Induced Resistance in Soybean to the Mexican Bean Beetle (Coleoptera: Coccinellidae): Comparisons of Inducing Factors

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ABSTRACT Induced resistance in soybean was investigated using mechanical injury and herbivory by the soybean looper, *Pseudoplusia includens* (Walker), as inducing factors. Dual-choice feeding-preference tests with the Mexican bean beetles, *Epilachna varivestis* Mulsant, were used to assess the induced resistance. Comparisons of leaves from plants treated by mechanical injury, soybean looper herbivory, and application of soybean looper larval regurgitate on mechanically wounded leaf surfaces revealed that herbivore-feeding injury was a better inducer than mechanical injury. The regurgitate of soybean looper larvae may contain factors that enhance induction of resistance. Tests using various types of mechanical injury as inducing factors showed that the level of induced resistance depended on the total number of wounded cells in contact with healthy cells and not on the total amount of plant tissue lost. We suggest that there is a positive correlation between the intensity of the inducing factor and the level of resulting resistance in soybean. Interplant transfer of inducing signals was tested, but no evidence was found that such transfer occurred.

KEY WORDS Insecta, *Epilachna varivestis*, soybean, induced resistance

INDUCED RESISTANCE in plants is the qualitative or quantitative enhancement of a plant's defense mechanism in response to extrinsic stimuli, such as pathogen infection, herbivory, or mechanical injury (Kogan & Paxton 1983). Plant defenses induced by previous herbivory or mechanical injury have physiological, behavioral, and ecological effects on insects (Fowler & Lawton 1985). Induction of resistance in plants results in chemical alterations that may change a plant's acceptability or decrease the nutritional quality of the plants to herbivores (Moran & Hamilton 1980, Kogan & Paxton 1983, Neuvonen & Haukioja 1984, Edwards et al. 1985, Ryan et al. 1986, Lin & Kogan 1990). Recent reviews of the literature on induced resistance by previous herbivory include Haukioja & Neuvonen (1987), Schultz (1988), and Karban & Myers (1989).

Several phytoalexins of soybean induced by fungal pathogens have various effects on soybean insect pests (Kogan & Paxton 1983). An example of induced resistance and interspecific competition between plant herbivore and pathogen was provided by Karban et al. (1987). They reported that populations of spider mites, *Tetranychus urticae* Koch, grew more slowly on cotton seedlings inoculated with a fungal pathogen, *Verticillium dahliae*, compared with noninoculated control plants. The same fungal pathogen was less likely to cause symptoms on cotton seedlings with previous mite infestation than on seedlings without previous infestation. Plant or fungal cell wall fragments that are produced during pest attack or mechanical injury have been suggested as inducers of resistance that activate a universal recognition system in plants and turn on gene expression of plant defense mechanisms (Ryan et al. 1986). Oligosaccharins, fragments of the plant cell wall, are plant molecules influencing plant resistance as they trigger the synthesis of phytoalexin (Albersheim & Darvill 1985).

Chiang et al. (1987) have shown that Mexican bean beetle, *Epilachna varivestis* Mulsant, herbivory induced increased levels of antixenosis to subsequent feeding and that the increase was positively correlated with total phenolic content of the plants. Soybean looper, *Pseudoplusia includens* (Walker), larvae that were fed on mechanically wounded plants had lower growth rates than those fed on unwounded plants (Reynolds & Smith 1985). In this work, we focused on four aspects of induced resistance in soybean: (1) induction of resistance in soybean plants to Mexican bean beetle by previous herbivory; (2) inducing factors and their effectiveness in the induction of resistance; (3) components of insect herbivory that elicit an inductive response in soybean; and (4) interplant transfer of inducing signals.

Materials and Methods

Insect and Plants. The Mexican bean beetle used in all experiments was obtained from a colony kept

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in the greenhouse on snapbean (*Phaseolus vulgaris* L.) seedlings. Only 1- to 2-wk-old female beetles were used in the feeding-preference tests. Beetles were starved for about 20 h before tests but were supplied with water.

Soybean loopers were obtained from a colony maintained on artificial medium (Henneberry & Kishaba 1966) at 26 ± 1°C, 70 ± 5% RH, and a 14:10 (L:D) photoperiod. The fourth instars were used to produce the feeding injury as a resistance-inducing factor.

Soybean, *Glycine max* (L.) Merrill, cv. Williams 82, was used in all experiments. Plants were seeded in 15-cm plastic pots, 80% full with a sterile soil mixture (1:1:1:1, top soil/peat/sand/perlite). Plants were grown in a greenhouse maintained at 30 ± 5°C, 60 ± 10% RH, and 14:10 (L:D) photoperiod with supplementary metal-halide illumination. Pots were watered at least once a day in the morning and with a 2% mixture fertilizer (water soluble N:P:K, 20:20:20) every Monday and Thursday. Definition of developmental stages of soybean plants follows Fehr et al. (1971).

Feeding-Preference Tests. Dual-choice tests were conducted to assess Mexican bean beetle feeding preferences according to procedures described by Kogan & Goeden (1970) and Kogan (1972). Six leaf disks from each pair of experimental plants, assigned as control (C) and treatment (T), were arranged in a Petri dish in an alternating pattern along a circle within the arena. Four starved female Mexican bean beetles were released into each Petri dish. The tests lasted 4 to 6 h, and the remaining leaf disk area was measured using a LICOR-3000 area meter (LICOR, Lincoln, Nebr.). The consumed leaf disk area of treatment (T) and control (C) was used to compute the statistical significance (*t* test) of differences in feeding preferences in paired comparisons between T and C and to calculate the feeding-preference index (PI) such that, $PI = 2T/T + C$ (Kogan & Goeden 1970, Kogan 1972). The PI value varies between 0 and 2, with $PI = 1$ indicating no feeding preference for either control or treatment disks, $PI > 1$ indicating preference for treatment leaf disks, and $PI < 1$ indicating preference for control leaf disks.

Experimental Procedures. A series of four experiments was conducted to compare induction of resistance by mechanical injury with resistance induced by direct herbivory. In addition, we tested the hypothesis that inducing signals may be transferrable from an injured to an uninjured plant.

Experiment 1 was conducted to compare resistance induced by various types of mechanical injury with induction by previous herbivory. Forty plants (one plant in each pot) at the V6 stage of growth were separated into four groups. One group (10 plants) received no injury and served as control (uninjured). The other three groups of 10 plants each received one of the following treatments: (1) soybean looper herbivory (SBL feeding), (2) tearing with a pair of forceps to produce about 40% removal of foliage tissue (torn), and (3) cutting off the two lateral leaflets of each trifoliolate at the base of the petiole (cut). Defoliation by herbivory was produced by placing 4–5 fourth-instar soybean loopers on the lower leaves of the plants; after 24 h the larvae usually had consumed about 30% of the leaf area from the first (bottom) to the fifth trifoliolates. Similarly, the first to fifth trifoliolates were treated by the mechanical procedures. The sixth trifoliolate was used for Mexican bean beetle feeding-preference tests 2 wk after plants were injured.

Experiment 2 was designed to test the role of soybean looper herbivory in the induction of resistance. Thirty plants (one plant in each pot) at the V6 stage of growth were separated into three groups. One group received no injury and served as control (uninjured). The other two groups received one of two treatments on the first through the fifth trifoliolates. The first type of treatment was done by puncturing the leaf surface of each leaflet (avoiding the main veins) with a bundle of 20 no. 1 insect pins fastened together with fiber tape (punctured). The second type of treatment was made by smearing regurgitate from sixth-instar soybean loopers on the leaf surface wounded by puncturing (punctured + regurgitate). The sixth trifoliolates of control and treatment plants were tested in paired comparisons 2 wk after the treatments.

Experiment 3 was conducted to study induced resistance by injuring cotyledons. Eight to 9 d after planting, the cotyledons of soybean seedlings in the control group received no injury (uninjured), and those in the treatment groups were treated as follows: (1) soybean looper feeding (SBL feeding) that resulted in about two-thirds loss of each cotyledon mass, (2) removal of two-thirds of each cotyledon's upper surface (cut) with a scalpel, (3) removal of cotyledon surface as in (2) and wetting the wounded surface with 30 µl distilled water (cut + water), (4) removal of cotyledon surface as in (2) and smearing the wounded surface with soybean looper larval regurgitate (cut + reg.), and (5) removal of cotyledon surface as in (2) and treating the wounded surface with about 30 µl suspension of *Phytophthora megasperma* f. sp. *glycinea* mycelia (Sharp et al. 1984) (cut + elicitor). Three days after the treatments, unifoliolates of the seedlings were tested using the Mexican bean beetle feeding-preference test. Ten pairs of seedlings were used in each test combination.

Experiment 4 was designed to test the hypothesis of interplant transfer of inducing signals. Twenty pots of experimental plants (two plants in each pot) were grouped in 10 pairs at the V6 stage of growth. Both plants in one pot of each pair were kept uninjured (uninjured no. 1). One plant of the other pot in the pair was infested by the fourth-instar soybean loopers as described in experiment 1 (SBL feeding). The other plant remained uninjured (uninjured no. 2). The uninjured plant grown in the

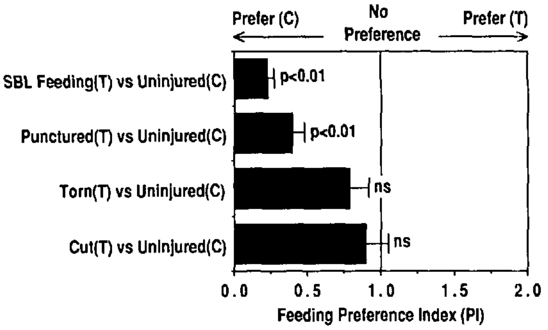

Fig. 1. Results of dual-choice preference tests—Experiment 1: Feeding on leaves from uninjured plants was compared with feeding on leaves from plants previously injured. Mean PI values ± SE derived from 10 replicates of each test combination. Values are significant at $P < 0.01$, torn (T) versus uninjured (C) and cut (T) versus uninjured (C) are not significant.

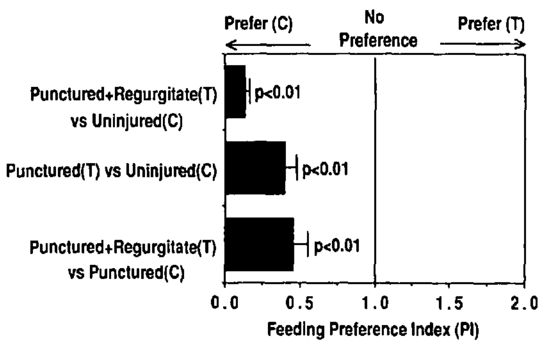

Fig. 2. Results of dual-choice preference tests—Experiment 2: Feeding on leaves from uninjured plants was compared with feeding on leaves from plants previously treated. Mean PI values ± SE derived from 10 replicates of each test combination. Values are significant at $P < 0.01$.

same pot as the injured plant was used to test the possible interplant transfer of inducing signals via root or foliar contact. Two weeks after treatment, with plants at the V9 stage, the uninjured sixth trifoliolates of all plants were tested for Mexican bean beetle feeding preference.

Results

The effect of herbivory in these experiments is measured by variations in acceptability of leaf tissue from injured plants in comparison with similar tissue from uninjured plants. For concision we refer to that effect as variations in resistance levels, although the dual-choice test only measures variations in relative preference, i.e., changes in antixenosis.

Results of experiment 1 demonstrated that different levels of resistance were induced by soybean looper herbivory and by different types of mechanical injury (Fig. 1). Increased resistance was significantly induced by soybean looper feeding (SBL feeding) compared with that of uninjured plants (uninjured): SBL feeding (T) versus uninjured (C), PI = 0.23 ± 0.04 ($\bar{x}$ ± SE), $P < 0.01$. Mechanical injury resulting from cutting two side leaflets of each trifoliolate (cut) did not induce plant resistance: cut (T) versus uninjured (C), PI = 0.89 ± 0.14, $P > 0.05$. Plants mechanically injured by tearing the leaf tissue with forceps (torn) showed a trend toward increased resistance, but differences were not statistically significant: torn (T) versus uninjured (C), PI = 0.78 ± 0.12, $P > 0.05$. Mechanical injury by puncturing the leaf surface of each leaflet with bundled insect pins (punctured) significantly increased resistance in treated plants compared with uninjured plants (uninjured): punctured (T) versus uninjured (C), PI = 0.43 ± 0.09, $P < 0.01$, but the effect was less accentuated than the effect obtained with actual soybean looper feeding.

Both soybean looper herbivory and puncturing injury induced plant resistance, but the effect of herbivory was greater. Therefore, experiment 2 was conducted to determine what components of insect herbivory, other than mechanical destruction of leaf tissue, are involved in the induction process. Results (Fig. 2) showed that resistance was significantly induced by puncturing leaves with or without addition of soybean looper larval regurgitate onto the wounded leaf surface, but the resistance induced by puncturing with addition of the looper regurgitate was stronger: punctured + regurgitate (T) versus uninjured (C), PI = 0.18 ± 0.07 ($\bar{x}$ ± SE), $P < 0.01$; punctured (T) versus uninjured (C), PI = 0.43 ± 0.09, $P < 0.01$. A comparison between leaves from plants treated by puncturing with and without addition of the looper regurgitate provided direct evidence that the looper regurgitate enhanced induction of resistance: punctured + regurgitate (T) versus punctured (C), PI = 0.51 ± 0.11, $P < 0.01$.

Results from experiment 3 showed that injury on cotyledons of 1-wk-old soybean seedlings induced resistance in unifoliolates (Fig. 3). Compared with uninjured seedlings (uninjured), level of resistance was significantly increased by induction due to: (1) soybean looper feeding on cotyledons (SBL feeding): SBL feeding (T) versus uninjured (C), PI = 0.04 ± 0.02 ($\bar{x}$ ± SE), $P < 0.01$; (2) removal of upper surface of cotyledons with application of the fungal elicitor (suspension of *P. megasperma* f. sp. *glycinea* mycelia) on the wounded cotyledon surface (cut + elicitor): cut + elicitor (T) versus uninjured (C), PI = 0.22 ± 0.07, $P < 0.01$; (3) removal of the upper surface of cotyledons with application onto the wound of soybean looper larval regurgitate (cut + reg.): cut + reg. (T) versus uninjured (C), PI = 0.06 ± 0.02, $P < 0.01$; and (4) removal of the upper surface of cotyledons (cut): cut (T) versus uninjured (C), PI = 0.64 ± 0.09, $P < 0.01$. Addition of water onto the wounded cotyledons (cut + water) did not af-

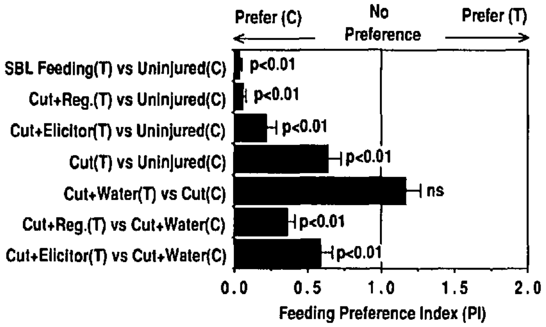

Fig. 3. Results of dual-choice preference tests—Experiment 3: Feeding on leaves from uninjured soybean seedlings was compared with feeding on leaves from seedlings the cotyledons of which were previously treated. Mean PI values ± SE derived from 10 pairs of seedlings in each test combination. Values are significant at $P < 0.01$, cut + water (T) versus cut (C) is not significant.

fect feeding preference: cut + water (T) versus cut (C), PI = 1.17 ± 0.10, $P > 0.05$. Comparisons among treatments consisting of the removal of cotyledon surface without (cut) and with addition of the fungal elicitor (cut + elicitor) or the looper regurgitate (cut + reg.) onto the wounded surface showed that stronger resistance was induced by the addition of either the elicitor: cut + elicitor (T) versus cut + water (C), PI = 0.59 ± 0.08, $P < 0.01$; or the regurgitate: cut + reg. (T) versus cut + water (C), PI = 0.36 ± 0.05, $P < 0.01$.

Results of experiment 4 (Fig. 4) testing the possibility of interplant transfer of inducing signals showed that leaves from plants previously injured by soybean looper herbivory (SBL feeding) were significantly less acceptable to the Mexican bean beetle than leaves from uninjured plants, whether grown in the different pots: SBL feeding (T) versus uninjured no. 1 (C), PI = 0.35 ± 0.08 ($\bar{x}$ ± SE), $P < 0.01$; or in the same pots: SBL feeding (T) versus uninjured no. 2 (C), PI = 0.37 ± 0.09, $P < 0.01$. Two types of uninjured plants—uninjured no. 2 (T) versus uninjured no. 1 (C)—showed no significant difference in Mexican bean beetle feeding-preference test (PI = 1.12 ± 0.16, $P > 0.05$). It appears that no resistance was induced in the uninjured plants grown in the same pots as the injured plants, suggesting that there was no transfer of inducing signals from injured plants to uninjured plants through root or foliage contact.

Discussion

Results of our experiments suggest that resistance in soybean is induced by previous herbivory, as well as by other stress factors. Consequently, induced resistance seems to be a nonspecific plant defense mechanism in soybean. Chiang et al. (1987) demonstrated that soybean resistance to Mexican bean beetle feeding is induced by previous Mexican bean beetle herbivory. Soybean resistance induced by soybean looper herbivory has antibiotic and antixenotic effects on the Mexican bean beetle and the soybean looper, but the effect on the Mexican bean beetle is stronger (Lin & Kogan 1990). We used the soybean looper feeding as the inducing factor in this study because it is easier to regulate the feeding behavior of this species. The Mexican bean beetle was chosen to perform the feeding-preference tests because it is an oligophagous species and is very sensitive to subtle changes in plant chemistry.

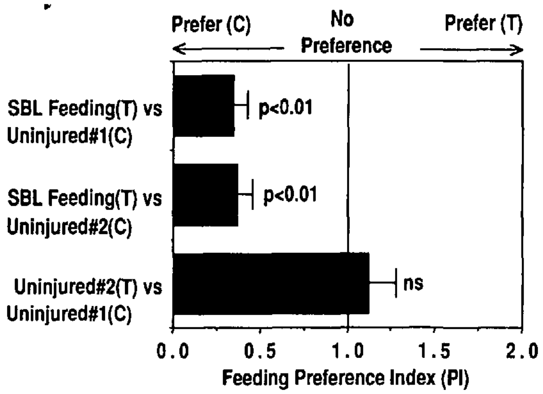

Fig. 4. Results of dual-choice preference tests—Experiment 4: Feeding on leaves from plants previously injured by soybean looper herbivory was compared with feeding on leaves from uninjured plants grown in different pots or in the same pots with the injured plants. Mean PI values ± SE derived from 10 replicates of each test combination. Values are significant at $P < 0.01$, uninjured #2 (T) versus uninjured #1 (C) is not significant.

We tested uninjured leaves that developed after the induction treatment was conducted. In so doing, we excluded the influence of any direct plant wounding-repair response and tested leaf quality affected by systemic induction.

Plant resistance may be induced by mechanical injury resulting in various effects on herbivores (Neuvonen & Haukioja 1984, Edwards et al. 1985, Karban 1985). Soybean looper larvae fed on soybean plants with mechanically wounded leaves had lower growth rates than larvae fed leaves grown on uninjured plants (Reynolds & Smith 1985). We observed that different types of mechanical injury induced different levels of resistance. Compared with leaves from uninjured plants, leaves from plants with leaflets removed at the petiole showed no detectable increase of resistance. Tearing portions of the leaf blade induced a moderate level of resistance. Puncturing leaves with bundled insect pins induced a stronger level of resistance than tearing. There was no apparent correlation between the level of resistance induced and the amount of plant leaf tissue lost from injury. Puncturing leaves resulted in little loss of plant leaf tissue but left many ruptured cells in contact with healthy cells. Removal of whole leaflets resulted in a considerable loss of plant leaf tissue, but left few ruptured cells in contact with healthy cells. We also observed that, at a similar defoliation level, soybean plants defoliated by the fourth-instar soybean loopers had a higher level of induced resistance than did plants defoliated by sixth instars (H.L. & M.K., unpublished data). Although the older larvae removed large portions of leaf tissue, the overall interface between injured and healthy cells was smaller than that resulting from feeding by younger instars. The fourth instars usually avoid main leaf veins and skeletonize leaves, causing many small wounds. We concluded that the level of resistance induced by injury depended on the number of injured cells that were in contact with healthy cells and not on the total leaf area lost.

Cell wall fragments of injured cells are further degraded by enzymatic action. Plant cell wall fragments, oligosaccharins, are believed to be activators of reception systems for defense (Albersheim & Darvill 1985, Ryan et al. 1986). The message apparently must be recognized by healthy cells to be transported throughout the plant for proper activation of the pathways that lead to the production of defense factors. Consequently, we speculate that as more tissue is wounded and more cell wall fragments are produced, more heathy cells receive the stimulus, and induced resistance is correspondingly stronger. Our experimental results can be explained by a correlation between the intensity of induction factors and strength of the resulting plant resistance.

In certain plant–herbivore systems, insect and mechanically produced injury are assumed to be equally effective as inducers of resistance (Ryan et al. 1986). However, it has been suggested that defoliated plants are affected by herbivore saliva, in addition to the mechanical destruction of plant tissue (Dyer & Bokhari 1976). Results of our experiments showed that soybean looper herbivory induced higher levels of resistance as compared with an equivalent level of injury caused by mechanical means. Furthermore, application of soybean looper larval regurgitate to mechanically injured leaf tissue induced stronger resistance than mechanical injury alone, suggesting that factors contained in the larval regurgitate may have enhanced the induction of resistance. Resistance induced by soybean looper herbivory seems to result from a combination of mechanical injury and some as yet unidentified factors in the larval regurgitate. Thus, insect herbivory is likely to induce resistance through the mechanical effect of feeding and the biochemical activation of inducing factors by regurgitate components. Finally, it also is conceivable that disruption of the plant surface by insect feeding also allows penetration of microorganisms that elicit induced responses.

There has been speculation about interplant communication of inducing signals (Baldwin & Schultz 1983, Rhoades 1983, but see Fowler & Lawton 1985). Therefore, we performed an experiment to test the possibility of close contact interplant transfer of the inducing signals. Our results, using Mexican bean beetle feeding-preference tests, showed that there was no detectable resistance induced in uninjured plants grown in the same pots as injured plants. Thus, we had no evidence that inducing signals were being transmitted or received either by foliage or through root contact.

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