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# Plant-mediated interactions in herbivorous insects: mechanisms, symmetry, and challenging the paradigms of competition past

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## Introduction

Interspecific interactions between insect herbivores can be either negative (competitive) or positive (facilitative) (Damman 1993, Denno *et al.* 1995). In the context of traditional community ecology, however, negative interactions have received the most attention (e.g., Lawton and Strong 1981, Schoener 1982, Strong *et al.* 1984, Denno *et al.* 1995) until quite recently (e.g., Lill and Marquis 2003, Nakamura *et al.* 2003). Nonetheless, the importance of interspecific competition as a factor structuring communities of insect herbivores has experienced a controversial history to say the least (Strong *et al.* 1984, Damman 1993, Denno *et al.* 1995). During the 1960s and 1970s, competition was revered as a central organizing force structuring communities of phytophagous insects (Denno *et al.* 1995). During these decades, field investigations into interspecific competition were heavily dominated by observational studies of resource partitioning as evidence for reduced competition and thus coexistence (e.g., McClure and Price 1976, Rathcke 1976, Waloff 1979). Notably, experimental field studies documenting the occurrence of interspecific competition between insect herbivores were scarce (but see McClure and Price 1975).

In the 1980s, the role of competition in structuring phytophagous insect communities was challenged severely, and within a few years it fell from a position of prominence to the status of a weak and infrequent process (Lawton

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and Strong 1981, Lawton 1982, Lawton and Hassell 1984, Strong *et al.* 1984). Two lines of criticism led to its downfall. The first had its roots in a theoretical paper by Hairston *et al.* (1960) who argued that because defoliation was infrequent, food must be rarely limiting for herbivores, and that natural enemies were largely responsible for maintaining herbivore densities below competitive levels. A second avenue of criticism that led to the demise of competition stemmed from the analysis of phytophagous insect distributions and co-occurrences. Cases of positive interspecific association and the presence of vacant niches led many ecologists to question the importance of competition (Strong 1981, Lawton 1982). During these times, it is noteworthy that the studies responsible for both the veneration and demise of interspecific competition were overwhelmingly observational, and nonexperimental (reviewed in Denno *et al.* 1995). By the mid 1980s the scientific community had responded to a plea for a more experimental approach, and many more manipulative investigations of competition between insect herbivores began to appear in the literature (e.g., McClure 1980, 1989, 1990, Kareiva 1982, Stiling and Strong 1984, Karban 1986, 1989, Crawley and Pattasudhi 1988, Denno and Roderick 1992). Along with such studies came the rejuvenated perception that herbivorous insects frequently compete and subsequent reviews reflect this reversal in thinking (Faeth 1987, Damman 1993).

In the mid 1990s, Denno *et al.* (1995) published a review based on experimental studies of interspecific competitive interactions between insect herbivores. This review examined 193 pair-wise interactions, and found strong evidence for competitive effects on performance and fitness. There was clear evidence for competitive effects in 93% of the studies involving sap-feeding herbivores (e.g., aphids, scale insects, planthoppers, and leafhoppers) and in 78% of the studies involving chewing herbivores (e.g., grasshoppers, caterpillars, beetles, and sawflies). Most surprising was the finding that over half of the cases of interspecific competition between mandibulate herbivores (52%) were examples of plant-mediated competition in which previous feeding by one species induced either nutritional or allelochemical changes in the plant that adversely affected the performance of another species feeding later in the season. Thus, one of the major outcomes of this review (Denno *et al.* 1995) and other contemporaneous assessments (Damman 1993) was that competitive effects were often plant-mediated via induced resistance and that failure to investigate such a mechanism may have vastly underestimated the possible importance of competition as a structuring force in communities of insect herbivores.

In the 1990s and thereafter, many more studies began to appear documenting that plant-mediated interactions were widespread and that insect herbivores frequently compete via induced resistance (e.g., Moran and Whitham 1990, Masters and Brown 1992, Rausher *et al.* 1993, Inbar *et al.* 1995, Salt *et al.* 1996,

Wold and Marquis 1997, Agrawal 1998, Heard and Buchanan 1998, Denno *et al.* 2000, Redman and Scriber 2000, Nykänen and Koricheva 2004, Van Zandt and Agrawal 2004b). Moreover, books on induced resistance also appeared during this time further highlighting that plants mediate interactions among insect herbivores (Tallamy and Raupp 1991, Karban and Baldwin 1997, Agrawal *et al.* 1999c). Thus, competition has re-entered the mix as a potentially important force influencing the structure of insect communities on plants.

Not only did reviews reveal that plants often mediate negative interactions between insect herbivores (competition via induced resistance or altered risk of natural enemy attack), but they also documented that plants can promote positive interactions (induced susceptibility) via altered plant nutrition (feeding facilitation), allelochemistry (leaf volatiles), architecture (leaf flush), or protective housing (leaf shelters) (Damman 1993, Denno *et al.* 1995, Nykänen and Koricheva 2004). Thus, in the context of a rapidly growing literature that documents the prevalence of plant-mediated interactions between insect herbivores, our objectives for this chapter are to: (1) identify the mechanisms underlying plant-mediated interactions between insect herbivores including induced resistance, induced susceptibility, and induced leaf volatiles and extrafloral nectar that alter risk of enemy attack, (2) outline herbivore traits (e.g., early colonization, tolerance of induced resistance, aggregation, dispersal, and feeding guild) that affect the symmetry of plant-mediated interactions between insect herbivores (e.g., competitive superiority), (3) explore the constraints that superiority in plant-mediated interactions (e.g., competitive dominance) may place on other life-history traits such as dispersal that ultimately affect landscape-scale population dynamics, and (4) discuss how plant-mediated interactions among insect herbivores increase the chances for interspecific interaction, yet challenge the paradigms of traditional competition theory. Last, we argue for a more all-encompassing approach to future studies that extends beyond a focus on pair-wise interactions and examines plant-mediated effects on multiple species at multiple spatial and temporal scales. Overall, we suggest that by considering plant-mediated interactions among insect herbivores, forces such as competition and facilitation will play an increasingly important role in structuring communities of phytophagous insects, albeit in nontraditional ways.

### **Mechanisms underlying plant-mediated interactions between insect herbivores**

The causal mechanisms of plant-mediated interaction between insect herbivores are diverse and include induced plant allelochemistry, nutrition, morphology, and altered natural-enemy attack. In this section we first consider mechanisms underlying negative interspecific interactions (competition via

induced resistance) and then we address those mechanisms promoting positive interactions (facilitation via induced susceptibility). In several cases of interspecific interaction, the precise mechanism of plant mediation is indeed known. However, much of the mechanistic work on induced resistance, especially earlier investigations, focused on intraspecific effects whereby previous feeding by one species had later consequences for conspecifics. On occasion, we also call on such intraspecific studies to provide a mechanistic understanding of induced effects, but emphasize that such mechanisms likely underlie interspecific effects as well.

*Induced resistance and plant-mediated competition between insect herbivores*

Induced allelochemistry

When herbivorous insects feed on plants, numerous allelochemicals can be induced with putative adverse effects on the performance or fitness of other herbivores that feed either contemporaneously or at a later time (Karban and Baldwin 1997, Constabel 1999). Allelochemicals known to be induced by herbivore feeding or mechanical wounding include defensive proteins (e.g., proteinase inhibitors, oxidative enzymes, cell-wall proteins, phenylpropanoid enzymes, lectins, and carbohydrate-binding enzymes), phenolics (phenolic acids, phenolic glycosides, furanocoumarins, coumarins, condensed and hydrolyzable tannins, lignin, and total phenolics), terpenoids (monoterpenes, diterpene aldehydes, phytoecdysteroids, and cucurbitacins), alkaloids (nicotine, quinolizidine, tropane, and hydroxamic acids such as DIMBOA), and indole glucosinolates (Karban and Baldwin 1997, Constabel 1999).

Induction of phytochemicals by herbivory can take place in two ways, either by the release of “preformed chemicals” or by “activated synthesis,” both of which can have adverse consequences for other herbivores (Karban and Baldwin 1997). Unlike most activated phytochemicals, the induction of “preformed defenses” does not result exclusively from changes in synthesis or degradation (Karban and Baldwin 1997). Rather, the release of preformed chemicals results from the disruption of tissues where such chemicals are compartmentalized or from the mixing of locally separated substrates and enzymes during tissue damage. Examples of preformed/compartmentalized allelochemicals include the monoterpenes stored in the resin ducts of conifers (Raffa 1991), the cardenolide-containing latex borne in the canal systems of a diversity of plant taxa (Dussourd and Denno 1991), and the furanocoumarins housed in oil tubes of wild parsnip plants (Berenbaum and Zangerl 1999, Zangerl 1999). When herbivores puncture such ducts, canals, or oil tubes during feeding, the compartmentalized allelochemicals are released, often with adverse effects. Examples of preformed allelochemicals that are induced by the mixing of separated substrates when plant tissue is damaged include the production of hydrogen cyanide in cyanogenic

plants (Conn 1979), the hydrolysis of glucosinolates to form thiocyanates in crucifers (Chew 1988), and the conversion of phenolic glycosides to more active feeding deterrents such as salicin in poplars (Clausen *et al.* 1989).

In the “activated” class of allelochemicals are proteinase inhibitors and many alkaloids that are synthesized following herbivory and result in an actual increase in the allelochemical pool (Karban and Baldwin 1997, Constabel 1999). The induced increase in allelochemistry can occur over a range of time intervals from a few hours or days (rapid induced response) to the next season (delayed induced response) (Karban and Baldwin 1997). Regardless, the distinction between “preformed” and “activated” induced responses is best viewed as a continuum (Karban and Baldwin 1997), because some allelochemicals have elements of both. For example, while furanocoumarins, monoterpenes, and glucosinolates are expressed constitutively (i.e., are preformed), they can be also induced several-fold by herbivory, suggesting induced synthesis (Lewinsohn *et al.* 1991, Agrawal *et al.* 1999b, Zangerl 1999). Rapid induced allelochemicals and the quick release of preformed allelochemicals are more likely to affect herbivores that feed contemporaneously on plants, whereas delayed plant responses offer the possibility of mediating interactions between herbivores that are temporally displaced.

Although there are numerous studies documenting the induction of specific allelochemicals by insect herbivores (reviewed in Karban and Baldwin 1997, Constabel 1999) and many others demonstrating plant-mediated competition between different herbivore species (Denno *et al.* 1995, I. Kaplan and R.F. Denno unpublished data), there are few reports linking the induction of a specific allelochemical by one species with a measured negative consequence for another herbivore species. Thus, the allelochemical mechanism underlying plant-mediated interspecific competition remains largely unknown for most interactions. Moreover, even when there is an association between an induced chemical and altered herbivore performance, the causal link is often ambiguous because only selected allelochemicals were measured (see Constabel 1999). Nonetheless, there are a few cases identifying the probable allelochemical involved in induced resistance.

Several examples involve the induction of defensive proteins. For instance, previous feeding by the fruitworm *Helicoverpa zea* induces increased levels of proteinase inhibitors and polyphenol oxidases in tomato *Lycopersicon esculentum*, which have adverse effects on the growth of a leaf-chewing lepidopteran and the density of aphids and a dipterous leaf miner (Stout and Duffey 1996, Stout *et al.* 1998). Similarly, feeding by the whitefly *Bemisia argentifolii* induces increases in defensive proteins in cabbage *Brassica oleracea* with negative consequences for the growth and survival of the cabbage looper *Trichoplusia ni*, and in *L. esculentum* with

negative effects on the oviposition, density, and survival of the leaf miner *Liriomyza trifolii* (Inbar *et al.* 1999a, 1999b, Mayer *et al.* 2002). Also, early season feeding by lepidopterans on oak induces increases in protein-binding capacity with negative density effects on a guild of lepidopteran species that feed in mid-to-late season (Wold and Marquis 1997).

There are other cases of induced resistance that implicate terpenoids, glucosinolates, and latex. For instance, root-feeding by the wireworm *Agriotes lineatus* induces increases in aboveground terpenoids in cotton *Gossypium herbaceum* which adversely affect the growth of the leaf-chewing lepidopteran *Spodoptera exigua* (Bezemer *et al.* 2003). Also, glucosinolates are induced by larvae of the imported cabbage worm *Pieris rapae* feeding on wild radish *Raphanus raphanistrum* that negatively affect the weight, colonization, and density of lepidopterans, aphids, and a dipterous leaf miner (Agrawal 1998, 1999, 2000). Likewise, feeding by monarch butterfly larvae *Danaus plexippus* induces latex production in milkweed *Asclepias syriaca* with adverse effects on the larval mass of the chrysomelid beetle *Labidomera clivicollis* and colonization by the aphid *Aphis nerii* (Van Zandt and Agrawal 2004b). Regardless of the specific mechanism, however, an important generality that emerges from this small collection of studies is that induced resistance conferred by allelochemistry can result in substantial competitive effects between insect herbivores that are taxonomically discrepant, temporally displaced, and spatially separated on the same plant.

#### Induced morphology

Early colonizing herbivores can induce changes in gross plant morphology (e.g., leaf flush, bud burst, branching architecture, floral traits, and leaf shelters) as well as small-scale surface structure (e.g., trichomes) that can have significant effects on the performance, survival, and density of other herbivores that feed later in the colonization sequence (Karban and Baldwin 1997). The induced morphological change can have either negative or positive effects (see below) on subsequent feeding herbivores. Two induced morphological changes that are known to adversely affect herbivores are changes in leaf trichome density (Agrawal 1998, 1999, Traw and Dawson 2002) and altered flower size and number (Strauss 1997). Because induced changes in plant morphology are expressed well after the initial bout of herbivory, their effects are likely to be felt by other herbivores that are temporally displaced from the inducing species, and significantly so in some cases. For example, when attacked by the chrysomelid beetle *Agelastica alni*, it is the reflushed leaves of grey alder *Alnus incana* that have a higher density of nonglandular trichomes (Baur *et al.* 1991). Also, the resprouted leaves of stinging nettle *Urtica dioica* carried a higher density of trichomes following damage than did noninduced leaves (Pullin and Gilbert

1989). Similarly, induced changes in floral and seed morphology often occur well after the initial bout of herbivory (Hendrix 1988, Strauss *et al.* 1996, Thalmann *et al.* 2003).

Notably, feeding by larvae of *Pieris rapae* induced increased trichome density in black mustard *Brassica nigra*, which had very adverse effects on the growth of conspecifics that fed several weeks later (Traw and Dawson 2002). Evidence from a similar study system links feeding-induced increases in leaf trichome density with the reduced performance of an assemblage of other herbivore species. Specifically, larvae of *P. rapae* induced trichomes in *R. raphanistrum* that had negative consequences for the growth and density of leaf-chewing lepidopterans, aphids, and dipterous leaf miners (Agrawal 1998, 1999, 2000).

Folivory-induced changes in floral traits are also likely to mediate interspecific interactions between insect herbivores with negative consequences for later-feeding species. For example, foliar herbivory can result in reduced flower size and number (Hendrix and Trapp 1989, Strauss *et al.* 1996, Lehtilä and Strauss 1997), and in pollen and nectar production (Strauss *et al.* 1996, Krupnick *et al.* 1999). Such induced changes have been viewed in the context of herbivore-pollinator interactions (Strauss 1997, Ohgushi 2005). However, one could argue that many pollinators (e.g., syrphid flies and bees) are indeed herbivores. The traditional focus has been on how folivory-induced changes in floral traits subsequently affect pollinator services to the plant (Strauss *et al.* 1996, Lehtilä and Strauss 1997, Krupnick *et al.* 1999). From the pollinator's perspective, it is less clear how herbivory-induced changes in floral morphology feed back to alter foraging strategies and ultimately pollinator fitness. Thus, the extent to which such interactions might represent plant-mediated competition remains plausible but open.

Most assuredly though, foliar herbivory can affect other herbivores that require a particular floral morphology for concealment and/or development. For instance, foliar herbivory can drastically reduce seed size (Hendrix 1988, Thalmann *et al.* 2003), and reduced seed size can have dire consequences for the growth and survival of seed-infesting herbivores (Szentesi and Jermy 1995, Moegenburg 1996, Willott *et al.* 2000). However, only one study involving weevils on musk thistle *Carduus nutans* provides a mechanistic link between folivore-induced changes in floral or seed morphology and their effects on an inflorescence/seed-feeder (Milbrath and Nechols 2004). Early-season feeding by the folivorous weevil *Trichosirocalus horridus* induced shorter flower stems, significantly fewer flower heads, and delayed flowering by one week, all of which had adverse effects (colonization, oviposition, and survival) on the seed-head-feeding weevil *Rhinocyllus conicus*.

## Altered nutrition and source–sink dynamics

When phloem-tapping herbivores such as aphids feed, they alter the source–sink dynamics of phloem transport (Way and Cammal 1970, Larson and Whitham 1991). Using  $^{14}\text{CO}_2$ -labeling experiments, it has been shown that aphids act as nutrient sinks by diverting assimilates from neighboring leaves and drawing them toward feeding sites where aphid performance is dramatically enhanced (Way and Cammal 1970, Larson and Whitham 1991, Inbar *et al.* 1995). The strength of the sink, and thus aphid performance, is influenced by the position of the feeding site such that aphids occupying the basal portion of the leaf (on the midrib) divert more assimilates than more distally located aphids (Larson and Whitham 1991, Inbar *et al.* 1995).

The manipulation of the phloem transport system provides the opportunity for plant-mediated exploitative competition between two phloem feeders because of where they feed on the plant with respect to one another. For example, the phloem-feeding aphid *Geoica* sp. forms galls at the base of wild pistachio *Pistacia palaestina* leaves where it diverts assimilates from the distal margins of leaves where another gall-forming aphid *Forda formicaria* develops (Inbar *et al.* 1995). The diversion of assimilates and the creation of basal nutrient sinks benefits *Geoica* but results in 84% mortality in distal *Forda* galls (Inbar *et al.* 1995).

Other phloem-feeding herbivores also compete via induced changes in plant nutrition, but the mechanism is quite different. For instance, the planthoppers *Prokelisia dolus* and *P. marginata* co-occur on intertidal marshes along the Atlantic coast of North America where they feed exclusively on the cordgrass *Spartina alterniflora* (Denno and Roderick 1992, Denno *et al.* 2000). Densities can be high and they often share the same plant where they feed together on the upper surfaces of the leaf blades (Denno *et al.* 2000). Previous feeding by *P. dolus* reduces the concentration of essential amino acids in cordgrass (Olmstead *et al.* 1997), which has very adverse effects on the performance and survival of *P. marginata* (Denno *et al.* 2000). Reciprocal effects are far less severe due to the ability of *P. dolus* to better tolerate low plant nitrogen via feeding compensation (Denno *et al.* 2000).

Induced reductions in plant nitrogen are also implicated in the interspecific triggering of emigrants (macropterous forms or alates) in both planthoppers (Denno and Roderick 1992, Matsumura and Suzuki 2003) and aphids (Itô 1960, Lamb and MacKay 1987). As populations grow, both crowding and induced changes in plant nutrition combine to stimulate nymphs to develop into dispersing morphs (Denno and Roderick 1992). Such interactions are competitive because one species stimulates the production of migrants in another, which promotes emigration from a shared plant resource (Denno and Roderick 1992).

Leaf-chewing herbivores also compete via induced changes in plant nutrition. For example, early-season feeding by lepidopterans induces reductions in foliar nitrogen that negatively affect the survival and performance of the late-season leaf miners and other free-living leaf-chewers on *Quercus robur* (West 1985, Hunter 1992). Likewise, previous feeding by the gypsy moth *Lymantria dispar* decreases plant nitrogen that has negative consequences for the growth and survival of the tiger swallowtail *Papilio canadensis* on quaking aspen *Populus tremuloides* (Redman and Scriber 2000). Like induced changes in plant allelochemistry and morphology, induced nutrition provides the opportunity for spatially and temporally displaced herbivores to compete.

Although feeding-induced changes in plant nutrition and source–sink dynamics can promote interactions between herbivore species, they should be viewed as “induced responses” (*sensu* Karban and Baldwin 1997) because the nutrient sinks created by aphids in fact compete with plants for assimilates by diverting nutrients away from developing fruits (Larson and Whitham 1991). Thus, from the plant’s perspective, whereas some induced allelochemicals and trichomes may benefit the plant and act as “induced defenses” (Agrawal 1998, 1999), known cases of induced nutrition do not clearly benefit the plant (Weis *et al.* 1988, Larson and Whitham 1991).

#### Altered risk of enemy attack

Feeding-induced changes in plant volatiles, extrafloral nectar, and morphology can also affect herbivore–herbivore interactions via altered risk of attack from natural enemies (Paré *et al.* 1999, Thaler 1999, Ness 2003). When herbivores feed on plants, volatiles such as terpenoids, green-leaf lipoxigenase products, and indole are either released from storage structures or are synthesized (Paré *et al.* 1999). Induced volatiles are then used by predators and parasitoids as cues to locate their habitats and hosts (Vinson 1998, Paré *et al.* 1999, Thaler 2002a). As a consequence, parasitism rates of herbivores on induced plants can as much as double (Thaler 1999). In some cases of induction, plants produce a herbivore-specific blend of volatiles that allow specialist parasitoids to distinguish between their host and close non-host relatives (De Moraes *et al.* 1998). For such cases involving specialists, parasitoids attack only the inducing herbivore and interspecific effects on other herbivore species are precluded. However, in other instances, damage by one herbivore species attracts generalist parasitoids (Thaler 2002a) or predators (Turlings *et al.* 1991, Paré *et al.* 1999) that have the potential to attack other co-occurring herbivore species. For example, damage of aspen leaves by gypsy moth larvae attracts generalist parasitoids that then parasitize larvae of swallowtail larvae as well as other caterpillar species (Redman and Scriber 2000). Apparently, volatiles emitted by wounded trees

attract a wide range of parasitoid species with broad host preferences (Schultz 1999, Redman and Scriber 2000). In another example, prior feeding by the mirid bug *Tupiocoris notatus* causes native tobacco plants to release volatile organic compounds that attract the generalist predator *Geocoris pallens*, which then selectively attacks caterpillars of the less mobile and co-occurring herbivore *Manduca quinquemaculata* (Kessler and Baldwin 2004).

Herbivory can also induce the flow of extrafloral nectar that subsequently attracts generalist natural enemies with negative effects on herbivores. For example, feeding by catalpa sphinx moth larvae *Ceratomia catalpae* induces two-fold increases in the volume of extrafloral nectar, which then results in a ten-fold increase in the density of attending ants *Forelius pruinosus* with subsequent reductions in the density of sphinx moth larvae (Ness 2003). Because such ants are generalist predators, the possibility remains that the density of other herbivore species was similarly reduced, but this interaction was not examined.

By altering plant morphology via building leaf shelters, herbivores can also enhance the density of natural enemies, an effect that cascades to adversely affect other herbivore species. For instance, several shelter-building caterpillars on willow *Salix miyabeana* promote the occurrence of specialist aphids *Chaitophorus saliniger* that feed preferentially within leaf shelters (induced susceptibility); the aphids in turn attract predaceous ants that then reduce the survival of the co-occurring leaf beetle larvae *Plagioderia versicolora* by 60% (indirect induced resistance) (Nakamura and Ohgushi 2003, Ohgushi 2005).

One of the frequent outcomes of induced resistance for insect herbivores is delayed development (Inbar *et al.* 1999b, Denno *et al.* 2000, Wise and Weinberg 2002), a result that may prolong exposure to natural enemies with increased risk of predation (Benrey and Denno 1997). Although the slow growth–high mortality hypothesis has been explored in the context of single predator–prey interactions (see review by Williams 1999), it remains largely untested in an interspecific framework whereby one herbivore induces a plant change that results in delayed growth and increased risk of attack in another herbivore species. Two studies, however, provide support (Kessler and Baldwin 2004, I. Kaplan *et al.* unpublished data). First, previous feeding by the mirid bug *Tupiocoris notatus* induces the accumulation of proteinase inhibitors in wild tobacco that are correlated with developmental delays in larvae of *Manduca quinquemaculata* making them more susceptible to attack by the generalist predator *Geocoris pallens* (Kessler and Baldwin 2004). In this system, the risk of predation in *Manduca* is further exacerbated because mirids also induce the production of volatile organic compounds that attract *Geocoris* to plants also occupied by *Manduca*. In a second study, previous feeding by potato leafhoppers *Empoasca fabae* induces chemical and morphological changes in potato plants that result in a significant developmental delay

for later-feeding larvae of Colorado potato beetles *Leptinotarsa decemlineata* (I. Kaplan *et al.* unpublished data). Moreover, slow-developing larvae on induced plants incur much higher mortality from the predaceous stinkbug *Podisus maculiventris* than larvae feeding on undamaged plants. Thus, developmental delays imposed on one herbivore by another via induced resistance can increase significantly risk of predation.

To assess the overall interspecific effect of induced resistance on a herbivore, one must know both the magnitude and direction of the direct (allelochemistry, nutrition, and morphology) and indirect effects (natural enemies). For example, in the potato system, feeding by leafhoppers has a negative effect on the growth and survival of potato beetles, an effect that is further exacerbated in the presence of *Podisus* predators. By contrast, if induced responses in plants affect herbivores adversely but also reduce the quality of herbivores for natural enemies (e.g., result in small host size), then the direct negative effect may be offset in part by a relaxed indirect effect from higher trophic levels (Thaler 2002b). Thus, to understand fully the consequences of interspecific herbivore interactions mediated via induced resistance, interactions among all the major players in the system must be taken into account. Nonetheless, there are clear cases where induced responses in plants enhance enemy effects on other herbivores in the system resulting in instances of diffuse competition (Thaler 1999, Redman and Scriber 2000, Kessler and Baldwin 2004, I. Kaplan *et al.* unpublished data).

*Induced susceptibility and plant-mediated facilitation between insect herbivores*

Induced allelochemistry

When previous feeding by one herbivore induces allelochemicals that are used by another to locate their host plants, induced susceptibility can occur. Induced susceptibility is evident when larvae of *Pieris rapae* feed on wild radish and induce glucosinolates and perhaps other volatile compounds that are used by the specialist flea beetle *Phyllotreta* sp. to locate its host, a response that results in increased beetle colonization, oviposition, and plant damage (Agrawal and Sherriffs 2001).

Induced susceptibility can also arise when one herbivore deactivates the preformed defenses of a plant thus providing another herbivore the opportunity to feed. For instance, feeding by jack pine budworms *Choristoneura pinus* severs resin canals thereby reducing resin flow and the concentration of monoterpenes (Wallin and Raffa 2001). Deactivation of the resin defense system by budworms promotes colonization by bark beetles *Ips grandicollis* and pine sawyers *Monochamus carolinensis* resulting in positive density associations among the three herbivores. A similar situation occurs on plants bearing latex canals. The vein-cutting and

trenching behaviors exhibited by a wide variety of insect herbivores depressurizes the latex-bearing canal system (Dussourd and Eisner 1987, Dussourd and Denno 1994). By feeding distal to the cuts, not only does the inducing herbivore benefit, but so can other species that feed on the undefended leaf tissue (Dussourd and Denno 1991, 1994). For example, armyworm larvae *Spodoptera ornithogalli* grow much more rapidly on the leaves of the latex bearing plant *Lactuca* following trenching by looper larvae *Trichoplusia ni* (Dussourd and Denno 1994). Given the prevalence of herbivores with behaviors that deactivate canal-borne defenses, and the abundance of plants with preformed defenses (Dussourd and Denno 1991, 1994), future research will undoubtedly discover more species of herbivores that take advantage of deactivated defenses and feed in association with trenching and vein-cutting species.

#### Induced morphology

Herbivores can also induce changes in plant morphology, such as increased branching and the re-flush of leaves, or alter architecture by building leaf shelters and leaf rolls that favor other herbivore species. Notably, induced changes in plant morphology usually occur well after the initial bout of herbivory or shelter construction providing the opportunity for temporally displaced herbivores to interact (Ohgushi 2005).

Regarding induced changes in plant morphology, damage to the apical meristem of goldenrod *Solidago altissima* by a guild of early-season gall-formers causes more branching that subsequently promotes increased colonization and densities of several aphids and spittlebugs (Pilson 1992). Similarly, there are studies showing that early-season herbivory by caterpillars on oaks and the gall-makers on willow stimulates a secondary leaf flush on which aphids, leaf beetles, and leaf rollers can flourish (Hunter 1992, Nakamura *et al.* 2003). In these examples, the mechanisms underlying facilitation extend beyond simply altered plant architecture. For instance, the regrowth leaves on which sap-feeders thrive are higher in nitrogen (Nakamura *et al.* 2003). Moreover, re-flushed leaves are tender and are easier for chewing herbivores to consume or construct leaf shelters with (Hunter 1992, Nakamura *et al.* 2003).

By constructing leaf shelters (rolls, folds, and ties) or forming leaf galls, herbivores create new habitats for other herbivores that often generate positive associations (Cappuccino 1993, Damman 1993, Martinsen *et al.* 2000, Fukui 2001, Lill and Marquis 2003, Ohgushi 2005). Positive interactions result because the shelters built by these so-called “ecosystem engineers” provide other colonizing herbivores with enemy-free space (Cappuccino 1993, Damman 1993), improved microclimate (Larsson *et al.* 1997), or improved food quality (Fukui 2001). Importantly, primary shelter-makers spend significant time and energy constructing

their leaf structures, expenditures that later shelter-users do not incur (Fukui 2001). The experimental addition of artificial leaf shelters designed to mimic the structures of early-season leaf-tying and leaf-rolling lepidopterans results in population increases in other shelter-building caterpillars (Lill and Marquis 2003) and non-shelter-building herbivores such as aphids, lepidopterans, sawflies, and beetles (Cappuccino 1993, Nakamura and Ohgushi 2003). In one instance, recruitment of previously occupied artificial ties by secondary leaf tyers is double that compared to never-occupied ties implicating feeding-related volatiles (Lill and Marquis 2003). Conversely, the removal of natural leaf shelters results in remarkable reductions in the densities of other insect herbivores (Cappuccino and Martin 1994, Martinsen *et al.* 2000, Lill and Marquis 2003). It is important to realize that the initiating shelter-builder can induce positive interactions with other shelter colonists (aphids), but negative associations with folivores (leaf beetles) that are adversely affected by ants that tend the aphids (Nakamura and Ohgushi 2003).

#### Altered nutrition and source–sink dynamics

When herbivores feed, particularly phloem feeders, they can induce nutrient sinks by diverting nutrients from surrounding leaves to their feeding site (Larson and Whitham 1991, Inbar *et al.* 1995). If other herbivores colonize and exploit surrounding sites, they are deprived of nutrients and their performance is often adversely affected (Inbar *et al.* 1995). On the other hand, if other herbivores co-occur locally along with the inducers at the site of the nutrient sink, they can benefit tremendously from the enhanced levels of assimilates. For instance, numerous aphid species either selectively colonize the specific feeding sites occupied by other aphid species or shift their feeding site to co-occur with another aphid species (Shearer 1976, Salyk and Sullivan 1982). The result is a pattern of positive interspecific association either within a plant or across plants in the field (Kidd *et al.* 1985, Formusoh *et al.* 1992, Montandon *et al.* 1993, Waltz and Whitham 1997). Similarly, leafhoppers *Idiocerus* sp. occur far more abundantly on poplar branches with *Pemphigus* gall aphids compared to branches where gall aphids are excluded, and leafhoppers are frequently observed feeding directly on galls (Waltz and Whitham 1997, G. Wimp personal communication). By occurring in close proximity to an induced nutrient sink, sap-feeders experience enhanced growth, body size, and survival (Forrest 1971, Shearer 1976, Kidd *et al.* 1985, Formusoh *et al.* 1992, Montandon *et al.* 1993).

Feeding-induced changes in source–sink dynamics can also benefit spatially separated herbivores on the same plant. Root-feeding coleopterans, for example, induce increases in aboveground leaf nitrogen that promotes increased growth, fecundity, and density of foliar-feeding aphids (Gange and Brown 1989, Masters

and Brown 1992) and inflorescence-feeding tephritid flies (Masters *et al.* 2001). Notably, most cases of plant-mediated facilitation via altered nutritional dynamics involve phloem-feeders, either as the inducing species or even more frequently as the beneficiary (Denno *et al.* 1995). The sensitivity of phloem-feeders to changes in amino nitrogen (Cook and Denno 1994) undoubtedly contributes to their overrepresentation in cases of plant-mediated facilitation involving altered source-sink dynamics.

#### Altered risk of natural-enemy attack

It is conceivable that one herbivore might induce allelochemicals that are then sequestered by another species for use in defense against natural enemies. This would represent a case of plant-mediated facilitation involving induced defenses and reduced enemy attack. Although no such cases are explicitly known, the scenario could result between leaf beetle species (*Galerucella lineola* and *Phratora vitellinae*) that co-occur on phenolic-glycoside-containing willows. Leaf beetles induce salicylates (Ruuholta 2001) and salicylates are the precursors of sequestered salicyl aldehyde that is excreted by *Phratora* as an effective defense against some invertebrate predators (Denno *et al.* 1990). Despite the possibility, however, pieces of this hypothetical interspecific scenario have not been linked.

#### Life-history traits promoting competitive superiority in plant-mediated interactions

Plant-mediated interactions between insect herbivores, both negative and positive, are overwhelmingly asymmetric (Denno *et al.* 1995). Competitive interactions, the ones we emphasize here, are particularly one-sided, with one species being clearly the superior competitor. Admittedly, however, many experimental designs examining plant-mediated effects between two herbivore species lack reciprocity (e.g., only examine the effects of spring feeders on late-season herbivores) and it is therefore not possible to separate competition from amensalism. Nonetheless, where designs have tested for reciprocal effects, these have been found even though interactions are strongly asymmetric (Tomlin and Sears 1992, Agrawal 2000). In this section we explore various herbivore traits that contribute to competitive superiority. It goes without saying that the various traits conferring competitive superiority may not be mutually exclusive and in fact may act in concert in some cases. In a forthcoming section, however, we provide evidence that trade-offs exist between certain traits (e.g., feeding compensation and dispersal), and that such trade-offs may constrain competitive superiority.

*Early-season exploitation of plant resources (breaking diapause and colonization)*

Early-season arrival/exploitation often provides a distinct advantage in plant-mediated competitive interactions (Denno *et al.* 1995). This advantage frequently involves the early breaking of diapause coupled with the rapid colonization and monopolization of optimal feeding sites (McClure 1980, Hunter 1992). The early exploitation of plant resources by one herbivore provides the opportunity for induced resistance with imposed effects on other herbivores that feed later (Denno *et al.* 1995, 2000). For instance, early colonization and feeding by nymphs of the scale *Fiorinia externa* significantly reduces the nitrogen available in young hemlock *Tsuga canadensis* foliage, which in turn dramatically decreases the survival of the co-occurring scale *Nuculaspis tsugae* (McClure 1980). Notably, when the advantage of early arrival is experimentally removed, competitive superiority is lost for *F. externa* (McClure 1980). The asymmetry of interspecific interactions between gall aphids (*Geoica* and *Forda*) results because competitive domination in *Geoica* is associated with the spring occupation of optimal leaf sites (leaflet base) where phloem transport is easily manipulated, nutrients are monopolized via nutrient sinks, and the distal galls of *Forda* suffer dramatically (Inbar *et al.* 1995). Although early-season feeding is clearly associated with competitive superiority in many plant-mediated interactions (Denno *et al.* 1995), there are admittedly no studies that have examined possible carry-over effects of late-season inducers on spring feeders. However, feeding by the spring defoliator *Epirrita autumnata* induces higher concentrations of total phenolic compounds in mountain birch (*Betula pubescens*) that carry over to the next season with adverse intraspecific effects on fecundity (Kaitaniemi *et al.* 1998, 1999). Thus, the possibility exists for induced interannual carry-over effects on other herbivore species.

*Tolerance of allelochemicals*

It goes without saying that insect herbivores induce resistance characteristics in plants that feed back to have adverse growth and fitness consequences for the inducing herbivore (Tallamy and Raupp 1991, Karban and Baldwin 1997, Agrawal *et al.* 1999c). In the context of interspecific interactions and competitive superiority, however, the question becomes one of differential tolerance. Specifically, competitive superiority can result because colonizing herbivores not only experience or create optimal feeding sites, but they are also relatively more tolerant of feeding-induced changes in plant physiology compared to later-feeding or co-occurring species. For instance, early-season feeding by the leaf beetle *Phratora vitellinae* induces increases in phenolic glycosides that it tolerates, but which adversely affect generalist herbivores such as *Operophtera brumata* (Ruuhola 2001). Similarly, the asymmetry of plant-mediated competition

between *Prokelisia* planthoppers is due to the ability of *P. dolus* to better tolerate feeding-depleted levels of plant nitrogen compared to its co-occurring congener *P. marginata* (Denno *et al.* 2000).

The mechanisms underlying tolerance, however, are diverse. Tolerance of induced allelochemistry involves detoxification, excretion, sequestration, and/or behavioral avoidance (Karban and Agrawal 2002). For example, furanocoumarins are expressed both constitutively but can be also induced several-fold by herbivory (Berenbaum and Zangerl 1999, Zangerl 1999). Adapted swallowtail larvae *Papilio polyxenes* that encounter furanocoumarins detoxify these compounds using cytochrome P450 monooxygenases (Cohen *et al.* 1992). Prior ingestion of furanocoumarins induces cytochrome P450 activity which then allows detoxification and leaf consumption (Cohen *et al.* 1989). Likewise, larvae of the specialist swallowtail *Battus philenor* induce high levels of aristolochic acid without physiological cost or increased mortality, but the mechanism underlying tolerance is unknown (Fordyce 2001).

Differences in tolerance to feeding-induced reductions in amino nitrogen between *Prokelisia* species result from dissimilarities in cibarial muscle mass (musculature associated with ingestion) that influence feeding compensation (Denno *et al.* 2000). The competitive superiority of *P. dolus* over *P. marginata* results from its greater commitment to cibarial muscle mass and increased ability to compensate for declining plant nitrogen via increased throughput of cell sap. Thus, in mixed-species crowds, not only does *P. dolus* contribute more to declines in plant nitrogen but it also tolerates such declines better and experiences fewer performance and fitness costs (Olmstead *et al.* 1997, Denno *et al.* 2000).

Also, feeding by the whitefly *Bemisia argentifolii* induces defensive proteins (e.g., chitinases, peroxidases, lysozymes) that have little effect on the whitefly but adversely affect the development and survival of the leaf-mining dipteran *Liriomyza trifolii* and the foliar-feeding lepidopteran *Trichoplusia ni* (Inbar *et al.* 1999a, 1999b, Mayer *et al.* 2002). Competitive superiority in this case results because sap-feeders, by virtue of their feeding style, are less exposed to defensive proteins (Raven 1983).

Regardless of the mechanism conferring tolerance, however, competitive superiority in several cases results from the selective ability of the inducing herbivore to tolerate or avoid induced plant responses better than other co-occurring species. Given that both generalists (*Bemisia*) and specialists (*Phra-tora* and *Prokelisia*) can dominate in plant-mediated competitive interactions, it seems unlikely that diet breadth will explain much of the variation underlying competitive superiority. On the other hand, it makes intuitive sense that generalists might be more likely to suffer from induced plant responses than adapted

specialists and thus be relegated to the role of inferior competitor, but this hypothesis remains untested (see Karban and Baldwin 1997).

#### *Aggregation*

Herbivores that aggregate are overrepresented in cases of demonstrated interspecific competition between insect herbivores (Damman 1993, Denno *et al.* 1995). Moreover, aggregation appears to confer competitive dominance in plant-mediated interactions, especially in small sap-feeding herbivores such as aphids and psyllids that compete via the formation of nutrient sinks that divert nutrients from other “competitors” (e.g., Shearer 1976, Salyk and Sullivan 1982, Inbar *et al.* 1995, Heard and Buchanan 1998). The ability of aphids to form nutrient sinks and benefit from enhanced nutrition is positively density dependent up to a certain aggregation size beyond which resource depletion occurs (Way and Cammell 1970). Optimal group size in some aphids, and therefore maximal nutrient manipulation, is maintained to some extent by a balance between on-site reproduction and emigration (Way and Cammell 1970).

Although aggregation appears to confer competitive superiority in sap-feeders that form nutrient sinks, it is unclear whether aggregation in chewing herbivores provides the same advantage, especially if allelochemicals are concerned. For instance, many plants become resistant after only small amounts of leaf tissue are removed (Karbon and Baldwin 1997). In other cases, resistance and damage are positively related (Karbon and Baldwin 1997). In these latter cases, aggregation may enhance resistance and thus confer competitive superiority if the inducing species is relatively more tolerant of the induced allelochemical. Because several of the chewing herbivores involved in cases of plant-mediated competition are both competitively superior and feed in groups (Denno *et al.* 1995), the possibility remains that aggregation imparts a competitive edge.

#### *Dispersal ability*

Although early colonization of plant resources confers competitive superiority in numerous interactions between insect herbivores, dispersal ability per se does not appear to do so (Denno *et al.* 1995). In fact, in a survey of interspecific competitive interactions at large among insect herbivores, the loser was a better disperser than the superior competitor in 10 of 13 interactions (Denno *et al.* 1995). Many of these interactions involved pairs of sap-feeders (aphids and planthoppers) in which competition was likely mediated via induced resistance (Itô 1960, Tamaki and Allen 1969, Addicott 1978, McClure 1980, 1990, Edson 1985, Denno and Roderick 1992). It has been suggested elsewhere that immobile insects owe their success to their ability to manipulate plant

physiology, particularly the mechanisms by which plants establish source–sink relationships (Karban and Baldwin 1997). Existing data for wing-dimorphic sap-feeders (aphids and planthoppers) suggest a phenotypic trade-off between competitive ability and dispersal capability, an issue that we develop in a forthcoming section.

#### *Feeding guild*

There is reason to expect that feeding guild (e.g., sap-feeder, free-living chewer, leaf miner, or root-feeder) could promote competitive superiority in plant-mediated interactions. This expectation arises because allelochemicals are much less concentrated in vascular tissue compared to leaf tissue (Raven 1983, Cook and Denno 1994). Thus, feeding and probing by sap-feeders may induce allelochemicals in tissues that they themselves do not experience or are exposed to in lower concentrations (Inbar *et al.* 1999a, 2003, de Ilarduya *et al.* 2003). Accordingly, sap-feeders may be advantaged over chewing herbivores that consume whole-leaf tissues. However, data at hand do not support this expectation. Indeed, there are three reports showing that sap-feeders (aphids and whiteflies) do impose adverse effects on the survival and performance of chewing herbivores (caterpillars and leaf-mining flies) (Mattson *et al.* 1989, Inbar *et al.* 1999a, 1999b, Mayer *et al.* 2002). There are conflicting data, namely five case studies, demonstrating that chewing herbivores induce plant responses that negatively affect sap-feeders (Ajlan and Potter 1992, Tomlin and Sears 1992, Stout and Duffey 1996, Agrawal 1998, Stout *et al.* 1998, Van Zandt and Agrawal 2004b). Moreover, the mechanisms underlying induced resistance in these studies are diverse, not guild specific, and include trichomes, defensive proteins, proteinase inhibitors, and glucosinolates.

Examples of competitive superiority in interactions between other feeding guilds are scant but no clear pattern prevails. For example, the belowground root-feeding coleopteran *Agriotes lineatus* imposed adverse effects on the aboveground leaf-chewer *Spodoptera exigua* in one case (Bezemer *et al.* 2003), but the reverse occurred in another instance where aboveground feeding by the leaf miner *Chromatomyia syngensiae* negatively affected the root-feeding scarab beetle *Phyllopertha horticola* (Masters and Brown 1992). Although the stem-boring weevil *Rhyssomatus lineaticollis* imposes adverse fitness effects on a variety of other feeding guilds (leaf-chewers, leaf miners, and sap-feeders) (Van Zandt and Agrawal 2004b), reciprocal effects have not been examined. Admittedly there are too few studies to draw a strong conclusion, but the data at hand do not suggest that feeding guild per se strongly confers competitive superiority in plant-mediated interactions involving insect herbivores.

### Competitive superiority, trade-offs, and constraints imposed on other life-history traits

Competitive superiority may constrain other life-history traits such as dispersal due to underlying phenotypic trade-offs, and thus have widespread consequences for population dynamics (Denno *et al.* 1995). Physiological trade-offs among life-history traits such as fecundity, age to first reproduction, egg size, and dispersal are common in herbivorous insects (Zera and Denno 1997). Here we argue that competitive superiority, especially for sap-feeders that interact via induced changes in plant nutrition, may limit dispersal. Our suspicion stems from the observation that competitive dominance and dispersal ability are inversely related in several species of sap-feeders (Denno *et al.* 1995).

For planthoppers, competitive superiority arises because of their ability to compensate for feeding-induced reductions in amino nitrogen by increasing their intake of phloem sap (Denno *et al.* 2000). This is made possible by a large commitment to the musculature associated with ingestion. Planthoppers and leafhoppers feed by inserting their stylets into phloem and xylem tissues respectively (Backus 1985, Cook and Denno 1994). Then using a cibarial pump (modified esophagus), they ingest cell sap. The cibarial pump is driven by a series of dilator muscles that insert on the interior of the face, and face size is positively related to the cross-sectional mass and thus the power of the cibarial muscles to ingest cell sap (Backus 1985). For *Prokelisia* planthoppers, *P. dolus* has a much broader face and commitment to subtending cibarial musculature than *P. marginata* (Denno *et al.* 2000). Thus, *P. dolus* is more capable of increasing food uptake in response to any reductions in plant nitrogen, either natural or those induced by previous feeding, than *P. marginata*. Furthermore, feeding by *P. dolus* may deplete plant nitrogen more than feeding by *P. marginata*, further enhancing the consequences for *P. marginata*. This supposition may explain why previous feeding by *P. dolus* has much more dire consequences on the fitness of *P. marginata* than the reverse situation. Moreover, the broad face and associated large commitment to cibarial muscles in *Delphacodes penedetector* (R.F. Denno unpublished data) likely explains why this planthopper does not suffer in plant-mediated interactions with *P. dolus* (Ferrenberg and Denno 2003).

Data for *Prokelisia* planthoppers suggest a trade-off between cibarial musculature and flight musculature and thus between competitive ability and dispersal. *Prokelisia dolus* is a very sedentary species with a high ratio of cibarial to flight muscle mass, which contrasts with the low ratio characteristic of the very dispersive *P. marginata* (Denno *et al.* 2000, A. F. Huberty and R. F. Denno unpublished data). Thus, competitive superiority is associated with feeding compensation

and tolerance of low plant nitrogen, whereas poor competitive ability is linked with intolerance of depleted nitrogen and high mobility (Denno *et al.* 2000). The two planthoppers cope with their nitrogen requirements in two very different ways, *P. dolus* by feeding compensation and *P. marginata* by dispersal to nitrogen-rich habitats elsewhere (Denno *et al.* 1996). We hypothesize that such trade-offs explain the inverse relationship between competitive ability and dispersal in sap-feeders. For sap-feeders, dispersal is also negatively correlated with other life-history traits such as fecundity and age to first reproduction (Denno *et al.* 1989, 1995). Thus, habitat factors (nonpersistence) that select for a high incidence of dispersal in populations should adversely affect both reproduction and competitive ability (Denno *et al.* 1996, 2000).

One can ask how widespread trade-offs between competitive ability and dispersal might be. The trade-off we report here has not been explored in species other than *Prokelisia*. However, if competitive ability is linked to feeding musculature, then there is every reason to expect such a trade-off in not only sap-feeders but in mandibulate herbivores as well.

### **Plant-mediated interactions challenge the past paradigms of competition theory**

Traditional competition theory posits that: (1) populations of herbivores frequently reach densities at which interspecific competition occurs, (2) species interact symmetrically by engaging in reciprocal struggles either via exploitation or interference over shared resources, (3) niche divergence (resource partitioning) diminishes competition, and (4) closely related species are more likely to compete because they share the same niche (reviewed in Denno *et al.* 1995). We suggest that when plants mediate “competitive interactions” between insect herbivores via induced resistance these traditional paradigms of community organization are often violated.

#### *Herbivore densities and competition*

Although plants generally become more resistant as herbivore damage increases, even very low amounts of damage can induce substantial levels of resistance in plants (reviewed in Karban and Baldwin 1997). Consequently, herbivores may interact with dire consequences even if their densities are not particularly high and apparent levels of herbivory are low. It is noteworthy that one of the major observations used by Hairston *et al.* (1960) to argue against the importance of competition between insect herbivores was that “defoliation” was rare, that food was not often limiting, and that natural enemies maintain herbivores below competitive levels. That insect herbivores can

induce resistance, and therefore compete at low to moderate densities, challenges the basis for this argument.

*Symmetry of interaction*

Plant-mediation pre-adapts competitive interactions for asymmetric outcomes. In fact, 84% of interactions between insect herbivores, many of which are plant-mediated, are asymmetric (Denno *et al.* 1995). Interference competition among insect herbivores, whereby individuals fight or vie for access to resources, tends to encourage more symmetric interactions (Denno *et al.* 1995). Plant-mediated interactions are fundamentally more exploitative in nature such that one herbivore influences the quality and thus quantity of available resources for another. Moreover, herbivores that compete via induced resistance are often spatially or temporally isolated and may never meet to vie for resources. Thus, early-season exploitation coupled with induced resistance and a diversity of tolerance mechanisms in the inducing herbivore often leads to competitive superiority.

*Niche divergence and resource partitioning*

Induced responses can be rapid (within a single herbivore generation) or quite delayed (across multiple generations) (Karban and Baldwin 1997), providing the opportunity not only for contemporaneous herbivores to interact but also those that occur in different seasons or perhaps even different years (Denno *et al.* 1995, Ohgushi 2005). Also, induced responses can be local, occurring in the damaged tissue, or they can be systemic where the response often carries beyond the damaged tissue to other nondamaged tissue, and in several cases even to different nondamaged tissue types (Inbar *et al.* 1995, Karban and Baldwin 1997, Karban and Kuć 1999). Thus, herbivores that co-occur locally as well as those that are spatially or temporally separated on the same plant can interact via feeding induced responses (Damman 1993, Denno *et al.* 1995, Ohgushi 2005). Needless to say, the conventional paradigm that “resource partitioning” minimizes “competitive interactions” is in serious jeopardy in the context of induced responses.

*Phylogenetic relatedness and competition*

Recent evidence from plant-mediated systems suggests that phylogenetically discrepant taxa of herbivores often compete intensely on the same plant (Tomlin and Sears 1992, Stout and Duffey 1996, Agrawal 1998, Stout *et al.* 1998, Inbar *et al.* 1999a, 1999b, Van Zandt and Agrawal 2004a, 2004b). Several characteristics of induced plant responses undoubtedly contribute to this pattern. First, many different cues can elicit an induced response in the same plant including feeding from a diversity of herbivore taxa (Karban and Kuć 1999, Stout and Bostock 1999). Second, although some induced responses are quite specific,

many are active against a wide variety of organisms including insect herbivores in multiple feeding guilds and orders (Karban and Baldwin 1997, Agrawal *et al.* 1999a, 2000, Karban and Kuć 1999, Stout and Bostock 1999). Although jasmonic acid is the primary pathway by which induced resistance mediates interactions between insect herbivores, and likewise the salicylic pathway for plant pathogens (Agrawal *et al.* 1999c, Karban and Kuć 1999), there are numerous cases whereby herbivores stimulate the salicylic pathway and pathogens the jasmonic (reviewed in Karban and Kuć 1999). Thus, a possible mechanistic explanation exists not only for interactions between diverse taxa of insect herbivores, but also for interphyletic interactions between arthropods and plant pathogens (Karban and Baldwin 1997, Stout and Bostock 1999, Ohgushi 2005).

All considered, plant mediation via induced resistance enhances significantly the probability for interspecific interaction between insect herbivores, a view corroborated by recent reviews (Denno *et al.* 1995, Ohgushi 2005). However, plant-mediated competition also defies the traditional views of competition theory in that interactions between insect herbivores occur even at low densities, are frequently asymmetric, are not often diminished by niche divergence on the same plant, and frequently occur between unrelated taxa.

#### **Looking ahead to more holistic approaches of community dynamics**

Almost all studies of interactions between insect herbivores, plant-mediated or otherwise, involve pair-wise assessments (reviewed in Damman 1993, Denno *et al.* 1995, Nykänen and Koricheva 2004). There are only a handful of studies that have considered multiple species interactions among the major co-occurring herbivores in any one system (Hunter 1992, Agrawal 2000, Van Zandt and Agrawal 2004b, Ohgushi 2005) and most of these (Ohgushi 2005 excepted) are very focused on plant-mediated lateral effects without much regard for higher trophic levels. Moreover, most studies assessing the relative strength of top-down and bottom-up forces on herbivores have largely excluded lateral effects (e.g., Stiling and Rossi 1997, Forkner and Hunter 2000, Denno *et al.* 2002). Despite the daunting experimental challenge, we must move beyond simple pair-wise assessments to a broader approach that includes not only interactions with multiple herbivores but also incorporates important top-down and bottom-up variables. Taking a keystone species perspective may simplify matters to some extent and make any experimental design more tractable (e.g., Hunter 1992, González-Megías and Gómez 2003). Moreover, because environmental factors (e.g., soil nutrient availability and stress) influence plant quality, a plant's ability to induce defenses against herbivores, and thus the relative strength of bottom-up controls (Karban and Baldwin 1997, Denno *et al.* 2002),

it will be critical to examine interaction strengths (both direct and indirect) and how environmental factors alter them. Only such a holistic approach will provide insights into the factors organizing community structure. Any predictive model of community structure will likely find plant-mediated responses at its core because plants mediate interactions not only among insect herbivores as shown here but also between herbivores and their natural enemies (Hunter and Price 1992, Denno *et al.* 2002, Ohgushi 2005).

Unraveling the food web ramifications of plant-mediated responses is further complicated by issues of temporal and spatial scaling. For instance, although induced resistance has been implicated in the cyclic fluctuations of forest defoliators and other insect herbivores, there is very little empirical evidence rigorously isolating the long-term carry-over effect of induced resistance as it might influence interspecific interactions and thus population dynamics across years (Karban and Baldwin 1997, Kaitaniemi *et al.* 1998, 1999, Underwood 1999). Similarly, spatial variation in plant responses to herbivory and its extended consequences is poorly understood in any context, let alone in a community-wide one. Future research on the spatial ecology of plant-mediated interactions would benefit from the broad experimental approaches used to explore spatially explicit variation in the strength of top-down and bottom-up controls and food web dynamics at large (Hacker and Bertness 1995, Uriarte and Schmitz 1998, Fagan and Bishop 2000, Denno *et al.* 2002).

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#### *References*

- Addicott, J.F. 1978. Niche relationships among species of aphids feeding on fireweed. *Canadian Journal of Zoology* 57:558–569.
- Agrawal, A.A. 1998. Induced responses to herbivory and increased plant performance. *Science* 279:1201–1202.
- Agrawal, A.A. 1999. Induced responses to herbivory in wild radish: effects on several herbivores and plant fitness. *Ecology* 80:1713–1723.
- Agrawal, A.A. 2000. Specificity of induced resistance in wild radish: causes and consequences for two specialist and two generalist caterpillars. *Oikos* 89:493–500.
- Agrawal, A.A., and M.F. Sherriffs. 2001. Induced plant resistance and susceptibility to late-season herbivores of wild radish. *Annals of the Entomological Society of America* 94:71–75.

- Agrawal, A. A., C. Kobayashi, and J. S. Thaler. 1999a. Influence of prey availability and induced host plant resistance on omnivory by western flower thrips. *Ecology* **80**: 518–523.
- Agrawal, A. A., S. Y. Strauss, and M. J. Stout. 1999b. Costs of induced responses and tolerance to herbivory in male and female fitness components of wild radish. *Evolution* **53**:1093–1104.
- Agrawal, A. A., S. Tuzun, and E. Bent (eds.) 1999c. *Induced Plant Defenses against Pathogens and Herbivores*. St. Paul, MN: American Phytopathological Society Press.
- Agrawal, A. A., R. Karban, and R. Colfer. 2000. How leaf domatia and induced plant resistance affect herbivores, natural enemies and plant performance. *Oikos* **89**:70–80.
- Ajlan, A. M., and D. A. Potter. 1992. Lack of effect of tobacco mosaic virus-induced systemic acquired-resistance on arthropod herbivores in tobacco. *Phytopathology* **82**:647–651.
- Backus, E. A. 1985. Anatomical and sensory mechanisms of leafhopper and planthopper feeding behavior, pp. 163–194 in L. R. Nault and J. G. Rodriguez (eds.) *The Leafhoppers and Planthoppers*. New York: John Wiley.
- Baur, R., S. Binder, and G. Benz. 1991. Nonglandular leaf trichomes as short-term inducible defense of the grey alder, *Alnus incana* (L.), against the chrysomelid beetle *Agelastica alni* L. *Oecologia* **87**:219–226.
- Benrey, B., and R. F. Denno. 1997. The slow growth–high mortality hypothesis: a test using the cabbage butterfly. *Ecology* **78**:987–999.
- Berenbaum, M. R., and A. R. Zangerl. 1999. Coping with life as a menu option: inducible defenses of wild parsnip, pp. 10–32 in R. Tolrian and C. D. Harvell (eds.) *The Ecology and Evolution of Inducible Defenses*. Princeton, NJ: Princeton University Press.
- Bezemer, T. M., R. Wagenaar, N. M. van Dam, and F. L. Wäckers. 2003. Interactions between above- and belowground insect herbivores as mediated by the plant defense system. *Oikos* **101**:555–562.
- Cappuccino, N. 1993. Mutual use of leaf-shelters by lepidopteran larvae on paper birch. *Ecological Entomology* **8**:287–292.
- Cappuccino, N., and M. A. Martin. 1994. Eliminating early-season leaf-tiers of paper birch reduces abundance of midsummer species. *Ecological Entomology* **19**:399–401.
- Chew, F. S. 1988. Biological effects of glucosinolates, pp. 155–181 in H. G. Cutler (ed.) *Biologically Active Natural Products: Potential Use in Agriculture*. Washington, DC: American Chemical Society.
- Clausen, T. P., P. B. Reichardt, J. P. Bryant, et al. 1989. Chemical model for short-term induction in quaking aspen (*Populus tremuloides*) foliage against herbivores. *Journal of Chemical Ecology* **15**:2335–2346.
- Cohen, M. B., M. R. Berenbaum, and M. A. Schuler. 1989. Induction of cytochrome P450-mediated detoxification of xanthotoxin in the black swallowtail. *Journal of Chemical Ecology* **15**:2347–2355.
- Cohen, M. B., M. A. Schuler, and M. R. Berenbaum. 1992. A host-inducible cytochrome P450 from a host-specific caterpillar: molecular cloning and evolution. *Proceedings of the National Academy of Sciences of the USA* **89**:10920–10924.

- Conn, E. E. 1979. Cyanide and cyanogenic glycosides, pp. 387–412 in G. A. Rosenthal and D. H. Janzen (eds.) *Herbivores: Their Interaction with Secondary Plant Metabolites*. New York: Academic Press.
- Constabel, C. P. 1999. A survey of herbivore-inducible defensive proteins and phytochemicals, pp. 137–166 in A. A. Agrawal, S. Tuzan, and E. Bent (eds.) *Induced Plant Defenses against Pathogens and Herbivores*. St. Paul, MN: American Phytopathological Society Press.
- Cook, A., and R. F. Denno. 1994. Planthopper/plant interactions: feeding behavior, plant nutrition, plant defense and host plant specialization, pp. 114–139 in R. F. Denno and T. J. Perfect (eds.) *Planthoppers: Their Ecology and Management*. New York: Chapman and Hall.
- Crawley, M. J., and P. Patrasudhi. 1988. Interspecific competition between insect herbivores: asymmetric competition between cinnabar moth and the ragwort seed-head fly. *Ecological Entomology* 13:243–249.
- Damman, H. 1993. Patterns of herbivore interaction among herbivore species, pp. 132–169 in N. E. Stamp and T. M. Casey (eds.) *Caterpillars: Ecological and Evolutionary Constraints on Foraging*. New York: Chapman and Hall.
- de Illarduya, O. M., Q. G. Xie, and I. Kaloshian. 2003. Aphid-induced defense responses in Mi-1-mediated compatible and incompatible tomato interactions. *Molecular Plant–Microbe Interactions* 16:699–708.
- De Moraes, C. M., J. Lewis, P. W. Paré, H. T. Alborn, and J. H. Tumlinson. 1998. Herbivore-infested plants selectively attract parasitoids. *Nature* 393:570–573.
- Denno, R. F., and G. K. Roderick. 1992. Density-related dispersal in planthoppers: effects of interspecific crowding. *Ecology* 73:1323–1334.
- Denno, R. F., K. L. Olmstead, and E. S. McCloud. 1989. Reproductive cost of flight capability: a comparison of life history traits in wing dimorphic planthoppers. *Ecological Entomology* 14:31–44.
- Denno, R. F., S. Larsson, and K. L. Olmstead. 1990. Host plant selection in willow-feeding leaf beetles (Coleoptera: Chrysomelidae): role of enemy-free space and plant quality. *Ecology* 71:124–137.
- Denno, R. F., M. S. McClure, and J. R. Ott. 1995. Interspecific interactions in phytophagous insects: competition revisited and resurrected. *Annual Review of Entomology* 40:297–331.
- Denno, R. F., G. K. Roderick, M. A. Peterson, *et al.* 1996. Habitat persistence underlies the intraspecific dispersal strategies of planthoppers. *Ecological Monographs* 66:389–408.
- Denno, R. F., M. A. Peterson, C. Gratton, *et al.* 2000. Feeding-induced changes in plant quality mediate interspecific competition between sap-feeding herbivores. *Ecology* 81:1814–1827.
- Denno, R. F., C. Gratton, M. A. Peterson, *et al.* 2002. Bottom-up forces mediate natural-enemy impact in a phytophagous insect community. *Ecology* 83:1443–1458.
- Dussourd, D. E., and R. F. Denno. 1991. Deactivation of plant defense: correspondence between insect behavior and secretory canal architecture. *Ecology* 72:1383–1396.

- Dussourd, D. E., and R. F. Denno. 1994. Host range of generalist Lepidoptera: larval trenching permits feeding on plants with secretory canals. *Ecology* 75:69–78.
- Dussourd, D. E., and T. Eisner. 1987. Vein-cutting behavior insect counterploy to the latex defense of plants. *Science* 237:898–901.
- Edson, J. L. 1985. The influences of predation and resource subdivision on the coexistence of goldenrod aphids. *Ecology* 66:1736–1743.
- Faeth, S. 1987. Community structure and folivorous insect outbreaks: the role of vertical and horizontal interactions, pp. 135–171 in P. Barbosa and J. C. Schultz (eds.) *Insect Outbreaks*. New York: Academic Press.
- Fagan, W. F., and J. G. Bishop. 2000. Trophic interactions during primary succession: herbivores slow a plant reinvasion at Mount St. Helens. *American Naturalist* 155:238–251.
- Ferrenberg, S. M., and R. F. Denno. 2003. Competition as a factor underlying the abundance of an uncommon phytophagous insect, the salt-marsh planthopper *Delphacodes penedetector*. *Ecological Entomology* 28:58–66.
- Fordyce, J. A. 2001. The lethal plant defense paradox remains: inducible host plant aristolochic acids and the growth and defense of the pipevine swallowtail. *Entomologia Experimentalis et Applicata* 100:339–346.
- Forkner, R. E., and M. D. Hunter. 2000. What goes up must come down? Nutrient addition and predation pressure on oak herbivores. *Ecology* 81:1588–1600.
- Formusoh, E. S., G. E. Wilde, and J. C. Reese. 1992. Reproduction and feeding-behavior of greenbug biotype-E (Homoptera: Aphididae) on wheat previously fed upon by aphids. *Journal of Economic Entomology* 85:789–793.
- Forrest, J. M. S. 1971. The growth of *Aphis fabae* as an indicator of the nutritional advantage of galling to the apple aphid *Dysaphis devecta*. *Entomologia Experimentalis et Applicata* 14:447–483.
- Fukui, A. 2001. Indirect interactions mediated by leaf shelters in animal–plant communities. *Population Ecology* 43:31–40.
- Gange, A. C., and V. K. Brown. 1989. Effects of root herbivory by an insect on a foliar-feeding species, mediated through changes in the host plant. *Oecologia* 81:38–42.
- González-Megías, A., and J. M. Gómez. 2003. Consequences of removing a keystone herbivore for the abundance and diversity of arthropods associated with a cruciferous shrub. *Ecological Entomology* 28:299–308.
- Hacker, S. D., and M. D. Bertness. 1995. A herbivore paradox: why salt marsh aphids live on poor-quality plants. *American Naturalist* 145:192–210.
- Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control, and competition. *American Naturalist* 44:421–425.
- Heard, S. B., and C. K. Buchanan. 1998. Larval performance and association within and between two species of hackberry nipple gall insects, *Pachypsylla* spp. (Homoptera: Psyllidae). *American Midland Naturalist* 140:351–357.
- Hendrix, S. D. 1988. Herbivory and its impact on plant reproduction, pp. 246–266 in J. Lovett-Doust and L. Lovett-Doust (eds.) *Plant Reproductive Ecology: Patterns and Strategies*. Oxford, UK: Oxford University Press.

- Hendrix, S. D., and E. J. Trapp. 1989. Floral herbivory in *Pastinaca sativa*: do compensatory responses offset reductions in fitness? *Evolution* **43**:891–895.
- Hunter, M. D. 1992. Interactions within herbivore communities mediated by the host plant: the keystone herbivore concept, pp. 287–325 in M. D. Hunter, T. Ohgushi, and P. W. Price (eds.) *Effects of Resource Distribution on Animal-Plant Interactions*. San Diego, CA: Academic Press.
- Hunter, M. D., and P. W. Price. 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology* **73**:724–732.
- Inbar, M., A. Eshel, and D. Wool. 1995. Interspecific competition among phloem-feeding insects mediated by induced host-plant sinks. *Ecology* **76**:1506–1515.
- Inbar, M., H. Doostdar, G. L. Leibee, and R. T. Mayer. 1999a. The role of plant rapidly induced responses in asymmetric interspecific interactions among insect herbivores. *Journal of Chemical Ecology* **25**:1961–1979.
- Inbar, M., H. Doostdar, and R. T. Mayer. 1999b. Effects of sessile whitefly nymphs (Homoptera: Aleyrodidae) on leaf-chewing larvae (Lepidoptera: Noctuidae). *Environmental Entomology* **28**:353–357.
- Inbar, M., R. T. Mayer, and H. Doostdar. 2003. Induced activity of pathogenesis related (PR) proteins in aphid galls. *Symbiosis* **34**:293–300.
- Itô, Y. 1960. Ecological studies on population increase and habitat segregation among barley aphids. *Bulletin of the National Institute of Agricultural Science, Series C* **11**:45–130.
- Kaitaniemi, P., K. Ruohomaki, V. Ossipov, E. Haukioja, and K. Pihlaja. 1998. Delayed induced changes in the biochemical composition of host plant leaves during an insect outbreak. *Oecologia* **116**:182–190.
- Kaitaniemi, P., K. Ruohomaki, T. Tammaru, and E. Haukioja. 1999. Induced resistance of host tree foliage during and after a natural insect outbreak. *Journal of Animal Ecology* **68**:382–389.
- Karban, R. 1986. Interspecific competition between folivorous insects on *Erigeron glaucus*. *Ecology* **67**:1063–1072.
- Karban, R. 1989. Community organization of *Erigeron glaucus* folivores: effects of competition, predation, and host plant. *Ecology* **70**:1028–1039.
- Karban, R., and A. A. Agrawal. 2002. Herbivore offense. *Annual Review of Ecology and Systematics* **33**:641–664.
- Karban, R., and I. T. Baldwin. 1997. *Induced Responses to Herbivory*. Chicago, IL: University of Chicago Press.
- Karban, R., and J. Kuć. 1999. Induced resistance against pathogens and herbivores: an overview, pp. 1–19 in A. A. Agrawal, S. Tuzun, and E. Bent (eds.) *Induced Plant Defenses against Pathogens and Herbivores*. St. Paul, MN: American Phytopathological Society Press.
- Kareiva, P. 1982. Exclusion experiments and the competitive release of insects feeding on collards. *Ecology* **63**:696–704.
- Kessler, A., and I. T. Baldwin. 2004. Herbivore-induced plant vaccination. I. The orchestration of plant defenses in nature and their fitness consequences in the wild tobacco *Nicotiana attenuata*. *Plant Journal* **38**:639–649.

- Kidd, N. A. C., G. B. Lewis, and C. A. Howell. 1985. An association between two species of pine aphid, *Schizolachnus pineti* and *Eulachnus agilis*. *Ecological Entomology* **10**:427–432.
- Krupnick, G. A., A. E. Weis, and D. R. Campbell. 1999. The consequences of floral herbivory for pollinator service to *Isomeris arborea*. *Ecology* **80**:125–134.
- Lamb, R. J., and P. A. MacKay. 1987. *Acyrtosiphon kondoi* influences alata production by the pea aphid, *A. pisum*. *Entomologia Experimentalis et Applicata* **45**:195–198.
- Larson, K. C., and T. G. Whitham. 1991. Manipulation of food resources by a gall-inducing aphid: the physiology of sink–source interactions. *Oecologia* **88**:15–21.
- Larsson, S., H. E. Hågström, and R. F. Denno. 1997. Preference for protected feeding sites by larvae of the willow-feeding leaf beetle *Galerucella lineola*. *Ecological Entomology* **22**:445–452.
- Lawton, J. H. 1982. Vacant niches and unsaturated communities: a comparison of bracken herbivores at sites on two continents. *Journal of Animal Ecology* **51**:573–595.
- Lawton, J. H., and M. P. Hassell. 1984. Interspecific competition in insects, pp. 451–495 in C. B. Huffaker and R. L. Rabb (eds.) *Ecological Entomology*. New York: John Wiley.
- Lawton, J. H., and D. R. Strong. 1981. Community patterns and competition in folivorous insects. *American Naturalist* **118**:317–338.
- Lehtilä, K., and S. Y. Strauss. 1997. Leaf damage by herbivores affects attractiveness to pollinators in wild radish, *Raphanus raphanistrum*. *Oecologia* **111**:396–403.
- Lewinsohn, E., M. Gijzen, and R. Croteau. 1991. Defense mechanisms of conifers: differences in constitutive and wound-induced monoterpene biosynthesis among species. *Plant Physiology* **96**:44–49.
- Lill, J. T., and R. J. Marquis. 2003. Ecosystem engineering by caterpillars increases insect herbivore diversity on white oak. *Ecology* **84**:682–690.
- Martinsen, G. D., K. D. Floate, A. M. Waltz, G. M. Wimp, and T. G. Whitham. 2000. Positive interactions between leafrollers and other arthropods enhance biodiversity on hybrid cottonwoods. *Oecologia* **123**:82–89.
- Masters, G. J., and V. K. Brown. 1992. Plant-mediated interactions between two spatially separated insects. *Functional Ecology* **6**:175–179.
- Masters, G. J., T. H. Jones, and M. Rogers. 2001. Host-plant mediated effects of root herbivory on insect seed predators and their parasitoids. *Oecologia* **127**:246–250.
- Matsumura, M., and Y. Suzuki. 2003. Direct and feeding-induced interactions between two rice planthoppers, *Sogatella furcifera* and *Nilaparvata lugens*: effects on dispersal capability and performance. *Ecological Entomology* **28**:174–182.
- Mattson, W. J., R. A. Haack, R. K. Lawrence, and D. A. Herms. 1989. Do balsam aphids (Homoptera: Aphididae) lower tree susceptibility to spruce budworm? *Canadian Entomologist* **121**:93–103.
- Mayer, R. T., M. Inbar, C. L. McKenzie, et al. 2002. Multitrophic interactions of the silverleaf whitefly, host plants, competing herbivores, and phytopathogens. *Archives of Insect Biochemistry and Physiology* **51**:151–169.
- McClure, M. S. 1980. Competition between exotic species: scale insects on hemlock. *Ecology* **61**:1391–1401.

- McClure, M. S. 1989. Biology, population trends, and damage of *Pineus boernerii* and *P. coloradensis* (Homoptera: Adelgidae) on red pine. *Environmental Entomology* **18**:1066–1073.
- McClure, M. S. 1990. Cohabitation and host species effects on the population growth of *Matsucoccus resinosae* (Homoptera: Margarodidae) and *Pineus boernerii* (Homoptera: Adelgidae) on red pine. *Environmental Entomology* **19**:672–676.
- McClure, M. S., and P. W. Price. 1975. Competition among sympatric *Erythroneura* leafhoppers (Homoptera: Cicadellidae) on American sycamore. *Ecology* **56**:1388–1397.
- McClure, M. S., and P. W. Price. 1976. Ecotope characteristics of coexisting *Erythroneura* leafhoppers (Homoptera: Cicadellidae) on sycamore. *Ecology* **57**:928–940.
- Milbrath, L. R., and J. R. Nechols. 2004. Indirect effect of early-season infestations of *Trichosirocalus horridus* on *Rhinocyllus conicus* (Coleoptera: Curculionidae). *Biological Control* **30**:95–109.
- Moegenburg, S. M. 1996. Sabal palmetto seed size: causes of variation, choice of predators, and consequences for seedlings. *Oecologia* **106**:539–543.
- Montandon, R., J. E. Slosser, and W. A. Frank. 1993. Factors reducing the pest status of the Russian wheat aphid (Homoptera: Aphididae) on wheat in the rolling plains of Texas. *Journal of Economic Entomology* **86**:899–905.
- Moran, N. A., and T. G. Whitham. 1990. Interspecific competition between root-feeding and leaf-galling aphids mediated by host-plant resistance. *Ecology* **71**:1050–1058.
- Nakamura, M., and T. Ohgushi. 2003. Positive and negative effects of leaf shelters on herbivorous insects: linking multiple herbivore species on a willow. *Oecologia* **136**:445–449.
- Nakamura, M., Y. Miyamoto, and T. Ohgushi. 2003. Gall initiation enhances the availability of food resources for herbivorous insects. *Functional Ecology* **17**:851–857.
- Ness, J. H. 2003. *Catalpa bignonioides* alters extrafloral nectar production after herbivory and attracts many bodyguards. *Oecologia* **134**:210–218.
- Nykänen, H., and J. Koricheva. 2004. Damage-induced changes in woody plants and their effects on insect herbivore performance: a meta-analysis. *Oikos* **104**:247–268.
- Ohgushi, T. 2005. Indirect interaction webs: herbivore-induced effects through trait change in plants. *Annual Review of Ecology, Evolution, and Systematics* **36**:81–105.
- Olmstead, K. L., R. F. Denno, T. C. Morton, and J. T. Romeo. 1997. Influence of *Prokelisia* planthoppers on the amino acid composition and growth of *Spartina alterniflora*. *Journal of Chemical Ecology* **23**:303–321.
- Paré, P. W., W. J. Lewis, and J. H. Tumlinson. 1999. Induced plant volatiles: biochemistry and effects on parasitoids, pp. 167–180 in A. A. Agrawal, S. Tuzun, and E. Bent (eds.) *Induced Defenses against Pathogens and Herbivores*. St. Paul, MN: American Phytopathological Society Press.
- Pilson, D. 1992. Aphid distribution and the evolution of goldenrod resistance. *Evolution* **46**:1358–1372.
- Pullin, A. S., and J. E. Gilbert. 1989. The stinging nettle, *Urtica dioica*, increases trichome density after herbivore and mechanical damage. *Oikos* **54**:275–280.

- Raffa, K.F. 1991. Induced defensive reactions in conifer–bark beetle systems, pp. 245–276 in D.W. Tallamy and M.J. Raupp (eds.) *Phytochemical Induction by Herbivores*. New York: Academic Press.
- Rathcke, B.J. 1976. Competition and coexistence within a guild of herbivorous insects. *Ecology* **57**:76–87.
- Rausher, M.D., K. Iwao, E.L. Simms, N. Ohsaki, and D. Hall. 1993. Induced resistance in *Ipomoea purpurea*. *Ecology* **74**:20–29.
- Raven, J.A. 1983. Phytophages of xylem and phloem: a comparison of animal and plant sapfeeders. *Advances in Ecological Research* **13**:135–234.
- Redman, A.M., and J.M. Scriber. 2000. Competition between the gypsy moth, *Lymantria dispar*, and the northern tiger swallowtail, *Papilio canadensis*: interactions mediated by host plant chemistry, pathogens, and parasitoids. *Oecologia* **125**:218–228.
- Ruuhola, T. 2001. *Dynamics of salicylates in willows and its relation to herbivory*. Ph.D. dissertation, University of Joensuu, Finland.
- Salt, D.T., P. Fenwick, and J.B. Whittaker. 1996. Interspecific herbivore interactions in a high CO<sub>2</sub> environment: root and shoot aphids feeding on *Cardamine*. *Oikos* **77**:326–330.
- Salyk, R.P., and D.J. Sullivan. 1982. Comparative feeding behavior of two aphid species: bean aphid (*Aphis fabae* Scopoli) and pea aphid (*Acyrtosiphon pisum* Harris) (Homoptera: Aphididae). *Journal of the New York Entomological Society* **90**:87–93.
- Schoener, T.W. 1982. The controversy over interspecific competition. *American Scientist* **70**:586–595.
- Schultz, J.C. 1999. Discussion, p. 19 in D.J. Chadwick and J.A. Goode (eds.) *Insect–Plant Interactions and Induced Plant Defense*. New York: John Wiley.
- Shearer, J.W. 1976. Effect of aggregations of aphids (*Periphyllus* spp.) on their size. *Entomologia Experimentalis et Applicata* **20**:179–182.
- Stiling, P., and A.M. Rossi. 1997. Experimental manipulations of top–down and bottom–up factors in a tri-trophic system. *Ecology* **78**:1602–1606.
- Stiling, P.D., and D.R. Strong. 1984. Experimental density manipulation of stem-boring insects: some evidence for interspecific competition. *Ecology* **65**:1683–1685.
- Stout, M.J., and R.M. Bostock. 1999. Specificity of induced responses to arthropods and pathogens, pp. 183–209 in A.A. Agrawal, S. Tuzun, and E. Bent (eds.) *Induced Defenses against Pathogens and Herbivores*. St. Paul, MN: American Phytopathological Society Press.
- Stout, M.J., and S.S. Duffey. 1996. Characterization of induced resistance in tomato plants. *Entomologia Experimentalis et Applicata* **79**:273–283.
- Stout, M.J., K.V. Workman, R.M. Bostock, and S.S. Duffey. 1998. Specificity of induced resistance in the tomato, *Lycopersicon esculentum*. *Oecologia* **113**:74–81.
- Strauss, S.Y. 1997. Floral characteristics link herbivores, pollinators, and plant fitness. *Ecology* **78**:1640–1645.
- Strauss, S.Y., J.K. Conner, and S.L. Rush. 1996. Foliar herbivory affects floral characteristics and plant attractiveness to pollinators: implications for male and female plant fitness. *American Naturalist* **147**:1098–1107.

- Strong, D. R. 1981. The possibility of insect communities without competition: hispine beetles on *Heliconia*, pp. 183–194 in R. F. Denno and H. Dingle (eds.) *Insect Life History Patterns: Habitat and Geographic Variation*. New York: Springer-Verlag.
- Strong, D. R., J. H. Lawton, and T. R. E. Southwood. 1984. *Insects on Plants*. Cambridge, MA: Harvard University Press.
- Szentesi, A., and T. Jermy. 1995. Predispersal seed predation in leguminous species: seed morphology and bruchid distribution. *Oikos* 73:23–32.
- Tallamy, D. W., and M. J. Raupp. 1991. *Phytochemical Induction by Herbivores*. New York: John Wiley.
- Tamaki, G., and W. W. Allen. 1969. Competition and other factors influencing the population dynamics of *Aphis gossypii* and *Macrosiphoniella sanborni* on greenhouse chrysanthemums. *Hilgardia* 39:447–505.
- Thaler, J. S. 1999. Jasmonate-inducible plant defenses cause increased parasitism of herbivores. *Nature* 399:686–688.
- Thaler, J. S. 2002a. Jasmonate-deficient plants have reduced direct and indirect defenses against herbivores. *Ecology Letters* 5:764–774.
- Thaler, J. S. 2002b. Effect of jasmonate-induced plant responses on the natural enemies of herbivores. *Journal of Animal Ecology* 71:141–150.
- Thalmann, C., J. Freise, W. Heitland, and S. Bacher. 2003. Effects of defoliation by horse chestnut leafminer (*Cameraria ohridella*) on reproduction in *Aesculus hippocastanum*. *Trees* 17:383–388.
- Tomlin, E. S., and M. K. Sears. 1992. Indirect competition between the Colorado potato beetle (Coleoptera: Chrysomelidae) and the potato leafhopper (Homoptera: Cicadellidae) on potato: laboratory study. *Environmental Entomology* 21:787–792.
- Traw, M. B., and T. E. Dawson. 2002. Reduced performance of two specialist herbivores (Lepidoptera: Pieridae, Coleoptera: Chrysomelidae) on new leaves of damaged black mustard plants. *Environmental Entomology* 31:714–722.
- Turlings, T. C. J., J. H. Tumlinson, R. R. Heath, A. T. Proveaux, and R. E. Doolittle. 1991. Isolation and identification of allelochemicals that attract the larva parasitoid, *Cotesia marginiventris* (Gesson), to the microhabitat of one of its hosts. *Journal of Chemical Ecology* 17:2235–2251.
- Underwood, N. 1999. The influence of induced plant resistance on herbivore population dynamics, pp. 211–229 in A. A. Agrawal, S. Tuzan, and E. Bent (eds.) *Induced Plant Defenses against Pathogens and Herbivores*. St. Paul, MN: American Phytopathological Society Press.
- Uriarte, M., and O. J. Schmitz. 1998. Trophic control across a natural productivity gradient with sap-feeding herbivores. *Oikos* 82:552–560.
- Van Zandt, P. A., and A. A. Agrawal. 2004a. Specificity of induced plant responses to specialist herbivores of the common milkweed *Asclepias syriaca*. *Oikos* 104:401–409.
- Van Zandt, P. A., and A. A. Agrawal. 2004b. Community-wide impacts of herbivore-induced plant responses in milkweed (*Asclepias syriaca*). *Ecology* 85:2616–2629.
- Vinson, B. 1998. The general host selection behavior of parasitoid hymenoptera and a comparison of initial strategies utilized by larvaphagous and oophagous species. *Biological Control* 11:79–96.

- Wallin, K.F., and K.F. Raffa. 2001. Effects of folivory on subcortical plant defenses: can defense theories predict interguild processes? *Ecology* **82**:1387–1400.
- Waloff, N. 1979. Partitioning of resources by grassland leafhoppers (Auchenorrhyncha, Homoptera). *Ecological Entomology* **4**:379–385.
- Waltz, A.M., and T.G. Whitham. 1997. Plant development affects arthropod communities: opposing impacts of species removal. *Ecology* **78**:2133–2144.
- Way, M.J., and M. Cammell. 1970. Aggregation behavior in relation to food utilization by aphids, pp. 229–247 in A. Watson (ed.) *Animal Populations in Relation to their Food Resources*. Oxford, UK: Blackwell Scientific Publications.
- Weis, A.E., R. Walton, and C.L. Crego. 1988. Reactive plant tissue sites and the population biology of gall makers. *Annual Review of Entomology* **33**:467–486.
- West, C. 1985. Factors underlying the late seasonal appearance of the lepidopterous leaf-mining guild on oak. *Ecological Entomology* **10**:111–120.
- Williams, I.S. 1999. Slow-growth, high-mortality: a general hypothesis, or is it? *Ecological Entomology* **24**:490–495.
- Willott, S.J., S.G. Compton, and L.D. Incoll. 2000. Foraging, food selection and worker size in the seed harvesting ant *Messor bouvieri*. *Oecologia* **125**:35–44.
- Wise, M.J., and A.M. Weinberg. 2002. Prior flea beetle herbivory affects oviposition preference and larval performance of a potato beetle on their shared host plant. *Ecological Entomology* **27**:115–122.
- Wold, E.N., and R.J. Marquis. 1997. Induced defense in white oak: effects on herbivores and consequences for the plant. *Ecology* **78**:1356–1369.
- Zangerl, A.R. 1999. Locally-induced responses in plants: the ecology and evolution of restrained defense, pp. 231–249 in A.A. Agrawal, S. Tuzun, and E. Bent (eds.) *Induced Plant Defenses against Pathogens and Herbivores*. St. Paul, MN: American Phytopathological Society Press.
- Zera, A.J., and R.F. Denno. 1997. Physiology and ecology of dispersal polymorphisms in insects. *Annual Review of Entomology* **42**:207–231.