CHAPTER TWO

PLANT INTERACTIONS WITH MULTIPLE ENEMIES

2.1 ABSTRACT

Plants are attacked by multiple enemies that can exert concerted, conflicted, or independent selection pressures on plant defense traits. Some plant defenses have very general effects on many enemies, others have affect several species but in opposite directions, whereas others are quite species-specific. Plant defense theory has yet to provide guidelines as to when we might expect a plant defense trait to have either of these effects, or which features of plant enemies group them into *enemy suites*, commonly affected by a given plant trait. I outline several hypotheses regarding *enemy suite* composition and review a variety of empirical methods that provide information on these questions from different perspectives. There is extensive literature that pertains to the question of plant defense against multiple enemies that is in need of synthesis, as much of it is generated to address different questions and is scattered in journals of fields of research that often (and lamentably) do not interact. I review some of the relevant information provided by different forms of evidence. The nature of a plant's response to a complex set of pressures bears on our understanding of the diversity and multiplicity of plant defense mechanisms, the maintenance of genetic variation in resistance within plant populations, on the nature of coevolution (whether it is pairwise or multispecies), and on our ability to breed plant varieties that can withstand damage by multiple agricultural pests.

2.2 PRELUDE

Biotic interactions play an central role in determining important features of a species' biology, including its density and population dynamics, its spatial distribution, the evolution of form and behavior, and the speciation process (Shoemaker et al. 1999; Werren and Jaenike 1995). The vast majority of studies consider interactions between a single pair of species because of the limited scope of the question or simply for the sake of tractability, but networks of biotic interactions when looked at in detail are generally found to be quite complex (Zamora 2000).

A focal species is engaged in numerous interactions with predators, parasites, symbionts, prey, etc. Plants, in particular, may compete with other plant species, succumb to seed predators, have symbiotic interactions with mycorrhizal fungi, pollinators and fruit dispersers, and have parasitic interactions with fungi, insects, nematodes, and mammals (and even parasitic plants) that feed on leaves, roots, stems, plant fluids and reproductive organs.

There is an increasing awareness of the importance of studying multiple interactions (Anderson and Paige 2003; Eubanks et al. 2002; Fellowes and Kraaijeveld 1998; Maleck and Dietrich 1999; Mitchell-Olds et al. 1995; Poitrineau et al. 2003; Sih et al. 1998). Examining a mere subset of a community network may limit our ability of understanding and predicting ecological and evolutionary dynamics (Inouye and Stinchcombe 2001). Interactions between a pair of species can be modified by the presence of other species. The model of *apparent competition* (Holt 1977) was developed in part to call attention to misidentified competition between prey, when ignoring their interactions via a common predator. The presence or absence of a predator may alter the interaction between a pair of species, altering competition between species (Werner and Anholt 1996), the rate of predation (Sih et al. 1998), or herbivory (Gastreich 1999; Peckarsky and McIntosh 1998; Schmitz et al. 1997). Herbivory rate can be altered by the presence of another herbivore that modifies the quantity (Preus and Morrow 1999), quality (Denno et al. 2000; Harrison and Karban 1986; Schultz and Baldwin 1982), or architecture of shared plant (Alonso and Herrera 1996; Larson and Whitham 1997). The presence of neighboring plants can change herbivory rates on host plants by affecting the herbivore's ability to locate its host (Hamback et al. 2000; Karban 1997). Species traits may have an effect upon community structure (Fritz 1992; Whitham et al. 2003), and within a community the thread of biotic interactions may stretch very far. In a study reminiscent of Darwin's indirect links drawn between cat and clover populations (Darwin 1859), Jones et al. (1998) recently suggested that the frequency of oak masting may be linked to outbreaks of lime disease, via population dynamics of gypsy moths, white footed mice, deer and ticks.

Considering multiple interactions is likewise important for understanding evolutionary dynamics. Ecological trade-offs between allocation of resources to different interactions is an inevitable alternative hypothesis (*cf.* interactions with single species, or physiological trade-offs) to explain the maintenance of genetic variation (Linhart and Thompson 1999; Strauss et al. 2002). The evolution of certain parasitic species cannot be understood without taking into account the mutualist interactions from which they've derived. For instance, the evolution of non-mutualist yucca moths appears to be driven in part by competitive interactions with mutualistic yucca-moths that favors a host shift (Pellmyr and Leebens-Mack 2000). Even in systems in which there appears to be a tight association between species pairs, certain phenomena can only be understood when taking into account interactions with additional species. For instance, life history evolution of Agonid fig pollinators may be influenced by biotic factors extrinsic to the tight-knit fig-fig wasp interaction, namely parasitic nematodes that infect the wasps (Herre 1993).

Understanding the nature of coevolution, whether it is multispecies (also termed diffuse or guild) or pairwise, requires considering the influence of multiple species. Janzen (1980) defines *diffuse coevolution* as the scenario “when either or both [interactants] are represented by an array of populations that generate a selective pressure as a group.” [I will use the term ‘multispecies’, as used by Gould (1988), rather than the more common designator ‘diffuse’. I find the latter an inaccurate term, as it suggests necessarily a form of non-directional evolution. However, if several species exert similar selection pressures, then their cumulative effect will result in directed evolution and adaptation to this functionally equivalent suite of enemies, originating a form of guild coevolution (Zamora 2000).] What are the unifying characteristics of a suite of species that exerts selection concertedly? How often do multiple species generate conflicting selection pressures? I will consider these issues in the context of plant defense against multiple enemies.

2.3 PLOTLINES: THE FOCUS & THE QUESTION

Plants have a diverse arsenal of weapons to prevent, avert, or curtail assaults and harm or kill their natural enemies attempting to feed, oviposit on or infect them. In the plant-insect literature, the term plant *resistance* commonly refers both to characters that repel or fail to attract an enemy (*antixenosis*), and characters that negatively affect an insect's biology (*antibiosis)*, including survival, development, and reproduction (Painter 1951; Panda and Khush 1995). Plant resistance traits can be *constitutive*, *i.e.*, following patterns of expression that are independent of damage, or *induced*, *i.e.*, expressed in response to damage (Karban and Baldwin 1997), and include multiple mechanisms:

(a) morphological traits, *e.g.*, trichomes (Gilbert 1971; Hoffman and McEvoy 1985; Levin 1973; Oghiakhe et al. 1992; Peeters 2002a; Ramalho et al. 1984), forms of plant architecture (Alonso and Herrera 1996), leaf vein structure (Scheirs et al. 1997; Shade and Wilson 1967), insect egg and herbivory mimicry (Niemela and Tuomi 1987; Shapiro 1981; Williams and Gilbert 1981), leaf shape (Rausher 1978; RiveroLynch et al. 1996).

(b) chemical traits, *e.g.*, a diverse and numerous set of secondary compounds produced from several biosynthetic pathways, including glucosinolates, alkaloids, terpenoids, and phenolics, which are deterrent or toxic to herbivores (*e.g.*, Rosenthal and Berenbaum 1991). In addition, plants produce proteinase inhibitors (PIs) that affect herbivore digestion (Broadway and Colvin 1992; Broadway et al. 1986), pigments that affect herbivore attraction to leaves, flowers, and fruits (Harborne 1993; Prokopy et al. 1983), slippery waxes that disrupt adherence to plant tissue (Eigenbrode and Espelie 1995; Stork 1980), resins and latexes that mechanically hinder feeding and contain toxins (Dussourd 1995; Dussourd and Hoyle 2000; Langenheim 1990; Langenheim et al. 1980), and compounds that recruit parasitoids that attack herbivores (De Moraes et al. 1998; Hoballah and Turlings 2001).

(c) phenological, *e.g.*, lack of overlap between enemy activity and host acceptability (Aide 1988; Tikkanen and Julkunen-Tiitto 2003; Tuomi et al. 1989), synchronous leaf production (Aide 1991), leaf expansion time (Moles and Westoby 2000), maintaining phenological variable populations (Tikkanen and Julkunen-Tiitto 2003).

(d) nutritional quality (Moran and Hamilton 1980), *e.g.*, low nutritional quality may discourage optimally foraging herbivores (Augner 1995; Lundberg and Astrom 1990), or increase their susceptibility to predation (Benrey and Denno 1997; Haggstrom and Larsson 1995; Loader and Damman 1991)

Plants also cope with enemy attacks by tolerating their damage without incurring significant losses in fitness (Stowe et al. 2000; Strauss and Agrawal 1999). Plant *tolerance* to disease or herbivore damage is most properly defined as a reaction norm, a function describing how a plant genotype's fitness is affected across levels of damage (Simms 2000). The slope of the reaction norm reflects the tolerance of a genotype, *i.e.*, a tolerant genotype has a very flat slope (or, to pursue the military analogy, is able to withstand attacks during a siege without great loss of prowess). There are several potential mechanisms associated with tolerance, including compensatory photosynthetic activity, utilization of stored reserves, phenological delays, and intrinsic growth rate (Tiffin 2000).

The term *defense* is restricted to resistance or tolerance traits that are adaptive, but term will be used on occasion as a more encompassing term without the adaptive implication. However, establishing whether resistance or tolerance traits are adaptations, traits that evolved by natural selection in response to damage imposed by natural enemies, or whether they have evolved for other purposes and happen fortuitously to provide some degree of resistance, is a question of significant importance. There has been some debate over the degree to which secondary compounds, in particular, are adaptive defenses (*e.g.*, Jermy 1993). It seems well established, however, that natural enemies can impose levels of damage that affect plant fitness (e.g., Marquis 1984; Marquis 1992; Parmesan 2000; Strauss 1991) and that certain plant traits can significantly affect the level of damage imposed by natural enemies (e.g., Agrawal 1998; Giamoustaris and Mithen 1995; Van Dam and Hare 1998). Several studies have demonstrated directly that natural enemies impose selection upon plant traits (*e.g.*, Mauricio and Rausher 1997; Shonle and Bergelson 2000).

Intriguingly, many populations have standing genetic variation for plant resistance traits (Fritz and Simms 1992), prompting a search for costs of resistance that might explain why natural selection has not exhausted genetic variation in these traits (Bergelson and Purrington 1996; Purrington 2000; Strauss et al. 2002). This had included multiple approaches, including the search for allocation costs (Mitchell-Olds et al. 1996), trade-offs between allocation to resistance and other physiological sinks, such as growth or reproduction (Herms and Mattson 1992), costs of plasticity in the case of induced defenses (Agrawal et al. 2002; Cipollini et al. 2003; Heil and Baldwin 2002), and trade-offs between different defense strategies, such as between resistance and tolerance (Fineblum and Rausher 1995; Mauricio et al. 1997; Tiffin and Rausher 1999). Increased resistance to a specific enemy may also imply an ecological cost, in terms of lower attraction of pollinators or other mutualists (Herrera et al. 2002; Strauss et al. 1999), or in terms of lower resistance to other enemies (Carroll and Hoffman 1980; Hare and Futuyma 1978; Nakamura et al. 1995).

The field of plant-insect herbivore interactions has been prolific in constructing general theories of plant defense that attempt to explain and predict either how plants change their allocation to defense under varying conditions in ecological time (phenotypic or ecological theories), or why plants have evolved a particular type of defensive strategy (genotypic or evolutionary theories) (Hartley and Jones 1997). These theories have had enormous heuristic value, but none has established itself as a theory of general scope (Berenbaum 1995). Nor have they incorporated a potentially important feature of plant biology and particular subject of this review, the multiplicity and diversity of multiple enemies that interact with plants.

About 40 species of arthropods feed on the bracken fern *Pteridium aquilinum* in the British Isles, with 10-12 species active at any one time in a given locality (Lawton 1976). Roughly 80 species attack leaves of tea, *Camellia sinensis* (Banerjee 1987), 138 species have been reported in the goldenrod herbivore fauna (Root and Cappuccino 1992), and more than 200 insect species have been identified for several tree species (Linhart 1989). Nearly one hundred phytophagous insects were encountered, in one farm, on collard over the course of three years (Root 1973). The later study reports, in addition, some 70 predaceous arthropods and over one hundred parasitic insects associated with the collard phytophages. Within these large arrays are species belonging to very different taxa, feeding modes, and levels of specialization. Such surveys often fail to account for belowground species, which can often play important biological roles (Blossey and Hunt-Joshi 2003). Likewise, enemies that the plant deters or even adaptively fails to attract or stimulate are undersampled. Regardless, these studies give us an idea of quite a diverse enemy community (Root 1973) and complex network of interactions stemming from a host plant.

How do plants cope with such a multitude of enemies? Naturally, not all of these species will impose significant damage or *per se* affect plant fitness. Linhart (1991) refers to species that are hosted by a plant and have on it a negative or positive impact as *dependent species*, in contrast to species that are merely associated with a host, having on it no effect. However, the accumulated damage of several low-impact species may impose, simultaneously or sequentially, a form of multi-species directional selection that may be an important force of selection on plant traits (Linhart and Thompson 1999). We still lack however the predictive tools that would allow us to recognize the unifying *similarities* between such enemies.

An analysis of the patterns of resistance to multiple enemies, by examining their response to host defense traits, will give us insights into the nature of plant resistance (Maddox and Root 1990). Do plants have general mechanisms of resistance against multiple enemies, referred to as horizontal resistance in the plant pathology literature (Horber 1979), or do plants have mechanisms that are specific to certain enemies (vertical resistance)? How often do resistance mechanisms have opposite effects against different enemies and thus give rise to ecological trade-offs? To what extent are ecological trade-offs responsible for the maintenance of genetic variation in resistance? What is the genetic architecture of resistance: does it entail many independent loci, and are there important pleiotropic effects? The structure of defense to multiple enemies may contribute to explaining the variation among localities in enemy communities (Fritz

1992), and the diversity of enemies in a locality, *e.g.*, a genetically diverse plant population composed of individuals that attract/repel different insects will sustain a more diverse assemblage of consumers than a uniform plant population (Linhart and Thompson 1999). In addition, the nature of resistance to multiple enemies is crucial to our understanding of the nature of coevolution: is it a pairwise process between a focal enemy and its host species, or are the evolutionary pressures and responses between a host and its community of enemies a multispecies process? Are plants constrained from adapting to a focal enemy by other enemies? (The term *focal enemy* is used here merely to refer to the species a researcher may be particularly interested in, not to its relative biological importance.)

The conditions for pairwise coevolution are quite stringent (Hougen-Eitzman and Rausher 1994; Iwao and Rausher 1997; Stinchcombe and Rausher 2001). It requires independence between resistance to different enemies, and that resistance to the focal enemy and the pattern of natural selection imposed by the focal enemy be independent of the presence/absence of other enemies. Thus, for instance, a common genetic basis or a pleiotropic effect on resistance to several enemies implies that an adaptive plant response to a focal enemy will affect resistance to other enemies. This may act as a constraint on adaptation, if the relationship in resistance is negative, or increase the response of selection, if correlations for resistance are positive, as many enemies acting in concert enforce a stronger selection pressure. Likewise, enemies may interfere with each others feeding behavior or the effects of combined damage on plant fitness may be nonadditive, such that selection imposed by a focal species may be different in the absence of other enemies.

In multispecies coevolution, a defense trait specific to a given enemy is less likely to evolve. A plant may respond to multiple and possibly conflicting selection pressures via generalized defenses effective against groups of enemies. Do plant resistance traits indeed thwart suites of enemies? Or, are interactions between plants and their enemies more specific, such that different enemies respond to different plant traits and plants have independent adaptations to different enemies?

With respect to the criteria for pairwise coevolution, I shall concentrate on the first criteria, that of independence of mechanism, but not restrict myself to the detection of genetic correlations. I shall not be considering studies of direct effects between enemies or plant-mediated interactions, by which attack by an enemy modifies plant properties that in turn change a plant's interaction to a second enemy. These phenomena, although important to the study of coevolution and ecological interactions, are uninformative with regard to the specificity of a given plant trait and have been reviewed by other authors (*e.g.*, Chang and Eigenbrode 2004; de Nooij et al. 1992; Hatcher 1995; Inouye and Stinchcombe 2001; Rostas et al. 2003; Werner and Peacor 2003).

An understanding of trade-offs in the context of multiple assaults is also of considerable importance in applied studies, particularly for agricultural systems. The questions surveyed in this review, in particular the potential trade-offs in resistance to different enemies, is crucial for long-term sustainable crops. Is it feasible to breed a cultivar that is resistant to most pests, or will a cultivar bred for enhanced resistance to the most important pest of the moment reveal susceptibility to non-target pests? This problem is critical even for plants bred with modern genetic engineering, where the specificity of genes expressed transgenically calls for gene pyramiding, *i.e.*, the combination of multiple mechanisms within a plant variety (Sharma et al. 2004). One of the most cultivated forms of transgenic plant are those genetically modified for resistance to insects with genes from *Bacillus thuringiensis* (Bt). The delta-endotoxins produced by these genes react with the gut lining of susceptible insects, but not vertebrates. However, these proteins are specific to the insects they affect. The most commonly used strain, Bt-kurstaki, is only effective against leaf- and needle-feeding caterpillars. A more recently developed strain, Bt-israelensis, is effective against dipteran larvae, whereas other strains are active against Colorado potato beetle and elm leaf beetle (Bt-san diego and Bt-tenebrionis, respectively). A strain of Bt-cotton, designed for resistance to the American bollworm, commonly planted in India has revealed susceptibility to leaf-curl and root-rot disease (Research Foundation for Science 2002) and the local pink bollworm has rapidly developed resistance to the crop, resulting in large yield losses (Ramachandran 2002).

In this review, I will focus on the question of whether plant defense mechanisms affect multiple enemies, the extent to which they are specialized vs. generalized, and whether there are any discernable patterns of association among enemies affected by similar defenses. I will concentrate on terrestrial plant interactions with insect herbivores, but will refer on occasion to plant interactions with other important enemy taxa.

2.4 STAGE DIRECTIONS: HYPOTHESES AND MODELS

As summarized in the previous section, plants are endowed with a rich and diverse arsenal of means of defense against natural enemies. One of the most remarkable features of plant biochemistry is the great intra-specific variability of plant secondary compounds (Hartmann 1996; Pichersky and Gang 2000). Although not all of these compounds play a role in defense at any time, they constitute a reserve of potentially active compounds. Some authors have gone so far as to argue that chemical diversity in itself is an adaptation maintained by natural selection (Jones and Firn 1991).

A diversity of defense mechanisms facing a multitude of natural enemies raises the question posed earlier: do defense mechanisms affect more than one enemy or, rather, do most mechanisms impact a single enemy, *i.e.*, might one expect correlations for defense against different enemies? If so, can we predict the composition of ‘enemy suites’, the set of enemies that respond similarly to plant traits? Can we predict which correlations for plant resistance to enemies are expected to be negative, positive, or null? In this section, we explore a number of hypotheses that predict patterns of association of enemies affected by plant defense. These ideas are by no means meant to be exclusive. Some are quite speculative. They are merely a heuristic organization of different ideas that hopefully will inspire discriminating experiments.

2.4.1 Taxonomic suites

As a starting hypothesis, consider that phylogenetically closely related enemies, sharing a low taxonomic rank, are more likely to be affected similarly by a plant defense than more distantly related enemies. Closely related taxa are more likely to possess comparable morphology, behavior, and physiology [what Linhart (1989) termed *desiderata*] that would make them similarly attracted or repelled, stimulated or deterred, susceptible or resistant to a plant trait.

2.4.2 Functional feeding guilds

Plant enemies consume plants in a variety of different manners. Mandibulate insects bite and chew different plant tissues, including leaves, stems, roots, flowers, and fruits. Among plant-chewers, galling insects modify plant development producing unique structures within which they feed. Sucking insects imbibe liquid nourishment, which they obtain by tapping into phloem (*e.g.*, aphids and leafhoppers), or xylem (*e.g.*, spittlebugs). Thrips rasp plant tissue and subsequently suck the cell content of epidermal or parenchymal cells. Plant gallers, belonging to many different taxa, manipulate plant development to feed upon modified tissues or provide these to their offspring. Plant-parasitic nematodes puncture plant root cells with long feeding stylets, or enter and move throughout the root feeding at many sites. Microbial pathogens, including fungi, bacteria and viruses, act at a much smaller scale, interacting enzymatically with plant cell walls and plant cell surface receptors.

Depending on their form of consumption and the tissues consumed, enemies are exposed to different plant morphological features and chemical components, and differ in the continuity, length, and intimacy of contact with the plant. This provides a basis for defining enemy functional guilds (Kennedy and Southwood 1984; Root 1967; Root and Cappuccino 1992), which include species that experience plants similarly. If members of different functional guilds respond to different plant traits, then within a variable plant population members of different functional guilds may covary negatively. One might expect positive correlations for plant resistance to members of the same guild, and negative or no correlations for resistance to members of different guilds.

The *a priori* definition of functional guilds varies across studies (Cornell and Kahn 1989; Peeters et al. 2001), as some classify enemies more finely and use different parameters. Furthermore, as our understanding of plant resistance traits improves, so might our definition of enemy guilds. Based on our knowledge of different plant-induced responses and which enemies activate each signaling pathway, Walling (2000) suggests that whiteflies, aphids, mites and other piercing/sucking insects are more akin to pathogens, than chewing insects. Mattson et al. (1998) rank insect feeding guilds according to their potential impact on plant fitness, taking into account the type of tissue the insect feeds on (and its value to the plant), the timing of attack (early season herbivory has less impact on fitness as it allows for compensatory growth), the size of the herbivore or its sociality, and whether damage facilitates the success of other enemies, particularly pathogens.

2.4.3 Specialist/Generalist divide

In perhaps the most oft cited article in the plant-insect literature, Ehrlich and Raven (1964) proposed a coevolutionary model to explain the diversification of host plants and their associated butterflies, and the pattern of specialization of butterflies on their host plants. The model can be summarized as a two-step sequential model: a key plant defensive trait allows a plant clade to escape herbivory and diversify, and subsequently a herbivore clade that adapts to the key plant trait will be able to shift hosts, and specialize and diversify on the new host clade.

The latter step implies that secondary compounds that are effective generalized plant defenses are ineffective towards specialist insects that have become adapted to their restricted host range (e.g., Agrawal 1999; Blau et al. 1978; Carroll and Hoffman 1980; Kliebenstein et al. 2002). In some cases, specialist herbivores are stimulated by compounds that function as deterrents to non-specialist herbivores (e.g., Giamoustaris and Mithen 1995), and some even sequester plant compounds, which they then use as defense against predators (e.g., Aliabadi et al. 2002; Duffey 1980; Hartmann et al. 1997).

This suggests a complementary pattern of distribution of specialists and generalists among hosts or plant genotypes and an independent or, most likely, inverse response to a plant defense mechanism.

2.4.4 Enemy mobility

Many plant defenses increase in concentration locally in areas of tissue damage or systemically in damaged plants (Karban and Baldwin 1997). Whereas highly mobile enemies are capable of coping with induced defenses by dispersing their feeding to different plant parts and different individual plants, enemies of low mobility are exposed to these induced defenses for longer periods of time (Duffy and Hay 1994). Less mobile enemy taxa may have been subject to stronger selection by plant toxins and be able to tolerate or even be stimulated by compounds that deter more mobile enemies (Hay and Fenical 1988). In addition, the type of defenses recruited against the two different groups of enemies may differ. Plants may recruit the most diverse and most specific defensive systems against insects that are enclosed within plant tissue, such as leaf miners, or have their mouth parts tapped into the vascular system for long periods, such as aphids. More general, less diverse defenses may be may be effective against most herbivores as they act as general deterrents by targeting external sensory systems or common physiological mechanisms. Mattson et al. (1998) suggest “that intimate interactions may select for more specific and more complex defenses because of the greater and more varied opportunities that the host plant has for regulating the lives of the intimate associates.” Thus one might expect a complementary association of mobile and sessile enemies among plant genotypes, and a greater likelihood of positive genetic correlations in resistance to more mobile enemies, a lack of correlations between mobile and insects that form intimate associations with plants, and no correlation (or negative correlations) in resistance to sessile enemies.

2.4.5 Enemy-free space

Among the explanations for host specialization is the notion that populations of parasites colonize novel hosts that provide a refuge from predators' or parasitoids' attack, an "enemy-free space" (Berdegue et al. 1996; Bernays and Graham 1988; Jeffries and Lawton 1984). While top-down ecological forces drive this evolutionary host-shift, plants may play a part in determining what constitutes an "enemy free-space". Upon damage, some plants emit compounds that attract parasitoids, which can be quite specific (Lill et al. 2002). For instance, tobacco, cotton, and maize releases distinct volatiles depending on whether they are fed on by *Heliothis virescens* or *Heliocoverpa zea*, attracting the specialist parasitoid *Cardiochiles nigriceps* only when it perceives the volatiles specific to its larval host, *H. virescens* (De Moraes et al. 1998). Additionally, several herbivores sequester compounds from their host plants that provide means of chemical defense against the herbivores' enemies (Duffey 1980).

A plant's habitat preference or the microenvironment a plant generates may create conditions that provide protection from predators and parasitoids. The possible role of plants in determining what constitutes an "enemy-free space" may promote the confluence of plant consumers that share predators or parasitoids upon certain plant species or genotypes, generating patterns of correlation between certain plant characters and their associated consumers.

2.4.6 Local enemy density

Plant populations will evolve and maintain defenses to insects that frequently damage plants and impose a consistent selection pressure. Insects that occur in low densities will have a small selective impact on plant defensive traits, and a plant will be better adapted to insects that generally have higher densities. Insect population densities can also be highly variable in time. A plant population may evolve better defenses against enemies with smoother fluctuations in herbivore pressure that impose steady selection pressures, and be more susceptible to enemies that fluctuate dramatically in density. In more general terms, as absolute density need not equate across taxa with strength of selection, one might expect a different pattern of plant defense against low- and high-impact enemies. For instance, according to several models, constitutive defenses are favored evolutionarily over induced responses when the damage is predictable and reliable (Astrom and Lundberg 1994; Clark and Harvell 1992). If the mechanisms of the two forms of defense are independent, then resistance to enemies with different population density patterns will be independent.

Some insects with very erratic population density fluctuations have years of extremely high density. During such outbreak years, herbivores may impose very strong selection. If there is a cost associated with the defense under conditions of relaxed selection during years of low herbivore frequency, the trait will return to pre-outbreak levels. However, an outbreak population could impose such hard selection as to strongly select for resistance and leave the population devoid of genetic variation, such that it would take many generations (in the absence of further outbreaks) to return to pre-outbreak levels of susceptibility. Such populations may become resistant to the outbreak species, and any others that share crucial characteristics with it, but be relatively undefended against other enemies.

2.4.7 Local enemy diversity

The local diversity of enemies a plant population must contend with may affect its effectiveness to defend against any single enemy. In localities of rich enemy diversity, the probability of any single plant defense's being ineffective against an enemy is higher. The effectiveness of a defense per unit of resource allocated may also decrease as the diversity of attack types and resource sinks increases (Jokela et al. 2000). Such host populations may evolve more general forms of resistance than those in enemy-poorer localities (Hay and Fenical 1988).

2.4.8 Species-specific defenses

Plant enemies exploit all parts of a plant, from roots to flowers, bark to leaves. Even those that use similar plant resources may respond to different cues and plant defense mechanisms (Linhart 1989). The within-host variability combined with interspecific differences in host preferences among enemies generates *in extremis* a context for a degree of specificity in which enemies associate with hosts independently from another. This extreme of specificity of plant defense would imply that enemies do not covary among plant genotypes nor would plants exhibit correlations for resistance to different enemies. One might consider this a null-model against which models predicting some degree of structure might be tested.

2.4.9 Interwoven storylines

Several of these hypotheses are confounded to some extent. Less mobile enemies, by the very nature of their more intimate host interaction, may tend to be more specialized than more mobile species. Likewise, level of specialization may overlap with taxonomy. Members of a given insect family and even order tend to share feeding mode, but feeding modes, unless defined very narrowly, are generally not exclusive of any taxon. For instance, tea cultivars, similar in phytochemistry and varying in leaf geometry/angle, have markedly different herbivore communities: sap-feeding species more common on erect leaf-cultivar, leaf miners occur only on semi-erect leaves, and horizontal leaves were the preferred sites for the leaf chewers (Banerjee 1987). However, guilds composed of congenerics also always show preference for same leaf type.

Untangling these factors is possible by studying (when possible) a diverse set of enemies that include different combinations of factors, e.g. the effects of taxonomy and feeding guild (Maddox and Root 1987; Maddox and Root 1990), or by holding one factor constant while focusing on variation in the factor being tested, e.g., studying a number of generalist species of different levels of mobility (Duffy and Hay 1994).

I suggested earlier that enemies belonging to similar feeding guilds may covary with plant genotypes expressing, for instance, different chemical attributes. Conversely, one might argue that enemies with similar consumer requirements and preferences will tend to experience greater interspecific competition (Simms and Fritz 1990). To the extent that plant genetic variation influences oviposition or feeding preference, it can in part determine overall herbivore density and the covariances between densities of species: if two species are attracted to same genotype they will tend to positively covary in density and compete more intensely. Weaker competitors may be displaced to less preferred (i.e., more resistant) genotypes, switch to an entirely different plant species, or become locally extinct. Observed enemy suites, under this framework, would be composed of few or unique members of different feeding guilds, although these species in fact have similar *desiderata*. Exclusion of strong competitors can alter the dependent community of a plant (Dickson and Whitham 1996), and exclusion of major pests with resistant crop varieties can promote secondary pests to high impact pests (Sharma et al. 2004).

2.4.10 Mechanistic-based predictions

Krischik et al. (1991) suggested that "the greater the toxicity of [a] plant allelochemicals (…) the more general the plant defense may appear." While some compounds appear to be effective against a broad spectrum of herbivores (e.g., Dyer et al. 2003; Schmitt et al. 1995), we lack an absolute scale of toxicity that might predict which chemical compounds have general effects. Furthermore, evolution has proven itself quite effective in creating resistant forms to the most noxious defenses, which attempt to disrupt even the most essential and universal biochemical pathways, via biochemcial and behavioral strategies (Wittstock and Gershenzon 2002).

However, a greater understanding of resistance mechanisms, revealed by the reductionist pharmacological and genetic approaches described in the next section, may provide insights into which traits might be expected to have species-specific versus general effects. This approach has been effective in other systems. Nonspecific export systems that eliminate a broad variety of compounds from the cell pre-adapt bacteria for multi-drug resistance (Poole 2001). We now understand the specific gene-for-gene interactions (Flor 1956) between plants and pathogens to be driven by the variety of pathogen elicitors and the corresponding specific plant receptor proteins (DeWit 1995; Martin et al. 2003). Resistance that occurs at other organizational levels, usually of a more polygenetic nature, tends to be less species-specific. A synthesis of resistance mechanisms to herbivores and of their effects upon multiple enemies may allow one make similar predictions for plant-herbivore interactions. For instance, are plant traits that attack herbivore physiology more general than those that affect herbivore behavior? Are traits that interfere mechanically with herbivore behavior more general than those that interact with the chemosensory system?

2.5 STAGECRAFT: TOOLS AND METHODS

There are multiple forms of data from which we can garner relevant evidence for the question of generality vs. specificity of plant defense traits. Some methods are more quantitative than others, with respect for instance to the estimation of genetic parameters, such as genetic correlations. Many, if not most, of the methods are used to address separate questions, yet provide some answers to the question at hand. Indeed, there is much untapped information in the literature and on researcher's desks and hard drives that would prove relevant for this issue. For instance, in the forest and agriculture science literature there are many dispersed studies on resistance of plant varieties to different enemies than have simply never been complied. Even studies that report simultaneously multiple resistance do not calculate correlations across varieties, their main interest being in identifying varieties that are multi-resistant not patterns across varieties. I have surveyed a broad set of types of studies, in part because they provide different perspectives on this issue and the different glances will hopefully produce a fuller picture, but also because any one given fraction of the literature has relatively few studies in which several enemies are sampled.

2.5.1 Traditional Quantitative Genetics

Genetic correlations are a central parameter in evolutionary quantitative genetics that provide insight into genetic constraints and how evolution may be deflected from the direction of natural selection (Lande and Arnold 1983; Price et al. 1993; Rausher 1992b). They are caused by pleiotropy or linkage disequilibrium, *i.e.*, a common or linked genetic basis between traits. The measurement of genetic correlations for resistance to different enemies requires submitting individual plants of known genealogical relatedness to a set of enemies. For instance, Roche and Fritz (1997) measured the natural abundance of 12 herbivores on several half-sib families of *Salix sericea*, the silky willow, over the course of three years. This study did not however measure resistance to each enemy separately, and thus plant resistance, measured as the reciprocal of herbivore abundances, may be confounded by interactions between herbivores.

There are many standard split-family designs for estimation of quantitative genetic parameters, many of which have been applied to this question: diallel crosses (Rausher and Simms 1989; Simms and Rausher 1989), full-sib families (Pilson 1996), half-sib families (Maddox and Root 1987; Roche and Fritz 1997), and clones (Fritz 1990; Mutikainen et al. 2002). A further possibility, applied to study the correlation between resistance and tolerance in the self-compatible *Ipomoea pupurea*, is the use of inbred lines (Fineblum and Rausher 1995), a procedure used frequently in the agronomic field (e.g., Elden and Lambert 1992; StMartin et al. 1994).

Heritabilities and genetic correlations have quite large confidence limits, and thus require large samples for precise estimations (Roff 1997). If one is to conduct a factorial design, with different enemies independently upon plants, then these experiments quickly become a great logistic burden. These methods vary in their statistical power and the degree to which dominance and maternal effects bias some of the parameters (Falconer and Mackay 1996; Lynch and Walsh 1998; Roff 1997). For instance, the use of clones, while offering some logistic advantages in the production of replicates, merely allow the estimation of total genetic variance, not the quantification of additive genetic variance, the relevant term for predicting responses to selection. [In addition, there is the possibility of topophysis, or non-genetic inheritance (Fritz 1992).] Half-sib designs are preferable to full-sib designs because in the former only one of the components of variance, the nested component, is biased by dominance effects.

Phenotypic correlations, while not allowing for the separation of genetic and environmental causes of variation, are much easier to estimate and have smaller standard errors. It has been argued that phenotypic correlations could be used as fair estimates of genetic correlations (Cheverud 1988; Koots and Gibson 1996; Roff 1995; Roff 1996); *c.f.*, (Willis et al. 1991). Maddox and Root (1990) found a strong correlation ($r=0.75$) between phenotypic and genetic correlations for resistance to 17 goldenrod herbivores. In contrast, Rausher and Simms (1989) found poor correspondence between the two types of correlation. Roche and Fritz (1997) also concluded phenotypic correlations were not particularly good predictors of genetic correlations. Within a year, they found a number of significant phenotypic correlations for herbivore abundance, but few significant genetic correlations, perhaps due to low statistical power given the low number of dams used in the study.

Finally, while these parameters are of interest to evolutionary and coevolutionary studies they are limited with regard to providing information about a common genetic basis of resistance to different enemies, for one must interpret the magnitude of the correlations appropriately. The absolute value of a correlation depends on the allele frequencies in a population. Thus differences in these frequencies within a population, driven by migration, mutation, selection, and drift, or between populations because of differences in local conditions, do not necessarily reflect differences in underlying genetic basis or mechanism of resistance. In addition, a correlation in resistance integrates over many plant characters that may vary in their contribution to the resulting correlation. An underlying mechanism that is strongly positively correlated over enemies, whose effects are combined with multiple mechanisms with small complementary effects, may result in an overall lack of detectable correlation. In short, a lack of correlation does not demonstrate a lack of causal connection and mechanisms with pleiotropic effects (Cheverud 1984; Mitchell-Olds and Rutledge 1986).

2.5.2 Measurement of selection gradients

An approach that follows from the quantitative genetic framework is the estimation of selection gradients, by measuring the covariances between a phenotypic trait, such as plant resistance, and individual fitness (Lande and Arnold 1983; Rausher 1992b). Recently, it has been suggested that in order to avoid the confounding effect of environmental covariances, one should estimate the covariance between fitness and breeding values, which requires the use of family groups described earlier (Mauricio and Mojonnier 1997; Rausher 1992a). Measuring whether the pattern of selection acting upon a trait varies with the presence and absence of an enemy is an important step in demonstrating that enemies are in fact driving evolution of resistance traits (Rausher 1996). A few studies have demonstrated that selection imposed by different enemies occurs in a multispecies, rather than pairwise, manner (Juenger and Bergelson 1998; Pigliucci 2003; Pilson 1996). Mauricio and Rausher (1997) used this approach to measure the selection gradients imposed on trichome density and glucosinolate content of *Arabidopsis thaliana* by the whole of its community of enemies. Stinchcombe and Rausher (2001) were able to separate the effects of different enemies by the use of an insecticide and fungicide. The phenotypic trait measured was deer herbivory, not any particular putative defense trait, but their study did report significant resistance to deer and generalist insect herbivory. Experiments combining the use of exclusionary devices to bar particular enemies and the measurement of putative defense traits would contribute to our understanding of enemy selection upon common defensive mechanisms.

2.5.3 Artificial selection experiments

Selection experiments provide a number of advantages over other methods for estimating genetic parameters. Positive responses to artificial selection directly demonstrates the heritability of the selected trait rather than rely on variance estimates, and avoids confounding errors due to unmeasured traits. Whereas split-family designs rely on estimation of variance and covariance components, an artificial selection design compares differences among line means, and thus offers greater statistical power for a similar number of individuals studied (Conner 2003). By measuring traits not subject to direct selection one can estimate genetic correlations between these traits and the trait targeted by selection. However, results from short-term selection experiments are limited for inferring long-term genetic constraints, as epistasis may cause the initial response to selection to differ from the response in inbreeding populations undergoing continuing selection (Mitchell-Olds and Rutledge 1986).

To address the issue of common mechanism in resistance to different enemies one can use two different approaches. One approach uses specific enemies to generate more resistant or susceptible populations and tests these populations against other enemies. As the populations resulting from artificial selection can be used in multiple separate experiments, the objective of studying multiple enemies becomes more feasible logistically. Mitchell-Olds et al. (1995) separately selected populations of *Brassica rapa* for resistance to three fungal pathogens, and then tested populations from each treatment for resistance to the other pathogens. In chapter two, I describe my experiment comparing control populations of *B. rapa* and those selected for increased resistance to cabbage leaf spot, *Alternaria brassicicola*, with regard to their resistance to a variety of insect herbivores. In addition, I tested for differences among treatments in glucosinolate content and profile, a potential resistance mechanism.

This ‘black box’ approach is not ideal for identifying mechanisms of resistance. More adequate for this purpose is to directly select upon a putative resistance trait and then compare populations with regards to their relative resistance to different enemies. Stowe (1998) selected populations of *Brassica rapa* for divergent leaf glucosinolate content and tested divergent populations for resistance to feeding by two species of lepidopteran larvae. In chapter three, I describe my experiment comparing populations selected for divergent vegetative expression of anthocyanins for resistance to a variety of enemies. While this approach does allow one to implicate a mechanism in multiple interactions, it does not allow for proper estimation of genetic correlations for resistance to different enemies. Several traits may have changed due to their correlations with the selected trait, but they may be uncorrelated among themselves. Thus, only correlations between the trait artificially selected and subsequently measured traits can be correctly estimated, not those between two unselected traits (Conner 2003).

2.5.4 Hybrid studies

The study of herbivory on hybrid plants has been gaining greater attention in the last decade (Boecklen and Spellenberg 1990; Dungey et al. 2000; Hanhimaki et al. 1994; Messina et al. 1996; Orians et al. 1997; Whitham et al. 1994). By comparing resistance between parental species and their interspecific hybrids, one can distinguish among the mechanisms of inheritance of resistance. Fritz et al. (1994) compared densities of eleven herbivores and a leaf rust pathogen on two willow species (*Salix sericea* and *S. eriocephala*) and their hybrids. Most species were more abundant on hybrids than on parental plants, but a few species followed an additive pattern – the hybrid intermediate between the parental species – or a dominance pattern – the hybrid more similar to one of the parental species. If two species have a similar pattern of abundance across genotypes, it does not imply they are responding to similar plant traits, but we do learn that species with different distribution patterns interact with traits of distinct genetic nature. Furthermore, one can determine whether species with similar patterns of abundance across genetic classes have similar characteristics, *e.g.*, feeding guild membership.

2.5.5 Changes in plant environment

Some insight into which plant features are relevant to enemies and which enemies respond similarly may be gathered by traditional ecological studies sampling and comparing enemy communities. Although there are certainly confounding factors, including interactions among enemies and their response to environmental factors, as well as the inability to distinguish dependent and 'tourist' species, enemy densities (or load *sensu* Root and Cappuccino 1992) are also a reflection of plant traits.

The level of fertilization, water or light availability, and other abiotic factors affects the allocation of plants resources to resistance or its ability to tolerate damage. Numerous experiments have attempted to measure the effects of manipulating these factors on resistance or tolerance against a given enemy (Gassmann 2003; Orians and Floyd 1997; Stowe et al. 1994; Throop 2002). Many of these were conducted in the context of testing physiological plant defense theories. Manipulative experiments of this sort, if combined with the measurement of effects upon several enemies, can provide an additional perspective on patterns of enemy response to plant traits. By analyzing which enemies respond similarly we may better understand the sensitivity of different groups, and the biotic dimensions that unite species into enemy suites. If information on the concrete mechanism is lacking, a set of enemies responding in concert to the manipulation of an abiotic factor may in fact be responding to different plant traits, which have responded similarly to the manipulation. However, a common enemy response does indicate enemies are sensitive to plant traits that have correlated responses to environmental factors, perhaps because they are linked metabolically.

These studies have an additional interest that derives from the empirical finding that plant responses to abiotic stress and biotic stress have common mechanisms (see below). Studying community changes along a gradient of abiotic stress could bring insights on the ecological manifestations of those underlying mechanisms.

2.5.6 Enemy community composition across host species

Although we are concerned with how a trait of a focal species affects its associated community of enemies, comparisons of such communities across hosts can also be informative. Such comparisons can reveal patterns of covariation between enemies across hosts, which could be a reflection of their common response to the homologous plant features. For instance, Peeters et al. (2002b) compared insect assemblages in 18 co-occurring plant species. By also measuring a number of plant traits, they were able to correlate densities of particular guilds with such traits, *e.g.*, external chewers were significantly negatively correlated with percent lignified area. The morphological traits measured were also found to be better predictors of community composition than leaf constituents such as nitrogen (Peeters 2002a).

2.5.7 Induced Responses to Herbivory

One of the most active fields recently within the study of plant-enemy interactions has been the study of induced resistance to natural enemies and the plant mechanisms that underlie these responses. These studies have changed our view of plants as static victims of offensives, protected only by whatever constitutive defenses they happen to posses, to a much more dynamic view of a plant actively mobilizing resources after enemy damage to influence enemy behavior or invasiveness (Karban and Baldwin 1997).

This approach has unveiled a complex set of physiological network pathways, from elicitation to signal transduction and local and systemic responses. Much of the research has centered on salicylate– and jasmonate-mediated responses (Bostock et al. 2001). The role of salicylic acid (SA) was revealed through studies of systemic acquired resistance (SAR) to plant pathogens, and the role of jasmonic acid (JA) largely through the study of wound induced responses. As result, these response pathways were thought initially to be quite taxa specific, but there is growing evidence of cross-talk between pathways (Felton and Korth 2000; Thaler et al. 2002b; Walling 2000).

Induced responses range from the *de novo* synthesis of compounds such as phytoalexins (low molecular weight plant antibiotics), active oxygen species (*e.g.*, hydrogen peroxide), proteinase inhibitors (PIs) and pathogen-related proteins (PRs), to programmed cell death (or hypersensitive response), cell wall modifications, and trichome growth (Agrawal 2000a; Hammerschmidt and Nicholson 1999; Karban and Baldwin 1997).

In the context of multiple enemies, one can consider the degree of specificity of resistance at different levels (Stout and Bostock 1999): recognition, signaling, and effect. *Specificity of recognition* refers to the plant's ability to distinguish between different types of assault. As a result of the interaction with an enemy, one or more signals (elicitors) are released. These can be a combination of plant molecules, released at the interaction surface (Ebel and Cosio 1994; Ham et al. 1995; Mendgen et al. 1995), enemy molecules, *e.g.*, elements of insect regurgitate (Alborn et al. 1997; McCloud and Baldwin 1997; Musser et al. 2002b), or microbial components (Meindl et al. 2000; Waspi et al. 1998). *Specificity of signalling* refers to differential signal transduction, the plant's ability to translate different elicitors into the activation of different responses cascades, *e.g.*, the activation of SAR- versus JA-mediated pathways trigger different response cascades and different downstream genes (Stout et al. 1994). Stout and Bostock (1999) consider these latter two phenomena jointly. However, they refer to different causal levels. Plants may produce similar responses because of a lack specificity in the types of elicitors produced during an interaction, or, there may be specificity in this regard but as a result of canalized responses to different elicitors, driven for example by extensive cross-talk between signal transduction pathways, a nonspecific response could be produced. Some species simultaneously induce alternative defense pathways that can confer resistance to the same pathogens and pests (Ellis et al. 2002). Finally, *specificity of effect* refers to the spectrum of enemies affected by the elicited response, a question that is similar to when one is considering the specificity of preformed, constitutive responses. Whereas the former two levels referred to the specificity of plant processes in reaction to assault, this level refers to the specificity of enemy reactions to a plant's response. Specificity of effect will depend upon the nature of the final response, what aspects of an enemy's biology it targets, and the degree to which enemies are themselves sensitive to such responses.

An inducible mechanism can respond to natural selection driven by an enemy via changes in elicitor detection mechanism, *e.g.*, a novel receptor co-opts an existing response mechanism, or evolution in the actual genes activated in response to an attack signal. If the effect of a plant response is nonspecific, then changes in the inducible mechanism due to selection driven by one enemy will have correlated effects on other enemies.

Concrete studies vary from strictly organismal studies, *e.g.*, in which plants are submitted to damage or infection and their resistance against a different enemies is subsequently tested (Agrawal 2000b), to more strictly biochemical or physiological experiments, *e.g.*, in which known elicitors are applied to the plant and gene expression is analyzed (Tamaoki et al. 2003). Plant-mediated effects among enemies and comparisons of induced responses to individual enemies (including gene expression, see below) may reveal common resistance mechanisms.

2.5.8 Pharmacological bioassays

There is a long tradition of testing the effects of extracted plant compounds on plant enemies. Compounds can be added to an insect's artificial diet or the growth media of a pathogen (*e.g.*, Pompermayer et al. 2001; Powell et al. 1993). These *in vitro* studies allow one to study the isolated effect of a compound, but exclude potentially important processes that occur *in* vivo. The large literature on these types of studies has hardly been synthesized with the specific aim of understanding patterns of effects on multiple plant enemies.

2.5.9 Genetic evidence

Modern molecular genetics and genomics offer a slew of different methods of studying ecologically relevant traits, such as the mechanisms of resistance (Hatcher and Paul 2000; Jackson et al. 2002). Mutants of model plant systems, particularly *Arabidopsis*, when tested against plant enemies have clarified the network of genes involved in induced pathway systems and the importance of these genes and pathways upon plant defense (e.g., Bowling et al. 1997; Ellis and Turner 2001; Frye and Innes 1998; Penninckx et al. 2003). Plants less amenable for mutant screening can be transgenically modified to express genes from model systems. For instance, transgenic white poplar (*Populas alba*) expressing a cysteine proteinase inhibitor gene from *A. thaliana* were more resistant to larvae of the chrysomelid beetle, *Chrysomela populi* (Delledonne et al. 2001).

Molecular techniques have also allowed the coarse mapping of loci that affect quantitative traits. Quantitative trait loci (QTL) represent a fairly large region of the genome (~10 centimorgans, ~500-600 genes in *A. thaliana*) and thus include one or more candidate genes actually affecting the studied trait. Plant genome maps are becoming gradually available supplying possible identification for candidate genes. This will become easier with the development of markers for fine-mapping of genes become available. However, QTLs associated with defense to an enemy or putative defensive traits can be used as markers to test for defense to other enemies. Kliebenstein et al. (2002) mapped QTLs controlling resistance to the specialist diamondback moth, *Plutella xylostella*, and the generalist cabbage looper, *Trichoplusia ni*. They identified QTLs specific to resistance to each insect and a single QTL controlling resistance to both herbivores. Furthermore, by comparing these QTLs with those mapped for controlling variation in glucosinolate production, they demonstrated that resistance to *P. xylostella* was uncorrelated with variation in this class of compounds shown to provide defense against *T. ni* and other generalist enemies.

Microarray analysis now permits one to measure the expression level of hundreds to thousands of genes simultaneously. By comparing plants subjected to different abiotic conditions or enemy assault with control plants, one can identify genes that are specifically expressed in response to those environments. Reymond (2000) compared microarray analysis from mechanically wounded plants to those damaged by larvae of the cabbage butterfly, *Pieris rapae*, and detected one gene specifically induced by insect feeding. Similar analyses using different enemies can unravel which proportion of genes are expressed specifically to a given enemy and which are expressed in response to a broader group of taxa. The application of microarry analysis to artificially selected populations may prove to be a powerful experimental strategy, as it would afford the prospect of analyzing gene expression correlated with change in complex traits over replicated populations.

2.5.10 Mathematical models

Theoretical models are a complementary tool to the many empirical approaches described thus far. In contrast with the deluge of empirical data on this topic that is in need of synthesis, there is a remarkable dearth of models dealing specifically with the context of defense against multiple enemies. This may derive from the lack of formulation of straightforward questions to be addressed. Some models from the host parasite evolution framework or from evolution of resistance to multiple pesticides are applicable. One question concerns the optimal level of resistance specificity when a host is attacked by multiple parasites. Frank (2000), for instance, modeled conditions favoring specific versus non-specific defense against parasite attack, and found conditions favoring hosts with specialized defenses, due to lower investment in more costly nonspecific defense. Lapchin (2002) simulated a fluctuating system in which the fitness of host and parasitoid varied with levels of resistance and virulence specificity. The optimal host strategy depended on the frequency of encounters with parasitoids, with a generalist resistance favored as a bet-hedging strategy to a fluctuating parasitoid population.

Poitrineau (2003) model the effects of mechanistic interference among two defenses to two enemies and of defensive synergy, *i.e.*, the engagement of defense against one enemy inducing resistance to other enemies. Conditions of high synergy and encounter rate with both enemies favor a maximal investment in one defense and an intermediate investment in the other defense. Interestingly, this tends to decouple the defense from the cues that induce it, and paradoxically a host that evolved in an environment with multiple enemies may become more susceptible to enemy attacks if the enemy community declines in diversity.

2.6 'TRAFFIC OF OUR STAGE': EVIDENCE FOR PATTERNS

In this section, I shall review data obtained with the methods described earlier. I will review some in greater detail than others. For instance, the review of changes in enemy communities across hybrids, different environments, and host plants, offers a comparatively small number of studies applicable to the theme of this review and I explain a few studies in some detail. In other sections, the relevant literature is extensive and dispersed and consequently I refer to important aspects, defer to recent reviews, and compile references in table format.

2.6.1 Correlations in resistance

I have collated and updated previous reviews (Fritz 1992; Linhart 1989; Rausher 1996) of genetic correlations for resistance to multiple enemies (see table 1). An overview reveals few negative genetic correlations, or indication of ecological trade-offs, and in a majority of cases correlations are non significant or positive. Taxonomy is a poor predictor of correlation in resistance. Stinchcombe and Rausher (2001), based on empirical measurements in *Ipomoea purpurea* of genetic correlations for resistance to herbivores, even suggest that trade-offs between mammalian and insect herbivores may be more common that those between resistance to different types of insects. There are some examples of negative correlations between specialists and generalist species (*e.g.*, Da Costa and Jones 1971; Kinsman 1982), however these also occur between generalists enemies. Significant correlations are on occasion along quite unexpected lines, as in the study by Wu and Ying (1997) in which the two positive genetic correlations found were between a moth and two fungal pathogens, the gall and blister rust.

2.6.2 Patterns of abundance

Whitham (1989) observed a large proportion of the aphid *Pemphigus betae* on hybrids of two *Populus* species and suggested that hybrids might constitute a sink for plant pests. In a review of 152 studies of hybridizing systems, nearly a third were consistent with this hypothesis (Whitham et al. 1999). Generalists were more likely than specialists to be found on hybrids, and specialists were more likely to have a dominance response, such that their abundance on hybrids as highest on those closest to the parent species on which they are specialists. A study of herbivore communities in a *Eucalyptus* hybrid sward found this same general pattern and correspondence with inheritance of leaf terpenoids (Dungey et al. 2000). This suggests a fundamental difference in the underlying genetics of resistance to specialists and generalists.

Many such studies rely on naturally occurring hybrids [identified with morphplogical or molecular methods (Hardig et al. 2000; Paige and Capman 1993)], but thus confound genetic and environmental effects. For this reason, Fritz (1999) argued for common garden and reciprocal transplant experiments with hybrids of known origin. In one such experiment, among *Salix* hybrids generated by hand-pollination, two sawflies and a leaf-galling midge were more abundant on hybrids and one of the parental species *S. caprea*, supporting the dominance pattern. Three other species exhibited no difference among classes. In contrast, hybrids were more infected by the rust *Melampsora* sp than either parent (one of the parents, *S. repens*, is totally resistant). The breakdown in rust resistance in hybrid plants suggests an epistatic breakdown that does not occur for any of the insect species.

Fritz et al. (2003) measured abundance of 14 species of herbivores among the willows *Salix sericea* and *S. eriocephala*, and their F_1, F_2, and backcross hybrids. By comparing the enemy communities among the different genetic classes, they tested whether resistance traits or host recognition traits determine host abundances. Epistatic combinations present in the parents are disassociated among the other genetic classes. If traits with antibiotic or antixenotic effects determine insect abundance, then the breakdown of epistasis of these resistance traits would result in higher herbivore abundance or damage. If cues or stimulants determine herbivore abundance, then the breakdown of epistasis would result in lower herbivore abundance or damage. Epistasis contributed to the patterns of 10 species, 4 species exhibited a pattern consistent with a breakdown of resistance, and 6 species with a breakdown of host recognition. As all of these six species use both parental species as hosts, this suggests herbivores use different cues in recognizing each host. The four remaining species exhibited a dominance pattern.

This study suggests a predominance of non-additive effects in plant-enemy interactions, which may impose constraints on plant defense evolution.

Orians and Floyd (1997) combine the use of *Salix* hybrids and varying nutrient levels to look genetic and environmental effects on herbivore densities. Plant susceptibility increased along a fertilization gradient, but this effect did not vary among the 5 insect herbivores and the fungal pathogen studied. Abundance patterns among genetic classes supported the dominance hypothesis: hybrid susceptibility to the rust *Melampsora* sp. And leaf miner *Phyllocnistis* sp. resembled that of *S. eriocephala*, whereas susceptibility to the sawfly *Phyllocolpa nigrita*, spider mite *Tetranychus sp.*, and leaf-chewing beetle *Popillia japonica* resembled *S. sericea*'s.

Meyer and Root (1996) compared densities of seventeen insect herbivores, from different feeding guilds, occurring upon *Solidago altissima* grown in fertilized and unfertilized plots. Most herbivores differed significantly in density among plots, but the effect was not strongly related to feeding guild, similarly to other studies in the same system (Maddox and Root 1990). But other studies have found differences among feeding guilds. Mazia et al. (2004) studied herbivore communites along a productivity gradient in northern Patagonian forests and found a predictable change of insect guild prevalence across the forest gradient. The xeric, least productive forests had greater total damage and this was accounted for largely by the prevalent leaf miners, whereas leaf chewers dominated in the more humid and productive forests.

Kopelke and Amendt (2002) studied the distribution of 43 species of gall-formers on 15 *Salix* species and two hybrids. Trees species most frequently hosted only two galling species, yet members of such species pairs tended to attack different individuals.

A comparison of *Eucaplyptus* herbivore community throughout a year revealed different seasonal responses among functional groups: some herbivorous groups responded to times of leaf production, and decomposers and fungus feeders respond to high moisture availability (Recher et al. 1996). The most valuable set of studies looking at herbivore communities across species are those that relate enemy distributions to plant traits (Peeters 2002a; Peeters 2002b; Peeters et al. 2001; Topp et al. 2002).

Larsson (1989) reviewed the effects of plant stress upon different guilds and found that while plant stress negatively affects gall-forming insects, it did not have any overall effect upon leaf-chewing or leaf-mining insects. A number of studies report a higher rate of colonization of stressed trees by bark beetles.

2.6.3 Pharmacological evidence

While the number of compounds and the corresponding literature is too vast to conduct a broad survey of the effects of specific compounds on different enemies, I will present some illustrative examples. I have selected a few compounds that are known to serve as host-plant selection cues (sinigrin) or that affect plant physiology (proteinase inhibitors and lectin). In so doing, we can survey the effects of a spectrum of compounds, but also address whether these two classes of compounds have different degrees of specificity of effect. I have avoided selecting broad categories of compounds, *e.g.*, glucosinolates, flavonoids, that include several thousand individual compounds, and whose diversity might confound any patterns. Insects interact with particular chemical compounds, although certainly blends of compounds are important sensory cues, however they are not exposed to entire families of compounds. However, in some cases I have broadened the search to include more than one chemical compound. Bibliographic searches were conducted in Web of Science, using as search keyword: (name of the compound) and (insect* or fung* or nemat* or pathog*), and complemented with relevant references in the bibliographies of these articles. While the references presented may not be exhaustive, I think they are representative.

2.6.3.1 Sinigrin

Sinigrin, or allyl glucosinolate, is found in numerous members of the Brassicaceae (crucifers). It is found to have both toxic/deterrent and stimulatory effects, on oviposition and feeding (see table 2.2). In general, generalists were affected negatively whereas crucifer specialists were affected positively by sinigrin, although it had relatively little impact upon feeding rate of larvae of the cabbage butterfly *Pieris rapae* (Blau et al 1978), the monophagous weevil *Ceutorhynchus inaffectatus* (Larsen et al. 1992) or the cabbage stem flea beetle, *Psylliodes chrysocephala* (Bartlet and Williams 1991). Interestingly, while it stimulated the specialist flea beetle *Phyllotreta nemorum* it had little effect on its congener *Phyllotreta cruciferae* (Nielsen et al. 2001). It’s effects were manifest on different feeding guilds, including the previously mentioned leaf-feeders and phloem feeders, such as the cabbage aphid, *Brevicoryne brassicae* (Gabrys and Tjallingii 2002). In summary, sinigrin appears to have a fairly broad deterrent effect, but stimulates feeding and oviposition of numerous specialists. Thus, pharmacological data seem consistent with the specialist/generalist hypothesis.

2.6.3.2 Protein Inhibitors (PI)

Plant protein inhibitors when ingested by insects catabolize insect midgut enzymes lead to hyperproduction of proteolytic enzymes by the insect, gradual decline in amino-acid availability, and reduction in growth and development (Broadway and Duffey

1986). There a are few categories of PIs, including cystein PI and trypsin CI, and isolated proteins. Their corresponding genes receive names corresponding to the plant species from which they were isolated. Due to the fairly toxic effects of these compounds, their genes have been used extensively to genetically-modify plants for increased resistance to insects, and many of the references found correspond to bioassays with transgenic plants (see table 2.3.). The fact that plant compounds expressed transgenically can affect enemies they might never encounter naturally is in itself evidence of the general effect of these compounds. Most have dose-dependent effects, *i.e.*, their antibiotic effect is reduced at low concentrations. In one case, *Spodoptera littoralis* larvae grown on leaves expressing low trypsin PI grew faster than control larvae (De Leo et al. 1998). Activity also depends on dietary quality (Pompermayer et al. 2003), physiological conditions of the midgut, and the structural compatibility with the proteinases of target insect (Ferry et al. 2003). Some species, *e.g.*, *Helicoverpa armigera*, have a complex gut proteinase composition (Patankar et al. 2001), or in the case of *Leptinotarsa decemlineata* respond by producing PI insensitive proteinases (Cloutier et al. 1999; Cloutier et al. 2000). Polyphagous species appear to be more invulnerable to nonhost PIs (Broadway and Villani 1995).

2.6.3.3 Lectins

The effectiveness of lectins stems from their resistance to gut proteolysis and a high and specific chemical reactivity with endogenous surface receptors of the epithelial cells of the gut of both higher animals and lower organisms. For instance, insecticidal activity of *Griffonia simplicifolia* leaf lectin II (GSII) is functionally linked to carbohydrate binding, presumably to the midgut epithelium or the peritrophic matrix, and to biochemical stability of the protein to digestive proteolysis (Zhu-Salzman et al. 1998).

However, the primary effects and the potency of lectins as biological signals are the direct result of their specific chemical reactivity with saccharides. For instance, Con A-induced production of pisatin (a phytoalexin) in pea tissues might be associated with activation of a signal-transduction pathway.(Toyoda et al. 1995). Although there is no direct correlation between toxicity and sugar specificity of the lectin (Rahbe et al. 1995), the binding reactions are predictable and as such the use of lectins as blockers of pathogens, immune stimulants, hormone modulators and metabolic agents in clinical-medical applications and as natural insecticides in transgenic plants offers great promise (Pusztai and Bardocz 1996).

2.6.3.4 Patterns from pharmacological data

A review of the literature confirmed that compounds that affect basic physiologic functions, such as proteinase inhibitor and lectins, have deterrent effects on a broad range of enemies, regardless of their level of specialization. Transgenic experiments demonstrate their effectiveness against enemies when expressed in transgenic host, *i.e.*, against enemies they did not specifically evolve to deter. That this broad pattern has occasional exceptions merely demonstrates the power of natural selection acting upon plant enemies to circumvent even the most cardinal of offenses.

Secondary compounds may have a different pattern of effects, deterring or injuring generalists while acting as host selection cues for specialists. This pattern seems to hold for sinigrin, a glucosinolate, which I reviewed, as well as other secondary compounds (Bernays and Chapman 1994). Systematic review of the effects of other secondary compounds on a broad array of enemies, rather than a collection of anecdotal evidence, must be done to further test the ‘specialist/generalist’ hypothesis.

Pharmacological studies rarely incorporate intra-specific variation. But it is this level of variation that pertains to enemy-driven natural selection in plant traits. One might expect generalists to be less sensitive to the more subtle intra-specific variation, but more sensitive to inter-specific variation (Futuyma and Saks 1981). Maddox and Root (1987) found no relationship between host breadth and response to genetic variation among *Solidago* clones. Ayres (1997) found no striking difference between the growth response of polyphagous versus oligophagous insects exposed to tannins from different woody plant species. Secondary compounds often also affect specialists, in a dose-dependent fashion. Several crucifer-specialists performed better at intermediate concentrations of glucosinolates, even though many of them use the compounds as host-selection cues .(Agrawal and Kurashige 2003; Siemens and MitchellOlds 1996). Specialists may simply be able to tolerate secondary compounds at higher levels, although even specialists have tolerance limits: *Ophraella communa*, a ragweed (*Ambrosia artemisiifolia*) specialist, had reduced performance on heavily fertilized plants that presumably expressed higher amounts of N-based sesquiterpenes (Throop 2002).

2.6.4 Genetic evidence

Analysis of plant genomes is revealing that a large number of genes are potentially involved in plant defense. The *Arabidopsis thaliana* genome contains an estimated 11.5% of its genes involved in defense (Arabidopsis Genome Initiative. 2000) (see fig. 1). Chromosome 1 and 4 of rice (*Oryza sativa*) have an estimated 3.3% of their identified genes dedicated to defense (Feng et al. 2002; Sasaki et al. 2002). In both cases, these numbers are preliminary as a large number of the genes have unassigned functions. It remains to be determined whether these genes have specific or general functions.

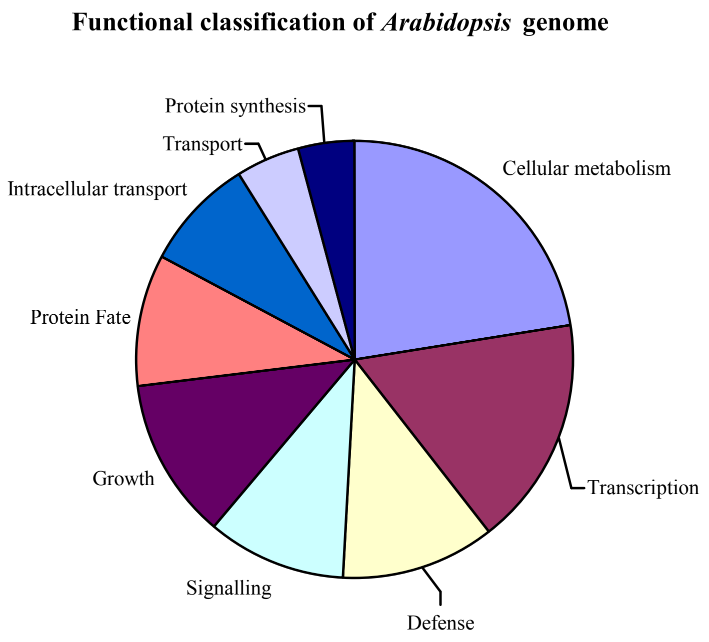

Fig. 2.1. Preliminary functional classification of the 17,833 identified genes in the *Arabidopsis thaliana* genome (Arabidopsis Genome Initiative. 2000)

However, in the case of chromosome 4 of *Arabidopsis*, the large proportion of defense genes is attributed to several clusters of leucine-rich repeat (LRR)-resistance specificity genes that produce proteins for specifically detecting pathogens another genes used for detecting abiotic and biotic stresses (Mayer et al. 1999). Disease resistance specificity may be associated with variation in these regions (Ellis et al. 2000). As more plant genomes become available, we will be able to reconstruct the history of the common plant ‘defensome’(Korth 2003; Moran et al. 2002; Reymond 2001; Schenk et al. 2000).

Comparing expression profiles is a technique that is bound to be very profitable in determining the degree of specificity of certain genes. The beet gene Hsl(pro-1) that specifically provides nematode resistance has also been identified in Arabidopsis (Thurau et al. 2003). The tomato resistance gene Mi has been found to confer resistance to both root knot nematode *Meloidogyne incognita*, the whitefly *Bemisia tabaci*, and the potato aphid *Macrosiphum euphorbiae* (Nombela et al. 2000; Rossi et al. 1998; Vos et al. 1998). Despite this broad effect on diverse taxa, Mi-mediated resistance did not extend to several populations of the potato aphid or to a generalist aphid that also attacks tomato, *Myzus persicae* (Goggin et al. 2001).

Although there seems to be significant specificity of recognition of attacks (Ebel and Mithofer 1998), there is a general lack of specificity in signaling pathways induced upon elicitation. Several genomic studies are demonstrating commonalities among plant response to pathogen and herbivore infection and to abiotic stress (Farmer 2000; Izaguirre et al. 2003). In addition, studies of plant induced responses are revealing substantial cross-talk between the JA and SAR pathways (Felton and Korth 2000; Rojo et al. 2003; Thaler et al. 2002b), with possible antagonism between them (Thaler et al. 2002a). Certain responses can be induced by arthropods and pathogenic micro-organisms (Marak et al. 2002). Even in instances of specificity of enemy recognition, the induced response tends to be more general in effect (Agrawal 2000b), but see van Zandt and Agrawal (2004). For instance, herbivore damage leads to the expression of genes involved in both in the JA-pathway and genes related to abiotic stress, pathogen infection and phytohormone signaling pathways (Zhang et al. 2004). There are several *Arabidopsis* mutants that the signal receptors knock-out or have constitutive expression of induced mechanisms, *e.g.*, the *coil* mutant is insensitive to JA and *cev1* has constitutive JA signaling. Ellis (2002) used these mutants to demostrate that JA-dependent defenses provide resistance to the biotrophic fungal pathogen *Erysiphe cichoracearum,* the bacterial pathogen *Pseudomonas syringae* pv. *maculicola*, and the green peach aphid *Myzus persicae*, independently of SA-dependent defenses.

Comparison across different studies can also reveal the general architecture of plant resistance. For instance, Kover and Caicedo (2001) looked at 85 studies that investigated the genetic architecture of plant disease resistance and found strong evidence that disease resistance in plants is polygenic and epistasis commonly affects resistance.

2.7 CURTAIN CALL: CONCLUSIONS

As is often the case with attempting to draw wide-ranging theories in biology, one is confronted with what appear to be taxon- and environment-specific phenomena. Distinct results may emerge if one studies different insect developmental stages (Renwick et al. 2001; Van Dam et al. 2001), different plant organs (Barnola et al. 1997; Hoy et al. 1998), phenological stages (Basset 2001; Kearsley and Whitham 1989; Lawrence et al. 2003; Waltz and Whitham 1997), or different times during the growing season (Pilson 1992).

Certain defense patterns may emerge only under given stressful environments (Waterman and Mole 1989). Local plant populations experience unique environments that can have a strong effect on their enemy associations (Stiling and Rossi 1995). The particular species composition of a plant's community of enemies will shape its overall defense strategy (Futuyma and Mitter 1996) and plants will experience different evolutionary histories, *e.g.*, different population size fluctuations, selection pressures experience different enemy communities (Thompson 1994). The constancy of the genetic variance-covariance matrix (G-matrix), as in the particular case of a matrix of correlations for resistance to different enemies, is still a question being dealt with empirically. Reviews reveal that species in different genera may have more similar matrices than congeners (Roff 1997).

A pattern between enemy species dictated by interaction with chemical components may be broken by behavioral adaptations. In a study of two leaf-chewing beetles that feed on *Cucurbita moschata*, cucurbitacins are rapidly mobilized to damaged leaves and stimulate feeding by the chrysomelid *Acalymma vittata* but inhibit feeding by the coccinelid *Epilachna tredecimnotata*. However, *E. tredecimnotata* feeds within a leaf area that it has previously trenched, which prevents its contact with the deterrents (Carroll and Hoffman 1980).

However, there are some general conclusions to be drawn from this survey of the literature. It is apparent that plant defense is often positively correlated among enemies, occasionally along unexpected lines. As our understanding of plant defense mechanisms increases it is becoming clear that while some levels are specific to certain enemies, many have broad effects. Together with increasing evidence of indirect affects among plants and nonadditive effects of damage on plant fitness, the existence of general defenses suggests a predominance of multispecies rather than pairwise coevolution between plants and their enemies (Hougen-Eitzman and Rausher 1994; Iwao and Rausher

1997; Stinchcombe and Rausher 2001). It is increasingly clear that plant defense constitutes an important bottom-up contributing effect in structuring communities (Agrawal 2003; Hochwender and Fritz 2004; Whitham et al. 2003).

Is there evidence for patterns of association among enemies along the lines of any of the hypothesis outlines earlier? We lack sufficient information to address some of the hypotheses outlined earlier. However, we can address some of the above hypotheses.

There appears to be little support for the taxonomic hypothesis. While the utility of taxonomy may to some extent be dependent on scale, there are a number of examples of closely related species showing distinct responses to resistance traits that advise prudence in using this criteria, for instance congeneric enemies responding differently to plant genotypes (e.g., Messina et al. 1996), or to different plant chemical components (e.g., Huang et al. 1993a; Huang et al. 1993b). In contrast, several cases document mechanisms having similar effects on very taxonomically distinct enemies, *e.g.*, a nematode and virus (Hunter et al. 1996),

Although chemical defenses seem to affect enemies regardless of their feeding guild, community studies show a strong correlation between plant structural features, such as pubescence, and guild composition (Andres and Connor 2003; Cornell and Kahn 1989; Peeters 2002b). "Species were no more likely to exhibit negative correlations with their guild mates than they were with members of other guilds. (...) Several species were positively associated with one another on the basis of similar habitat requirements or the use by one species of conditions created by the presence of another" (Root and Cappuccino 1992). Feeding guilds are partly a human construct and those that may appear evident to investigators may in fact include a greater degree of subtlety in forms of interaction. For instance, leaf chewers vary in whether or not they damage leaf veins, feed on both leaf surfaces, or prefer different stages of leaf development they prefer. Different forms of leaf damage, whether clumped or dispersed, are known to affect plant physiology and fitness (Mauricio et al. 1993; Meyer 1998).

As our understanding of plant mechanisms and their effects on multiple enemies increases, we will be able to test hypotheses of patterns in relation to certain classes of mechanisms. Our analysis of pharmacological effects seems consistent with the notion that antibiotic mechanisms involved in host-selection follow a generalist/specialist divide, whereas antixenotic mechanisms that affect enemy physiology are broader in effect, being less effective against polyphagous species.

Overall, this certainly suggests a word of caution to the experimenter that one cannot simply use one enemy in a study and assume that answers apply to any other enemy, or use a representative species to selected for a resistant plant breed and expect it to come to have broad resistance. Researchers should refrain from generalizing based upon studies with a single species and encouraged to ‘bite the logistic bullet’ and sample a broader set of enemies. Groups of enemy species may interact with plant defense mechanisms in modes that are unaccounted for by the suggested hypotheses or some combination thereof. An apparently idiosyncratic pattern may also indicate there are plant-dictated principles which we are unable to discern. Only with more multi-enemy studies and additional synthetic work can one hope to understand what constitutes enemy suites.

Comparison with analogous fields of inquiry may provide further insights, including the generality of immune response (e.g., Blount et al. 2003; Schmid-Hempel and Ebert 2003; Yunis et al. 2002), and the responses of prey to multiple predators (Relyea 2003; Sih et al. 1998) and to multiple parasites (Fellowes and Kraaijeveld 1998). The aquatic and marine literature contains many relevant studies (Hay 1996; Hay and Fenical 1988; Schmitt et al. 1995). There is extensive literature on resistance to multiple herbicides (*e.g.*, Brogdon et al. 1999; Kuk et al. 2000; Sibony and Rubin 2003; Walsh et al. 2004) and insecticides (*e.g.*, Andreev et al. 1999; Oakeshott et al. 2003; Soderlund and Knipple 1995). Bacterial resistance to multiple antibiotics is an important medical issue, however we need more studies of resistance of proteins and natural bacterial isolates to antibiotics that is due to pleiotropy rather than acquisition of novel plasmids (Faichild and Cowan 1991; Feldgarden and Riley 1999).

While understanding the mechanisms and genetics of resistance is enlightening, it is important to bear in mind that natural selection perceives ‘resistance’ as a composite trait. From an evolutionary perspective, it is this combination of mechanisms that relates level of enemy damage to plant fitness that fuels evolution. Our understanding of the maintenance of genetic variation within populations and the sheer multiplicity of resistance mechanisms relies on being able to look upon resistance simultaneously at the mechanistic and phenomenological level.

Plant Species	Enemies	Experimental design	Pattern	# enemies	Signnificant correlations			Reference
					-	0	+	
Solidago altissima	17 insect herbivores, from different feeding guilds	Clones	Positive correlations did not cluster herbivores according to feeding guild	17	9	100	27	(Maddox and Root 1990)
Ipomoea purpurea	Specialist tortoise beetles (*Deloyala guttata* and *Metriona bicolor*) and sweet-potato flea beetle (*Chaetocnema confinis*), generalist corn earworm (*Heliothis zea*), generalist folivores (including grasshoppers)	Replicated partial-diallel cross		4	0	6	0	(Simms and Rausher 1989)
	Same as above and in addition the fungal pathogen *Colleotrotricum dematium*	Replicated partial-diallel cross	Significant correlation between anthracnose and tortoise beetle resistance	5	0	4	1	(Simms and Rausher 1993)
	C. confinis, *H. zea*, and generalist herbivores	Inbred lines		3	0	2	0	(Fineblum and Rausher 1995)
	The specialists *D. guttata* and the sweet potato leaf miner *Bedellia somnulentella*	Inbred lines		2	0	1	0	(Hougen-Eitzman and Rausher 1994)
	Deer and generalist insect damage	Half-sib design		2	1	0	0	(Stinchcombe and Rausher 2001)
Mimulus guttatus	Spittlebug *Philaenus spumarius* and Cucumber Mosaic virus	Half-sib design		2	1	0	0	(Eubanks et al. 2002)
Brassica rapa	Three fungal pathogens: Peronospora parasitica, Albugo candida and Leptosphaeria maculans	Artificial selection for disease resistance	Singificant positive genetic correlation between resistance to *Peronospora* and *Leptosphaeria*	3	0	2	1	(Mitchell-Olds et al. 1995)
	Flea beetle Phyllotreta cruciferae and weevil Ceutorhynchus assimilis	Half-sib design	Although no significant correlation in resistance to the two beetles was detected, there was a significant negative correlation between tolerance to weevil damage and resistance to flea beetles.	2	0	1	0	(Pilson 2000)
	Fungal pathogen *Alternaria*, and cecidomyid seed predator	Family		2	1	0	0	(Nakamura et al. 1995)

Xanthium strumarium	Two insect seed predators, Phaneta imbridana and Euaresia aequalis			2	1	0	0	(Hare and Futuyma 1978)
Trifolium repens	Molluscs, sheep, a weevil, and two fungal pathogens (*Cymadothea trifolii* and the rust *Uromyces trifolii)*	Cyanogenic and acyanogeic clones	Acyanogenic morphs were preferred by molluscs, *U.t.* preferred cyanogenic morphs. Remaining species exhibited variable or no preferred association	5	1	9	0	(Dirzo and Harper 1982)
Curcubita moschata	Chrysomelid beetle, *Acalymma vittata*, and coccinelid beetle *Epilachna tredecimonotata*		Curcurbitacins stimulate feeding by *A.v.* and inhibit feeding by *E.t.*	2	1	0	0	(Carroll and Hoffman 1980)
Cucumis sativus	Two-spotted mite *Tetranychus urticae* and cucumber beetle *Diabrotica spp*	Isogenic lines	Cucurbitacines attract specialist beetle and are toxic to generalist mite	2	1	0	0	(Da Costa and Jones 1971)
Oenothera biennis	Two specialists: the noctuid *Schinia florida* and the aphid *Macrosiphum gaurae*; and the generalist japanese beetle *Popillia japonica*, sap sucking plant bugs *Lygus lineolaris* and *Plagiognathus* spp.	Two genotypes, one resistant the other susceptible to the specialist herbivores	Genotype preferred by both specialists were least preferred by generalist herbivores	5	6	0	4	(Kinsman 1982)
Betula pendula	Voles and insect herbivores	Multiple genotypes		2	0	0	1	(Pusenius et al. 2002)
	Geometrid moth, *Epirrita autumnata*, and two mammals (vole and hare)	Clones		3	0	2	1	(Mutikainen et al. 2002)
	Hare Lepus timidus, vole Microtus agrestris, weevils Polydrosus mollis and Phyllobius aregentatus, fly Phytobia betulae, leaf miner moth Eriocrania spp., two phloem feeding aphids, Euceraphis betulae and Symydobius oblongus, and leaf feading moth Operophtera brumata	Clones	No correlation on clone resistance to herbivores. Two clones exhibited opposite response to mammals, and aphids and leaf miner.	9				(Rousi et al. 1997; Tikkanen et al. 2003)
Pinus contorta	Three fungal pathogens, the western gall rust, *Endocronartium harknessii*, the stalactiform blister rust *Cronartium coleosporioides*, and the needle cast *Lophodermella concolor*, and sequoia pitch moth *Synanthedon sequoiae*	Half-sib	Positive correlations in resistance between pitch moth and blister rust and between moth and gall rust	4	0	4	2	(Wu and Ying 1997)

Pinus radiata	Black-tailed deer Odocoileus hemionus and porcupine Erethizon dorsatum	Clones		2	1	0	0	(Hood and Libby 1980)
Salix laiolepis	Four closely related gall-forming sawflies: the stem-galling *Euura lasiolepis*, the petiole galler *Euura* sp., the leaf-galling *Pontania* sp., and the leaf-folding sawfly *Phyllocolpa* sp.	Clones		4	0	2-5[1]	1-4	(Fritz and Price 1988)
	idem	Clones		4	0	1-5[2]	1-5	(Fritz 1990)
Salix sericea	Leaf miner, *Phyllonorycter salicifoliella*, the leaf-galling *Pontania* sp., and the leaf-folding sawfly *Phyllocolpa* sp.	Clones	Negative correlation between the leaf miner and leaf galler, positive correlation between leaf miner and leaf-folder	3	1	1	1	(Fritz 1992)
Salix phylicifolia	Mountain hare Lepus timidus, grey-sided vole Clethrionomys rufocanus, and autumnal moth Epirrita autumnata		Hares and voles may select willows at least partly on the same basis, but there was no correlation between palatability of the trees to the mammals and the growth rate of the larvae of the autumnal moth on the same trees	3	0	2	1	(Suomela et al. 1997)
Pseudotsuga menziesii	Black-tailed deer *Odocoileus hemionus* and snowshoe hare *Lepus americanus*	Clones		2	0	1	0	(Dimock et al. 1976)
	Wooly aphid, Gilletteella cooleyi and needle cast fungus Rhabdocline pseudotsugae	Among populations		2	1	0	0	(Stephan 1987)
Quercus ruber	13 species of Cynipini oak galling wasps	Phenotypic correlations		13	0	60	18	(Ananthakrishnan 1984)

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[1] Study includes samples in two year.

[2] Study included two sites samples in two years.

Camellia sinensis	80 spp of phytophagous insects	Tea cultivars varying in leaf geometry	Defoliators and leaf chews feed mostly on cultivars with horizontal leaves; leaf rollers and miners colonize only semi-erect leaves; sap feeders prefer cultivars with erect leaves but inhabit all three types					(Banerjee 1987)
Glycine max	Velvetbean caterpillar *Anticarsia gemmatalis*, sybean looper *Pseudoplusia includens*, tobacco budworm *Heliothis virescens*, and corn earworm *Heliothis zea*	Agricultural varieties	Genotype showing resistance to one of the insect species also showed resistance to the other three species.	4	0	0	6	(Lambert and Kilen 1984)
Medicago sativa	Three root rot fungi Fusarium avenaceum, F. oxysporum, and F. solani, bacterial wilt Clavibacter michiganense and Verticillium wilt Verticillium albo-atrum	Half-sib design	Resistancse to *Fusarisum* spp were positively correlated. Resistance to *V.a.* was correlated with resistance to some *Fusarium* sp.	6	0	9	6	(Millergarvin and Viands 1994)

Table 2.1 Survey of reported correlations for resistance to natural enemies. For the purpose of this table, correlation should be understood broadly to include quantified genetic and phenotypic correlations and correlations inferred from artificial selection experiments or comparisons among genotypes. This table includes entries from previous reviews (Fritz 1992; Linhart 1989; Rausher 1996) and additional references I compiled for this review. When more than two enemies were studied, I briefly describe the pattern of correlations among species. Only statistically significant correlations are noted in the positive and negative correlation columns. Some studies (e.g., Fritz 1990, Fritz 1992) include multiple correlation matrices, calculated in different environments or years. In these cases I have supplied the range of the number of correlations in each category.

Effect of compound	Enemy species
Negative effects on survival	specialist *Papilio polyxenes* (Blau et al. 1978), sheep (Duncan and Milne 1993)
Negative effects on development	Generalists: *Spodoptera eridania* (Blau et al. 1978), Bertha armyworm *Mamestra configurata* (McCloskey and Isman 1993), cabbage looper *Trichoplusia ni* (Shields and Mitchell 1995), pea aphid, *Acyrthosiphon pisum* (Gabrys and Tjallingii 2002), the nematode *Heterodera schachtii* (Lazzeri et al. 1993), and variety of pathogens (Mari et al. 1993; Mayton et al. 1996)
No impact	Generalist: *Spodoptera eridania*(Li et al. 2000) Crucifer specialists: *Pieris rapae* (Blau et al 1978) and flea beetle *Phyllotreta cruciferae* (Nielsen et al. 2001)
Feeding stimulant	Generalist: desert locust *Schistocerca gregaria* (Leberre and Tira 1977) Crucifer specialists: weevil *Ceutorhynchus inaffectatus* (Larsen et al. 1992) cabbage stem flea beetle, *Psylliodes chrysocephala* (Bartlet and Williams 1991), cabbage aphid, *Brevicoryne brassicae* (Gabrys and Tjallingii 2002), and flea beetle *Phyllotreta nemorum*
Oviposition stimulant	Crucifer specialists: *Pieris rapae*, *Pieris napi* (Huang and Renwick 1994; Traynier and Truscott 1991) and diamondback moth *Plutella xylostella*

Table 2.2. Effect of sinigrin (a glucosinolate) on plant natural enemies.

Effect of compound	Enemy species
Negative effects on survival	Antibiotic resistance (Calatayud et al. 1994)
Negative effects on development	Generalists: European corn borer *Ostrinia nubilalis* (Abouzaid et al. 1993), noctuid *Anticarsia gemmatalis* (Gazzoni et al. 1997) Specialists: *Manduca sexta* (Horwath and Stamp 1993; Stamp and Horwath 1992)
No impact	Generalists: *Trichoplusia ni* (Krischik et al. 1991) and *Heliothis virescens* (Bi et al. 1997) Specialists: *Manduca sexta* (Krischik et al. 1991)
feeding stimulant	Generalist acridid *Schistocerca americana* (Bernays et al. 1991), polyphagous japaness beetle *Popillia japonica* (Fulcher et al. 1998), *Galerucella vittaticollis* (Ohta et al. 1998), growth stimulant of mycorrhyzae *Pisolithus* hyphal growth (Lagrange et al. 2001)
Oviposition stimulant	*Papilio xuthus* (Ohsugi et al. 1991)

Table 2.3. Effect of rutin (a flavonoid) on several plant natural enemies.

Plant	Enemy species	Effect of compounds	Reference
Nicotiana attenuata expressing TPI from potato	hornworm *Manduca sexta* and mirids *Tupiocoris notatus*	Negative effects on growth rate and survirorship	(Zavala et al. 2004)
Vigna spp. with different expression of CPI	Bruchid *Callosobruchus maculatus*	No effect	(Sulehrie et al. 2003)
Medicago sativa expressing OC-I and OC-II	Root-lesion nematodes *Globodera pallida*	Negative effect on population size	(Samac and Smigocki 2003)
Soybean *Glycine max* PI in artificial diet	moth *Diatraea saccharalis*	Negative effect, but weaker effect when larvae fed on PI in a richer artificial diet	(Pompermayer et al. 2003)
Sugar cane *Saccharum officinarum*	sugarcane borer *Diatraea saccharalis*	Negative effect on larval growth.	(Falco and Silva 2003)
Potato expressing OC-I	potato cyst nematodes *Globodera pallida* and *Globodera rostochiensis*, and *Eupteryx aurata*	Enhanced levels of resistance to nematodes but negligible impact on the nontarget herbivore *E. aurata*.	(Cowgill and Atkinson 2003)
Potato with OC-I	Colorado potato beetle *Leptinotarsa decemlineata*	No effect on adult survival, incidence of diapause, relative growth rate, or female reproductive fitness. Beetles compensated their lower conversion efficiency by increasing foliage consumed and adapting their digestive proteolytic system, *e.g.*, producing OCI-insensitive proteases.	(Cloutier et al. 1999; Cloutier et al. 2000)
Oak expressing TPI	oak leafroller *Tortrix viridana* and gypsy moth *Lymantria dispar*		(Ivashov et al. 2001)
Tobacco expressing MTI-2	Moth *Spodoptera littoralis*	No effects on larval development but significant reduction in adult fertility	(De Leo and Gallerani 2002)
Tobacco *Nicotiana alata*	budworm *Helicoverpa punctigera* and black field cricket *Teleogryllus commodus*	Reduced growth and increased mortality	(Heath et al. 1997)
Tobacco and pea expressing tobacco PI	*Helicoverpa armigera*	larvae exhibited higher mortality and extended development.	(Charity et al. 1999)
Tobacco expressing SBTI	*Helicoverpa armigera*	No effect, despite negative in vitro proteolytic effects of SBTI on *H. armigera* gut enzyme activity	(Nandi et al. 1999)
Chickpea *Cicer arietinum*	Podborer *Helicoverpa armigera*	No effect, *H. armigera* produced inhibitor-insensitive proteinases that digest chickpea PIs	(Giri et al. 1998)

Arabidopsis expressing OC-I	slug *Deroceras reticulatum*	Decreased growth	(Walker et al. 1999)
Brassica napus expressing OC-I	pea aphid *Acyrthosiphon pisum*, cotton/melon aphid *Aphis gossypii*, peach potato aphid *Myzus persicae*,	Negative effect on weight and fecundity	(Rahbe et al. 2003)
Oilseed rape *Brassica rapa* expressing OC-I	Diamondback moth *Plutella xylostella*	No effect as *P. xylostella* uses serine digestive proteases, nor on its predator Ladybird predator *Harmonia axyridis*, although *in vitro* studies demonstrated effect of OC-1 on *H. axyridis* proteases.	(Ferry et al. 2003)
Brassica rapa expressing OC-I or SBBI	Beetle *Phaedon cochleariae*	*In vitro* effects of PIs on beetle proteinases, but *in vivo* PIs were cleaved by insect serine proteinases	(Girard et al. 1998b)
Brassica rapa expressing OC-I	two strains of cabbage seed weevil *Ceutorhynchus assimilis*	*In vitro* effects of PIs on beetle proteinases, but one strain showed an increased growth rate when fed the transgenic seeds, while the other strain remained unaffected.	(Girard et al. 1998a)
Brassica rapa expressing OC-I	Beetle *Psylliodes chrysocephala*	increase in weight gain accompanied by 2-fold increase in both cysteine and serine proteolytic activity	(Girard et al. 1998c)
Brassica rapa expressing OC-I	Weevil *Baris coerulescens*	OC-I inhibits completely the cysteine proteinase activity in vitro, but growth and survival of larvae feeding on transformed *B. rapa* was not affected. Larvae compensated by decreasing activity of cysteine proteinase and increasing serine proteinase activity by more than 2-fold	(Bonade-Bottino et al. 1999)
Damaged leaves of maize *Zea mays* accumulate maize PI	*Spodoptera littoralis*	inhibitor of mammalian and insect elastase and of insect chymotrypsin, but not mammalian chymotrypsin	(Tamayo et al. 2000)
Winter wheat *Triticum aestivum*	Root rot *Fusarium* spp.	Wheat PIs neutralized *Fusarium* proteases providing rot resistance	(Klechkovskaya et al. 1998)
Barley *Hordeum vulgare*	aphids *Schizaphis graminum* and *Rhopalosiphum padi*	Aphids induce chymotrypsin inhibitor production in barley leaves. When fed the PI in artificial diets, only *R. padi* showed decreased survival	(Casaretto and Corcuera 1998)
Rice expressing BTI-CMe	rice weevil *Sitophilus oryzae*	Reduced survival rate	(Alfonso-Rubi et al. 2003)
Rice expressing SKTI	brown planthopper *Nilaparvata lugens*	Increased plant resistance	(Lee et al. 1999)
Rice *Oryza sativa*	Beetle *Callosobruchus chinensis* and seed bug *Riptortus clavatus*	Reduced growth and increased mortality	(Kuroda et al. 1996)
Rice expressing potato PI	pink stem borer *Sesamia inferens*	Increased resistance to stem borer	(Duan et al. 1996)
Poplar (*Populus tremula* x *P. tremuloides*) expressing OC-I	Beetle *Chrysomela tremulae*	Increased resistance to beetle	(Leple et al. 1995)

Artificial diet with soybean CPI	western corn rootworm *Diabrotica virgifera*	inhibits growth and development	(Zhao et al. 19967)
Artificial diet containing potato PI-II	black field cricket *Teleogryllus commodus*	Slower growth and nd damage to midgut	(Sutherland et al. 2002)
Artificial diet with soybean PI	sugarcane borer, *Diatraea saccharalis*	Retardation of growth and development rates but no effect on survival	(Pompermayer et al. 2001)
Artificial diet with SKTI	oriental beetle *Exomala orientalis*, European chafer *Rhizotrogus majalis*, Phyllophaga white grub *Phyllophaga anxia*, cranberry root grub *Lichnanthe vulpina*, Japanese beetle *Popillia japonica*, Asiatic garden beetle *Maladera castanea*, and the black cutworm *Agrotis ipsilon*	STI did not influence larval survival for those species with relatively generalized feeding habits (i.e., oriental beetle, European chafer)	(Broadway and Villani 1995)
Artificial diet with SBBI	Honey bee, *Apis mellifera*	No major toxic effects but elicited a large decrease in trypsin activity	(Belzunces et al. 1994)
Artificial diet with SBBI, POT-1, POT-2, BTI or CPI, with 3 different levels of casein	black field cricket *Teleogryllus commodus*	High levels of mortality at low concentrations on diets with low or moderate casein. Efficacy in reducing cricket growth was strongly influenced by the level of dietary casein	(Burgess et al. 1994)
Artificial diet with SKTI, SBBI, or a CPI	rice weevil, *Sitophilus oryzae*	CPI decreased survival and delayed development. Weevils fed SKTI and SBBI, developed normally.	(Pittendrigh et al. 1997)

Table 2.4. Effect of in vivo proteinase inhibitors (PI) on different plant enemies. Articles that only reported in vitro studies of the effect of PIs on insect proteinases, e.g., Burgess et al (2003), were not included. Abbreviations. BTI-CMe: barley trypsin inhibitor; CPI: cysteine proteinase inhibitor (cystatin); MTI: mustard trypsin inhibitor; OC: a rice CPI (oryzacystatin I), e.g., OC-I; SKTI: soybean Kunitz trypsin inhibitor; SBBI: soybean Bowman-Birk inhibitor; SBTI: Soybean trypsin inhibitor; TPI: trypsin protease inhibitors.

Plant	Enemy species	Effect of compounds	Ref
winged bean *Psophocarpus tetragonolobus*	seed weevil, *Callosobruchus maculatus*	Toxic to larvae, toxicity correlated with lectin's haemagglutinating activity	(Gatehouse et al. 1991)
Common Bean *Phaseolus vulgaris*	Azuki-Bean Weevil, *Callosobruchus chinensis*	Inhibition of larval growth	(Ishimoto and Kitamura 1991)
Stinging nettle *Urtica dioica*	Fungus *Phycomyces blakesleeanus*	No reduction of mycelial growth but changes in cell wall structure and chitinase production.	(Vanparijs et al. 1992)
transgenic tobacco expressing high levels of GNA	Peach potato aphid *Myzus persicae*	Increased resistance	(Hilder et al. 1995)
Transgenic tobacco expressing GNA	potato aphid *Aulacorthum solani*	Slower development and decrease in adult fecundity	(Down et al. 1996)
Transgeneic tobacco expressing GNA	Nematode G*lobodera pallida*	Increased resistance	(Burrows et al. 1998)
transgenic potato plants expressing GNA	tomato moth, *Lacanobia oleracea*	Reduced leaf damage, total insect biomass per plant, and slight reduction in larval survival	(Gatehouse et al. 1997)
Transgeneic potato expressing Con A	tomato moth *Lacanobia oleracea* and peach-potato aphid *Myzus persicae*	Delayed development of both insects, increased *L. oleracea mortality*	(Gatehouse et al. 1999)
transgenic potato plants expressing GNA	Noctuid *Lacanobia oleracea*	slowed larval development and lower survival	(Fitches et al. 1997)
Transgeneic rice expressing GNA	Rice brown planthopper *Nilaparvata lugens*	decreased survival and delayed development, and overall deterrent effect	(Rao et al. 1998)
Purified lectins from eleven plant sources	Three fungi Neurospora crassa, *Aspergillus amstelodami*, and *Botryodiplodia theobromae.*	sensitivity to osmotic lysis, adventicious branching of spore germ tubes, and inhibition of germ tube elongation	(Brambl and Gade 1985)
Artificial diet with WGA	European Corn-Borer *Ostrinia nubialis*, Southern Corn-Rootworm *Diabrotica undecimpunctata*, *Callosobruchus maculates* Cowpea Weevil and rice brown planthopper *Nilaparvata lugens*	Inhibition of larval growth	(Czapla and Lang 1990; Murdock et al. 1990; Powell et al. 1993)
Potato lectin STA	fungal potato pathogen *Fusarium oxysporum*	irreversibly inhibits conidia germination and alters the germ tubes	(Gozia et al. 1993)
Eranthis hyemalis lectin	alfalfa mosaic virus, and southern corn rootworm, *Diabrotica undecimpunctata*	Antiviral and larvicidal	(Kumar et al. 1993)

Artificial diets with GNA or WGA	rice brown planthopper *Nilaparvata lugens*, rice green leafhopper *Nephotettix cinciteps*	antimetabolic effects	(Powell et al. 1993)
WGA, UDA and agglutinin from thorn apple *Datura stramonium*	Rat	interfered with metabolism and function, including hypertrophic growth of the pancreas and caused thymus atrophy	(Pusztai et al. 1993)
Artificial diet with Con A	Aphid *Acyrthosiphon pisum*	significant toxicity and growth inhibition	(Pusztai et al. 1993)
Artificial diet with WGA	Honey bee, *Apis mellifera*	No major toxic effects but elicited a large decrease in trypsin activity	(Belzunces et al. 1994)
Artificial diet with WGA and 3 different levels of casein	black field cricket *Teleogryllus commodus*	High levels of mortality at low concentrations on diets with low or moderate casein. Efficacy in reducing cricket growth was strongly influenced by the level of dietary casein	(Burgess et al. 1994)
Artificial diet with WGA or lectin from *Brassica spinescens*	Aphid *Brevicoryne brassicae*	Insecticidal	(Cole 1994)
Artificial diet with Con A	Pathogen *Magnaporthe grisea*	Suppression of appressorium formation, but not conidial germination and adhesion.	(Xiao et al. 1994)
	European Corn-Borer *Ostrinia nubialis*	significant mortality or a decrease in weight gain, also bound strongly brush border membrane proteins	(Harper et al. 1995)
Artificial diet with GNA, WGA, PSA, NPA, ASA, OSA, or UDA.	Rice brown planthopper, *Nilaparvata lugens*	GNA was most effective antifeedant, reducing honeydew excretion by 96%, followed by NPA, WGA, and ASA. With time some recovery took place. PSA, OSA, and UDA had no significant effect.	(Powell et al. 1995a; Powell et al. 1995b)
Thirty lectins, including Concanavalin A	pea aphid *Acyrthosiphon pisum*. Concanavalin A tested on five other aphids: *Aphis gossypii*, *Aulacortum solani*, *Macrosiphum euphorbiae*, *Macrosiphum albifrons* and *Myzus persicae*	Most exhibited low toxicity, but some, *e.g.*, concanavalin A, lectins from amaranth, lentil and snowdrop, induced significant mortality. Dose-response curves to concanavalin A differed substantially between aphid species.	(Rahbe et al. 1995)
Artificial diet with WGA and GNA	Scarab sugarcane whitegrub *Antitrogus parvulus*	insecticidal and growth inhibiting	(Allsopp and McGhie 1996)
Five lectins	silverleaf whitefly, Bemisia argentifolii	Not insecticidal	(Davidson et al. 1996)

Artificial diet with GNA, NPA, or ASA	Peach potato aphid *Myzus persicae*	GNA caused mortality, and NPA and ASA reduced growth	(Sauvion et al. 1996)
Lectin from *Griffonia simplicifolia*	cowpea weevil, *Callosobruchos maculatus*	Insecticidal	(Zhu et al. 1996)
Artificial diets with PNA	Stem borer *Chile partellus*	Peanut lectin bound to epithelial cells in the mid-gut of C. Partellus and increased mortality	(Law and Kfir 1997)
Artificial diet with lectin from *Griffonia simplicifolia*	rice weevil, *Sitophilus oryzae*	No effect	(Pittendrigh et al. 1997)
In vitro assays with extract from transgeneic tobacco expressing UDA	Germinated spores of the fungi *Botrytis cinerea, Trichoderma viride*, and *Colletotrichum lindemuthianum*	growth inhibition at a specific phase of fungal growth	(Does et al. 1999)
Artificial diets with 25 lectins from 15 plant families	legume pod borer, *Maruca vitrata*	16 lectins had detrimental effects pertaining either to larval survival, weight, feeding inhibition, pupation, adult emergence and/or fecundity. LOA and *Galanthus nivalis* (Amaryllidaceae) agglutinin were effective against for all six parameters examined	(Machuka et al. 1999)

Table 2.5. Effects of lectins on plant natural enemies. Some of the articles describe in vitro fluorescence binding and agglutination assays. Abreviations. ASA: dimer Garlic *Allium sativum* agglutinin; BPA: *Bauhinia purpurea* agglutinin; Con A: Jack Bean *Canavalia ensiformis* concanavalin A; GNA: tetramer Snowdrop *Galanthus nivalis* agglutinin; LOA: common twayblade *Listera ovata* agglutinin (Orchidaceae); NPA: trimer Daffodil *Narcissus pseudonarcissus* agglutinin; OSA: dimeric *Oryza sativa* agglutinin; PNA: peanut *Arachis hypogaea* agglutinin PSA: *Pisum sativum* agglutinin; UDA: monomeric *Urtica dioica* agglutinin; WGA, Wheat Germ *Triticum aestivum* agglutinin

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