Changes in fall armyworm (Lepidoptera: Noctuidae) fitness over five generations after larval feeding on resistant tropical landrace sorghum[1]

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Abstract. There is evidence of some levels of resistance in Honduran landrace sorghum to fall armyworm (FAW), *Spodoptera frugiperda* (J. E. Smith), but the stability of this resistance through several generations is unknown. A study was conducted to measure the development and fitness of FAW when fed a resistant tropical honduran landrace sorghum cultivar, San Bernardo III, and AF-28, a resistant sorghum cultivar from Brazil, through five generations. A susceptible sorghum cultivar, Cacho de Chivo-169, and a susceptible maize cultivar, Maicito, both from Honduras, were included for comparisons. Larvae fed AF-28 or San Bernardo III had higher larval and pupal mortality in the second, fourth, and fifth generations than larvae fed the susceptible sorghum or maize cultivars. Lowest pupal weight and fecundity were recorded for FAW fed San Bernardo III in all generations except the first. San Bernardo III and AF-28 appeared to have similar negative influences on FAW fitness, expressed as low net reproductive rate and low intrinsic rate of natural increase, compared with the susceptible sorghum and maize cultivars. However, insects fed AF-28 had a lower intrinsic rate of natural increase in the third and fifth generations compared with insects fed San Bernardo III. These results indicate that San Bernardo III and AF-28 maintained initial levels of antibiosis resistance to FAW through five generations.

Key words: Insect tolerance, plant resistance, *Spodoptera frugiperda*, *Sorghum bicolor*

Resumen. Existe evidencia de ciertos niveles de resistencia al gusano cogollero *Spodoptera frugiperda* (J.E. Smith) en variedades criollas hondureñas de sorgo, pero la estabilidad de esta resistencia a través de varias generaciones es desconocida. Un estudio fue conducido para medir el desarrollo y estado físico del cogollero cuando las larvas fueron alimentados con la variedad criolla resistente hondureña, San Bernardo III y AF-28 una variedad resistente proveniente de Brasil, durante cinco generaciones. Un cultivar susceptible de sorgo, Cacho de Chivo– 69 y una variedad susceptible de maíz, Maicito, ambos hondureños, fueron incluidos en la comparación. Las larvas alimentadas con San Bernardo III o AF-28 tuvieron tasas de mortalidad para las larvas y pupas, más altas que las variedades susceptibles en la segunda, cuarta y quinta generación. Los pesos más bajos de pupa y tasas de fecundidad fueron encontrados en cogollero alimentado en San Bernardo III con excepción de la primera generación. San Bernardo III y AF-28 aparentan tener efectos negativos similares en el desarrollo del cogollero, expresado como baja tasa neta de reproducción y baja tasa de incremento natural, comparada con variedades susceptibles. Sin embargo, insectos alimentados con AF-28 tuvieron tasa neta de reproducción e incremento natural en la tercera y quinta generación más bajos comparado con San Bernardo III. Estos resultados indican que San Bernardo III y AF-28 mantuvieron los mismos niveles de resistencia por cinco generaciones.

Palabras claves: Insectos tolerantes, plantas resistentes, *Spodoptera frugiperda*, *Sorghum bicolor*

INTRODUCTION

Maxwell and Jennings (1980) reported that plants with antibiosis resistance produce an adverse effect on insect populations; the effects are specific, cumulative, and persistent. Leuck and Perkins (1972) reported a positive correlation between pupal size and fecundity of fall armyworm (FAW), *Spodoptera frugiperda* (J. E. Smith). Luginbill (1928) and Pitre and Hogg (1983) reported that populations of FAW fed on grasses had shorter pupal

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developmental times and heavier pupae than FAW developed on other hosts. Fall armyworm development on resistant plants may be influenced by antibiosis (Painter 1951), or possibly non-feeding preference ("antixenosis") (Kogan and Ortman 1978). Development may be influenced by fundamental differences in FAW races. Pashley (1986) identified races of FAW which developed at different rates on rice and maize.

According to Meckenstock *et al.* (1991), FAW fed AF-28, a resistant sorghum cultivar from Brazil, had heavier pupae than FAW fed San Bernardo III, a tropical Honduran landrace sorghum cultivar with some resistance to this pest. The general assumption is that female insects developed from heavy pupae will probably have greater fecundity and have a higher intrinsic rate of natural increase than adults developed from pupae that weigh less.

Although there is evidence of FAW resistance in Honduran landrace sorghum, the stability of this resistance through several generations is unknown. This study evaluated the fitness of FAW and the potential for the insects to overcome antibiosis resistance conferred by San Bernardo III through multiple generations. Knowledge of ability of the FAW to overcome resistance mechanisms in the landrace sorghums will assist in defining future selection of genetic materials for evaluation in host plant resistance programs directed against this pest.

MATERIALS AND METHODS

Five successive generations of FAW (beginning with the first laboratory generation in culture) were evaluated for growth and development on susceptible and resistant sorghum and maize. Two resistant sorghums were used; these were San Bernardo III, a caudatum-durra landrace accession from Honduras (a selection from the "Liberal" landrace initially collected near the rural community of San Bernardo) and AF-28, a resistant cultivar from Brazil (Lara *et al.* 1980). San Bernardo III is late maturing with relatively low yield potential and drought resistance, but well adapted to intercropping with maize. A third sorghum, Cacho de Chivo-169, a susceptible cultivar from Guatemala, was included. A susceptible maize cultivar, Maicito (collected near Tierra Blanca in southern Honduras) was included because many farmers intercrop this early maturing cultivar.

Both sorghum and maize were planted on five dates. Plantings were synchronized with each FAW generation to have enough plant food for larvae in each developmental stage through the entire study period. Soil was characterized to have pH 5.7, organic matter 1.8%, nitrogen 0.19%, phosphorous 13.0 ppm, and potassium 420 ppm. A commercially available fertilizer (18-46-0 of NPK) was applied by hand at planting at a rate of 180-kg/ha and nitrogen (urea 46%N) at 52 kg/ha was applied 30 days after planting.

The four cultivars were planted in a randomized complete block with four replications on each of the five planting dates. Each plot was one row, 5 m long and 80 cm between rows. To reduce competition among plants and to ensure better quality food for the larvae, plots were thinned to 30 plants per row. The environmental conditions were different for each test period (insect generation) due to differences in planting dates. Since temperature, rainfall, and photoperiod are key factors in plant development, this information is presented (Table 1) for

Table 1. Average environmental conditions in the field prior to and during periods that sorghum was fed to larvae in each of five fall armyworm generations. El Zamorano, Honduras.

	Plant age	Rainfall, mm		Temperature			Photoperiod, (h)	
Insect generation	D[a]	Rb[b]	Rd[c]	EC		std	Pb[d]	Pd[e]
1	23	231	83	24.1	±	4.9	12.8	12.7
2	28	119	260	21.9	±	8.5	12.7	12.4
3	29	284	208	23.8	±	4.9	12.3	11.8
4	32	181	55	22.8	±	6.0	11.7	11.2
5	26	14	5	21.4	±	5.0	11.3	11.2

[a] = Plant age (days) when test initiated.
[b] = Rainfall 14 days before planting date.
[c] = Rainfall during period that plants were fed to larvae.
[d] = Photoperiod (light) 14 days before planting date.
[e] = Photoperiod (light) during period that plants were fed to larvae.

consideration in assessing positive or negative correlations with parameters of antibiosis resistance.

The FAW used in this study were originally collected on landrace sorghum in a production field at El Conchal, Honduras, located on the Pacific coastal plain (ca. sea level) near the border with El Salvador. The insects were maintained on a modified pinto bean diet (Burton and Perkins 1989) until the second generation (first laboratory generation) when tests were initiated.

The plant growth stages used in each test were identified according to Vanderlip and Reeves (1972). When plants attained 23 to 32 days of age (Table 1), fresh leaf material (the two youngest whorl leaves from the stock of food plants) was collected daily. Whorl leaf material was cut from the respective treatment plots, wrapped in moist paper, placed in paper bags, labeled accordingly, and taken immediately to the laboratory in a refrigerated box to be used in the study. Leaves were first washed with distilled water, then with a 5% hypochlorite solution, and finally with distilled water to remove the chemical residue. Sorghum leaf tissue (ca. 60-80 cm^2) was placed inside individual plastic cups (29.6 ml) containing 5 ml of agar to provide moisture for the leaves. Each cup contained 0.28 g of corncob-grit treated with 0.03% griseoflavin, 0.04% phaltan, and 0.03% tetracyclin. The antibiotics reduced contamination by microorganisms. Leaves were replaced daily until FAW pupation.

One FAW egg mass was selected from the rearing colony and used for each replication in each test. Eight neonates were randomly selected at hatch for each treatment and individually placed in plastic cups with the plant material. Treatments were randomly assigned to a holding tray and trays were placed in a randomized complete block design in a rearing room in the laboratory. Each treatment was replicated 10 times and the tests were conducted at 26 ± 2° C and 14:10 L:D photoperiod.

Parameters measured for each generation included larval plus pupal mortality, larval developmental time, larval plus pupal developmental time (considered as generation time), pupal weight (measured on a Mettler AC 100 analytical balance), fecundity, net reproductive rate, and intrinsic rate of natural increase.

Fecundity (F) was estimated using the formula reported by Leuck and Perkins (1972):

$$F = 5.33wp - 423.23 \qquad [1]$$

where wp is the female pupal weight (mg).

The net reproductive rate (R_0), a measure of the rate of increase of a population per generation rather than per unit of time, was calculated using fecundity and survivorship (Birch 1948):

$$R_0 = F\,Lx \qquad [2]$$

where Lx = 1- Pm (Pm is combined larval and pupal mortality/100).

The intrinsic rate of natural increase (r_m) was estimated according to Birch (1948):

$$r_m = [\mathrm{Log}_e (R_0)] / T \qquad [3]$$

where T = generation time (number of days from egg hatch until adult emergence).

Lower values of r_m represent a lower rate of increase in FAW population (i.e., reduced fitness) which may be

Table 2. Effect of three sorghum cultivars and one maize cultivar on development of fall armyworm during the first laboratory generation at 26 ± 2° C and 14:10 L:D.

Cultivar	% larval + pupal mortality (Pm)	Developmental time, d: Larva	Developmental time, d: Larva + Pupa (T)	Female Pupal wt (mg)	Fecundity (F)	Net reproductive rate (R_0)	Intrinsic rate of increase (r_m)
San Bernardo III[1]	33.0 a[5/]	15.4 b	26.4 c	193.1 a	605.7 a	422.6 a	0.228 a
AF-28[2]	29.0 a	15.3 b	27.3 a	190.1 a	590.1 a	419.8 a	0.220 a
Cacho de Chivo-169[3]	34.0 a	17.1 a	26.8 b	186.7 a	571.9 a	374.1 a	0.218 a
Maicito maize[4]	33.0 a	15.5 b	26.5 c	205.1 a	670.1 a	451.5 a	0.229 a

1/ Resistant tropical Honduran landrace sorghum cultivar
2/ Resistant sorghum cultivar from Brazil
3/ Susceptible landrace sorghum cultivar from Honduras
4/ Susceptible maize cultivar from Honduras
5/ Means within a column not followed by the same letter are significantly different at the 0.05 level by Duncan's multiple range test (n=80 larvae/treatment).

attributed to diet (i.e., antibiosis of the plant). The intrinsic rate of natural increase provides a basis for measuring relative fitness because it is a measure of the rate of growth of the population that incorporates the effects of all factors affecting fitness.

Data were analyzed with ANOVA (Steel and Torrie 1983) using the GLM procedure of SAS (SAS Institute 1985). Means were separated with Duncan's multiple range test (Duncan 1955) at the 0.05 level. Pearson correlation analysis was used to correlate environmental factors with insect performance (SAS Institute 1985).

RESULTS AND DISCUSSION

The first laboratory generation of FAW fed San Bernardo III, AF-28, Cacho de Chivo-169, or maize showed no differences in mortality, female pupal weight, fecundity, net reproductive rate, or intrinsic rate of natural increase (Table 2). Insects fed AF-28 had the longest generation time compared with insects fed the other test sorghum or maize cultivars.

Second generation FAW fed AF-28 or San Bernardo III had similar mortality rates, but significantly greater mortality than when fed maize (Table 3). Generation times were only somewhat longer for insects fed AF-28 or San Bernardo III than for insects fed maize. Female pupal weight was lowest for insects fed San Bernardo III and highest for insects fed AF-28; pupal weights for insects fed AF-28, Cacho de Chivo-169, or maize were not different. Similar results were recorded by Meckenstock *et al.* (1991). There were no differences among treatments for fecundity or net reproductive rate. However, insects fed AF-28 or San Bernardo III had significantly lower intrinsic rates of natural increase than insects fed maize or Cacho de Chivo-169, which is evidence of reduced fitness attributed to antibiosis resistance.

FAW in the third generation which were fed test cultivars had similar mortality, fecundity, and net reproductive rate (Table 4). Insects fed maize or San Bernardo III had the longest larval developmental times, while Cacho de Chivo-169 and AF-28 had the shortest developmental times. However, a significantly longer generation time (ca. 2 d) was recorded for FAW fed AF-28 compared with San Bernardo III. Insects fed AF-28 had greater pupal weight than insects fed San Bernardo III, but similar pupal weight for insects fed Cache de Chivo-169 or maize. Insects fed AF-28 had a lower intrinsic rate of natural increase compared with insects fed San Bernardo III. These results contribute to our recognition of AF-28 as being more resistant to FAW than San Bernardo III.

In the fourth generation, FAW fed San Bernardo III or AF-28 had greater mortality than those fed the susceptible sorghum or maize (Table 5). Although no single test cultivar significantly influenced FAW larval developmental time, female pupal weight, or fecundity more than any other cultivar, insects fed San Bernardo III had the lowest net reproductive rate and the lowest intrinsic rate of natural increase, although the latter was not significantly different from AF-28.

Table 3. Effect of three sorghum cultivars and one maize cultivar on development of fall armyworm during the second laboratory generation at 26 ± 2° C and 14:10 L:D.

Cultivar	% larval + pupal mortality (Pm)	Developmental time, d Larva	Larva + Pupa (T)	Female pupal wt (mg)	Fecundity (F)	Net reproductive rate (R_0)	Intrinsic rate of increase (r_m)
San Bernardo III[1]	72.0 a[5]	15.1 ab	24.6 ab	179.6 b	534.1 a	210.7 a	0.206 b
AF-28[2]	69.0 ab	16.0 a	24.7 a	193.2 a	606.3 a	331.0 a	0.212 b
Cacho de Chivo-169[3]	56.0 b	16.0 a	24.0 b	186.3 a	569.6 a	249.9 a	0.227 a
Maicito maize[4]	46.0 c	14.8 b	23.8 b	185.9 a	567.4 a	302.4 a	0.237 a

1/ Resistant tropical Honduran landrace sorghum cultivar
2/ Resistant sorghum cultivar from Brazil
3/ Susceptible landrace sorghum cultivar from Honduras
4/ *Susceptible maize cultivar from Honduras*
5/ Means within a column not followed by the same letter are significantly different at the 0.05 level by Duncan's multiple range test (n=80 larvae/treatment).

Table 4. Effect of three sorghum cultivars and one maize cultivar on development of fall armyworm larvae and pupae during the third laboratory generation at 26 ± 2° C and 14:10 L:D.

Cultivar	% larval + pupal mortality (Pm)	Developmental time, d Larva	Larva + Pupa (T)	Female Pupal wt (mg)	Fecundity (F)	Net reproductive rate (R_o)	Intrinsic rate of increase (r_m)
San Bernardo III[1]	31.0 a[5]	19.0 a	25.5 c	188.9 b	583.8 a	398.2 a	0.232 a
AF-28[2]	29.0 a	17.8 b	28.3 a	201.0 a	648.0 a	488.4 a	0.216 b
Cacho de Chivo-169[3]	35.0 a	17.7 b	25.6 c	198.6 ab	635.0 a	405.5 a	0.228 ab
Maicito maize[4]	39.0 a	19.3 a	26.2 b	199.9 a	642.0 a	388.7 a	0.228 ab

1/ Resistant tropical Honduran landrace sorghum cultivar
2/ Resistant sorghum cultivar from Brazil
3/ Susceptible landrace sorghum cultivar from Honduras
4/ Susceptible maize cultivar from Honduras
5/ Means within a column not followed by the same letter are significantly different at the 0.05 level by Duncan's multiple range test (n=80 larvae/treatment).

Table 5. Effect of three sorghum cultivars and one maize cultivar on development of fall armyworm larvae and pupae during the fourth laboratory generation at 26 ± 2° C and 14:10 L:D.

Cultivar	% larval + pupal mortality (Pm)	Developmental time, d Larva	Larva + Pupa (T)	Female Pupal wt (mg)	Fecundity (F)	Net reproductive rate (R_o)	Intrinsic rate of Increase (r_m)
San Bernardo III[1]	76.0 a[5]	19.5 a	29.6 c	181.3 a	543.3 a	144.4 d	0.163 b
AF-28[2]	55.0 b	18.5 a	31.8 a	184.1 a	558.0 a	250.3 c	0.172 b
Cacho de Chivo-169[3]	21.0 c	19.5 a	30.3 b	188.1 a	579.3 a	458.8 b	0.202 a
Maicito maize[4]	8.0 d	18.3 a	30.4 b	189.4 a	586.5 a	540.0 a	0.206 a

1/ Resistant tropical Honduran landrace sorghum cultivar
2/ Resistant sorghum cultivar from Brazil
3/ Susceptible landrace sorghum cultivar from Honduras
4/ Susceptible maize cultivar from Honduras
5/ Means within a column not followed by the same letter are significantly different at the 0.05 level by Duncan's multiple range test (n=80 larvae/treatment).

Fifth generation laboratory FAW fed Cacho de Chivo-169 had the shortest generation time and highest intrinsic rate of natural increase compared with FAW fed the other test sorghum cultivars (Table 6). Insects fed resistant AF-28 had somewhat greater mortality and lower net reproductive rate than insects fed the susceptible cultivars; San Bernardo III was intermediate in measures of these parameters.

Correlation analyses among environmental factors in the field and parameters of antibiosis were performed to help describe the effects of these factors on the development of FAW when fed the various plant cultivars. Fall armyworms fed AF-28 showed a negative correlation between temperature and mortality (r = -0.964), and between rainfall before initiation of feeding and mortality (r = -0.873). Mortality was highest when temperature and rainfall were lowest. Fall armyworms fed San Bernardo III or maize showed negative correlations [San Bernardo III (r = -0.884) and maize (r = -0.912) between photoperiod and generation time. As photoperiod increased, generation time decreased. This relationship can have a negative effect on sorghum resistance to FAW, as the pest can have an increase in number of generations per season. Also, San Bernardo III showed a positive correlation between temperature and female pupal weight, and between temperature and fecundity (r = 0.918). This

Table 6. Effect of three sorghum cultivars and one maize cultivar on development of fall armyworm larvae and pupae during the fifth laboratory generation at 26 ± 2° C and 14:10 L:D.

Cultivar	% larval + pupal mortality (Pm)	Developmental time, d Larva	Larva + Pupa (T)	Female Pupal wt (mg)	Fecundity (F)	Net reproductive rate (R_o)	Intrinsic rate of increase (r_m)
San Bernardo III[1]	50.0 ab[5]	29.7 ab	41.4 a	180.4 a	538.3 a	292.5 ab	0.134 b
AF-28[2]	66.0 a	31.4 a	42.8 a	184.6 a	560.7 a	189.5 b	0.121 c
Cacho de Chivo-169[3]	41.0 b	27.7 b	38.4 b	185.3 a	564.5 a	335.6 a	0.150 a
Maicito maize[4]	53.0 ab	30.6 a	41.3 a	185.4 a	564.9 a	263.2 ab	0.133 bc

1/ Resistant tropical Honduran landrace sorghum cultivar
2/ Resistant sorghum cultivar from Brazil
3/ Susceptible landrace sorghum cultivar from Honduras
4/ Susceptible maize cultivar from Honduras
5/ Means within a column not followed by the same letter are significantly different at the 0.05 level by Duncan's multiple range test (n=80 larvae/treatment).

suggests that low temperature influences FAW through low female pupal weight and fecundity. Consequently, low populations of FAW might be expected for subsequent generations when this insect undergoes development on San Bernardo III at lower temperatures.

Positive correlations for FAW fed AF-28 were identified between temperature and net reproductive rate (r = 0.920), between rainfall and net reproductive rate (r = 0.904), and between photoperiod and intrinsic rate of natural increase (r = 0.901). Insects fed San Bernardo III had a positive correlation between photoperiod and intrinsic rate of natural increase (r = 0.906). The correlation coefficients calculated were based on observations of parameters measured and did not consider the influence of specific environmental factors on plant nutrition, an important factor in understanding growth and development when insects are fed various diets.

Larval plus pupal mortality was greater for FAW fed the resistant San Bernardo III or AF-28, than when fed the susceptible Cacho de Chivo-169 through five laboratory generations. Differential mortality levels were apparent in second, fourth, and fifth generations. When comparing FAW development on AF-28 or San Bernardo III through five generations, insects fed AF-28 had longer generation time than insects fed the other test cultivars, while San Bernardo III had longer generation time than Cacho de Chivo-169 only in the second and fifth generations. This suggests that FAW development was consistently affected by AF-28 and this relationship could have an influence in reducing the number of FAW generations per season, while San Bernardo III did not show the same consistency in its effects on the pest. Low pupal weight and associated low fecundity for FAW fed San Bernardo III contributed to low reproductive rates from the second through fifth generations, while similar relationships were observed for FAW fed AF-28 in the fourth and fifth generations. Low intrinsic rates of natural increase were observed for FAW fed San Bernardo III and AF-28 in the second, fourth, and fifth generations.

San Bernardo III and AF-28 proved to have a relatively consistent level of resistance to FAW through five consecutive generations. This suggests that the FAW may not overcome the type of antibiosis resistance expressed in AF-28 sorghum over a short period of time, e.g., where this pest may have a limited number of generations. San Bernardo III, the Honduran landrace sorghum, did not influence FAW populations with the same intensity in each generation. However, according to Meckenstock *et al.* (1991) the fitness of a FAW population fed San Bernardo III had a negative influence on the intrinsic rate of natural increase, showing a level greater than that for FAW fed AF-28.

Meckenstock *et al.* (1991) discussed the possible selection of genes that confer antiobiosis resistance in tropical landrace sorghum in crop production systems in nature. They hypothesized that because there is an abundance of plant species serving as hosts for FAW larvae that develop in a small number of generations on sorghum, there is a differential selection process for resistant-virulent genes in the host-insect population in which all sorghum is subject to FAW feeding but not all FAW larvae are forced to develop on sorghum. Consequently, resistance genes are selected in sorghum, but virulence genes that enable FAW to overcome resistance are diluted by a much larger insect population which develops on hosts plants other than sorghum.

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