

## Chapter 3

### WHY INDUCED DEFENSES MAY BE FAVORED OVER CONSTITUTIVE STRATEGIES IN PLANTS

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#### Abstract

Although induced resistance has been documented in over 100 species of plants, why plants employ facultative defense strategies is not well understood. Although it has been widely accepted that induction may be a means of reducing resource allocations to defense when not needed, this explanation is not exclusive of a wide array of hypotheses for the advantages of induced defenses. In an attempt to shift attention away from the “allocation cost” model, here we focus on several alternative hypotheses for the benefits of induction. Given that most plants interact with multiple specialist and generalist herbivores, various pathogens, microbes, and mutualists, a host of constraints on maintaining constantly high levels of resistance arise. The temporal and spatial variability in food quality for phytophages created by induction may be especially important. Variability may hinder herbivore performance in ecological time as well as the evolutionary ability of herbivores to adapt to host plants. Research on the various benefits of induced defenses seems to be the obvious next step in understanding why so many plants employ induction.

## Introduction

This chapter examines the potential of induced responses to maximize plant defense and focuses on factors that may have favored induced over constitutive defenses. Induced responses to herbivory are common and well documented in plants (reviewed by Karban and Baldwin, *in press*). We define induced resistance to herbivory as a plant response that leads to a reduction in the performance or preference of an herbivore that feeds on a damaged plant. We reserve the term “induced defense” for responses that confer resistance against herbivores and increases plant fitness. The study of induced responses is rich with examples of induced resistance across many taxa of plants and affecting various herbivores (e.g., Karban and Carey 1984, Haukioja and Neuvonen 1985, Zangerl 1990, Baldwin 1991, Bryant et al. 1991, Rausher et al. 1993). However, there are almost no clear examples of induced responses increasing the fitness of induced plants compared to uninduced controls in the presence of herbivores (but see Raffa and Berryman 1982). Demonstration of such effects on fitness components is necessary (but not sufficient) to infer that induced responses are the result of adaptations to herbivory.

In addition to the lack of evidence for induced responses affecting plant fitness (i.e., induced defense), there has been surprisingly little exploration of the various constraints and selection pressures that could favor an inducible over a constitutive strategy of defense (see Rhoades 1979, Karban and Myers 1989, Tuomi et al. 1991, Parker 1992, Adler and Karban 1994, Åström and Lundberg 1994, Padilla and Adolph 1996). If induced responses are effective at deterring and/or killing herbivores, why are they not on all of the time? Measurement of increased plant fitness of damage-induced plants

compared to damaged but uninduced plants can demonstrate that induced responses are defensive, but not that inducibility would necessarily be favored over a constitutive strategy. Nearly all previous explanations for the evolution of induced defenses have implicated saving of allocation costs as the key factor. Other benefits have been less well explored. In this chapter we outline several potential benefits of induced responses to herbivory. Measuring the benefits of induced responses will allow us to: 1) evaluate the ecological consequences of induction, and 2) begin to identify the selection pressures that may have resulted in inducible rather than constitutive defenses.

There are many reasons why inducible defenses may be favored over constitutive ones (Table 3.1.A). Induced defenses may be favored or maintained by selection because they are more effective than constitutive strategies. Inducibility can be viewed as an effective strategy if it minimizes costs (in the broadest sense) or if it maximizes benefits to the plant for a given level of investment in defense. These potential benefits do not demonstrate that induced responses are defensive, but rather that induced defenses may be favored over constitutive defenses. In Table 3.1.B, we indicate mechanisms of induced responses that may benefit plant fitness and provide evidence for defense. Below we focus on the benefits described in Table 3.1.A and henceforth only consider defensive responses.

### The Role of Allocation Costs

The hypothesis for the evolution of induced defenses that has been widely accepted posits that defense is maintained as a facultative trait because expression of defense traits diverts essential resources from growth and reproduction (Zangerl and Bazzaz 1992). In the absence of herbivory, plants that do not

allocate resources to defense traits are predicted to have higher levels of resources available for growth and reproduction (Herms and Mattson 1992, Rausher 1996). Experimental attempts to find such allocation costs of induction have met with limited support (Brown 1988, Simms 1992, Karban 1993b, A. Agrawal et al. unpublished manuscript, but see Baldwin et al. 1990). Although there is limited support for the “savings of allocation cost” argument, research on other benefits of induced defenses is currently lacking. Furthermore, many researchers continue to interpret patterns and develop mathematical models and verbal defense theories based largely on the notion that defense as an induced trait is a strategy to reduce allocation costs (Herms and Mattson 1992, Zangerl and Bazzaz 1992, Rausher et al. 1993, Zangerl and Rutledge 1996). Below we suggest that this interpretation may not be correct, or at least that it may not be complete, and that alternative factors favoring the evolution of induced defenses should be considered. Realistically, why might allocation costs be minimal or undetectable?

Selection can minimize initial costs of resistance. Numerous examples from taxa other than plants have demonstrated this phenomena and are reviewed by Simms (1992) and McKenzie (1996). In a recent study, Schrag and Perrot (1996) worked with bacteria that evolved resistance to an antibiotic. Two lines of resistant bacteria initially showed fitness reductions (costs) of 14% and 19%, respectively, in the absence of the antibiotic. Quite surprisingly, in bacterial cultures without the antibiotics but with both resistant and wild types (not resistant), the wild type bacteria did not dominate the cultures. To the contrary, after 135 generations, all of the colonies assayed were resistant. After an additional 45 generations (in the absence of antibiotics) the resistant bacterial strains evolved further and

minimized the cost of resistance until fitness was indistinguishable from wild types. In our own studies of costs of induction, we are finding that plants exhibit variation for costs among half sibs grown in a common environment, suggesting that cost may be subject to selection (A. Agrawal et al., unpublished data). Our interpretation of this is that costs of resistance are not universal and can be minimized by selection if they exist early in the evolutionary process.

In an extensive survey of costs of plant resistance, Bergelson and Purrington (1996) found that only 33% of the studies reviewed demonstrated costs of resistance to herbivores. Other reviews of costs of plant resistance, discussions of additional explanations for “no cost defenses”, and problems with detecting costs can be found elsewhere (Parker 1992, Simms 1992, Karban 1993b, Antonovics and Thrall 1994, Mole 1994) and are not discussed further in this chapter.

Do the absence of allocation costs defy logic, or just a paradigm? In the late 1970's, ecologists studying species interactions held competition as a ubiquitous phenomenon, a paradigm of ecology (reviewed in Salt 1983). The view that competition was so important led some experimentalists who did not find competition between species to reject their experiments before rejecting the hypothesis that competition was occurring (Strong 1980). Allocation costs of plant resistance may be a similar paradigm. We view repeated failure to experimentally find significant allocation costs of plant resistance as a genuine contribution to plant-herbivore studies and as a window for new avenues of research on constraints and selection pressures on plant defense.

Even where detectable or undetectable allocation costs exist, they may not necessarily be the most important constraint favoring the evolution of induced defenses (Parker 1992, Simms 1992, Karban 1993b,

Mole 1994). The importance of allocation costs for the evolution of induced defenses will be determined not only by attempts to detect such costs, but by comparing costs of maintaining induced versus constitutive defenses. If costs of induced and constitutive defenses are comparable, their relevance is dubious. Given our current state of knowledge, it seems short-sighted to overlook non-exclusive alternative hypotheses. In subsequent sections we consider less explored hypotheses for the evolutionary origin and/or maintenance of induced defenses in plants.

### **Induced Defenses Reduce Host Finding by Specialist Herbivores**

Here we focus on situations where induced responses to herbivory lead to both resistance and susceptibility and might be a mixed blessing for the plant. Evidence from several systems suggests that damaged plants may sometimes become more attractive or of better quality to herbivores (Danell and Huss-Danell 1985, Apriyanto and Potter 1990, Haukioja et al. 1990, Karban and Niho 1995, Baur et al. 1996). This is termed induced susceptibility. For example, some phytochemicals that are implicated in resistance against generalist herbivores also serve as attractants for specialized herbivores. Thus, a potential benefit of employing induced defenses is that defense chemicals are used when needed, but specialist herbivores are not as attracted to plants in the uninduced state. Below we discuss a system where this may be occurring.

Induced responses and resistance to generalist herbivores have been studied in many brassicaceous plants including Brassica napus, B. rapa, B. nigra, B. juncea, Raphanus raphanistrum, R. sativus, Lepidium virginicum, and Sinapis alba (Koritsas et al. 1991, Bodnaryk 1992, Doughty et al. 1995, R. Mithen, personal communication, A. Agrawal unpublished data). A general pattern of increased indole glucosinolates following

damage and increased resistance against generalist herbivores has been found. There are also many studies demonstrating that glucosinolates are important stimulants of oviposition and larval feeding in pierid butterflies and other specialist herbivores (e.g., flea beetles and diamondback moths) of the Brassicaceae (David and Gardner 1966, Feeny 1977, Blau et al. 1978, Chew 1980, Lamb 1989, Huang and Renwick 1993, Chew and Renwick 1995, Giamoustaris and Mithen 1995).

The question then arises, do plants with induced responses that result in elevated levels of glucosinolates suffer more damage from specialist herbivores and less from generalized feeders? Evidence comes from Baur et al. (1996) who demonstrated that damage to two different Brassica host plant species resulted in increased preference of the hosts to cabbage root flies (Delia radicum). In simultaneous choice tests, root flies laid more eggs on plants that experienced previous feeding. Other studies have shown that root fly feeding and mechanical damage resulted in induction of glucosinolates (Griffiths et al. 1994, Birch et al. 1996) and that such glucosinolates are important oviposition cues (Roessingh et al. 1992). Taken together, these studies indicate that maintaining high levels of glucosinolates all of the time may increase the susceptibility of Brassica hosts to some specialist herbivores.

In an excellent study, Giamoustaris and Mithen (1995) bred 28 lines of Brassica napus with continuous variation from low to high levels of glucosinolates. In field experiments, strong negative relationships were found between glucosinolates and herbivory by generalist slugs and pigeons. However, strong positive relationships were found between total glucosinolates and damage by specialist flea beetles and incidence of Pieris rapae larvae. This study demonstrates how plant resistance chemicals can functionally serve as

“double agents”. Because many brassicaceous plants exhibit an accumulation of glucosinolates following damage, individual plants can naturally vary in their levels of glucosinolates over time. A benefit of employing an inducible strategy may be to use resistance chemicals when necessary, without attracting specialist herbivores when the plant is not under attack. The same chemical strategies may mediate interactions between plants and pathogens (see Giamoustaris and Mithen 1997).

This phenomenon is not likely to be a special case for brassicaceous plants which employ inducible glucosinolates. For example, plants in the family Cucurbitaceae, that also employ suites of induced responses, are likely to be more resistant to generalists and more susceptible to specialists in the induced state (Da Costa and Jones 1971, Metcalf and Lapman 1989, Tallamy 1985, Apriyanto and Potter 1990, Tallamy and McCloud 1991). Carroll and Hoffman's (1980) classic paper demonstrated this double edged cost of induction in Cucurbita moschata. Additional examples of this phenomena from other plant families can be found in Alados et al. (1996), Landau et al. (1994), Matsuki and MacLean (1994), Pasteels and Rowell-Rahier (1992), and Wink (1998).

### **Induced Defenses Improve Resistance against Different Enemies**

Most plants are subject to attack, not only by multiple herbivores, but also by suites of damaging nematodes, fungi, bacteria, and viruses (Barbosa et al 1991, Hatcher 1995). There are often different defense pathways of production and defense products that are activated in response to the various sets of plant attackers (Bennett and Wallsgrove 1994, Doares et al. 1995a,b, Benhamou 1996, Kunkel 1996). For example, the salicylic acid pathway which induces production of defense

responses against some pathogens in brassicaceous plants produces different suites of glucosinolates than does the pathway that responds to insect damage (Doughty et al. 1995). Similarly, it is thought that there are multiple pathways of induction in Solanaceous plants such as tomato, and accumulation of induction products following attack by arthropods and fungal pathogens can be strikingly divergent (M. Stout, personal communication). It has recently been discovered that some of these pathways inhibit each other, although the physiological, ecological, and evolutionary reasons have not yet been explored (Doherty et al. 1988, Pena-Cortes et al. 1993, Doares et al. 1995a,b). For example, in both tomato and tobacco plants, exogenous application of salicylic acid inhibits induced defenses against herbivores but is likely to provide defense against fungal pathogens (Ward et al. 1991, Baldwin et al. 1997, M. Stout, personal communication).

A striking case of the potential incompatibility of plant resistance to pathogens and herbivores is the Solanum dulcamara - eriophyid mite system. Westphal and colleagues (1991) have demonstrated that gall induction by Aceria cladophthirus mites induced resistance to subsequent attack by A. cladophthirus as well the rust mite, Thamnacus solani. Resistance to these mites in the Solanum system, however, is mediated by a hypersensitive plant response (Fernandes 1990) which leads to decreased leaf tissue damage and/or growth of the mites (Westphal et al. 1991). The hypersensitive response was associated with increased peroxidase activity and other pathogenesis-related proteins in S. dulcamara (Bronner et al. 1991a,b). Such plant responses are most often associated with resistance against pathogens (i.e., Kuc 1987). If the plant pathways responding to pathogens and other herbivores inhibit each other (Doherty et al. 1988, Pena-Cortes et al. 1993, Doares et al. 1995a,b), we predict that S.

dulcamara plants infested with galling mites may become more susceptible to other herbivores. Indeed, Westphal et al. (1992) found that leaves of S. dulcamara damaged by the galling mites became more susceptible to the generalist two-spotted spider mite, Tetranychus urticae. T. urticae females were stimulated to oviposit and had significantly higher fecundity on leaves expressing the hypersensitive response. These results suggest that when plants respond to attack by producing pathogenesis-related defenses, they may become more susceptible to attack by other insect herbivores.

There has also been a considerable number of studies on the effects of arthropod and pathogen induced responses, their interaction, and their biological effects in the cucumber system. Infection of cucumber by anthracnose fungus induced systemic resistance to at least 13 pathogens including various fungi, viruses, and bacteria (Kuc et al. 1975, Kuc 1982, 1983, 1987). However, induced responses by anthracnose did not provide any resistance against spider mites, armyworms, or aphids (Ajlan and Potter 1991). In the reverse scenario, induction following spider mite and armyworm feeding did not provide resistance against anthracnose. Although there was no evidence of pathogen attack increasing plant susceptibility to herbivores, these studies provide additional evidence that there may be alternative pathways and different effects of induction by pathogens and herbivores. Similar results have been found for interactions between pathogens and arthropods on tobacco (Ajlan and Potter 1992).

Apriyanto and Potter (1990) report on another study on cucumber in which tobacco necrosis virus (TNV) was found to induce resistance against anthracnose. Consistent with the idea of multiple induction pathways, it was found that induction by TNV affected neither performance of spider mites and

armyworms, nor preference of whiteflies and armyworms. Although cucurbitacins were not found to be induced in infected plants, leaves of infected plants were more susceptible to feeding by striped cucumber beetles, specialists on the Cucurbitaceae. In summary, cucurbits seem to have multiple induction pathways. Pathogens induce resistance against a diverse array of pathogens but not against arthropods and arthropod induction can cause resistance against arthropods (Tallamy 1985, A. Agrawal unpublished), but does not seem to cause resistance to pathogens (Ajlan and Potter 1991). Finally, induction following both pathogen and arthropod attack appears to result in susceptibility to some specialist arthropod herbivores (Carroll and Hoffman 1980, Apriyanto and Potter 1990, Tallamy and McCloud 1991). From the plant's perspective, such divergent results may be unavoidable and therefore may favor the facultative expression of resistance.

Changes in plant quality caused by herbivores or pathogens do not always result in such trade-offs in effects on different plant parasites. For example, there are a great number of examples of generalized induced responses that appear to provide resistance against many herbivores and pathogens (see extensive reviews in Barbosa et al. (1991) and by Hatcher (1995)). Especially within different guilds of plant enemies, there appear to be some generalized responses that confer resistance against several attackers. However, where multiple pathways do play a role, plant physiological constraints may favor inducible defenses against multiple attackers because alternative defense strategies may not be compatible. Adler and Karban (1994) theorize that inducible defense phenotypes would be favored over constitutive strategies when defenses against some attackers are ineffective against others. In summary, if defense-related products make plants more

susceptible to specialist herbivores or if particular defense pathways inhibit other pathways, induced strategies may be favored.

### **Induced Defenses Create Variability in Food Quality**

Variability, such as that imposed by induced defenses, could pose difficulties for herbivores. Induced plant responses can create variability in many ways (Table 3.2). Plant defenses can be variable because they are induced and then relaxed over different temporal and spatial scales. In addition, biotic and abiotic factors can strongly affect the expression of induced defenses within and among individual plants. Factors listed in section A of Table 3.2 make individual plants and populations more variable, while those in section B only have the potential to make populations of plants more variable. Below we consider the potential benefits of variability created by induced defenses.

Stockhoff (1993) provides the strongest evidence that performance of an herbivore cannot be simply predicted by the average food quality that it experiences in a heterogeneous environment. Extremely polyphagous gypsy moth larvae were unable to compensate for variability in food quality, resulting in decreased pupal mass and slowed development time when fed increasingly variable diets with the same mean nitrogen level. Stockhoff (1993) pointed out that unselective foragers would suffer the direct fitness decrement of natural variation in food quality, while selective foragers may experience other costs associated with increased movement (see below). In either case, more variable plants should be better defended and thus favored by selection.

In addition to only partially compensating for food quality variation, herbivores often cannot respond well to large shifts in plant quality (Brattsten et al. 1983, Lindroth 1991). This is due in part to the

enzymes used to detoxify plant defense chemicals which themselves can be inducible in herbivore guts (e.g., Berenbaum and Zangerl 1994); variation in plant defense chemicals may present herbivores with food environments not well matched with their current enzymatic capabilities. Furthermore, Brattsten et al. (1983) demonstrated that some herbivores may be able to compensate for heavy doses of defense chemicals, as long as they are increased in small increments; larger shifts in defense chemicals can poison the herbivore. Finally, many herbivores self-select appropriate diets (Waldbauer and Friedman 1991) and are able to learn to avoid lower quality food. Variability created by induced responses may reduce the ability of herbivores to use such learned self-selection information and has the potential to maintain herbivores on sub-optimal diets (Jones and Ramnani 1985). Where plant variability hinders herbivore performance in ecological time, we predict that variable plants will out-perform more homogeneous genotypes.

### **Variability Itself Improves Resistance**

By definition, induced defenses create temporal variability in the food quality experienced by herbivores (Table 3.2). Below we consider a simplified model of plant defense to demonstrate how variability *per se*, as created by induced responses, could maximize defense. Consider the common case where levels of foliage toxins increase following herbivory (Baldwin 1994). If the level of secondary compounds is analyzed on a scale of 0 to 10, where 0 is no chemicals and 10 is a high dose of chemicals, then a herbivore on a plant with induced defenses may experience level 2 and level 8, before and after induction, respectively. If these compounds have a linearly negative effect on herbivores (i.e., from 0 to 10) then a herbivore exposed to these levels for equal times

experiences a realized food quality at the mean toxin level, 5. A herbivore on a plant constitutively expressing chemical level 5 should have the same fitness as a herbivore faced with equal time eating variable levels 2 and 8.

However, consider food quality as a declining concave function of plant toxins, where a small amount of a chemical has little impact on the herbivore and higher chemical doses have exponentially increasing deleterious impacts on herbivore performance. A relationship of increasing effectiveness of toxins with higher doses has been reported from several plant-herbivore systems (reviewed by Karban, Agrawal, and Mangel, *in press*). In this case, a herbivore experiencing chemical levels 2 and 8 experiences quantitatively poorer food quality than a herbivore feeding constantly at level 5. This inequality stems from the fact that higher chemical levels result in exponentially worse food quality. This model developed by Karban et al. (*in press*) demonstrates that variability, such as that created by induced defenses, could be favored because it increases the effectiveness of defense chemicals. In this model, as in all others considered in this chapter, plants must still be constrained to some level of defense; a plant expressing toxin level 10 would obviously be the most defended. However, no matter how the plant might be constrained, variation in defense could maximize the toxic effects of a given level of defense chemicals.

In conclusion, if the variability created by induced responses maximizes defense, then variable plants may be selected for by two mechanisms: 1) variable plants will have less damage and higher fitness because of direct negative effects on herbivores, and 2) variable plants will be avoided by herbivores and therefore have higher fitness. In addition to the potentially negative biological effects of variability (previous section), variability in

itself may increase the quantitative effectiveness of defenses.

## **Induced Defenses Slow Adaptation of Herbivores**

“Variation as a defense may place plant pests in an evolutionary ‘squeeze play’ that even rapidly evolving pests cannot easily surmount” (Whitham 1983). In the early 1980’s, variation in plant defense was suggested as an important component of plant-herbivore interactions (Denno and McClure 1983). It was hypothesized and later mathematically modelled that variability in plant genotype, defense, or *Bacillus thuringiensis* expression at the individual or population levels could slow the evolutionary adaptation of herbivorous insects (Whitham and Slobodchikoff 1981, Whitham 1983, Whitham et al. 1984, Gould 1986a, b, 1995, Gould and Anderson 1991, Gould et al. 1991, Liu and Tabashnik 1997). Yet, the idea that induced defenses create natural variation in plant defense is still in its infancy.

Variability in defense created by induction could potentially weaken the selection pressure for herbivores to adapt to plant defenses. Because selection will not always be strong, individuals not adapted to the defenses will continue to reproduce. Recombination and interbreeding between more and less adapted herbivores could thwart population level adaptation (Gould 1995). On the other hand, constitutively defended plants may impose a consistent directional selection pressure causing herbivores to adapt rapidly (e.g., Gould 1979, Fry 1989). However, it is not clear whether more slowly evolving pests on variable plants, in itself, could explain the evolution of induced defenses. For example, in order to avoid a group selection argument, inducibility must have arisen because of other selection pressures in short-lived plants. If, on the other hand, plants live long enough to have pests adapted to individuals (e.g.,

inducible *Quercus* spp., see Faeth 1991, Mopper et al. 1995), individuals with inducible defenses may have higher lifetime fitness than conspecifics with constitutively expressed defenses because they have fewer adapted herbivores.

### **Induced Defenses Disperse Damage and Increase Herbivore Movement**

Induced responses may force herbivores to move following a bout of herbivory. If herbivores move as a result of induction, dispersing their damage, and dispersed damage reduces plant fitness less than concentrated damage, then induction may be favored indirectly. This benefit is especially plausible in cases where there are localized induced responses such as some of those in birch (Tuomi et al 1988), wild parsnip (Zangerl and Berenbaum 1994/5), sunflower (Olson and Roseland 1991), and tomato (Stout et al. 1996). Because methods to inhibit induced defenses are still being developed and have not been extensively used in ecological studies (see Baldwin 1988, Baldwin et al. 1990, Hartley 1988, Karban et al. 1989, Doares et al. 1995a,b), it has been difficult to test how localized responses influence herbivore feeding patterns because the null model has not been obvious. Studies that have measured herbivore feeding patterns on previously induced foliage (e.g., Wratten et al. 1990) did not measure the reaction of herbivores to induction following a bout of their own herbivory, but rather the reaction of herbivores to systemically induced leaves (i.e., the herbivore simply experiences a highly resistant plant). However, Bergelson et al. (1986) did find that herbivores were likely to move away from damage sites on leaves. Other demonstrations of damage-induced movement are reviewed in Edwards et al. (1991). If induction is hypothesized to be favored over a constitutive strategy because it forces herbivores to move, experiments will

have to demonstrate that inhibition of induced responses causes herbivores to feed in a more concentrated fashion.

Experimental and theoretical evidence does suggest that concentrated damage can be more detrimental to plant fitness than the same amount of damage spread more widely (Lowman 1982, Marquis 1992, 1996, Mauricio et al. 1993, Lehtilä 1996). This finding is potentially due to the ability of plants to compensate locally for small amounts of damage. Although it is still not clear if this is a general result, others have suggested that the relationship between concentrated and dispersed damage will not always be as described above, but rather that the relationship will simply not be linear (P. Kareiva, personal communication). As long as different leaves or even different parts of individual leaves have different resource pools or productivity values for the plant, concentrated damage may decrease or increase plant fitness compared to plants with dispersed damage.

Increased herbivore movement promoted by induced responses may not only disperse damage, but also may lead to higher rates of predation and parasitism of herbivores (Edwards and Wratten 1983, Schultz 1983). Again, this is a difficult hypothesis to test because one must demonstrate: 1) that herbivores are moving more following induction than herbivores on uninduced controls, and 2) that this movement (and not other cues associated with induction) is attracting predators and parasites. Although Bergelson and Lawton (1988) found that herbivores only moved away from the immediate sites of damage, caterpillars experimentally forced to move suffered higher predation by ants. Other cues associated with induced responses may benefit the plant via increased attraction of natural enemies (Table 3.1.B, Turlings et al. 1991, Whitman and Norlund 1994, Drukker et al. 1995,

Takabayashi and Dicke 1996); however, it is not obvious that this would benefit plants more than a constitutive strategy that was always attractive.

In summary, induced defenses may be favored over constitutive defenses if: 1) patterns of herbivore feeding/movement change following induction, and either 2a) the subsequent effect of herbivory on the plant or 2b) the subsequent level of predation and parasitism on the herbivore, is influenced by the pattern of feeding. Presently, all of the individual links appear to have been satisfied in various systems; however, there have been no complete demonstrations of this potential benefit of induced defenses for any one system.

### **Induced Defenses Reduce Autotoxicity**

Autotoxicity of plant secondary metabolites has been discussed as a possible physiological cost of plant defense since the 1970's (Chew and Rodman 1979, Fowden and Lea 1979). Karban and Myers (1989) suggested that one benefit of an induced defense over a constitutive defense strategy is that autotoxicity is avoided when the plants are not under attack and do not need the defenses. Some plant defense chemicals that are thought to be autotoxic, such as hydrogen cyanide (HCN) in clover, are stored as precursors and separated from catalyzing enzymes in vacuoles (reviewed by Duffey and Felton 1989). Feeding damage to such plants induces the defense by puncturing vacuoles; enzymes mix with cyanogenic glucosides to form HCN. Jones (1972) has hypothesized that noncyanogenic morphs of clover may be favored to reduce autotoxicity in environments where cell disruption and subsequent production of HCN frequently occurs by abiotic processes.

Minimizing autotoxicity by inducing defenses may also be a strategy in other plant

species where defense compounds are produced *de novo* following damage. Baldwin and Callahan (1993) provide evidence that nicotine, which is produced in response to herbivore feeding in wild tobaccos, *Nicotiana sylvestris* and *N. glauca*, can reduce the photosynthetic capacity of the plants. These experiments used uninduced plants that were hydroponically fed realistic levels of nicotine to isolate the specific effects of autotoxicity. Indirect evidence also comes from Rasmussen et al. (1991) who demonstrated that salicylic acid (a known autotoxin) is produced following bacterial infection; natural heavy salicylic acid production or experimental endogenous injection is followed by veinal chlorosis and stunting of the leaves. Although not all plant defense compounds cause autotoxicity, the presence of compounds that do may favor inducible defenses.

### **Induced Defenses Reduce Deleterious Effects on Natural Enemies**

Compatibility of biological control and plant resistance has been of long standing interest to entomologists (reviewed in Boethel and Eikenbary 1986, Hare 1992, Duffey et al. 1995). In addition to the agricultural importance, a negative interaction between plant resistance to herbivores and predation and parasitism of herbivores could act as an evolutionary constraint favoring inducible defenses over constitutive strategies. Plant resistance traits have the potential to deter predators and parasites, interfere with their movement, and poison them when they consume plant parts or herbivores. Although several positive and even synergistic interactions between plant resistance and natural enemies of herbivores have been found (Table 3.1.b., Boethel and Eikenbary 1986, Hare 1992, Duffey et al. 1995), here we focus on the negative interactions to highlight

a potential constraint on constitutive plant defenses.

Since many important predators are to some degree omnivorous they may have reduced preference for herbivores on resistant plants (Stoner 1970, Kiman and Yeargam 1985). Development in plant tissue is fairly common among predaceous bugs making the predators potentially very sensitive to plant defenses (Coll 1996). Many omnivores, such as the western flower thrips, often feed heavily on plants and they are also important predators of herbivores (Agrawal and Karban 1997). In such cases, generalized plant defenses may have a negative effect on preference of predators and parasites.

Several studies have highlighted the direct and indirect impacts of plant resistance on interference with predators and parasites. For example, Kauffman and Kennedy (1989) found that parasitoids suffered high mortality due to plant trichomes on wild tomato plants. In addition, plant resistance in the tomato system has been reported to negatively affect parasitoids indirectly through the herbivore (Campbell and Duffey 1979, Barbour et al. 1993). Even for herbivores that do not sequester chemicals from their host plants, consumption of herbivores feeding on more resistant plants led to decreased survival and fecundity, and increased development time of predators and parasites (Barbosa et al. 1991, Stamp 1993, Stamp et al. 1997). Pathogens of herbivores may also be affected by plant resistance traits (Duffey et al. 1995). For example, Hunter and Schultz (1993) have found that herbivore induced responses in oak trees negatively affected the ability of a nuclear polyhedrosis virus, a pathogen of gypsy moths, to kill moth larvae. Induction may be favored as a strategy to reduce such negative impacts of plant resistance on natural enemies of herbivores.

## **Induced Defenses Reduce Pollinator Deterrence**

Secondary metabolites from some plants may be found in floral parts and nectar (Baker and Baker 1975, Stephenson 1982, Landolt and Lenczewski 1993, Langenheim 1994, Giamoustaris and Mithen 1996, F. Stermitz, personal communication). Such chemicals have been known to decrease floral visitation by certain pollinators (Baker and Baker 1975, Giamoustaris and Mithen 1996). For example, alkaloids can be found in the nectar and flower parts of many plants, and may even be toxic to some honeybees and lepidopteran visitors (Baker and Baker 1975). Levels of glucosinolates in the inflorescences of Brassica napus had strong negative effects on incidence of a pollen beetle (Giamoustaris and Mithen 1996). In addition, other volatile or surface compounds in fruits and foliage have the potential to deter particular pollinators. Chambliss and Jones (1966) found that cucumbers that did not express the bitter gene, and subsequent production of cucurbitacins, were significantly more attractive to bees and wasps than bitter controls. If such effects of secondary metabolites in vegetative plant parts decrease pollinator visitation and subsequent plant fitness, inducibility may be favored as a strategy to minimize pollinator deterrence.

Recent research has suggested that leaf damage may affect the pollination biology of plants (Quesada et al. 1995, Mutikainen and Delph 1996, Strauss et al. 1996). Although some of these effects on pollination caused by leaf damage are the likely result of changes in floral number and architecture, other effects may be due to changes in plant defense chemicals in foliage, flowers, nectar, and pollen (e.g., Baldwin and Karb 1995). Because of constraints on vascular architecture, plants may be unable to control where certain plant defense chemicals go

(e.g., Jones et al. 1993). Lehtilä and Strauss (unpublished manuscript) have recently demonstrated that damaged wild radish plants suffered reduced visitation by syrphid flies even when differences in flower number and size were controlled. If such results are general and are caused by changes in plant chemistry, and if pollinator visitation affects plant fitness, then the evolution of plant defenses may be constrained by pollinator deterrence and induction may be favored.

## Conclusions

Research on induced responses has broadened our knowledge of plant-herbivore interactions: plants are more dynamic than once thought and they employ complex and variable defensive phenotypes that herbivores must deal with. Induced defenses provide variability within and among individual plants. Therefore, we must first understand the factors that create and influence this variability. The listing in Table 3.2 only begins to detail how and why plants are variable with regard to what herbivores perceive. The benefits of such variability are likely to be manifold. Given the constraints outlined in this chapter, we expect that in various systems, each of these many benefits may have contributed to favoring the induced defense strategy.

At this stage it would be difficult to assess the relative importance of these factors in promoting the evolutionary origin and maintenance of induced defenses, since the evidence for each of the benefits is circumstantial at best. It is likely that “reduced host finding” is at least important in certain plant families with highly specialized herbivores such as the Brassicaceae and Cucurbitaceae. Similarly, induction favored as a strategy to reduce large “autotoxic effects” of secondary compounds may be restricted to particular plant families with classes of chemicals such as cyanogenic

glucosides, glucosinolates, and certain alkaloids. Maximizing defense against multiple plant enemies, dispersing herbivory, and taking advantage of the effects of variability may, on the other hand, be more general and widespread factors influencing the deployment of induced defenses. Although induction may have been favored as a strategy to “minimize herbivore adaptation” in long-lived plants with intimately associated herbivores, this benefit may only be important in maintaining induced defenses (and not necessarily in its evolutionary origin) in populations of shorter lived plants. In systems where natural enemies are important regulating factors of herbivores, selection for reduced or inducible defenses may be common (see also Strong and Larsson 1994). Finally, “avoidance of poisoning the pollinator” may be a common constraint on plant defense, especially in plants which cannot control where particular compounds flow (i.e., Jones et al. 1993, and some parasitic plants, L. S. Adler, personal communication). In this chapter we have emphasized alternatives to the widely accepted explanation of induced defenses as a means of minimizing allocation costs. Although support for the role of allocation costs is surprisingly poor, we believe that further attempts to evaluate this hypothesized selective agent are important. However, we speculate that studying other potential benefits and constraints may be required to truly understand induced defenses in plants.

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## References

- Adler, F. R., and R. Karban. 1994. Defended fortresses or moving targets? Another model of inducible defenses inspired by military metaphors. *Am. Nat.* 144: 813-832.
- Agrawal, A. A., and R. Karban. 1997. Domatia mediate plant-arthropod mutualism. *Nature* 387:562-563.
- Ajlan, A. M., and D. A. Potter. 1991. Does immunization of cucumber against anthracnose by *Colletotrichum lagenarium* affect host suitability for arthropods? *Entomol. Exp. Appl.* 58: 83-92.
- Ajlan, A. M., and D. A. Potter. 1992. Lack of effect of tobacco mosaic virus-induced systemic acquired resistance on arthropod herbivores in tobacco. *Phytopathology* 82: 647-651.
- Alados, C. L., F. G. Barroso, A. Aguirre, and J. Escos. 1996. Effects of early season defoliation of *Anthyllis cytisoides* (a Mediterranean browse species) on further herbivore attack. *J. Arid Environ.* 34:455-463.
- Alarcon, J. J. and M. Malone. 1995. The influence of plant age on wound induction of proteinase inhibitors in tomato. *Physiologia Plantarum* 95: 423-427.
- Antonovics, J., and P. H. Thrall. 1994. The cost of resistance and the maintenance of genetic polymorphism in host-pathogen systems. *Proc. R. Soc. Lond. B Biol. Sci.* 257: 105-110.
- Apriyanto, D., and D. A. Potter. 1990. Pathogen-activated induced resistance of cucumber: Response of arthropod herbivores to systemically protected leaves. *Oecologia* 85: 25-31.
- Åström, M., and P. Lundberg. 1994. Plant defence and stochastic risk of herbivory. *Evo. Ecol.* 8: 288-298.
- Baker, H. G., and I. Baker. 1975. Studies of nectar-constitution and pollinator-plant coevolution. Pages 100-140, in L. E. Gilbert and P. H. Raven (eds.), *Coevolution of Animals and Plants*. University of Texas Press, Austin.
- Baldwin, I. T. 1988. Short-term damage-induced increases in tobacco alkaloids protect plants. *Oecologia* 75: 367-370.
- Baldwin, I. T. 1991. Damage-induced alkaloids in wild tobacco. Pages 47-69, in D. W. Tallamy and M. J. Raupp (eds.), *Phytochemical Induction by Herbivores*. Wiley, New York.
- Baldwin, I. T. 1994. Chemical changes rapidly induced by folivory. Pages 1-23, in E. Bernays, (ed.), *Insect Plant Interactions*. V. CRC Press, Baton Rouge.
- Baldwin, I. T., and P. Callahan. 1993. Autotoxicity and chemical defense: nicotine accumulation and carbon gain in solanaceous plants. *Oecologia* 94: 534-541.
- Baldwin, I. T., and M. J. Karb. 1995. Plasticity in allocations of nicotine to reproductive parts in *Nicotiana attenuata*. *J. Chem. Ecol.* 21: 897-909.

- Baldwin, I. T., C. L. Sims, and S. E. Kean. 1990. The reproductive consequences associated with inducible alkaloidal responses in wild tobacco. *Ecology* 71: 252-262.
- Baldwin, I. T., Z. Zhang, N. Diab, T. E. Ohnmeiss, E. S. McCloud, G. Y. Lynds, E. A. Schmelz. 1997. Quantification, correlations, and manipulations of wound-induced changes in jasmonic acid and nicotine in *Nicotiana sylvestris*. *Planta* 201:397-404.
- Barbosa, P., V. A. Krischick, and C. G. Jones, editors. 1991. *Microbial Mediation of Plant-Herbivore Interactions*. Wiley, New York.
- Barbosa, P., P. Gross, and J. Kemper. 1991. Influence of plant allelochemicals on the tobacco hornworm and its parasitoid, *Cotesia congregata*. *Ecology* 72:1567-1575.
- Barbour, J. D., R. R. Farrar, Jr., and G. G. Kennedy. 1993. Interaction of *Manduca sexta* resistance in tomato with insect predators of *Helicoverpa zea*. *Entomol. Exp. Appl.* 68:143-155.
- Boethel, D. J., and R. D. Eikenbary. 1986. Interactions of plant resistance and parasitoids and predators of insects, pp. 224. Wiley, New York.
- Baur, R., V. Kostal, and E. Städler. 1996. Root damage by conspecific larvae induces preference to oviposition in cabbage root flies. *Entomol. Exp. Appl.* 80: 224-227.
- Benhamou, N. 1996. Elicitor-induced plant defence pathways. *Trends Plant Sci.* 1: 233-240.
- Bennett, R. N., and R. M. Wallsgrave. 1994. Tansley review no. 72. Secondary metabolites in plant defence mechanisms. *New Phytol.* 127: 617-633.
- Berenbaum, M. R., and A. R. Zangerl. 1994. Costs of inducible defense: protein limitation, growth, and detoxification in parsnip webworms. *Ecology* 75: 2311-2317.
- Bergelson, J., S. Fowler, and S. Hartley. 1986. The effects of foliage damage on casebearing moth larvae, *Coleophora serratella*, feeding on birch. *Ecol. Entomol.* 11: 241-250.
- Bergelson, J. M., and J. H. Lawton. 1988. Does foliage damage influence predation on the insect herbivores of birch? *Ecology* 69: 434-445.
- Bergelson, J., and C. B. Purrington. 1996. Surveying patterns in the cost of resistance in plants. *Am. Nat.* 148: 536-558.
- Birch, A. N. E., D. W. Griffiths, R. J. Hopkins, and W. H. M. Smith. 1996. A time-course study of chemical and physiological responses in *Brassicacae* induced by turnip root fly (*Delia floralis*) larval feeding. *Entomol. Exp. Appl.* 80: 221-223.
- Blau, P. A., P. Feeny, L. Contardo, and D. S. Robson. 1978. Allylglucosinolate and herbivorous caterpillars: a contrast in toxicity and tolerance. *Science* 200: 1296-1298.
- Bodnaryk, R. P. 1992. Effects of wounding on glucosinolates in the cotyledons of oilseed rape and mustard. *Phytochemistry* 31: 2671-2677.
- Brattsten, L. B., J. H. Samuelian, K. Y. Long, S. A. Kincaid, and C. K. Evans. 1983. Cyanide as a feeding stimulant for the southern armyworm, *Spodoptera eridania*. *Ecol. Entomol.* 8: 125-132.
- Bronner, R., E. Westphal, and F. Dreger. 1991a. Enhanced peroxidase activity associated with the hypersensitive response of *Solanum dulcamara* to the gall mite *Aceria cladophthirus* (Acari: Eriophyoidea). *Can. J. Bot.* 69:2192-2196.
- Bronner, R., E. Westphal, and F. Dreger. 1991b. Pathogenesis-related proteins in *Solanum dulcamara* L. resistant to the gall mite *Aceria cladophthirus* (Nalepa) (synonym *Eriophyes cladophthirus* Nal.). *Physiol. Mol. Plant Pathol.* 38:93-104.
- Brown, D. G. 1988. The cost of plant defense: an experimental analysis with inducible proteinase inhibitors in tomato. *Oecologia* 76: 467-470.
- Bryant, J. P., K. Danell, F. Provenza, P. B. Reichardt, T. A. Clausen, and R. A. Werner. 1991. Effects of mammal browsing on the chemistry of deciduous woody plants. Pages 135-154, in D.

- W. Tallamy and M. J. Raupp (eds.), *Phytochemical Induction by Herbivores*. John Wiley, New York.
- Campbell, B. C., and S. S. Duffey. 1979. Tomatine and parasitic wasps: Potential incompatibility of plant-antibiosis with biological control. *Science* 205:700-702.
- Carroll, C. R., and C. A. Hoffman. 1980. Chemical feeding deterrent mobilized in response to insect herbivory and counteradaptation by *Epilachna tredecimnotata*. *Science* 209:414-416.
- Chambliss, O. L., and C. M. Jones. 1966. Cucurbitacins: specific insect attractants in Cucurbitaceae. *Science* 153: 1392-1393.
- Chew, F. S. 1980. Foodplant preferences of *Pieris* caterpillars. *Oecologia* 46: 347-353.
- Chew, F. S., and J. A. A. Renwick. 1995. Host plant choice in *Pieris* butterflies. Pages 214-238, in W. J. Bell and R. T. Cardé (eds.), *Chemical Ecology of Insects II*. Chapman and Hall, New York.
- Chew, F. S., and J. E. Rodman. 1979. Plant resources for chemical defense. Pages 271-307, in G. A. Rosenthal and D. H. Janzen (eds.), *Herbivores: Their Interaction With Secondary Plant Metabolites*. Academic Press, New York.
- Coll, M. 1996. Feeding and ovipositing on plants by an omnivorous insect predator. *Oecologia* 105:214-220.
- Da Costa, C. P. and C. M. Jones. 1971. Cucumber beetle resistance and mite susceptibility controlled by the bitter gene in *Cucumis sativus* L. *Science* 172: 1145-1146.
- Danell, K and K Huss-Danell. 1985. Feeding by insects and hares on birches earlier affected by moose browsing. *Oikos* 4: 75-81.
- David, W. A. L. and B. O. C. Gardiner. 1966. Mustard oil glucosides as feeding stimulants for *Pieris brassicae* larvae in a semi-synthetic diet. *Entomol. Exp. Appl.* 9: 247-255.
- Denno, R. F. and M. S. McClure, (eds.). 1983. *Variable Plants and Herbivores in Natural and Managed Systems*. Academic Press, New York.
- Doares, S. H., J. Narvaez-Vasquez, A. Conconi, and C. A. Ryan. 1995a. Salicylic acid inhibits synthesis of proteinase inhibitors in tomato leaves induced by systemin and jasmonic acid. *Plant Physiol.* 108: 1741-1746.
- Doares, S. H., T. Syrovets, E. W. Weiler, and C. A. Ryan. 1995b. Oligogalacturonides and chitosan activate plant defensive genes through the octadecanoid pathway. *Proc. Nat. Acad. Sci. USA* 92: 4095-4098.
- Doherty, H. M., R. R. Selvendran, and D. J. Bowles. 1988. The wound response of tomato plants can be inhibited by aspirin and related hydroxybenzoic acids. *Physiol. Mol. Plant Pathol.* 33: 377-384.
- Doughty, K. J., G. A. Kiddle, B. J. Pye, R. M. Wallsgrove, and J. A. Pickett. 1995. Selective induction of glucosinolates in oilseed rape leaves by methyl jasmonate. *Phytochemistry* 38: 347-350.
- Downum, K. R. 1992. Tansley review no. 43. Light-activated plant defence. *New Phytol.* 122: 401-420.
- Drukker, B., P. Scutareanu, and M. W. Sabelis. 1995. Do anthocorid predators respond to synomones from *Psylla*-infested pear trees under field conditions? *Entomol. Exp. Appl.* 77: 193-203.
- Duffey, S. S., and G. W. Felton. 1989. Plant enzymes in resistance to insects. Pages 289-313, in J. R. Whitaker and P. E. Sonnet (eds.), *Biocatalysis in Agricultural Biotechnology*. American Chemical Society, Toronto.

- Duffey, S. S., K. Hoover, B. Bonning, and B. D. Hammock. 1995. The impact of host plant on the efficacy of baculoviruses. Pages 137-275 in R. M. Roe and R. J. Kuhr (eds.) Review of Pesticides and Toxicology, Volume 3. Toxicology Communications, Raleigh.
- Edwards, P. J., and S. D. Wratten. 1983. Wound induced defenses in plants and their consequences for patterns of insect grazing. *Oecologia* 59: 88-93.
- Edwards, P. J., S. D. Wratten, and R. M. Gibberd. 1991. The impact of inducible phytochemicals on food selection by insect herbivores and its consequences for the distribution of grazing damage. Pages 205-221, in D. W. Tallamy and M. J. Raupp (eds.), *Phytochemical Induction by Herbivores*. Wiley, New York.
- Faeth, S. H. 1991. Variable induced responses: direct and indirect effects on oak folivores. Pages 293-323, in D. W. Tallamy and M. J. Raupp (eds.), *Phytochemical Induction by Herbivores*. Wiley, New York.
- Feeny, P. 1977. Defensive ecology of the Cruciferae. *Ann. Miss. Bot. Gar.* 64: 221-234.
- Fernandes, G. W. 1990. Hypersensitivity: A neglected plant resistance mechanism against insect herbivores. *Environ. Entomol.* 19:1173-1182.
- Fowden, L. and P. J. Lea. 1979. Mechanism of plant avoidance of autotoxicity by secondary metabolites, especially by nonprotein amino acids. Pages 135-160, in G. A. Rosenthal and D. H. Janzen (eds.), *Herbivores: Their interaction with secondary plant metabolites*. Academic Press, New York.
- Fry, J. D. 1989. Evolutionary adaptation to host plants in a laboratory population of the phytophagous mite *Tetranychus urticae* Koch. *Oecologia* 81: 559-565.
- Giamoustaris, A., and R. Mithen. 1995. The effect of modifying the glucosinolate content of leaves of oilseed rape (*Brassica napus* ssp. *oleifera*) on its interaction with specialist and generalist pests. *Ann. Appl. Biol.* 126: 347-363.
- Giamoustaris, A., and R. Mithen. 1996. The effect of flower colour and glucosinolates on the interaction between oilseed rape and pollen beetles. *Entomol. Exp. Appl.* 80:206-208.
- Giamoustaris, A., and R. Mithen. 1997. Glucosinolate and disease resistance in oilseed rape (*Brassica napus* ssp. *oleifera*). *Plant Pathol.* 46:271-275.
- Gould, F. 1979. Rapid host range evolution in a population of the phytophagous mite *Tetranychus urticae* Koch. *Evolution* 33: 791-802.
- Gould, F. 1986a. Simulation models for predicting durability of insect-resistant germ plasm: a deterministic diploid, two-locus model. *Environ. Entomol.* 15: 1-10.
- Gould, F. 1986b. Simulation models for predicting durability of insect-resistant germ plasm: Hessian fly (Diptera: Cecidomyiidae) resistant winter wheat. *Environ. Entomol.* 15: 11-23.
- Gould, F. 1995. The evolutionary potential of crop pests. Pages 190-201, in M. Slatkin (ed.), *Exploring Evolutionary Biology: Readings From American Scientist*. Sinauer Associates, Sunderland.
- Gould, F., and A. Anderson. 1991. Effects of *Bacillus thuringiensis* and HD-73 delta-endotoxin on growth, behavior, and fitness of susceptible and toxin-adapted strains of *Heliothis virescens* (Lepidoptera, Noctuidae). *Environ. Entomol.* 20: 30-38.
- Gould, F., G. G. Kennedy, and M. T. Johnson. 1991. Effects of natural enemies on the rate of herbivore adaptation to resistant host plants. *Entomol. Exp. Appl.* 58: 1-14.
- Griffiths, D. W., A. N. E. Birch, and W. H. Macfarlane-Smith. 1994. Induced changes in the indole glucosinolate content of oilseed and forage rape (*Brassica napus*) plants in response to either

- turnip root fly (*Delia floralis*) larval feeding or artificial root damage. *J. Sci. Food Agri.* 65: 171-178.
- Hare, J. D. 1992. Effects of plant variation on herbivore-natural enemy interactions. Pages 278-300 in R. S. Fritz and E. L. Simms, editors. *Plant Resistance to Herbivores and Pathogens. Ecology, Evolution, and Genetics.* University of Chicago Press, Chicago.
- Hartley, S. E. 1988. The inhibition of phenolic biosynthesis in damaged and undamaged birch foliage and its effect on insect herbivores. *Oecologia* 76: 65-70.
- Hatcher, P. E. 1995. Three-way interactions between plant pathogenic fungi, herbivorous insects and their host plants. *Biol. Rev.* 70: 639-694.
- Haukioja, E., and S. Neuvonen. 1985. Induced long-term resistance of birch foliage against defoliators: defensive or incidental? *Ecology* 66: 1303-1308.
- Haukioja, E., K. Ruohomaki, J. Senn, J. Suomela, and M. Walls. 1990. Consequences of herbivory in the mountain birch (*Betula pubescens* ssp. *tortuosa*): Importance of the functional organization of the tree. *Oecologia* 82: 238-247.
- Harms, D. A., and W. J. Mattson. 1992. The dilemma of plants: to grow or defend. *Quart. Rev. Biol.* 67: 283-335.
- Hjalten, J., K. Danell, and L. Ericson. 1994. The impact of herbivory and competition on the phenolic concentration and palatability of juvenile birches. *Oikos* 71: 416-422.
- Huang, X., and J. A. A. Renwick. 1993. Differential selection of host plants by two *Pieris* species: The role of oviposition stimulants and deterrents. *Entomol. Exp. Appl.* 68: 59-69.
- Hunter, M. D., and J. C. Schultz. 1993. Induced plant defenses breached? Phytochemical induction protects an herbivore from disease. *Oecologia* 94:195-203.
- Hunter, M. D. and J. C. Schultz. 1995. Fertilization mitigates chemical induction and herbivore responses within damaged oak trees. *Ecology* 76: 1226-1232.
- Jones, C. G., R. F. Hopper, J. S. Coleman, and V. A. Krischik. 1993. Control of systemically induced herbivore resistance by plant vascular architecture. *Oecologia* 93: 452-456.
- Jones, D. A. 1972. Cyanogenic glucosides and their function. Pages 103-124, in J. B. Harborne, (ed.), *Phytochemical Ecology.* Academic Press, London.
- Jones, D. A., and A. D. Ramnani. 1985. Altruism and movement of plants. *Evo. theory* 7: 143-148.
- Karban, R. 1993a. Induced resistance and plant density of a native shrub, *Gossypium thurberi*, affect its herbivores. *Ecology* 74: 1-8.
- Karban, R. 1993b. Costs and benefits of induced resistance and plant density for a native shrub, *Gossypium thurberi*. *Ecology* 74: 9-19.
- Karban, R., and I. T. Baldwin. *in press*. *Induced Responses to Herbivory.* University of Chicago Press, Chicago.
- Karban, R., A. K. Brody, and W. C. Schnathorst. 1989. Crowding and a plant's ability to defend itself against herbivores and diseases. *Am. Nat.* 134: 749-760.
- Karban, R., and J. R. Carey. 1984. Induced resistance of cotton seedlings to mites. *Science* 225: 53-54.
- Karban, R., and J. H. Myers. 1989. Induced plant responses to herbivory. *Ann. Rev. Ecol. Syst.* 20: 331-348.
- Karban, R., and C. Niiho. 1995. Induced resistance and susceptibility to herbivory: plant memory and altered plant development. *Ecology* 76: 1220-1225.
- Karban, R., A. A. Agrawal, and M. Mangel. *in press*. The benefits of induced defenses against herbivores. *Ecology* 78.

- Kauffman, W. C. and G. G. Kennedy. 1989. Toxicity of allelochemicals from wild insect-resistant tomato, Lycopersicon hirsutum f. glabratum to Campoletis sonorensis, a parasitoid of Heliothis zea. *J. Chem. Ecol.* 15:2051-2060.
- Kiman, Z. B. and K. V. Yeargan. 1985. Development and reproduction of the predator Orius insidiosus (Hemiptera: Anthocoridae) reared on diets of selected plant material and arthropod prey. *An. Entomol. Soc. Am.* 78:464-467.
- Koritsas, V. M., J. A. Lewis, and G. R. Fenwick. 1991. Glucosinolate responses of oilseed rape, mustard and kale to mechanical wounding and infestation by cabbage stem flea beetle (Psylliodes chrysocephala). *Ann. Appl. Biol.* 118: 209-222.
- Kuc, J. 1982. Induced immunity to plant disease. *BioScience* 32: 854-860.
- Kuc, J. 1983. Induced systemic resistance in plants to disease caused by fungi and bacteria. Pages 191-221, in J. A. Bailey and B. J. Deverall (eds.), *The Dynamics of Host Defense*. Academic Press, New York.
- Kuc, J. 1987. Plant immunization and its applicability for disease control. Pages 255-273, in I. Chet (ed.), *Innovative Approaches to Plant Disease Control*. Wiley, New York.
- Kuc, J., G. Schockley, and K. K. Kearney. 1975. Protection of cucumber against Colletotrichum lagenarium by Colletotrichum lagenarium. *Physiol. Plant Path.* 7: 195-199.
- Kunkel, B. N. 1996. A useful weed put to work: Genetic analysis of disease resistance in Arabidopsis thaliana. *Trends Genet.* 12: 63-69.
- Lamb, R. J. 1989. Entomology of oilseed Brassica crops. *Ann. Rev. Ent.* 34: 211-230.
- Landau, I., H. Muller-Scharer, and P. I. Ward. 1994. Influence of cnicin, a sesquiterpene lactone of Centaurea maculosa (Asteraceae), on specialist and generalist insect herbivores. *J. Chem. Ecol.* 20:929-942.
- Langenheim, J. H. 1994. Higher plant terpenoids: a phytocentric overview of their ecological roles. *J. Chem. Ecol.* 20: 1223-1280.
- Landolt, P. J., and B. Lenczewski. 1993. Lack of evidence for the toxic nectar hypothesis: A plant alkaloid did not deter nectar feeding by Lepidoptera. *Florida Entomol.* 76:556-566.
- Lehtilä, K. 1996. Optimal distribution of herbivory and localized compensatory responses within a plant. *Vegetatio* 127:99-109.
- Lindroth, R. L. 1991. Differential toxicity of plant allelochemicals to insects: roles of enzymatic detoxification systems. Pages 1-33, in E. A. Bernays (ed.), *Insect-plant interactions*. Volume III. CRC Press, Baton Rouge.
- Liu, Y and B. E. Tabashnik. 1997. Experimental evidence that refuges delay insect adaptation to Bacillus thuringiensis. *Proc. R. Soc. Lond. B.* 264:605-610.
- Lowman, M. D. 1982. Effects of different rates and methods of leaf area removal on rain forest seedlings of coachwood (Ceratopetalum apetalum). *Aust. J. Bot.* 30: 477-483.
- Malcolm, S. B. and M. P. Zalucki. 1996. Milkweed latex and cardenolide induction may resolve the lethal plant defense paradox. *Entomol. Exp. Appl.* 80: 193-196.
- Marquis, R. J. 1992. A bite is a bite is a bite? Constraints on response to folivory in Piper arieianum (Piperaceae). *Ecology* 73: 143-152.
- Marquis, R. J. 1996. Plant architecture, sectoriality, and plant tolerance to herbivores. *Vegetatio* 127:85-97.
- Matsuki, M., and S. F. MacLean, Jr. 1994. Effects of different leaf traits on growth rates of insect herbivores on willows. *Oecologia* 100:141-152.

- Mauricio, R., M. D. Bowers, and F. A. Bazzaz. 1993. Pattern of leaf damage affects fitness of the annual plant Raphanus sativus (Brassicaceae). *Ecology* 74: 2066-2071.
- McKenzie, J. A. 1996. *Ecological and Evolutionary Aspects of Insecticide Resistance*. Landes, Austin.
- Metcalf, R. L., and R. L. Lampman. 1989. The Chemical Ecology of Diabroticites and Cucurbitaceae. *Experientia* 45: 240-247.
- Mole, S. 1994. Trade-offs and constraints in plant-herbivore defense theory: a life-history perspective. *Oikos* 71: 3-12.
- Mopper, S., M. Beck, D. Simberloff, and P. Stiling. 1995. Local adaptation and agents of selection in a mobile insect. *Evolution* 49: 810-815.
- Mutikainen, P. and L. F. Delph. 1996. Effects of herbivory on male reproductive success in plants. *Oikos* 75: 353-358.
- Oleszek, W. 1987. Allelopathic effects of volatiles from some Cruciferae species on lettuce, barnyard grass, and wheat growth. *Plant and Soil* 102: 271-273.
- Olson, M. M., and C. R. Roseland. 1991. Induction of the coumarins scopoletin and ayapin in sunflower by insect-feeding stress and effects of coumarins on the feeding of sunflower beetle (Coleoptera: Chrysomelidae). *Environ. Entomol.* 20: 1166-1172.
- Padilla, D. K., and S. C. Adolph. 1996. Plastic inducible morphologies are not always adaptive: the importance of time delays in a stochastic environment. *Evol. Ecol.* 10: 105-117.
- Parker, M. A. 1992. Constraints on the evolution of resistance to pests and pathogens. Pages 181-197, in P. G. Ayres (ed.), *Environmental Plant Biology Series: Pests And Pathogens: Plant Responses To Foliar Attack*; Meeting, Lancaster, England, Uk, April 9-10, 1992. Bios Scientific Publishers Ltd., Oxford.
- Pasteels, J. M., and M. Rowell-Rahier. 1992. The chemical ecology of herbivory on willows. *Proc. R. Soc. Edin. Sec. B* 98:63-73.
- Pena-Cortes, H., T. Albrecht, S. Prat, E. W. Weiler, and L. Willmitzer. 1993. Aspirin prevents wound-induced gene expression in tomato leaves by blocking jasmonic acid biosynthesis. *Planta* 191:123-128.
- Quesada, M., K. Bollman, and A. G. Stephenson. 1995. Leaf damage decreases pollen production and hinders pollen performance in Cucurbita texana. *Ecology* 76: 437-443.
- Raffa, K. F. and A. A. Berryman. 1982. Accumulation of monoterpenes and associated volatiles following inoculation of grand fir with a fungus transmitted by the fir engraver, Scolytus ventralis (Coleoptera: Scolytidae). *Can. Entomol.* 114: 797-810.
- Rasmussen, J. B., R. Hammerschmidt, and M. N. Zook. 1991. Systemic induction of salicylic acid accumulation in cucumber after inoculation with Pseudomonas syringae pv syringae. *Plant Physiol.* 97: 1342-1347.
- Rausher, M. D., K. Iwao, E. L. Simms, N. Ohsaki, and D. Hall. 1993. Induced resistance in Ipomoea purpurea. *Ecology* 74: 20-29.
- Rausher, M. D. 1996. Genetic analysis of coevolution between plants and their natural enemies. *Trends Genet.* 12: 212-217.
- Rhoades, D. F. 1979. Evolution of plant chemical defense against herbivores. Pages 3-54, in G. A. Rosenthal and D. H. Janzen (eds.), *Herbivores: Their Interaction With Secondary Plant Metabolites*. Academic Press, New York.

- Roessingh, P., E. Städler, G. R. Fenwick, J. A. Lewis, J. K. Nielsen, J. Hurter, and T. Ramp. 1992. Oviposition and tarsal chemoreceptors of the cabbage root fly are stimulated by glucosinolates and host plant extracts. *Entomol. Exp. Appl.* 65: 267-282.
- Ruohomaki, K., F. S. Chapin, III, E. Haukioja, S. Neuvonen, and J. Suomela. 1996. Delayed inducible resistance in mountain birch in response to fertilization and shade. *Ecology* 77:2302-2311.
- Sadras, V. O. 1997. Interference among cotton neighbours after differential reproductive damage. *Oecologia* 109:427-432.
- Salt, G. W. (ed.). 1984. *Ecology and Evolutionary Biology*. University of Chicago Press, Chicago.
- Schrag, S. J., and V. Perrot. 1996. Reducing antibiotic resistance. *Nature* 381: 120-121.
- Schultz, J. C. 1983. Habitat selection and foraging tactics of caterpillars in heterogeneous environments. Pages 61-90, in R. F. Denno and M. S. McClure (eds.), *Variable Plants and Herbivores in Natural and Managed Systems*. Academic Press, New York.
- Simms, E. L. 1992. Costs of plant resistance to herbivores. Pages 392-425, in R. S. Fritz and E. L. Simms (eds.), *Plant Resistance to Herbivores and Pathogens*. Ecology, Evolution, and Genetics. University of Chicago Press, Chicago.
- Stamp, N. E. 1993. A temperate region view of the interaction of temperature food quality and predators on caterpillar foraging. Pages 478-508 in N. E. Stamp and T. M. Casey (eds.). *Caterpillars: Ecological And Evolutionary Constraints On Foraging*. Chapman and Hall, London.
- Stamp, N. E., Y. Yang, and T. P. Osier. 1997. Response of an insect predator to prey fed multiple allelochemicals under representative thermal regimes. *Ecology* 78:203-214.
- Stephenson, A. G. 1982. Iridoid glycosides in the nectar of *Catalpa speciosa* are unpalatable to nectar thieves. *J. Chem. Ecol.* 8:1025-1034.
- Stockhoff, B. A. 1993. Diet heterogeneity: Implications for growth of a generalist herbivore, the gypsy moth. *Ecology* 74: 1939-1949.
- Stoner, A. 1970. Plant feeding by a predaceous insect, *Geocoris punctipes*. *J. Econ. Entomol.* 63:1911-15.
- Stout, M. J., J. Workman, and S. S. Duffey. 1994. Differential induction of tomato foliar proteins by arthropod herbivores. *J. Chem. Ecol.* 20: 2575-2594.
- Stout, M. J., K. V. Workman, and S. S. Duffey. 1996. Identity, spatiality, and variability of induced chemical responses in tomato plants. *Entomol. Exp. Appl.* 79: 255-271.
- Stout, M. J., K. V. Workman, J. S. Workman, S. S. Duffey. *in press*. Temporal and ontogenetic aspects of protein induction in foliage of the tomato, *Lycopersicon esculentum*. *Biochem. Ecol. Syst.*
- Strauss, S. Y., J. K. Conner, and S. L. Rush. 1996. Foliar herbivory affects floral characters and plant attractiveness to pollinators: Implications for male and female plant fitness. *Am. Nat.* 147: 1098-1107.
- Strong, D. R. 1980. Null hypotheses in ecology. *Synthesé* 43: 271-285.
- Strong, D. R. and S. Larsson. 1994. Is the evolution of herbivore resistance influenced by parasitoids? Pages 261-278 in B. A. Hawkins and W. Sheehan (eds.) *Parasitoid Community Ecology*. Oxford University Press, Oxford.
- Takabayashi, J. and M. Dicke. 1996. Plant-carnivore mutualism through herbivore-induced carnivore attractants. *Trends Plant Sci.* 1: 109-113.

- Tallamy, D. W. 1985. Squash beetle feeding behavior: an adaptation against induced cucurbit defenses? *Ecology* 66: 1574-1579.
- Tallamy, D. W., and E. S. McCloud. 1991. Squash beetles, cucumber beetles, and inducible cucurbit responses. Pages 155-181, in D. W. Tallamy and M. J. Raupp, (eds.), *Phytochemical Induction by Herbivores*. Wiley, New York.
- Tuomi, J., T. Fagerström, and P. Niemelä. 1991. Carbon allocation, phenotypic plasticity, and induced defenses. Pages 85-104, in D. W. Tallamy and M. J. Raupp (eds.), *Phytochemical Induction by Herbivores*. Wiley, New York.
- Tuomi, J., P. Niemela, M. Rousi, S. Siren, and T. Vuorisalo. 1988. Induced accumulation of foliage phenols in mountain birch branch response to defoliation. *Am. Nat.* 132: 602-608.
- Turlings, T. C. J., J. H. Tumlinson, and W. J. Lewis. 1990. Exploitation of herbivore-induced plant odors by host-seeking parasitic wasps. *Science* 250: 1251-1253.
- Van Dam, N. M., and K. Vrieling. 1994. Genetic variation in constitutive and inducible pyrrolizidine alkaloid levels in *Cynoglossum officinale* L. *Oecologia* 99: 374-378.
- Waldbauer, G. P. and S. Fiedman. 1991. Self-selection of optimal diets by insects. *Ann. Rev. Ent.* 36: 43-63.
- Ward, E. R., S. J. Uknes, S. C. Williams, S. S. Dincher, D. L. Wiederhold, D. C. Alexander, P. Ahl-Goy, J. Métraux, and J. A. Ryals. 1991. Coordinate gene activity in response to agents that induce systemic acquired resistance. *The Plant Cell* 3: 1085-1094.
- Westphal, E., F. Dreger, and R. Bronner. 1991. Induced resistance in *Solanum dulcamara* triggered by the gall mite *Aceria cladophthirus* (Acari: Eriophyoidea). *Exp. Appl. Acarol.* 12:111-118.
- Westphal, E., M. J. Perrot-Minnot, S. Kreiter, and J. Gutierrez. 1992. Hypersensitive reaction of *Solanum dulcamara* to the gall mite *Aceria cladophthirus* causes an increased susceptibility to *Tetranychus urticae*. *Exp. Appl. Acarol.* 15:15-26.
- Whitham, T. G. 1983. Host manipulation of parasites: Within-plant variation as a defense against rapidly evolving pests. Pages 15-41, in R. F. Denno and M. S. McClure (eds.), *Variable Plants and Herbivores in Natural and Managed Systems*. Academic, New York.
- Whitham, T. G. and C. N. Slobodchikoff. 1981. Evolution by individuals, plant-herbivore interactions, and mosaics of genetic variability: the adaptive significance of somatic mutations in plants. *Oecologia* 49: 287-292.
- Whitham, T. G., A. G. Williams, and A. M. Robinson. 1984. The variation principle: individual plants as temporal and spatial mosaics of resistance to rapidly evolving pests. Pages 15-51 in P. W. Price, C. N. Slobodchikoff and W. S. Gaud (eds.). *A new ecology: novel approaches to interactive systems*. John Wiley, New York.
- Whitman, D. W., and D. A. Nordlund. 1994. Plant chemicals and the location of herbivorous arthropods by their natural enemies. Pages 133-159, in T. N. Ananthakrishnan (ed.), *Functional Dynamics of Phytophagous Insects*. Oxford & IBH, New Delhi.
- Wink, M. 1988. Plant breeding importance of plant secondary metabolites for protection against pathogens and herbivores. *Theor. Appl. Gen.* 75:225-233.
- Wittmann, J., and F. Schoenbeck. 1996. Studies of tolerance induction in wheat infested with powdery mildew or aphids. *Zeitschrift fuer Pflanzenkrankheiten und Pflanzenschutz (Journal of Plant Disease and Protection)* 103:300-309
- Wratten, S. D., P. J. Edwards, and A. M. Barker. 1990. Consequences of rapid feeding-induced changes in trees for the plant and the insect: individuals and populations. Pages 137-145, in A.

- D. Watt, S. R. Leather, M. D. Hunter, and N. A. C. Kidd (eds.), *Population Dynamics of Forest Insects*. Intercept Ltd., Andover.
- Zangerl, A. R. 1990. Furanocoumarin induction in wild parsnip: Evidence for an induced defense against herbivores. *Ecology* 71: 1926-1932.
- Zangerl, A. R., and F. A. Bazzaz. 1992. Theory and pattern in plant defense allocation. Pages 363-391, in R. S. Fritz and E. L. Simms (eds.), *Plant Resistance to Herbivores and Pathogens. Ecology, Evolution, and Genetics*. University of Chicago Press, Chicago.
- Zangerl, A. R., and M. R. Berenbaum. 1990. Furanocoumarin induction in wild parsnip: Genetics and populational variation. *Ecology* 71: 1933-1940.
- Zangerl, A. R., and M. R. Berenbaum. 1994/5. Spatial, temporal, and environmental limits on xanthotoxin induction in wild parsnip foliage. *Chemoecology* 5/6: 37-42.
- Zangerl, A. R., and C. E. Rutledge. 1996. The probability of attack and patterns of constitutive and induced defense: a test of optimal defense theory. *Am. Nat.* 147: 599-608.

**Table 3.1.** Inducibility may be favored as a defense strategy over constitutive defenses if inducibility is more beneficial to plants (A). If induced responses benefit plants in environments with herbivores, induced plants should have higher fitness than uninduced plants. Although evidence for induced resistance is strong, effects on plant fitness have rarely been demonstrated (B).

BENEFIT	MECHANISM	EVIDENCE	REFERENCES
<b>A -Factors favoring an induced defense</b>			
Reduces allocation costs	Resource allocation to growth and reproduction is saved when not induced	mixed	Simms 1992, Karban 1993b
Reduces host finding by specialists	Specialist herbivores that are attracted to resistance related compounds are avoided when the plant is not in the induced state	weak	Apriyanto & Potter 1990, Giamoustaris & Mithen 1995
Reduces susceptibility to pathogens	Herbivore resistance can inhibit pathogen resistance and vice versa	weak	Westphal et al. 1992, Doares et al. 1995a,b
Creates beneficial variability	Herbivores cannot deal with temporally and/or spatially variable food quality	weak	Brattsten et al. 1993; Lindroth 1991
Increases effectiveness of resistance	If resistance chemicals have exponentially increasing effects on herbivore performance, variation around a mean level provides more resistance than the mean level constitutively	theoretical	Karban, Agrawal, & Mangel, <u>in press</u>
Slows evolution of herbivore adaptation	Weak (non-directional) selection pressure on herbivores to adapt to plants	theoretical	Whitham 1983
Disperses herbivory	Concentrated damage has a higher fitness cost than dispersed damage	moderate	Marquis 1992, Mauricio et al. 1993
Increases herbivore movement/predation	Moving herbivores are more visible to natural enemies	moderate	Bergelson & Lawton 1988
Reduces autotoxicity	Induction reduces plant exposure to autotoxic effects of secondary compounds	moderate	Baldwin & Callahan 1993
Reduces deleterious effects on predators and parasites	Plant resistance may negatively impact preference, provide a physical deterrence, or poison natural enemies of herbivores	mixed	Hare 1992, Duffey et al. 1995
Reduces pollinator deterrence	Defense chemicals leak into flower parts and deter pollinators	none	Baker & Baker 1975, Stephenson 1982
<b>B - Effects of induced responses on plants</b>			
Less damage to plants	Herbivores avoid or are poisoned by induced plants	strong	reviewed in Karban & Baldwin, <u>in press</u>
Increases competitive ability	Allelopathic inhibition of competitors	weak	Oleszek 1987, Sadras 1996
More tolerant to damage	Subsequent herbivory has less of a negative effect on plant fitness	theoretical	Lehtilä 1996, Wittmann & Schoenbeck 1996
Increases predation and parasitism	Natural enemies are attracted by volatiles released from induced plants	moderate	reviewed in Takabayashi & Dicke 1996

**Table 3.2.** How induced responses create variability in plant quality faced by herbivores. Induced responses can make individuals and populations of plants more variable (A). Abiotic and neighborhood effects can make induced responses in populations of plants more variable (B).

CAUSE OF VARIATION	NATURE OF VARIATION	EVIDENCE FOR VARIATION
<b>A - Within and among plants</b>		
Induction itself	Induction and relaxation create temporal variation	Baldwin 1991, 1994, Malcolm and Zalucki 1996
Induction itself	Spatial: local vs. systemic responses	Jones et al. 1993, Stout et al. 1994, 1996
Induction itself	Different structures are more or less inducible	Zangerl and Rutledge 1996, Baldwin and Karb 1995
Unpredictable induction	Highly variable change in quality following herbivory	Stout et al. 1996, Van Dam and Vrieling 1994
Developmental state	Inducibility may change with plant age	Alarcon and Malone 1995, Stout et al., <i>in press</i>
Fungal infection	Fungal infection may inhibit induced defenses to herbivory	Westphal et al. 1992, Doares et al. 1995a,b, Hatcher 1995
Other herbivores	Other guilds may induce resistance or susceptibility	Stout et al. 1996, Karban and Niho 1995, Hatcher 1995
Plant genotype	Induction threshold and strength of inducibility	Zangerl and Berenbaum 1990
Type of feeding	Induction products and the intensity of induction	Stout et al. 1994, 1996
<b>B - Among plants</b>		
Nutrient regime	Fertilized or shaded plants may be more or less inducible	Haukioja and Neuvonen 1985, Hunter and Schultz 1995, Ruohomaki et al. 1996
Plant density	Crowded plants may be less inducible	Karban et al. 1989, Karban 1993a, Hjalten et al. 1994
Light regime	UV light may affect expression of defenses	reviewed in Downum 1992