Costs of induced responses in plants

Don Cipollini1,*, Colin B. Purrington2 and Joy Bergelson3

1 Department of Biological Sciences, Wright State University, Dayton, Ohio, USA
2 Department of Biology, Swarthmore College, Swarthmore, Pennsylvania USA
3 Department of Ecology and Evolution, University of Chicago, Chicago, Illinois USA

Received November 1, 2001 · Accepted February 15, 2002

Abstract

Induced responses to herbivores in plants are thought to be a form of adaptive phenotypic plasticity, whereby plants save metabolic costs by expressing defenses only when they are necessary. Although costs of being inducible have never been examined, there have been many studies of costs of induced responses, with approaches ranging from the manipulation of induction with herbivores or wounding, and more recently, with chemical elicitors. While some early studies reported no significant costs of induced responses, evidence for significant costs of induced responses in both wild and agricultural species has recently increased in the literature. Recent studies have made it clear that benefits of induced responses in the field in the presence of herbivores can counterbalance costs of induced responses seen in the absence of herbivores. Moreover, as has been shown for constitutive resistance, costs of induced responses may vary with environmental conditions, including the presence of competitors and altered resource availability. Ecological costs of induced responses may include increased susceptibility to untargeted herbivores, either through the altered attraction of specific herbivores or due to defense pathway cross-talk, but the actual fitness consequences of such ecological costs have been little studied. Mutant and transgenic plants altered in induced responses are increasingly being identified or produced, as are specific elicitors of direct and indirect defenses. Their use, coupled with the increasing ability to analyze global gene expression in plants, will advance studies on the specificity, magnitude, and mechanisms of costs of induced responses.


*Corresponding author: Don Cipollini, Department of Biological Sciences, Wright State University, Dayton, Ohio, 45435 USA, Phone: +1-937-775-3805, Fax: +1-937-775-3320, e-mail: don.cipollini@wright.edu

1439-1791/03/04/01-079 $ 15.00/0
oder transgene Pflanzen mit veränderter induzierter Antwort werden mehr und mehr identifiziert oder produziert. Auch der Kenntnisstand über Elicitoren der direkten und indirekten Verteidigung erweitert sich zunehmend. Wenn genetisch veränderte Pflanzen genutzt werden und die Kenntnisse über die Elicitoren ebenso eingesetzt werden wie die Fähigkeit zur Analyse der Genexpression in Pflanzen, dann können die Untersuchungen zur Spezifität, zum Ausmaß, und den Mechanismen der Kosten von induzierten Antworten der Pflanzen auf Herbivorenbefall Fortschritte machen.

Key words: costs of resistance – elicitors – herbivores – pathogens – systemic acquired resistance – transgenic plants

Introduction

It is widely assumed that the constitutive expression of resistance in plants is accompanied by fitness costs that accrue when pests and pathogens are absent (Rhoades 1979, Simms & Rausher 1987, Herms & Mattson 1992, Simms 1992, Bergelson & Purrington 1996, Purrington 2000). The magnitude of these costs may explain why susceptible genotypes persist in many plant populations (Dirzo & Harper 1982, Berenbaum et al. 1986, Jones 2001). Inducible resistance, whereby plants mount morphological or biochemical defenses only when they are attacked, is a form of adaptive phenotypic plasticity that may allow plants to minimize fitness costs of resistance (Karban & Baldwin 1997, Baldwin 1998, 1999, Cipollini 1998, Agrawal 1999, Agrawal et al. 1999b). The role of costs in the evolution of induced responses is examined in more detail by Zangerl (2003). Because agronomists and others frequently consider the ability to induce a resistance response “cost free”, it is important to emphasize that there are well-documented costs associated with induced responses. Recent reviews on costs of resistance in plants have given increased attention to costs of induced responses (Purrington 2000, Heil 2001, Heil & Baldwin 2002). The aim of this review is to highlight the current state of knowledge on costs of induced responses in plants and to explore directions in which future experimental investigations are likely to focus. While recent research has shown that plants can exhibit induced responses to ovipositing herbivores (Meiners & Hilker 2000, Hilker et al. 2002), the emphasis of this review is on costs of plant responses to feeding herbivores, with some discussion of responses induced by pathogens.

The cost of an induced response is typically measured as a reduction in plant fitness (e.g., survivorship and seed production) in the absence of herbivores that is due to the production of elevated levels of defense. These costs are generally envisioned to be due to allocation of resources toward defense production and away from primary metabolism (Bazzaz et al. 1987, Herms & Mattson 1992). Another source of costs, invoked sometimes in the context of constitutive resistance, is autotoxicity of defensive chemicals (McKey 1974, Baldwin & Callahan 1993). Negative effects of induced responses on a plant's interaction with other plants, plant consumers, or plant mutualists are referred to as “ecological” costs, and have been the focus of several recent studies and reviews (Felton et al. 1999, Thaler et al. 1999, Felton & Korth 2000, Heil 2001, Cipollini 2002a, Siemens et al. 2002). Costs of simply being inducible, which would be reflected in costs of inducibility in the absence of induction and in the absence of herbivore attack, have never been examined (Bergelson & Purrington 1996, Cipollini 1998, Purrington 2000).

Wounding has often been used to assess costs of induced responses

Typically, studies on costs of induced responses have involved the controlled application of an insect herbivore to induce a response, followed by its removal and an assessment of the performance of the plant. This approach is sometimes accompanied by measurement of putative morphological or biochemical defenses, or by an assessment of levels of resistance achieved by the induction in a bioassay. In some cases, the occurrence of natural damage early in the season is simply correlated with both later damage (to estimate the induction of resistance by early damage) and plant fitness (Karban 1993). While biologically realistic, this latter approach can be ripe with flaws. First, the distribution of damage early in the season is simply correlated with both later damage (to estimate the induction of resistance by early damage) and plant fitness (Karban 1993). While biologically realistic, this latter approach can be ripe with flaws. Second, even if plants receive a similar amount and pattern of damage, there can be a great degree of specificity in induced responses to different herbivores, even in controlled laboratory experi-
ments on closely related individuals (Stout et al. 1998, Stout & Bostock 1999, Agrawal 2000, Dicke et al. 2003). Any study that pools all herbivore damage, especially damage inflicted by different feeding styles, would miss potentially important sources of variation. This variability makes it important that defensive traits are assessed directly in cost studies to insure that plants are indeed induced. It also suggests that the presence and magnitude of costs are highly dependent upon the identity of the inducing organism, even in controlled laboratory experiments.

Mechanical wounding itself has been shown to induce resistance in many plants and has been used in several studies on costs. Indeed, a fitness cost associated with the induction of nicotine in tobacco by mechanical wounding was one of the first demonstrations of fitness costs of an induced response (Baldwin et al. 1990). Using this approach, it is possible to carefully control the amount, timing, and pattern of inducing damage. The disadvantage is that mechanical wounding often does not cause the same induced responses as actual herbivory (Baldwin 1990, Stout et al. 1998, Stout & Bostock 1999, Dicke et al. 2003). In studies utilizing some form of damage, either natural or artificial, to induce a response, it can also be difficult to account for costs produced by the damage itself (i.e. fitness decreases due to removal of resources stored in plant tissues and by loss of assimilatory tissues). Fitness costs of damage are known to vary with plant genotype, plant and leaf age, and environment (e.g., Rosenthal & Kotanen 1994). In some plants, rapid whole-leaf removal (as opposed to persistent mechanical damage or herbivore feeding) does not induce resistance traits (Agrawal et al. 1999b, Cipollini & Sipe 2001), allowing some authors to use leaf damage treatments to control for costs of leaf removal itself (Agrawal et al. 1999b). In the absence of such controls, other authors have used techniques, such as pin pricks, that effectively induce the plant with a minimum of leaf area loss and physical damage (Zangerl et al. 1997).

**Chemical elicitors of induced responses are increasingly being used**

Chemical elicitors capable of stimulating induced responses have been used in numerous studies. Brown (1988) used chitin injections to induce defense responses in tomato in one of the first studies to assess fitness costs of an induced response. Since this study, the identification of signaling molecules, such as jasmonic acid (JA), that regulate the wound-inducible expression of defense genes (Creelman et al. 1992, Farmer et al. 1992, McConn et al. 1997), has advanced the study of costs of induced responses. In fact, the application of JA or its methyl ester to induce defenses has now been employed in numerous recent cost studies (e.g., Baldwin 1998, van Dam & Baldwin 1998, 2001, Agrawal et al. 1999b, Thaler 1999, Cipollini & Sipe 2001, Redman et al. 2001, Cipollini 2002a). Costs of induced responses to the application of molecules that regulate other inducible resistance pathways, such as salicylic acid (SA) or its mimics, are also increasing in the literature (Tally et al. 1999, Heil et al. 2000, Cipollini 2002a). The relative delay in studies on costs of SA-induced responses is surprising, however, given the multitude of studies on the role of SA in systemic acquired resistance to pathogens (e.g. Delaney et al. 1994, Delaney 1997, Mauch-Mani & Metraux 1998, Heil 1999, 2001).

The manipulation of chemical elicitors offers the advantage of uncoupling costs of induced responses from the less controllable (and typically unmeasured) costs of damage, and enables a high degree of control over the spatial and temporal aspects of induction. Moreover, application of different doses of an elicitor allows for the quantitative assessment of costs (Baldwin 1998, Redman et al. 2001, Cipollini 2002a). Gauging the correct amount of elicitor to apply to reasonably mimic that produced endogenously in response to damage can be a challenge, however, and requires knowledge of elicitor uptake and metabolism in planta. Some authors have done a good job of this (Baldwin et al. 1997), although most have just used estimates based on the degree to which certain levels of elicitor induce resistance. Regardless, extending defense phenotypes beyond the average with high doses of elicitor can still provide valuable information about costs, and might provide forecasts about the effects of engineering constitutive expression of inducible resistance in transgenic plants.

Despite its advantages, the use of chemical elicitors possesses flaws of its own. First, signal transduction cascades that are part of the induction of defense (e.g. mitogen-activated protein kinase cascades) are mediated by numerous molecules, many of which interact in complex ways (Xu et al. 1994, Thomma et al. 1998, Tena et al. 2001). Application of one mediator of these signaling cascades that, for example, exerts its effects only midway through a pathway may not fully, or not properly, initiate a biologically relevant resistance phenotype. Second, chemical elicitor treatment may produce secondary effects on plant primary or secondary metabolism that can in turn affect plant fitness. For example, in addition to its effects on defense expression, JA is known to affect processes ranging from photosynthesis to pollen fertility (Creelman & Mullet 1997). However, because increased levels of endogenous JA are required for many defense responses...
plants, *Arabidopsis thaliana* has been used in several studies of costs of constitutive resistance (Purrington & Bergelson 1997, Mauricio 1998), but it was used for the first time to study costs of induced responses only recently (Cipollini 2002a). Although there is considerable interest in the inducible resistance phenotypes of trees (e.g., Haukioja & Honkanen 1997, Clérivet & Alami 1999), no study of costs of induced responses for a woody plant has yet been reported, likely because of the difficulty in estimating fitness in long-lived plants. Defense costs and benefits are believed to explain patterns of constitutive resistance in long-lived woody plants across species and resource environments (Feeny 1976, Coley et al. 1985). The fact that damage-induced increases in thorn length in *Acacia drepanolobium* will eventually relax after the removal of herbivores suggests that costs may modulate the expression and distribution of induced responses in woody plants as well (Young & Okello 1998). Obviously, the assessment of costs of induced responses needs to occur over much longer temporal scales in woody plants than in short-lived herbaceous plants.

As work on the molecular genetics of inducible response pathways has progressed, numerous mutants that vary in their competence to induce resistance have either been identified or produced using transgenic technology (e.g. Delaney 1997, Cao et al. 1998). Manipulation of such experimental subjects provides a novel way to assess costs (and benefits) of inducible responses in plants (Voelckel et al. 2001b, Cipollini 2002a). For example, manipulation of non-inducible mutants (e.g. Staaswick et al. 1992, Delaney et al. 1995) with an elicitor enables the assessment of secondary effects of elicitors on plant fitness that are unrelated to defense expression (Purrington 2000, Cipollini 2002a). In turn, assessment of the fitness of mutants that constitutively express inducible responses (e.g. Cao et al. 1998, Cipollini 2002a) would provide information on costs of high levels of defense expression and autotoxicity. The costs of induction, while being interesting to evolutionary biologists, are of applied importance to crop breeders attempting to produce high-yielding yet well-protected crops. One rather easy way to produce plants with induced resistance is to spray crop fields with chemical elicitors, many of which are available commercially (e.g., Actigard®/BION® from Novartis) and that can invoke costs such as those detailed above (Tally et al. 1999, Heil et al. 2000, Oostendorp et al. 2001). A second strategy is to clone genes involved in pest perception, or subsequent signalling cascades, and engineer them with strong promoters prior to plant transformation, a strategy that would also entail costs of constitutively expressing resistance genes (but see Cao et al. 1998).
Costs have been estimated in numerous ways

An ongoing debate on costs of resistance has centered on the currency of cost. Because interest in costs of resistance is generally motivated by a desire to understand evolutionary dynamics, most studies have quantified costs using correlate(s) of fitness such as plant size, flower production, pollen production, fruit and seed production, fruit ripening, and seed germination (e.g. Baldwin 1998, Agrawal et al. 1999b, Redman et al. 2001, Cipollini 2002a). However, by examining only fitness correlates, the mechanisms leading to changes in fitness can not be determined at a physiological level (Gershenzon 1994, Purrington & Bergelson 1999). Other traits examined in studies on costs of induced responses have included physiological traits such as photosynthesis, respiration, and nitrogen uptake and utilization (Zangerl et al. 1997, Baldwin et al. 1998, Baldwin & Hamilton 2000, van Dam & Baldwin 2001). In studies that address costs of induced responses in a purely agricultural context, the relevant trait to measure may be some aspect of vegetative growth or plant “quality”, rather than a more direct measure of fitness (Thaler 1999, Tally et al. 1999).

With so many potential traits to measure, it is obvious that the choice of the measured trait and the focus on certain defenses can determine the outcome of the study. For example, Agrawal et al. (1999b) found that responses induced by JA in wild radish had no effect on female fitness traits, but negatively affected male fitness traits such as pollen production. Because female fitness has been assessed much more frequently than male fitness in studies of costs of induced responses, many effects on male fitness have likely been missed. Moreover, Agrawal (2001) found that responses induced by herbivores in wild radish can extend into the next generation, suggesting that some costs of induced responses in maternal plants may not show up until the performance of their offspring can be assessed. The magnitude of costs to any given fitness trait can potentially be influenced by many factors, including the degree of induction, mechanism of resistance, and environmental conditions. For example, the effects of reduced nutrient availability on costs of induced responses may be more pronounced on female fitness than on male fitness. This makes it difficult to broadly compare the magnitude of costs of induced responses between different plants, environments, and responses. When defense levels have been quantified and associated with costs, the emphasis in empirical studies has been on the expression of direct defenses. On the other hand, it has been suggested that employment of indirect defenses, such as the induced release of predator- or parasitoid-attracting volatiles (Dicke et al. 1990, Alborn et al. 1997, DeMoraes et al. 1998, Turlings et al. 2000, Dicke et al. 2003), may be metabolically cheaper than the employment of direct defenses (Dicke & Sabelis 1992). The two attempts to estimate the metabolic costs of induced volatiles have indeed substantiated this claim (Dicke & Sabelis 1989, Halitschke et al. 2000). No study has yet empirically addressed these costs in terms of fitness, however, although protocols to assess their costs would likely be similar to those used to assess costs of direct defenses. Induced indirect defenses have been less well-studied than induced direct defenses, but plants are not restricted to producing only one or the other. In fact, direct and indirect defenses may act synergistically to protect the plant (Baldwin & Preston 1999). If plants produce both direct and indirect defenses in response to damage, then some portion of fitness costs of induced responses may be due to the production of predator-attracting volatiles that have gone unmeasured in most studies. In fact, it is possible to experimentally manipulate and assess costs of direct and indirect defenses in some systems where mechanical damage and herbivore damage differentially induce direct and indirect defenses (Dicke et al. 1990, Kahl et al. 2000). The most important costs of the employment of induced predator-attracting volatiles, however, may be due to the risk that herbivores would use such cues in long-range host detection or host avoidance (Takahayashi & Dicke 1996, Dicke & Vet 1999, Baldwin & Preston 1999, DeMoraes et al. 2001, Kessler & Baldwin 2001). In turn, because the benefits to the plant of the production of induced volatiles are highly dependent upon the predator and parasitoid community, reliance on indirect defenses may be costly if no protectors are there to respond to alarm signals. Two recent studies have indicated that under the right circumstances, however, parasitoid attraction can benefit fitness of induced plants (van Loon et al. 2000, Hoballah-Fritzche & Turlings 2001).

Costs are increasingly being reported although mechanisms are often unknown

While some early studies reported no significant costs of induced responses (Brown 1988, Karban 1993), evidence for significant fitness costs of induced responses has increased in the literature in the last four years (e.g. Heil & Baldwin 2002). This may represent better experimental control (perhaps through the use of specific elicitors on single genotypes of plants), use of elicitors with more secondary effects on metabolism and growth, or a bias against the publication of studies where insignificant costs have been found. Regardless of the system, most studies on costs have been unable
to determine the exact mechanism responsible for reduced fitness in plants expressing inducible defenses, although resource allocation tradeoffs have been most widely supported. For example, Zangerl et al. (1997) were able to directly associate damage-induced increases in respiration rate and reductions in growth in wild parsnip with the energetic costs of induced furanocoumarin production. In tobacco, damage-induced increases in nicotine content can account for 6% of the plant’s total nitrogen (Baldwin et al. 1998), and high levels of nicotine can be autotoxic (Baldwin & Callahan 1993). Because induction typically leads plants to alter the production of numerous proteins, compounds, and structures, it is not surprising that it is difficult to quantitatively associate costs with the expression of particular defenses. Recent experiments utilizing either differential display or microarrays to analyze gene expression have shown that induction by wounding or insect feeding in plants usually involves the coordinate upregulation of many defense-related transcripts, and the downregulation of transcripts involved in primary metabolism or other “housekeeping” roles (Reymond et al. 2000, Hermsemeier et al. 2001). This finding supports the long-held assumption that, upon induction, resources are allocated toward defense and wound healing, and away from primary metabolism; redirections that can lead to fitness costs. Understanding patterns of expression of genes after induction provides targets for genetic manipulation, whereby individual genes can be up- or down-regulated to see which are most important in resistance, and which are most costly (Delaney 1997, Martin 1999, Melchers & Stuiver 2000, Kuc 2001, Tuzun 2001, Voelckel et al. 2001b).

In order to consider inducible responses adaptive, it is necessary that a benefit of induced responses in the field can be demonstrated. Fitness benefits of induced resistance have only rarely been measured, but at least a couple of recent studies make clear that such benefits in the presence of herbivores can counterbalance costs of induced responses seen in the absence of herbivores (Agrawal 1998, 1999, Baldwin 1998). The inability to control (potentially unknown) benefits of induced responses could have contributed to the lack of significant costs of induced responses reported in some studies (Brown 1988, Karban 1993).

Costs may be contingent upon the environment

Ecological costs of induced responses may include increased susceptibility to untargeted herbivores, either through the altered attraction of specific herbivores or due to defense pathway cross-talk that may alter responsiveness to certain attackers. For example, cucumber plants induced to produce cucurbitacins may become more resistant to generalist arthropod herbivores, but more susceptible to specialist beetles that use cucurbitacins as feeding stimulants (Agrawal et al. 1999a). The same could be said for glucosinolates, which tend to deter generalist arthropod herbivores but may be used as oviposition stimulants and host acceptance by specialist lepidopterans (Renwick & Lopez 1999, Siemens et al. 2002). The sometimes-negative interaction between SA- and JA-mediated inducible response pathways could make plants more resistant to some herbivores but more susceptible to others (Doares et al. 1995, Felton et al. 1999, Thaler et al. 1999, Felton & Korth 2000). The fitness consequences of such ecological costs of induced responses have not yet been demonstrated. However, evolutionary maintenance of the apparent prioritization of SA-mediated responses over JA-mediated responses when both are induced suggests that activation of these pathways may vary in costliness or in effectiveness.

As has been shown for constitutive resistance (e.g. Bergelson 1994), costs of induced responses may vary with growing conditions, including the presence of competitors and otherwise altered resource availability. For example, Heil et al. (2000) showed that induction of pathogen defense in wheat with BION®, an elicitor that mimics the action of SA, was most costly under nitrogen deprivation. An interesting set of recent studies with tobacco have indicated that the neighbors of focal plants induced with JA benefit because they take advantage of temporary reductions in the ability of induced plants to compete for nitrogen (van Dam & Baldwin 1998, 2001, Baldwin & Hamilton 2000). This makes induction not only costly to the induced focal plant but also beneficial to the neighbors. In contrast, other studies have found little effect of external resource levels on costs of induced responses. Brown (1988) found that nitrogen availability (manipulated according to several regimes) had no effect on costs of induced responses in tomato. Recent studies on Arabidopsis, Arabis, and Brassica have found that defense responses induced by chemical elicitors or insect herbivory were either no more costly or were less costly in competing plants than in plants grown alone (Cipollini 2002a, Siemens et al. 2002, D. Siemens, unpublished data). These authors suggested that pleiotropic effects of the signal molecules may have had positive effects on competitive ability in induced plants, or that some of the “anti-herbivore” defenses induced in these plants served a direct role in competition. For example, elevated glucosinolate level is a common inducible response in the Brassicaceae, of which each of these plants are members. Glucosinolates can possess allelopathic properties (Brown &
Costs of inducibility remain unexamined

Despite the general interest in examining the costs of induction, there are a variety of costs of inducibility that are often ignored, yet are potentially large (Bergelson & Purinton 1996, Cipollini 1998, Purinton 2000). These mechanisms include the production and maintenance of sensing, response, and defense storage systems, the production of enzymes that can protect from autotoxicity, and lag-time costs (DeWitt et al. 1997, Glazebrook 2001, Tena et al. 2001). These mechanisms could make phenotypic plasticity in resistance no less costly than the expression of constitutive resistance, but perhaps more effective in other ways (e.g., there might be a benefit in avoiding the simultaneous production of compounds that separately are effective against particular pests) (Karban et al. 1997, see Zangerl 2003). In some amphibians (e.g. wood frogs), costs of plasticity in the induction of a predator-induced phenotype can be widespread (Reylea 2002). To date, no published study on plants examines whether there are detectable genetic or phenotypic costs of phenotypic plasticity in herbivore resistance. It would likely be difficult to separate such costs from costs associated with the actual expression of constitutive or inducible defenses without careful control over induction, and would require comparison of closely related genotypes (or genetically manipulated genotypes) that vary only in defense plasticity. Because it is believed that many inducible response pathway mechanisms may have been co-opted from other plant developmental processes (Tena et al. 2001), the component of costs due to the production and maintenance of some signaling systems may be minimal (Cipollini 1998). Phenotypic plasticity in inducible defenses may minimize fitness costs of resistance by limiting the expression of defense, but it may be accompanied by unique costs in itself.

Polymorphism in induced resistance has been identified quite frequently in agricultural crops. In fact, the rate and level at which crop genotypes can mount inducible defenses, or the identity of the defenses produced, often differentiates “susceptible” vs. “resistant” cultivars (e.g., Hammerschmidt et al. 1984, Velozo et al. 1999, Forslund et al. 2000). Polymorphism in induced responses has been examined less frequently in wild plants, although it has been detected in a few studies (Zangerl & Berenbaum 1990, van Dam & Vrieling 1994, Bergelson et al. 2001, Glazebrook 2001). Polymorphisms in induced resistance to particular attackers may arise through variation in the recognition of herbivore and pathogen presence, variation in signal transduction networks and metabolic pathways controlling synthesis of defenses, and variation in effective deployment of defense. If induced responses themselves can vary among plant genotypes within species, then genotypes may also vary in costs of induced responses. This would be especially true if cost-saving mechanisms exist and genotypes employ them differentially. Agricultural plant genotypes that can exhibit high levels of induced resistance at minimal costs to yield would be highly desirable to identify. Unfortunately, such polymorphism has never been examined in either agricultural or wild plants.

Conclusions

The ability to experimentally manipulate the expression of induced responses in plants has led to several recent demonstrations of costs of resistance in plants, although the mechanisms of costs remain elusive. Induced indirect defenses have received much attention recently, but their fitness costs have gone unmeasured, as have the fitness consequences of ecological costs of induced responses. Continued identification of specific elicitors of induced responses, incorporation of response mutant and transgenic plants, and the analysis of global gene expression in plants will increase the ability of researchers to determine the mechanisms and magnitude of costs of induced responses. The best studies will examine costs in ecologically-relevant contexts to examine the contingencies of costs and benefits of induced responses, and the fitness effects of ecological costs. Studies that examine costs of induced responses over multiple spatial and temporal scales, and in woody plants are needed, as are studies on costs of inducibility. Progress in the study of costs of induced responses is not only interesting to evolutionary ecologists, but also important to agronomists interested in maximizing resistance and yield in cultivated plants where the phenotypic and genetic manipulation of induced responses as a resistance strategy has become increasingly popular.
Acknowledgements. We thank Monika Hilker, Marcel Dicke, Martin Heil and one anonymous reviewer for helpful comments on the manuscript. We acknowledge financial support during the writing of this manuscript from USDA NRI-CGP grant 01-02783 (to D.C.), and NIH grants GM57994 and GM62504 (to J.B.).

References


