

Nora Underwood · William Morris · Kevin Gross
John R. Lockwood III

Induced resistance to Mexican bean beetles in soybean: variation among genotypes and lack of correlation with constitutive resistance

Received: 30 November 1998 / Accepted: 25 June 1999

Abstract Fourteen genotypes (varieties) of soybean (*Glycine max*) were screened for levels of induced resistance to Mexican bean beetle (*Epilachna varivestis*) damage, and a subset of 6 of those varieties was screened for levels of constitutive resistance to Mexican bean beetles. Experiments were carried out in the greenhouse, with damage imposed by Mexican bean beetle larvae, and levels of resistance measured by a choice test bioassay with adult beetles. We found significant variation among soybean genotypes in levels of both induced and constitutive resistance. We found no significant correlation between levels of induced and constitutive resistance measured in the same genotypes. We compare these results to past work on resistance in the soybean-Mexican bean beetle system, consider the implications of variation in both types of resistance for plant-herbivore interactions in agricultural and natural systems, and discuss the relationship between induced and constitutive resistance.

Key words Induced resistance · Constitutive resistance · Soybean · Mexican bean beetle · Bioassay

Introduction

Plants have two modes of resistance to herbivores: constitutive resistance, which remains at a constant level re-

gardless of herbivore attack, and induced resistance, which is triggered to increase by herbivore damage. Many studies have shown that constitutive resistance varies among plant species and among genotypes within a species (Fritz and Simms 1992). There are fewer data on variation in induced resistance, although the timing and strength of induced responses are known to vary both among and within species (Karban and Baldwin 1997). Relatively few studies have examined the range of variation in induced resistance among more than two genotypes within a species (Shapiro and DeVay 1987; Anderson et al. 1989; Zangerl and Berenbaum 1990; Raffa 1991; Brody and Karban 1992; Bi et al. 1994; van Dam and Vrieling 1994; English-Loeb et al. 1998).

Understanding genetic variation for resistance is important because the amount of this variation is a determinant of the response of resistance to artificial and natural selection. Genetic variation in constitutive resistance has been widely used to artificially select for pest-resistant crop plants (Kennedy and Barbour 1992). The use of induced resistance to control insect herbivores in agricultural systems is beginning to be explored (Karban and Baldwin 1997), for which, the existence of genetic variation is a prerequisite. Variation in induced resistance among artificially selected varieties derived from the same parent species may also indicate the potential extent to which natural selection can shape induced resistance in natural populations.

We report here the results of experiments showing that there is a wide range of variation among genotypes of soybean (*Glycine max*) in their induced responses to Mexican bean beetle (*Epilachna varivestis*) damage. In several other studies, we have used this genetic variation to examine ecological questions about the effect of plant quality in general and induced resistance in particular on herbivore population dynamics in time (Underwood 1997) and space (W. Morris, unpublished data). In this paper we also take advantage of variation in constitutive resistance among genotypes to take a preliminary look at the relationship between induced and constitutive resistance in this system.

N. Underwood (✉) · W. Morris · K. Gross · J.R. Lockwood III
Department of Zoology, Duke University, Box 90325,
Durham, NC 27708-0325, USA

Present addresses:

N. Underwood, Center for Population Biology,
University of California, Davis, CA 95616, USA,
e-mail: nunderwood@ucdavis.edu,
Tel.: +1-530-7522800, Fax: +1-530-7521537

Kevin Gross, Department of Zoology,
University of Wisconsin-Madison, Birge Hall, 430 Lincoln Drive,
Madison, WI 53706, USA

J.R. Lockwood, Department of Statistics,
Carnegie Mellon University, Pittsburgh, PA 1521, USA

Models for the evolution of plant resistance assume that resistance has both costs (due to limited resources) and benefits (due to increased fitness in the presence of herbivores) (e.g., Simms and Rausher 1987; Adler and Karban 1994). Assuming that both constitutive and induced resistance involve costs, and that both kinds of resistance yield the same benefit of reducing herbivory, a single genotype (or single plant part) would be predicted to have one or the other, but not both kinds of resistance (Herms and Mattson 1992; Zangerl et al. 1997). Only three studies have looked for the expected negative correlation between induced and constitutive resistance across genotypes (Brody and Karban 1992; English-Loeb et al. 1998) or species (Thaler and Karban 1997). In all three cases, no significant correlation between induced and constitutive resistance has been found. Here we address this question by determining the level of constitutive resistance in a subset of the genotypes screened for induced resistance and asking if there is any correlation between the strengths of the two types of resistance in the soybean-Mexican bean beetle system.

Methods

System

Soybean (*G. max*: Fabaceae) seeds for this experiment were obtained from T. Carter and J. Burton (North Carolina State University, N.C.), from L. Lambert (USDA-ARS-SIML, Miss.) and from R. Nelson (USDA Soybean Germplasm Collection Urbana, Ill.). In all experiments, soybeans were grown in 4-inch plastic pots in a mixture of soil, peat, perlite, sand, and lime. Plants were grown in the Duke University greenhouses under a 14-h daylength with supplemental lighting (430-W high-pressure sodium lamps). This daylength was sufficient to prevent the plants from becoming reproductive. Plants were watered as needed and fertilized with Peters soluble fertilizer (20-10-20) approximately weekly. Plants were not inoculated with *Rhizobium*, but haphazard sampling of roots indicated that plants often had nodules that appeared to be active. We tested 14 genotypes for induced resistance (Bragg, Braxton, Centennial, Clark, Cook, Davis, Dillon, Gasoy 17, Johnston, PI 416937, Stonewall, Tracy-M, Williams, Young) and a subset of 6 genotypes for constitutive resistance (Bragg, Davis, Gasoy 17, PI 416937, Tracy-M). With the exception of PI 416937, all of these genotypes are considered, based primarily on field trial data, to be constitutively susceptible to Mexican bean beetles (T. Carter, personal communication). Williams has been previously found to exhibit some induced resistance to Mexican bean beetles (Kogan and Fischer 1991). Both constitutive and induced resistance were measured by feeding preference bioassay, as described below.

Mexican bean beetles (*E. varivestis*: Coccinellidae) are specialists on legumes and economic pests of soybeans in many areas. The beetles lay their eggs on the host plant and both larvae and adults feed on foliage. Beetles used in these experiments were obtained from T. Dorsey (New Jersey Department of Agriculture, Trenton, N.J.) and were reared in an environmental chamber with a 14-h daylength at 28°C. Beetles used in these experiments were reared on common snap bean plants (*Phaseolus vulgaris*) to prevent them from developing preferences for any particular soybean genotypes.

Measuring induced resistance

We used a bioassay rather than chemical analysis to measure induced resistance because the focus of our studies is the effect of

induced resistance on the herbivore. The induction response of soybeans is physiologically complex (Felton et al. 1994), and it is not yet clear what chemical changes in the plant should be measured to best represent effects on the beetles. Using the response of the beetles themselves is the most direct way to obtain information on the impact of induced resistance on the herbivore.

Experiments measuring induced resistance were carried out in three rounds over a period of approximately 2 years. For each soybean variety used in a given round of the experiment, 24 plants were grown in the greenhouse as described above. When the plants had one fully expanded trifoliolate leaf and a partially expanded second trifoliolate (their first two true leaves are simple leaves), half the plants were randomly chosen to receive damage. Four or more third- or fourth-instar Mexican bean beetle larvae were placed on the first trifoliolate of each damaged plant and confined there with a mesh bag. We used enough larvae to completely consume the trifoliolate within 48 h, adding larvae to some plants after 24 h to ensure that damage was completed. One fully eaten trifoliolate constitutes damage to approximately 60% of the leaf area of the plant at that stage of growth. The 60% damage level was chosen because it has been shown to cause induced resistance in many genotypes of soybeans (N. Underwood, unpublished data). All control plants also had their first trifoliolates bagged, but no larvae were added. Three days after larvae were removed from the plants, 12 pairs of damaged and control plants from each genotype were randomly chosen, and leaf disks were cut from their most recently expanded undamaged trifoliolates for use in a bioassay. Because leaves collected from the damaged plants had not received any direct damage, the bioassay tested for systemic induced resistance. Leaf disks were cut with a cork borer, which has been shown not to cause induces resistance in the disks (Kogan and Fischer 1991). Plants were discarded after being sampled, so that no plant was used more than once in the experiment.

We measured induced resistance as beetle feeding preference for leaf tissue from a control plant over tissue from a damaged plant (method derived from Kogan 1972). Two leaf disks from one randomly chosen control plant and two disks from a randomly chosen damaged plant were placed in a petri dish lined with damp filter paper. Control and "damaged" disks were arranged opposite each other at the edges of the dish and one female Mexican bean beetle, previously starved for 24 h at 28°C, was placed in the dish. Adult females were used because they have been shown to eat more tissue and to be more discriminating than males (Smith et al. 1979). The beetles were allowed to feed until approximately 25% of the total leaf area in the dish was consumed, or for 24 h, whichever came first. Dishes in which no disk had greater than 3% of its area damaged were not included in analyses. This sometimes resulted in sample sizes less than 12. The area of tissue consumed was measured using a computerized image analysis program (Image 1, Universal Imaging Corporation 1991) on an IBM Gateway 486 computer with a BURLE black-and-white video camera (model TC7311). Two choice tests (two petri dishes) were run for each plant pair to minimize lost data due to beetles occasionally not eating. The measures of induced resistance from the two dishes from each plant pair were averaged to form a single observation (replicate).

Analysis

For consistency with previous studies of induced resistance in soybeans (Kogan 1972; Underwood 1998), we calculated a preference index $[PI=2(c/(c+d))]$ where c and d indicate the amount of damage to the control and damaged disks in each dish, respectively. A PI of 1 indicates no preference (no difference in feeding between damaged and undamaged plants) and PIs higher than 1 indicate a preference for the control (rejection of previously damaged plants). The mean PI of all observations from a single variety indicates the degree of induced resistance for that variety. Statistical analyses were performed on the ratio of amounts of the control and damaged disks eaten ($c/c+d$) rather than the PIs, and these ratios were arcsine square-root transformed before analysis to nor-

malize their distributions (Zar 1984). We tested each variety separately for induced resistance (PI significantly greater than 1) using one-sample, one-tailed *t*-tests. We report results of these tests both for $\alpha=0.05$ and $\alpha=0.004$ (corrected for multiple comparisons using the Bonferroni method). Because all 14 genotypes were not represented in each round of the experiment, we used nested analysis of variance (GLM procedure of SAS; SAS 1989) to determine whether genotypes differed significantly in their induced response to beetle damage, with round and genotype nested within round as factors.

Measuring constitutive resistance

Using the results from our tests for induced resistance, we selected six varieties (Bragg, Davis, Gasoy 17, PI 416937, Tracy-M) spanning the range of induced responses and tested these varieties for constitutive resistance. For consistency with our measure of induced resistance, we measured constitutive resistance as beetle feeding preference for undamaged plants of one variety over another.

Plants were grown in the greenhouse under the conditions described above. This experiment was carried out in 15 temporal blocks of 30 plants each (5 plants \times 6 varieties), from fall 1995 through spring 1996. When the majority of plants had fully expanded their second trifoliolate, the most recently expanded trifoliolate was collected for use in the bioassay. Due to small asynchronies in growth rates among individuals, the collected leaf was usually, but not always, the second trifoliolate; occasionally either the first or third trifoliolate was used.

The bioassays for constitutive resistance were the same as the assays for induced resistance (described above) with the following exception. Each beetle was presented with two disks from a single individual of one variety and 2 disks from an individual of a different variety, rather than disks from damaged and control individuals of the same variety. All 15 possible pairings of the 6 varieties were tested, with each pairing tested once in each block. As with induced resistance, each pair of plants was tested in two dishes. As in the induced-resistance experiments, the area of each disk eaten was measured using image analysis software.

Analysis

To describe constitutive resistance, we used a PI analogous to the one used to describe induced resistance. For each pair of two varieties, the variety whose name came first alphabetically was used as the "reference" variety (*y*). We then calculated the PI for each dish as the amount of tissue of the non-reference variety (*x*) as a proportion of the total tissue eaten in that dish ($x+y$): $PI=2(x/(x+y))$. For the PI for constitutive resistance, values less than 1 indicate that the beetle preferred the reference variety (i.e., the reference variety had less antifeedant resistance) and values greater than 1 indicate discrimination against the reference variety (i.e., the reference variety had more resistance than the other variety). The PIs from the two dishes for each pair of varieties were averaged to form a single observation. Prior to statistical analysis PIs were divided by 2 and arcsine square-root transformed to normalize their distributions (Zar 1984). Individual pairs of varieties were tested using a two-tailed *t*-test to determine if there was a significant preference for one variety over the other (i.e., whether the PI differed from 1).

We also ranked each variety along an axis of constitutive resistance in the following way. For each variety, we computed the average PI when this variety was used as the reference variety in pairings with each other variety. These five averages were then averaged to yield an overall measure of preference for (or against) the variety under consideration. Thus varieties that had a low average PI when measured against the other varieties used in the experiment were considered to have a relatively high level of constitutive resistance.

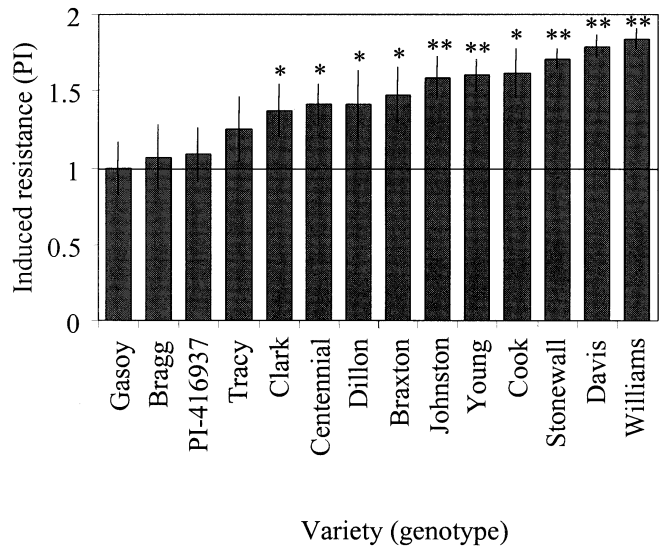


Fig. 1 The level of induced resistance (as measured by preference index, *PI*) in 14 varieties of soybean. The *PI* ranges from 0 to 2. A *PI* of 1 indicates no induced resistance (damaged and undamaged plants equally preferred by beetles), values less than 1 would indicate induced susceptibility, and values greater than 1 indicate induced resistance (undamaged plants preferred over damaged plants). Error bars indicate 1 SE and sample sizes for each bar range from 8 to 12. Asterisks indicate varieties for which there was significant induced resistance [$PI > 1$, one-tailed *t*-test, * $\alpha=0.05$, ** $\alpha=0.004$ (corrected for 14 comparisons)]

Results

We found substantial variation among varieties in the strengths of their induced responses to Mexican bean beetle damage (Fig. 1). These responses ranged from no detectable induced resistance (e.g., Gasoy) to very strong induced responses (e.g., Davis). Eleven of the 14 varieties showed significant induced resistance at the $\alpha=0.05$ level, and 5 of these showed significant induced resistance at the $\alpha=0.004$ level (corrected for multiple comparisons). Analysis of variance confirmed that soybean varieties differed significantly in the strength of their induced response to beetle damage (effect of variety nested within round, $F_{12,142}=3.07$, $P=0.0007$), and that there was no difference in induced resistance among the three rounds of the experiment in which we screened varieties for induced resistance (effect of round, $F_{2,142}=0.19$, $P=0.83$).

We also found variation in constitutive resistance among 6 varieties. Nine out of 15 choice tests between pairs of varieties yielded a significant preference for one variety at the $\alpha=0.05$ level (Table 1). If the α level is corrected using the highly conservative Bonferroni approach for 15 multiple comparisons (corrected $\alpha=0.003$), only one pairing (Gasoy versus Tracy) remains significantly different. The preferences of the beetles for undamaged leaf tissue from the six varieties tested were remarkably consistent. If beetles significantly preferred variety A over B and B over C, they never preferred C over A. This can be seen by constructing a table (Fig. 2) in

Table 1 Results of Mexican bean beetle choice tests measuring relative constitutive resistance of six soybean varieties. Constitutive resistance was measured as relative beetle preference for one variety over the other (as described by the preference index). Preference index values less than 1 indicate preference for the variety listed first in the pair, values above 1 indicate preference for the second variety (*n.p.* no significant preference)

Pair	<i>n</i>	Preference index (± 1 SE)	<i>P</i> ($\alpha=0.05$, two-tailed)	Preferred variety
Bragg/Davis	11	0.83 (0.16)	<0.5	<i>n.p.</i>
Bragg/Gasoy	11	1.15 (0.19)	<0.5	<i>n.p.</i>
Bragg/PI 416937	9	0.47 (0.17)	<0.02	Bragg
Bragg/Stonewall	10	1.43 (0.19)	<0.05	Stonewall
Bragg/Tracy-M	11	0.68 (0.17)	<0.1	<i>n.p.</i>
Davis/Gasoy	10	1.16 (0.16)	<0.25	<i>n.p.</i>
Davis/PI 416937	11	0.61 (0.12)	<0.02	Davis
Davis/Stonewall	11	0.85 (0.18)	<0.5	<i>n.p.</i>
Davis/Tracy-M	11	0.63 (0.17)	<0.05	Davis
Gasoy/PI 416937	11	0.51 (0.18)	<0.05	Gasoy
Gasoy/Stonewall	10	1.18 (0.18)	<1.0	<i>n.p.</i>
Gasoy/Tracy-M	9	0.44 (0.08)	<.001	Gasoy
PI 416937/Stonewall	11	1.49 (0.17)	<0.02	Stonewall
PI 416937/Tracy-M	8	1.21 (0.19)	<0.05	Tracy-M
Stonewall/Tracy-M	9	0.45 (0.13)	<0.01	Stonewall

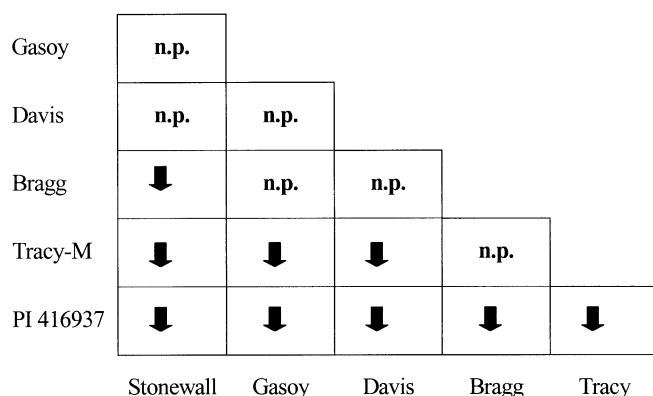


Fig. 2 The preference hierarchy of Mexican bean beetles for six varieties of soybean. Arrows point to the variety that was significantly preferred when beetles were given a choice between leaf disks taken from undamaged plants from the varieties in the corresponding row and column (*n.p.* no preference; see Table 1 for statistical tests)

which the varieties are ordered from lowest mean preference index (Stonewall) to highest mean preference index (PI 416937); all of the arrows in the table point in the same direction. As a consequence of this consistent preference, the six soybean varieties can be ranked along an axis of constitutive resistance. Stonewall has the lowest constitutive resistance, because it was significantly preferred over the three most resistant varieties (although there was no preference for Stonewall over Gasoy or Davis). Next in order of constitutive resistance is the pair of equally preferred varieties, Gasoy and Davis, which were both significantly preferred to the two most resistant varieties but not to Bragg. Bragg was preferred to PI 416937 but not to Tracy-M. Finally, beetles preferred all other varieties to PI 416937.

Because beetle preferences were consistent among the six varieties, we could use the mean PI for each variety tested against the other five as an overall measure of constitutive resistance. Even though the six varieties we tested ranged widely in both induced and constitutive resistance, the correlation between induced and constitu-

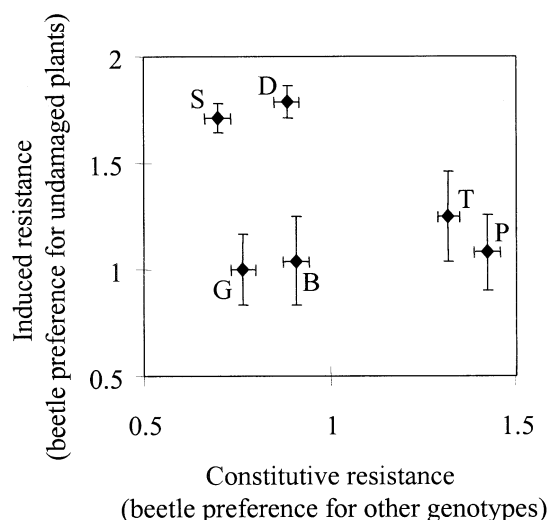


Fig. 3 The relationship between levels of constitutive and induced resistance in six varieties of soybeans. Both types of resistance were measured by preference index (PI). For induced resistance, the PI indicates the relative preference of beetles for undamaged over damaged plants, and for constitutive resistance the PI indicates the relative preference of beetles for other varieties over the variety under consideration. Error bars indicate 1 SE; sample sizes for each point range from 8 to 12 (B Bragg, D Davis, G Gasoy, P PI 416937, S Stonewall, T Tracy-M)

tive resistance ($R=-0.37$) did not differ significantly from 0 ($F_{4,4}=2.17$, $P>0.2$). However, none of the varieties we tested appear to have very high levels of both constitutive and induced resistance (Fig. 3). Our power to determine whether a correlation of $R=-0.37$ between induced and constitutive resistance differs significantly from 0 with these data was 0.9.

Discussion

We found substantial variation among 14 soybean varieties for induced resistance to Mexican bean beetle damage (Fig. 1), and among six varieties of soybeans in their

relative constitutive resistance (Fig. 3). We found no evidence of a correlation between induced and constitutive resistance, though the trend is towards a negative correlation. Below, we place our results in the context of past work on resistance in the soybean-Mexican bean beetle system, explore the implications of variation in both types of resistance for plant-herbivore interactions in agricultural and natural systems, and discuss the relationship between induced and constitutive resistance.

Our method of measuring both induced and constitutive resistance was a choice-test bioassay, which measures antifeedant resistance, not antibiosis. Although induced and constitutive resistance in soybean are known to affect both the feeding preference and performance of Mexican bean beetles and other insects (e.g., Kogan and Fischer 1991; Nault et al. 1992), the exact strength of the correlation between preference and beetle performance is not known.

Our findings are consistent with many previous demonstrations that soybean genotypes vary in constitutive resistance (e.g., Van Duyn et al. 1971; Barney and Rock 1975; Kraemer and Rangappa et al. 1988; Kraemer et al. 1994). Our results for the constitutive resistance of particular varieties are largely consistent with previous ratings. In particular, our ranking of Tracy-M as preferable to PI 416937 but less preferred than Bragg follows results of a field trial of these varieties in 1994 (Kraemer et al. 1994). The fact that beetle preferences were consistent among varieties (Fig. 2) suggests that beetles may base their feeding choices on either a single plant trait or a set of traits that are correlated among the six varieties we tested. In principle, insects could prefer variety A to variety B and variety B to variety C on the basis of different traits, in which case they might not prefer A to C. If insect preferences were not consistent, it might be difficult to say categorically that one variety is the most resistant, which would complicate deciding which varieties to select when breeding for constitutive resistance in agricultural crops. Our results suggest that this may not be a problem for breeding antifeedant resistance to Mexican bean beetles into soybeans. Additional experiments are needed to determine whether the consistency in bean beetle preference holds in comparisons involving larger numbers of soybean varieties.

Few previous studies have looked for variation in induced resistance among soybean genotypes, but our results are consistent with work in other systems that demonstrates genotypic variation for induced resistance (Shapiro and DeVay 1987; Anderson et al. 1989; Zangerl and Berenbaum 1990; Raffa 1991; Brody and Karban 1992; Bi et al. 1994; van Dam and Vrieling 1994; English-Loeb et al. 1998). Interpreting differences in induced resistance among genotypes can be complicated. If genotypes differ in the timing of their responses to damage (e.g., rates of onset and decay of induced resistance, duration of the resistance), differences in timing could be incorrectly interpreted as differences in the strength of response. Likewise, if genotypes differ in the relationship between induced resistance and amount of

damage, differences at one damage level could be interpreted incorrectly as differences in peak response. For the soybean-Mexican bean beetle system, it is known that for at least four genotypes (Bragg, Centennial, Clark, and Williams), the timing of induced resistance does not vary among genotypes (Underwood 1998). Assuming that this result applies to all the genotypes used in this experiment, variation among genotypes in our study is likely to be due to genotype differences in the magnitude, rather than the timing, of induced resistance. We also know that the strength of induced resistance in soybeans varies with the magnitude of damage (Underwood, in press), and that the shape of this relationship differs among genotypes. Although damage was constant across genotypes in the experiments reported here, some of the observed variation in induced resistance could thus be due to variation in the threshold level of damage necessary to provoke induced resistance. To reduce this possibility, the level of damage used in this experiment was chosen to exceed most of the thresholds that have been measured for soybeans (N. Underwood, unpublished data).

Variation in induced responses to herbivore damage among genotypes can provide a powerful experimental tool for addressing evolutionary and ecological questions about induced resistance, including the correlation of induced and constitutive resistance. Varieties tested in this paper are being used to test for effects of induced resistance on herbivore population dynamics (N. Underwood, unpublished data), and have been used to look at effects of induced resistance on herbivore spatial spread (W. Morris, unpublished data). Genetic variation for induced resistance has also been used by other workers to determine if related varieties share resistance traits (e.g., Thaler and Karban 1997; English-Loeb et al. 1998).

Levels of induced and constitutive resistance were not significantly correlated in the six varieties of soybeans tested in this study, although the trend was towards a negative correlation (no varieties had very strong levels of both types of resistance; Fig. 3). With only six varieties, our experiment had a power of only 0.9 to determine whether the observed correlation of $R = -0.37$ is significantly different from 0, so we can be only 90% certain that no significant correlation exists. Our data do, however, strongly suggest that the correlation between the two types of resistance in this system is not positive. This supports the idea that induced and constitutive resistance may be physiologically distinct processes in soybean (Wheeler and Slansky 1991), so that having one type of resistance does not automatically mean that a plant also produces the other type.

The lack of correlation between levels of induced and constitutive resistance observed in this system is consistent with the findings of three previous studies that have looked for such correlations, among ten varieties of cotton (Brody and Karban 1992), in 21 species of *Gossypium* (Thaler and Karban 1997), and in nine varieties of grapes (English-Loeb et al. 1998). However, two of these

three studies (Brody and Karban 1992; English-Loeb et al. 1998) and the current study have looked for these correlations in crop plants. Crop plants may not be good analogs for wild species in this type of study because they are subject to strong artificial, rather than natural, selection. Artificial selection may favor different traits or trait values than natural selection (Kennedy and Barbour 1992). Environmental conditions in an agricultural setting, such as fertilization and spraying of insecticides, might also interfere with the expression of costs and benefits for each type of resistance (Kennedy and Barbour 1992). A lack of correlation between induced and constitutive resistance in crops may thus not be representative of plants subjected to natural selection. In a study conducted in a population of wild parsnip, Zangerl and Berenbaum (1990) found that correlations between induced and constitutive levels of furanocoumarins were positive.

If induced and constitutive resistance are in fact uncorrelated or positively correlated in most systems, this would indicate either that one or both of the two types of resistance are not particularly costly, or that the two types of resistance provide different benefits to the plant. Measuring costs of resistance is an active field of research (see for example Simms and Rausher 1987; Zangerl et al. 1997) and it is still unclear whether resistance characters, especially induced resistance, are in general costly. To our knowledge, the relative benefits of constitutive and induced resistance have never been measured in a single system.

Given that induced resistance in soybeans has been shown to affect not only preference but also the performance of Mexican bean beetles and other insects (Kogan and Fischer 1991), induced resistance has at least the potential to be useful in protecting crops from pests (Karbon 1991). The range of genetic variation for induced resistance found in our experiments suggests that breeding for high levels of this trait should be possible. The suggestion of a lack of negative correlation between induced and constitutive resistance in soybeans also suggests that it might be possible to breed for genotypes with high levels of both types of resistance. Plants with both types of resistance might have advantages over plants with only one type, although none of the six varieties for which we measured both induced and constitutive resistance had high levels of both (Fig. 3). Constitutive resistance should lower mean rates of pest reproduction, and induced resistance might provide a density feedback that could contribute to pest population regulation, or reduce the likelihood of pests developing tolerance to plant resistance.

Acknowledgements We thank T. Dorsey and the NJ Department of Agriculture for providing Mexican bean beetles for these experiments. We also thank the following people for supplying soybean seed: T. Carter and J. Burton (NC State University, Raleigh, N.C.), R. Nelson (USDA Soybean Germplasm Collection, Urbana, Ill.), and L. Lambert and W. Solomon (USDA-ARS-SIML, Miss.). This work was supported by NRI Competitive Grants Program/USDA grant 94-37302-0463 to W. Morris and NRI Competitive Grants Program/USDA grant 94-37302-0348 to M. Rausher.

References

- Adler FR, Karban R (1994) Defended fortresses or moving targets? Another model of inducible defenses inspired by military metaphors. *Am Nat* 144:813–832
- Anderson SS, McCrea KD, Abrahamson WG, Hartzel LM (1989) Host genotype choice by the ball gallmaker *Eurosta solidaginis* (Diptera: Tephritidae). *Ecology* 70:1048–1054
- Barney WP, Rock GC (1975) Consumption and utilization by the Mexican bean beetle of soybean plants varying in levels of resistance. *J Econ Entomol* 68:497–501
- Bi JL, Felton GW, Mueller AJ (1994) Induced resistance in soybean to *Helicoverpa zea*: role of plant protein quality. *J Chem Ecol* 20:183–198
- Brody AK, Karban R (1992) Lack of a tradeoff between constitutive and induced defenses among varieties of cotton. *Oikos* 65:301–306
- Dam NM van, Vrieling K (1994) Genetic variation in constitutive and inducible pyrrolizidine alkaloid levels in *Cynoglossum officinale* L. *Oecologia* 99:374–378
- English-Loeb G, Karban R, Walker MA (1998) Genotypic variation in constitutive and induced resistance in grapes against spider mite (Acari: Tetranychidae) herbivores. *Environ Entomol* 27:297–304
- Felton GW, Summers CB, Mueller AJ (1994) Oxidative responses in soybean foliage to herbivory by bean leaf beetle and three-cornered alfalfa hopper. *J Chem Ecol* 20:639–650
- Fritz RS, Simms EL (eds) (1992) Plant resistance to herbivores and pathogens: ecology, evolution, and genetics. University of Chicago Press, Chicago
- Hermes DA, Mattson WJ (1992) The dilemma of plants: to grow or defend. *Q Rev Biol* 67:283–335
- Karbon R (1991) Inducible resistance in agricultural systems. In: Tallamy DW, Raupp MJ (eds) *Phytochemical induction by herbivores*. Wiley, New York, pp 403–419
- Karbon R, Baldwin IT (eds) (1997) *Induced responses to herbivory*. University of Chicago Press, Chicago
- Kennedy GG, Barbour JD (1992) Resistance variation in natural and managed systems. In: Fritz RS, Simms EL (eds) *Plant resistance to herbivores and pathogens: ecology, evolution, and genetics*. University of Chicago Press, Chicago, pp 13–41
- Kogan M (1972) Intake and utilization of natural diets by the Mexican bean beetle, *Epilachna varivestis* – a multivariate analysis. In: Rodriguez JG (ed) *Insect and mite nutrition: significance and implications in ecology and pest management*. North-Holland, Amsterdam, pp 107–126
- Kogan M, Fischer DC (1991) Inducible defenses in soybean against herbivorous insects. In: Tallamy DW, Raupp MJ (eds) *Phytochemical induction by herbivores*. Wiley, New York, pp 347–378
- Kraemer ME, Rangappa M, Benepal PS, Mebrahtu T (1988) Field evaluation of soybeans for Mexican bean beetle resistance. I. Maturity groups VI, VII, and VIII. *Crop Sci* 28:497–499
- Kraemer ME, Mebrahtu T, Rangappa M (1994) Evaluation of vegetable soybean genotypes for resistance to Mexican bean beetle (Coleoptera: Coccinellidae). *J Econ Entomol* 87:252–257
- Nault BA, All JN, Boerma HR (1992) Resistance in vegetative and reproductive stages of a soybean breeding line to three defoliating pests (Lepidoptera: Noctuidae). *J Econ Entomol* 85:1507–1515
- Raffa KA (1991) Induced defensive reactions in conifer-bark beetle systems. In: Tallamy DW, Raupp MJ (eds) *Phytochemical induction by herbivores*. Wiley, New York, pp 245–276
- SAS (1989) *SAS/STAT user's guide*. SAS Institute, Cary, NC
- Shapiro AM, DeVay JE (1987) Hypersensitivity reaction of *Brassica nigra* L. (Cruciferae) kills eggs of *Pieris* butterflies (Lepidoptera: Pieridae). *Oecologia* 71:631–632
- Simms EL, Rausher MD (1987) Costs and benefits of plant resistance to herbivory. *Am Nat* 130:570–581
- Smith CM, Wilson RF, Brim CA (1979) Feeding behavior of Mexican bean beetle on leaf extracts of resistant and susceptible soybean genotypes. *J Econ Entomol* 72:374–377

- Thaler JS, Karban R (1997) A phylogenetic reconstruction of constitutive and induced resistance in *Gossypium*. *Am Nat* 149: 1139–1146
- Underwood N (1997) The interaction of plant quality and herbivore population dynamics. PhD thesis, Duke University, Durham, NC
- Underwood NC (1998) The timing of induced resistance and induced susceptibility in the soybean Mexican bean beetle system. *Oecologia* 114:376–381
- Underwoods N (in press) Density dependence in induced plant resistance to herbivore damage: threshold, strength and genetic variation. *Oikos*
- Van Duyn JW, Turnipseed SG, Maxwell JD (1971) Resistance in soybeans to the Mexican bean beetle. I. Sources of resistance. *Crop Sci* 11:572–573
- Wheeler GS, Slansky F Jr (1991) Effect of constitutive and herbivore-induced extractables from susceptible and resistance soybean foliage on nonpest and pest noctuid caterpillars. *J Econ Entomol* 84:1068–1079
- Zangerl AR, Berenbaum MR (1990) Furanocoumarin induction in wild parsnip: genetics and populational variation. *Ecology* 71: 1933–1940
- Zangerl AR, Arntz AM, Berenbaum MR (1997) Physiological price of an induced chemical defense: photosynthesis, respiration, biosynthesis, and growth. *Oecologia* 109:433–441
- Zar JH (1984) *Biostatistical analysis*. Prentice Hall, Englewood Cliffs, NJ