Effects of Previous Insect Feeding Injury to Sweet Potato on Resistance to Sweet Potato Weevil (Coleoptera: Curculionidae) and Storage Root Chemistry[1]

Lixin Mao, Richard N. Story,[2] Abner M. Hammond, Joseph K. Peterson[3] and Don R. Labonte[4]

Department of Entomology, Louisiana Agricultural Experiment Station, Louisiana State University Agricultural Center, Baton Rouge, LA 70803 USA

J. Entomol. Sci. 38(1): 72-83 (January 2003)

Abstract The effects of root and foliage feeding on sweet potato resistance to sweet potato weevil, *Cylas formicarius* (F.), and on the levels of resin glycoside and caffeic acid in sweet potato storage root periderm tissues were studied. Genotypes ("Beauregard," "Excel," "W-244," "W250," and "Sumor") with varying levels of sweet potato weevil resistance were evaluated. Adult banded cucumber beetle, *Diabrotica balteata* LeConte, and larval *Spodoptera latifascia* (Walker) were introduced onto caged sweet potato plants in the field to elicit root feeding and defoliation on plants. Storage roots were evaluated for sweet potato weevil resistance by quantifying sweet potato weevil adult feeding, oviposition, larval survival, and pupal weight. Both root and foliage injuries were associated with an increase in oviposition (significant in 1998 but not in 1997), but there was no association with adult feeding, larval survival and pupal weight. Genotype had a significant effect on adult feeding, oviposition, and larval survival but not on pupal weight. Root and foliage injuries did not have a significant effect on the levels of resin glycoside and caffeic acid in storage roots. The levels of these compounds differed significantly among genotypes, but there was no apparent relationship between sweet potato weevil resistance (antibiosis) and the levels of these compounds.

Key Words Sweet potato weevil, host plant resistance, resin glycoside, caffeic acid, induced response

The sweet potato weevil, *Cylas formicarius* (F.), is the most destructive insect pest of sweet potato, *Ipomoea batatas* (L.) Poir., worldwide. It attacks storage roots directly in the field and during storage. Larvae feed internally and induce terpenoid production that imparts a bitter taste and renders damaged roots unfit for consumption (Chalfant et al. 1990). Researchers have attempted to develop resistant cultivars for decades; however, little success has been achieved, partly because of the inconsistency of the expressed resistance (Talekar 1987, Collins et al. 1991).

Herbivorous insects rarely encounter host plants that are free of other herbivores.

[1]Received 16 February 2002; accepted for publication 15 June 2002.

[2]To whom reprint requests are to be addressed (email: rstory@agctr.lsu.edu).

[3]U.S. Department of Agriculture, Agricultural Research Service, US Vegetable Laboratory, 2875 Savannah Highway, Charleston, SC 29414 USA.

[4]Department of Horticulture, Louisiana Agricultural Experiment Station, Louisiana State University Agricultural Center, Baton Rouge, LA, 70803.

The presence or feeding damage of one insect species often influences the feeding, oviposition, survivorship, and development of other herbivorous insect species through the induction of chemical, physical, or phenological responses of the plants (Karban and Baldwin 1997). Induced resistance has been documented in many insect-plant systems, where plants respond to herbivory by reducing the suitability of their tissue to subsequent herbivores (Raupp and Denno 1984, Olson and Roseland 1991, Inbar et al. 1999). On the other hand, herbivory by insects may increase plant susceptibility and stimulate insect population growth (Williams and Myers 1984, Faeth 1992, Messina et al. 1993).

Sweet potato has a rich and diverse insect fauna (Talekar 1992). Banded cucumber beetle, *Diabrotica balteata* LeConte, is an important sweet potato pest in the southern United States whose larvae feed upon storage roots in the soil (Schalk et al. 1991). *Spodoptera latifascia* (Walker) is polyphagous and frequently causes extensive defoliation to many ornamental and agricultural plants including sweet potato (Levy and Habeck 1976). In 1997 and 1998, these insects were abundant in Louisiana sweet potato fields. Their feeding on sweet potato plants may affect the suitability of the plants to sweet potato weevil and hence influence the expression of resistance to sweet potato weevil. The objectives of this study were to examine the effect of previous root feeding or defoliation to sweet potato plants on sweet potato weevil resistance as measured by adult feeding, oviposition, larval survival, and development (pupal weight) on storage roots. Five genotypes with varying levels of sweet potato weevil resistance were evaluated. Resin glycoside and caffeic acid levels in the storage root periderm tissue were measured, because these two compounds are believed to be related to insect resistance (antibiosis) in sweet potato (Peterson and Harrison 1992, Peterson et al. 1998, Jackson and Peterson 2000).

Materials and Methods

Field experiment. Field experiments were conducted at Burden Research Center, Louisiana State University Agricultural Center, Baton Rouge, LA, using a complete randomized split-plot design. Six replications of 4 main treatment levels were randomly applied to 24 main plots (1.8 × 1.8 m) arranged in a row. The main treatments were (1) root feeding by banded cucumber beetle larvae, (2) defoliation by *S. latifascia* larvae, (3) cage only control (no introduced insects), and (4) no cage control. Plots of the first 3 treatments were covered by saran cages (1.8 × 1.8 × 1.8 m) to confine the introduced insects and exclude other organisms. Within each main plot, 4 three-plant subplots (sweet potato genotypes) were randomly arranged in 2 rows with 0.3 m spacing within rows and 1.0 m spacing between rows. In 1997, 2 cultivars, "Beauregard" and "Excel," and 2 breeding lines, "W-250" and "W-244," (obtained from the soil insect resistance sweet potato breeding program of Janice R. Bohac, U.S. Vegetable Laboratory, USDA-ARS, 2875 Savannah Hwy., Charleston, SC) were used. Beauregard is susceptible to sweet potato weevil. The other genotypes have shown a slight to moderate level of resistance (Mao et al. 1998, 2000, Story et al. 1999a, b, c, Story et al. 2000). In 1998, the cultivar "Sumor" was used in place of W-250 because the sweet potato weevil resistance of W-250 was absent in the 1997 experiment. The resistance of Sumor was higher and more consistent than that of W-250 in field tests conducted during 1997 and 1998 (Mao et al. 1998, 2000, Story et al. 2000). Sweet potato slips were planted on 26 June 1997, and 17 July 1998, with different randomization plans for both main-plots and subplots. Banded cucumber

beetle adults or second and third instar *S. latifacia* larvae collected from nearby sweet potato fields were released into their designated cages. For the banded cucumber beetle treatment, 144 adults per cage were released in a 30-day period beginning at 40 days after transplant (DAT) in 1997; 96 adults per cage were released during the same period of time in 1998. For the *S. latifacia* treatment, 150 larvae were released into each cage at 40 DAT. Visual inspections were made twice a week to assess *S. latifacia* population development and determine whether to add or remove some of the larvae to reach a visual rating of 90% leaf area removal at harvest. Control plots received insecticide applications (permethrin, 48.3 g AI/ha, Ambush®, Zeneca Agricultural Products, Wilmington, DE) weekly to prevent any unwanted insect feeding. Storage roots were harvested by hand at 116 DAT in 1997 and at 111 DAT in 1998, then cured (30°C, 90% RH for 7 d) and stored at 15 ± 2°C until laboratory bioassays and chemical analysis.

Insect rearing. The sweet potato weevil colony was established in January of 1997 from field-collected infested storage roots (about 500 insects) and maintained in the laboratory on storage roots of Beauregard in plastic containers (5.6 L) with screen covers at 28 ± 2°C and 85 ± 10% RH. Voucher specimens were stored in the insect museum of the Entomology Department, Louisiana State University. In preparing experimental insects, 5 fresh storage roots (US #1 grade) were exposed to about 1000 unsexed adults for 5 d, then removed and the roots maintained under the conditions described above. Emerging adults were collected weekly and held with fresh storage roots. Female adults 3 to 4 wk old were used in the bioassays to ensure adequate egg-laying capability (Wilson et al. 1988).

Feeding and oviposition. The bioassay technique was an adaptation of one previously described by Mullen et al. (1980), and it has been used in several sweet potato weevil feeding and oviposition studies (Nottingham et al. 1987, Wilson et al. 1988). This technique consisted of a 24-well tissue culture plate (12.5 × 8.5 × 2.0 cm; Falcon® model 3047, Becton Dickenson and Co., Lincoln Park, NJ) placed in a rectangular clear plastic container (17 × 12 × 6 cm; Tri-State Plastic, Dixon, KY). Cores were cut from storage roots harvested from the field plots with a cork borer (1.6 cm diam) and inserted into the wells so that only the surface of the periderm was exposed. The diameters of the cores were the same diameter as the wells, providing a close fit. Female adults were kept without food for 3 h before being introduced into the arena at the rate of 2 weevils per root core. A moist cotton ball was placed in the container to maintain 90 to 100% RH and prevent desiccation of the root cores. After 24 h, the number of feeding punctures on each core was recorded, and after 48 h, the number of eggs was counted. One root core from one genotype was presented to the weevils in no-choice tests. Choice tests were conducted by presenting 16 root cores cut from one root of each treatment combination. The 16 cores were randomly arranged on the plate. Unoccupied wells were left open. Tests were repeated 4 times for each field plot using a different storage root from that plot each time for both no-choice and choice tests. Some of the field plots were not tested because of lack of storage roots. For the banded cucumber beetle treatment, roots with feeding damage holes (range from 1 to 10 holes) were used. All tests were conducted at 28 ± 2°C, 85 ± 10% RH under total darkness to eliminate light as a variable.

Larval survival and development bioassay. Sweet potato weevils were reared individually in Petri dishes (60 × 15 mm) by transferring a single egg into a root section (about 1.5 × 1.5 × 1.5 cm) with a small cavity (1 to 2 mm deep, 4.0 mm diam, cut with a No. 1 cork borer) for its reception. The cavity penetrated the periderm (skin) of the

root, but not the cortex layer which is 5 to 7 mm wide. The depth of the cavity was selected so as to simulate the natural depth of egg placement by weevils. Eggs were obtained by exposing Beauregard storage roots to about 500 females (3 to 4 wk old) for 24 h. A needle-nosed forceps was used to transfer eggs. At 12 d after egg deposition, root sections were examined to determine if eggs had hatched. Nonviable eggs or rotten root sections were discarded. At 25 d after oviposition, root sections were dissected for pupae. Larval survival and pupal weight were recorded. Two replications of each treatment combinations were conducted with sample sizes ranging from 19 to 32 eggs each because of egg mortality. Bioassays were conducted under conditions of 28 ± 2°C and 85 ± 10% RH with total darkness.

Chemical analysis. The chemical analysis was conducted in the USDA Vegetable Laboratory, Charleston, SC. Roots were carefully washed under flowing water and dried. Periderm tissue was gently scraped off with a scalpel, dried at 50°C, and ground to a fine powder using a mortar and pestle while covered with liquid nitrogen. Subsequently the powder was re-dried at 40°C and stored in vials under nitrogen at −20°C until analysis. Powder samples were weighed (200 mg) into Teflon-lined, screw-capped test tubes and 2.0 ml of methanol was added containing 0.08 mg of chrysin (recrystallized from amyl alcohol), used as an internal standard. Test tubes were ultrasonicated for 20 min while the surrounding water was ice-cooled. The tubes were then centrifuged and the supernatant was filtered through Nylon-66 membrane filters (0.20 μm; Pierce Chemical Company, Rockville, IL) into auto injector vials. Resin glycoside and caffeic acid concentrations were analyzed by reversed phase HPLC using 20 μl of the solution. For resin glycoside, a H_2O/MeOH linear gradient from 60% to 100% MeOH in 15 min was used and held at 100% MeOH for 25 min; flow rate was 1 ml min^{-1} and detection was at 230 nm. For caffeic acid, a second injection of 20 μl was made, using the same sample as was used for the resin glycoside analysis. A H_2O/MeOH linear gradient from 10% to 100% MeOH in 35 min was used and held at 100% MeOH for 25 min; flow rate was 1 ml min^{-1} and detection was at 340 nm. Each solvent contained 0.1% H_3PO_4. The column was a Beckman Ultrasphere C_{18}, 5 μm (4.6 × 250 mm; Beckman and Coulter, Fullerton, CA). Purified reference substances were used as external standards to determine response factor versus chrysin for quantification. Reference glycoside material was purified using Sephadex column chromatography followed by semi-preparative HPLC as described previously (Peterson et al. 1998). Reference caffeic acid was purchased from Aldrich Chemical Company (Milwaukee, WI).

Data analysis. All data were analyzed using SAS mixed linear model analysis of variance (PROC MIXED) followed by Tukey's procedure for mean separation (SAS 1990). Contrast statements were used to test the cage effect. A square-root transformation was used for larval survival data. The significance level was $\alpha = 0.05$.

Results

Feeding and oviposition. In 1997, insect injury treatments did not have a significant effect on sweet potato weevil feeding and ovipostion in both choice tests (feeding punctures: $F = 0.33$; df = 3,16; $P = 0.8027$, eggs: $F = 2.64$; df = 3,16; $P = 0.0849$) and no-choice tests (feeding punctures: $F = 1.24$; df = 3,20; $P = 0.3215$, eggs: $F = 0.31$; df = 3,20; $P = 0.8193$). However, there was a tendency for more eggs to be deposited on insect-injured plants in the choice tests (Table 1). Genotype had a significant effect on the number of feeding punctures under both testing conditions (choice test: $F =$

Table 1. The effect of banded cucumber beetle and *S. latifascia* feeding injury to sweet potato plants on sweet potato weevil adult feeding and oviposition behavior on four sweet potato genotypes in 1997

Main effects	No-choice test		Choice test	
	No feeding punctures*	No. eggs*	No. feeding punctures*	No. eggs*
BCB**	22.6 ± 1.43a	8.8 ± 0.55a	24.8 ± 1.67a	8.9 ± 0.50a
SL**	19.7 ± 1.33a	8.5 ± 0.58a	25.2 ± 1.95a	9.1 ± 0.47a
Cage only	24.1 ± 1.06a	8.0 ± 0.33a	24.4 ± 1.48a	6.5 ± 0.37a
No cage	20.3 ± 1.44a	8.0 ± 0.52a	21.9 ± 1.33a	7.6 ± 0.53a
Beauregard	24.5 ± 1.32a	8.8 ± 0.49a	25.7 ± 1.39a	8.0 ± 0.50a
Excel	17.2 ± 0.93b	7.0 ± 0.50b	23.2 ± 1.49ab	7.8 ± 0.52a
W-244	19.6 ± 0.89b	8.6 ± 0.40ab	20.2 ± 1.16b	8.0 ± 0.48a
W-250	25.4 ± 1.45a	8.9 ± 0.54a	27.2 ± 1.99a	8.1 ± 0.59a

* Mean ± SEM. Means followed by the same letter are not significantly different ($P > 0.05$, Tukey).
** BCB = Banded cucumber beetle, *Diabrotica balteata;* SL = *Spodoptera latifascia.*

8.08; df = 3,48; $P = 0.0002$. no-choice test: $F = 20.85$; df = 3,60; $P < 0.0001$), but only had a significant effect on oviposition in no-choice tests (no-choice test: $F = 4.47$; df = 3,60; $P = 0.0067$. choice test: $F = 0.17$; df = 3,48; $P = 0.9179$). W-244 and Excel had fewer feeding punctures and eggs than Beauregard and W-250 (Table 1). Treatment by genotype interaction and cage effect was not significant ($P = 0.1078$ to 0.8677).

The same trend was present with the main treatment effects in 1998. Insect injury treatments did not significantly affect the number of feeding punctures in both choice and no-choice tests (choice test: $F = 0.51$; df = 3,16; $P = 0.6840$, no-choice test: $F = 0.13$; df = 3,16; $P = 0.9424$). However, insect injury significantly affected the number of eggs deposited in the choice tests ($F = 5.97$; df = 3,16; $P = 0.0062$), in which significantly more eggs were deposited in roots of plants fed upon by *S. latifascia* (Table 2). The effect was not significant in no-choice tests ($F = 1.70$; df = 3,16; $P = 0.2077$) although the same trend was present. The genotype effect was highly significant ($P < 0.0001$) for all categories, where Beauregard received more feeding punctures (choice test: $F = 71.44$; df = 3,4; $P < 0.0001$, no-choice test: $F = 54.17$; df = 3,48; $P < 0.0001$) and more eggs (choice test: $F = 23.59$; df = 3,48; $P < 0.0001$, no-choice test: $F = 43.14$; df = 3,48; $P < 0.0001$) than the other genotypes (Table 2). In contrast to 1997, the interaction between treatment and genotype was significant for oviposition in choice tests ($F = 3.78$; df = 9,48; $P = 0.0012$) and in no-choice tests ($F = 2.39$; df = 9,48; $P = 0.0249$) in 1998. No significant cage effects were detected ($P = 0.1040$ to 0.7310).

Larval survival and development. Insect injury treatments did not have a significant effect on sweet potato weevil larval survival (1997: $F = 0.88$; df = 3,4; $P = 0.5247$, 1998: $F = 0.02$; df = 3,4; $P = 0.9953$) and pupal weight (1997: $F = 3.37$; df = 3,4; $P = 0.1356$, 1998: $F = 0.01$; df = 3,4; $P = 0.9979$). The genotype effect was significant for larval survival (1997: $F = 10.55$; df = 3,12; $P = 0.0011$, 1998: $F = 12.29$; df = 3,12; $P = 0.0006$) with lower survival present for resistant genotypes (Excel, W-244 and Sumor) (Table 3). W-250 was not significantly different from Beauregard

Table 2. The effect of banded cucumber beetle and *S. latifascia* feeding injury to sweet potato plants on sweet potato weevil adult feeding and oviposition behavior on four sweet potato genotypes in 1998

Main effects	No-choice test		Choice test	
	No. feeding punctures*	No. eggs*	No. feeding punctures*	No. eggs*
BCB**	27.3 ± 2.00a	9.9 ± 0.48a	36.5 ± 2.54a	9.8 ± 0.33ab
SL**	28.7 ± 2.00a	10.5 ± 0.51a	35.9 ± 2.78a	10.6 ± 0.32a
Cage only	27.3 ± 1.97a	8.8 ± 0.54a	33.0 ± 2.61a	8.5 ± 0.58b
No cage	26.8 ± 1.87a	9.3 ± 0.74a	32.0 ± 3.37a	8.9 ± 0.55b
Beauregard	37.3 ± 1.51a	12.7 ± 0.54a	44.9 ± 2.17a	11.4 ± 0.32a
Excel	27.4 ± 1.44b	9.2 ± 0.38b	40.5 ± 2.31a	8.8 ± 0.43b
W-244	25.3 ± 1.32b	8.2 ± 0.39b	32.1 ± 1.60b	8.1 ± 0.48c
Sumor	20.2 ± 1.14c	8.3 ± 0.34b	19.9 ± 1.18c	9.5 ± 0.38b

* Mean ± SEM. Means followed by the same letter are not significantly different ($P > 0.05$, Tukey).
** BCB = Banded cucumber beetle, *Diabrotica balteata;* SL = *Spodoptera latifascia.*

Table 3. The effect of banded cucumber beetle and *S. latifascia* feeding injury to sweet potato plants on sweet potato weevil larval survival and pupal weight on four sweet potato genotypes in 1997 and 1998

Main effect	1997		1998	
	Larval survival* (%)	Pupal weight* (mg)	Larval survival* (%)	Pupal weight* (mg)
BCB**	91.7 ± 2.18a	7.78 ± 0.17a	93.9 ± 2.06a	7.45 ± 0.06a
SL**	92.5 ± 2.42a	7.23 ± 0.14a	93.5 ± 1.70a	7.43 ± 0.12a
Cage only	94.4 ± 1.31a	7.00 ± 0.18a	93.6 ± 1.76a	7.43 ± 0.15a
No cage	91.7 ± 1.67a	7.38 ± 0.17a	93.2 ± 1.49a	7.41 ± 0.11a
Beauregard	98.0 ± 0.87a	7.21 ± 0.10a	99.0 ± 0.64a	7.34 ± 0.12a
Excel	91.3 ± 1.56bc	7.59 ± 0.16a	9.28 ± 1.59b	7.38 ± 0.07a
W-244	87.2 ± 1.86c	7.48 ± 0.20a	90.2 ± 1.00b	7.48 ± 0.06a
W-250	93.8 ± 0.73ab	7.10 ± 0.24a	—	—
Sumor	—	—	92.2 ± 1.52b	7.54 ± 0.11a

* Mean ± SEM. Means followed by the same letter are not significantly different ($P > 0.05$, Tukey).
** BCB = Banded cucumber beetle, *Diabrotica balteata;* SL = *Spodoptera latifascia.*

(Table 3). No significant genotype effects were detected for pupal weight (1997: $F = 1.99$; df = 3,12; $P = 0.1698$, 1998: $F = 0.97$; df = 3,12; $P = 0.4384$). Treatment by genotype interaction was not significant for larval survival (1997: $F = 0.93$; df = 9,12; $P = 0.5354$, 1998: $F = 1.56$; df = 9,12; $P = 0.2320$) and pupal weight (1997: $F = 0.65$; df = 9,12; $P = 0.7372$, 1998: $F = 0.58$; df = 9,12; $P = 0.7919$). No significant cage effects were detected ()$P = 0.5119$ to 0.8945).

Resin glycoside and caffeic acid contents. In 1997, insect injury treatment

significantly affected the levels of resin glycoside ($F = 6.87$; df = 3,18; $P = 0.0028$) and caffeic acid ($F = 8.05$; df = 3,18; $P = 0.0013$). The *S. latifascia* treatment tends to have the higher level of resin glycoside and the banded cucumber beetle treatment tends to have the higher level of caffeic acid although the differences were not always significant (Table 4). A significant insect injury effect was not present in 1998 (resin glycoside: $F = 2.73$; df = 3,20; $P = 0.0709$, caffeic acid: $F = 1.68$; df = 3,20; $P = 0.2043$), but the trend was similar to that of 1997 (Table 4).

The levels of resin glycoside and caffeic acid were different among the tested sweet potato genotypes in 1997 (resin glycoside: $F = 61.82$; df = 3,29; $P < 0.0001$, caffeic acid: $F = 11.95$; df = 3,29; $P < 0.0001$) and in 1998 (resin glycoside: $F = 36.87$; df = 3,40; $P < 0.0001$, caffeic acid: $F = 30.92$; df = 3,40; $P < 0.0001$). Excel consistently had the highest resin glycoside content in both years, followed by Beauregard and W-244 in 1997, and by Beauregard, W-244, and Sumor in 1998. In 1997, W-250 had the highest level of caffeic acid followed by Beauregard and Excel. In 1998, Sumor had the highest level of caffeic acid followed by Beauregard and W-244 (Table 4).

Treatment by genotype interaction was significant with resin glycoside ($F = 3.60$; df = 9,29; $P = 0.0041$) in 1997, but not with caffeic acid ($F = 0.91$; df = 9,29; $P = 0.5327$). No interaction effects were significant in 1998 (resin glycoside: $F = 1.28$; df = 9,40; $P = 0.2782$, caffeic acid: $F = 1.04$; df = 9,40; $P = 0.4272$). The cage effect was significant with resin glycoside levels in 1997 ($F = 15.14$; df = 1,18; $P = 0.0011$), with caged plants having higher levels of resin glycoside than non-caged plants. The effect was not present in 1998 ($F = 0.13$; df = 1,20; $P = 0.7175$). The cage had no significant effect on caffeic acid (1997: $F = 2.49$; df = 1,18; $P = 0.1322$, 1998: $F = 2.00$; df = 1,20; $P = 0.1730$).

Discussion

Insect herbivory has the potential to induce changes in host plants that are either detrimental or beneficial to subsequent herbivores. Insect feeding or mechanical damage that induces plant resistance to insects has been documented in many insect-plant systems where insects were adversely affected (Karban and Myers 1989, Karban and Baldwin 1997). Rausher et al. (1993) reported that *Ipomoea purpurea* Roth, a close relative of sweet potato, had insect-induced resistance to both its generalist and specialist herbivores. In other cases, insect feeding or mechanical damage to plants has been found to improve the performance of herbivorous insects. Messina et al. (1993) reported that the Russian wheat aphid, *Diuraphis noxia* (Mordvilko), had lower mortality and a higher population growth rate on previously defoliated host plants. We found that root feeding and defoliation on sweet potato plants increased sweet potato weevil oviposition on storage roots by 10 to 25% in choice tests (although these differences were not always significant) but had no effect on adult feeding, larval survival, and pupal weight. These induced effects might vary among genotypes because the interaction effect of genotype by insect injury treatment on the number of eggs deposited was significant in 1998 (Table 2).

Induced effects on herbivorous insects can be explained by changes of plant chemistry (Smith 1988, Karban and Baldwin 1997). Sweet potato plants contain numerous secondary compounds that are produced either constitutively or upon induction by external agents (Kays 1992). Resin glycoside and caffeic acid are two compounds found in the periderm and cortex tissues of sweet potato storage roots that

Table 4 The effect of genotype and banded cucumber beetle and *S. latifascia* feeding injury on resin glycoside and caffeic acid contents in periderm tissues of sweet potato storage roots in 1997 and 1998

	1997		1998	
Main effect	Resin glycoside* (% DW)*	Caffeic acid* (% DW)**	Resin glycoside* (% DW)**	Caffeic acid* (% DW)**
BCB***	2.67 ± 0.417(17)a	0.44 ± 0.013(17)a	2.13 ± 0.218(17)a	0.49 ± 0.021(17)a
SL***	5.50 ± 1.181(10)a	0.35 ± 0.026(10)ab	3.02 ± 0.487(16)a	0.47 ± 0.032(16)a
Cage only	1.88 ± 0.371(15)b	0.40 ± 0.020(15)a	1.99 ± 0.120(20)a	0.43 ± 0.022(20)a
No cage	3.10 ± 0.516(21)a	0.34 ± 0.024(21)b	2.63 ± 0.275(23)a	0.42 ± 0.028(23)a
Beauregard	3.10 ± 0.462(16)b	0.40 ± 0.019(16)b	2.36 ± 0.220(22)b	0.44 ± 0.019(22)b
Excel	5.41 ± 0.602(19)a	0.35 ± 0.021(19)bc	4.32 ± 0.365(15)a	0.31 ± 0.016(15)c
W-244	2.55 ± 0.324(13)b	0.31 ± 0.024(13)c	1.88 ± 0.160(18)bc	0.44 ± 0.030(18)b
W-250	0.55 ± 0.104(15)c	0.46 ± 0.011(15)a	—	—
Sumor	—	—	1.63 ± 0.103(21)c	0.56 ± 0.010(21)a

* Mean ± SEM (n). Means followed by the same letter are not significantly different ($P > 0.05$, Tukey).

** DW = dry weight.

*** BCB = Banded cucumber beetle, *Diabrotica balteata;* SL = *Spodoptera latifascia.*

possess antibiotic qualities (Peterson and Harrison 1992, Johnson and Felton 1996, Peterson et al. 1998). Jackson and Peterson (2000) reported that sweet potato resin glycoside is toxic to first and second instars of *Plutella xylostella* L. and has sublethal effects that slow larval development and reduce pupal weight and lifetime fecundity. Summers and Felton (1994) reported that caffeic acid had adverse effects on *Helicoverpa zea* (Boddie), a generalist herbivore. Therefore, there is a possibility that these two compounds may play a role in sweet potato weevil resistance in the form of an antibiotic effect on larvae. The effect of resin glycoside and caffeic acid on the sweet potato weevil has not been investigated. Son et al. (1991) reported that the level of caffeic acid did not appear to be correlated to sweet potato weevil resistance using resistant genotypes identified in field tests. Our results show that the concentration of resin glycoside and caffeic acid in the periderm differed among genotypes, but there was no evidence of any relationship with sweet potato weevil feeding, oviposition, larval survival, and pupal weight. The levels of sweet potato resin glycoside and caffeic acid have been shown to increase under certain stresses, such as insect feeding or attack by microorganisms (Uritani 1953, Peterson and Harrison 1992). We observed that higher levels of resin glycoside were associated with defoliation, and higher levels of caffeic acid were associated with root feeding (these differences were not always significant). The effects of insect feeding on resin glycoside levels would likely differ among genotypes since the interaction effect was significant in 1997. The significant cage effect on resin glycoside in 1997 suggests that the concentration of the compound might be influenced by the environment.

The periderm tissue of sweet potato storage roots also contains boehmeryl acetate, which has been identified as a sweet potato weevil oviposition stimulant (Wilson et al. 1991). In our study, the slightly higher number of eggs found on sweet potatoes in insect injury treatments suggests that herbivory by other insects during the growing season may trigger changes in storage roots that increase the oviposition stimulants in amount, efficiency, or both, or decrease the effect of unidentified deterrent(s). However, boehmeryl acetate levels were not measured in this study. Higher number of weevil eggs in banded cucumber beetle treatments may be caused by root feeding, which can cause water stress that may enhance plant suitability to herbivorous insects (White 1984, Gange and Brown 1989). Further studies are needed before any conclusion can be made.

The sweet potato weevil resistant and susceptible genotypes used in this study were identified in earlier studies (Ratnayake 1995, Mao et al. 1998, 2000, Story et al. 1996, Story et al. 1999a, b). Excel (W-221) and Sumor (W-201) possess multiple resistances to insects and plant diseases (Dukes et al. 1987, Jones et al. 1989). W-244 and W-250 are breeding lines selected for multiple pest resistance combined with good horticultural traits (Janis Bohac, U.S. Vegetable Laboratory, USDA-ARS, Charleston, SC, pers. comm.). The presence of sweet potato weevil resistance in Excel, Sumor, W-244, and W-250 was shown over a 3-yr period in both field and laboratory studies (Mao et al. 1998, 2000, Story et al. 1996, 1999a, b, c.). The performance of these lines varied from year to year, with Sumor being the most consistent of all genotypes through all 3 yrs (range of 47 to 100% reduction in damage compared to Beauregard). Ratnayake (1995) categorized W-250 as moderately resistant to sweet potato weevil. Story et al. (1999a) also showed that this genotype supported lower number of sweet potato weevils, but in subsequent tests its performance was marginal. We failed to find any reduction in adult feeding, oviposition, larval survival, and pupal weight with this genotype in 1997, indicating that sweet

potato weevil resistance in W-250 is highly variable. Sumor, Excel, and W-244 had significantly lower feeding and oviposition when compared to Beauregard in 1998, but not in 1997, suggesting that the expression of resistance (antixenosis) is also variable in these genotypes. Sumor, Excel, and W-244 had significantly lower larval survival (5 to 10% reduction) in both years, indicating the presence of antibiosis resistance.

Acknowledgments

We thank Janice Bohac for letting us use W-244 and W-250 sweet potato breeding lines and Jeff Murray and Aboubacar Diagne for their assistance in conducting the study. We also thank Michael J. Stout, Arthur Q. Villordon, and Rich Goyer for their comments on the manuscript. Approved for publication by the Director of the Louisiana Agricultural Experiment Station as manuscript number 02-17-0007.

References Cited

Chalfant, R. B., R. K. Jansson, D. R. Seal and J. M. Schalk. 1990. Ecology and management of sweet potato insects. Annu. Rev. Entomol. 35: 157-180.

Collins, W. W., A. Jones, M. A. Mullen, N. S. Talekar and F. W. Martin. 1991. Breeding sweet potato for insect resistance: A global overview, Pp. 379-397. *In* R. K. Jansson and K. V. Raman [Eds.], Sweet potato pest management: a global perspective. Westview Press, Inc. Boulder, CO.

Dukes, P. D., M. G. Hamilton, A. Jones and J. M. Schalk. 1987. "Sumor"—a multiple-use sweet potato. HortScience 22: 170-171.

Faeth, S. H. 1992. Do defoliation and subsequent phytochemical responses reduce future herbivory on oak trees? J. Chem. Ecol. 18: 915-925.

Gange, A. C. and V. K. Brown. 1989. Effects of root herbivory by an insect on a foliar-feeding species, mediated through changes in the host plant. Oecologia 81: 38-42.

Inbar, M., H. Doostdar and R. T. Mayer. 1999. Effects of sessile whitefly nymphs (Homoptera: Aleyrodidae) on leaf-chewing larvae (Lepidoptera: Noctuidae). Environ. Entomol. 28: 353-357.

Jackson, D. M. and J. K. Peterson. 2000. Sublethal effects of resin glycosides from the periderm of sweet potato storage roots on *Plutella xylostella* (Lepidoptera: Plutellidae). J. Econ. Entomol. 93: 388-393.

Johnson, K. S. and G. W. Felton. 1996. Physiological and dietary influences on midgut redox conditions in generalist lepidopteran larvae. J. Insect Physiol. 42: 191-198.

Jones, A., P. D. Dukes and J. M. Schalk. 1989. "Excel" sweet potato. HortScience 24: 171-172.

Karban, R. and I. T. Baldwin. 1997. Induced resistance against herbivores, Pp. 104-166. *In* R. Karban and I. T. Baldwin, Induced responses to herbivory. The University of Chicago Press, Chicago, IL.

Karban, R. and J. H. Myers. 1989. Induced plant responses to herbivory. Annu. Rev. Eco. Systm. 20: 331-348.

Kays, S. J. 1992. The chemical composition of the sweet potato, Pp. 201-262. *In* W. A. Hill, C. K. Bonsi and P. A. Loretan [Eds.], Sweet potato Technology for the 21st Century. Tuskegee Univ., Tuskegee, AL.

Levy, R. and D. H. Habeck. 1976. Descriptions of the larvea of *Spodoptera sunia* and *S. latifascia* with a key to the mature *Spodoptera* larvae of the Eastern United States (Lepidoptera: Noctuidae). Annu. Entomol. Soc. Am. 69: 585-588.

Mao, L., R. N. Story, A. M. Hammond and D. R. LaBonte. 1998. Evaluation of sweet potato cultivars for resistance to sweet potato weevil, 1997. Arthropod Management Tests 23: 384.

2000. Evaluation of sweet potato cultivars for resistance to sweet potato weevil, 1999. Arthropod Management Tests 25: 429-430.

Messina, F. J., T. A. Jones and D. C. Nielson. 1993. Performance of the Russian wheat aphid (Homoptera: Aphididae) on perennial range grasses: effects of previous defoliation. Environ. Entomol. 22: 1349-1354.

Mullen, M. A., A. Jones, R. Davis and G. C. Pearman. 1980. Rapid selection of sweet potato lines resistant to the sweet potato weevil. HortScience 15: 70-71.

Nottingham, S. F., D. D. Wilson, R. F. Severson and S. J. Kays. 1987. Feeding and oviposition preferences of the sweet potato weevil, *Cylas formicarius elegantulus,* on the outer periderm and exposed inner core of storage roots of selected sweet potato cultivars. Entomol. Exp. Appl. 45: 271-275.

Olson, M. M. and C. R. Roseland. 1991. Induction of the coumarius scopoletin and ayapon in sunflower by insect-feeding stress and effects of coumarins on the feeding of sunflower beetle (Coleoptera: Chrysomelidae). Environ. Entomol. 20: 1166-1172.

Peterson J. K. and H. F. Harrison, Jr. 1992. Chemical factors involved in sweet potato pest resistance and allelopathy, Pp. 263-272. *In* W. A. Hill, C. K. Bonsi and P. A. Loretan [Eds.], Sweet potato technology for the 21st century. Tuskegee Univ., Tuskegee, AL.

Peterson J. K., H. F. Harrison, Jr., and A. E. Muckenfuss. 1998. Sweet potato [*Ipomoea batatas* (L.)] resin glycosides: evidence of antibiosis effects in the diamondback moth *Plutella xylostella* L. (Lepidoptera: Plutellidae). Allelopathy J. 5: 43-52.

Raupp, M. J. and R. F. Denno. 1984. The suitability of damaged willow leaves as food for the leaf beetle, *Plagiodera versicolora.* Ecol. Entomol. 9: 443-448.

Rausher, M. D., K. Iwao, E. L. Simms, N. Ohsadi and D. Hall. 1993. Induced resistance in *Ipomoea purpurea.* Ecology 74: 20-29.

Ratnayake, B. M. 1995. Determination of categories of host plant resistance to the sweet potato weevil, *Cylas formicarius elegantulus,* in various genotypes of sweet potato (*Ipomoea batatas*). MS Thesis, Mississippi State Univ., Mississippi State, MS.

SAS Institute. 1990. SAS/STAT user's guide, release 6.12. SAS Institute, Cary, NC.

Schalk, J. M., A. Jones, P. D. Dukes and J. K. Peterson. 1991. Approaches to the control of multiple insect problems in sweet potato in the Southern United States, Pp. 283-302. *In* R. K. Jansson and K. V. Raman [Eds.], Sweet potato pest management: a global perspective. Westview Press, Inc., Boulder, CO.

Smith, C. M. 1988. Effects of mechanical damage to plants on insect populations, Pp. 321-340. *In* E. A. Heinrich (Ed.), Plant stress-insect interactions. John Wiley & Sons, New York, NY.

Son, K. -C., R. F. Severson, M. E. Snook and S. J. Kays. 1991. Root carbohydrate, organic acids, and phenolic chemistry in relation to sweet potato weevil resistance. HortScience 26: 1305-1308.

Story, R. N., A. M. Hammond, J. Murray, L. H. Rolston and D. LaBonte. 1996. Selection for host plant resistance in sweet potatoes to the sweet potato weevil, 1995, Pp. 71-79. *In* Sweet potato Research 1996. Louisiana Agricultural Experiment Station Mimeo Series No. 117.

Story, R. N., A. M. Hammond, D. LaBonte, P. Thompson and J. Bohac. 1999a. Evaluation of sweet potato germplasm for resistance to sweet potato weevil, 1996. Arthropod Management Tests 24: 436-437.

1999b. Evaluation of sweet potato germplasm for resistance to sweet potato weevil, 1997. Arthropod Management Tests 24: 437-438.

1999c. Evaluation of sweet potato germplasm for resistance to sweet potato weevil, 1998. Arthropod Management Tests 24: 438-439.

Story, R. N., A. M. Hammond and M. J. Murray. 2000. Evaluation of sweet potato germplasm for resistance to sweet potato weevil, 1999. Arthropod Management Tests 25: 430-432.

Summers, C. B. and G. W. Felton. 1994. Prooxidant effects of phenolic acids on the generalist herbivore *Helicoverpa zea* (Lepidoptera: Noctuidae): potential mode of action of phenolic compounds in plant anti-herbivore chemistry. Insect Biochem. Molec. Biol. 24: 943-953.

Talekar, N. S. 1987. Feasibility of the use of resistant cultivar in sweet potato weevil control. Insect Sci. Applic. 8: 815-817.

1992. Insect factors in breeding and cultivation of sweet potato, Pp. 143-154. *In* W. A. Hill, C. K. Bonsi and P. A. Loretan [Eds.], Sweet potato technology for the 21st century. Tuskegee Univ., Tuskegee, AL.

Uritani, I. 1953. Phytopathological chemistry of black-rotted sweet potato. Part 7. Isolation and identification of polyphenols from the injured sweet potato. Nippon Nougeikagaku Kaishi 27: 29-33.

White, T. C. R. 1984 The abundance of invertebrate herbivores in relation to the availability of nitrogen in stressed food plants. Oecologia 63: 90-105.

Williams, K. S. and J. H. Myers. 1984. Previous herbivore attack of red alder may improve food quality for fall webworm larvae. Oecologia 63: 166-170.

Wilson, D. D., R. F. Severson, K. -C. Son and S. J. Kays. 1988. Oviposition stimulant in sweet potato periderm for the sweet potato weevil, *Cylas formicarius elegantulus.* Environ. Entomol. 17: 691-693.

Wilson, D. D., R. F. Severson and S. J. Kays. 1991. Oviposition stimulant for *Cylas formicarius* in sweet potato: isolation, identification, and development of analytical screening method, Pp. 221-234. *In* R. K. Jansson and K. V. Raman [Eds.], Sweet potato pest management: a global perspective. Westview Press, Inc., Boulder, CO.