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The Varied Roles of Induced Plant Responses in Species Interactions

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The Varied Roles of Induced Plant Responses in Species Interactions

THESIS SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF MASTER'S OF BIOLOGICAL SCIENCES

UNIVERSITY OF SOUTHERN MAINE

DEPARTMENT OF BIOLOGY

BY

JUSTINE B. ROTH

2013

Acknowledgements

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The other members of my graduate committee have also contributed significantly to this project. I am grateful for the participation of Dr. Mike Mazurkiewicz, whose extensive knowledge of natural history has always inspired me. His enthusiastic love of ecology is infectious and reminds me to stop and wonder at the amazing natural world we live in. In particular, his interest in insect ecology was part of the spark that lit my own interest in this topic. I am also appreciative of the contributions of Dr. Joseph Staples. His willingness to take part in my committee as I neared completion of my degree has been greatly appreciated. His feedback and ideas have strengthened the quality of my work.

It is with great sadness in the passing of Dr. Tom Knight that I acknowledge his influence on my graduate education and this paper. He was an excellent teacher and a dedicated researcher who often took the time to discuss the physiological aspects of plant-insect interactions with me. It was through his influence that I deepened my appreciation and interest in the biochemical and physiological aspects of plant-mediated interactions.

While there are numerous other individuals that have supported me throughout this process, I would like to thank the USM Biology Department faculty as a whole. I have taken courses from many of the faculty over the years, participated in their research or relied on their support in other significant ways. Many of them have contributed greatly to my development as a scientist and as a person; my life has been enriched through my interactions with all of them. I sincerely thank all of the faculty that have contributed to my education.

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Preface

It has been a long journey from the day that I decided to return to higher education in pursuit of a Master's Degree in Biology to the completion of this paper. I initially planned on a much different project and on a much shorter timescale. Life however has many unexpected surprises for all of us, and my path through graduate school has been no exception. My initial research interest was in the evolution and ecology of plant-mediated indirect interactions. I found the interplay between plants and insects endlessly fascinating, as I do to this day.

With the help of Terry Theodose and the rest of my committee, I planned an ambitious research project, intent on making an original contribution to this exciting and growing field. I was also eager to do my research in a salt marsh, the location of my undergraduate research experience and an environment that I am deeply passionate about. With the support of my committee, research permits in hand, locations scouted out and a field assistant secured, I embarked on my project.

At the very beginning of the field season, I developed severe pain while walking. I persisted on field work for several weeks with increasing pain and decreasing mobility. Initially diagnosed with tendonitis, I was told to keep off my feet indefinitely, until the pain subsided. A year later, with no research project to show for that time, I was finally diagnosed with severe arthritis in both feet. While with a correct diagnosis I could now manage the pain, it was not feasible to continue field research, especially in a setting as challenging to navigate on foot as a salt marsh.

It was with great disappointment concerning giving up my original thesis that I began to look for other research projects. I followed up with several of these with the support of the faculty and my committee, however I lacked the passion for them that I had for my original research project. The combination of a year or more off my feet and the lack of a research direction had taken the wind out of my sails.

As a result, after completing my coursework, I took a hiatus from working on a thesis project. I re-entered the work force and discovered a new passion in the field of special education. However, giving up on completing my graduate studies in biology was never an option for me. With the support of my friends and family as well as my adviser, Terry, I eventually went back to my original interest—the interplay between insect herbivores and plants— and began to write this literature review. While it is a far different project from the original research that I had hoped to contribute to this field when I entered graduate school, I hope that it provides a synthesis of this diverse and complex topic and that it captures in some small part the abiding appreciation that I have for the rich and fascinating natural world around us.

Abstract

In this review, I will discuss indirect species interactions that occur as a result of herbivore-induced trait changes in plants. Species interactions are at the very core of the field of ecology. In particular, plant–insect herbivore interactions are of central importance as these two groups together consist of over 75% of the macroscopic diversity on earth. Historically, research has focused on pair-wise direct interactions however, more recently, the importance of indirect interactions has been widely acknowledged. Indeed, indirect interactions may be as strong and as common as direct interactions. Indirect interactions have been actively investigated in plant–insect systems, which are the primary focus of this paper. Plants exhibit multiple responses to insect herbivory, including changes in chemistry, morphology and physiology. These changes provide the mechanisms for trait-mediated indirect interactions between organisms that utilize the same host plant, whether for food, shelter or oviposition. Indirect plant-mediated interactions include competition and facilitation between insect herbivores as well as interactions that involve higher trophic levels, such as natural enemy attraction. Recent research has begun to elucidate community-level effects of plant responses to insect herbivory, including plant-mediated connections between aboveground and belowground communities.

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Introduction

The interactions between organisms have been actively studied throughout the history of ecology from early descriptive ecology through recent experimental research. In addition, many other disciplines have contributed to this field, including evolutionary biology, biochemistry, and molecular biology. Early work focused on direct interactions between two organisms, such as predation and interference competition. In recent years, indirect interactions resulting from density and trait changes of a mediating species or those involving more than three species have been well documented (Miner 2005). Interaction theory is being continuously revised to reflect this richer understanding of the complex mechanisms of species interactions and the complicated roles they play within ecological communities.

The study of trait-mediated indirect interactions has been a particularly active area of research and a large body of work concerning their importance in a broad range of ecological communities has accumulated (Bolker *et al.* 2003, Werner and Peacor 2003). Early studies focused on behavior-mediated predator–prey interactions but an increasingly important focus is on the dynamic interactions between herbivores and plants. Although technically not classified as behaviors, the diverse responses of plants to herbivory can impact other species in the community.

Understanding species interactions can be extremely difficult due to multiple, complicating factors. First, many disciplines have contributed to this field and as a result the terminology is inconsistent and potentially confusing. Different

authors can use the same terminology in different ways and various terms are often used to describe the same concept. Second, the interacting organisms are themselves highly complex with each having unique variations in biochemistry, physiology, morphology, behavior and evolutionary history, the very factors that drive interactions. Third, all interactions take place in a larger ecological context with other biotic and abiotic factors impacting and being impacted by the interactions themselves. Therefore the emergent properties arising from an interaction between just two organisms can have ramifications throughout the entire ecological community.

Species interactions have been broadly classified as either those that are direct or those that are indirect. While definitions of each of these terms vary (see Appendix A), direct interactions typically involve two species while indirect interactions typically involve three (or more) species. In this paper, I will be using the terms direct interactions and indirect interactions as outlined by Abrams (1995), who takes a more nuanced approach. A direct interaction is one in which a change in one species produces a change in another without any intermediary species required (see Fig. 1; Abrams 1995). In contrast, an indirect interaction involves an initiating species that produces a change in an intermediate species which then produces a change in a receiving species (Fig. 2; Abrams 1995).

Indirect interactions are likewise separated into two types by most authors (but see Appendix A for further discussion), namely trait-mediated indirect interactions (TMII) and density-mediated indirect interactions (DMII). Density-mediated indirect interactions are those that are mediated by changes in

abundance of the mediating species while TMII are mediated by trait changes in the mediating species, such as those in behavior, chemistry, morphology and phenology.

Here I review research on trait-mediated indirect interactions with a focus on plant trait-mediated interactions involving plants and insect herbivores. Plants and insects are two of the most diverse and ecologically important macroscopic taxa on Earth, so the interactions between them have been extensively researched (Strong *et al.* 1984, Agrawal 2004). I will first discuss direct interactions between plants and insect herbivores, which are the building blocks of indirect interactions, focusing on the myriad responses of plants to herbivory, their various manifestations, and the effects of those responses on the insect herbivores. I will then turn to the topic of plant-mediated indirect interactions, concentrating on those involving two insect herbivores, above- and belowground indirect interactions, and those involving higher trophic levels. Finally, I will discuss the recent research on community level effects of plant-mediated indirect interactions and future research in this burgeoning field.

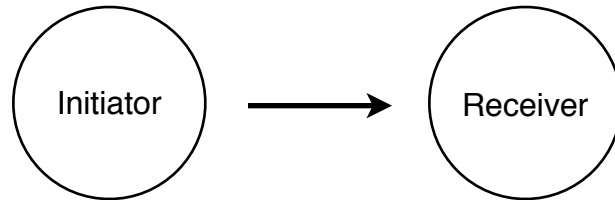


Fig. 1. A model depicting a simple direct interaction. While this model only depicts the effect of the initiating species on the receiving species, reciprocal interactions generally occur (Abrams 1995). In symmetric interactions, interaction strength is equal in both directions while in asymmetric interactions, interaction strength is weaker in one direction.

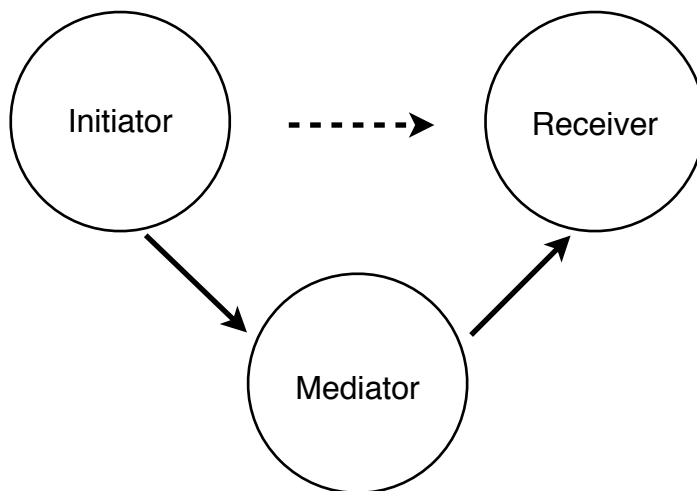


Fig. 2. A model depicting a simple indirect interaction. Solid lines illustrate direct interactions and the dashed line illustrating the indirect interaction. Note that indirect interactions require at least one intermediary species between the initiating and receiving species (Abrams 1995). As in Figure 1, reciprocal effects are likely to occur in nature although not shown in this model.

Direct plant–insect herbivore interactions: the roles of plant responses

Plants have evolved multiple ways of coping with the challenges of being literally rooted in one location. Herbivory represents just one of those challenges but it is a particularly complex one. As the foundation for the passage of solar energy and carbon flux into food webs, herbivory plays a pivotal role in the ecosystem. Thus most plant species have numerous herbivores from a diversity of taxa. In the face of this onslaught, plants are not passive targets, but have evolved multiple layers of defense. These layers can be classified based on permanence in plant tissue, mechanism of defense, and the impact on the herbivore.

Induced plant responses to insect herbivory

Plant defenses can be classified according to how permanent they are in plant tissue. Constitutive defenses are those which are present even in the absence of herbivory. In contrast, plant defenses may also be induced by herbivory. Induced plant responses are broadly defined as changes following any kind of damage or stress, including drought, freezing and light damage in addition to herbivory (Karban and Myers 1989, Karban and Baldwin 1997, Van Zandt and Agrawal 2004a).

While many induced plant responses to herbivory may be assumed to be defenses, only those that can be shown to increase plant fitness are technically considered induced defenses (Karban and Baldwin 1997, Agrawal and Karban

1999). Surprisingly, some induced responses increase plant susceptibility to subsequent herbivory or otherwise decrease plant fitness (Poelman *et al.* 2010). Herbivore-induced plant changes, whether defensive or not, are the building blocks of the trait-mediated indirect interactions that will be discussed later.

If plants already have constitutive defenses, what additional functions do induced responses play? There are multiple hypotheses about the adaptive functions of induced responses and they often address the topic of defense costs but also the strategic advantage to a plant dealing with multiple consumers. Indeed, the earliest and most prevalent ideas about the evolution of induced responses centered on cost (Karban and Myers 1989, Agrawal and Karban 1999).

Surprisingly, many studies have failed to demonstrate any costs of defense (Agrawal and Karban 1999, Arnold 2003) while others were able to demonstrate fitness costs particularly under laboratory conditions (Baldwin and Hamilton 2000). One weakness of many of these studies is that they were not conducted under natural conditions and some did not include an herbivory treatment. For instance, in a greenhouse study utilizing transformed wild tobacco (*Nicotiana attenuata*) with reduced expression of trypsin proteinase inhibitors (TPIs), Zavala *et al.* (2004) demonstrated reproductive and growth costs for both constitutive and induced TPI expression in the untransformed lines when grown under competition. However, these fitness costs may be ameliorated in a natural setting that includes herbivory (Zavala *et al.* 2004). On the other hand, additional costs may also be present in the natural setting, such as decreased

attractiveness to pollinators and other mutualists or increased susceptibility to specialist herbivores (Zavala et al 2004, Agrawal 2011).

As expected, the relative fitness costs of constitutive and induced plant defenses is an active area of research and debate (Cipollini 2003, Agrawal 2011). Costs can be either biosynthetic, ecological or both, with ecological costs potentially being more common and probably much higher than biosynthetic costs (Fatouros 2005, Karban 2011). However, due to relative ease of study, biosynthetic costs have been examined in greater detail. Constitutive defenses are assumed to be costly in the absence of herbivory due to resources being permanently allocated to defense that could otherwise go towards growth and reproduction. However, because some constitutive defenses have dual roles in the plant, there may be little additional cost in maintaining them. Examples include cellulose, lignin and waxes. However other constitutive traits appear to serve the sole function of defense, such as thorns, spines and many plant chemicals that do not have a known primary metabolic function. Evolution, then, may favor induced defenses because the plant can adjust its defenses during periods of herbivore attack rather than defending continuously. This may result in lower overall fitness costs to the plant in the long term.

Although the allocation costs of constitutive defenses may be obvious, induced responses can also carry costs, such as allocation away from primary metabolism. In addition, ecological costs may also accrue, such as changes to interactions with other, beneficial, species. For example, plant defenses may be toxic to certain pollinators and therefore deter them (Agrawal and Karban 1999,

Karban 2011). Positive interactions with microbial symbionts and seed dispersers may also decrease (Strauss *et al* 2002, Agrawal 2011). Likewise, indirect mutualists, such as predators and parasitoids of herbivores, may also be negatively affected by plant toxins, such as when toxins are sequestered by the herbivore and used for its own defense (Agrawal and Karban 1999, Karban 2011).

If cost reduction does not adequately explain the benefit of induced responses over constitutive defense, what other factors may be important? Some plant resistance traits, such as putative defense chemicals, attract specialist herbivores (Robert *et al.* 2012). Thus constitutive expression of these traits can make the plant conspicuous, favoring the evolution of induced expression. Induced defenses may make the plant less apparent to specialist herbivores (Agrawal 1998, Agrawal and Karban 1999, Lankau 2007). To illustrate this, brassicaceous plants have constitutive glucosinolates that actually attract and stimulate feeding and oviposition by specialist herbivores (Feeny 1970, Slansky and Feeny 1977, Agrawal and Karban 1999).

Inducible defenses may also provide a more flexible strategy than constitutive defenses in response to the great variety of challenges plants face in the larger ecological context. Most plants must defend against a range of herbivores and pathogens that can attack simultaneously or sequentially. Different biochemical pathways can provide specific defenses against these diverse challenges. However, some of these pathways are antagonistic within the plant making it unlikely that a single phenotype has the capacity to defend

against the full range of potential challengers at all times. Inducible defenses, then, allow the plant to tailor a response to the current attack without sacrificing its future ability to defend against attack by other organisms (Agrawal and Karban 1999, Ruiz *et al.* 2002).

Plant variability in herbivore food quality is another factor favoring inducible responses. Herbivores, including specialists, can be negatively affected by variability in the food source, including variability in chemical defenses (Brattsten *et al.* 1983, Stockhoff 1993, Shelton 2004, Karban 2011). Induced defenses increase both the spatial and temporal nutritional variability of plant tissue in a way not possible with constitutive defenses (Agrawal and Karban 1999, Shelton 2005). Variability itself may also be an effective strategy over evolutionary time scales as herbivores and pathogens must adjust their counterstrategies to cope with a moving target rather than a fixed phenotype (Karbon and Myers 1989, Adler and Karban 1994, Agrawal and Karban 1999). Thus inducibility potentially slows the counter-adaptation of herbivores to plant defenses. On the other hand, in an environment with predictable and constant levels of herbivory, constitutive defenses may be favored (Karbon and Myers 1989, Ruiz *et al.* 2002).

Inducibility may also affect herbivore feeding behavior. For instance, induced defenses may cause herbivores to relocate following damage, dispersing subsequent damage to other parts of the plant or to nearby plants (Karbon 2011). Dispersed damage may be more favorable to the plant than concentrated damage. Increased herbivore movement may also increase

parasitism and predation rates providing an indirect benefit to the plant (Agrawal and Karban 1999).

All of the above-mentioned advantages of inducibility may have favored its evolution and may explain the prevalence of this strategy in plants. However, because of the dynamic environment plants face, employing a combination of constitutive and induced defenses may be the most adaptive. In a 2004 meta-analysis exploring trade-offs between the two kinds of defense, Koricheva *et al.* (2004) found evidence for trade-offs but they also acknowledged that constitutive and induced defenses are not mutually exclusive. Indeed, constitutive and induced defenses may not be redundant, but together can provide a highly effective defense strategy. For instance, constitutive defenses can provide an immediate defense during the lag time typical of most induced responses (Ruiz *et al.* 2002).

Mechanisms of induced plant responses to herbivory

Plant defenses are also classified based on whether they are morphological (such as thorns, spines or trichomes), chemical (such as alkaloids or proteinase inhibitors), or phenological (such as early growth or reproduction to escape herbivory). Surprisingly, seemingly permanent aspects of morphology can be induced by herbivory. Common induced morphological responses include changes in branching, leaf flush, bud burst, floral traits, shoot regrowth, growth of spines or thorns and changes in trichome or pigment gland density (Agrawal and Karban 2000, Denno and Kaplan 2006). Induced changes in plant morphology generally take more time than the relatively rapid changes in plant chemistry.

Changes in plant defense chemistry are probably the most widely known and actively researched induced responses to herbivory. Herbivory can increase the concentrations of putative defense chemicals include defensive proteins, phenolics, terpenoids, alkaloids and indole glucosinolates through the activation of biosynthetic pathways (Denno and Kaplan 2006). Volatile organic compound (VOC) composition and quantity may also change as a result of herbivory. While not directly defensive, we will see that herbivore induced VOCs are an important component of plant responses to herbivory. Preformed defense chemicals may be released by herbivore damage although some herbivores may also deactivate preformed chemical defenses (Denno and Kaplan 2006). As an example, some insects cut latex-bearing veins on plant leaves rendering the downstream tissue free of latex (Dussourd and Eisner, Agrawal and Konno 2009). Chemical changes frequently occur rapidly after damage, on a time scale of minutes to a few days (Karban and Myers 1989, Karban and Baldwin 1997, Underwood 1998, Gomez *et al.* 2010).

Herbivory can also alter plant nutrition and source-sink dynamics (Denno and Kaplan 2006). For instance, aphids divert phloem from the plant, acting as a nutrient sink. Other herbivores have been shown to increase or decrease plant nitrogen, particularly in new plant growth.

Herbivore induced plant responses do not generally occur in only a single trait; rather, multiple plant traits are generally altered at the same time. The concept of plant defense syndromes has been proposed to explain the suites of traits that may co-occur most frequently (Kursar and Coley 2003, Agrawal and

Fishbein 2006). Kursar and Coley (2003) suggested, based on their work in tropical rainforests, that plants fall along an escape/defense continuum. The escape syndrome is typified by weak chemical defenses, lower nutrition and higher growth rates while the defense syndrome is characterized by higher levels of defense and slower growth rates. As plant tissue is most vulnerable to herbivory in early developmental stages, faster growth rates provide a means of reducing the period of time a plant is vulnerable to herbivory. In contrast, slower growth rates increase the period of vulnerability and is often associated with highly defended tissue (Kursar and Coley 2003). Agrawal and Fishbein (2006) determined that 3 possible defense syndromes occur in 24 species of *Asclepias*. Two of their described syndromes correlate with Kursar and Coley's (2003) defense strategy, in each case involving high defense and high concentrations of tissue nitrogen. These two "defense" syndromes differed in that the first involved primarily physical defenses such as high trichome densities and latex while the second involved high levels of cardenolides (Agrawal and Fishbein 2006). In contrast, Agrawal and Fishbein's (2006) third possible syndrome involved low nutritional quality and low digestibility. Agrawal and Fishbein (2006) proposed a "defense syndrome triangle" as a model that includes the escape and defense syndromes described by Kursar and Coley (2003) and also the low nutritional quality syndrome that they described. The low nutritional quality syndrome is closely related to the group of traits described by Feeny (1976) for highly apparent plants. Further research is merited in this area to determine whether these correlations are adaptive and widespread.

Researchers are increasingly using molecular techniques such as microarray analysis and genetically transformed plants to study the mechanisms of plant defense (Halitschke and Baldwin 2002, Roda and Baldwin 2003, Zhu-Salzman *et al.* 2005). There are multiple, well-studied biosynthetic pathways involved in induced plant responses. Induced plant responses are produced by mechanical damage in combination with insect-specific elicitors. This elicitation triggers cascading pathways that result in up-regulation of defense responses (Halitschke and Baldwin 2005). The jasmonic acid (JA) and salicylic acid (SA) pathways have been studied in great detail with ongoing research focusing on signaling compounds such as ethylene, auxin, abscisic acid and methanol (Utsumi 2010). Wounding alone can produce a defense response, however insect elicitors typically induce a larger or different response than wounding alone (Zhu-Salzman *et al.* 2005).

The JA and SA pathways are differentially induced within the same plant. Feeding guild seems to be one of the most important factors determining which pathway responds. The JA pathway is generally triggered by chewing insects while the SA pathway is generally induced by sucking insects or pathogens (Thaler *et al.* 1999, Walling 2000, Heidel and Baldwin 2004, Ali and Agrawal 2012, Thaler *et al.* 2012). Heidel and Baldwin (2004) investigated molecular plant responses from 5 different herbivores in three feeding guilds using microarray analysis. Lepidopteran leaf-chewers induced a pattern consistent with JA induction, while a cell-content puncture feeder elicited an SA-type pattern. Aphids induced little responses in contrast to other studies in which phloem feeders elicit

the SA pathway. Some phloem feeders may induce the SA pathway while others induce the JA pathway (Thaler *et al.* 2012). In 2000, Walling reviewed induction by various feeding guilds and found that phloem feeders like aphids induce a response similar to pathogens while induction by chewers and cell content feeders most closely resembles the wound-signaling response.

Current research supports differential induction by various feeding guilds and hints at the mechanistic reasons behind the pattern. In a review of 13 recent studies, Ali and Agrawal (2012) found that phloem-feeders induced fewer JA genes, suppressed more genes in total and induced weaker overall plant responses than chewers. This response is consistent with pathogen-induced plant responses and probably occurs because phloem-feeders typically cause only minor tissue damage as compared to chewers. In contrast, chewing herbivores induced few genes typical of the SA pathway and induced stronger overall plant responses than suckers, consistent with the idea that the greater tissue damage induces a response similar to the wound-signaling response. Both SA and JA can be applied exogenously to plants resulting in induction of their respective pathways (Thaler *et al.* 1999) and this technique is frequently used to elucidate mechanisms.

There is evidence that these two response pathways interact antagonistically, as demonstrated in laboratory experiments of tomato, tobacco and *Arabidopsis thaliana* (Thaler *et al.* 2002) and documented in 17 total plant species (Thaler *et al.* 2012). The antagonism between pathways occurs when induced with exogenous JA and SA application and has also been demonstrated

a few times in plants induced by herbivores (Thaler *et al.* 2002, Thaler *et al.* 2012).

Specificity of plant responses may be due in part to cross-talk between pathways providing plants with mechanisms to tune a specific response to a particular attacker (Halitschke and Baldwin 2002). In *Arabidopsis*, SA is prioritized over JA but this can be modified with ethylene which promotes the JA pathway (Thaler *et al.* 2012). In other species, JA tends to suppress the SA pathway (Thaler *et al.* 2012). Besides ethylene, various other hormones also modulate either the JA pathway, SA pathway or both pathways. These hormones include abscisic acid, auxin, gibberellins, cytokinins and brassinosteroids (Erb *et al.* 2012, Thaler *et al.* 2012).

The interaction between the two biochemical pathways may also depend on timing and strength of induction and compensation can occur when one pathway is disabled (Thaler *et al.* 2002, Thaler *et al.* 2012). While cross-talk is generally considered adaptive, it may also lead to induced susceptibility in certain situations (Thaler *et al.* 2012). In a test of four different herbivores' performance on plants induced with both an SA analog and JA, there was a positive effect on cabbage looper performance due to attenuation of the JA pathway. There was no effect of attenuated plant resistance on the performance of thrips, spider mites or hornworm caterpillars (Thaler *et al.* 2002). More research is needed to test the hypothesis that the JA–SA antagonism is adaptive (Thaler *et al.* 2012).

Variation in plant responses to insect herbivory

The expression of induced plant responses to herbivory can be altered by multiple factors, including herbivore density, location of damage, herbivore identity and damage type.

The magnitude of induced plant responses can depend on the density of the attacking herbivore. For instance, spider mites feeding on cotton plant cotyledons induced changes in the density of pigment glands on cotyledons, first and second true leaves in a density-dependent manner. These pigment glands contain defense chemicals including gossypol and other terpenoid aldehydes (Agrawal and Karban 2000). Density dependence is not necessarily a linear effect; in a recent study (Robert *et al.* 2012), the authors found that medium densities of a root herbivore (*Diabrotica virgifera virgifera*) produced peak emissions of several induced VOCs. While herbivore density is an important consideration, induced plant responses can and do occur at very low levels of herbivory (Kaplan and Denno 2007, Ohgushi 2008).

Herbivore-induced plant responses can either occur locally to the damaged tissue or systemically with induction occurring even in distant non-damaged tissue (Schilmiller and Howe 2005). The vascular architecture of the plant is involved with systemic induction, with plant parts that share vascular connection more likely to have similar levels of induction (Orians 2005). However, induction is not entirely dependent on these connections. Induction can also occur in distant plant parts or even neighboring plants as a result of herbivore-

induced volatile organic compound (VOC) emission (Baldwin *et al.* 2006, Heil and Karban 2010).

Plants responses depend in part on the type of damage and herbivore identity. Some studies have shown that simple mechanical damage can be sufficient to induce plant responses. For instance, in an early study Silkstone (1987) applied mechanical damage to birch leaves and measured subsequent leaf damage by herbivores. Experimental leaves received less overall herbivory and had less tissue loss due to herbivory than controls, providing evidence of plant response to mechanical damage. However, the earlier observation that mechanical damage was not equivalent to herbivore damage (Haukioja and Neuvonen 1985) led to research on herbivore-specific plant responses (Agrawal 2000).

Variation in plant response to different herbivores has been termed specificity of elicitation (Viswanathan *et al.* 2005). Plant traits that vary depending on herbivore identity include defensive proteins, nutrient concentrations, latex production, trichome density and VOC production and composition (Viswanathan 2007). For instance, different insect species induce different chemical defense responses in tomato plants (Stout *et al.* 1996, Stout *et al.* 1998). Tomato plants induced by the noctuid caterpillar *Helicoverpa zea* had increased levels of polyphenol oxidase and proteinase inhibitors (Stout *et al.* 1996). In contrast, induction by the aphid *Macrosiphum euphorbiae* increased peroxidase and lipoxygenase levels (Stout *et al.* 1998).

Specificity of elicitation is a result of signals from both the type of damage inflicted on the plant and herbivore-associated chemical elicitors (Agrawal 2000, Kessler and Halitschke 2007, Poelman 2008). Damage type is strongly associated with the plant response, with characteristic responses induced by different feeding guilds such as leaf chewers, cell content feeders and phloem feeders (Walling 2000, Ali and Agrawal 2012). Chemical elicitors have been identified from insect regurgitant, saliva and oviposition secretions. Known elicitors include β -glucosidase, fatty acid-amino acid conjugates, inceptins, bruchins and caeliferins (Doss *et al.* 2000, Kessler and Baldwin 2002, Kessler and Halitschke 2007, Ali and Agrawal 2012).

Specificity of elicitation may also relate to whether the herbivore is a specialist or generalist of the host plant. Specialists may induce a more specific plant response as compared to generalists. In a 2012 review, Ali and Agrawal found few studies that rigorously tested this hypothesis and those found little support for it.

Some recent work suggests that plant responses to herbivory can be passed down to plant offspring, reducing the lag time for induction (Agrawal *et al.* 1999, Agrawal 2001, Agrawal 2002, Holeski *et al.* 2012). For example, offspring of herbivore-induced wild radish (*Raphanus* spp.) plants had more trichomes per leaf than offspring of control plants (Agrawal *et al.* 1999). This was not an anomalous finding; in 2012, Holeski reviewed additional studies that demonstrate transgenerational induction. While many of these studies examined induction by pathogens, transgenerational induction by herbivores has been demonstrated in

Arapidopsis, tomato (*Solanum lycopersicum*) and monkeyflower (*Mimulus guttatus*) in addition to wild radish (Agrawal *et al.* 1999, Holeski 2012).

Effects of induced plant responses on insect herbivores

Induced plant responses may be considered from the herbivore point of view as either induced resistance or induced susceptibility. Induced resistance is an induced response that decreases herbivore preference or performance (Karban and Baldwin 1997, Agrawal and Karban 1999, Underwood 1999). In contrast, induced susceptibility is a plant response that has a positive effect on herbivore performance or preference (Karban and Baldwin 1997, Karban and Myers 1989). Examples of induced resistance and induced susceptibility occur for each of the induced plant response types discussed above.

While many studies have investigated the effect of induced plant responses on herbivores, few demonstrate the mechanism of the effect. However, general patterns have emerged. For instance, changes in plant chemistry may decrease herbivore fitness or preference but also may attract specialist herbivores. Changes in morphology may deter herbivores as in the case of increased trichome density but may also benefit herbivores as in the case of leaves flushed after herbivory that are more tender and nutritious than older tissue. New shoot growth is often favorable for oviposition, potentially due to being less tough than older shoots.

In addition, different herbivores may elicit different plant responses. In addition, herbivores may respond differently to a given plant response. This phenomenon is known as specificity of effect (Karban and Baldwin 1997, Stout *et*

al. 1998, Van Zandt and Agrawal 2004a). Karban and Baldwin (1997) categorize specificity of effect based on which herbivores are impacted: whether on the inducing herbivore alone (high specificity) or on many different herbivores (low specificity). It is predicted that in cases of high specificity of effect, conspecifics of the inducing herbivore should be more affected than other herbivores. In contrast, some induced plant defenses can have a very broad generality of effect, such as the cucurbitacins found in the squash family. These chemicals defend against a wide variety of organisms including spider mites, roaches, beetles, caterpillars and even mice (Agrawal and Karban 2000). Latex is another example; it occurs in approximately 10% of all plant species and negatively impacts a range of herbivores due to both its physical and chemical characteristics (Agrawal and Konno 2009, Agrawal and Heil 2012). Other responses may only impact a subset of the full range of potential herbivores. For instance, hypersensitive response, which consists of plant cell death surrounding the site of attack, is associated with non-mobile herbivores that are intimately associated with plant tissue such as galling insects and leaf miners (Fernandes and Negreiros 2001).

Indirect interactions between insects mediated by plant trait change

Indirect interactions are a direct result of herbivore-induced plant responses which provide the mechanism to mediate a range of interactions between the inducing species and species that are subsequently affected by the plant responses. Here we will remain focused on insect herbivore-induced plant responses, although it is worth noting that plants may be induced by other stressors, including mammalian herbivores, pathogens and mechanical damage. Likewise, diverse organisms may be at the receiving end of the interactions, including pollinators, pathogens and non-insect herbivores.

Plant-mediated indirect interactions between insect herbivores

Plants mediate interactions ranging from mutualisms to competition, although the focus of research has been on the latter. In 1960, Hairston *et al.* published a seminal theoretical paper that altered the conventional view of the factors limiting herbivore abundance. Prior to that time, herbivore abundance was assumed to be limited primarily by resource availability (bottom-up hypothesis), so that competition with other herbivores for resources was considered the most important interaction. However, Hairston *et al.* (1960) argued that herbivore abundance is unlikely to be limited by resource competition because plants are clearly abundant and rarely consumed entirely. They proposed instead that herbivore abundance was dictated by interactions with higher trophic levels, such as predation and parasitism.

This idea that top-down forces control herbivore populations, known as the “Green World” hypothesis, persisted for decades. This view has slowly shifted as understanding of plant trait changes induced by herbivory has grown. Induced resistance provides a mechanism for competition between herbivores that does not depend solely on food quantity but rather on the herbivore-induced changes in food quality. In addition, ecologists are beginning to recognize that positive indirect interactions are also quite common and may be equally important in structuring ecological communities. Induced susceptibility provides a mechanism for positive indirect interactions between insect herbivores, as mediated by the plant food source.

Plant-mediated indirect interactions do not necessarily depend on two insect species utilizing the same part of the plant or sharing the same plant simultaneously. As induced responses can occur at time scales ranging from hours to years, the length of temporal separation can be highly variable. Altered plant chemistry generally occurs quite quickly and may relax to constitutive levels within days or weeks. Morphological changes including increased trichome densities or new growth may occur quite slowly in comparison but they generally persist for a much longer time span.

Interactions between temporally separated herbivores have been reported since at least 1986 when Faeth documented asymmetric competition between early and late season herbivores of *Quercus emoryi*. He found that early-season leaf chewers negatively impacted late-season leaf miners. This impact occurred more frequently on intact leaves rather than damaged leaves because damaged

leaves had higher tannin and lower protein concentrations compared to intact leaves. The observed interaction between the two herbivores was strongly asymmetric, approaching amensalism.

Since publication of Faeth's 1986 paper, many other researchers have documented interactions between temporally separated herbivores as mediated by plants. There are examples of both negative and positive interactions involving a variety of herbivores including aphids, beetles, planthoppers, weevils, sawflies, galling insects and thrips (Ohgushi 2005). For instance, a stem-boring moth (*Archinara geminipuncta*) induced narrow side shoots in common reed (*Phragmites australis*) which were then utilized by the gall-making midge *Giraudiella inclusa* which prefers thin shoots. Prior moth damage was correlated with increased midge egg survival and abundance, demonstrating induced susceptibility (Tscharntke 1988).

More recent work has focused on how sequence of arrival modifies interactions. A few studies (Voelkel and Baldwin 2004, Viswanathan *et al.* 2007) have indicated that sequence of arrival may be an important factor in indirect interactions, however few have tested this explicitly. A recent meta-analysis of aboveground–belowground interactions found that the sequence of arrival strongly influenced interactions between aboveground (AG) and belowground (BG) herbivores. BG herbivores had a positive effect on AG herbivore performance when they arrived simultaneously but not when either arrived first. AG herbivores on the other hand had a negative effect on BG herbivore performance when AG herbivores arrived first (Johnson 2012). In a study of the

interaction between leaf- and root-feeders on teosinte and cultivated maize, the leaf herbivore only negatively impacted colonization and growth by the root-feeder when the leaf herbivore arrived first. When the root-feeder arrived first, larval performance was not affected although adult emergence was reduced. The authors proposed that feeding deterrent or repellent secondary metabolites are the cause (Erb *et al.* 2011). In general, the competitive advantage goes to the earliest colonizing herbivores.

Plant mediated interactions frequently occur between insect herbivores that do not utilize the same plant part. Like temporal separation, spatial separation between interacting species is highly variable as induced plant responses may be localized to the damaged tissue or be systemic. The scale of variability in plant tissue quality ranges from within a single leaf to the entirety of the plant body (Shelton 2005). Spatially separated herbivores may even be mediated by different plants, with plant-plant signaling inducing defense responses across individuals. Spatial separation also encompasses interactions between members of different feeding guilds that frequently utilize different parts of the host plant, such as interactions between phloem-feeders and leaf chewers, as well as interactions between herbivores and pollinators, or herbivores and ovipositing insects.

Case study: aboveground–belowground plant-mediated insect interactions

Since by definition herbivory does not kill the plant, interactions are temporally and spatially separated insect species are frequent. Aboveground (AG) – belowground (BG) herbivore interactions provide an excellent case study of

plant-mediation involving both spatial and temporal separation. In addition, since most research involving AG–BG interactions is very recent, it provides a snapshot of the current work in this field. In this section, I will use AG–BG interactions to examine general principles and current understanding of plant-mediated indirect interactions.

Early work on potential aboveground–belowground interactions centered on the idea that BG herbivores could provoke a plant response similar to that of drought stress due to reduction in plant root biomass. The drought stress response results in increased concentration of AG nitrogen and carbohydrates. Therefore it was predicted that BG herbivores could have a positive impact on AG herbivores which would benefit from the improved nutritional quality of plant tissue aboveground. Conversely, AG herbivores could negatively impact BG herbivores as reduction in AG plant tissue would reduce allocation to belowground biomass (Masters 1992, 1993). This hypothesis was tested by Masters and Brown (1992) with a study of the interaction between a root chewer (*Phyllopertha horticola*) and a leaf miner (*Chromatomyia syngenesiae*) on common sow thistle (*Sonchus oleraceus*). They found that root herbivory increased pupal weight of the leaf miner while leaf herbivory reduced growth rate of the root herbivore, a contramensal interaction. While they did not find a difference in total leaf nitrogen, they proposed that the BG herbivore increased leaf quality whereas leaf mining decreased root biomass, a likely cause of the negative part of the interaction.

However, further testing of this “stress response hypothesis” has not been as promising. For instance, Hunt-Joshi and Blossey (2005) tested it using purple loosestrife (*Lythrum salicaria*) and its specialist herbivores, a leaf-feeding chrysomelid beetle and a root-feeding weevil. They demonstrated negative effects of leaf herbivory on the weevil in a potted plant study but not under field conditions. They found no effect on the AG beetle in response to the BG weevil in either the potted plant experiment or four-year long field study. The authors suggest that the AG herbivore would be most likely to negatively impact the BG herbivore in cases of extreme defoliation, which would result in partial or complete death of BG tissue (Hunt-Joshi and Blossey 2005).

Also contrary to the expectations of the stress response hypothesis, Bezemer *et al.* (2003) found that root herbivory had a negative effect on an aboveground herbivore. They investigated the impact of leaf and root herbivory on terpenoid concentrations in cotton (*Gossypium herbaceum*). Root herbivory increased terpenoid levels throughout the plant while foliar herbivory increased terpenoids primarily in young leaves. As a result, in the foliar herbivory treatment, the AG herbivore shifted its feeding from young to mature leaves. No response was seen in the BG herbivory treatment. Thus the consumption and growth rate of the AG herbivore was reduced on plants exposed to root herbivory.

In a review of the available literature, Blossey and Hunt-Joshi (2003) suggest that the success of the stress response hypothesis may depend on the study system. The bulk of studies supporting the hypothesis were short term and conducted in early successional communities predominated by annual species.

Blossey and Hunt-Joshi argue that as resource availability and root herbivore populations increase in maturing communities the hypothesis may no longer apply (Blossey and Hunt-Joshi 2003).

The mechanisms governing these patterns may not be adequately predicted by the stress response hypothesis, but some general patterns have begun to emerge. BG organisms can increase or decrease concentrations in AG tissue of putative defense compounds such as terpenoids, glucosinolates and phenolics. For instance, most studies of root-chewing insects show an overall increase in plant chemistry (Bezemer and van Dam 2005, Kaplan *et al.* 2008).

In contrast to the effect of BG herbivores on AG defenses, the effect of AG herbivores on BG defenses appears to be weak (Soler *et al.* 2007, Kaplan *et al.* 2008). There are studies that document either increased or decreased levels of defense chemistry in plant roots as a result of AG herbivory. The quality of root exudates may also be altered by AG herbivory (Bezemer and Van Dam 2005, Soler *et al.* 2007). These changes may be responsible for changes in belowground soil communities. For instance, foliar application of JA and SA have been shown to reduce the numbers of root-feeding grape phylloxera and root-knot nematodes respectively (Bezemer and Van Dam 2005).

In a recent meta-analysis (Johnson 2012) identified four factors that most influenced experimental results of AG–BG interactions: 1) sequence of herbivore arrival (discussed previously), 2) performance parameter measured, 3) plant and study type, and 4) herbivore type. The performance parameter measured was important when examining effects of AG herbivores on BG herbivores. For

instance, AG herbivory negatively impacted BG survival but positively affected BG population growth rates. In contrast, BG herbivore effects on AG herbivores did not depend on which performance parameters were measured. This finding indicates that researchers should measure multiple performance parameters in order to demonstrate positive or negative interactions between insect herbivores.

The most consistent results were obtained in lab studies rather than field experiments although it did not matter whether the plant was a natural species or an agricultural plant. Plant type also affected study results with AG herbivores negatively impacting BG herbivores on annuals, but not on perennials. Currently, much of the existing research has been done on annual plant systems. Additional work is needed to understand perennial plant systems.

Herbivore taxa also influenced outcome, perhaps through specificity of elicitation. BG dipterans negatively affected AG herbivores while BG coleopterans had positive impacts on AG homopterans and negative impacts on AG hymenopterans. AG herbivore type did not appear to have significant effects on BG herbivory. Further research that integrates AG–BG experimental designs with work on specificity of elicitation might clarify this complexity.

Plant-mediated indirect interactions involving natural enemy recruitment

In addition to mediating interactions between two insect herbivores, plants may mediate more complex interactions involving additional trophic levels. Several mechanisms by which plants can mediate these interactions have been

identified. Induced plants may alter the herbivore quality or other traits as perceived by predators or parasitoids of herbivores. Plants may also recruit natural enemies of herbivores, such as parasitoids or predators, thereby reducing herbivore damage or abundance.

While natural enemy attraction is generally considered an indirect defense, only a few studies actually link natural enemy attraction to improved plant fitness (Van Der Meijden and Klinkhamer 2000, Kessler and Baldwin 2002). Several studies have demonstrated increased seed production on plants with parasitized caterpillars lending credence to the adaptivity of parasitoid attraction (Dicke et. al 2003). However, parasitism of insect herbivores may have some negative impacts on plant fitness. In particular, koinobont parasitoids (those that permit their host to continue development) may slow down herbivore development, resulting in longer feeding time on the host plant (Dicke 2000). There is some evidence that hosts parasitized by solitary parasitoid species consume less plant material than unparasitized herbivores. However, hosts parasitized by gregarious parasitoids may consume the same or slightly more than unparasitized hosts (Dicke 2000).

Methods of natural enemy attraction include the release of volatile organic compounds (VOCs) and non-volatile contact cues as well as the secretion of extrafloral nectar (EFN). Upon damage by herbivores, most plants emit VOCs. There is ample evidence that predators and parasitoids use VOCs for host location (De Moraes *et al.* 1998, Dicke 2000, Rutledge 1996). Infochemicals (including VOCs and contact cues) may be classified into several types (Dicke

and Sabelis 1988, Rutledge 1996). Kairomones, such as plant VOCs used as natural enemy attractants, benefit both the emitting and receiving organisms. On the other hand, synomones benefit only the receiving organism. For example, parasitoids may use herbivore-derived infochemicals for host location. However, herbivore-based cues are generally more difficult to detect than plant-based cues as there is an evolutionary disadvantage for the herbivore to broadcast its location (Vet and Dicke 1992). In contrast, plants potentially benefit from releasing host-location cues (Kessler and Heil 2011). Parasitoid search behavior has been connected to the composition of VOCs as blends are often specific to the initiating herbivore and can be modified by subsequent or simultaneous herbivory.

Natural enemies also use VOCs to discriminate between plants either damaged by previously parasitized or unparasitized hosts. Fatouros (2005) demonstrated that the parasitoid wasps *Cotesia rubecula* and *C. glomerata* land preferentially on plants in an unparasitized host treatment rather than the parasitized host treatment. Plants produced larger quantities of VOCs in the unparasitized host treatment, potentially as an adaptation to reduce induction costs once natural enemies have been recruited (Fatouros 2005).

VOC-mediated enemy attraction has most commonly been studied aboveground, but research of belowground systems demonstrates that root VOCs can also attract natural enemies. In a recent study by Rasmann *et al.* (2011), entomopathogenic nematodes were attracted by VOCs released by plant roots damaged by a root-boring beetle. With nematodes present, beetle survival

rate was reduced, leading to no change in aboveground biomass relative to control plants. Without nematodes, the beetles survived and reduced AG biomass by over 40% (Rasmann *et al.* 2011). Since AG herbivory can affect BG root exudates and potentially BG VOCs, it is possible that AG herbivory can impact BG indirect defenses. Bezemer and Van Dam (2005) reported that no studies had yet been done to address that question, which could be an important area of future research.

VOCs communicate plant location to insects from a distance. In contrast, contact cues assist parasitoids in detecting a suitable host insect once on the plant. Shiojiri *et al.* (2001) found that two species of specialist endoparasitic wasps discriminated between plants depending on whether plants had been damaged by host or non-host species. Both wasps spent more time searching on plant leaves damaged by their hosts than on those damaged by nonhost larvae or artificially damaged. Simultaneous damage by their hosts altered both chemical cues and parasitoid preference. *Cotesia glomerata* was more attracted to and had higher parasitism rates on plants with simultaneous herbivory than control plants. The responses of *Cotesia plutellae* to simultaneous herbivory were the opposite (Shiojiri *et al.* 2001, Shiojiri *et al.* 2002).

The use of VOCs to attract natural enemies does not come without cost to the plant. In addition to the physiological costs of VOC induction for the plant, there are potential ecological costs as herbivores may also use VOCs to locate the plant (Dicke 2000).

Recent work shows that plants also recruit natural enemies through the secretion of extrafloral nectar (EFN; Kessler and Heil 2011). While studies of this are increasingly common, there is far less research on this type of indirect defense than on VOC emissions (Heil *et al.* 2001, Dicke *et al.* 2003). Extrafloral nectar has been documented in at least 104 plant families (Kessler and Heil 2011) and it has been shown to attract diverse organisms, most commonly ants, wasps, mosquitoes and other insects (Kost and Heil 2005). The induction of EFN through herbivory has been demonstrated in some plants although others express EFN constitutively (Heil *et al.* 2001). EFN can indirectly reduce herbivory through the recruitment of ants and wasps that defend the plant from other insects, including herbivores. For example, Kost and Heil (2005) demonstrated that the application of artificial nectar (simulating natural levels of EFN production) increased the presence of ants, wasps and flies on lima bean plants (*Phaseolus lunatus*). This resulted in a significant reduction in the rate of herbivory on plants treated with artificial nectar relative to control plants.

Surprisingly, induced plant responses may negatively impact natural enemies. For instance, in one study (Thaler 2002), fewer adult parasitoids emerged from host caterpillars on induced plants than on controls. This decrease was attributed to decreased herbivore quality on induced plants. In the same study, induced tomato plants decreased the abundance of an aphid predator, possibly due to decreased aphid densities. In addition, VOCs occasionally deter rather than attract natural enemies although attraction does seem to be more prevalent (Dicke 2000).

Greater effects of plant-mediated insect interactions

Species interactions occur in the greater context of multiple species living in diverse ecological communities. Increased knowledge of the dynamic responses of plants to herbivory has altered scientific understanding of the pivotal role plants can play in community dynamics. Plant-mediated indirect interactions can have diverse and rippling effects on multiple species and ultimately the larger ecological community. This very recent field of study reveals the full range of positive, negative and neutral interactions mediated by plant responses and the impacts these have throughout ecological communities. The complexity of these multispecies interactions will only be elucidated through further study, as we move beyond the previous paradigm that focused only on pair-wise interactions.

Plant-mediated interactions that involve more than two insect species

Compared to the research discussed thus far, there is far less empirical work on more complex multispecies interactions mediated by plants. In the natural enemy recruitment scenarios discussed above, an herbivore induced a plant response that then attracted a predator or parasitoid of the herbivore. Likewise, parasitized and unparasitized hosts elicited specific plant responses, ultimately influencing additional enemy recruitment and plant fitness. In an example of the complex ripple effects of indirect interactions, Poelman *et al.* (2011) demonstrated an indirect interaction between two parasitoids, ultimately

mediated by changes in plant quality. In this study, the endoparasitoid *Cotesia glomerata* had higher mortality on plants fed on by hosts parasitized by *Cotesia rubecula*; *C. rubecula* survival was unaffected by prior herbivory of either parasitized or unparasitized hosts. The authors propose that differences in level of damage by parasitized hosts and differences in caterpillar regurgitate can explain the differences in plant quality which cascade up to the parasitoids. This interaction is an example of asymmetric competition with *C. glomerata* as the inferior competitor. The authors cite a study which demonstrates that *C. glomerata* in fact avoids plants previously damaged by hosts parasitized by *C. rubecula*. In the same study system, a previous study (Fatouros et al. 2005) demonstrated that *C. glomerata* discriminates between plants previously damaged by *C. rubecula*-parasitized hosts using VOCs and avoids those plants.

As mentioned previously, some work has illustrated how indirect defenses can involve the belowground community. Plants can mediate interactions between herbivores that are spatially separated, including root and shoot herbivores. Plants can also mediate interactions between these communities at upper trophic levels. Most commonly, studies have examined the impact of BG herbivory on AG communities. For instance, Masters *et al.* (2001) used a soil-insecticide treatment to show that root-feeding insects can increase the abundance of both a seed predator and its parasitoids. While both the seed predator and the parasitoids were more abundant on plants subject to root herbivory, the rate of parasitism did not differ between treatments.

Indirect plant defenses may be one method by which BG herbivory impacts multiple AG species. Bezemer *et al.* (2005) studied the impacts of BG herbivory on higher AG trophic levels. In a greenhouse study, nematodes reduced the number of aphid offspring, but the aphids were larger and parasitoid survival was higher. Since parasitoid performance and preference have been linked to host size, the impact of nematodes on aphid size may have positively affected parasitoids in this study.

Less commonly, researchers are exploring the impact of AG herbivory on BG communities. Soler *et al.* (2007) studied the impact of AG herbivory by *Pieris brassicae* (large cabbage white butterfly, a leaf chewer) on the root-chewing herbivore *Delia radicum* (cabbage root fly) and its endoparasitoid *Trybliographa rapae*. They demonstrated that prior AG herbivory negatively affected the BG herbivore and its parasitoid. Survival and performance of both *D. radicum* and its parasitoid decreased when reared on black mustard plants (*Brassica nigra*) that had been previously exposed to *P. brassicae* larvae for six days. Neither root biomass nor root nitrogen was affected by *P. brassicae* herbivory, however there was an increase in indole glucosinolates in the roots, a possible mechanism for the interaction.

Effects of plant-mediated interactions on ecological communities

Increasingly, the importance of indirect interactions has been realized by ecologists and research has begun to incorporate the role of indirect interactions into community ecology (Utsumi 2011). Some of this work centers around new ways to explore interaction webs, including non-trophic and indirect interactions

rather than only consumer-resource interactions. This is a very important endeavor but will not be explored in greater detail here. Some excellent recent reviews of this topic include those by Utsumi and colleagues (2010) and Ohgushi (2008). Other community level work focuses on changes to community composition and other community level parameters that change as a result of indirect interactions.

Utsumi and Ohgushi (2009) observed that community level impacts rely on three factors. First, plant responses to herbivory can alter the performance and preference of other herbivores. As we have seen, this can be either induced resistance or induced susceptibility, thus having positive or negative effects on subsequent herbivores. Second, plant responses can alter abundance, species richness and species composition of herbivores. Third, the indirect effects between herbivores (mediated by plant responses) can alter interactions between other members of the larger community, affecting predator abundance or species richness, for instance (Utsumi and Ohgushi 2009).

Insect herbivores potentially play an important role in structuring communities. Because plant responses to herbivory are dependent at least in part on herbivore identity and sequence of herbivore arrival, early season herbivory can alter the composition of the subsequent community. The initial herbivore has been shown to change community level parameters in several model systems. The community of herbivores that utilize monarchs varies depending on initial herbivory by monarchs, weevils or leaf beetles (Van Zandt and Agrawal 2004b). Initial herbivore identity also impacts subsequent

colonization of bittersweet nightshade (*Solanum dulcamara*) while mechanical damage does not (Viswanathan *et al.* 2005). Utsumi and colleagues (Utsumi and Ohgushi 2009, Utsumi *et al.* 2009) investigated the moth-induced regrowth of willow shoots and the subsequent structure of herbivore and predator communities. Abundance and species richness of herbivores increased on regrown shoots, potentially due to increased nitrogen content of the new leaves. Predator abundance and richness also increased. Shelter-builders also potentially increase abundance and species richness. For instance, the presence of leaf rolls increased arthropod species richness and abundance on cottonwoods (Martinsen *et al.* 2000).

Feeding guild also potentially affects changes in species richness and abundance. Removal of an aphid species from cottonwoods reduced species richness and abundance while removal of a leaf-feeding beetle increased species richness and abundance (Waltz and Whitham 1997). While the mechanisms were not investigated, aphids may have increased species richness through provision of honeydew, as well as through altered source-sink dynamics. In contrast, the beetle consumed large quantities of foliage and may have negatively affected plant quality (Waltz and Whitham 1997).

Mammalian herbivores also impact community structure. For instance, Bailey and Whitham (2003) studied the community impacts of elk browsing on aspen (*Populus tremuloides*). Elk browsing reduced gall density of the leaf-edge galling sawfly *Phyllocolpa bozemanii*. Sawfly gall density was associated with both increased arthropod species richness and increased bird predation. Thus

elks negatively impacted both the arthropod community and avian foraging. In an earlier study, Roininen *et al.* (1997) documented induced susceptibility of two members of the Salicaceae to sawflies following browsing by moose and hares. Leaf-folding sawfly densities increased after browsing, possibly due to the regrowth of longer shoots.

Because herbivore-induced plant responses have community level manifestations, they can potentially impact the success of invasive species. For example, Ando *et al.* (2011) documented the mechanism by which the exotic aphid (*Uroleucon nigrotuberculatum*) affects the late season dominance of native insects in Japan. This aphid, found in Japan since about 1990, is a specialist of tall goldenrod (*Solidago altissima*), which was introduced to Japan about 100 years ago. The aphids feed on tall goldenrod in the spring, which the authors found induced increased plant tissue nitrogen levels later in the growing season. Thus in the fall, aphid-induced plants were dominated by leaf chewers while non-induced plants were dominated by sap-suckers. Therefore the induced plant response was the mechanism by which aphids impacted other insect species in the community, even after the aphids were no longer present. If such interactions are widespread, increased knowledge of plant-mediated mechanisms could be an important tool for managing exotic insects and the ecosystems in which they occur.

The role of herbivore-induced plant responses may be particularly relevant to the success and community-level impacts of insect biocontrol agents used on invasive plants. Induced plant responses are being actively investigated for the

proposed biocontrol of several plants in the United States, including purple loosestrife (*Lythrum salicaria*) and common reed (*Phragmites australis*) (Hunt-Joshi and Blossey 2005, Park and Blossey 2008). In the future, the knowledge gleaned by these and similar studies may enhance the success of biocontrol and mitigate possible negative impacts on native insect communities.

Conclusion

The study of herbivore induced plant responses and the resulting indirect interactions has progressed dramatically since the earliest observations of these phenomena. Initially controversial, the idea that plants are able to respond to herbivores is now universally accepted and the ripple effects of these responses on communities are well-documented. However, there is still a great deal of work to do in this field.

While the biochemical pathways and similar mechanisms behind plant responses have been well-researched, there are still many knowledge gaps in concerning the cross-talk between pathways and how these pathways are modified by other signaling compounds. In addition, most of the molecular work has been conducted on just a small number of cultivated species such as tomato, *Arabidopsis*, and tobacco. More research is needed on wild plants that have not undergone strong artificial selection and on plants that vary in evolutionary history. For example, some taxa utilize unique biochemical pathways for other aspects of metabolism such as the synthesis of betalains within the Caryophyllales and the C₄ Carbon fixation pathway found in many members of the Poaceae. Because diversity within the plant kingdom is so great, it is likely that biochemical pathways of herbivore-induced response also vary. Thus a wide sampling of taxa is needed in order to represent the breadth of plant responses to insect herbivores.

Although hundreds of biochemical and molecular studies have informed understanding on plant responses to herbivory, most have been conducted in

greenhouses or growth chambers. If biochemical and molecular studies were to move out of the lab and into natural settings, they could begin to capture the full complexity of plant responses and interactions. This movement is already occurring with some workers embracing “lab techniques” in field studies, such as the use of genetically transformed plants and microarray analysis. However, more work is needed on wild plants in their natural habitat to truly grasp the evolutionary and ecological significance of plant responses to herbivory.

Studies which seek to bridge the biochemical/molecular literature with the ecological literature are necessary for an integrative understanding of plant-mediated interactions. There are several recent contributions from the field of molecular ecology that have particular relevance. The phenomenon known as “priming of plant responses”, or increased readiness to defend, is an area of molecular research that may modify current understanding of induced plant responses, including the timing of induction. This phenomenon has only been documented since 2004, however multiple mechanisms have already been investigated and the evidence that priming is widespread among plant families is rapidly accumulating (Holeski *et al.* 2012, Kim and Felton 2012).

Transgenerational induction is a related field with similar implications for understanding the timing and mechanisms of plant responses.

Research on community level effects of plant-mediated interactions is still in its infancy, but this area may have broad ramifications for community ecology as a whole. However, only a few sample communities have been explored in much detail (e.g. *Asclepias syriaca* and *Phragmites australis*). In addition,

continued work on the plant-mediated connections between entire aboveground and belowground communities will be important as belowground herbivory is an important but often overlooked component of both agricultural and natural communities. Finding the connections between plant responses and the numerous organisms in the surrounding community will be a fruitful endeavor towards elucidating the mechanisms of community structure and informing management of natural and agricultural systems.

Useful metrics for measuring and comparing interaction strength within an ecological community need to continue to be developed, as discussed in Appendix A. Such metrics would help ecologists assess the relative importance of interactions in a given community, which could in turn assist with making informed policy and conservation decisions. For example, understanding the relative strength of top-down and bottom-up forces on an insect herbivore could potentially help inform management of invasive species.

Lastly, models of indirect interaction webs should continue to be developed and revised as these tools have the potential to convey large amounts of sophisticated information for researchers and managers. There are currently a multitude of approaches that vary greatly in their depictions, such as whether interaction strength is incorporated or how clearly multiple interaction types are shown (Figs. 3-6). Although these methods vary in their strengths and weaknesses, a standardized approach that optimizes the best of each method would go far in enhancing a generalized understanding of indirect interactions in communities. Additional discussion and input will be needed from the research

community to promote the wider acceptance, development and use of these relatively new types of models.

Overall, it is vital that ecologists continue to move away from the central paradigm of pair-wise consumer-resource interactions. Species interactions are far more complex and intertwined than a simple assemblage of pair-wise building blocks. The emergent properties of interactions mediated by trait-change have ramifications throughout ecological communities that we are only beginning to understand. By incorporating the tools and knowledge of multiple disciplines and emphasizing a role for indirect interactions that rivals that of direct interactions, this field will continue to enhance our understanding and appreciation of the fascinating interplay between organisms in ecosystems.

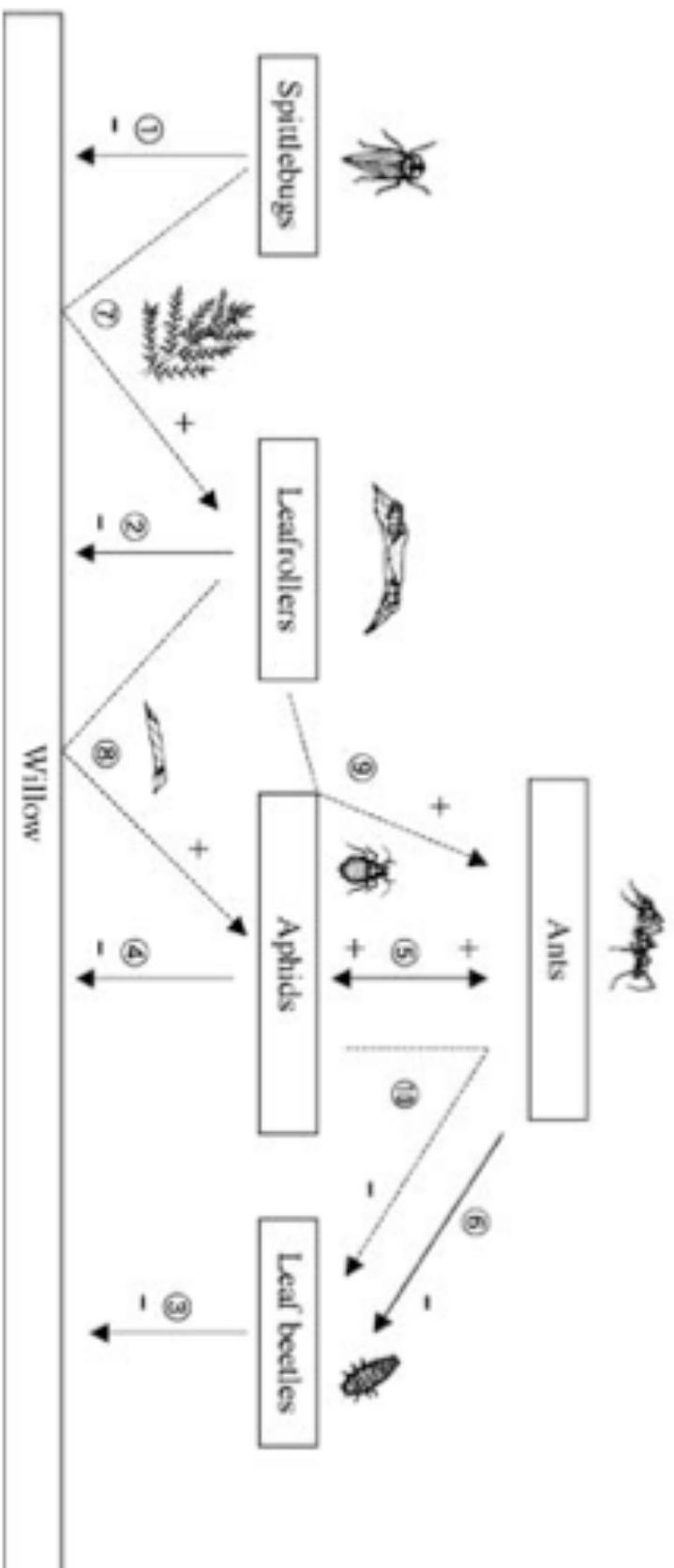


Fig. 3. Indirect interaction web (from Ohgushi 2005), numbers illustrate sequence and (+ -) symbols indicate net positive and negative effects on receivers.

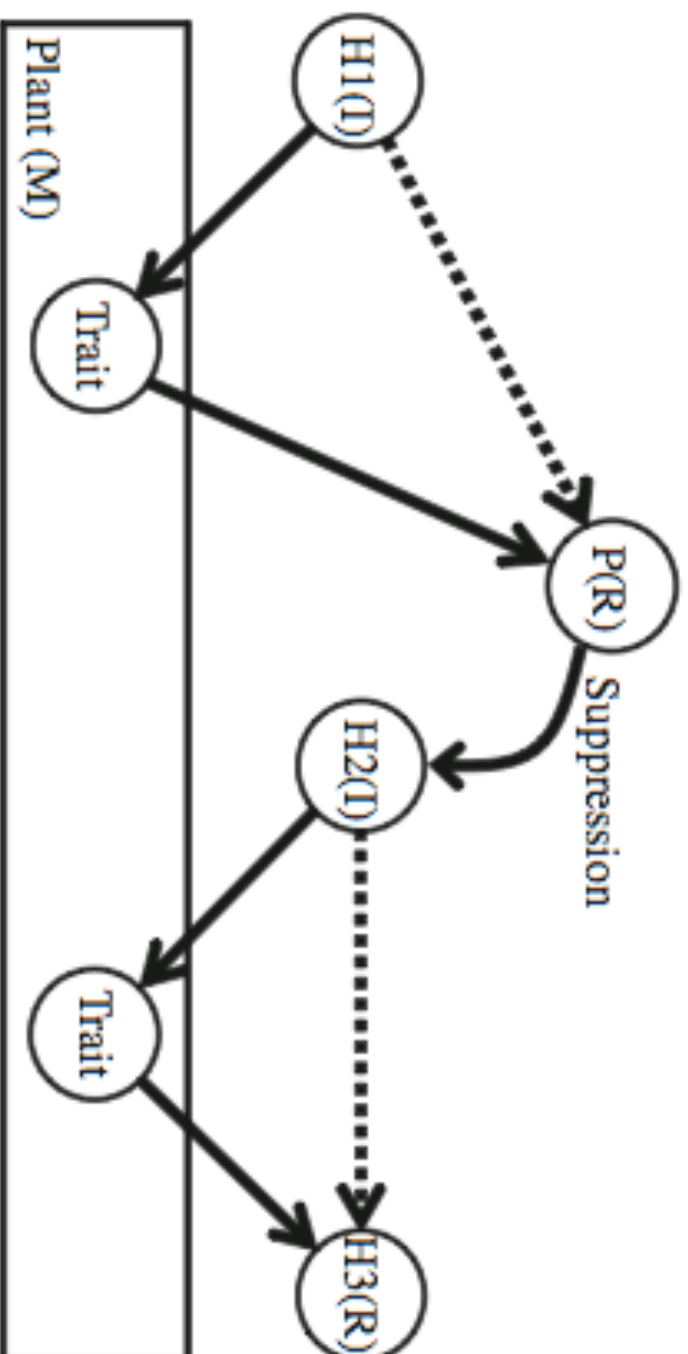


Fig. 4. Indirect interaction web (from Utsumi *et al.* 2010), model depicts two indirect interactions and the linkage between them.

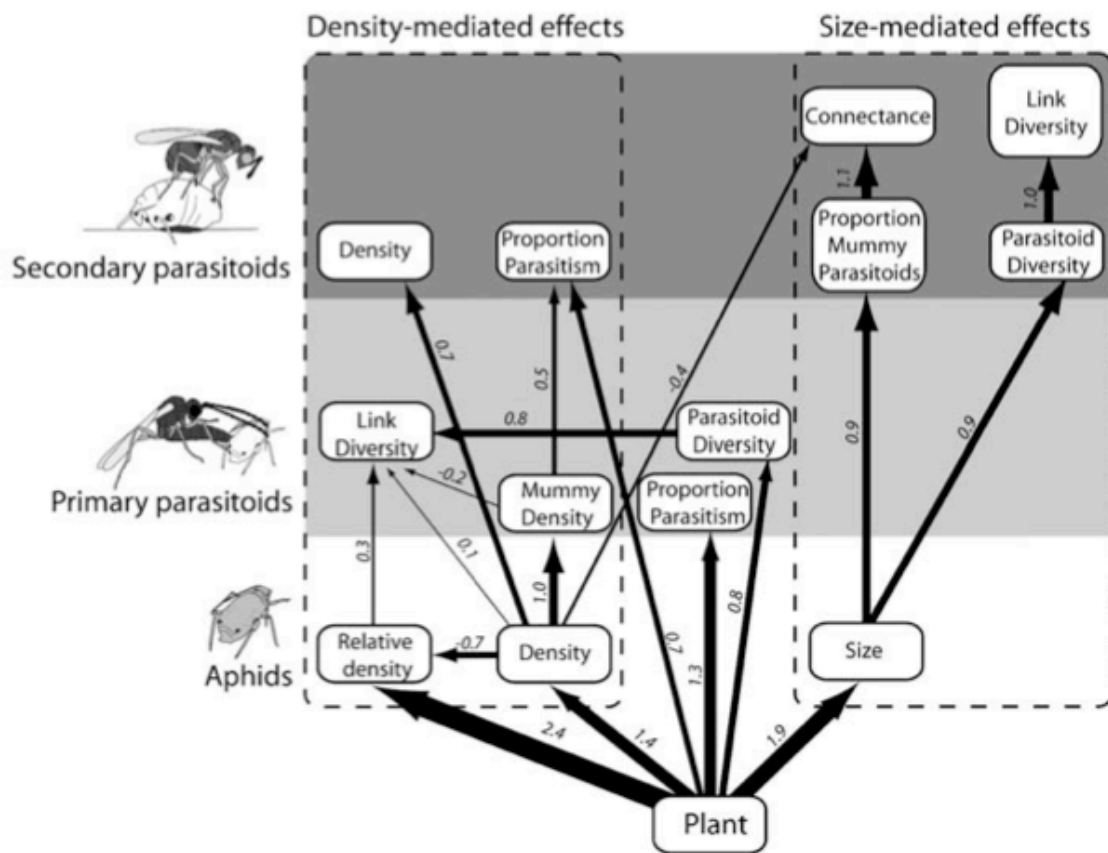


Fig. 5. Interaction web (from Bukovinsky *et al.* 2008), arrow thickness illustrates relative interaction strength and effects are categorized as either density or size-mediated.

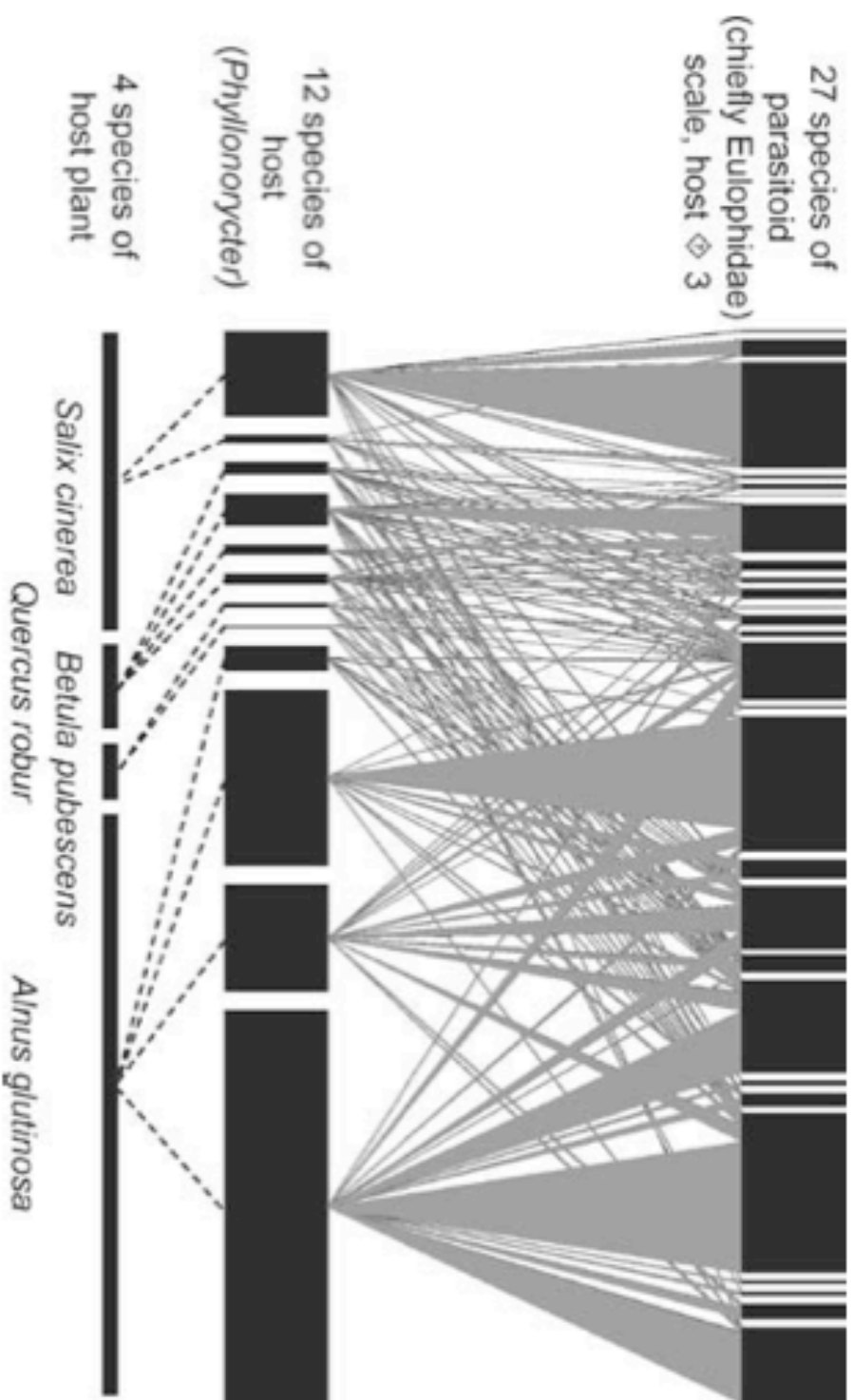


Fig. 6. Quantitative food web (from Van Veen *et al.* 2006), the width of each black bar indicates relative density of that species and the size of each wedge indicates the relative importance of each host. Quantitative food webs may be used to assess the relative importance of indirect interactions between communities

Appendix A: Classification Schemes

Interactions between organisms have been classified in multiple ways, leading to complicated and sometimes conflicting nomenclature schemes. The terms used to describe interactions have shifted as the field has matured. It is worthwhile to examine the history of classification and the way interactions have been defined as this will lead to a richer understanding of the current research. There is a large body of work on interactions from many disciplines and spanning decades, often with different authors or disciplines using different terms and classifications to refer to similar concepts.

Interactions are generally classified as either direct or indirect. Within these two categories, more specific types of interactions are defined based on either mechanism or effect. For example, interference competition has been classified as direct, apparent competition and exploitation competition have been classified as indirect while all are classified as (– –) interactions.

Historically, the delineation between direct and indirect interactions has been muddy with little agreement between workers. Wootton (1994) produced an apparently simple definition of a direct interaction that specifies a physical interaction between two species. In contrast, Abrams (1995) defines direct interactions more broadly as those involving two species in which a change in the initiating species produces a response in the receiving species without a necessary change in any other species. This definition includes interactions such as competition for resources that do not depend on physical contact between two species. Other authors include interactions like resource competition in their

definition of indirect interactions (Strauss 1991). Menge (1995) defines direct interactions as those in which changes in abundance of one species result from its interaction with another species, while neglecting changes in effects other than abundance. Some agreed upon examples of direct interactions (therefore involving physical interaction) include consumption and interference competition (Wootton 1994).

The generally accepted types of direct interaction are interference competition (– –), predation (+ –), herbivory (+ –), parasitism (+ –), mutualism (+ +), commensalism (+ 0), amensalism (– 0) and neutralism (0 0). The last four types are defined by effect rather than mechanism and can be either direct or indirect interactions. Neutralism is strictly speaking not an interaction at all (rather the absence of interaction), but is frequently included in classification schemes (Arthur and Mitchell 1989). Occasionally, the (+ –) interaction is referred to as contramensalism, a term first introduced by Arthur (1986), particularly when the mechanism is nontrophic. Some authors prefer this term for any (+ –) interaction as it is effect rather than mechanism based (Arthur and Mitchell 1989). Predation is a flexible term, sometimes used strictly to talk about the predator/prey relationship and sometimes also including herbivory and parasitism. Predator is also used in these two senses, sometimes including herbivores and parasites or parasitoids. Competition is another term with varying interpretations, but frequently used for all (– –) interactions rather than to refer to a specific mechanism. Interference competition is clearly a direct interaction, however other types (exploitative and apparent competition) are indirect. This distinction

between mechanism and effect should be made for clarity when discussing competition (Arthur and Mitchell 1989). All of these categories reflect combinations of positive, negative and neutral interactions between the two interacting species.

The six possible types of interactions based on the combinations of positive (+), negative (–) and neutral (0) interaction signs are frequently summarized using an interaction grid (Fig. 7). However, the interaction grid does not adequately reflect the dynamic nature of species interactions. Holland and DeAngelis (2009) advocate for the use of an interaction compass as an alternative (Fig. 8). The interaction compass more accurately depicts the possible shifts between interaction types that can occur given different biotic and abiotic conditions. For instance, competition (– –) may become strongly asymmetric under a give set of conditions and be better described as amensalism (– 0).

| | | Species 1 | | |
|-----------|---|-----------------|-------------|------------|
| | | + | – | 0 |
| Species 2 | + | mutualism | | |
| | – | contramensalism | competition | |
| | 0 | commensalism | amensalism | neutralism |

Fig. 7. Interaction grid of the six possible types of species based on the positive, negative or neutral effect on each species. The general term *contramensalism* includes all (+ –) interactions such as predation, herbivory, and parasitism.

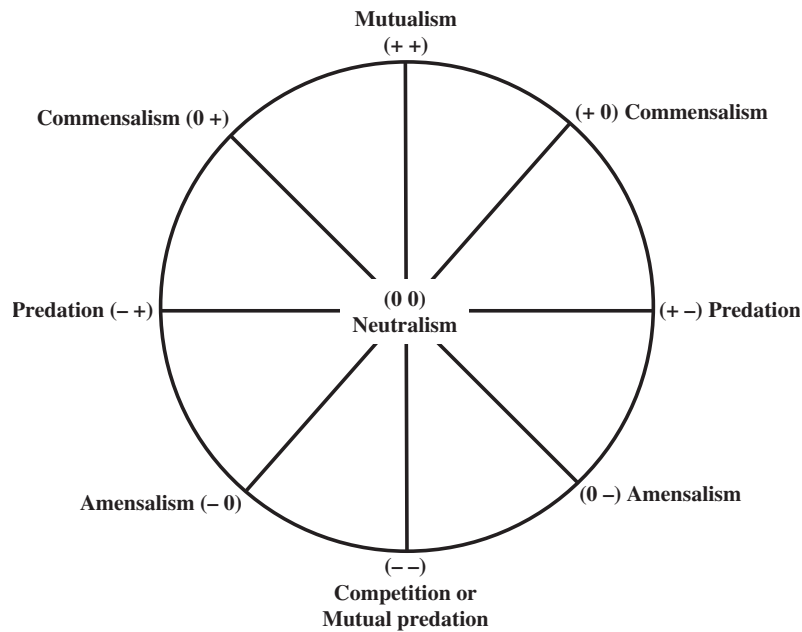


Fig. 8. Interaction compass model (from Holland and DeAngelis 2009). The compass depicts the same six possible types of interactions as in Fig. 4 but emphasizes the continuity between them.

There is even less consensus on the definitions of indirect interactions but most (but not all), definitions include a third species. Wootton (1994) defines indirect effects as the impact of one species on another that requires the presence of a third; Miller and Kerfoot (1987) define them as “how and to what degree pairwise species interactions are influenced by the presence and density of other species in the community”, and Abrams’ (1995) definition includes one (or more) transmitting species that is (are) intermediate to the initiating and receiving species. For Abrams, some property (or properties) of the transmitting species must be changed by the initiator and this change in the transmitter then alters some property (or properties) of the receiver.

Some authors allow mediation by a chemical or physical variable without the presence of an intermediate species (Strauss 1991) while others include such interactions in their definition of direct interactions (Abrams 1987, Abrams 1995). For instance, a plant may alter the soil through allelopathy or reduction in nutrients. These changes in the soil can then alter the success of surrounding plants without involving a physical interaction between them. Notice that this example would fall under Abrams' definition of a direct interaction. In order to separate biotic and abiotic intermediaries some authors refer to the latter as indirect effects rather than indirect interactions although this distinction is inconsistent in the literature. Strauss (1991) suggests that in fact all interactions are indirect with the exceptions of predation (including herbivory and parasitism), interference competition and some mutualisms. Wootton (1994) discusses the same issue but states that indirect effects include only those mediated by a third species. Both Strauss (1991) and Wootton (1994) agree that it is more important to account for physical and chemical variables than to assign them firmly as either direct or indirect effects.

Indirect interactions are occasionally referred to as higher order interactions. This phrase is particularly ambiguous as it is sometimes used to refer to non-linear direct interactions and sometimes to refer to interactions of three or more species (Wootton 1994, Abrams 1995). Abrams advocates for the latter use of the term.

More specific interaction types have been organized by either the mechanism of interaction (such as consumption of a shared resource or

predation) or the population level effect of the interaction (such as effect on population size, population growth rate or individual fitness) (Abrams 1987). Abrams refers to these two approaches as mechanism definitions and effect definitions respectively (1987).

While the same interaction can be classified either by mechanism or by effect, in practice these two models vary greatly. Classification based on mechanism can be arbitrary, as in the distinction between parasitism and predation or between parasitism and disease (Abrams 1987). However, mechanistic classification has the advantage that interaction mechanisms are often readily observable while effects can be difficult to measure. A confounding factor of the mechanism approach is that several mechanisms can be involved in a given interaction and this complexity may not be taken into account. This is especially true with regard to indirect effects.

In contrast to mechanistic classifications, those classifications based on effect are inclusive of all mechanisms involved in an interaction. Categorization is also more straightforward as the categories are simply the six possible pair-wise combinations of (+, −, 0). For instance, predation would be categorized as a (+ −) effect, as would parasitism and herbivory (Abrams 1987). Thus there are multiple mechanisms for each effect category. Theoretically, competition is not the only mechanism that produces (− −) effects for instance, although other mechanisms are frequently overlooked by researchers, including indirect effects such as apparent competition (Abrams 1987).

Effect classification schemes have the added complication that the interaction sign may depend on what effect measurement is chosen (*e.g.* individual fitness, population density or population growth rate). Likewise, the sign may vary over different time scales. Abrams (1987) provides an example of a predator that consumes both a prey species and a strong competitor of that prey species. Over the short term, the predator has a negative impact on the prey's population growth rate but over the longer term may have a positive effect if it consumes enough of the strong competitor.

To complicate matters, indirect interactions can be further classified into types. There have been multiple classification systems proposed. The two types proposed by Wootton (1993, 1994) are interaction chains and interaction modifications. Interaction chains are made up of a series of direct interactions between species pairs (Wootton 1993). The direct interactions result in changes of abundance that indirectly affect another species. The trophic cascade is a classic example: a predator that reduces the abundance of an herbivore positively affects the food plant. In contrast to an interaction chain, an interaction modification is the impact of a third species on the direct interaction itself that occurs between two others without changing the abundance of either. For example, a predator may alter the behavior of its prey so that the prey becomes more susceptible to predation by another predator. The first predator does not alter the abundance of the prey, but rather changes its behavior and the interaction between it and the second predator.

Wootton (1993) used barnacles, limpets and birds as a study system to distinguish between these two types of indirect interactions. The birds consumed limpets; limpets and barnacles competed for space, with limpets being the superior competitor. Bird consumption of limpets increased barnacle abundance, an example of an interaction chain as the indirect effect of birds on barnacles is through a series of direct interactions involving abundance. However, limpets and barnacles have similar coloration. The presence of barnacles makes limpets more difficult for the birds to find. Thus barnacle presence alters the interaction between birds and limpets, an example of an interaction modification. In each case an indirect effect exists (in both cases between barnacles and birds) however the mechanism is different.

Janssen *et al.* (1998) proposed a different categorization of indirect interactions, namely numerical indirect interactions and functional indirect interactions. Numerical indirect interactions are consistent with Wootton's interaction chains, involving a series of changes in abundance. Functional indirect interactions are the change in function of an interaction between two species caused by the presence of a third, as mediated by changes in distribution, behavior, morphology or physiology, similar to Wootton's interaction modifications. Janssen *et al.* point out that their new terms are analogous to the terms "numerical response" and "functional response" used in population ecology and that the terms are consistent with how interactions can be modeled. They also propose that direct interactions be categorized as numerical or functional interactions, taking into account direct interactions that are not based on changes

in abundance. For instance, the presence of a predator may change the behavior of prey without altering its abundance (Janssen 1998).

Strauss (1991) adapted her classification from that of Miller and Kerfoot (1987), defining 4 categories of indirect effects: a) abundance, b) behavioral/morphological/chemical/physiological, c) environmental and d) response. The environmental subtype includes interactions mediated by a non-living resource (also known as a priority effect or historical effect) such as the alteration of water quality by one species that subsequently impacts another species (Strauss 1991). Environmentally-mediated interactions are more typically regarded as direct effects as most authors define indirect interactions as those requiring an intermediate species (Abrams 1995, Wootton 1994). The fourth subtype, response, is akin to Wootton's interaction modification in that the presence of a third species modifies the interaction between two others (without altering abundance, behavior, etc. or the environment (Strauss 1991).

Currently, the most prevalent classification scheme for defining indirect interactions divides interactions into two types: density-mediated indirect interactions (DMII) and trait-mediated indirect interactions (TMII; Abrams 1995, 2007, Werner and Peacor 2003). Additional terms that are analogous to DMII include trophic linkage, ecological, abundance, population or species interaction indirect effects; terms analogous to TMII include behavioral indirect effects and higher order interactions (Janssen 1998, Menge 1997, Wootton 1994). DMII and TMII are based on Abrams' definitions of trait and density mediated effects (Abrams 1995), although Peacor and Werner (1997) later change the word effect

to interaction and introduced the commonly used acronyms (Abrams 2007). In 2007, Abrams clarified the use of TMII and DMII, advocating these terms to describe pathways within an interaction. He notes that TMII when used to refer to an entire interaction generally include a DMII component as well. For clarity, the term TMII should only be used to refer to the specific pathway within the interaction. For instance, the basal member of a three species food chain receives both density-mediated and trait-mediated effects from the middle member of the chain. The problem arises if the term trait-mediated indirect interaction is used to describe the entire interaction between the top member of the chain and the basal member. While Abrams makes a sound argument, common usage of TMII and DMII referring to interactions rather than pathways prevails.

Abrams (2007) also addresses the use of trait-mediated interaction (TMI) and density-mediated interaction (DMI) as terms intended to encompass both direct and indirect interactions. Bolker (2003) defines TMIs as interactions “in which trophic and competitive interactions depend on individual traits as well as on overall population densities” while Bolnick and Preisser (2005) prefer the definition “strategic changes in prey behavior, morphology, or physiology, in response to the presence of a predator” (Bolnick and Preisser 2005, Preisser *et al.* 2005). DMIs are defined by Preisser *et al.* (2005) as the reduction in prey population densities through direct consumption.

Abrams (2007) states that this use of “mediated” is not true to the original definitions, where the term was used to refer to the role of the the transmitting

(mediating) species in an indirect interaction. Abrams' definition therefore requires a third, mediating, species. To use TMI and DMI in this way is inaccurate and a better term would be trait-modified to refer to the role of trait change in direct interactions. He also notes that density-modified is not an appropriate counterpart to trait-modified as all interactions have a density component. He also discusses whether consumptive and non-consumptive effects (CE and NCE) are adequate replacements for DMI and TMI in regards to predator effects. Janssen's (1998) definitions of functional and numerical direct interactions seem to be equivalent to the intent of other authors use of TMI and DMI without the misuse of the term "mediation" or the possible confusion of "modified". However, this language does not appear to have been widely adopted.

More specific types of indirect interactions include apparent competition, exploitation competition, keystone predation, indirect mutualism, indirect commensalism, habitat facilitation, trophic cascade, indirect defense, and apparent predation (Menge 1995). Like the types of direct interactions, these are defined based on mechanism and/or effect.

Apparent competition has often been considered the quintessential indirect interaction. This mechanism has been recognized at least as early as 1957 (Williamson). Defined by Holt (1977), apparent competition is mediated by a shared enemy (predator, herbivore or parasite) reducing the equilibrium abundance of both prey (in the loose sense, which also includes plants and hosts). The initiating species enhances the impact of the shared enemy, with a negative effect on the receiving species. The two species may also be direct

competitors with each other (Holt 1977). Chaneton (2000) gives 12 examples of apparent competition between plants mediated by various herbivores. Most of those interactions were non-reciprocal (-0) interactions (thus amensalism rather than competition) or asymmetric competitive interactions. In a manipulative study, Rand (2003) demonstrated apparent competition between *Salicornia europaea* and *Atriplex patula* mediated by a leaf beetle herbivore, *Erynephala maritima*. The presence of *S. europaea* near individuals of *A. patula* increased beetle herbivory on the latter. In an earlier study, Rand (2002) had shown that beetle herbivory on *A. patula* reduced survival and seed production.

Refuge-mediated apparent competition is a variant in which a plant provides a resource other than food (such as cover from predation) to a shared consumer that thereby increases consumption on another plant (Orrock *et al.* 2010). There are additional models that are highly similar to classic apparent competition, such as a single predator of several victim species in addition to the focal species and several predators of the focal species and multiple additional victim species (Holt and Lawton 1994). By any definition, apparent competition is a consumer-mediated interaction between an initiating resource species and other resources.

Exploitation competition has been discussed in the ecological literature for decades however it was not until the 1980s and early 1990s that it was recognized as an indirect interaction (Menge 1995, Strauss 1991). Exploitation competition occurs when the reduction of a consumer results from the reduction of a resource by another consumer (Menge 1995). Referring to competitive

interactions between herbivores, Kaplan and Denno (2007) state that exploitation competition is an indirect interaction in which the quantity of plant tissue removed is the mechanism of competition. They refer to competitive interactions mediated by changes in plant quality simply as plant-mediated interactions.

Keystone predation occurs when a predator increases the abundance of its prey's competitor by reducing the abundance of its prey (Menge 1995). There has been debate over whether species other than top carnivores, such as herbivores, can be considered keystone predators (Davic 2002, Higdson 2002) based on the original keystone concept as proposed by Paine (1966, 1969). To be a keystone species, the species must exert top-down pressure and reduce competition in lower trophic levels, providing a stabilizing effect on community diversity (Paine 1969, Davic 2002). As an herbivore has the potential to exert both top-down effects and to maintain species diversity through the amelioration of competition, Davic (2002) argued that it is plausible for an herbivore to act as keystone predator.

Trophic cascades have also commonly been referred to as tritrophic interactions. In general, a trophic cascade is an increase in plant abundance caused by a decrease in herbivores due to predation (Menge 1995). Trophic cascades can be both density- and trait-mediated (Schmitz *et al.* 2004). The presence of a predator may cause the herbivore to choose between feeding and predator avoidance, for instance, reducing the impact on plants without altering the density of the herbivore. The herbivore may also shift habitats, potentially utilizing a less preferred host with lower predation risk. Historically, trophic

cascades have been considered the primary mechanism by which plant species diversity and abundance has been maintained (Hairston *et al.* 1960). This idea has commonly been referred to as the green world hypothesis, which states that plants are abundant because predators limit herbivores and that competition between herbivores is uncommon and of minor importance because plants are not a limiting resource (Hairston *et al.* 1960).

Indirect mutualism is the positive effect on two species from predation on the competitor of each other's primary prey species (Vandermeer 1980, Menge 1995). Similar to keystone predation, a consumer releases a resource from competition by consumption of its competitor. Reciprocally, another consumer reduces the abundance of the competitor, positively impacting the original resource and indirectly also benefiting the original consumer. This benefits both consumers in the case of indirect mutualism. In order for this to occur, the competition between the two resources must be symmetric, otherwise it is likely that the interaction is indirect commensalism (Dethier and Duggins 1984).

Indirect commensalism is related to indirect mutualism with one of the predators consuming both prey species (Menge 1995). However, Sanders and Van Veen (2012) document an indirect commensal relationship between two parasitoids of two aphids. Both parasitoids utilize only one aphid species (in contrast to Menge's definition whereby one of the parasitoids should use both potential aphid hosts). Sanders and Van Veen were able to demonstrate a positive indirect effect on one parasitoid but not on the other, meeting the definition of commensalism. In an earlier study, Dethier and Duggins (1984)

examined a rocky intertidal system consisting of a chiton, two limpet species, macroalgae and diatoms. In this system, chitons consume both macroalgae and diatoms while limpets consume diatoms. Using removal and addition of the chiton, the authors demonstrated a positive effect of the chiton on the limpets due to macroalgae removal, permitting diatom growth. In the removal experiments, chiton removal cause limpet populations to fall to near zero while in chiton addition experiments, limpet abundance increased. The interaction between macroalgae and diatoms is strongly asymmetric; macroalgae cover prevents diatom growth, however diatoms have little or no effect on macroalgae.

Holt (1977) proposed that indirect (+ –) interactions be called apparent predation to distinguish them from direct predation. Predation (as discussed elsewhere) has been used to describe any (+ –) interaction which leads to confusion when used to describe effect rather than a particular mechanism. Arthur's (1986) proposed term contramensalism has the advantage of being non-mechanistic and consistent with other effect-based terminology.

Habitat facilitation occurs when one organism improves the habitat of a second by altering the abundance of a third organism (Fairweather 1990, Menge 1995). For instance, whelks that kill barnacles create habitat for invertebrate and algal species that utilize the empty barnacle tests. When the tests are removed, gastropod species graze the newly exposed areas (Fairweather 1990).

Interactions, whether direct or indirect, are not static and may shift between types as biotic and abiotic conditions change (Holland and DeAngelis 2009). Unlike the interaction grid of the six basic combinations of (–, + 0) which

simply summarizes these interactions, an interaction compass has been used to describe the possible transitions between interaction types along each axis, emphasizing the dynamic nature of interactions and how fluid the types really are in nature (Holland and DeAngelis 2009).

Interaction strength is an important area of research, especially in regards to the comparative strength between direct and indirect effects and between TMIs and DMIs. Interaction strength can be very difficult to quantify, partly because the sign of the effects may either be the opposite or the same thus either canceling each other out or reinforcing each other. In addition, there are multiple ways to define interaction strength, confounding the development of a consistent method of measuring interaction strength (Wootton and Emmerson 2005). Most methods focus on trophic interactions, with few studies including non-trophic interactions such as interference competition (Werner and Peacor 2003, Wootton and Emmerson 2005).

One common approach for determining direct and indirect interaction strength is the combination of press and pulse experiments (Bender 1984, Abrams 1995). In pulse experiments, the density of one species is changed but not maintained, as for instance in a one-time removal of all individuals of a species. The effects are then observed prior to return to the original state. Press experiments also alter the density of a species but this change is maintained with observations being made after the system reaches equilibrium. In this case, all individuals of a species may be removed and maintained over several

generations (Strauss 1991). Pulse experiments are intended to measure direct effects while press experiments measure net impact of direct and indirect effects.

There is an underlying assumption that direct effects operate more quickly relative to indirect effects. Abrams (1995) states that these experiments are not a good basis for comparison because trait changes can be slow or fast in ecological time. There are multiple examples in the literature of indirect effects that are very rapid. Menge (1997) studied whether indirect effects occur during the same observational period as direct effects. He used press experiments in rocky intertidal webs to examine detection of direct vs indirect effects during experimental observation over periods ranging from 1.9 to 31 months. Indirect effects usually occurred either simultaneously with or shortly after direct effects. At least in rocky intertidal systems, it appears that direct and indirect effects are observable over similar time scales (Menge 1997).

In addition, pair-wise species interactions occur in a complex web of interactions, direct and indirect, with other members of the ecological community. Each of those interactions occurs at different temporal and spatial scales, leading to difficulty in assessing the results of a press-pulse or other species deletion experiment (Wootton and Emmerson 2005). It is no longer sufficient to assume that interaction strength is independent of the community (Werner and Peacor 2003).

Trait changes can affect interactions independent of changes in density, with consequences beyond the focal species pair (Werner and Peacor 2003). For instance, a single predator may have a very strong effect on prey behavior

without altering prey density. This large change in behavior may have large impacts on other members of the interaction web (Werner and Peacor 2003).

Various other empirical approaches have been utilized, including field, laboratory and observational methods. Wootton (2005) proposed using more readily quantifiable properties to estimate interaction strength. For instance, body size potentially scales with interaction strength (Wootton 2005). Berlow *et al.* (2009) incorporated metabolic body mass and biomass into a predictive model of food webs from 10-30 species with good success, although this model only incorporates consumer-resource interactions, neglecting non-trophic interactions. Rall *et al.* (2011) used size but also included taxonomy in a model that addressed non-linear interaction strength. This study attempted to incorporate the strengths of size-based approaches frequently used in marine ecology with the taxonomy-based approach used in terrestrial systems (Rall *et al.* 2011). Research continues to address more refined ways to assess interaction strength in complex webs. Much of the work has focused on predator-prey interactions and often neglects non-trophic interactions (Berlow *et al.* 2004) and indirect effects (Gorman 2010).

Although methods are inconsistent and problems exist with accurately quantifying interaction strength, a general pattern has begun to emerge. In general, per capita interaction strength distribution is skewed, with many weak interactions and few strong interactions (Wootton 2005, Gorman 2010). This pattern appears to contribute to community stability (Gorman 2010). More work is needed in this area to further generalize patterns of interaction strength and to arrive at methods that are comparable between studies. Indeed, a 2006 panel

convened by the National Science Foundation identified the investigation of interaction strengths in multiple contexts as one of three important areas in great need of ecological research over the next decade (Agrawal *et al.* 2007).

Appendix B: Final Approval

THE UNIVERSITY OF SOUTHERN MAINE DEPARTMENT OF BIOLOGICAL SCIENCES

Date: 5/10/13

We hereby recommend that the thesis of Justine Roths, entitled:

The Varied Roles of Induced Plant Responses in Species Interactions

be accepted as partial fulfillment of the requirements for the degree of

Master of Science in Biology

Signatures

Author:

Justine B. Roths Date: 5/10/13

Advisory Committee:

[Signature] Date: 6/5/13 (Primary Advisor)

Joseph K. Staples Date: 5/10/2013

Michael Mazurkiewicz Date: 5/10/2013

Chair of the Department of Biological Sciences:

Lin Mou Date: 6/7/2013

Dean of the College of Arts and Sciences

[Signature] Date: 7-1-2013

References

- Abrams, P. A. 1987. On classifying interaction between populations. *Oecologia* **73**:272-281.
- Abrams, P. A. 1995. Implications of dynamically variable traits for identifying, classifying, and measuring direct and indirect effects in ecological communities. *American Naturalist* **146**:112 - 134.
- Abrams, P. A. 2007. Defining and measuring the impact of dynamic traits on interspecific interactions. *Ecology* **88**:2555-2562.
- Adler, F. R. and R. Karban. 1994. Defended fortresses or moving targets? Another model of inducible defenses inspired by military metaphors. *American Naturalist* **144**:813-832.
- 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. 2001. Transgenerational consequences of plant responses to herbivory: an adaptive maternal effect? *American Naturalist* **157**:555-569.
- Agrawal, A. A. 2002. Herbivory and maternal effects: mechanisms and consequences of transgenerational induced plant resistance. *Ecology* **83**:3408-3415.
- Agrawal, A. A. 2004. Plant defense and density dependence in the population growth of herbivores. *American Naturalist* **164**:113-120.
- Agrawal, A. A. 2011. Current trends in the evolutionary ecology of plant defence. *Functional Ecology* **25**:420-432.
- Agrawal, A. A., D. D. Ackerly, F. Adler, A. E. Arnold, C. Cáceres, D. F. Doak, E. Post, P. J. Hudson, J. Maron, K. A. Mooney, M. Power, D. Schemske, J. Stachowicz, S. Strauss, M. G. Turner, and E. Werner. 2007. Filling key gaps in population and community ecology. *Frontiers in Ecology and the Environment* **5**:145-152.
- Agrawal, A. A. and M. Fishbein. 2006. Plant defense syndromes. *Ecology* **87**:S132-S149.
- Agrawal, A. A. and R. Karban. 1999. Why induced defenses may be favored over constitutive strategies in plants. Pages 45-61 *in* R. Tollrian and C. D. Harvell, editors. *The ecology and evolution of inducible defenses*. Princeton University Press, Princeton.

- Agrawal, A. A. and R. Karban. 2000. Specificity of constitutive and induced resistance: pigment glands influence mites and caterpillars on cotton plants. *Entomologia Experimentalis et Applicata* **96**:39-49.
- Agrawal, A. A. and K. Konno. 2009. Latex: a model for understanding mechanisms, ecology, and evolution of plant defense against herbivory. *Annual Review of Ecology, Evolution and Systematics* **40**:311-331.
- Agrawal, A. A. and N. S. Kurashige. 2003. A role for isothiocyanates in plant resistance against the specialist herbivore *Pieris rapae*. *Journal of Chemical Ecology* **29**:1403-1415.
- Agrawal, A. A., C. Laforsch, and R. Tollrian. 1999. Transgenerational induction of defences in animals and plants. *Nature* **401**:60-63.
- Ali, J. G. and A. A. Agrawal. 2012. Specialist versus generalist insect herbivores and plant defense. *Trends in Plant Science* **17**:293-302.
- Ando, Y., S. Utsumi, and T. Ohgushi. 2011. Community-wide impact of an exotic aphid on introduced tall goldenrod. *Ecological Entomology* **36**:643-653.
- Arnold, T. M. 2003. To grow and defend: lack of tradeoffs for brown algal phlorotannins. *Oikos* **100**:406-408.
- Arthur, W. 1986. On the complexity of a simple environment: competition, resource partitioning and facilitation in a two-species *Drosophila* system. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* **313**:471-508.
- Arthur, W. and P. Mitchell. 1989. A revised scheme for the classification of population interactions. *Oikos* **56**:141-143.
- Baldwin, I. T., R. Halitschke, A. Paschold, C. C. Von Dahl, and C. A. Preston. 2006. Volatile signaling in plant-plant interactions: "talking trees" in the genomics era. *Science* **311**:812-815.
- Baldwin, I. T. and W. Hamilton III. 2000. Jasmonate-induced responses of *Nicotiana sylvestris* results in fitness costs due to impaired competitive ability for nitrogen. *Journal of Chemical Ecology* **26**:915-952.
- Ballhorn, D. J., S. Kautz, U. Lion, and M. Heil. 2008. Trade-offs between direct and indirect defences of lima bean (*Phaseolus lunatus*). *Journal of Ecology* **96**:971-980.
- Bender, E. A., T. J. Case, and M. E. Gilpin. 1984. Perturbation experiments in community ecology: theory and practice. *Ecology* **65**:1-13.
- Berlow, E. L., J. A. Dunner, N. D. Martinez, P. B. Starl, R. J. Williams, and U. Brose. 2009. Simple prediction of interaction strengths in complex food webs. *Proceedings of the National Academy of Sciences* **106**:187-191.
- Berlow, E. L., A.-M. Neutel, J. E. Cohen, P. C. De Ruiter, B. Ebenman, M. Emmerson, J. W. Fox, V. A. A. Jansen, J. I. Jones, G. D. Kokkoris, D. O. Logofet, A. J. McKane, J. M. Montoya, and O. Petchey. 2004. Interaction

- strengths in food webs: issues and opportunities. *Journal of Animal Ecology* **73**:585-598.
- Bezemer, T. M., G. B. De Deyn, T. M. Bossinga, N. M. Van Dam, J. A. Harvey, and W. H. Van der Putten. 2005. Soil community drives aboveground plant–herbivore–parasitoid interactions. *Ecology Letters* **8**:652-661.
- Bezemer, T. M. and N. M. Van Dam. 2005. Linking aboveground and belowground interactions via induced plant defenses. *Trends in Ecology and Evolution* **20**:617-624.
- 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.
- Blossey, B. and T. R. Hunt-Joshi. 2003. Belowground herbivory by insects: influence on plants and aboveground herbivores. *Annual Review of Entomology* **48**:521-547.
- Bolker, B., M. Holyoak, V. Krivan, L. Rowe, and O. Schmitz. 2003. Connecting theoretical and empirical studies of trait-mediated interactions. *Ecology* **84**:1101-1114.
- Bolnick, D. I. and E. L. Preisser. 2005. Resource competition modifies the strength of trait-mediated predator–prey interactions: a meta-analysis. *Ecology* **86**:2771-2779.
- Brattsten, L. B., J. H. Samuelian, K. Y. Long, S. A. Kincaid, and C. K. Evans. 1983. Cyanide as a feeding stimulant for the southern armyworm, *Spodoptera eridania*. *Ecological Entomology* **8**:125-132.
- Bukovinsky, T., F. J. F. Van Veen, Y. Jongema, and M. Dicke. 2008. Direct and indirect effects of resource quality on food web structure. *Science* **319**:804-807.
- Chaneton, E. J. and M. B. Bonsall. 2000. Enemy-mediated apparent competition: empirical patterns and the evidence. *Oikos* **88**:380-394.
- Cipollini, D., C. B. Purrington, and J. Bergelson. 2003. Costs of induced responses in plants. *Basic and Applied Ecology* **4**:79-85.
- Cipollini, M. L., E. Paulk, and D. F. Cipollini. 2002. Effect of nitrogen and water treatment on leaf chemistry in horsenettle (*Solanum carolinense*), and relationship to herbivory by flea beetles (*Epitrix* spp.) and tobacco hornworm (*Manduca sexta*). *Journal of Chemical Ecology* **28**:2377-2398.
- Davic, R. D. 2002. Herbivores as keystone predators. *Conservation Ecology* 6(2): r8. [online] URL: <http://www.consecol.org/vol6/iss2/resp8/>
- De Moraes, C. M., W. 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 I. Kaplan. 2006. Plant-mediated interactions in herbivorous insects: mechanisms, symmetry, and challenging the paradigms of competition past. Pages 19-50 *in* T. Ohgushi, T. P. Craig, and P. W. Price, editors. Indirect interaction webs: nontrophic linkages through induced plant traits. Cambridge University Press, Cambridge.
- Denno, R. F., M. A. Peterson, C. Gratton, J. Cheng, G. A. Langellotto, A. F. Huberty, and D. L. Finke. 2000. Feeding-induced changes in plant quality mediate interspecific competition between sap-feeding herbivores. *Ecology* **81**:1814-1827.
- Dethier, M. N. and D. O. Duggins. 1984. An "indirect commensalism" between marine herbivores and the importance of competitive hierarchies. *American Naturalist* **124**:205-219.
- Dicke, M. and M. W. Sabelis. 1988. Infochemical terminology: based on cost-benefit analysis rather than origin of compounds? *Functional Ecology* **2**:131-139.
- Dicke, M. and J. J. A. Van Loon. 2000. Multitrophic effects of herbivore-induced plant volatiles in an evolutionary context. *Entomologia Experimentalis et Applicata* **97**:237-249.
- Dicke, M., R. M. P. Van Poecke, and J. G. De Boer. 2003. Inducible indirect defence of plants: from mechanisms to ecological functions. *Basic and Applied Ecology* **4**:27-42.
- Doss, R. P., J. E. Oliver, W. M. Proebsting, S. W. Potter, S. Kuy, S. L. Clement, R. T. Williamson, J. R. Carney, and E. D. DeVilbiss. 2000. Bruchins: insect-derived plant regulators that stimulate neoplasm formation. *Proceedings of the National Academy of Sciences* **97**:6218-6223.
- Dussourd, D. E. and T. Eisner. 1987. Vein-cutting behavior: insect counterploy to the latex defense of plants. *Science* **237**:898-901.
- Erb, M., S. Meldau, and G. A. Howe. 2012. Role of phytohormones in insect-specific plant reactions. *Trends in Plant Science* **17**:250-259.
- Erb, M., C. A. M. Robert, B. E. Hibbard, and T. C. J. Turlings. 2011. Sequence of arrival determines plant-mediated interactions between herbivores. *Journal of Ecology* **99**:7-15.
- Faeth, S. H. 1986. Indirect interactions between temporally separated herbivores mediated by the host plant. *Ecology* **67**:479-494.
- Fairweather, P. G. 1990. Is predation capable of interacting with other community processes on rocky reefs? *Australian Journal of Ecology* **15**:453-464.
- Fatouros, N. E., J. J. A. Van Loon, K. A. Hordijk, H. M. Smid, and M. Dicke. 2005. Herbivore-induced plant volatiles mediate in-flight host discrimination by parasitoids. *Journal of Chemical Ecology* **31**:2033-2047.

- Feeny, P. 1970. Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. *Ecology* **51**:565-581.
- Feeny, P. 1976. Plant apparency and chemical defense. Pages 1-40 in J. W. Wallace and R. L. Mansell, editors. *Biochemical interaction between plants and insects*. Plenum, New York, New York.
- Fernandes, G. W. and D. Negreiros. 2001. The occurrence and effectiveness of hypersensitive reaction against galling herbivores across host taxa. *Ecological Entomology* **26**:46-55.
- Fornoni, J. 2011. Ecological and evolutionary implication of plant tolerance to herbivory. *Functional Ecology* **25**:399-407.
- Gómez, S., W. Van Dijk, and J. F. Stuefer. 2010. Timing of induced resistance in a clonal plant network. *Plant Biology* **12**:512-517.
- Gorman, E. J., U. Jacob, T. Jonsson, and M. C. Emmerson. 2010. Interaction strength, food web topology and the relative importance of species in food webs. *Journal of Animal Ecology* **79**:682-692.
- Hairton, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control, and competition. *American Naturalist* **94**:421-425.
- Halitschke, R. and I. T. Baldwin. 2005. Jasmonates and related compounds in plant–insect interactions. *Journal of Plant Growth Regulation* **23**:238-245.
- Haukioja, E. and S. Neuvonen. 1985. Induced long-term resistance of birch foliage against defoliators: defensive or incidental. *Ecology* **66**:1303-1308.
- Heidel, A. J. and I. T. Baldwin. 2004. Microarray analysis of salicylic acid- and jasmonic acid-signalling in responses of *Nicotiana attenuata* to attack by insects from multiple feeding guilds. *Plant, Cell and Environment* **27**:1362-1373.
- Heil, M. and R. Karban. 2010. Explaining evolution of plant communication by airborne signals. *Trends in Ecology and Evolution* **25**:137-144.
- Heil, M., T. Koch, A. Hilpert, B. Fiala, W. Boland, and K. E. Linsenmair. 2001. Extrafloral nectar production of the ant-associated plant, *Macaranga tanarius*, is an induced, indirect defensive response elicited by jasmonic acid. *Proceedings of the National Academy of Sciences* **98**:1083-1088.
- Higdon, J. W. 2002. Functionally dominant herbivores as keystone species. *Conservation Ecology* 6(2): r4. [online] URL: <http://www.consecol.org/vol6/iss2/resp4/>
- Holeski, L. M., G. Jander, and A. A. Agrawal. 2012. Transgenerational defense induction and epigenetic inheritance in plants. *Trends in Ecology and Evolution* **27**:618-626.
- Holland, N. J. and D. L. DeAngelis. 2009. Consumer-resource theory predicts dynamic transitions between outcomes of interspecific interactions. *Ecology Letters* **12**:1357-1366.

- Holt, R. D. 1977. Predation, apparent competition and the structure of prey communities. *Theoretical Population Biology* **12**:197-229.
- Holt, R. D. 1984. Spatial heterogeneity, indirect interactions, and the coexistence of prey species. *American Naturalist* **124**:377-406.
- Holt, R. D. and J. H. Lawton. 1994. The ecological consequences of shared natural enemies. *Annual Review of Ecology and Systematics* **25**:495-520.
- Hunt-Joshi, T. R. and B. Blossey. 2005. Interactions of root and leaf herbivores on purple loosestrife (*Lythrum salicaria*). *Oecologia* **142**:554-563.
- Janssen, A., A. Pallini, M. Venzon, and M. W. Sabelis. 1998. Behaviour and indirect interactions in food webs of plant-inhabiting arthropods. *Experimental & Applied Acarology* **22**:497-521.
- Johnson, S. N., K. E. Clark, S. E. Hartley, T. H. Jones, S. W. McKenzie, and J. Koricheva. 2012. Aboveground–belowground herbivore interactions: a meta-analysis. *Ecology* **93**:2208-2215.
- Kaplan, I. and R. F. Denno. 2007. Interspecific interactions in phytophagous insects revisited: a quantitative assessment of competition theory. *Ecology Letters* **10**:977-994.
- Kaplan, I., R. Halitschke, A. Kessler, S. Sardanelli, and R. F. Denno. 2008. Constitutive and induced defenses to herbivory in above- and belowground plant tissues. *Ecology* **89**:392-406.
- Karban, R. 2011. The ecology and evolution of induced resistance against herbivores. *Functional Ecology* **25**:339-347.
- Karban, R. and I. T. Baldwin. 1997. Induced responses to herbivory. University of Chicago Press, Chicago, Illinois, USA.
- Karban, R. and J. H. Myers. 1989. Induced plant responses to herbivory. *Annual Review of Ecology and Systematics* **20**:331-348.
- Kessler, A. and I. T. Baldwin. 2002. Plant responses to insect herbivory: the emerging molecular analysis. *Annual Review of Plant Biology* **53**:299-328.
- Kessler, A. and R. Halitschke. 2007. Specificity and complexity: the impact of plant responses on arthropod community structure. *Current Opinion in Plant Biology* **10**:409-414.
- Kessler, A. and M. Heil. 2011. The multiple faces of indirect defences and their agents of natural selection. *Functional Ecology* **25**:348-357.
- Kim, J. and G. W. Felton. 2012. Priming of antiherbivore defensive responses in plants. *Insect Science*. doi: 10.1111/j.1744-7917.2012.01584.x
- Koricheva, J., H. Nykänen, and E. Gianoli. 2004. Meta-analysis of trade-offs among plant antiherbivore defenses: are plants jacks-of-all-trades, masters of all? *American Naturalist* **163**:E64-E75.

- Kost, C. and M. Heil. 2005. Increased availability of extrafloral nectar reduces herbivory in Lima bean plants (*Phaseolus lunatus*, Fabaceae). *Basic and Applied Ecology* **6**:237-248.
- Kursar, T. A. and P. D. Coley. 2003. Convergence in defense syndromes of young leaves in tropical rainforests. *Biochemical Systematics and Ecology* **31**:929-949.
- Lankau, R. A. 2007. Specialist and generalist herbivores exert opposing selection on a chemical defense. *New Phytologist* **175**:176-184.
- 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., V. K. Brown, and A. C. Gange. 1993. Plant-mediated interactions between above- and below-ground insect herbivores. *Oikos* **66**:148-151.
- 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.
- Menge, B. A. 1995. Indirect effects in marine rocky intertidal interaction webs: patterns and importance. *Ecological monographs* **65**:21-74.
- Menge, B. A. 1997. Detection of direct versus indirect effects: were experiments long enough? *American Naturalist* **149**:801-823.
- Miller, T. E. and W. C. Kerfoot. 1987. Redefining indirect effects. Pages 33-37 in W. C. Kerfoot and A. Sih, editors. *Predation: direct and indirect impacts on aquatic communities*. University Press of New England, Hanover.
- Miner, B. G., S. E. Sultan, S. G. Morgan, D. K. Padilla, and R. A. Relyea. 2005. Ecological consequences of phenotypic plasticity. *Trends in Ecology and Evolution* **20**:685-692.
- Ohgushi, T. 2005. Indirect interaction webs: herbivore-induced effects through trait change in plants. *Annual Review of Ecology, Evolution and Systematics* **36**:81-105.
- Ohgushi, T. 2008. Herbivore-induced indirect interaction webs on terrestrial plants: the importance of non-trophic, indirect, and facilitative interactions. *Entomologia Experimentalis et Applicata* **128**:217-229.
- Orians, C. 2005. Herbivores, vascular pathways, and systemic induction: facts and artifacts. *Journal of Chemical Ecology* **31**:2231-2239.
- Orrock, J. L., R. D. Holt, and M. L. Baskett. 2010. Refuge-mediated apparent competition in plant–consumer interactions. *Ecology Letters* **13**:11-20.

- Paine, R. T. 1966. Food web complexity and species diversity. *American Naturalist* **100**:65-75.
- Paine, R. T. 1969. A note on trophic complexity and community stability. *American Naturalist* **103**:91-93.
- Park, M. G. and B. Blossey. 2008. Importance of plant traits and herbivory for invasiveness of *Phragmites australis* (Poaceae). *American Journal of Botany* **95**:1557-1568.
- Peacor, S. D. and E. E. Werner. 1997. Trait-mediated indirect interactions in a simple aquatic food web. *Ecology* **78**:1146-1156.
- Petersen, M. K. and J. P. Sandström. 2001. Outcome of indirect competition between two aphid species mediated by responses in their common host plant. *Functional Ecology* **15**:525-534.
- Poelman, E. H., C. Broekgaarden, J. J. A. Van Loon, and M. Dicke. 2008. Early season herbivore differentially affects plant defence responses to subsequently colonizing herbivores and their abundance in the field. *Molecular Ecology* **17**:3352-3365.
- Poelman, E. H., R. Gols, T. A. L. Snoeren, D. Muru, H. M. Smid, and M. Dicke. 2011. Indirect plant-mediated interactions among parasitoid larvae. *Ecology Letters* **14**:670-676.
- Poelman, E. H., J. J. A. Van Loon, N. M. Van Dam, L. E. M. Vet, and M. Dicke. 2010. Herbivore-induced plant responses in *Brassica oleracea* prevail over effects of constitutive resistance and result in enhanced herbivore attack. *Ecological Entomology* **35**:240-247.
- Preisser, E. L., D. I. Bolnick, and M. F. Benard. 2005. Scared to death? The effects of intimidation and consumption in predator-prey interactions. *Ecology* **86**:501-509.
- Rall, B. C., G. Kalinkat, D. Ott, O. Vucic-Pestic, and U. Brose. 2011. Taxonomic versus allometric constraints on non-linear interaction strengths. *Oikos* **120**:483-492.
- Rand, T. A. 2002. Variation in insect herbivory across a salt marsh tidal gradient influences plant survival and distribution. *Oecologia* **132**:549-558.
- Rand, T. A. 2003. Herbivore-mediated apparent competition between two salt marsh forbs. *Ecology* **84**:1517-1526.
- Rasman, S., A. C. Erwin, R. Halitschke, and A. A. Agrawal. 2011. Direct and indirect root defences of milkweed (*Asclepias syriaca*): trophic cascades, trade-offs and novel methods for studying subterranean herbivory. *Journal of Ecology* **99**:16-25.
- Renwick, J. A. A. and K. Lopez. 1999. Experience-based food consumption by larvae of *Pieris rapae*: addiction to glucosinolates? *Entomologia Experimentalis et Applicata* **91**:51-58.

- Robert, C. A. M., M. Erb, B. E. Hibbard, B. W. French, C. Zwahlen, and T. C. J. Turlings. 2012. A specialist root herbivore reduces plant resistance and uses an induced plant volatile to aggregate in a density-dependent manner. *Functional Ecology* **26**:1429-1440.
- Roda, A. L. and I. T. Baldwin. 2003. Molecular technology reveals how the induced direct defenses of plants work. *Basic and Applied Ecology* **4**:15-26.
- Rodriguez-Saona, C., J. A. Chalmers, S. Raj, and J. S. Thaler. 2005. Induced plant responses to multiple damagers: differential effects on an herbivore and its parasitoid. *Oecologia* **143**:566-577.
- Roininen, H., P. W. Price, and J. P. Bryant. 1997. Response of galling insects to natural browsing by mammals in Alaska. *Oikos* **80**:481-486.
- Ruiz, N., D. Ward, and D. Saltz. 2002. Calcium oxalate crystals in leaves of *Pancratium sickenbergeri*: constitutive or induced defence? *Functional Ecology* **16**:99-105.
- Rutledge, C. 1996. A survey of identified kairomones and synomones used by insect parasitoids to locate and accept their hosts. *Chemoecology* **7**:121-131.
- Sanders, D. and F. J. F. Van Veen. 2012. Indirect commensalism promotes persistence of secondary consumer species. *Biology Letters* **8**:960-963.
- Schilmiller, A. L. and G. A. Howe. 2005. Systemic signaling in the wound response. *Current Opinion in Plant Biology* **8**:369-377.
- Schmitz, O. J., V. Krivan, and O. Ovadia. 2004. Trophic cascades: the primacy of trait-mediated indirect interactions. *Ecology Letters* **7**:153-163.
- Schoener, T. W. 1983. Field experiments on interspecific competition. *American Naturalist* **122**:240-285.
- Shelton, A. L. 2004. Variation in chemical defences of plants may improve the effectiveness of defence. *Evolutionary Ecology Research* **6**:709-726.
- Shelton, A. L. 2005. Within-plant variation in glucosinolate concentrations of *Raphanus sativus* across multiple spatial scales. *Journal of Chemical Ecology* **31**:1711-1732.
- Shiojiri, K., J. Takabayashi, S. Yano, and A. Takafuji. 2001. Infochemically mediated tritrophic interaction webs on cabbage plants. *Population Ecology* **43**:23-29.
- Shiojiri, K., J. Takabayashi, S. Yano, and A. Takafuji. 2002. Oviposition preferences of herbivores are affected by tritrophic interaction webs. *Ecology Letters* **5**:186-192.
- Silkstone, B. E. 1987. The consequences of leaf damage for subsequent insect grazing on birch (*Betula* spp.). A field experiment. *Oecologia* **74**:149-152.

- Slansky, F., Jr. and P. Feeny. 1977. Stabilization of the rate of nitrogen accumulation by larvae of the cabbage butterfly on wild and cultivated food plants. *Ecological monographs* **47**:209-228.
- Soler, R., T. M. Bezemer, A. M. Cortesero, W. H. Van der Putten, L. E. M. Vet, and J. A. Harvey. 2007. Impact of foliar herbivory on the development of a root-feeding insect and its parasitoid. *Oecologia* **152**:257-264.
- Staley, J. T. and S. E. Hartley. 2002. Host-mediated effects of feeding by winter moth on the survival of *Eucera phis betulae*. *Ecological Entomology* **27**:626-630.
- Stockhoff, B. A. 1993. Diet heterogeneity: implications for growth of a generalist herbivore, the gypsy moth. *Ecology* **74**:1939-1949.
- 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.
- Stout, M. J., K. V. Workman, and S. S. Duffey. 1996. Identity, spatial distribution, and variability of induced chemical responses in tomato plants. *Entomologia Experimentalis et Applicata* **79**:255-271.
- Strong, D. R., J. H. Lawton, and R. Southwood. 1984. *Insects on plants: community patterns and mechanisms*. Harvard University Press, Cambridge, MA.
- Strauss, S. Y. 1991. Indirect effects in community ecology: their definition, study and importance. *Trends in Ecology and Evolution* **6**:206-210.
- Strauss, S., J. A. Rudgers, J. A. Lau, and R. E. Irwin. 2002. Direct and ecological costs of resistance to herbivory. *Trends in Ecology and Evolution* **17**:278-285.
- Takabayashi, J., Y. Sato, M. Horikoshi, R. Yamaoka, S. Yano, N. Ohsaki, and M. Dicke. 1998. Plant effects on parasitoid foraging: differences between two tritrophic systems. *Biological Control* **11**:97-103.
- Thaler, J. S. 1999. Jasmonate-inducible plant defences cause increased parasitism of herbivores. *Nature* **399**:686-688.
- Thaler, J. S., A. L. Fidantsef, S. S. Duffey, and R. M. Bostock. 1999. Trade-offs in plant defense against pathogens and herbivores: a field demonstration of chemical elicitors of induced resistance. *Journal of Chemical Ecology* **25**:1597-1609.
- Thaler, J. S., P. T. Humphrey, and N. K. Whiteman. 2012. Evolution of jasmonate and salicylate signal crosstalk. *Trends in Plant Science* **17**:260-270.
- Thaler, J. S., R. Karban, D. E. Ullman, K. Boege, and R. M. Bostock. 2002. Cross-talk between jasmonate and salicylate plant defense pathways: effects on several plant parasites. *Oecologia* **131**:227-235.

- 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.
- Tscharntke, T. 1988. Attack by a stem-boring moth increases susceptibility of *Phragmites australis* to gall-making by a midge; mechanisms and effects on midge population dynamics. *Oikos* **55**:93-100.
- Turlings, T. C. J., J. H. Loughrin, P. J. McCall, U. S. R. R  se, W. J. Lewis, and J. H. Tumlinson. 1995. How caterpillar-damaged plants protect themselves by attracting parasitic wasps. *Proceedings of the National Academy of Sciences* **92**:4169-4174.
- Underwood, N. C. 1998. The timing of induced resistance and induced susceptibility in the soybean–Mexican bean beetle system. *Oecologia* **114**:376-381.
- Underwood, N. C. 1999. The influence of induced plant resistance on herbivore population dynamics. Pages 211-230 in A. A. Agrawal, S. Tuzun, and E. Bent, editors. *Inducible plant defenses against pathogens and herbivores: biochemistry, ecology, and agriculture*. American Phytopathological Society Press, St. Paul, Minnesota.
- Utsumi, S. 2011. Eco-evolutionary dynamics in herbivorous insect communities mediated by induced plant responses. *Population Ecology* **53**:23-34.
- Utsumi, S., Y. Ando, and T. Miki. 2010. Linkages among trait-mediated indirect effects: a new framework for the indirect interaction web. *Population Ecology* **52**:485-497.
- Utsumi, S., M. Nakamura, and T. Ohgushi. 2009. Community consequences of herbivore-induced bottom-up trophic cascades: the importance of resource heterogeneity. *Journal of Animal Ecology* **78**:953-963.
- Utsumi, S. and T. Ohgushi. 2009. Community-wide impacts of herbivore-induced plant regrowth on arthropods in a multi-willow system. *Oikos* **118**:1805-1815.
- Van Dam, N. M., C. E. Raaijmakers, and W. H. Van der Putten. 2005. Root herbivory reduces growth and survival of the shoot feeding specialist *Pieris rapae* on *Brassica nigra*. *Entomologia Experimentalis et Applicata* **115**:161-170.
- Van der Meijden, E. 1996. Plant defence, an evolutionary dilemma: contrasting effects of (specialist and generalist) herbivores and natural enemies. *Entomologia Experimentalis et Applicata* **80**:307-310.
- Van der Meijden, E. and P. G. L. Klinkhamer. 2000. Conflicting interests of plants and the natural enemies of herbivores. *Oikos* **89**:202-208.

- Van Veen, F. J. F., R. J. Morris, and H. C. J. Godfray. 2006. Apparent competition, quantitative food webs, and the structure of phytophagous insect communities. *Annual Review of Entomology* **51**:187-208.
- 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.
- Vandermeer, J. 1980. Indirect mutualism: variations on a theme by Stephen Levine. *American Naturalist* **116**:441-448.
- Vet, L. E. M. and M. Dicke. 1992. Ecology of infochemical use by natural enemies in a tritrophic context. *Annual Review of Entomology* **37**:141-172.
- Viswanathan, D. V., O. A. Lifchits, and J. S. Thaler. 2007. Consequences of sequential attack for resistance to herbivores when plants have specific induced responses. *Oikos* **116**:1389-1399.
- Viswanathan, D. V., A. J. T. Narwani, and J. S. Thaler. 2005. Specificity in induced plant responses shapes patterns of herbivore occurrence on *Solanum dulcamara*. *Ecology* **86**:886-896.
- Voelckel, C. and I. T. Baldwin. 2004. Herbivore-induced plant vaccination. Part II. Array-studies reveal the transience of herbivore-specific transcriptional imprints and a distinct imprint from stress combinations. *The Plant Journal* **38**:650-663.
- Walling, L. L. 2000. The myriad plant responses to herbivores. *Journal of Plant Growth Regulation* **19**:195-216.
- Werner, E. E. and S. D. Peacor. 2003. A review of trait-mediated indirect interactions in ecological communities. *Ecology* **84**:1083-1100.
- Williamson, M. H. 1957. An elementary theory of interspecific competition. *Nature* **180**:422-425.
- 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. *Ecological Entomology* **27**:115-122.
- Wootton, J. T. 1993. Indirect effects and habitat use in an intertidal community: interaction chains and interaction modifications. *American Naturalist* **141**:71-89.
- Wootton, J. T. 1994. Predicting direct and indirect effects: an integrated approach using experiments and path analysis. *Ecology* **75**:151-165.
- Wootton, J. T. and M. Emmerson. 2005. Measurement of interaction strength in nature. *Annual Review of Ecology, Evolution and Systematics* **36**:419-444.

- Zavala, J. A., A. G. Patankar, K. Gase, and I. T. Baldwin. 2004. Constitutive and inducible trypsin proteinase inhibitor production incurs large fitness costs in *Nicotiana attenuata*. *Proceedings of the National Academy of Sciences* **101**:1607-1612.
- Zhu-Salzman, K., J.-L. Bi, and T.-X. Liu. 2005. Molecular strategies of plant defense and insect counter-defense. *Insect Science* **12**:3-15.