EFFECT OF SWEETPOTATO GENOTYPE, STORAGE TIME AND PRODUCTION SITE ON FEEDING AND OVIPOSITION BEHAVIOR OF THE SWEETPOTATO WEEVIL, *CYLAS FORMICARIUS* (COLEOPTERA: APOINIDAE)

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ABSTRACT

The effect of sweetpotato genotype, storage time and production site on *Cylas formicarius* (Fab.) feeding and oviposition was investigated. Sweetpotato genotype had a significant effect on feeding and oviposition rates in both no-choice and choice arenas. Beauregard and Centennial were uniformly susceptible across all age groups. W-250 had the least number of feeding punctures and eggs at 7 and 25 days after harvest. At 85 days after harvest, W-244 had the least number of feeding punctures and eggs, while W-250 was not significantly different from Beauregard and Centennial. Roots of the same genotype grown in different locations differed in the number of feeding punctures and eggs. These results suggest that antixenosis is responsible for at least part of the sweetpotato weevil resistance. Storage time and production sites appeared to affect the expression of the resistance, but the outcomes depended on the genotypes.

Key Words: host plant resistance, antixenosis, storage time, production site

RESUMEN

Fue investigado el efecto de genotipo del camote, la duración de almacenamiento y el lugar de producción sobre la alimentación y oviposición de *Cylas formicarius* (Fab.). El genotipo del camote tuvo un efecto significativo sobre la alimentación y velocidad de oviposición dadas las opciones de raíz y no raíz. Beauregard y Centennial fueron igualmente susceptibles entre los genotipos evaluados. W-250 tuvo un menor numero de agujeros y huevos a 7 y 25 días después del cosechado. A 85 días después de cosechado, W-244 tuvo menos agujeros y huevos, mientras que W-250 no tuvo diferencias significativas con Beauregard y Centennial. Raíces del mismo genotipo sembradas en diferentes localidades tuvieron diferente numero de agujeros y huevos. Los resultados sugieren que antixenosis es responsable al menos en parte por la resistencia del picudo del camote. La resistencia al picudo del camote parece ser afectada por el tiempo de almacenaje y las localidades de producción, pero los resultados finales dependen mas en los genotipos.

Sweetpotato weevil (SPW), *Cylas formicarius* (Fab.), is a major constraint to sweetpotato [*Ipomoea batatas* (L.) Lam.] production worldwide (Chalfant et al. 1990; Jansson & Raman 1991). It attacks sweetpotato both in the field and during storage. Adults make feeding and oviposition punctures on the root surface that can reduce root quality and market value. Larval tunneling in roots induces terpenoid production that renders even slightly damaged roots unfit for human and animal consumption (Cockerham et al. 1954; Uritani et al. 1975). Due to the concealed nature of the feeding habit, control of SPW is difficult. The use of resistant sweetpotato cultivars is a potentially viable option that could be an economical component in the integrated management of SPW (Martin & Jones 1986; Collins et al. 1991).

Many studies have been conducted on SPW resistance in sweetpotato indicating variable resistance in the field (Rolston et al. 1979; Mullen et al. 1980b, 1981, 1982, 1985; Taleker 1987b) and laboratory (Mullen et al. 1980a; Barlow & Rolston 1981; Nottingham et al. 1987, 1989; Ratnayake 1995; Story et al. 1996, 1999a, b, c). However, little success has been realized in the development of resistant cultivars, partly because of inconsistencies in the performance of selected breeding lines (Talekar 1987a, b) and a lack of understanding of the resistance mechanisms.

The expression of insect resistance can be influenced by many environmental factors (Smith 1989). Identification of these factors would help to explain the inconsistent performance of resistant genotypes. Such information would also be useful in facilitating the development of resistant cultivars and understanding the underlying mechanisms of resistance. In temperate growing areas like the United States, storage roots are cured by

keeping them in a specially designed facility maintained at about 30°C and 85% to 90% RH for 4 to 7 days. Cured roots are often evaluated over a period of several months in sweetpotato breeding programs. Thus curing and storage time may affect the outcome of SPW resistance evaluations because physical and chemical changes occur in the roots (Bouwkamp 1985). In addition, sweetpotato is grown throughout a wide geographic range. Wide variations in SPW resistance between production sites have been observed in field plots (Talekar 1987b). However, until this study, no comparative study has been done under controlled laboratory conditions to determine the effect of storage and production site on SPW feeding and oviposition. We evaluated 4 sweetpotato genotypes ("Beauregard", "Centennial", "W-244", and "W-250") to determine the effects of storage and production site on SPW feeding and oviposition.

Materials and Methods

Insect rearing

A SPW colony was established from a field collected population (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. In preparing experimental insects, 5 fresh storage roots (US #1) were exposed to about 1000 adults (male and female) for 5 days, then were removed and kept under the conditions described above. Emerging adults (male and female) were collected weekly and held with fresh storage roots. Female adults 3-4 weeks old were used in the bioassays to ensure adequate egg-laying capability (Wilson et al. 1988).

Bioassay

The assay technique was an adaptation of one previously described by Mullen et al. (1980a) and has been used in several SPW feeding and oviposition studies (Nottingham et al. 1987; Wilson et al. 1988). It consisted of a 24-well tissue culture plate (12.5 × 8.5 × 2.0 cm; Falcon®) placed in a rectangular clear plastic container (17 × 12 × 6 cm). Cores were cut from selected roots with a cork borer (1.6 cm diameter) and inserted into the wells so that only the surface of the root periderm was exposed. The cores had the same diameter as the wells, providing a close fit. Female adults were kept without food for 3 hours 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 90-100% RH and prevent desiccation of the root cores. After 24 hours the number of feeding punctures on each core was recorded, and after 48 hours the number of eggs was counted. All tests were conducted at 28 ± 5°C, 85 ± 10% RH under total darkness to eliminate light as a variable. Cores from only one genotype were presented to the weevils in no-choice tests. In choice tests, one core from each genotype was randomly arranged on the plate and presented to the insects.

Four sweetpotato genotypes were chosen according to their performance in no-choice whole-root laboratory evaluations (Story et al. 1996). W-244 and W-250 were breeding lines shown to be resistant to SPW. Beauregard and Centennial were two susceptible cultivars. To determine the effect of curing and storage time, bioassays were conducted with roots of the following groups: non-cured 7 days after harvest (DAH), cured 25 DAH, and cured 85 DAH. Storage roots were produced using standard practices at Burden Research Plantation, Baton Rouge, Louisiana. Slips were planted on July 5, 1996 with 0.3 m spacing in 20-plant plots with rows separated by 1.2 m. Storage roots were harvested on November 1, 1996, cured (30°C, 90% RH for 7 days), and stored at 15 ± 2°C. At each test date, both no-choice and choice tests were conducted with complete randomized experimental designs and 8 replications (8 US#1 roots for each genotype).

Three sweetpotato growing regions were chosen to evaluate the effect of production site on the expression of SPW resistance. They were Baton Rouge, Louisiana (LA), Edisto, South Carolina (SC), and Pontotoc, Mississippi (MS). Storage roots were produced at each site using similar production practices. Non-cured 7 DAH roots of all 4 genotypes from LA and MS and cured 25 DAH roots of 3 genotypes (Beauregard, Centennial and W-250) from LA and SC were used. No-choice tests were conducted with 8 replications.

Data Analysis

All data (average number of feeding punctures or number of eggs per root core) were analyzed with the PC SAS General Linear Model (GLM) procedure (SAS Version 6.12 1990), followed by Tukey multiple range tests for mean separations. The effect of storage time was tested as a fixed block effect by pooling data from all 3 age groups. Curing effect was tested using a contrast statement. Production site effect was analyzed as a fixed block effect in a randomized complete block design. In all tests the significance level was $\alpha = 0.05$.

Results

Genotype, Curing and Storage Time Effects

Significant differences in both choice and no-choice tests in feeding and oviposition were found among the 4 genotypes. In both no-choice and choice tests, W-250 had the lowest number of feeding punctures and eggs at 7 and 25 DAH (Table 1). At 85 DAH, W-244 had the least numbers of feed-

TABLE 1. EFFECT OF GENOTYPE AND STORAGE TIME (DAH = DAYS AFTER HARVEST) ON THE NUMBER OF FEEDING PUNCTURES AND THE NUMBER OF EGGS OF SWEETPOTATO WEEVIL UNDER NO-CHOICE AND CHOICE TEST CONDITIONS.

	No-choice test		Choice test	
Genotype	Feeding puncture[1]	Eggs[1]	Feeding puncture[1]	Eggs[1]
		Non-cured 7 DAH roots		
Beauregard	17.8 b	9.8 b	15.8 b	7.6 a
Centennial	23.1 a	12.4 a	21.8 a	8.9 a
W-250	9.0 c	5.7 c	3.4 d	2.0 c
W-244	20.9 ab	9.0 b	9.7 c	3.9 b
		Cured 25 DAH roots		
Beauregard	19.2 a	7.7 a	14.5 a	5.5 a
Centennial	20.4 a	7.6 a	18.3 a	6.6 a
W-250	11.9 b	4.0 c	4.7 b	1.8 b
W-244	17.4 a	6.2 b	13.5 a	6.3 a
		Cured 85 DAH roots		
Beauregard	23.3 a	10.5 a	20.1 a	7.0 a
Centennial	24.5 a	12.8 a	18.9 a	7.1 a
W-250	19.6 a	11.1 a	13.6 a	5.6 a
W-244	10.0 b	5.6 b	4.5 b	2.7 b

[1]Means followed by the same letter within a column of each storage time category are not significantly different ($p > 0.05$, Tukey).

ing punctures and eggs while W-250 was not significantly different from Beauregard and Centennial (Table 1). The curing process did not have a significant effect on feeding and oviposition in both choice and no-choice tests. Storage time had a significant effect on the number of eggs deposited in no-choice tests ($F = 61.52$, $df = 2,84$, $P = .0001$), but not in choice tests. Storage time did not have an effect on feeding punctures. Cultivar and storage time interaction effect was significant in all cases. W-250 had some resistance relative to the susceptible cultivars when the roots were non-cured 7 DAH and cured 25 DAH, but the resistance factors were diminished in cured 85 DAH roots (Table 1). The opposite trend was found with W-244, in which significant differences in the number of punctures and eggs were detected only with cured 85 DAH roots when they were compared with the susceptible cultivars. Beauregard and Centennial were uniformly susceptible across the three root age groups.

Production Site Effects

Non-Cured Roots. A significant production site effect was found for the number of feeding punctures ($F = 5.72$, $df = 1,56$, $P = 0.0202$) on the non-cured roots from Louisiana and Mississippi where Mississippi roots received higher number of feeding punctures than Louisiana roots (Table 2). However, the number of eggs deposited was not significantly different ($F = 0.05$, $df = 1,56$, $P = 0.8915$). The interaction effect of genotype and production site was highly significant for both feeding and oviposition ($F = 4.63$, $df = 3,56$, $P = 0.0058$, $F = 6.33$, $df = 3,56$, $P = 0.0009$, respectively), indicating that the feeding and oviposition rates among the 4 genotypes were different

TABLE 2. EFFECT OF GENOTYPE AND PRODUCTION SITE (LOUISIANA, MISSISSIPPI) ON THE NUMBER OF FEEDING PUNCTURES AND EGGS OF SWEETPOTATO WEEVIL ON NON-CURED ROOTS UNDER NO-CHOICE TEST CONDITIONS.[1]

	Feeding puncture[2]		Eggs[2]	
Genotype	Louisiana	Mississippi	Louisiana	Mississippi
Beauregard	15.8 b	24.3 a	7.6 a	8.5 a
Centennial	21.8 a	16.9 b	8.9 a	6.0 b
W-250	3.4 d	9.5 c	2.0 c	4.4 b
W-244	9.7 c	11.2 c	3.9 b	3.9 b

[1]The tests were conducted using non-cured roots 7 days after harvest.
[2]Means followed by the same letter within production site are not significantly different ($p > 0.05$, Tukey).

between these two sites (Table 2). For Louisiana grown roots, all 4 genotypes were significantly different from each other in number of feeding punctures, while no significant difference was found between Beauregard and Centennial in the number of eggs laid. Centennial had the most feeding punctures and eggs. For Mississippi grown roots, significant differences were found between the two susceptible cultivars in both number of feeding punctures and eggs. Significant differences were not found between W-244 and W-250 but they were different from susceptible cultivars. Beauregard was the preferred genotype for both feeding and oviposition.

Cured Roots. A significant production site effect was found between the number of eggs deposited ($F = 4.38$, $df = 1,42$, $P = 0.0424$) in Louisiana and South Carolina cured roots where South Carolina roots had higher number of eggs (Table 3). The number of feeding punctures was not significantly affected by production site ($F = 1.90$, $df = 1,42$, $P = 0.1723$). Although no statistically significant production site and genotype interaction effects were found, there was a trend toward different performance of W-250 from these two locations. Roots grown in Louisiana had significantly fewer punctures and eggs for W-250 when compared to Beauregard and Centennial. However, no differences were detected among the 3 genotypes grown in South Carolina.

Discussion

Plant resistance to insects may be due to antibiosis, antixenosis (nonpreference), tolerance, or escape. All these types have been reported in sweetpotato resistance to SPW (Waddill & Conover 1978; Barlow & Rolston 1981; Mullen et al. 1981; Talekar 1987b; Ratnayake 1995). This study evaluated antixenosis effects (plants lack the characteristics that attract insects and are avoided by insects) on feeding and oviposition by female adult of SPW. We found that Beauregard and Centennial were preferred by SPW with respect to both feeding and oviposition. These results are consistent with previous reports that have shown the susceptibility of Beauregard (Ratnayake 1995; Story et al. 1996) and Centennial (Mullen et al. 1980b; Nottingham et al. 1989; Rolston et al. 1979) in both field and laboratory tests. W-244 and W-250 are two breeding lines with resistance to SPW (Ratnayake 1995; Story et al. 1999a). The lower numbers of feeding punctures and eggs on the roots of these two lines suggests that antixenosis was responsible for at least part of SPW resistance and that the resistant factor(s) may have a broad spectrum. Talekar (1987a) argued against the feasibility of nonpreference in sweetpotato. He pointed out that it had little value because weevils lack choices among sweetpotato genotypes in commercial plantings. We found that SPW exhibited feeding and oviposition differences among sweetpotato genotypes under no-choice conditions, suggesting the possibility of utilizing antixenosis in SPW management.

No-choice and choice are the two experimental settings for evaluating plant resistance to insects. Sometimes, results from these two kinds of tests appear to be contradictory. Resistant genotypes identified under choice conditions can receive more feeding damage than susceptible genotypes when insects are forced to feed on only one genotype (Tingey 1986). Usually, under choice conditions, susceptible plants receive higher levels of damage than resistant plants when compared to the results of no-choice conditions. This results in a larger variance among genotypes under the choice conditions. We found no significant differences in number of feeding punctures ($F_s = 1.2513$, $df_1 = df_2 = 95$, $P = 0.13818$) and eggs ($F_s = 1.2781$, $df_1 = df_2 = 95$, $P = 0.11679$) between choice and no-choice tests when testing for equal variance as described by Sokal and Rohlf (1981).

Curing and storage are common postharvest procedures for sweetpotato in temperate growing areas. During these processes many physical and chemical changes may occur in the roots. For example, curing promotes wound periderm formation on injured surfaces, thus reducing decay and water loss (Bouwkamp 1985). Storage has been reported to induce changes in carbohydrate composition, enzyme activities and cell wall components (Takahata et al. 1995; Walter & Palma 1996). Our study shows that curing had no effect

Table 3. Effect of genotype and production site (Louisiana, South Carolina) on the number of feeding punctures and eggs of sweetpotato weevil on cured roots under no-choice test conditions.[1]

	Feeding puncture[2]		Eggs[2]	
Genotype	Louisiana	South Carolina	Louisiana	South Carolina
Beauregard	14.5 a	15.5 a	5.5 a	6.1 a
Centennial	16.3 a	14.2 a	6.6 a	6.8 a
W-250	4.7 c	13.1 a	1.8 b	5.7 a

[1]The tests were conducted using cured roots 25 days after harvest.
[2]Means followed by the same letter within production site are not significantly different ($p > 0.05$, Tukey).

on SPW feeding and oviposition behaviors. However, as storage time lengthened, SPW feeding and oviposition rates changed among genotypes. This suggests that storage time may influence the expression of SPW resistance, but the effect differs with each genotype.

The importance of environmental factors in the expression of SPW resistance has been noted by Talekar (1987 b). Our study also had some significant production site effects and the interactions of genotype and production site on SPW feeding and oviposition. Previous studies have related SPW resistance to the presence and concentration of a pentacyclic triterpene, boehmeryl acetate, in the periderm tissues of sweetpotato roots. This chemical has been identified as a SPW oviposition stimulant (Son 1989; Wilson et al. 1989). Our study suggests the possibility of the presence of deterrent(s) or repellent(s) in the resistant genotypes or a reduction of boehmeryl acetate. Environmental factors very likely influence such phytochemicals and hence alter the level of resistance.

In conclusion, SPW exhibited different feeding and oviposition preferences among sweetpotato genotypes. Curing, storage time, and production site influenced SPW feeding and oviposition behavior. When screening for SPW resistance, all conditions associated with testing materials (storage roots) and environmental conditions should be kept as consistent as possible. Potentially resistant lines should be evaluated under multiple sets of environmental conditions over a period of several years.

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