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Inheritance of Resistance to the First and Second Broods of the European Corn Borer in Corn¹

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The European corn borer is one of the most destructive insect pests of corn. Our objective was to determine the inheritance of host resistance in corn to the first and second broods of the European corn borer with Design III and S₁ progeny analyses. All estimates of additive and dominance genetic variances were significantly different from zero except for the dominance variance for second-brood cavity counts. Additive genetic variance, however, was the major component of the total genotypic variance in the F₂ population for all traits. Average level of dominance was in the partial range for the date of anthesis (0.74), first-brood leaf feeding (0.81), and second-brood cavity counts (0.53), but in the range for complete dominance (1.09) for the second-brood visual rating. Some genes have dominance action in conditioning resistance to first and second broods of the European corn borer. Selection procedures that emphasize selection for additive genetic variance in the population for first- and second-brood larval feeding resistance would be effective for improving host resistance.

INDEX DESCRIPTORS: *Zea mays* L., genetic variance, level of dominance, genotypic and phenotypic correlations, heritability.

Development of corn (*Zea mays* L.) cultivars resistant to the European corn borer (*Ostrinia nubilalis*, Hübner) larval feeding is one of the most effective methods for control of his insect. Inheritance of resistance to first and second broods of the European corn borer was shown to be polygenic (10, 17, 18) and indicated that additive gene action was more important than nonadditive gene action in conditioning resistance to first-brood leaf feeding (7, 11, 14, 19). Average level of dominance also was estimated to be in the partial range for first-brood leaf feeding (11, 19). Genetic information, however, is limited for second-brood larval feeding. A 10-line diallel mating system (7) and a generation mean analysis (8) were the only studies that estimated the relative importance of additive to nonadditive gene action in the expression of resistance to second-brood larval feeding. Estimates of additive and dominance genetic variances and the average level of dominance have not been reported for host resistance to the second brood. Our objectives were: 1) to study the inheritance of resistance to the first and second broods of the European corn borer with a Design III mating plan and S₁ progeny analysis and 2) to compare estimates of genetic parameters obtained with Design III and S₁ analyses.

MATERIALS AND METHODS

The reference population was the F₂ population generated by crossing inbreds B52 and CI31A. CI31A is highly resistant to first-brood leaf feeding and intermediate in resistance to second-brood larval feeding. B52 is highly resistant to second-brood larvae but intermediate in resistance to first-brood leaf feeding. Experimental materials were produced from backcrosses of unselected F₂ plants used

as the male parents. F₂ plants were backcrossed to CI31A and B52 and selfed to obtain F₃(S₁) progenies. From each of the three progeny groups (two groups of Design III and one group of S₁ progenies), 108 families were chosen for evaluation on the basis of adequate seed supply. Each of the 108 families had a common F₂ parent in the other groups.

The experimental design was a randomized incomplete block with three replications within each set. Each of the three groups of 108 progenies was divided into six sets of 18 progenies. Each set was arranged in a split plot with subplots nested within main plots. Main plots included the three types of progeny groups; subplots included 18 entries within each main plot. The three progeny groups were separated in different blocks to avoid competition effects. Main plots were randomized within each replication, and subplots were randomized within main plots. Each single-row plot was 381 cm (16 hills) long, with 25.4 cm between hills and 76.2 cm between rows. The plots were overplanted and thinned to one plant per hill. Stand density was equivalent to 45,925 plants/ha.

Two entries were added to the 18 entries in each group in each set. These entries were used for the field arrangements and were later excluded from the analysis of variance for each group. The entries included with the Design III progenies were B52 and CI31A, whereas F₂ seeds were included with the S₁ progenies.

Progenies were evaluated in 1978 and 1979. Sixteen entries were replaced with 16 others in 1979 because of insufficient seed. Data were collected in 1978 for leaf-feeding rating of first-brood borers, stalk cavity counts and visual rating for sheath-collar feeding damage of second-brood borers, and date of anthesis. Data were taken only for the leaf feeding of the first-brood larvae in 1979.

In 1978, the first five plants at one end of each plot were infested with first-brood egg masses at the whorl stage of plant development; five plants on the opposite end were infested with second-brood egg masses when half the plants in a plot were shedding pollen. Techniques for production of egg masses and artificial infestation by first- and second-brood corn borers were described by Guthrie et al. (4). Each plant received 8 and 10 first-brood egg masses (ca. 200-250 eggs) in 1978 and 1979, respectively. Ten plants per plot were infested with first-brood egg masses in 1979. Sixteen egg masses (ca. 400 eggs) were applied per plant for the second-brood study with eight applications of two egg masses in 1-day intervals.

Leaf-feeding ratings for the first brood were made on an individual-plant basis about 3 weeks after egg hatch. A nine-class rating scale was

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used (3); class "one" represents the most resistant, and class "nine" the most susceptible plants (3).

Stalks were dissected longitudinally 50 to 60 days after egg hatch to permit counting and measurement of cavities made by the second-brood corn borers. A cavity 2.5 cm long was counted as one cavity; a cavity 15 cm long counted as six cavities. The visual rating for sheath-collar feeding of the second-brood borers was made with a nine-class scale (5) on a plot-mean basis. Class "one" represents little or no sheath-collar feeding, whereas class "nine" represents extensive sheath-collar feeding. Date of anthesis was recorded as the number of days from planting until 50% of the plants in each plot had shed pollen.

Data were analyzed on a plot-mean basis for all traits. Each set was analyzed separately, and the sums of squares and degrees of freedom were pooled across sets. From the analysis of variance of the Design III progenies, estimates of additive and dominance genetic variances, average levels of dominance, and heritabilities were obtained for all traits on the basis of the procedure of Comstock and Robinson (1). Genotypic variances and heritabilities also were obtained from the analysis of S₁ progenies. In addition, coefficients of variation, genotypic and phenotypic correlations, and standard errors of genetic parameters (9) were estimated. Standard errors of the heritabilities were determined by the method presented by Dickerson (2). Genotype-year interaction variances also were estimated for host responses to the first-brood leaf feeding.

RESULTS

Means and coefficients of variation (C.V.) for all traits are given in Table 1. The mean pollen shedding of B52 was 4 days earlier than that of CI31A. Earliness was dominant as expressed in the S₁ and Design III backcross progeny means. Resistance to larval feeding of the second brood was related to direction of cross, with the S₁ progenies near the midparent. First-brood ratings were in the resistant range with the means of the S₁ progenies, F₂, and backcross to CI31A having a rating closer to the more resistant parent (CI31A). Coefficients of variation (C.V.) were high for first- and second-brood larval feeding. High C.V.'s were common for corn borer resistance studies (7, 16).

Analyses of variance for individual years and of data combined over years (not presented) showed that all pertinent mean squares for Design III and S₁ analyses were statistically significant except for the males-years interaction for the first-brood leaf feeding. Genetic

variance among males is one-fourth of the additive genetic variance in the Design III mating system. Thus, the existence of significant additive genetic variance in the F₂ population was indicated. Significance of males by lines variance component suggests that some of the genes conditioning resistance to the first and second broods also exhibit dominance gene action. Interaction of additive genetic effects with years was not significant, but significance of males by lines by years interaction suggested the existence of an interaction between dominance deviations and years for the first brood. Estimates of additive and dominance by years interaction variances confirmed the results from the analysis of variance. The genetic effects by years interactions, however, were small compared with the estimates of genetic variances (Table 2). All estimates of additive and dominance genetic variances were significantly different from zero except for dominance variance for the second-brood cavity counts. Estimates of additive genetic variances, however, were at least three times greater than the dominance genetic variances except for the second-brood visual rating (additive variance was 1.6 times greater than dominance). The relative importance of additive to dominance genetic variance also was shown from the ratios of dominance to additive genetic variances (Table 2).

Estimates of the average level of dominance for the date of anthesis (0.74) and first-brood leaf feeding (0.81) were in the partial range, but they were not significantly different from the hypothesis of complete dominance. The average level of dominance was complete (1.09) for the second-brood visual rating, whereas it was in the partial range (0.53) for the second-brood cavity counts (Table 2).

Estimates of $\sigma_A^2 + \frac{1}{4}\sigma_D^2$ from the Design III analysis and genotypic variances from the analysis of S₁ progenies are shown in Table 3. Most of the estimates from S₁ progenies were similar to those from the Design III analysis.

All heritability estimates, on an entry-mean basis, were significantly different from zero (Table 4). Narrow-sense heritabilities from the Design III and heritability estimates from S₁ progeny analysis were high for all traits except for visual rating of second-brood damage. Heritability estimates from both methods of estimation were in good agreement.

Genotypic and phenotypic correlations were in close agreement in both sign and magnitude for all pairs of traits (Table 5). The phenotypic correlations of first-brood leaf feeding with second-brood visual rating and cavity counts were either small or zero. Most of the phenotypic correlations were significant but low in magnitude. These

Table 1: Means and coefficients of variation (C.V.) for days to anthesis and evaluations for response to European corn borer feeding for five generations of corn.

Trait	Population means						C.V. %
	S ₁	B52 x F ₂	CI31A x F ₂	F ₂	B52	CI31A	
Days to anthesis†	79.8 ± 0.05	77.8 ± 0.05	78.7 ± 0.05	78.6 ± 0.17	78.8 ± 0.17	82.9 ± 0.17	2
Second-brood‡ visual rating	6.7 ± 0.05	4.8 ± 0.05	6.6 ± 0.05	5.9 ± 0.17	5.2 ± 0.17	8.7 ± 0.17	15
Second-brood§ cavity counts	14.0 ± 0.17	10.6 ± 0.17	13.6 ± 0.17	12.1 ± 0.56	10.2 ± 0.56	18.4 ± 0.56	24
First brood‡ leaf feeding	1.6 ± 0.02	2.4 ± 0.02	1.2 ± 0.02	1.6 ± 0.07	3.7 ± 0.07	1.2 ± 0.07	26

†Days from planting to 50% anthesis.

‡Rated on a scale of 1 to 9 with 1 resistant and 9 susceptible and 2-year means for first-brood leaf feeding.

§Number of cavities.

Table 2. Estimates of genetic parameters and their standard errors from the Design III and S₁ progenies

Trait	Estimates			
	$\hat{\sigma}_A^2$	$\hat{\sigma}_D^2$	$\frac{\hat{a}}{\hat{a}}$	$\hat{\sigma}_A^2\hat{\sigma}_D^2$
Design III				
Days to Anthesis	1.95 ± 0.37	0.53 ± 0.12	0.74	0.27
Second-brood visual rating	0.53 ± 0.12	0.20 ± 0.07	1.09	0.59
Second-brood cavity counts	8.10 ± 2.07	1.12 ± 0.64	0.53**	0.14
First-brood† leaf feeding	0.26 ± 0.06 (0.04 ± 0.02)‡	0.08 ± 0.02 (0.05 ± 0.02)‡	0.81	0.33
S ₁ progenies				
First-brood† leaf feeding	0.15 ± 0.03§ (0.05 ± 0.02)‡	—	—	—

**Significant deviation from the hypothesis of $\hat{a} = 1$ at 1% probability level (a two-tailed F-test).

†Estimates obtained from 2-year combined analysis.

‡Estimates of interaction with years.

§Assuming either $p = q = 0.5$ or no dominance effects.

correlations probably have little biological meaning and merely reflect the large number of degrees of freedom involved in the test of significance.

DISCUSSION

The major portion of the total genetic variance was due to additive genetic variance for both first- and second-brood larval feeding. Although the Design III mating plan was a powerful design in the estimation of dominance genetic variances (1), estimates of dominance variance were smaller than the estimates of additive genetic variances. Other studies also have reported greater additive genetic variance compared with dominance genetic variance for first-brood leaf-feeding resistance (11, 14, 19). Our estimates of heritability were relatively high for resistance to first- and second-brood larvae, which agrees with other reports (16, 19). Selection methods that emphasize selection for additive effects would seem effective in improving the resistance level of the population to either brood of the European corn borer. No studies have been reported on the effectiveness of mass selection in improving populations for first- or second-brood resistance, but S₁ recurrent selection has been effective for first- (12, 15) and second-brood resistance (15).

The population under study was an F₂ of two inbred lines. It would

Table 3. Estimates of $(\sigma_A^2 + \frac{1}{4}\sigma_D^2)$ from the Design III analysis and genotypic variances from S₁ progenies

Trait	Design III	S ₁
	$\hat{\sigma}_A^2 + \frac{1}{4}\hat{\sigma}_D^2$	$\hat{\sigma}_G^2 = \sigma_A^2 + \frac{1}{4}\sigma_D^2$ †
Days to anthesis	2.08	2.08
Second-brood visual rating	0.38	0.49
Second-brood cavity counts	8.38	10.82
First-brood leaf feeding (1978)	0.27	0.12
First-brood leaf feeding (1979)	0.84	0.52
First-brood leaf feeding (combined)	0.28	0.15

†For $p = q = 0.5$.

Table 4. Estimates of heritabilities (h²) for four traits on an entry-mean basis

Trait	Design III		
	h ²		S ₁ progenies
	Narrow sense	Broad sense	h ²
Days to anthesis	0.70 ± 0.13	0.88 ± 0.14	0.87 ± 0.14
Second-brood visual rating	0.42 ± 0.15	0.67 ± 0.18	0.65 ± 0.14
Second-brood cavity counts	0.65 ± 0.16	0.74 ± 0.18	0.77 ± 0.14
First-brood leaf feeding, 1978	0.69 ± 0.14	0.84 ± 0.15	0.66 ± 0.14
First-brood leaf feeding, 1979	0.68 ± 0.11	0.93 ± 0.12	0.87 ± 0.14
First-brood leaf feeding, combined	0.61 ± 0.15	0.81 ± 0.16	0.70 ± 0.16

not be, therefore, a useful source population in a practical breeding program in the U.S. Corn Belt because the lines are late in maturity and have below-average combining ability. A synthetic variety could be constructed that includes B52 and CI31A and other lines of good agronomic performance and above-average resistance to the first- or second-brood borers. Improvement of the synthetic variety should make it possible to extract resistant inbred lines having above-average agronomic performance.

The statistical significance of the males by lines interaction in the analysis of variance and partial to complete average levels of dominance indicated that some genes act in a dominant manner in conditioning host resistance to first- and second-broods of the European corn borer. Because heterosis is a function of the level of dominance, it would be desirable to test the extracted inbred lines in hybrid combinations for first- and second-brood resistance.

Additive and dominance genetic variances and the average levels of dominance were estimated with the assumptions of no epistasis and no linkage or linkage equilibrium in the presence of linkage. These estimates are biased if the assumptions were not valid. Horner et al. (6) studied, theoretically, the effects of epistasis on the estimation of genetic parameters in the Design III. In three of the most commonly known types of epistasis (duplicate, complementary, and multiplicative), the amount and direction of bias was the same for the additive and dominance genetic variances. Inheritance studies of the first- and second-brood resistance have shown that epistasis was negligible or, when present, was not the major source of genetic variation (8, 14, 19). Thus, the presence of epistatic bias does not seriously bias the

Table 5. Phenotypic (upper number) and genotypic (lower number) correlations for traits studied in 1978.

Trait	Second-brood visual rating	Second-brood cavity counts	Days to anthesis
First-brood leaf feeding	-0.01 -0.08	0.17** 0.26	-0.13* -0.16
Second-brood visual rating		0.30** 0.44	0.26** 0.39
Second-brood cavity counts			-0.22** -0.22

*, **Statistically significant at the 5% and 1% levels of probability.

estimates of additive and dominance genetic variances and the average level of dominance.

Coupling phase linkage contributes to an overestimation of additive and dominance genetic variances, whereas repulsion phase linkages cause an underestimation of additive and overestimation of dominance genetic variances (1, 13). Estimates of additive genetic variance were greater than the estimates of dominance variance in our study. If linkage effects were important, coupling phase linkages would bias the estimates similarly. Repulsion phase linkages would bias the estimates differently, but the estimates of additive genetic variances were greater than dominance variances in all instances. Conclusions would not change if linkage effects were not present. Also, the average level of dominance will be estimated with no bias or with upward biases in the presence of linkages (1, 13). Values of less than one for first-brood leaf feeding, second-brood cavity counts, and date of anthesis and of 1.09 for second-brood visual rating indicated that the average level of dominance for these traits was not in the overdominance range in the presence of linkages. Average levels of dominance for first-brood leaf feeding also have been reported to be in the partial range (11, 19).

The small correlations of first-brood leaf feeding with second-brood larval feeding suggest a lack of pleiotropism or linkage among genes causing resistance to both broods. Russell et al. (16) also reported correlations close to zero between first- and second-brood resistance. The independent inheritance at these traits suggests the possibility of developing cultivars resistant to both broods. Russell and Guthrie (15) developed an F_7 line from pedigree selection of 200 F_3 lines from the cross of B52 \times Oh43. This line was better than Oh43 for first-brood resistance and was equal to B52 for second-brood resistance. Recent emphasis has been to develop populations resistant to both broods of the European corn borer through S_1 recurrent selection. The progress from this program, after two cycles, has been encouraging.

The similarity of estimates obtained from the S_1 and the Design III mating system indicated that the estimate of genotypic variance among S_1 families is a reliable indication of additive genetic variance in the population. S_1 recurrent selection would effectively exploit the additive genetic variance in populations for first- and second-brood larval feeding. S_1 recurrent selection has been effective for both broods (12, 15). The S_1 recurrent selection would be especially useful in the early cycles of selection if adequate additive genetic variance is available. Later, an alternative breeding scheme might be considered to exploit the small, nevertheless, significant dominance genetic variance. One cycle of selection could be completed each year for first-brood resistance, but a minimum of 2 years would be required for second-brood resistance.

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