

GENETIC STUDIES OF RESISTANCE FOR CORN
EARWORM [Heliothis zea (Boddie)] IN
SOYBEAN [Glycine max (L.) Merr.]

By

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EARWORM [*Heliothis zea* (Boddie)] IN
SOYBEAN [*Glycine max* (L.) Merr.]

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INTRODUCTION

The two chapters of this dissertation are separate and complete manuscripts. Chapter I and Chapter II are to be submitted to the Crop Science for publication.

CHAPTER I

Inheritance and Combining Ability of
Resistance for Corn Earworm
in Soybean

Inheritance and Combining Ability
of Resistance for Corn Earworm
in Soybean

ABSTRACT

Corn earworm [*Heliothis zea* (Boddie)] is one of the most destructive pests of soybean [*Glycine max* (L.) Merr.]. Its infestation sometimes can cause complete crop loss. Corn earworm management programs for soybean are emphasizing the development of corn earworm resistant cultivars since promising sources of resistance for this insect have been identified. Two experiments were conducted in the present study. In experiment 1, five adapted soybean cultivars (Oksoy, Essex, Forrest, Douglas, and Sohoma), one corn earworm resistant line (N80-50232), their 15 F₁ hybrids, and 15 F₂ populations were evaluated. In experiment 2, three adapted cultivars (Oksoy, Douglas, and Sohoma), the corn earworm resistant line (N80-50232), their six F₁ hybrids, their six F₂ populations, and twelve backcrosses [six BC₁ (P₁ X F₁) and six BC₂ (P₂ X F₁)] were evaluated. The objectives were: to determine the relative resistance to corn earworm among the soybean genotypes and to estimate general (GCA) and specific (SCA) combining ability effects for corn earworm resistance in soybean as determined by larval and

pupal survival, larval and pupal weight, and length of larval and pupal stage. Seeds of these genotypes were space planted at two locations, Stillwater and Perkins, Oklahoma, in a randomized complete block design with 9 replications in the summer of 1987. Antibiosis was studied in a growth chamber using leaves of these plant genotypes and corn earworm larvae obtained from a laboratory-reared colony. The corn earworm resistance of N80-50232 and its hybrids resulted in higher larval mortality, smaller larvae and pupae, and a longer larval stage. The responses of F₁ hybrids involving N80-50232 were intermediate between N80-50232 and the other parents for larval and pupal weight, indicating additive gene effects. Based on length of larval stage results, Sohoma and Oksoy appeared to have an intermediate level of resistance to the corn earworm, however much additional evidence would be needed before these two cultivars could be recommended as additional sources of corn earworm resistance. The corn earworm resistant line (N80-50232) had desirable GCA effects for larval and pupal weight and length of larval stage. The SCA effects of Oksoy/N80-50232 and Douglas/Sohoma for length of larval stage were significant and desirable, while these effects for Douglas/N80-50232 and Oksoy/Sohoma were significant, but undesirable, for this character.

Additional index words: Glycine max, Heliothis zea, general and specific combining abilities, additive gene action.

INTRODUCTION

Corn earworm [*Heliothis zea* (Boddie)] is one of the most destructive pests of soybean. Resistance to several damaging insects of soybean [*Glycine max* (L.) Merr.] has been identified (4, 5, 8, 9, 22, 23). Variation in resistance to corn earworm exists in soybean genotypes. The resistance has been determined to be antibiosis and/or non-preference (1, 8, 16). Since promising sources of resistance to the corn earworm have been identified, control through genetically mediated resistance would be an economically and ecologically superior insect pest management technique.

Van Duyn et al. (22, 23) determined that soybean plant introductions (PIs) 171451, 227687 and 229358 are resistant to the Mexican bean beetle, *Epilachna varivestis* (Mulsant). Clark et al. (4) found that the same 3 PIs have resistance to the corn earworm, *Heliothis zea* (Boddie), bean leaf beetle *Cerotoma trifurcat* (Forster) and striped blister beetle *Epicauta vittata* (F.). The mechanism of resistance was determined to be antibiosis. Also, Hatchett et al. (8), when studying leaf feeding resistance in soybean, determined that these three plant introductions are resistant to the corn earworm and the tobacco budworm *Heliothis virescens*

(Fabricius). They further concluded that antibiosis was the mechanism responsible for higher larval mortality, smaller larvae and pupae, and increased length of larval stage in both corn earworm and tobacco budworm. Likewise, Luedders and Dickerson (17) concluded that the three plant introductions were significantly more resistant to leaf feeding by second-instar cabbage looper larvae *Trichoplusia ni* (Hubner) than the two commercial cultivars included in their study. Studies conducted by Lambert and Hamer (14) indicated that there are significant differences among cultivars for level of resistance to soybean looper and velvetbean caterpillar.

In host plant resistance, determination of the value of the parent for resistance is very important. This value is determined mainly by two factors: the performance of the parent with respect to corn earworm resistance and the behavior of the parent in hybrid combinations. Information on the combining ability of corn earworm resistant genotypes for corn earworm resistance would help in selecting parents for future hybridization programs.

Significant levels of general and specific combining ability were reported from a diallel analysis of six sweet corn inbreds for corn earworm injury (25). Also, from a two year study, Widstrom (24) reported highly significant GCA and SCA mean squares separately and from the combined analysis. He further mentioned that all interactions of genetic effects with years were highly significant,

indicating that response to environment was not consistent from year to year. Also Widstrom and Hamm (26) reported that GCA effects were highly significant in two sets of diallel crosses among sweet corn lines. SCA estimates were generally low.

These studies were conducted to determine the relative resistance to corn earworm among the soybean genotypes and to estimate general (GCA) and specific (SCA) combining ability effects for corn earworm resistance in soybean as determined by larval and pupal survival, larval and pupal weight, and length of larval and pupal stage.

MATERIALS AND METHODS

Experiment 1:

In the summer of 1985 and 1986, N80-50232, an advanced soybean breeding line resistant to the corn earworm (2), and five adapted soybean cultivars [Oksoy (11), Essex (21), Forrest (7), Douglas (18), and Sohoma (12)] were crossed in a diallel fashion with no reciprocals.

Seeds of the six parents, 15 F₁s, and 15 F₂ populations were space planted at the Agronomy Research Stations located near Stillwater and Perkins, Oklahoma on 18 May and 16 June 1987, respectively. Test plants were arranged in a randomized complete block design with 9 replications. Each replication consisted of one plant from each parent, one plant from each F₁, and three plants from each F₂ (a total of 66 plants per replication).

Antibiosis was studied using the leaves of these plant genotypes and corn earworm larvae reared in the laboratory. Tests were conducted in a growth chamber maintained at 27 ± 1° C in constant darkness with relative humidity of 60%. The experimental design and number of replications were the same as used in the field.

The tests were started when plants were in the V₇ stage of development (6), using a bioassay technique described by

Hatchett et al. (8) with some modifications. The upper fully expanded trifoliolate was excised from each plant and placed in a 150 ml plastic vial with a lid. A moistened sponge was placed in the bottom of each vial to maintain relative humidity for the larva and to retard water loss from the leaflet. Filter paper was placed on top of the sponge to provide a smoother surface, to minimize water loss, and to make cleaning of the vials easier.

Corn earworm larvae used in the test were obtained from laboratory colonies reared on an artificial diet (3). Three newly hatched (<4 hours) larvae were placed in each vial with an artist's fine brush.

After three days, larvae were reduced to one per vial. After the first feeding, the old leaflet was removed, and a fresh leaflet was added to each vial every 48 hours during larval development.

After the initial feeding, the second, third, and fourth trifoliolates below the pinched trifoliolate were used for each feeding, respectively. After the fourth feeding, an effort was made to feed leaflets of approximately the same age at each feeding, but newly developed trifoliolates were avoided.

Criteria for antibiosis were: larval survival, larval weight at day 12, length of larval stage, pupal weight on the third day after pupation, length of pupal stage, and pupal survival.

After pupal weights were taken, pupae were transferred to cups containing wheat germ then returned to the growth chamber.

Experiment 2:

The experimental plant materials for this study were derived from a diallel cross (with no reciprocals) made in the summer of 1985 using N80-50232, Oksoy, Douglas, and Sohoma as parents. Backcrosses to each parent were made and F_2 seeds were produced in the summer of 1986.

The seeds of the four parents, six F_1 , six F_2 , and twelve backcrosses [six BC_1 ($P_1 \times F_1$) and six BC_2 ($P_2 \times F_1$)] were space planted at the Agronomy Research Stations located near Stillwater and Perkins, Oklahoma on 18 May and 22 June 1987, respectively. Test plants were arranged in a randomized complete block design with nine replications. Each replication consisted of one plant from each parent, one plant from each F_1 , three plants from each F_2 , and one plant from each backcross (a total of 40 plants per replication).

Methods for determining antibiosis were the same as used for Experiment 1.

To double the number of observations and increase the reliability of the results, statistical analyses were conducted on the data combined over locations and experiments, utilizing the four parents and six F_1 hybrids of experiment 2 which were also included in experiment 1.

Locations and experiments were considered as random factors and genotypes as a fixed factor. To have comparatively conservative tests, in cases of significant interaction (at 0.25 probability level) between genotypes X locations or genotypes X experiments, the genotypes and all other populations included in the genotypes were tested against genotypes X locations or genotypes X experiments mean square. Also, in cases of significant interaction (at 0.25 probability level) between genotypes X locations X experiments, the genotypes and all other populations included in the genotypes were tested against the pooled (genotypes X locations + genotypes X experiments + genotypes X locations X experiments) mean square.

RESULTS AND DISCUSSION

The mean squares for larval weight, length of larval stage, and pupal weight for the data combined over locations and experiments are given in Tables 1, 2, and 3, respectively. There were statistically significant differences among genotypes for larval weight, length of larval stage, and pupal weight. The overall heterosis was nonsignificant for these three characters. There were statistically significant differences among the parents and between N80-50232 and the adapted cultivars. The differences among the adapted cultivars for length of larval stage were statistically significant. For larval and pupal weight, differences among the adapted cultivars were not statistically significant. The differences among the F_1 s were statistically significant for length of larval stage, while the differences among the F_1 s were nonsignificant for larval and pupal weight. Also, the interaction of genotypes X locations for larval weight and the interaction of genotypes X experiments for pupal weight were declared significant at the 0.25 and 0.05 levels of probability, respectively, indicating that the genotypes performed differently relative to one another over the locations and the experiments for larval and pupal weight. The

interaction of genotypes X locations X experiments was significant for length of larval stage, revealing that the relative performance of the genotypes was not stable over the locations and experiments.

The numerical value used for larval and pupal survival was 1 and for larval and pupal mortality was 0. Because statistical differences were not detected for % larval and pupal survival and for length of pupal stage the mean squares are not given; however, the entry means are presented in Appendix Table 1.

The mean performance of the parents and their F_1 s for larval and pupal weight and for length of larval stage (Table 4) indicated that larvae reared on leaves from N80-50232 weighed significantly less, needed a longer larval stage, and resulted in smaller pupae than all other parents. These results are consistent with the results obtained by others (1, 9, 15, 20). The data also indicated that larvae reared on leaves from Sohoma and Oksoy weighed less, needed a longer larval stage, and produced smaller pupae when compared with Douglas; however, these three cultivars were not significantly different from each other statistically for larval and pupal weight.

Larvae reared on leaves from F_1 s involving N80-50232 as one of their parents produced smaller larvae, and resulted in smaller pupae, than larvae reared on the leaves from the adapted cultivars and the F_1 s derived from the adapted cultivars. When comparisons between N80-50232, the adapted

cultivars, and the derived intercrosses were made, it was determined that resistance was N80-50232 > F₁s involving N80-50232 as one of the parents > adapted cultivars and their derived F₁s. These results are similar to those obtained in other studies (10, 13, 15, 19).

Larvae reared on leaves from N80-50232 and the crosses involving N80-50232 survived relatively less than all other genotypes, although these differences were not statistically significant (Appendix Table 1). Similar results have been reported (1, 15, 20). There was not clear distinction among the effects of parents and their intercrosses on the percent pupal survival. Also, there were no distinct differences among the genotypes for length of pupal stage.

Combining Ability:

The mean square for general combining ability (GCA) was statistically significant for larval weight (Table 1). The mean square for specific combining ability (SCA) was statistically significant for length of larval stage (Table 2).

The GCA effect of N80-50232 for larval weight was highly significant statistically and desirable (-69.17), indicating that larvae reared on the leaves involving this genotype weighed less, hence N80-50232 is considered resistant to the corn earworm based on this character and the resistance could be transferred to adapted cultivars (Table 5). On the other hand, the GCA effects for the other

parents were nonsignificant and in the undesirable direction. The GCA effects of N80-50232 for length of larval stage and pupal weight were statistically significant at the 0.05 and 0.01 probability levels, respectively. These effects as shown in Table 5 were also in the desirable direction indicating that larvae reared on leaves involving N80-50232 took longer to pupate (0.51) and resulted in smaller pupae (-31.38). This also indicates that resistance could be transferred to adapted cultivars. On the other hand, the GCA effects of the other parents were of opposite sign and different magnitudes than N80-50232, and were statistically not different from zero.

The GCA and SCA mean squares for length of pupal stage and larval and pupal survival were nonsignificant, therefore, tables for these mean squares were not given. However, the estimates of both GCA and SCA effects are presented in Appendix Table 2.

The SCA effects for larval weight for Oksoy/N80-50232 and Douglas/Sohoma were in the desirable direction (each -23.12) although none of the SCA effects for larval weight were significant statistically (Table 5).

The SCA effects of Oksoy/N80-50232 and Douglas/Sohoma for length of larval stage shown in Table 5 were highly significant and desirable (each 0.85), indicating that larvae reared on the leaves from these genotypes needed significantly more days to pupate than all other crosses. Hence, based on this character, these genotypes could be

considered resistant to the corn earworm. This means that corn earworm resistant segregates may be derived from these crosses, based on the length of larval stage. On the other hand, the SCA effects of Douglas/N80-50232 and Oksoy/Sohoma were significant, but undesirable (each -0.48), indicating that larvae reared on these genotypes needed significantly fewer days to pupate. These genotypes can be considered susceptible to the corn earworm and resistant segregates can not be derived from these crosses based on the results of this character. The SCA effects of Sohoma/N80-50232 and Oksoy/Douglas were in the undesirable direction, but not statistically significant. These results suggest that resistance in soybean to the corn earworm, based on the length of larval stage, could be controlled by other than additive gene action. For pupal weight, SCA effects were in the undesirable direction for Douglas/N80-50232 and Oksoy/Sohoma but in the desirable direction for the other four crosses. However, none of the SCA effects were of significance at the 0.05 level for pupal weight.

From the results of these experiments, it can be concluded that N80-50232 does possess resistance to the corn earworm and that this resistance is transmitted to, and expressed in, F_1 intercrosses involving N80-50232. Thus, the resistance appears to be an inherited trait and should be transferable to other genotypes. Also, it was declared that additive gene action is controlling the resistance in soybean to the corn earworm based on larval and pupal weight

since the F_1 s showed an intermediate response. Based on the length of larval stage results, Sohoma and Oksoy appeared to have an intermediate level of resistance to the corn earworm, however much additional evidence would be needed before these two cultivars could be recommended as additional sources of corn earworm resistance. Based on the results obtained under the conditions of these experiments it can be concluded that larval and pupal survival and length of pupal stage are not good characters to use in studying the expression of corn earworm resistance in soybean. Significant GCA effects of N80-50232 in a desirable direction for larval and pupal weight and length of larval stage indicated that resistance based on these characters could be transferred to other genotypes. Also, significant SCA effects of Oksoy/N80-50232 and Douglas/Sohoma for length of larval stage indicated that corn earworm resistant segregates may possibly be derived from these crosses.

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Table 1: Mean squares for larval weight for the data combined over locations and experiments.

Source	df	MS
Locations(L)	1	141340
Experiments(E)	1	75503
L X E	1	3684
Replications(L E)	32	48841
Genotypes(G)§	9	118053 *
Generations	1	3079
Parents	3	208080 **
N80- vs Adap.cv.	1	427976 **
Adap.cv.	2	98123
F ₁	5	87031
GCA	3	122235 *
SCA	2	23200
G X L§	9	27586 +
G X E§	9	20761
G X L X E†	9	13898
Residual	234	19773
Total	305	

+,*,** significant at 0.25, 0.05, and 0.01 probability levels, respectively.

† G X L X E was tested against residual MS.

§ G X L and G X E were tested against the pooled (G X L X E + Residual MS).

§ Because the interaction of G X L was significant at 0.25 level of probability, genotypes and all other populations included in the genotypes were tested against G X L MS (27586).

Table 2: Mean squares for length of larval stage for the data combined over locations and experiments.

Source	df	MS
Locations(L)	1	105.65
Experiments(E)	1	3.96
L X E	1	25.63
Replications(L E)	32	7.01
Genotypes(G)§	9	19.57 **
Generations	1	9.52
Parents	3	31.74 **
N80- vs Adap.cv.	1	56.31 **
Adap.cv.	2	19.46 *
F ₁	5	14.28 *
GCA	3	6.05
SCA	2	24.53 *
G X L§	9	2.00
G X E§	9	7.34
G X L X E†	9	6.89 *
Residual	184	3.31
Total	255	

*,** significant at 0.05 and 0.01 probability levels, respectively.

† G X L X E was tested against residual MS.

§ G X L and G X E were tested against G X L X E MS.

§ Because the interaction of G X L X E was significant at 0.05 level of probability, genotypes and all other populations included in the genotypes were tested against the pooled (G X L + G X E + G X L X E) MS (5.41).

Table 3. Mean squares for pupal weight for the data combined over locations and experiments.

Source	df	MS
Locations(L)	1	2878
Experiments(E)	1	12157
L X E	1	9869
Replications(L E)	32	5041
Genotypes(G)\$	9	22604 *
Generations	1	874
Parents	3	42814 *
N80- vs Adap.cv.	1	103020 **
Adap.cv.	2	12712
F ₁	5	14824
GCA	3	21145
SCA	2	3318
G X L\$	9	1548
G X E\$	9	7104 *
G X L X E†	9	3202
Residual	184	3183
Total	255	

*,** significant at 0.05 and 0.01 probability levels, respectively.

† G X L X E was tested against residual MS.

\$ G X L and G X E were tested against the pooled (G X L X E + Residual MS).

§ Because the interaction of G X E was significant at .05 level of probability, genotypes and all other populations included in the genotypes were tested against G X E MS (7104).

Table 4. Means of parents and their F₁ hybrids for larval and pupal weight and length of larval stage for the data combined over locations and experiments.

Genotypes	LWT	LofLStg	PWT
	(mg)	(days=24 h)	(mg)
N80-50232	276	18.71	239
Oksoy	406	17.37	311
Douglas	462	15.94	340
Sohoma	391	17.14	309
Oksoy/N80-50232	308	18.05	271
Douglas/N80-50232	346	16.15	287
Sohoma/N80-50232	348	16.58	287
Oksoy/Douglas	447	15.91	313
Oksoy/Sohoma	427	16.13	334
Douglas/Sohoma	401	17.06	309

Standard error for LWT, LofLStg, and PWT = 31.00, 0.51, and 18.00, respectively.

Table 5. Estimates of GCA and SCA effects for larval and pupal weight and length of larval stage for the data combined over locations and experiments.

Parent	GCA		
	LWT	LofLStg	PWT
N80-50232	-69.17 **	0.51 *	-31.38 **
Oksoy	28.18	-0.01	14.49
Douglas	27.41	-0.35	3.30
Sohoma	13.57	-0.14	13.58

*,** significant at the 0.05 and 0.01 probability levels, respectively.

Cross	SCA		
	LWT	LofLStg	PWT
Oksoy/N80-50232	-23.12	0.85 **	-6.46
Douglas/N80-50232	10.58	-0.48 *	9.48
Sohoma/N80-50232	12.54	-0.37	-3.02
Oksoy/Douglas	12.54	-0.37	-3.02
Oksoy/Sohoma	10.58	-0.48 *	9.48
Douglas/Sohoma	-23.12	0.85 **	-6.46

*,** significant at the 0.05 and 0.01 probability levels, respectively.

CHAPTER II

Heritability of Resistance for Corn Earworm
and Correlations Between
Characters in Soybean

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ABSTRACT

Determination and knowledge of the heritability of resistance to corn earworm [*Heliothis zea* (Boddie)] in soybean [*Glycine max* (L.) Merr.] is very important for development of improved cultivars. Two experiments were conducted in the present study. In experiment 1, five adapted soybean cultivars (Oksoy, Essex, Forrest, Douglas, and Sohoma), one corn earworm resistant line (N80-50232), their 15 F₁ hybrids and 15 F₂ populations were evaluated. In experiment 2, three adapted cultivars (Oksoy, Douglas, and Sohoma), the corn earworm resistant line (N80-50232), their six F₁ hybrids, their six F₂ populations, and 12 backcrosses [six BC₁ (P₁ X F₁) and six BC₂ (P₂ X F₁)] were evaluated. The objectives were: to estimate broad-sense heritability for larval and pupal survival, larval and pupal weight, and length of larval and pupal stage, and to estimate the correlations among these characters. Seeds of these plant genotypes were space planted at two locations, Stillwater and Perkins, Oklahoma, in a randomized complete block design with 9 replications in the summer of 1987.

Antibiosis was studied in a growth chamber using the leaves of these plant genotypes and corn earworm larvae obtained from a laboratory-reared colony. The numerical values of 0 or 1 were given for larval and pupal mortality or survival, respectively. Length of pupal stage was measured on a day basis, i.e. 24 hour increments. Because the values recorded for these three characters did not satisfactorily distinguish the variation, broad-sense heritability was not estimated and correlations involving these characters were not determined. The magnitude of the broad-sense heritability estimates for larval weight, length of larval stage, and pupal weight were quite variable over the six crosses ranging from -0.32 to 0.29, from -0.04 to 0.57, and from -0.03 to 0.52, respectively. In general, the broad-sense heritability estimates of crosses involving N80-50232 were higher than the other populations. Hence, selection for resistance would be more effective in F₂ populations involving the resistant line. Larval weight and pupal weight were positively correlated, and each was negatively correlated with length of larval stage.

Additional index words: [*Glycine max* (L.) Merr.], [*Heliothis zea* (Boddie)], broad-sense heritability estimates and correlation.

INTRODUCTION

Development of resistant host plants of soybean is one of the best means for effective management of corn earworm in soybean fields. Pathak (13) compared host plant resistance with other methods of control. He emphasized that resistant plants are more desirable than other control methods, because insects on resistant plants are often restless, less vigorous, and more susceptible to environmental variations, predators, and insecticides. Kea et al. (6) indicated that although high levels of resistance, especially in the form of pest mortality, are desirable, evidence suggests that much lower levels can effectively reduce the general vigor of the pest while increasing the efficiency of pesticide treatments.

Evidence provided by several studies (7, 10, 14) indicated that corn earworm resistance in the soybean plant introduction (PI) 229358 is an inherited trait, although the genetic basis of this resistance is still not fully understood.

Sisson et al. (14) concluded that the resistance of soybean to Mexican bean beetle [*Epilachna varivestis* (Mulsant)] was quantitatively inherited. They determined that population means of F₃ progeny were not significantly

different from their midparent values, suggesting additive gene action. They determined broad-sense heritability estimates which ranged from 44 to 81%. Luedders and Dickerson (11) worked on the resistance of soybean to the cabbage looper larvae. They determined that heritability estimates for leaf-feeding ranged from 6 to 41%. They added that limited population size may have been the major factor because heritability tended to increase with number of progeny. They concluded that linkage between resistance and maturity genes would not be a factor in transferring the resistance from the late-maturing plant introductions to genotypes adapted in more northern latitudes.

Widstrom and McMillian (16) studied the genetic effects of resistance of corn to corn earworm. They determined that broad-sense heritability estimates, on an individual plant basis, were 29% for both sweet and dent groups. They further indicated that additive gene effects among sweet corn crosses and dominance effects among dent corn crosses are involved in controlling the resistance.

The objectives of these studies were: to estimate broad-sense heritability for larval and pupal survival, larval and pupal weight, and length of larval and pupal stage, and to estimate the correlations between these characters.

MATERIALS AND METHODS

Experiment 1:

In the summer of 1985 and 1986, N80-50232, an advanced soybean breeding line resistant to the corn earworm (1), and five adapted soybean cultivars [Oksoy (8), Essex (15), Forrest (4), Douglas (12), and Sohoma (9)] were crossed in a diallel fashion with no reciprocals. F₂ seeds were produced in the summer of 1986 and winter of 1986-87.

Seeds of the six parents, 15 F₁'s, and 15 F₂'s were space planted at the Agronomy Research Stations located near Stillwater and Perkins, Oklahoma on 18 May and 16 June 1987, respectively. Test plants were arranged in a randomized complete block design with 9 replications. Each replication consisted of one plant from each parent, one plant from each F₁, and three plants from each F₂ (a total of 66 plants per replication).

Antibiosis was studied using the leaves of these plant genotypes and corn earworm larvae reared in the laboratory. Tests were conducted in a growth chamber maintained at 27 ± 1° C in constant darkness with relative humidity of 60%. The experimental design and number of replications were the same as used in the field.

The tests were started when plants were in the V₇ stage of development (3), using a bioassay technique described by Hatchett et al. (5) with some modifications. The upper fully expanded trifoliolate was excised from each plant and placed in a 150 ml plastic vial with a lid. A moistened sponge was placed in the bottom of each vial to maintain relative humidity for the larva and to retard water loss from the leaflet. Filter paper was placed on top of the sponge to provide a smoother surface, to minimize water loss, and to make cleaning of the vials easier.

Corn earworm larvae used in the test were obtained from laboratory colonies reared on an artificial diet (2). Three newly hatched (<4 hours) larvae were placed in each vial with an artist's fine brush.

After three days, larvae were reduced to one per vial. After the first feeding, the old leaflet was removed and a fresh leaflet was added to each vial every 48 hours during larval development.

After the initial feeding, second, third, and fourth trifoliolates below the pinched trifoliolate were used for each feeding, respectively. After the fourth feeding, an effort was made to feed leaflets of approximately the same age at each feeding, but newly developed trifoliolates were avoided.

Criteria for antibiosis were: larval survival, larval weight at day 12, length of larval stage, pupal weight on

the third day after pupation, length of pupal stage, and pupal survival.

After pupal weights were taken, pupae were transferred to cups containing wheat germ then returned to the growth chamber.

Experiment 2:

The plant materials for this study were derived from a diallel cross (with no reciprocals) made in the summer of 1985 using N80-50232, Oksoy, Douglas, and Sohoma as parents. Backcrosses to each parent were made and F_2 seeds were produced in the summer of 1986.

The seeds of the four parents, six F_1 , six F_2 , and twelve backcrosses [six BC_1 ($P_1 \times F_1$) and six BC_2 ($P_2 \times F_1$)] were planted at the Agronomy Research Stations located near Stillwater and Perkins, Oklahoma on 18 May and 22 June 1987, respectively. Test plants were arranged in a randomized complete block design with nine replications. Each replication consisted of one plant from each parent, one plant from each F_1 , three plants from each F_2 , and one plant from each backcross (a total of 40 plants per replication).

Methods for determining antibiosis were the same as used for experiment 1.

To double the number of observations and increase the reliability of the results, broad-sense heritabilities and correlations between characters were estimated on the data combined over locations and experiments, utilizing the four

parents, six F₁, and six F₂ generations of experiment 2 which were also included in experiment 1. Locations and experiments were considered as random factors and genotypes as a fixed factor in deriving the variances which were used for broad-sense heritability calculations. The numerical values of 0 and 1 were given for larval and pupal mortality or survival, respectively. Length of pupal stage was measured on a day basis, i.e. 24 hour increments. Because the values recorded for these three characters did not satisfactorily distinguish the variation, broad-sense heritability was not estimated and correlations involving these characters were not determined.

Broad-sense heritability estimates (h^2_{bs}) on a plant basis were calculated as:

$$h^2_{bs} = \frac{VF_2 - \frac{1}{3} (VP_1 + VP_2 + VF_1)}{VF_2}$$

where VF₂, VP₁, VP₂, and VF₁ = variance of F₂, parent one, parent two, and F₁, respectively. Variance for broad-sense heritability estimates was computed as:

$$Vh^2_{bs} = \left[\frac{2}{(VF_2)^2 (9)} \right] \left[\frac{(VP_1)^2}{dfP_1} + \frac{(VP_2)^2}{dfP_2} + \frac{(VF_1)^2}{dfF_1} + \frac{(VP_1+VP_2+VF_1)}{dfF_2} \right]$$

where dfP₁, dfP₂, dfF₁, and dfF₂ = degrees of freedom for parent one, parent two, F₁, and F₂, respectively. A standard error for each broad-sense heritability estimate was calculated by taking the square root of the variance for the broad-sense heritability estimate.

If the magnitude of a broad-sense heritability estimate exceeds its standard error by two times, then it is statistically different from zero at the 0.05 probability level. If this magnitude exceeds its standard error by three or more times, then it is statistically different from zero at the 0.01 probability level.

Phenotypic correlations (r_p) on a plant basis were calculated as:

$$r_p = \frac{\text{Cov}(x,y)_{F_2}}{[(Vx)_{F_2} (Vy)_{F_2}]^{.5}}$$

where $\text{cov}(x,y)_{F_2}$ represents the covariance between the character x and y of the F_2 , $(Vx)_{F_2}$ and $(Vy)_{F_2}$ denote the variances of x and y of the F_2 , respectively.

Environmental correlations (r_e) on a plant basis were calculated as:

$$r_e = \frac{\text{Cov}(x,y)_E}{[(Vx)_E (Vy)_E]^{.5}}$$

where $\text{Cov}(x,y)_E$ represents the covariance between the character x and y of the environment, $(Vx)_E$ and $(Vy)_E$ represent the variances of x and y of the environment, respectively.

$$\text{Cov}(x,y)_E = \frac{\{dfP_1[\text{Cov}(x,y)_{P_1} + dfP_2[\text{Cov}(x,y)_{P_2} + dfF_1[\text{Cov}(x,y)_{F_1}]]\}}{dfP_1 + dfP_2 + dfF_1}$$

Genotype correlations (r_g) on a plant basis were calculated as:

$$r_g = \frac{\text{Cov}(x,y)_{F_2} - \text{Cov}(x,y)_E}{[(Vx)_{F_2} - (Vy)_E]^{.5} [(Vy)_{F_2} (Vy)_E]^{.5}}$$

A standard error for the genotypic correlations was calculated as:

$$\begin{aligned}
 SE(r_g) = r_g \{ & \frac{[(\text{Cov}(x,y)F_2)^2 + (Vx)F_2 (Vy)F_2] /}{dfF_2 + [\text{Cov}(x,y)_E^2 + (Vx)_E (Vy)_E] / df_E} \\
 + & \frac{[(Vx)F_2]^2 / dfF_2 + [(Vx)_E]^2 / df_E}{2[(Vx)F_2 - (Vx)_E]^2} + \frac{[(Vy)F_2]^2 / dfF_2 + [(Vy)_E]^2 / df_E}{2[(Vy)F_2 - (Vy)_E]^2} \\
 - & \frac{2[\text{Cov}(x,y)F_2 (Vx)F_2] / dfF_2 + 2[\text{Cov}(x,y)_E (Vx)_E] / df_E}{(Vx)F_2 - (Vx)_E} \\
 - & \frac{2[\text{Cov}(x,y)F_2 (Vy)F_2] / dfF_2 + 2[\text{Cov}(x,y)_E (Vy)_E] / df_E}{(Vy)F_2 - (Vy)_E} \\
 + & \frac{[\text{Cov}(x,y)F_2]^2 / dfF_2 + [\text{Cov}(x,y)_E]^2 / df_E}{[(Vx)F_2 - (Vx)_E] [(Vy)F_2 - (Vy)_E]} \}^{.5}
 \end{aligned}$$

If the magnitude of a genetic correlation exceeds its standard error by two times, then it is said to be statistically different from zero at the 0.05 probability level. If this magnitude exceeds its standard error by three or more times, then it is statistically different from zero at the 0.01 probability level.

RESULTS AND DISCUSSION

Broad-sense heritability:

In soybean [*Glycine max* (L.) Merr.] determination of heritability for corn earworm [*Heliothis zea* (Boddie)] resistance is very important for deciding appropriate strategies to be used in future selection programs for corn earworm resistance.

Broad-sense heritability estimates for larval and pupal weight and length of larval stage are presented in Table 1. The magnitudes of the heritability estimates for larval weight, length of larval stage, and pupal weight were quite variable over all crosses ranging from -0.32 to 0.29, from -0.04 to 0.57, and from -0.03 to 0.52, respectively.

For larval weight, the estimated heritability values of Oksoy/N80-50232 and Douglas/N80-50232 were significantly different from zero, indicating the presence of more variability for resistance to corn earworm in these populations than in other populations. Similarly, the heritability estimates of Oksoy/N80-50232, Douglas/N80-50232, Sohoma/N80-50232, and Douglas/Sohoma for length of larval stage were statistically significantly different from zero, which also indicates the presence of more genetic variability for corn earworm resistance in these

populations. For pupal weight, the heritability estimates of Oksoy/N80-50232, Douglas/N80-50232, Sohoma/N80-50232, and Oksoy/Douglas were statistically different from zero, revealing the presence of more genetic variability for resistance to corn earworm in these populations. Selection for corn earworm resistance based on larval and pupal weight and length of larval stage, would be more effective in populations containing higher levels of genetic variability for resistance.

Correlations between characters:

Phenotypic (r_p), genotypic (r_g), and environmental (r_e) correlation coefficients among the three characters, with the data combined over locations and experiments, are given in Tables 2, 3, and 4, respectively.

Phenotypic correlation is the relationship between values of two characters on the same insect reared on the leaves from one genotype. The genetic correlation, on the other hand, is the relationship between an insect's genetic value for one character and the same insect's genetic value for the other character. Environmental correlation could be defined as the relationship between an insect's environment for one character and the same insect's environment for the other character.

When phenotypic correlation coefficients between two characters are significant, it indicates that the two characters are associated. When calculating genetic

correlations from variance components, it is possible to derive estimates numerically greater than 1. This happens primarily between characters with relatively high phenotypic correlations, but with low heritability estimates.

Genotypic correlation coefficients could not be estimated for characters that had negative heritability estimates. Also, standard errors for genotypic correlations for some crosses could not be estimated due to the negative genetic variances.

Larval weight was negatively correlated phenotypically with length of larval stage and this correlation was statistically highly significant in all populations, ranging from -0.50 to -0.66. The genetic correlation between these two characters for Douglas/N80-50232 was also highly significant (-0.63). The correlation coefficient between these two characters for Douglas/Sohoma was strongly influenced by the environment.

Larval weight was positively correlated phenotypically with pupal weight and this correlation was highly significant in all populations, ranging from 0.53 to 0.70. The genotypic correlation between these two characters (0.52) was significant for Oksoy/N80-50232. It seems that environment had some influence on the correlation between these two characters in Oksoy/Douglas.

Length of larval stage was negatively correlated with pupal weight and this correlation was statistically highly significant for all populations, ranging from -0.48 to

-0.60. These two characters were also correlated genotypically and the correlation was significant and highly significant (-0.55 and -0.73) for Oksoy/N80-50232 and Douglas/N80-50232, respectively. The influence of environment on the correlations of length of larval stage and pupal weight was minimal.

From the results of these experiments it can be concluded that significant levels of genetic variability were present for larval and pupal weight and length of larval stage, but not in all populations. Hence, selection for corn earworm resistance would be more effective in F_2 populations containing the genetic variability based on these three characters. In general, heritabilities for length of larval stage and pupal weight were higher than for larval weight, indicating that selection based on the former two characters would be more effective for corn earworm resistance. Environment influenced the genetic variability in some crosses for larval weight, length of larval stage, and pupal weight. Positive correlation existed between larval weight and pupal weight. Negative correlation existed between larval weight and length of larval stage and between length of larval stage and pupal weight. More research is required to determine the genetic relationship of larval weight with length of larval stage, larval weight with pupal weight, and length of larval stage with pupal weight.

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Table 1. Estimates of broad-sense heritability and their standard errors for larval and pupal weight and for length of larval stage for the data combined over locations and experiments.

Cross	LWT	LofLStg	PWT
Oksoy/N80-50232	.29 ± .11 *	.37 ± .12 **	.35 ± .13*
Douglas/N80-50232	.26 ± .11 *	.57 ± .11 **	.52 ± .09 **
Sohoma/N80-50232	.14 ± .16	.41 ± .12 **	.28 ± .14*
Oksoy/Douglas	.22 ± .13	.13 ± .16	.27 ± .13*
Oksoy/Sohoma	-.32 ± .21§	-.04 ± .18§	.12 ± .15
Douglas/Sohoma	.18 ± .15	.35 ± .13 *	-.03 ± .18§

*,** Significant at 0.05 and 0.01 probability levels, respectively.

§ Value < 0 may be interpreted as 0.

Table 2. Phenotypic correlations among three characters in six soybean crosses for the data combined over locations and experiments.

Cross	LWT vs LofLStg	LWT vs PWT	LofLStg vs PWT
Oksoy/N80-50232	-.66 **	.53 **	-.50 **
Douglas/N80-50232	-.53 **	.70 **	-.57 **
Sohoma/N80-50232	-.58 **	.63 **	-.54 **
Oksoy/Douglas	-.58 **	.57 **	-.55 **
Oksoy/Sohoma	-.51 **	.62 **	-.60 **
Douglas/Sohoma	-.50 **	.57 **	-.48 **

** Significant at 0.01 probability level.

Table 3. Genotypic correlations among three characters in six soybean crosses for the data combined over locations and experiments.

Cross	LWT vs LofLStg	LWT vs PWT	LofLStg vs PWT
Oksoy/N80-50232	-.67§	.52 ± .22 *	-.55 ± .20*
Douglas/N80-50232	-.63 ± .11**	.88§	-.73 ± .10**
Sohoma/N80-50232	-.76§	2.14§	-.92§
Oksoy/Douglas	-.96§	.48§	-.83§
Oksoy/Sohoma	----†	----†	----†
Douglas/Sohoma	-.30 ± .51	----†	----†

*,** Significant at 0.05 and 0.01 probability levels, respectively.

§ Because of the negative genotypic variances, standard error could not be calculated.

† Genotypic correlation could not be calculated because of negative h^2_{bs} estimates.

Table 4. Environmental correlations among three characters in six soybean crosses for the data combined over locations and experiments.

Cross	LWT vs LofLStg	LWT vs PWT	LofLStg vs PWT
Oksoy/N80-50232	-.64 **	.54 **	-.48 **
Douglas/N80-50232	-.45 **	.57 **	-.39 **
Sohoma/N80-50232	-.63 **	.46 **	-.38 **
Oksoy/Douglas	-.50 **	.60 **	-.49 **
Oksoy/Sohoma	-.69 **	.55 **	-.41 **
Douglas/Sohoma	-.59 **	.50 **	-.52 **

** Significant at 0.01 probability level.

APPENDIXES

Appendix Table 1. Means of parents and their respective F_1 hybrids for larval and pupal survival and length of pupal stage for the data combined over locations and experiments.

Genotype	L. Sur.	LofPStg	P. Sur.
	(%)	(days=24 h)	(%)
N80-50232	0.58	11.91	0.86
Oksoy	0.78	11.64	0.88
Douglas	0.86	11.45	0.82
Sohoma	0.77	11.43	0.92
Oksoy/N80-50232	0.75	11.66	0.81
Douglas/N80-50232	0.67	11.95	0.92
Sohoma/N80-50232	0.68	11.31	0.92
Oksoy/Douglas	0.84	11.42	0.85
Oksoy/Sohoma	0.82	11.47	0.95
Douglas/Sohoma	0.84	11.60	0.85

Standard error for L. Sur., LofPStg, and P. Sur. = 0.5183, 0.3136, and 0.0719, respectively.

Appendix Table 2. Estimates of GCA and SCA effects for larval and pupal survival and length of pupal stage for the data combined over locations and experiments.

Parent	GCA		
	L. Sur.	LofPStg	P. Sur.
N80-50232	-0.09 *	-0.01	-0.01
Oksoy	0.05	-0.07	-0.02
Douglas	0.03	0.10	-0.02
Sohoma	0.01	-0.02	0.05

* significant at 0.05 probability level.

Cross	SCA†		
	L. Sur.	LofPStg	P. Sur.
Oksoy/N80-50232	0.02	0.10	-0.05
Douglas/N80-50232	-0.01	0.10	0.05
Sohoma/N80-50232	-0.01	-0.21	0.00
Oksoy/Douglas	-0.01	-0.21	0.00
Oksoy/Sohoma	-0.01	0.10	0.05
Douglas/Sohoma	0.02	0.10	-0.05

† SCA of all crosses are nonsignificant at 0.05 probability level.

VITA

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