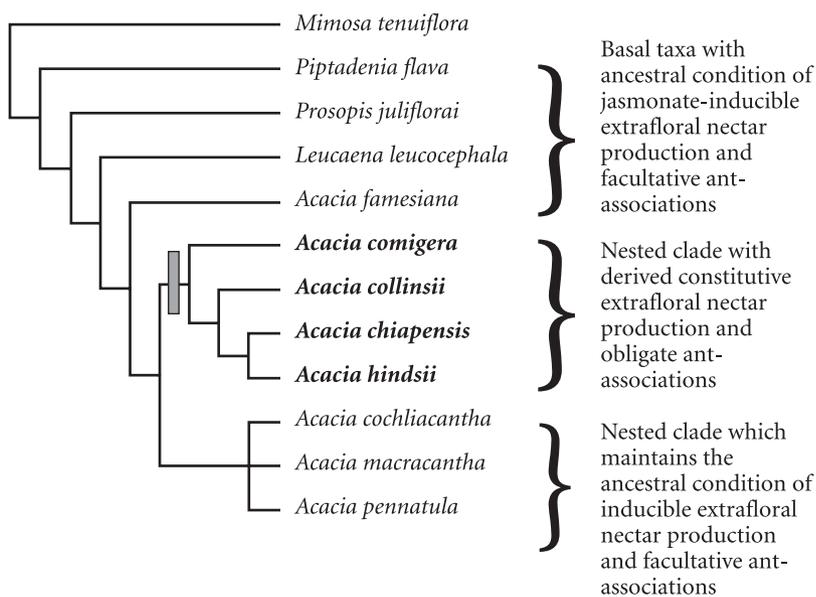
Only two studies to date have attempted to examine the phylogenetics of induced responses. Thaler & Karban (1997) examined the constitutive and induced resistance of 21 *Gossypium* species to herbivory by spider mites. *Gossypium* spp. are distributed world-wide, and are of economic importance, as several species are cultivated for cotton lint. Although not entirely clear, constitutive resistance appeared to be the ancestral state. No ecological or biogeographical correlates of induction were detected, and induction apparently evolved independently several times.

In a recent study, Heil et al. (2001, 2004) examined the macro-evolution of constitutive and induced extrafloral nectar production (an indirect defense) in Central American *Acacia* species (Figure 5). Although historically it was thought that extrafloral nectar production is a constitutively expressed trait, recent work has demonstrated its inducibility in many taxa (Agrawal & Rutter, 1998; Heil et al., 2001, 2004). *Acacia* species having facultative associations with defensive ants show inducible nectar production following herbivory and the application of

jasmonates. However, plant species with obligate associations with ants show constitutive expression of high levels of nectar secretion (and are not responsive to jasmonates). Heil et al.'s phylogenetic analysis revealed that induction (and facultative ant associations) were ancestral, and that constitutive expression was derived, probably in a single origin. This result, although opposite to the original predictions about induction being derived, is consistent with other predictions (Agrawal & Rutter, 1998). Most critically, where ant defense is most reliable (i.e., the environment is least variable) constitutive strategies prevail. Although it is clear that the derived state is constitutive, and this evolved from inducible ancestors, it is unclear whether the true ancestral state, further back in evolutionary time, was constitutive or inducible.

#### Holism or mechanism?

In this paper three areas of research that promise to advance our understanding of induced plant responses to herbivory are outlined. The questions and hypotheses put forward can be addressed using holistic and mechanistic approaches. Holistic approaches are usually those involving experiments in complex field environments, considering multi-species interactions, and patterns across ecological and evolutionary time. Mechanistic approaches may involve experiments in highly controlled environments, the use of genetically modified organisms, and bioassays of behavior and growth. An important caveat to this apparent delineation is that each approach is weak without a connection to the other. For example, an examination of insect abundance patterns in the field provides little means for effectively



**Figure 5** A schematic cladogram depicting the evolutionary relationships between Central American *Acacia* species, modified from Heil et al. (2001, 2004). The rectangle represents the evolutionary transition from inducible to constitutive traits. Such phylogenetic analyses reveal the importance of evolutionary history and ecological associations in driving the phenotypes of species.

manipulating plant–herbivore interactions in agricultural systems. Conversely, a detailed understanding of the hormonal interactions between two organisms that never co-occur in the field may provide a deceptive picture of nature. Kessler et al. (2004) provided a fine example of the fruitful partnership between the mechanistic and holistic approaches. The discovery that jasmonic acid co-regulates direct and indirect defenses, from defensive proteins and glucosinolates to volatile terpenes and extrafloral nectar, is a triumph of the mechanistic approach. It is quite clear that molecular biology will be able to make increasing contributions to the advancement of our field. As a brief cautionary note, however, it is important to recognize that an increasingly mechanistic approach, focusing on a few model organisms in the absence of ecological interactions, is not likely to lead to generality and predictability. After all, the diversity of species generated by adaptive radiation over evolutionary time and co-existing in ecological time, is maintained by ecological differences. It is these differences with which biologists must grapple, i.e., finding general principles that yield a predictive science, while recognizing the complexity of species diversity.

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