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Combining ability in maize for fall armyworm and southwestern corn borer resistance based on a laboratory bioassay for larval growth

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Abstract The fall armyworm, *Spodoptera frugiperda* (J. E. Smith), and southwestern corn borer, *Diatraea grandiosella* Dyar, are major insect pests of maize, *Zea mays* L., in the southern USA. Both insects feed extensively on leaves of plants in the whorl stage of growth. A diallel cross of seven inbred lines with different levels of susceptibility to leaf feeding damage in the field was evaluated in a laboratory bioassay for fall armyworm and southwestern corn borer larval growth. Diets were prepared from lyophilized leaf tissue of field-grown plants of the inbred lines and their 21 F_1 hybrids. One inbred line, Tx601, exhibited heavy leaf damage in field tests but showed moderate resistance in the laboratory bioassay. Both general and specific combining ability were highly significant sources of variation in the inheritance of fall armyworm and southwestern corn borer larval growth in the laboratory bioassay. Tx601 showed excellent general combining ability for reduced larval growth of both species.

Key words Combining ability · Host plant resistance Maize · Fall armyworm · Southwestern corn borer

Introduction

The fall armyworm, *Spodoptera frugiperda* (J.E. Smith), and the southwestern corn borer, *Diatraea grandiosella* Dyar, are major insect pests of maize, *Zea mays* L., in the southern USA. Larvae of both species feed extensively on leaves of plants that are in the whorl stage of growth. Several germ plasm lines with resistance to these pests have been developed by visually selecting for reduced leaf feeding among maize genotypes artificially infested with fall armyworm and southwestern corn borer (Scott and Davis 1981, Williams and Davis 1982, 1984, Williams et al. 1990a).

Although visual ratings of leaf damage have been effective for selecting among genotypes in breeding programs, their subjective nature has made them less useful in genetic analyses. Williams et al. (1989) reported the results of an analysis of a diallel cross evaluated in the field for reaction to fall armyworm and southwestern corn borer. Larvae recovered from resistant hybrids were smaller than those recovered from susceptible hybrids. They concluded that general combining ability, but not specific combining ability, was important in the inheritance of resistance to these insects when reduced weight was used as an indicator of resistance.

Because some aspects of the genetic and chemical basis of resistance can be more thoroughly investigated in the laboratory, a bioassay using lyophilized leaf tissue of resistant and susceptible genotypes was developed (Williams et al. 1990b). Fall armyworm and southwestern corn borer larvae reared on diets containing tissue of susceptible genotypes were significantly heavier than those reared on diets containing tissue of resistant genotypes. Further investigation revealed that when fall armyworm larvae were fed diets composed of mixtures of susceptible and resistant leaf tissue, the larvae were intermediate in weight (Williams and Buckley 1992).

This study was undertaken to investigate the inheritance of resistance in maize to fall armyworm and southwestern corn borer when resistance is measured as reduced larval growth on diets composed of lyophilized leaf tissue. Specific objectives were to determine the relative importance of general and specific combining ability (GCA and SCA, respectively) in the inheritance of resistance to fall armyworm and southwestern corn borer.

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Materials and methods

Four inbred lines with resistance to leaf feeding by the fall armyworm and southwestern corn borer, Mp496, Mp704, Mp705, and Mp708, and three susceptible inbred lines, Ab24E, SC229, and Tx601, were selected as parents of a diallel cross. Field experiments were conducted at Mississippi State in 1992 and 1993 to evaluate the inbred lines for leaf feeding damage by fall armyworm and southwestern corn borer. Separate experiments for each insect were planted in a randomized complete block design with three replications in a Leeper silty clay loam (fine montmorillonitic, nonacid, thermic Lertic Haplaquept) soil on 14 April 1992 and 23 April 1993. The single-row plots were approximately 5 m long, spaced 1 m apart, and thinned to 20 plants. Standard corn production practices were followed.

Plants were infested in the midwhorl stage of growth with 30 larvae each. Larvae were mixed with corn cob grits and placed in the plant whorl with a mechanical dispenser (Wiseman et al. 1980). Leaf feeding damage was visually rated 14 days after infestation on a scale of 0–9, where 0 indicated no visible damage and 9, extensive damage (Williams et al. 1989).

Ten additional rows of each inbred line and 5 rows of each of the 21 F_1 hybrids were grown to provide leaf tissue for laboratory bioassays. Whorls of these plants were harvested at the same stage of growth at which the other plants were infested. The whorls were trimmed to about 15 cm in length, placed in plastic freezer bags, packed in ice, and transported to the laboratory where they were stored at –18°C until lyophilized. The lyophilized leaf tissue was ground to a fine powder using a laboratory mill with a 1-mm mesh screen.

Laboratory bioassays were conducted as described by Buckley et al. (1991). Diets were prepared by combining 250 ml distilled water, 2400 mg agar, 12.5 mg gentamicin sulfate, 132 mg sorbic acid, 528 mg ascorbic acid, and 10 g lyophilized leaf tissue. The mixture was dispensed in aliquots of 10 ml into 30-ml plastic cups.

On 19 February 1993 and 10 February 1994, 20 cups of diet were prepared from each inbred line and each hybrid. On the following day, each cup was infested with one neonate fall armyworm larva and covered with a paperboard lid. Any inherent differences among larvae were assumed to occur randomly among treatments. Cups were arranged in a randomized complete block design with 20 replications and placed in an environmental chamber at 29°C and a photoperiod of 12:12 (L:D). Larvae were weighed 10 days later.

Similar experiments to determine southwestern corn borer larval growth were initiated 24 March 1993 and 25 January 1994. The southwestern corn borer larvae were weighed, however, after 14 rather than 10 days.

Plot means for leaf feeding ratings from each of the field experiments were calculated and used in an analysis of variance. Data for the 2 years were combined for the analysis. For the laboratory experiments, data for inbreds and hybrids were analyzed separately. Variation in fall armyworm and southwestern corn borer larval weights among hybrids was partitioned into GCA and SCA components using Griffing's Method 4, Model I (1956) diallel analysis. Because of highly significant genotype × environment interactions in the laboratory data, data from the 2 years are reported separately.

Table 1 Leaf feeding damage sustained by parental inbred lines infested with fall armyworm and southwestern corn borer larvae in field tests conducted at Mississippi State in 1992 and 1993

Inbred	Fall armyworm	Southwestern corn borer
Ab24E	8.5[a]	7.8
SC229	8.4	8.7
Tx601	7.8	8.5
Mp496	7.0	7.5
Mp704	6.3	5.6
Mp705	5.7	6.8
Mp708	5.7	6.3
LSD (0.05)	1.0	1.4

[a] Leaf feeding damage was visually rated on a scale of 0 (no damage) to 9 (extensive damage) 14 days after infestation with 30 larvae per plant

Table 2 Weights of fall armyworm and southwestern corn borer larvae reared in a laboratory on diets containing lyophilized leaf tissue of inbred lines grown in 1992 and 1993 at Mississippi State

Inbred	Fall armyworm[a]		Southwestern corn borer[b]	
	1992	1993	1992	1993
	mg			
Ab24E	346	377	138	124
SC229	213	416	107	111
Tx601	190	326	70	80
Mp496	170	321	92	91
Mp704	147	213	58	59
Mp705	145	256	47	49
Mp708	120	182	59	75
LSD (0.05)	38	56	14	12

[a] Fall armyworm larvae were fed the laboratory diets for 10 days
[b] Southwestern corn borer larvae were fed laboratory diets for 14 days

Results and discussion

Leaf feeding damage ratings for the seven inbred lines grown in 1992 and 1993 (Table 1) indicate that although Mp496 was released as a source of resistance to southwestern corn borer, it sustained heavy damage by both southwestern corn borer and fall armyworm (Scott and Davis 1981). Mp704, Mp705, and Mp708 sustained moderate damage. Genotype × environment interactions were not significant for leaf feeding damage ratings.

Genotype × environment interactions were significant, however, for larval weights in the laboratory bioassays in which larvae were fed lyophilized leaf tissue of the inbred lines. Therefore, mean larval weights for both fall armyworm and southwestern corn borer are presented separately for 1992 and 1993 (Table 2). Neither weights of larvae fed leaf tissue of Tx601 and Mp496 nor leaf feeding damage sustained by them differed significantly for either insect in 1992 or 1993. On the basis of leaf feeding damage, Mp496 appears to be susceptible to both insects but, on the basis of larval weights in this bioassay, Tx601 appears to be more appropriately grouped with the resistant inbred lines than with the susceptible ones. The bioassay apparently measures some aspects of resistance that differ from those expressed in levels of damage in the field. These results are consistent with earlier findings by Williams and Buckley (1992) for laboratory bioassays with Tx601. Both fall armyworm and southwestern corn borer larvae fed on Mp496 leaf tissue were larger than those fed on Mp704, Mp705, and Mp708 in both years. This provides further evidence of the lower level of resistance of Mp496.

Table 3 Weights of fall armyworm and southwestern corn borer larvae reared in a laboratory on diets containing lyophilized leaf tissue of F_1 hybrids grown in 1992 and 1993 at Mississippi State

Hybrid	Fall armyworm[a]		Southwestern corn borer[b]	
	1992	1993	1992	1993
	mg			
Ab24E×SC229	330	299	130	116
Ab24E×Tx601	277	262	94	91
Ab24E×Mp496	314	266	118	91
Ab24E×Mp704	304	147	91	58
Ab24E×Mp705	247	185	83	59
Ab24E×Mp708	334	164	131	50
SC229×Tx601	259	208	95	70
SC229×Mp496	371	323	124	96
SC229×Mp704	141	314	91	89
SC229×Mp705	214	320	90	79
SC229×Mp708	174	333	100	96
Tx601×Mp496	207	140	99	57
Tx601×Mp704	146	231	57	71
Tx601×Mp705	115	96	56	39
Tx601×Mp708	162	176	69	64
Mp496×Mp704	225	186	72	53
Mp496×Mp705	152	237	67	66
Mp496×Mp708	265	318	80	89
Mp704×Mp705	217	253	77	79
Mp704×Mp708	241	271	75	79
Mp705×Mp708	238	242	61	74
LSD (0.05)	46	57	13	12

[a] Fall armyworm larvae were fed laboratory diets for 10 days
[b] Southwestern corn borer larvae were fed laboratory diets for 14 days

Table 4 Estimates of general combining ability effects for weights of fall armyworm and southwestern corn borer larvae fed in a laboratory on diets containing lyophilized leaf tissue of maize hybrids grown in 1992 and 1993

Inbred	Fall armyworm		Southwestern corn borer	
	1992	1993	1992	1993
	mg		mg	
Ab24E	79.4	−19.4	23.2	3.6
SC229	16.0	75.2	19.6	19.7
Tx601	−49.0	−61.3	−12.3	−11.2
Mp496	25.0	9.8	5.8	1.0
Mp704	−27.0	−3.6	−13.7	−3.8
Mp705	−45.2	−17.4	−19.6	−10.1
Mp708	0.9	16.8	−3.0	0.8
LSD (0.05)	19.5	24.1	5.7	4.8

Genotype × environment interactions were also significant when larvae were fed on lyophilized leaf tissue of the F_1 hybrids. Larvae fed on diets containing leaf tissue of hybrids between Tx601 and the leaf feeding resistant inbreds were among the smallest for both insects both years (Table 3). This provides additional evidence of the unique behavior of Tx601; it tends to fit the susceptible classification when judged on the basis of leaf feeding damage and the resistant classification when judged on the basis of larval growth on lyophilized leaf tissue.

Table 5 Estimates of specific combining ability effects for weights of fall armyworm and southwestern corn borer larvae fed in a laboratory on lyophilized leaf tissue of maize hybrids grown in 1992 and 1993

Hybrid	Fall armyworm		Southwestern corn borer	
	1992	1993	1992	1993
	mg			
Ab24E×SC229	−0.2	6.5	−1.3	18.2**
Ab24E×Tx601	11.4	106.1**	−5.8	24.3**
Ab24E×Mp496	−25.0	38.6*	0.2	11.5**
Ab24E×Mp704	16.7	−66.4**	−6.6	−16.4**
Ab24E×Mp705	−21.7	−14.4	−9.1*	−8.6**
Ab24E×Mp708	18.8	−70.4**	22.5**	−29.0**
SC229×Tx601	57.0**	−43.0**	−0.7	−13.5**
SC229×Mp496	94.9**	1.1	10.0**	1.1
SC229×Mp704	−82.5**	5.7	−3.8	−1.7
SC229×Mp705	8.2	25.1	1.1	−5.2
SC229×Mp708	−77.3**	4.7	−5.4	1.1
Tx601×Mp496	−4.3	−44.8**	17.2**	−6.6*
Tx601×Mp704	−12.9	59.7**	−5.7	11.5**
Tx601×Mp705	−26.1*	−62.0**	−0.5	−14.4**
Tx601×Mp708	−25.1	−16.1	−4.5	−0.5
Mp496×Mp704	−7.5	−57.1**	−8.5*	−19.1**
Mp496×Mp705	62.3**	7.8	−7.9*	0.9
Mp496×Mp708	4.2	54.5**	−11.0**	12.9**
Mp704×Mp705	54.3**	37.2*	21.3**	18.7**
Mp704×Mp708	31.9*	20.9	3.3	6.9*
Mp705×Mp708	47.6*	6.4	−4.9	8.6**

*, ** Significantly different from zero at the 0.05 and 0.01 levels of probability, respectively

Partitioning the variation among hybrids into general and specific combining ability components indicated that both were highly significant sources of variation in the inheritance of fall armyworm and southwestern corn borer larval weights. Estimates of GCA effects are given in Table 4. The large negative values for Tx601 in 1992 and 1993 for both insects indicate that this line imparted a high level of resistance to its hybrids. Mp704 and Mp705 also imparted resistance to their hybrids. SC229 and Ab24E, except in 1993 for fall armyworm, contributed to heavier larvae.

Estimates of SCA effects (Table 5) further reveal the importance of specific combining ability in some hybrid combinations. Differences between years, such as those exhibited in fall armyworm weights for SC229×Tx601 and southwestern corn borer weights for Ab24E×Mp708 and Mp496×Mp708, indicate why significant genotype × environment interactions were found. On the other hand, weights of both species of larvae were consistently greater for the hybrid Mp704×Mp705 than would have been expected from the average performance of the lines.

The results of this investigation illustrate the importance of recognizing the complex nature of insect resistance. Although Tx601, like Ab24E and SC229, sustained heavy damage from both fall armyworm and southwestern corn borer in field tests (Table 1), larvae fed on leaf tissue of Tx601 were significantly smaller than those fed on Ab24E in all tests and on SC229 in all tests except the 1992 fall armyworm test (Table 2). The large, negative estimates for GCA effects for Tx601 are quite different from those for Ab24E and SC229 (Table 4).

These bioassays were initiated to gain a better understanding of resistance in maize to these insects. The results indicate that both additive and nonadditive types of gene action are important in larval growth rates. The bioassays provide strong evidence of differences among inbred lines that appear to be quite similar when only leaf feeding damage ratings are considered. Consideration of additional components of resistance and different methods of measuring resistance and susceptibility will be especially important when undertaking investigations of the chemical nature of resistance.

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