Specificity of induced resistance in wild radish: causes and consequences for two specialist and two generalist caterpillars

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Inducible plant resistance against herbivores is becoming a paradigm of plant–herbivore ecology. Fundamental to understanding induced resistance and its evolutionary ecology is specificity of "induction" and "effects". Specificity in the induction of resistance refers to whether plant damage by various herbivores causes the same response in plants. Specificity in the effects of induced resistance refers to whether induction has the same consequences (i.e., reduced preference or performance) for various herbivores. I examined both specificity of induction and effect employing four lepidopteran herbivores and wild radish plants, a system for which fitness benefits and costs of induction have been documented for the plant. Variation in the specificity of induction and effects of induced plant resistance was found; however, this variation was not associated with diet specialization in the herbivores (i.e., specialists vs generalists). Induction caused by *Plutella* (specialist) and *Spodoptera* (generalist) resulted in general resistance to all of the herbivores, induction caused by *Pieris* (specialist) induced resistance only to *Spodoptera* (generalist) and *Pieris*, and plant damage by *Trichoplusia* (generalist) failed to induce resistance and reduce the performance of any of the herbivores. To the contrary, plants damaged by *Trichoplusia* supported enhanced growth of subsequently feeding *Trichoplusia* compared to uninduced controls. These results add a novel level of complexity to interactions between plants and leaf chewing caterpillars. Within the same guild of feeders, some herbivores cause strong induced resistance, no induced resistance, or induced susceptibility. Similarly, caterpillar species were variable in the level to which induced resistance affected their performance. Such interactions limit the possibility of pairwise coevolution between plants and herbivores, and suggest that coevolution can only be diffuse.

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Induced plant resistance to herbivores is a general phenomenon found in many plants and is characterized by reduced preference or performance of herbivores on previously damaged plants compared to that on controls (Karban and Baldwin 1997). Such plasticity in plant resistance has been shown to be adaptive in several instances: induced plants had relatively higher fitness (seed production) than uninduced controls in the presence of herbivores and relatively lower fitness than controls in the absence of herbivores (Agrawal 1998,

1999a, b, c, Agrawal et al. 1999). An important component of the ecology and evolution of induced plant resistance is the specificity of the response. As early as 1981, McIntyre et al. demonstrated that induced resistance in tobacco caused by Tobacco Mosaic Virus increased plant resistance to viral, fungal, and bacterial pathogens and aphids. Such apparently generally effective defenses may be more economical for the plant than more specific defenses. However, general defenses may lack the precision of specific defenses and thereby

may make the plant more susceptible to particular attackers than plants with specific defenses. Specificity of induced resistance can be examined from two perspectives: 1) how does a particular herbivore respond to plants damaged by different herbivores (specificity of induction), and 2) how does damage by a particular herbivore affect resistance to other herbivores (specificity of effect) (Karban and Baldwin 1997, Stout et al. 1998). When specificity of induction is defined as such, the observed specificity may be caused by variation in a plant's response to herbivory or in the inducing herbivore's way of feeding. Specificity of effect is a measure of the challenge herbivore's performance on plants with a particular induced response.

Part of the impetus for studies of the specificity of induction stems from procedural tests of the effects of artificial damage to plants. For example, Haukioja and Neuvonen (1985) demonstrated that caterpillar herbivory on birches caused greater levels of induced resistance than did manual leaf clipping with scissors. Many other studies have found a lack of correspondence between artificial herbivory and actual damage, with induced responses being minimized or amplified by clipping, depending on the system (Hartley and Lawton 1987, 1991, Mattson and Palmer 1988, Baldwin 1990, Agrawal 1998, 1999a, b). In addition to making herbivory studies more difficult, these results indicate that particular qualities of damage may be perceived by the plant, and affect the plant's response.

Herbivores also differ in the way in which they damage plants. For example, the type of plant tissue fed upon varies from phloem and xylem suckers to cell content feeders and chewing herbivores. Within each of these guilds, herbivores may vary in their salivary constituents, the number of leaf cells damaged, and the timing and pattern of damage, each of which may influence the level of induction (Lin et al. 1990, Bodnaryk 1992, Dussourd 1993, Mattiacci et al. 1995, Alborn et al. 1997, Korth and Dixon 1997). There is limited evidence that different herbivores within a feeding guild may influence plant responses differentially, and it has been speculated that such differences may be associated with the diet breadth (specialization) of the herbivores (Hartley and Lawton 1987, Bowers and Stamp 1993, Agrawal and Karban 1999).

Specialist and generalist herbivores may also respond differently to induced plant responses. In some cases, induced phytochemicals that inhibit feeding by some herbivores are feeding stimulants or toxins sequestered by specialists (Agrawal and Karban 1999). For example, Carroll and Hoffman (1980) showed that induced cucurbitacins in *Cucurbita moschata* attracted some herbivores while inhibiting feeding by others. Well-developed examples of this double-edged nature of induced plant responses are also found in Brassicaceae–herbivore interactions (Palaniswamy and Lamb 1993, Vaughn and Hoy 1993, Baur et al. 1996). It should be noted that although specialist herbivores may be attracted to plants with high levels of secondary compounds (i.e., Bowers 1992), they may still be susceptible to the toxic effects of the phytochemicals (Adler et al. 1995).

In this study, I focused on four lepidopteran herbivores of wild radish plants to address the specificity of induced plant resistance. Two of the herbivores have a restricted diet breadth, feeding only on plants within the Brassicaceae, while the two other herbivores are generalist feeders. For each of the four herbivores I asked the following question: how does damage to the plants by each caterpillar species affect the subsequent larval growth of each of the four caterpillars? The sum of the experiments presented here represents each herbivore species being assayed on control plants and plants damaged by each of the four species. Thus, data on the specificity of induction (how does a particular herbivore respond to plants damaged by different herbivores) and effect (how does damage by a particular herbivore affect resistance to other herbivores) are presented in a factorial manner.

Materials and methods

Wild radish plants, *Raphanus sativus* (Brassicaceae), are fast-growing, herbaceous annuals common to disturbed sites. The species is thought to have been introduced to North America from Eurasia in the late 1800s and is now common on six continents. Several guilds of herbivores attack wild radish, including leaf and root chewers, suckers, and cell content feeders. This study focused on four leaf-chewing lepidopteran herbivores that feed on wild radish plants in Northern California: *Pieris rapae* (Pieridae, s.f. Pierinae), *Plutella xylostella* (Yponomeutidae), *Spodoptera exigua* (Noctuidae, s.f. Amphipyrrinae), and *Trichoplusia ni* (Noctuidae, s.f., Plusiinae). *Pieris* and *Plutella* caterpillars are restricted to feeding on plants in the Brassicaceae, while *Spodoptera* and *Trichoplusia* are generalist herbivores which are known to feed on plants in up to 20 families each (Tietz 1972, Sutherland and Greene 1984). All caterpillars were grown on artificial diet and were obtained from colonies as follows: *Pieris* (U.C. Davis), *Plutella* (USDA, Columbia, MO), *Spodoptera* (USDA, Stoneville, MS), and *Trichoplusia* (U.C. Davis).

The following general procedure was used to study specificity of induction. The experiment described below was conducted four times, each time with one of the four caterpillar species as the inducing agent, and all four of the caterpillar species in the challenge. Seeds were collected in August 1997 from a large population of wild radish growing in the Orchard Park vicinity of the U.C. Davis campus. Seeds were sown in 0.8-L pots using U.C. soil mix in a greenhouse and randomly

divided into "control" and "induced" groups. At the four-leaf stage, one caterpillar was confined to one leaf of the induced plants using a clip-cage, and the larva consumed the entire leaf. Clip-cages were made from the tops of ventilated Petri dishes (5 cm) attached to either side of a hair clip. The cage structure was supported by a wooden stake, so as not to weigh down the leaves. Control plants received a sham clip-cage without the caterpillar.

Four days after the inducing caterpillar was removed, control and induced plants were randomly divided into four groups each, to be challenged by a single *Pieris*, *Plutella*, *Spodoptera*, or *Trichoplusia* caterpillar. For each experiment, there were eight treatment combinations involving control and induced plants crossed with a challenge by four herbivores. All challenge caterpillars were freshly hatched larvae. All the treatments were completely randomized over two greenhouse benches, and plant leaves were not allowed to touch each other. Challenge caterpillars were allowed to feed over the entire plant for four days, and no cages were used. After four days of feeding, the caterpillars were removed from the plants, frozen, and weighed to 0.1 μg using a Mettler-Toledo UMT-2 balance (Hightstown, NJ). Caterpillar weights at egg hatch were assumed to be equal and thus only final weights were measured.

This experiment was repeated four times during a six-week period, each time with one of the four species of caterpillar as the inducing agent. All four challenge species were used in each trial. In each of the four trials, 12–20 plants were used in each of the eight treatments. In each trial, plants were damaged and assayed at the same growth stage. Two-way ANOVAs were conducted separately for each trial, with induction and herbivore species challenged as the fixed main effects, and weight of the caterpillars as the response variable.

A separate experiment was conducted in which the goal was to replicate a portion of the first set of experiments in one trial. For this experiment, 180 wild radish plants were grown and equally divided into three groups: 1) undamaged controls, 2) one leaf consumed by a caged *Trichoplusia*, and 3) one leaf consumed by a caged *Spodoptera*. As in the previous experiment, four days after the inducing caterpillar was removed, I added a newly hatched challenge caterpillar to each plant. Each of the treatments was further divided into three challenge groups consisting of *Pieris*, *Trichoplusia*, and *Spodoptera*. This experiment was conducted one year after the original set of experiments and the source of caterpillars changed as follows: *Pieris* (a colony from newly collected individuals at U.C. Davis), *Trichoplusia* (Entopath Inc., Easton, PA), *Spodoptera* (U.C. Davis). Weight gain of the caterpillars after four days was analyzed as a two-way ANOVA with induction and herbivore challenge species as main effects.

Because several separate experiments were conducted to test for the effects of induction on the four species of caterpillars, I used Fisher's method for combining probabilities from different experiments to create an overall test for significance of induction effects on each caterpillar (Fisher 1954). This approach is advocated by Sokal and Rohlf (1995: 794) and is a form of meta-analysis. Natural log probability values from each experiment are summed and multiplied by -2, based on the fact that $-2 \ln P$ is distributed as $\chi^2_{[2]}$. With two degrees of freedom associated with each probability value, the total value can be analyzed using a table of the critical values of the chi-square distribution.

Results

In three out of the four initial experiments, there was an overall effect of induction, which reduced the weight

Table 1. Analyses of variance for the effects of induction by A) generalist and B) specialist herbivores on growth of four herbivore species. The "Herbivore" term refers to the four species of caterpillars that were used to challenge the plants following the establishment of control and induced treatments.

A.	Induced by *Trichoplusia*				Induced by *Spodoptera*			
Source	df	ms	F	P	df	ms	F	P
Induction (I)	1	79 723	0.22	0.643	1	1 720 719	4.59	0.035
Herbivore (H)	3	42 796 700	115.83	<0.001	3	24 515 200	65.40	<0.001
I×H	3	567 934	1.54	0.208	3	752 759	2.00	0.118
Error	130	369 468			93	374 873		

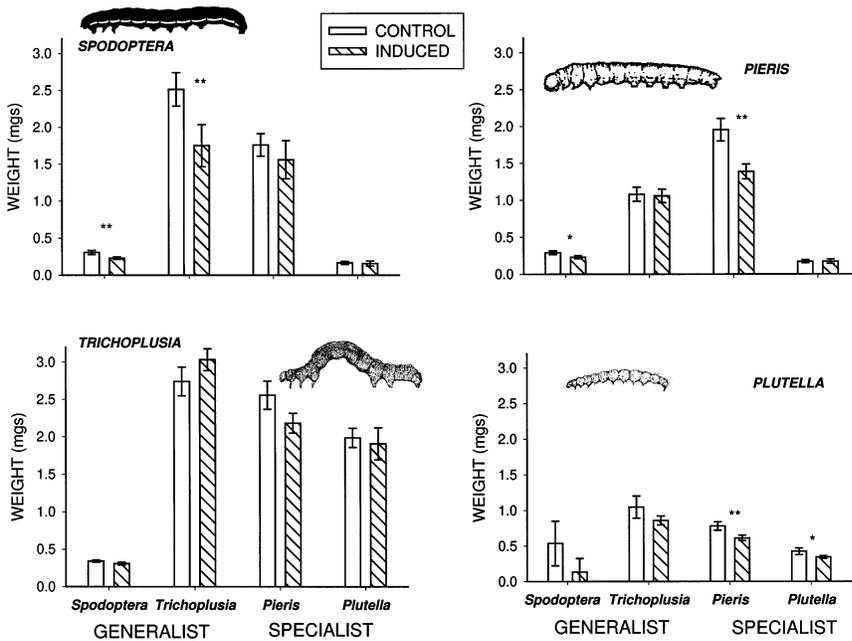| B.	Induced by *Pieris*				Induced by *Plutella*			
Source	df	ms	F	P	df	ms	F	P
Induction (I)	1	0.635	7.64	0.007	1	1.145	3.40	0.068
Herbivore (H)	3	12.292	147.81	<0.001	3	2.078	6.18	0.001
I×H	3	0.453	5.45	0.002	3	0.127	0.38	0.769
Error	91	0.083			99	0.337		

Fig. 1. Growth of two specialist (*Pieris* and *Plutella*) and two generalist (*Spodoptera* and *Trichoplusia*) caterpillars on control and induced wild radish plants. Each graph represents a trial in which the plants were induced by a single caterpillar species (shown on top of each graph) and challenged by four species (shown on bottom). Bars shown are mean $\pm$ SEM. * represents $P < 0.1$ and ** represents $P < 0.05$ for comparisons of the effects of induction on caterpillar weights for individual species.

gain of caterpillars (Table 1, Fig. 1). Only when plants were damaged by *Trichoplusia* was there no detectable effect of previous damage on subsequent growth of the four caterpillar species, providing evidence for specificity of induction. In all experiments, the effect of caterpillar species used for the challenge (after treatments were established) was highly significant, indicating that the different species grew at different rates (Tables 1, 2).

Further evidence for specificity in induction is that *Plutella* were only affected by induction in the case where *Plutella* caterpillars were the inducing agent (Figs 1, 2). Similarly, *Pieris* and *Spodoptera* were strongly negatively affected (29% and 25% reductions, respectively) when they were the respective inducers, and less so when other species induced the plants (Figs 1, 2). However, *Trichoplusia*, experienced mild reductions in growth when plants were induced by other species, but actually had 11% greater weight (although not statistically significant) when grown on plants damaged by *Trichoplusia* compared to controls.

Specificity of effect was detected in the experiment where plants were induced by *Pieris*. In this case, there was a significant induction by challenge herbivore interaction, indicating that some caterpillars were affected by induction, while others were not. One of the specialists (*Pieris*) and one of the generalists (*Spodoptera*) was negatively affected by induction. Conversely, damage by the other specialist herbivore, *Plutella*, resulted in generalized induced resistance against all of the herbivores (although this was only statistically significant for *Pieris*, see Fig. 1).

In the additional experiment conducted with plants damaged by *Trichoplusia* and *Spodoptera* on the same date, there were strong overall effects of induced resistance, herbivore species, and a highly significant interaction. However, in contrast analyses, induced resistance was only detectable against *Pieris* (Fig. 3, Table 2). Many of the non-significant trends in this experiment were consistent with results from the last experiment, i.e., higher growth of *Trichoplusia* on plants damage by *Trichoplusia*.

Fisher's method of combining probabilities from different experiments indicated that *Spodoptera* (d.f. = 12, $\chi^2 = 22.6$, $P < 0.05$) and *Pieris* (d.f. = 12, $\chi^2 = 47.6$, $P < 0.001$) were consistently susceptible to negative effects of induced plant responses, while *Trichoplusia* (d.f. = 12, $\chi^2 = 14.5$, $P > 0.1$) and *Plutella* (d.f. = 8, $\chi^2 = 5.7$, $P > 0.5$) were not. This provides additional support for specificity in the effects of induction in wild radish plants.

Both specificity of induction and effects of induction were measured in this study. However, there were no general patterns in specificity of induction for specialist versus generalist caterpillars. Similarly, the magnitude

Table 2. Analysis of variance for the effects of induction by *Trichoplusia* and *Spodoptera* on growth of three herbivore species (*Trichoplusia*, *Spodoptera*, and *Pieris*). The "Herbivore" term refers to the three species of caterpillars that were used to challenge the plants following the establishment of control and induced treatments.

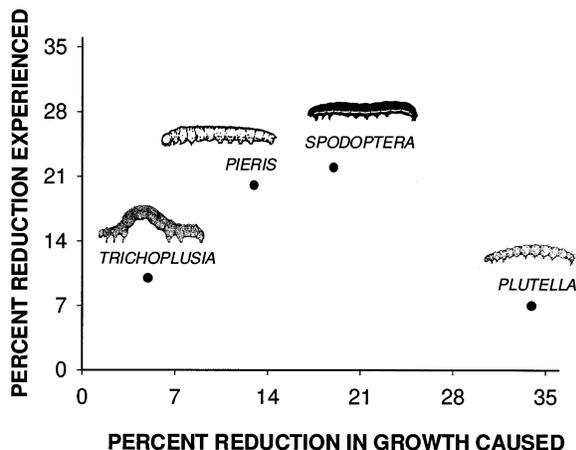| Source	df	ms	F	P
Induction (I)	2	4 334 414	8.003	<0.001
Herbivore (H)	2	20 354 368	37.583	<0.001
I × H	4	4 782 600	8.831	<0.001
Error	149	541 584		

Fig. 2. Specificity of induced plant resistance plotted by species in terms of "induction caused" and "effect experienced". Each point represents the average reductions in growth caused by induction by that species on four species of caterpillars (*x*-axis), and average reductions in growth for that species when feeding on plants induced by each of the four caterpillar species relative to that on a control (*y*-axis).

of effects of induction were not explained consistently by diet breadth (Fig. 2). Herbivory and subsequent induction caused by *Plutella* is of special interest because it caused the strongest, most generalized induced resistance, and it is also the species that was least affected by induction. Conversely, induction caused by *Trichoplusia* was the weakest and it was minimally affected by induction (compare to *Plutella* in Fig. 2).
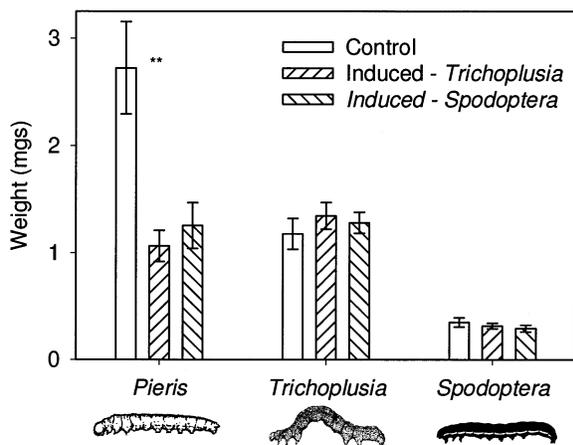

Fig. 3. An additional experiment in which growth of *Pieris*, *Trichoplusia*, and *Spodoptera* was assayed on control and induced (by *Trichoplusia* and *Spodoptera*) wild radish plants. Bars shown are mean ± SEM. ** represents *P* < 0.05 for comparisons of the effects of induction on caterpillar weights for individual species.

Discussion

Plant responses to herbivory are now viewed as a nearly ubiquitous defense strategy that, under some circumstances, are likely to be adaptive. However, the complexities of the herbivore effects on plants and vice versa are still being documented. Specificity of induced responses corresponds to different herbivores causing different responses in plants, while specificity in the effects of induction corresponds to the consequences for different herbivores. In the present study variation in induction and effects were found for four lepidopteran herbivores of wild radish. Specificity of induction can be caused by the type of feeding damage (Hartley and Lawton 1987, 1991, Bowers and Stamp 1993, Dussourd 1993, Felton et al. 1994, Stout et al. 1994, 1998, Takabayashi and Dicke 1996), salivary constituents (Hartley and Lawton 1987, 1991, Turlings et al. 1990, Mattiacci et al. 1995, Alborn et al. 1997, Korth and Dixon 1997), and the extent of damage imposed by the herbivore (Karban 1987, Lin et al. 1990, Bodnaryk 1992). Specificity in the effects of induction may be due to variation in herbivore tolerance and detoxification ability (i.e., post-ingestive effects) (Rosenthal et al. 1978, Ivie et al. 1983, Lindroth 1991, Berenbaum and Zangerl 1993, Glendinning and Slansky 1995).

Different herbivore species are likely to be highly variable in the way they eat leaves, the phytochemicals they induce, and the way induction affects their performance. The current study sought to detect specificity within a feeding guild of leaf-chewing caterpillars. Even at this level, there may be large differences in the ways that larvae feed (e.g., Parrella et al. 1985). Bernays and Janzen (1988) showed that caterpillars in the Saturniidae tended to use simple cutting methods to eat leaves, while caterpillars in the Sphingidae tended to tear and crush leaves. Such differences may cause differential induction of plant defense responses. Early studies of cotton plant–spider mite interactions showed that congeneric herbivores, *Tetranychus urticae* and *T. turkestani*, differentially induced resistance in plants (Karban and Carey 1984). Induced resistance caused by *T. turkestani* feeding was much stronger than induced resistance caused by *T. urticae* feeding, even when half the number of mites were used to induce the plants. A recent field experiment with cotton and tobacco plants found that plants infested with *Heliothis virescens* attracted significantly more parasitoids than plants infested with *Helicoverpa zea* or undamaged controls (De Moraes et al. 1998). In this case, the parasitoid, *Cardiochiles nigriceps*, is only a parasitoid of *H. virescens* and the attraction was correlated with differences in the induced volatiles following herbivory by *H. virescens* and *H. zea*. Such specificity in induced plant responses may even occur within a single species of herbivore. Corn plants damaged by early versus late instars of *Pseudaletia separata* produced distinct induced plant

responses (Takabayashi et al. 1995). This effect was mediated by changes in the caterpillars' salivary constituents, not differences in their feeding styles.

Induced responses in wild radish include many changes following herbivory, including shifts in the profiles of defensive mustard oil glycosides (glucosinolates) (Agrawal et al. 1999) and an increases in trichome densities on newly formed leaves of damaged plants compared to undamaged controls (Agrawal 1999a). In the current study, only chemical or physiological responses were likely to underlie induced resistance because challenge caterpillars were put on plants four days after the initial damage, not leaving time for the development of new leaves. Generally, I found that specialist *Plutella* caused the greatest level of induced resistance and was the least affected by induction (Fig. 2). Growth of *Plutella* was only reduced by induction when plants were initially damaged by *Plutella*. However, data for the other specialist herbivore, *Pieris*, were quite different. *Pieris* caused an intermediate level of induction, and was negatively affected by induction on plants induced by each of the four caterpillars. These specialist caterpillars are generally thought to be tolerant of glucosinolates and other defensive constituents in the Brassicaceae (Blau et al. 1978, Chew 1988, Louda and Mole 1992, Talekar and Shelton 1993, Coleman et al. 1996, Bodnaryk 1997; but see Renwick 1996). Plants selected for higher levels of glucosinolates actually experienced greater numbers of *Pieris* in field experiments with *Brassica napus* (Giamoustaris and Mithen 1995). In the current study I found no evidence that larvae of the specialist herbivores were stimulated by induced responses in wild radish (but see a review of the phenomena in Agrawal and Karban 1999). It is possible that although glucosinolates have a stimulatory effect on specialist herbivores, other induced phytochemicals deter these herbivores. For example, *Pieris* and *Plutella* were negatively affected by proteinase inhibitors, which are resistance compounds known to be inducible in the Brassicaceae (Broadway and Colvin 1992, Broadway 1995).

Generalist herbivores are thought to be more susceptible to effects of plant resistance than specialist herbivores. My data for *Spodoptera* support this contention, as growth was negatively affected by induction in both experiments. Coleman et al. (1996) failed to find effects of induced resistance in *Brassica oleracea* on species of *Pieris* or *Spodoptera*. One source of variation within my own experiments and compared to those of Coleman et al. is that the caterpillars were obtained from different sources, with each source population potentially having different abilities to exploit plants. Perhaps the most surprising result of the current experiment is that generalist *Trichoplusia* caterpillars caused the lowest level of induction and were hardly affected by induction (tied with *Plutella*, see Figs 2, 3). In another study, induced flavonoids in the mouse-eared cress, *Arabidopsis*

thaliana, deterred feeding by *Pieris*, but not by *Trichoplusia* (Grant-Petersson and Renwick 1996). Although *Trichoplusia* is known to employ "trenching" behavior which helps the caterpillar circumvent plant deployment of defenses via secretory canals (Dussourd and Denno 1994, Dussourd 1997), no such trenching behavior was observed in this study. When *Trichoplusia* damaged plants they induced susceptibility to themselves (although this effect was marginal). There was specificity in this interaction: *Trichoplusia* was the only caterpillar species to induce susceptibility, and *Trichoplusia* was the only caterpillar species to benefit from this induction. I am aware of one other study that has documented specificity in induced plant susceptibility (Williams et al. 1998). *Myzus persicae* aphids on sugar beet (*Beta vulgaris*) plants with previous infestations of *M. persicae* had 50% higher survival than *M. persicae* on plants without previous infestations of *M. persicae* (i.e., induced susceptibility). However, no such induced susceptibility was observed for *M. persicae* on plants previously infested with a different aphid species, *Aphis fabae*, compared to controls.

The results of the current experiment have direct relevance to the debate characterizing plant-insect coevolution as "pairwise" or "diffuse" (Janzen 1980, Fox 1981, 1988, Rausher 1992, Thompson 1994). Pairwise coevolution can occur when a plant and a herbivore impose reciprocal selection on each other, causing the pair of species to evolve jointly. Diffuse coevolution is thought to act in cases where more than one herbivore may affect plant fitness and likewise where plant defense mechanisms may act generally against more than one plant parasite. Unless plant susceptibility to different herbivores is genetically uncorrelated, and the pattern of selection exerted by each herbivore (on the plant) is independent of the presence of other herbivores, coevolution can only be diffuse (Hougen-Eitzman and Rausher 1994). More specifically, if the presence of one herbivore affects the amount of plant damage by other herbivores, then coevolution will be diffuse (Iwao and Rausher 1997). Although the presence of induced resistance between different herbivores, itself, satisfies this criterion, the results presented in this paper further show that induced resistance caused by herbivore species (that all commonly feed on the plant) is variable and is sometimes general. Because induced resistance in wild radish can be caused and experienced by multiple herbivores, pairwise coevolution is even less likely to occur.

An alternative view of coevolution that has recently been advocated by Thompson (1994, 1997, 1998) states that coevolution is likely to be pairwise, but may be geographically structured such that different herbivores may be coevolving with a particular plant species in different populations. This geographic view suggests that at the species level coevolution may appear to be diffuse; however, at the population level it may be

pairwise. The current study did not investigate geographical patterns of the plant–herbivore association. However, other workers studying Brassicaceae – herbivore interactions have found evidence for geographic structure in herbivore pressure and even genetic differentiation among plant populations for levels of defense (Mithen et al. 1995, Nielsen 1997).

Conclusion

Progress in understanding the evolutionary ecology of induced plant resistance is being made quickly. The documentation of phenotypic benefits and costs of induction shows that such plasticity in defense is likely adaptive under some circumstances. The next step will be to document genetic variation in induction and ask which biotic and abiotic environments favor particular plant resistance patterns. The current study, which addresses specificity of induction and effects of induced plant resistance contributes to the understanding of complex plant–herbivore interactions. Understanding these interactions adds a level of complexity to our knowledge and may help predict how natural selection will act on plants in variable herbivore environments. In wild radish, different leaf-chewing caterpillars differentially induced plant resistance and were themselves differentially affected by induction of resistance.

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