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EVALUATION OF RICE CULTIVARS FOR ANTIBIOSIS AND TOLERANCE RESISTANCE TO FALL ARMYWORM (LEPIDOPTERA: NOCTUIDAE)

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ABSTRACT

The effects of antibiosis on the growth of fall armyworm (FAW), *Spodoptera frugiperda* (J. E. Smith), larvae by rice, *Oryza sativa* L., seedlings at different plant stages and the tolerance of seedlings to artificial defoliation at the 7-leaf stage were evaluated in five plant introductions (PI) and the check cultivar 'Mars'. FAW larvae fed 5-leaf stage foliage had significantly lower larval, pupal, and adult weights than larvae fed 3-leaf stage foliage. The effects of antibiosis on the growth of FAW were evident in PIs 160842, 160827, 346833, and 346839, but not in PI 160823 or Mars. PIs 160842, 160827, and 160823 exhibited higher tolerance in plant regrowth after defoliation than PI 346833, 346839, or Mars. PIs 160842 and 160827 exhibited both the antibiosis and tolerance resistance.

RESUMEN

Se evaluó en cinco plantas introducidas (PI) y en la variedad testigo 'Mars', el efecto de antibiosis en el crecimiento de larvas del gusano cogollero, *Spodoptera frugiperda* (J. E. Smith), en plantas de semillero de diferentes etapas de crecimiento del arroz, *Oriza sativa* L., y de la tolerancia de las plantas a la defoliación artificial en la etapa de 7-hojas. Larvas, pupas, y adultos del gusano cogollero alimentadas con follaje de la etapa de 5-hojas, tuvieron significativamente un peso menor que las larvas que se alimentaron con follaje de la etapa de 3-hojas. El efecto de antibiosis en el crecimiento del gusano cogollero fue evidente en PI 160842, 160827, 346833, y en 346839, pero no en PI 160823 o Mars. PI 160842, 160827, y 160823 tuvieron una tolerancia más alta en el crecimiento de la planta después de la defoliación que PI 346833, 346839, o Mars. PI 160842 y 160827, ambas dfemostraron resistencia de tipo de antibiosis y tolerancia.

The fall armyworm (FAW), *Spodoptera frugiperda* (J. E. Smith), is a polyphagous insect which is an important pest on many crops (Luginbill 1928). However, cereals and grasses are the most preferred among its host plants (Crumbs 1927). On rice, *Oryza sativa* L., the FAW defoliates the leaf particularly at the seedling stage and is a sporadic pest in the southern U.S.A. (Bowling 1978, Smith et al. 1986). Severe damage by FAW to rice has been reported in Puerto Rico (Chandler et al. 1977), and several countries in South America (Navas 1966, Gallego 1967, Machado 1978).

Plant resistance to FAW has been studied on many crops as reviewed by Davis (1980). Pantoja et al. (1986) evaluated over 5,000 rice plant introductions for resistance to FAW defoliation. In their study, 11 plant introductions (PI) were found resistant in choice and no-choice experiments in the greenhouse and field.

The antixenosis, antibiosis, and tolerance resistance are all important to the implementation of resistant cultivars into an insect pest management program. Both rice stands and yield are reduced due to the damage caused by FAW feeding during the seedling stage (Bowling 1978). For this reason, the ability of rice to regrow after damage by FAW is an useful indicator for evaluating the tolerance resistance of rice germplasm. Similarly, the defoliation of rice by FAW or by artificial methods has differential effects on rice yield. Upland rice in Panama tolerates substantial artificial or FAW defoliation without incurring significant yield loss (Navas 1976). Artificial defoliation of the upper 2/3 of the plants of a leafy rice variety, N.P. 130, increased yields by 10-34% depending on the age of the plants at defoliation (Tripathi et al. 1973). Mukerji (1973) reported that rice plants pruned at the seedling stage have slight reductions in yield.

The objectives of this study were to evaluate the effects of rice plant growth stage on the growth of FAW larvae and to evaluate antibiosis and tolerance of five rice PIs found to have antixenosis resistance by Pantoja et al. (1986).

Materials and Methods

Four resistant PIs (160842, 346833, 346839, and 160823), one susceptible PI 160827, and check cultivar 'Mars' (PI 009945) were selected from the study of Pantoja et al. (1986). Seeds were pregerminated in an oven at 30°C for 3 d before being sown into pots in a greenhouse.

In the antibiosis test, pregerminated seeds were sown into the center of a plastic pot (5.1 by 5.1 by 5.1 cm) with ca. four to six seeds per pot. Baccto® potting soil was used, but no fertilizers were applied during the experiment. Pots were set in plastic-lined benches in the greenhouse, and the water level in benches was maintained at a height of 2-3 cm. Pots were moved to the labortory when most of the plants reached the 3-leaf stage (Yoshida 1981). All of the plants in each pot were confined in a transparent plastic tub (2.5 cm diam., 45.0 cm high). One FAW neonate larva per pot was introduced onto plants inside the tube with a camel's hair brush. A total of 20 pots of seedlings of each PI were used. Infested plants were placed inside an incubator at 28±2°C, 14:10 L:D, and 70% RH. Larval weights were measured daily from the 8th day until larvae became prepupae. Pupal weights were recorded within 24 h after the pupation of each larva. The duration and mortality of the entire larval stage, the prepupal stage, and the pupal stage were also recorded. Individual larvae on severely consumed plants were transferred into cages with plants of the same stage to ensure that enough fresh plants were provided throughout the larval stage.

The same procedures were repeated using rice seedlings at the 5-leaf stage of growth. Effects of rice plant growth stage on growth of FAW larvae were compared by a t test (SAS Institute 1985). Means of measurements were subjected to Duncan's multiple range test (Duncan 1955) to compare antibiosis effects among PIs.

In the tolerance test, pregerminated seeds were sown into plastic pots (15 cm diam., 15 cm high) with six to tn seeds per pot. The soil was a mixture of rice field soil and Baccto® potting soil at a 4:1 ratio. No fertilizers wer applied to the soil during this test. Pots were set in plastic-lined benches in greenhouse, and the water level in the benches was maintained at ca. 10 cm. The number of seedlings was thinned to two plants per pot at the 4-leaf stage. Leaf blades were removed with scissors at rates of 0, 33, 66, and 99% dfoliation at the 7-leaf stage, and pots were flooded after defoliation. This experiment was conducted with a split-plot design with four replications. The six PIs were the whole plots and the different percent defoliation levels were the subplots. There were three pots for 0% defoliation (control) and two pots for each of the remaining treatments in each replication. Four weeks after defoliation, plants were removed from pots and soil was washed from the roots. The number of tillers, vegetation wet weight, root wet weight, and root volume were measured in each pot. Plant dry weights were measured after drying at 55°C for 4 d.

Analysis of variance (ANOVA) was performed to compare the effects of different defoliation levels on plant growth among and within rice PIs (SAS Institute 1985). The relationships between plant growth measurements and rice PIs were quantified by correlation analysis (SAS Institute 1985). The percent reduction in plant dry weight,

$$\frac{\text{(Dry Wt. of Uninfested Plant} - \text{Dry Wt. of Infested Plant)}}{\text{Dry Wt. of Uninfested Plant}} \times 100\%,$$

where plant dry weight = dry weight of vegetative parts + dry weight of roots, was calculated to compare tolerance among PIs (Panda & Heinrichs 1983). The relationship between antibiosis and tolerance among PIs was quantified by regrssing the last day larval weight (maximum larval weight) at the 5-leaf stage (antibiosis index) on the average percent plant loss in dry weight (tolerance index) (SAS Institute 1985). This relationship was used to measure the relative contributions of the antibiosis and tolerance components of resistance in each of the tested PIs (Ortega et al. 1980).

RESULTS

Rice plant growth stage had a significant effect on the growth of FAW (Table 1). Larvae fed 5-leaf stage foliage weighed significantly less and had a longer duration of the larval stage than larvae fed 3-leaf stage foliage. The prepupal duration was longer on 5-leaf stage foliage than on 3-leaf stage foliage; however, the duration of the pupal stage was not different. Both pupal and adult weights of larvae fed on 5-leaf stage foliage were also lower than weights of larvae fed on 3-leaf stage foliage. The ovrall mortality of FAW was ca. 10% and showed no differences due to the rice plant growth stage. No larval mortality was observed, with the exception of one larva fed 5-leaf stage 'Mars' foliage. Most of the mortality was observed in the pupal stage. Adults emerging from larvae fed both plant growth stages appeared normal.

The effects of rice PI on larval and pupal weights and th duration of the larval and pupal stage were significant at both the 3-leaf and 5-leaf stages (Table 2). Larvae exhibited different trends in growth on different PIs tested. Therefore, the larval weight at the last larval day (maximum larval weight) was used to compare antibiosis effects. Maximum larval weights on PIs 346833 and 346839 were lower than those on all other PIs in the 3-leaf stage of growth. The same trend appeared among weights of larvae fed 5-leaf stage foliage, except that the maximum larval weight of FAW larvae fed PI 160827 was the same as that of larvae fed PI 346833. The duration of larval

TABLE 1. EFFECTS OF RICE PLANT GROWTH STAGE ON THE GROWTH AND DEVELOPMENT OF FALL ARMYWORM.

FAW Growth Index	Plant Growth Stage 3-leaf	Plant Growth Stage 5-leaf	t Test t	t Test df	t Test P>F
8th day larval wt. (mg)	147.22	109.66	4.58	218	0.0001**
Last day larval wt. (mg)	424.17	388.92	4.62	233	0.0001**
Larval duration (day)	11.62	12.36	–3.91	196	0.0001**
Prepupal duration (day)	1.87	2.01	–3.10	226	0.0022**
Pupal duration (day)	7.30	7.49	–1.84	193	0.0665^NS
Pupal wt. (mg)	172.10	145.06	7.99	210	0.0001**
Adult wt. (mg)	81.93	67.30	6.63	207	0.0001**
Percent mortality	9.60	10.00	0.67	7	0.5188^NS

**highly significant at α = 0.05; ^NS not significant at α = 0.05.

development appeared to be correlated to the larval weight at the 8th day of development. The lower the larval weight on day 8, the longer the larval duration and vice versa ($r = -0.805$, $P = 0.0001$, $n = 235$). Pupal weights were not correlated to the duration of development among larvae fed rice at the 3-leaf stage ($r = 0.007$, $P = 0.940$, $n = 115$) or the 5-leaf stage ($r = -0.165$, $P = 0.080$, $n = 113$) of growth. However, pupal weights were significantly correlated to maximum larval weights (3-leaf stage; $r = 0.736$, $P = 0.001$, $n = 115$; 5-leaf stage; $r = 0.755$, $P = 0.001$, $n = 113$). FAW larvae had the highest pupal mortality when fed foliage of PI 160827 at both stages of rice growth.

In the tolerance test, the effects of PI were significant in relation to the number of tillers ($F = 15.04$; $df = 5,15$; $P = 0.0001$), vegetation wet weight ($F = 10.47$; $df = 5,15$;

TABLE 2. GROWTH AND MORTALITY OF FALL ARMYWORM LARVAE FED FIVE RICE PLANT INTRODUCTIONS (PI) AND THE CULTIVAR 'MARS' AT TWO PLANT GROWTH STAGES.

PI Number	Larval Weight (mg) 8th Day	Larval Weight (mg) Last Day	Duration (d) Larva	Duration (d) Pupa	Pupal Wt. (mg)	% Mortality
			3-leaf stage			
160842	57.7 d[1]	458.6 a	13.2 a	7.6 a	179.4 ab	0
346833	105.0 c	400.0 bc	12.0 b	7.7 a	165.4 bc	5.0
346839	179.2 b	385.3 c	10.7 c	7.4 a	162.5 c	10.5
160823	202.6 ab	433.2 ab	10.9 c	6.6 b	173.9 abc	10.0
Mars	123.6 c	446.7 a	11.9 b	7.8 a	186.2 a	5.3
160827	218.8 a	438.0 a	10.9 c	6.4 b	164.9 c	31.6
			5-leaf stage			
160842	105.3 c	388.2 bc	12.2 c	7.4 a	138.2 c	0
346833	66.5 d	354.4 c	13.7 b	7.7 a	131.8 c	0
346839	185.8 a	381.8 bc	10.4 e	7.8 a	139.9 b	0
160823	145.6 b	448.0 a	11.3 d	7.0 b	181.3 a	11.8
Mars	42.7 e	406.0 b	14.7 a	7.8 a	154.2 b	5
160827	108.7 b	354.4 c	12.0 c	7.0 b	128.4 c	22.2

[1]Means followed by the same letters in each column for each plant growth stage are not significantly different (P = 0.05; Duncan's [1955] multiple range test).

$P = 0.0002$), vegetation dry weight ($F = 14.50$; $df = 5,15$; $P = 0.0001$), root wet weight ($F = 9.18$; $df = 5,15$; $P = 0.0004$), root dry wight ($F = 3.42$; $df = 5,15$; $P = 0.0294$), and root volume ($F = 3.58$; df $= 5,15$; $P = 0.0248$). Defoliation also significantly affected the number of tillers ($F = 12.62$; $df = 3,54$; $P = 0.0001$), vegetation wet weight ($F = 27.50$; $df = 3,54$; $P = 0.0001$) and dry weight ($F = 27.50$; $df = 3,54$; $P = 0.0001$), root wet weight ($F = 8.69$; $df = 3,54$; $P = 0.0001$) and dry weight ($F = 6.21$; $df = 3,54$; $P = 0.0011$), and root volume ($F = 9.70$; $df = 3,54$; $P = 0.0001$). Interactions of PI and defoliation were not significant across any rice plant growth measurements. Among the PIs tested, 346833 and 160823 had higher growth measurement values than the remaining PIs (Table 3), indicating that these two PIs have a larger biomass than the other PIs tested.

The 33% defoliation rate did not induce a significant effect among PI on percent reduction in plant dry weight, but the 66% and 99% defoliation rates did ($\alpha = 0.10$) (Table 4). In general, PIs 160842 and 160827 had the lowest reductions among all rice PIs tested. PI 160823 had a moderate reduction in plant dry weight, whereas the susceptible cultivar 'Mars' had the highest plant dry weight reduction across all three defoliation levels.

The linear relationship between the average percent reduction in plant dry weight and the maximum weight of larvae fed foliage of plants at the 5-leaf stage of growth (Fig. 1) had a very small slope. Among the five PIs tested, only the plotted values of PIs 160842 and 160827 fell within the region in which both antibiosis and tolerance were present. Values of PIs 346833 and 346839 fell in the region in which only antibiosis was present. PI 160823 had the highest larval weight among the PIs tested, but still plotted just within the tolerance quadrant. Values for the susceptible cultivar Mars fell within the region in which neither antibiosis nor tolerance was expressed.

Discussion

The use of whole rice seedling plants proved to be a useful bioassay technique to evaluate the antibiosis effects of rice on the growth of FAW. During the experiment, the first, second, and third instars fed exclusively on leaf blades while the fourth and fifth instars fed randomly on leaf blades or leaf sheaths. Pupal cells were built successfully under the base of plants by pooling plant fragments, frass, and soil. No prepupal mortality was observed during the test.

The significant differences in the growth of FAW fed rice plants of different stages indicated that plant growth stage affects the growth of FAW on rice. Older 5-leaf stage seedlings had more detrimental effects on the growth of FAW than younger 3-leaf

TABLE 3. Effects of artificial defoliation on the regrowth of five rice plant introductions and the cultivar 'Mars'[1].

PI Number	No. of Tillers	Vegetation Weight Wet (g)	Vegetation Weight Dry (g)	Root Weight Wt (g)	Root Weight Dry (g)	Root Volume (ml)
160842	9.3 c[2]	65.5 b	8.6 c	96.7 b	17.6 bc	86.4 bc
346833	13.5 b	94.4 a	12.2 a	181.9 a	35.7 a	135.1 a
346839	10.6 c	62.0 b	7.5 c	71.1 b	14.0 c	66.1 c
160823	17.8 a	84.2 a	11.8 ab	166.6 a	33.9 ab	127.4 ab
Mars	10.1 c	67.8 b	8.9 c	106.8 b	20.0 bc	86.6 bc
160827	13.1 b	71.9 b	10.6 b	89.7 b	24.0 bc	84.8 bc

[1]Plants were defoliated at the rate of 0, 33, 66, and 99% at the 7-leaf stage of growth. Plant growth measurements were taken 4 weeks after defoliation.

[2]Means followed by the same letters are not significantly different (P = 0.05; Duncan's [1955] multiple range test).

TABLE 4. PERCENT REDUCTION IN PLANT DRY WEIGHT OF FIVE RICE PLANT INTRODUCTIONS AND THE CULTIVAR 'MARS' AFTER DIFFERENT RATES OF ARTIFICIAL DEFOLIATION.

PI Number	Defoliation Rate			
	33%	66%	99%	Average
Mars	33.28	51.35 a[1]	83.16 a	56.02 a
346839	30.33	44.17 ab	56.07 b	43.47 a
346833	2.01	50.42 a	62.13 ab	36.00 ab
160823	27.75	5.62 b	54.95 b	31.61 b
160827	–0.95	22.17 ab	48.44 b	23.78 b
160842	–14.23	18.82 ab	50.41 b	19.70 b
$F=$	0.82	2.28	2.55	3.64
$df=$	5, 14	5, 15	5, 15	5, 80
$P=$	0.5544	0.0987	0.0733	0.0485

[1]Means followed by the same letters are not significantly different (P = 0.10; Duncan's [1955] multiple range test).

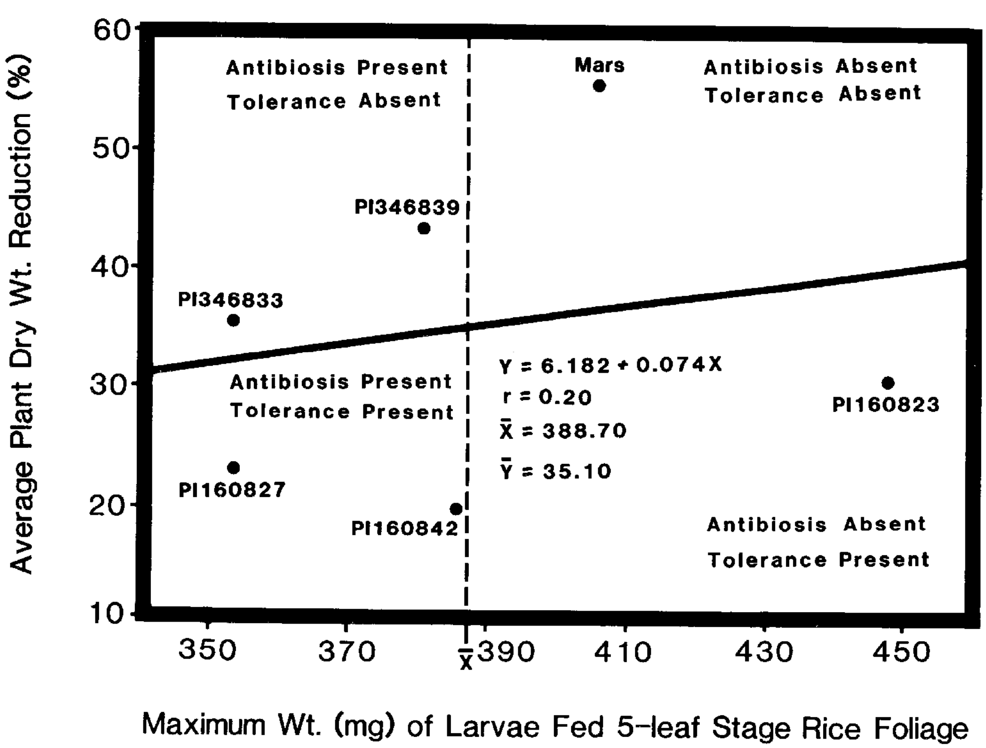

Fig. 1. Relationship between percent rice plant dry weight reduction (tolerance) and maximum larval weight of fall armyworms (antibiosis) fed foliage of five rice plant introductions and the cultivar 'Mars' at the 5-leaf stage of development.

stage seedlings. Hardy et al. (1986) reported that both neonate and fourth instar FAW larvae feed more on new growth than on older growth of tall fescue grass. FAW larvae also prefer young corn leaves over old leaves as a food source (Garner & Lynch 1981). Similarly, the resistance level of rice plants may vary as the plants mature. In our study, the maximum larval weight of FAW larvae on PI160827 was among the highest when fed 3-leaf stage foliage, but became the lowest when larvae were fed 5-leaf stage foliage.

Larval weight has been used previously as an indicator of rice plant resistance to insects. Oliver & Gifford (1975) studied the effects of seven rice lines on the larval weight of the rice stalk borr, *Chilo plejadellus* Zincken, and identified two cultivars as potential sources of stalk borer resistanc. In our study, the maximum larval weights of FAW fed 5-leaf stage foliage of PIs 346833 and 160827 were the lowest among the five PIs tested, indicating that these two PIs are more resistant to FAW than the other PIs. In general, PIs 160842, 346833, 346839, and 160827 had more antibiotic effects on FAW growth than Mars and PI160823, based on the maximum larval weight of FAW fed 5-leaf stage foliage.

The percent reductions in plant dry weight of the five rice PIs tested were lower than that of the check cultivar 'Mars'. PI 160827, which did not exhibit antixenosis (Pantoja et al. 1986), had an antibiotic effect on FAW growth and was tolerant to defoliation as indicated by its low percent reduction in plant dry weight. These results indicate that the resistance by one cultivar cannot be justified by a single category of resistance. The relationships between antibiosis and tolerance (Fig. 1) demonstrate the relative contributions of each type of FAW resistance in PIs tested. PIs 346833 and 346839 have antibiosis but no tolrance to FAW damage. PIs 160842 and 160827 appear to be sources of antibiosis and tolerance resistance to FAW; however, PI160842 appears to be the most promising PI to use for development of lasting resistance to FAW, because it also has the antixenosis resistance reported by Pantoja et al. (1986).

Acknowledgment

The authors thank Drs. E. A. Heinrichs, J. R. Fuxa, and T. J. Riley for their critical review of the manuscript. This research was supported by funds from the Louisiana Agricultural Experiment Station and USDA Special Grant no. 85-CRSR-2-2621 and is approved for publication by the Director of the Louisiana Agricultural Experiment Station as manuscript number 88-17-2067.

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