GENETIC STUDIES OF AGRONOMIC CHARACTERS

IN SOYBEANS [GLYCINE MAX (L.) MERR.]

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CHAPTER I

INTRODUCTION

The soybean, a native of eastern Asia, has become a major grain crop in the United States in the past half century. The United States presently accounts for about 50 percent of the world production of soybeans. Soybeans are an economically important crop in many areas of the world. Soybeans are used for human consumption, animal food, and several industrial uses. Soybean seed consists of approximately 40 percent protein and 20 percent oil.

The primary goal of a soybean breeder is to increase seed yield to help insure a sufficient food supply to meet the growing human requirements. A better understanding of the mode of inheritance for agronomic characters is necessary if further improvements are to be accomplished.

Heterosis and inbreeding depression for seed yield have been reported in soybeans, suggesting that it may be worthwhile to search for favorable heterozygous gene combinations. Information pertaining to the nature of heterosis, inbreeding depression, and combining ability for seed yield and yield components is presented in Chapter II. A four-parent diallel mating system is used for the studies in Chapters II and III. Chapter III involves heterosis, inbreeding depression, and combining ability of plant height, plant yield, and harvest index.

In Chapter IV, broad-sense heritability estimates for agronomic

characters are reported. The associations of seed yield with other agronomic characters are reported in terms of phenotypic and genetic correlation coefficients.

Chapter V concerns the inheritance of plant height and height components in a soybean cross. Broad-sense and narrow-sense heritability estimates, as well as phenotypic and genetic correlations between height and its components, are also presented.

Chapters II, III, IV, and V are presented in a form acceptable to the Crop Science Society of America.[1] Chapter VI is a general summary of the four studies. Additional data are presented in a tabular form in the Appendix.

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[1]Publications Handbook and Style Manual, ASA, CSSA, SSSA. (1984).

CHAPTER II

Heterosis, Inbreeding Depression, and Combining Ability
for Yield and Yield Components in Soybeans[1]

ABSTRACT

Information on hybrid soybeans [Glycine max (L.) Merr.] in the
Southern Great Plains of the United States is limited. A four-parent
diallel study was conducted to study heterosis, inbreeding depression,
and combining ability for yield and its primary components in soybeans.
Six F_1 hybrids (all combinations except reciprocals) of 'Douglas',
'Essex', 'Forrest', and 'York' were space-planted along with their
parents in 1982 and 1983. The 1983 experiment also included six
F_2 hybrids. The field layout was a randomized complete block design
with four and eight blocks in 1982 and 1983, respectively. Heterosis
and inbreeding depression were greater for yield than for any other
character. Number of pods/plant expressed the greatest heterotic
response and inbreeding depression of the yield components. Significant
F_2 deviations were found for yield and pods/plant from combined data
suggesting that both dominance and epistatic effects could be involved
for these two characters. When averaged over years and crosses,
midparent heterosis for yield, pods/plant, seeds/pod, and seed weight
were 25.4, 18.9, 0.2 and 3.2%, respectively. High-parent heterosis for

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[1]To be submitted for publication.

yield, pods/plant, seeds/pod, and seed weight were 20.9, 9.0, -3.5, and -6.5%, respectively. General combining ability (GCA) estimates were significant for pods/plant, seeds/pod, and seed weight. Specific combining ability (SCA) estimates were significant for yield and pods/plant. Year x GCA and Year x SCA interactions were not significant for any character studied. The relatively high levels of heterosis for yield found in this study suggest that if economical large-scale method of producing F_1 seed could be found, the commercial production of hybrid soybeans should be favorable.

For successful commercial production of hybrid cultivars in soybeans (<u>Glycine</u> <u>max</u> (L.) Merr.), two requirements should be satisfied: (i) an economical large-scale method of producing hybrid seed must be found, and (ii) there must be sufficient heterosis for seed yield to offset cost of seed production. With the finding of genetic male sterility in soybeans (4), interest has developed in the potential productivity of hybrid soybeans. A method for producing experimental quantities of hybrid soybean seed using genetic male sterility and green seed embryo was suggested by Burton and Carter (5).

Heterosis and inbreeding depression have been reported in soybeans, suggesting that it may be worthwhile to search for favorable heterozygous gene combinations. Studies have shown the average high-parent heterosis for seed yield/plant of hybrid soybeans to range from 8% (17) to 26% (6) with most values ranging between 13 and 23% (3,16,20,21,22). High-parent heterosis for yield has been reported to range from -52% (13) to +90% (21). However, Brim (2) suggested that in most cases pure lines were more productive than F_1 hybrids. Very little heterosis has been found for seed weight (6,15,17,20,21) or number of seeds/pod (6,17,20). Information about hybrid soybeans in the Southern Great Plains of the United States has been limited.

In soybeans, significant general (GCA) and specific combining ability (SCA) estimates have been observed for yield/plant, pods/plant, and seed weight (14,18,19). Studies from China (18) also found significant GCA and SCA estimates for number of seeds/pod and ratios of GCA to SCA mean squares for yield/plant, pods/plant, seeds/pod, and seed weight of 3.4, 3.8, 16.2, and 12.3, respectively. Paschal and Wilcox (17) found significant GCA estimates for yield/plant, pods/plant,

seeds/pod, and seed weight, and significant SCA estimates for seed weight.

The objectives of the present study were (i) to provide additional information on the magnitude of heterosis and inbreeding depression for seed yield and yield components in soybeans, and (ii) to determine the relative importance of GCA and SCA in soybeans grown in the Southern Great Plains.

MATERIALS AND METHODS

Four soybean cultivars, Douglas, Essex, Forrest, and York, were hand-crossed in a diallel system, i.e., all possible crosses without reciprocals. The four cultivars are well adapted to growing conditions in Oklahoma and the Southern Great Plains. Each of the F_1 hybrids could be a prospective commercial soybean hybrid.

The study was conducted at the Agronomy Research Station, Perkins, Oklahoma in the summers of 1982 and 1983. The four parents and their six F_1 hybrids were grown in the field in 1982 and 1983. In addition, the six F_2 hybrids were included in the 1983 experiment. The experimental design was a randomized complete block with four blocks in 1982 and eight blocks in 1983. In each block, all experimental plants were randomly planted; therefore, each plant was an experimental unit. Plantings were made using a hand planter with an adjusted depth of 3.5 cm on 13 June 1982 and 6 June 1983 on a Teller loam soil (fine-loamy, mixed, thermic Udic Argiustolls) with a pH of 6.5. Based on soil tests, there were sufficient nutrients for the growth of soybeans. The spacing between plants and rows was 76 x 76 cm. Each row consisted of six experimental plants in 1982 and 13 experimental plants in 1983. Each block consisted of 192 experimental plants in 1982 and 234 experimental plant in 1983. Each block was bordered by rows of a standard variety with the same spacing as that of the experimental planting. A total of 80 plants from each entry were grown in 1982. A total of 64 plants from each parent, 50 to 80 plants from each F_1 hybrid, and 192 plants from each F_2 hybrid were grown in 1983. When a plant died, it was replaced by a healthy border plant to minimize competition effects on surrounding

plants. Measurements on a per-plant basis were recorded for the following characters:

Seed yield. Weight of air-dried seed expressed in g/plant.

Number of pods/plant. Calculated as [seed yield/(seed weight /100)]/no. of seeds per pod i.e. (g/plant ÷ g/seed) ÷ no. seeds/pod.

Number of seeds/pod. Obtained by counting seeds from 20 randomly selected pods/plant.

Seed weight. Weight in g per 100 random whole seeds.

All statistical analyses were made on an entry-block mean basis. In the analyses of variance, years and genotypes were assumed fixed and blocks were assumed random. The data were analyzed through the use of a computer program, using the Statistical Analysis System (SAS). Diallel analyses were obtained using Gardner and Eberhart's Analysis III (10). The F_1 hybrids were partitioned into GCA and SCA, using Griffing's analysis method 4 (one set of F_1's and no reciprocals) (11). The pooled error mean square was used to test the significance of the genotypes and the years x genotypes interaction, and block within years was used to test years. When both GCA and SCA mean squares were significant, GCA/SCA equivalent components of mean squares as suggested by Baker (1) were used to assess the relative importance of GCA and SCA. The equivalent component of mean square is the component of mean square in the fixed model that is equivalent to the component of variance in the random model.

Percent heterosis, inbreeding depression, and F_2 deviations for individual crosses were computed as follows:

Percent midparent heterosis = 100 (F_1 - Midparent)/Midparent

Percent high-parent heterosis = 100 (F_1 - High-parent)/High-parent

Percent inbreeding depression = $100 \; (F_1 - F_2)/F_1$

Percent F_2 deviations = $100 \; [F_2 - 1/2 \; (F_1 + \text{Midparent})] \; / \; 1/2 \; (F_1 + \text{Midparent})$

The F-LSD (protected LSD) (7,9) procedure was used to test for the significances of high-parent heterosis and inbreeding depression within each year. Orthogonal contrasts were used to test for significances of the midparent heterosis within each year. Orthogonal contrasts were also used to test for the significances of heterosis responses and interaction of heterosis x years in the combined data. Average midparent heterosis, inbreeding depression, and F_2 deviation effects were calculated similarly to those of individual crosses except the generation mean for the character was used instead of the entry mean. Orthogonal contrasts were also used to test for the significances of these estimates.

RESULTS AND DISCUSSION

The combined 2-years analyses of variance for parents and F_1 hybrids indicated that the mean squares were significant for most sources of variation (Table 1). Significant differences among the parents were observed for all characters except yield; however, significance for yield was observed in 1982 (P=0.04) and 1983 (P=0.09). Differences among the F_1 hybrids were highly significant (P$\leq$0.01) for all characters.

Significant year x parent interactions were found for all characters, but year x F_1 hybrid interactions were not significant for any character. These results indicated that the F_1 hybrids were more stable in performance over years than their parents for yield, pods/plant, seeds/pod, and seed weight. The interactions with years were due primarily to differences in rank of genotypes from one year to the next (Table 2).

Heterosis and Inbreeding Depression

Highly significant mean squares of parents vs. F_1's were found for yield and pods/plant (Table 1). The parents vs. F_1's component reflects overall heterosis of all crosses relative to the midparent and is also attributable totally to nonadditive gene effect (10,12). Thus, the overall midparent heterosis was highly significant for yield and pods/plant when analyzed over the two years.

Midparent heterosis x year interactions were not significant for any character, except for number of seeds/pod in the Forrest/York cross. This significant interaction was probably due to differences in the magnitude of responses for the two years.

General trends for means and heterotic responses, averaged over the two years, are presented in Tables 3 and 4. Five out of six hybrids (all except Douglas/Forrest) yielded significantly higher than their respective high-parent in 1982 and 1983 and also in the combined two-years data (Table 2). There was no significant difference among these five hybrids within each year nor in the combined two-years data. Douglas/Forrest was the only hybrid that was not significantly different from the midparent value for yield and number of pods/plant in both years. Average mid-parent heterosis over years and crosses for yield was 25.4% with the range between 10.0 and 38.1% (Table 4). Average high-parent heterosis over all crosses and years for yield was 20.9% with the range between 5.4 and 38.0%. This averaged value is comparable to the high-parent heterosis of 19.6% estimated by Veatch (20) and 20.2% by Brim and Cockerham (3). However, the high-parent heterosis value is larger than those usually reported for a hybrid developed from two adapted parents.

The Douglas/Essex hybrid was significantly higher than the high-parent for pods/plant in 1982 and was significantly higher than the midparent in 1983 (Table 2). This hybrid was also significantly higher than the high-parent for pods/plant averaged over the two-years (Table 3). Douglas/York was significantly higher than the midparent for pods/plant only in 1983 (Table 2), but was not significantly higher than the midparent averaged over the two-years (Table 3). Essex/York was significantly higher than the high-parent for pods/plant in 1982 and was significantly higher than the midparent in 1983. This hybrid was significantly higher than the high-parent averaged over both years. Forrest/Essex was significantly higher than the midparent for pods/plant

within each year and was significantly higher than the high-parent when averaged over both years. Forrest/York was significantly higher than the high-parent for pods/plant in 1982 and was significantly higher than the midparent in 1983 and when averaged over both years. Average midparent and high-parent heterosis over years and crosses for this character was 18.9 and 9.0%, respectively (Table 4).

None of the hybrids was significantly different from the midparent for number of seeds/pod within each year and when averaged over the two-years. Most of the F_1 hybrids tended to be intermediate between their parents for seeds/pod. Averaged midparent and high-parent heterosis over years and crosses for this character were near zero (0.2 and -3.5% respectively).

Douglas/Essex exhibited significant midparent heterosis for seed weight in 1983 (Table 2) and significant high-parent heterosis over both years (Table 3). Douglas/Forrest and Douglas/York produced significantly larger seeds than the midparents in 1982 (Table 2), and the same results were obtained when averaged over the two-years (Table 3). No significant midparent heterosis was observed in either year for Essex/York, but this hybrid had significantly smaller seeds than the midparent when averaged over both years. Forrest/York had significantly smaller seeds than the midparent in 1983; however, this hybrid did not differ significantly from the midparent for seed weight when averaged over the two-years. When averaged over years and crosses (Table 4), midparent and high-parent heterosis for this character was 3.2 and -6.5%, respectively.

Average midparent heterosis, inbreeding depression, and F_2 deviations for 1983 are summarized in Table 5. Parental and F_2 means

were consistently lower than the F_1 mean for all characters except seeds/pod. Average midparent heterosis and inbreeding depression were highly significant for yield and pods/plant. Heterosis (23%) and inbreeding depression (16%) for yield were greater than that for any other character. Pods/plants exhibited the greatest heterosis and inbreeding depression of the yield components. The four characters were ranked similarly based on midparent heterosis and inbreeding depression estimates. The number of crosses showing significant heterosis, inbreeding depression, and F_2 deviation effects was greater for yield and pods/plant than other characters (Table 5). Significant F_2 deviation effects for yield and pods/plant suggested that both dominance and epistatic effects could be involved for these two characters in the combined data over all crosses (8). Weber et al. (21) also reported that gene action other than additive was operating for yield in soybeans. These results indicate that superior hybrids will need to be selected on the basis of their performance rather than on the performance of their parents. The presence of nonadditive gene effects suggests that hybrid cultivars may provide a desirable alternative to pure lines for higher potential yields.

Combining Ability

Mean squares for the combining ability analyses over both years are presented in Table 6. The SCA mean square was significant for yield, but the GCA mean square was not. The highest SCA effects (7.79) for yield were detected in crosses of Douglas/Essex and Forrest/York. Both GCA and SCA mean squares were highly significant for pods/plant. The ratio of GCA to SCA equivalent components of mean squares for this

character was 2.2, indicating that GCA was more important than SCA in determining the progeny performance. Essex and Forrest had the highest GCA effects for pods/plant (30.89 and 27.01), respectively. The highest SCA effects (20.2) for pods/plant were associated with Douglas/Essex and Forrest/York hybrids. Forrest/York also had the highest yield (Table 3) with the second highest high-parent heterosis (29.4%) when averaged over both years. Douglas/Essex had the second highest yield with the highest high-parent heterosis (38.1%). Therefore, Forrest/York and Douglas/Essex were the best yielding hybrids based on their means, heterotic responses, and SCA effects.

GCA mean squares were significant for seeds/pod and seed weight but SCA mean squares were not indicating that the performance of a single-cross progeny could be sufficiently predicted on the GCA basis (1). Douglas and York had the highest GCA effects (0.09 and -0.01) for seeds/pod, respectively. York and Douglas also had the highest GCA effects (1.25 and 0.97) for seed weight, respectively.

Year x GCA and year x SCA interactions were not significant for any character evaluated. These results indicated that both types of combining ability were stable in performance over both years for the four characters.

In summary, five out of six F_1 hybrids yielded significantly ($P \leq 0.05$) higher than the high parent. Heterosis and inbreeding depression were greater for yield than for any other character. When averaged over years and crosses, midparent and high-parent heterosis for yield were 25.4 and 20.9%, respectively. Yield, pods/plant, seed weight, and seeds/pod were ranked similarly from highest to lowest based on midparent heterosis and inbreeding depression

estimates. Significant GCA estimates were found for pods/plant, seeds/pod and seed size. SCA estimates were significant for yield and pods/plant. Forrest/York and Douglas/Essex were considered the best yielding hybrids based on their means, heterotic responses, and SCA effects. The year x GCA interaction and the year x SCA interaction were not significant for any character studied.

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LIST OF TABLES

Table 1. Analyses of variance for parents and hybrids for yield and yield

    components in soybeans averaged over two years.

Source of variation	df	Mean squares			
		Yield/plant	No. of pods/plant	No. of seeds/pod	Seed weight
Years(Y)	1	84.1	5 806.8	0.698	1.7
Blocks	10	772.6**	7 934.1**	0.253**	2.5*
Entries	9	2 724.0**	·32 572.8**	0.124**	46.1**
Parents(P)	3	462.2	32 459.0*	0.268**	105.5**
P vs. F_1's	1	17 727.2**	79 268.1**	0.002	3.8
F_1's	5	1 080.4**	23 302.0**	0.061**	26.2**
Y x entries	9	370.8	4 311.5†	0.037*	3.0**
Y x P	3	870.9*	8 726.4**	0.073**	7.0**
Y x (P vs F_1's)	1	133.3	975.5	0.006	2.0**
Y x F_1's	5	118.3	2 329.7	0.022	0.8
Pooled error	90	284.6	2 268.2	0.017	1.1

†,*,**Significant at the 0.10, 0.05, 0.01 probability levels, respectively.

Table 2 Means of parents and hybrids for yield and yield components in

   soybeans in 1982 and 1983.

Entry	Year	Yield	No. of pods/plant	No. of seeds/pod	seed weight
		g/plant			g/100 seeds
Douglas	1982	103.1	263.1	2.76	14.2
	1983	87.6	238.5	2.54	14.8
Essex	1982	83.5	249.0	2.30	15.0
	1983	107.4	342.9	2.35	13.6
Forrest	1982	100.6	326.3	2.63	11.7
	1983	107.5	368.6	2.41	12.3
York	1982	113.7	265.3	2.50	17.4
	1983	102.4	242.1	2.17	20.0
Douglas/Essex	1982	131.7*	317.5*	2.66	15.6
	1983	131.8*	361.5†	2.42	15.3†
Douglas/Forrest	1982	115.4	290.6	2.64	15.2†
	1983	104.0	308.6	2.39	14.4
Douglas/York	1982	128.0*	278.0	2.64	17.6†
	1983	125.6*	288.7†	2.46	18.0
Essex/York	1982	126.0*	337.4*	2.43	15.5
	1983	126.1*	346.3†	2.32	15.9
Forrest/Essex	1982	124.2*	386.1†	2.41	13.5
	1983	128.4*	408.3†	2.34	13.3
Forrest/York	1982	143.3*	409.7*	2.42	14.4
	1983	131.2*	364.9†	2.38	15.1‡
CV,%	1982	12.0	13.9	5.30	5.7
	1983	15.6	15.1	5.40	7.4

*significantly larger than the high-parent at the 0.05 probability
 level.

†significantly larger than the midparent-value at the 0.05 probability
 level.

‡significantly smaller than the midparent-value at the 0.05 probability
 level.

Table 3. Means of parents and hybrids for yield and yield components in soybeans averaged over two years.

Entry	Yield	No. of pods/plant	No. of seeds/pod	seed weight
	g/plant			g/100
Douglas	95.3	250.8	2.65	14.5
Essex	95.4	295.9	2.33	14.3
Forrest	104.1	347.5	2.52	12.0
York	108.1	253.7	2.33	18.7
Douglas/Essex	131.7*	339.5*	2.54	15.4*
Douglas/Forrest	109.7	299.6	2.52	14.8†
Douglas/York	126.8*	283.4	2.55	17.8†
Essex/York	126.0*	341.9*	2.38	15.7‡
Forrest/Essex	126.3*	397.2*	2.37	13.4
Forrest/York	137.2*	387.3†	2.40	14.7
CV,%	14.6	14.8	5.40	6.9

*significantly larger than the high-parent at the 0.05 probability level.

†significantly larger than the midparent value at the 0.05 probability level.

‡significantly smaller than the midparent value at the 0.05 probability level.

Table 4. Average F_1 heterosis over years and crosses for yield and yield components in soybeans.

Character	Average midparent heterosis	Range for midparent heterosis	Average high-parent heterosis	Range for high-parent heterosis
			%—————————	
Yield	25.4	10.0 – 38.1	20.9	5.4 – 38.0
No. of pods/plant	18.9	0.2 – 28.9	9.0	–13.8 – 14.7
No. of seeds/pod	0.2	– 2.6 – 2.4	– 3.5	– 5.7 – 1.9
seed weight	3.2	– 4.9 – 11.7	– 6.5	–21.0 – 6.4

Table 5. Average performance of parental, F_1, and F_2 generations and average midparent heterosis, inbreeding depression, and F_2 deviations for yield and yield component in soybeans in 1983.

Character	Parental mean	F_1 mean	F_2 mean	Midparent heterosis	Inbreeding depression	F_2 deviations	No. of crosses significant (.05)		
					%—————		Midparent heterosis	Inbreeding depression	F_2 deviations
Yield(g)	101.2	124.6	104.6	23.0**	16.0**	-7.3**	5	4	1
No. of pods/plant	298.0	346.4	295.7	16.2**	14.6**	-8.2**	5	4	2
No. of seeds/pod	2.39	2.38	2.39	0.8	-0.4	0.7	1	0	0
Seed weight(g/100)	15.15	15.33	15.14	1.2	1.2	-0.6	2	0	0

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

Table 6. Mean squares for general (GCA) and specific combining

ability (SCA) and interactions with years for yield and yield

components in F_1 hybrid soybeans averaged over two years.

Source of variation	df	Yield	No. of pods/plant	No. of seeds/pod	seed weight
GCA	3	690.1	32 313.9**	0.098**	42.4**
SCA	2	1 665.7*	9 784.1**	0.007	1.8
Year x GCA	3	143.4	3 597.4	0.033	1.1
Year x SCA	2	80.5	428.4	0.006	0.2
Error	50	393.0	3 174.3	0.021	1.2

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

CHAPTER III

Heterosis, Inbreeding Depression, and Combining Ability

for Height, Plant Weight, and Harvest Index in Soybeans[1]

ABSTRACTS

Little information is available on heterosis in soybeans [Glycine max (L.) Merr.] in the Southern Great Plains of the United States. Our objective was to study heterosis, inbreeding depression, and combining ability for height, plant weight and harvest index in soybeans. Six F_1 hybrids (all combinations except reciprocals) of the cultivar Douglas, Essex, Forrest, and York were space-planted along with their parents in 1982 and 1983. The experiment also included the six F_2 hybrids in 1983. The field layout corresponded to a randomized complete block design with four and eight blocks in 1982 and 1983, respectively. Average midparent heterosis and inbreeding depression were significant for plant weight, height, and harvest index. When averaged over years and crosses, midparent heterosis values for height, plant weight, and harvest index were 14.6, 21.5, and 3.8%, respectively. Average high-parent heterosis values for height, plant weight, and harvest index were 9.5, 15.6, and 1.1%, respectively. GCA estimates were significant only for height. SCA estimates were significant only for plant weight. GCA x year and SCA x year interactions were not

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significant for height or plant weight suggesting that both types of combining ability were equally stable over the two years. The year x GCA interaction was significant for harvest index; whereas, the year x SCA interaction was not significant suggesting that SCA was more stable across years than GCA.

Additional index words: Glycine max (L.) Merr., Hybrid soybean, Diallel crosses, Genotype x environment interaction.

Heterosis has been observed for height and other agronomic characters in soybeans (Glycine max (L.) Merr.). Most of the reports on hybrid soybeans have come from the midwestern and the southeastern sections of the United States. Very little information has been reported on hybrid soybeans in the Southern Great Plains.

Several investigators have found that the height of the hybrid is between the midparental value and the taller parent (2,12,15,16); however, significant high-parent heterosis for height has also been observed (3,11,13,17). Significant high-parent heterosis for plant weight has been observed (12). Very little heterosis has been found for harvest index (12,15,16).

Significances of both general (GCA) and specific combining ability (SCA) estimates have been observed for plant height in diallel analyses (12,13,14,16). Little information has been reported on combining ability estimates for plant weight and harvest index; nevertheless, Paschal and Wilcox (12) found significant GCA estimates for both characters.

The objectives of this study were (i) to investigate the degree of heterosis and inbreeding depression for height, plant weight, and harvest index, and (ii) to determine the relative importance of general and specific combining ability of adapted soybean parents for these characters.

MATERIALS AND METHODS

The experiments were performed at the Agronomy Research Station, Perkins, Oklahoma in the summer of 1982 and 1983. Six F_1 hybrids (all combinations except reciprocals) of 'Douglas', 'Essex', 'Forrest', and 'York' were spaced-planted along with their parents in a randomized complete block design with four blocks in 1982 and eight blocks in 1983. In addition, six F_2 hybrids were included in 1983. In each block, all plants were randomly planted; therefore, each plant was an experimental unit. Plantings were made using a hand planter with an adjusted depth of 3.5 cm on 13 June 1982 and 6 June 1983 on a Teller loam soil (fine-loamy, mixed, thermic Udic Argiustolls) with a pH of 6.5. Based on soil tests, there were sufficient nutrients for the growth of soybeans. The spacing between plants and rows was 76 x 76 cm. Each row consisted of six experimental plants in 1982 and 13 experimental plants in 1983. A total of 80 plants from each entry were grown in 1982. A total of 64 plants from each parent, 50 to 80 plants from each F_1 hybrid, and 192 plants from each F_2 hybrid were grown in 1983. Each block was bordered by rows of a standard variety with the same spacing as that of the experimental planting. When a plant died, it was replaced with a healthy border plant to minimize competition effects on surrounding plants. Measurements for the following characters were made on individual plants:

Height. The length in cm of a plant from the ground to the tip of the mainstem at maturity.

Plant weight. Total air-dried weight of the above ground portion of the plant at maturity measured in g.

Harvest index. The ratio of seed yield to plant weight.

All statistical analyses were made on an entry-block mean basis. In the analysis of variance, years and genotypes were assumed fixed and blocks were assumed random. The 1982 and 1983 experiments were analyzed separately as well as in combination for all traits.

Diallel analyses were conducted using Gardner and Eberhart's Analysis III (7). The F_1 hybrids were partitioned into GCA and SCA using Griffing's analysis method 4 (one set of F_1's and no reciprocals) (8). The pooled error mean square was used to test the significance of the genotypes and the year x genotype interaction, and the blocks within year mean square was used to test years.

Percent of heterosis, inbreeding depression, and F_2 deviations for individual crosses were calculated as follows:

Percent midparent heterosis = $100(F_1 - \text{Midparent})/\text{Midparent}$

Percent high-parent heterosis = $100(F_1 - \text{High-parent})/\text{High-parent}$

Percent inbreeding depression = $100(F_1 - F_2)/F_1$

Percent F_2 deviations = $100[F_2 - 1/2(F_1 + \text{Midparent})] / 1/2(F_1 + \text{Midparent})$

Average midparent heterosis, inbreeding depression, and F_2 deviations were computed similarly to those of individual values except the generation mean for the character was used instead of the entry mean. Significant differences were determined by either the F-LSD (protected LSD) (4,6) or orthogonal contrasts.

RESULTS AND DISCUSSION

The combined analyses of variance over two years (Table 1) shows significant mean squares for most sources of variation. Significant differences among the parents and among the F_1's were observed for all characters. Significant year x entry interactions were observed for all characters evaluated. The year x entry interaction was due to changes in magnitude and/or direction of response for the two years. Year x parent and year x hybrid interactions were not significant for height and plant weight indicating that the parents and F_1 hybrids were stable over years for the two characters. However, year x parent and year x hybrid interactions were both significant for harvest index.

Heterosis and Inbreeding Depression

Highly significant ($p \leq 0.01$) mean squares of parents vs F_1's were observed for height, plant weight, and harvest index (Table 1). The parents vs. F_1's component reflects the average heterosis of all crosses relative to the midparent and is attributable totally to non-additive gene effect (7,9).

Two hybrids (Douglas/Essex and Douglas/Forrest) were significantly taller than their high-parents within each year and when averaged over the two years (Table 2). Douglas/York was significantly taller than its taller-parent in 1982 and was significantly taller than the midparent in 1983. When averaged over both years, this hybrid was significantly taller than the high-parent (Table 2). Forrest/York was significantly taller than the midparent in 1982 and when averaged over years even though it was not significantly different from the midparent in 1983.

When averaged over years and crosses, midparent heterosis for height was 14.6% with the range between -1.8 and 33.2% (Table 3). Average high-parent heterosis for this character was 9.5% with the range between -5.6 and 29.8%.

Three hybrids (Douglas/Essex, Forrest/Essex, and Forrest/York) showed significant high-parent heterosis for plant weight when averaged over the two years (Table 2). These three hybrids also yielded significantly higher than their high-parent values when averaged over the two years (10). The other three hybrids produced plants of significantly greater weights than their midparental values averaged over both years. Midparent and high-parent heterosis values for this character were 21.5 and 15.6%, averaged over years and crosses (Table 3).

When averaged over years and crosses, Douglas/York was the only hybrid that was significantly higher than the high-parent for harvest index (Table 2). Essex/York was also significantly higher than the midparent for this character. Average midparent and high-parent heterosis for this character over years and crosses was 3.8 and 1.1%, respectively (Table 3).

Average midparent heterosis, inbreeding depression, and F_2 deviations for 1983 are summarized in Table 4. The F_1 hybrids have higher means than the midparents or the F_2 hybrids for all characters. The F_2 means fell between the midparent and F_1 means for all characters. Average midparent heterosis and inbreeding depression were significant for all of the characters. Heterosis and inbreeding depression for plant weight were greater than that for any other character. The three characters ranked similarly based on both midparent heterosis and

inbreeding depression. Significance of F_2 deviation effect for harvest index suggested that both dominance and epistatic effects could be involved in this character for the combined data over all crosses (5).

Combining Ability

Mean squares for combining ability analyses over the two years are presented in Table 5. Mean squares for GCA were significant only for height suggesting that the performance of a single cross progeny could be adequately predicted on the basis of GCA (1). Douglas expressed the highest positive GCA effect for this character both within each year and averaged over both years. Essex had the lowest GCA effect (negative) for this character when averaged over both years. Mean square for SCA was significant only for plant weight averaged over both years. Douglas/Essex and Forrest/York exhibited the highest SCA effects for this character.

The year x GCA and the year x SCA interaction were not significant for height or plant weight, indicating that both types of combining ability were stable over years. The year x SCA interaction was significant for harvest index, but the year x GCA interaction was not, indicating that SCA was more stable than GCA for this character.

In summary, height, plant weight, and harvest index were ranked similarly from highest to lowest based on heterosis and inbreeding depression. Average midparent heterosis and inbreeding depression were significant for height, plant weight, and harvest index. Significance of F_2 deviation estimates for harvest index suggested that both dominance and epistatic effects could be involved for this character in the combined data over all crosses. When averaged over years and

crosses, midparent heterosis values for height, plant weight and harvest index were 14.6, 21.5, and 3.8%, respectively. Average high-parent heterosis values for height, plant weight, and harvest index were 9.5, 15.6, and 1.1%, respectively averaged over years and crosses. GCA estimates were significant only for height. SCA estimate was significant only for plant weight. GCA and SCA did not exhibit significant interactions with years for height or plant weight, indicating that both types of combining ability were stable over the two years. GCA showed a significant interaction with years for harvest index but SCA did not, suggesting that SCA was more stable across years than GCA for this character.

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Table 1. Two-year combined analyses of variance of four parents and their six F_1 hybrids for height, plant weight, and harvest index.

Source of variation	df	Mean squares		
		Ht	Plant wt	Harvest index
Years(Y)	1	599.3**	24 696.9*	0.055 1**
Replication/Y	10	42.0	3 617.8**	0.002 1**
Entries	9	1 067.7**	10 279.0**	0.004 2**
Parents(P)	3	297.4**	4 115.8**	0.006 1**
P vs. F_1's	1	1 879.0**	60 679.9**	0.012 4**
F_1's	5	1 367.6**	3 893.2*	0.001 5*
Y x entries	9	75.1*	3 394.7*	0.002 8**
Y x P	3	76.7	3 219.6	0.002 3**
Y x (P vs. F_1's)	1	106.4	5 869.2*	0.005 2**
Y x F_1's	5	67.9	3 004.9	0.002 7**
Pooled error	90	30.8	1 458.5	0.000 5

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

Table 2. Means of parents and F_1's for height, plant weight, and harvest index in soybeans, 2-year average.

Entry	Ht	Plant wt	Harvest index
	cm	gm	
Douglas	63.3	234.0	0.408
Essex	54.5	211.3	0.451
Forrest	60.0	245.5	0.425
York	54.4	265.6	0.410
Douglas/Essex	74.1*	298.4*	0.443
Douglas/Forrest	82.1*	273.4†	0.413
Douglas/York	73.0*	283.8†	0.452*
Essex/York	53.4	279.8†	0.451†
Forrest/Essex	56.6	283.7*	0.447
Forrest/York	61.4†	321.2*	0.432
CV,%	8.9	14.4	5.1

* Significantly larger than the high-parent at the 0.05 probability level.

† Significantly larger than the midparent value at the 0.05 probability level.

Table 3. Average F_1 heterosis over all crosses for height, plant weight, and harvest index in soybeans, 2-year average.

character	Average midparent heterosis	Range for midparent heterosis	Average high-parent heterosis	Range of high-parent heterosis
		———————————— % ————————————		
Ht	14.6	-1.8 - 33.2	9.5	-5.6 - 29.8
Plant wt	21.5	13.6 - 34.0	15.6	5.3 - 27.5
Harvest index	3.8	-0.9 - 10.5	1.1	-2.9 - 10.3

Table 4. Average performance of parental, F_1, and F_2 generations and average midparent heterosis, inbreeding depression, and F_2 deviations for height, plant weight, and harvest index in soybeans, 1983.

Character	Parental mean	F_1 mean	F_2 mean	Midparent heterosis	Inbreeding depression	F_2 deviations
				——————————— % ———————————		
Ht (cm)	56.9	63.6	58.6	11.7**	7.8**	-2.7
Plant wt (g)	233.0	268.8	240.1	15.4**	10.7**	-4.3
Harvest index	0.438	0.468	0.440	6.8**	6.0**	-2.9*

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

Table 5. Mean squares for general (GCA) and specific combining ability

(SCA) and interactions with years for height, plant weight, and

harvest index averaged over two years.

Source of variation	df	Ht	Plant wt	Harvest index
GCA	3	2 236.6**	1 127.0	0.001 4
SCA	2	64.1	7 892.0*	0.001 7
Year x GCA	3	80.1	4 529.2	0.003 9**
Year x SCA	2	49.7	718.4	0.000 9
Error	50	30.3	2 017.6	0.000 6

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

CHAPTER IV

Heritability of Agronomic Characters and their

Associations with Yield in Soybeans[1]

ABSTRACT

Knowledge of heritability estimates of agronomic characters and their associations with seed yield in soybeans [Glycine max (L.) merr.] is useful for planning more efficient breeding programs. The objective of this study was to determine the magnitude of heritability estimates and the associations of seed yield with other agronomic characters in soybeans. Six F_1 and F_2 populations obtained from a diallel cross (all combinations except reciprocals) of the cultivars Douglas, Essex, Forrest, and York were space-planted along with their parents at the Agronomy Research Station, Perkins, Okla., in the summer of 1983. The field layout was a randomized complete block design with six blocks. When averaged over all crosses, the magnitudes of heritability estimates were as follows: 0.66 (height), 0.64 (days to flowering), 0.56 (harvest index), 0.54 (seed yield), 0.53 (number of pods/plant), 0.51 (seed weight), 0.49 (plant weight), and 0.10 (number of seeds/pod). In general, genotypic correlations between yield and other agronomic characters were larger than phenotypic correlations. High yield was positively associated with larger number of pods/plant

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and with increases in plant weight and plant height. Genetic correlations of yield with plant weight and pods/plant were the highest. Significant positive correlations for yield with seeds/pod, seed weight, and harvest index were found in three populations. Both positive and negative associations were observed for yield and days to flowering.

In soybeans [Glycine max (L.) Merr.], increasing seed yield potential is the primary objective in most breeding programs. Information concerning heritability estimates of quantitatively inherited characters and their associations with yield is useful for planning more efficient breeding programs for the future.

Heritability estimates for yield in soybeans have generally been low, ranging from 0.03 (8) to 0.58 (2). Heritability estimates ranged from 0.21 to 0.51 for number of pods/plant and from 0.59 to 0.60 for number of seeds/pod (6). Heritability estimates for seed weight (g/100 seeds) ranged from 0.44 (8) to 0.94 (4). Information on heritability estimates for plant weight and harvest index is limited. However, Dinkins (3) found heritabilities of plant weight and harvest index to be 0.15 and -0.16, respectively. Estimates of heritability for plant height have ranged from 0.66 (4) to 0.90 (2). Heritability estimates for days to flowering ranged from 0.65 and 0.91 (1).

Several agronomic characters in soybeans are affected less by environment than is yield, and such characters might be valuable indicators of yield if they were consistently correlated with yield. Correlations of yield with various agronomic characters have been variable. Positive correlations have been observed for yield with number of pods per plant (1,3,7,9), number of seeds per pod (1,3,9,11) plant weight (3,9), and harvest index (3,9). Yield has been both positively and negatively correlated with seed weight (1,2), height (2), and days to flowering (12).

The objectives of this study were (i) to estimate broad-sense

heritability values for agronomic characters and (ii) to determine the phenotypic and genotypic correlations of yield with other agronomic characters in soybeans.

MATERIALS AND METHODS

Four soybeans cultivars, Douglas, Essex, Forrest, and York were hand-crossed in a diallel system, i.e. all possible crosses without reciprocals. The four cultivars are well adapted to growing conditions in Oklahoma and the Southern Plains. The study was conducted at the Agronomy Research Station, Perkins, Oklahoma, in the summer of 1983. Four parents and their six F_1 and F_2 populations were planted in a randomized complete block design with eight blocks. Plantings were made using a hand planter with an adjust depth of 3.5 cm on 6 June on a Teller loam soil (fine-loamy, mixed, thermic Udic Argiustolls) with a pH of 6.5. Based on soil tests, there were sufficient nutrients for the growth of soybeans. The spacing between plants and rows was 76 x 76 cm. Each row consisted of 13 experimental plants. Each block consisted of 234 experimental plants. In each block, all experimental plants were randomly planted; therefore, each plant was an experimental unit. Each block was bordered by rows of a standard variety with the same spacing as that of the experimental planting. A total of 64 plants from each parent, 50 to 80 plants from each F_1 hybrid, and 192 plants from each F_2 hybrid were grown in the experiment. When a plant died, it was replaced by the standard variety to minimize competition effects on surrounding plants. Sprinkle irrigation was provided throughout the growing season as needed. The following data were collected on individual plants:

Seed yield. Weight of air-dried seed expressed in g/plant.

Number of pods/plant. Calculated as [seed yield/(seed weight/ 100)]/ number of seeds per pod, i.e. (g/plant ÷ g/seed) ÷ no. of seeds/pod.

Number of seeds/pod. Obtained by counting seeds from randomly selected 20 pods/plant.

Seed weight. Weight in g per 100 random whole seeds.

Plant weight. Total air-dried weight (g) of the above ground portion of the plant at maturity.

Harvest index. The ratio of seed yield to plant weight.

Height. The length in cm of a plant from the ground to the tip of the main stem at maturity.

Days to flowering. The number of days after planting until the first open flower on the plant appeared.

Broad-sense heritability estimates (h^2_{bs}), on a plant basis, were computed as: $h^2_{bs} = (V_{F_2} - V_E) / V_{F_2}$ where V_{F_2} = the F_2 variance and V_E = environmental variance. $V_E = [df_{P_1}(V_{P_1}) + df_{P_2}(V_{P_2}) + df_{F_1}(V_{P_1})]/(df_{P_1} + df_{P_2} + df_{F_2})$. V_{P_1}, V_{P_2} and V_{F_1} = the variances of the two parents and F_1, respectively; and df_{P_1}, df_{P_2}, and df_{F_1} = the degrees of freedom of the error mean squares for the two parents and F_1, respectively. The variances were estimated by the corresponding error mean squares in the analyses of variances. A standard error for the broad-sense heritability estimate was computed as: $SE(h^2_{bs}) = V_E\{[2(df_{F_2})^2(df_{F_1} + df_{F_2} - 4)/df_E(df_{F_2} - 2)^2(df_{F_2} - 4)]\}^{1/2} / V_{F_2}$.

The phenotypic correlation coefficient (r_p), on a plant basis, was computed as: $r_p = Cov(x,y)_{F_2} / [(V_{x_{F_2}})(V_{y_{F_2}})]^{1/2}$. The genotypic correlation coefficient (r_g), on a plant basis, was computed as: $r_g = [Cov(x,y)_{F_2} - Cov(x,y)_E]/[(V_{x_{F_2}} - V_{x_E})^{1/2}(V_{y_{F_2}} - V_{y_E})^{1/2}]$ where $Cov(x,y)_{F_2}$ and $Cov(x,y)_E$ represent the covariances between character x and y of the F_2 and environment, respectively; $Cov(x,y)_E = [df_{P_1}(Cov(x,y)_{P_1}) +$

$df_{P_2}(Cov(x,y)_{P_2}+df_{F_1}(Cov(x,y)_{F_1})]/(df_{P_1}+df_{P_2}+df_{F_2})$; Vx_{F_2} and Vy_{F_2} denote the variances of x and y of the F_2; Vx_E and Vy_E denote the environmental variances and were calculated similarly to those in the heritability estimates. The covariances were estimated by the corresponding error mean products in the analyses of covariances. A standard error for the genotypic correlation (r_g) was calculated as :

$$SE(r_g)=r_g\left\{\frac{[(Cov(x,y)_{F_2})^2+Vx_{F_2}Vy_{F_2})]/df_{F_2}+[(Cov(x,y)^2_E+Vx_EVy_E)]/df_E}{[Cov(x,y)_{F_2}-Cov(x,y)_E]^2}\right.$$

$$+\ \frac{(Vx_{F_2})^2/df_{F_2}+(Vx_E)^2/df_E}{2(Vx_{F_2}-Vx_E)^2}\ +\ \frac{(Vy_{F_2})^2/df_{F_2}+(Vy_E)^2/df_E}{2(Vy_{F_2}-Vy_E)^2}$$

$$-\ \frac{2[Cov(x,y)_{F_2}(Vx_{F_2})]/df_{F_2}+2[Cov(x,y)_E(Vx_E)]}{[Cov(x,y)_{F_2}-Cov(x,y)_E](Vx_{F_2}-Vx_E)}$$

$$-\ \frac{2[Cov(x,y)_{F_2}(Vy_{F_2})]/df_{F_2}+2[Cov(x,y)_E(Vy_E)]}{[Cov(x,y)_{F_2}-Cov(x,y)_E](Vy_{F_2}-Vy_E)}$$

$$+\ \left.\frac{[Cov(x,y)_{F_2}]^2/df_{F_2}\ +\ [Cov(x,y)_E]^2/df_E}{[Cov(x,y)_{F_2}-Vx_E][Vy_{F_2}-Vy_E]}\right\}^{1/2}$$

RESULTS AND DISCUSSION

Broad-sense heritability estimates for the characters studied in the six crosses are given in Table 1. The magnitude of heritability estimates for a particular character varied from one cross to another. In general, a higher heritability estimates occurred in the cross involving parents with greater differences for that character. Negative heritability estimates were found for number of seeds/pod in the crosses of Douglas/Forrest and Douglas/York. These negative values were due to the high variance estimates for the environments (P_1, P_2 and F_1) and the relatively low corresponding variance estimates of the phenotypes (F_2) in the two crosses. The data from Table 1 suggest that selection effectiveness for the eight characters in the F_2 generation may vary with each cross.

When averaged over all crosses, the magnitude of heritability estimates were as follows: 0.66 (height), 0.64 (days to flowering), 0.56 (harvest index), 0.54 (seed yield), 0.53 (number of pods/plant), 0.51 (seed weight), 0.49 (plant weight), and 0.10 (number of seeds/pod) (Table 1). The average heritability estimates for yield, seed size, height, and days to flowering were higher than the expected heritability estimates by Johnson and Bernard (5). Their expected heritabilities were based on available data and observations of several soybean breeders and geneticists. The average heritability estimate for pods/plant was higher. However, the estimate for seeds/pod was lower than the estimates by Johnson et al. (6). The average heritability estimates for plant weight and harvest index were greater than previously reported (3). The average heritability estimates for yield, pods/plant, seed weight, plant weight, and harvest index were similar in

magnitude, suggesting that early selection would be equally effective for these five characters. The average heritability estimates for these five characters were greater than that of seeds/pod but were less than those of height and harvest index, suggesting that early selection for these five characters would be more effective than for seeds/pod but less effective than for height or days to flowering.

Correlation

Phenotypic correlation coefficients between yield and other agronomic characters are presented in Table 2. Significant phenotypic correlations indicate the two characters were associated. Genotypic correlation coefficients (r_g) are given in Table 3. These coefficients (r_g) provide a measure of the genotypic association between characters. Phenotypic and genotypic correlations agreed both in direction and magnitude except in the Forrest/Essex cross for seed weight with yield. With a few exceptions, genotypic correlations were the same or higher than phenotypic correlations in the six crosses which are in agreement with the results of others (1,7,8). These results indicated that the correlations between yield and other characters studied were primarily genetic. Significant positive phenotypic correlations for yield with pods/plant and plant weight were detected in all crosses. Genetic correlation coefficients of yield with pods/plant and plant weight were highest in magnitude and were consistently high over all crosses. The range of r_g for yield and pods/plant was from 0.84 to 0.93 and for yield and plant weight was from 0.88 to 0.96. The consistent positive genetic correlations of yield with pods/plant and plant weight are well recognized (1,3,9,7). These results indicated that an increase

in yield should be obtained by selecting for increases in pods/plant and plant weight.

Both phenotypic and genotypic correlation coefficients of yield with seeds/pod, seed weight, harvest index, height, and days to flowering varied with each cross in magnitude and in a few cases in direction. These results also have been reported by others (1,7,8). Therefore, the associations of yield with seeds/pod, seed weight, harvest index, height, and days to flowering may be characteristics of the specific population. There would be no reason to expect constant associations between yield and these characters in other populations of soybeans.

Phenotypic correlations of yield with seeds/pod were significant in three crosses. Seeds/pod exhibited a high genetic correlation with yield in the Douglas/Essex cross; however, its standard error was also high. Genetic correlation coefficients for seeds/pod with yield could not be estimated in crosses of Douglas/Forrest and Douglas/York due to higher estimates of the environmental variances than estimates of the phenotypic variances in these two crosses. Moderate (r_g=0.43), low (r_g=0.02), and 0 values of genetic correlations between seeds/pod and yield were observed in crosses of Essex/York, Forrest/Essex, and Forrest/York, respectively. In addition, the heritability estimates for seeds/pod were lower than for yield for all crosses. The results suggested that seeds/pod may not be useful as an indirect selection for yield.

Phenotypic correlations of seed weight with yield were significant in Douglas/Forrest, Douglas/York, and Essex/York. Seed weight also had positive genetic correlations with yield in these three crosses. The

heritability estimates for seed weight in these three crosses were similar in magnitude to yield. These results suggested that an increase in yield in these three populations should be obtained by selecting for an increase in seed weight. Phenotypic correlations for yield with seed weight were not significant in Douglas/Essex, Forrest/Essex, and Forrest/York. In addition, genotypic correlation for yield with seed weight in these three crosses were relatively small, indicating that selection for high seed weight may not result in an increase in yield in these three populations.

Significant phenotypic correlations of yield with harvest index were detected in three crosses. Positive phenotypic and genotypic correlations between harvest index and yield were found for all crosses which are in agreement with the results of others (3,9). However, Schapaugh and Wilcox (10) found both positive and negative correlations between harvest index and yield in different years.

Phenotypic correlations of height with yield were observed for all crosses. Height also had a positive genetic correlation with yield for all crosses, indicating that taller genotypes were higher in yield. Significant positive phenotypic correlations of days to flowering and yield were found in Douglas/Essex and Douglas/York. Positive genetic correlations between days to flowering and yield were also found in these two crosses, which indicated that later genotypes tended to be higher in yield for these two populations. Negative phenotypic and genotypic correlations between days to flowering and yield were detected in Forrest/York.

In conclusion, the magnitude of heritability for a certain character varied from one population to another for most of the

characters. These results suggested that the selection effectiveness for the eight characters studied may not be the same for different populations. Heritability estimates were moderately high for height and days to flowering, intermediate for yield, pods/plant, seed weight, plant weight, and harvest index, and low for seeds/pod. The heritability estimates presented here are in the broad-sense and are useful at first approximations, not as definitive values, for heritability of yield and other agronomic characters in soybeans.

In general, genotypic correlations were larger than phenotypic correlations, indicating that the correlations between yield and other characters studied were primarily genetic. Significant positive phenotypic correlations for all populations of yield with pods/plant, plant weight and height were observed, which indicate that selection for high yield may be accomplished by selecting tall plants with high values of pods/plant and plant weight. Number of pods/plant and plant weight were closely related to yield. Genetic correlations of yield with pods/plant, plant weight, and harvest index tended to vary slightly from one population to another, while the correlations between yield with number of seeds/pod, seed weight and height tended to vary moderately. Significant positive correlations for yield with seeds/pod, seed weight and harvest index were found in three populations while the correlations in the other three populations were not significant. Both positive and negative correlations were observed between yield and days to flowering. The heritability and correlation values presented in this study were computed from individual spaced plants; therefore, they may be different from those obtained from plants grown in conventional row

culture. Nevertheless, F_2 populations are often grown under space planted conditions. The results obtained from this study should provide useful information for early selection in soybeans.

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Table 1. Estimates of broad-sense heritability and their standard errors for eight characters in six soybean crosses.

	Cross						
Character	Douglas/ Essex	Douglas/ Forrest	Douglas/ York	Essex/ York	Forrest/ Essex	Forrest/ York	Average
Seed yield	0.77+0.06	0.64+0.09	0.37+0.15	0.57+0.09	0.49+0.10	0.39+0.12	0.54
No. of Pods/plant	0.65+0.09	0.45+0.13	0.42+0.14	0.55+0.09	0.55+0.09	0.56+0.12	0.53
No. of seeds/pod	0.06+0.23	-0.01+0.24	-0.36+0.31	0.21+0.16	0.43+0.11	0.29+0.15	0.10
Seed weight	0.77+0.06	0.60+0.10	0.59+0.09	0.41+0.12	0.38+0.12	0.32+0.14	0.51
Plant weight	0.69+0.08	0.57+0.10	0.33+0.16	0.47+0.11	0.47+0.10	0.40+0.12	0.49
Harvest index	0.67+0.08	0.69+0.07	0.55+0.11	0.51+0.10	0.41+0.12	0.55+0.09	0.56
Height	0.88+0.03	0.87+0.03	0.85+0.03	0.35+0.13	0.48+0.10	0.51+0.10	0.66
Days to flowering	0.88+0.03	0.69+0.07	0.80+0.05	0.48+0.10	0.43+0.11	0.55+0.09	0.64

Table 2. Phenotypic correlation coefficients (r_p) for seven characters with yield in six soybean crosses.

	Cross						
Character corr-elated with yield	Douglas/ Essex	Douglas/ Forrest	Douglas/ York	Essex/ York	Forrest/ Essex	Forrest/ York	Average
No. of pods/plant	0.85**	0.87**	0.88**	0.91**	0.91**	0.90**	0.89
No. of seeds/pod	0.25**	0.25**	0.05	0.26**	0.08	0.05	0.16
Seed weight	0.17	0.27**	0.19*	0.23**	0.09	0.06	0.17
Plant weight	0.91**	0.90**	0.91**	0.95**	0.94**	0.93**	0.92
Harvest index	0.22**	0.12	0.16	0.27**	0.17*	0.04	0.16
Height	0.51**	0.44**	0.45**	0.53**	0.29**	0.40**	0.44
Days to flowering	0.26**	0.16	0.31**	0.05	0.03	-0.25**	0.09

*,**Significant at the P=0.05 and 0.01 levels, respectively.

Table 3. Genotypic correlation coefficients (r_g) with their standard errors for seven characters with yield in six soybean crosses.[†]

Character corr-elated with yield	Cross						
	Douglas/Essex	Douglas/Forrest	Douglas/York	Essex/York	Forrest/Essex	Forrest/York	Average
No. of pods/plant	0.92±0.04	0.92±0.05	0.84±0.08	0.91±0.03	0.93±0.03	0.88±0.04	0.92
No. of seeds/pod	0.99±1.89	–	–	0.43±0.30	0.02±0.13	0.00±0.35	0.36
Seed weight	0.16±0.13	0.35±0.17	0.43±0.25	0.43±0.21	-0.18±0.26	0.01±0.31	0.20
Plant weight	0.93±0.02	0.88±0.04	0.89±0.07	0.96±0.02	0.94±0.03	0.88±0.05	0.91
Harvest index	0.31±0.14	0.32±0.17	0.33±0.26	0.47±0.18	0.28±0.22	0.19±0.23	0.32
Height	0.53±0.09	0.49±0.11	0.57±0.15	0.08±0.18	0.15±0.20	0.37±0.21	0.49
Days to flowering	0.35±0.11	0.39±0.17	0.70±0.24	0.27±0.21	0.48±0.27	-0.09±0.23	0.35

[†]No test for significance is available for genotypic correlations.

CHAPTER V

INHERITANCE OF PLANT HEIGHT AND HEIGHT
COMPONENTS IN A SOYBEAN CROSS[1]

ABSTRACT

Information on the inheritance of height components in soybeans [Glycine max (L.) Merr.] is limited. Parental, F_1, F_2 and backcross (BC_1 and BC_2) generations of a 'Douglas'/'Essex' cross were studied in a field experiment grown on the Agronomy Research Station at Perkins, Okla., in the summer of 1983. The objectives of this study were: (i) to determine the inheritance of plant height and its components, and (ii) to investigate phenotypic and genotypic associations between plant height and its components. The field layout was a randomized complete block design with six blocks. The F_1 was significantly taller and had significantly greater number of nodes than the midparental value, indicating that a sizable amount of non-additive gene action was involved for these two characters. A large amount of transgressive segregation was also observed for plant height and number of nodes. The F_2 population was distributed over the entire range of the two parents for internode length. Broad-sense heritability estimates for height, number of nodes, and internode length were 0.82, 0.81 and 0.40, respectively. Narrow-sense heritability estimates for height, number of

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nodes, and internode length were 0.15, 0.21, and 0, respectively. Significant positive correlations were observed for plant height versus number of nodes, plant height versus internode length, and number of nodes versus internode length suggesting that the two characters contrasted were probably not inherited independent of each other. Genotypic correlation was greater than phenotypic correlation for all cases indicating that the associations between height and its components were primarily genetic.

Additional index words: Glycine max (L.), Merr., number of nodes, internode length, transgressive segregation, heritability, phenotypic correlation, genotypic correlation.

The cultivated soybeans (<u>Glycine</u> <u>max</u> (L.) Merr.) is an erect, bushy leguminous annual plant. The plant varies in height from 3.0 cm to 2 m (5). Plant height is determined by two components: number of nodes and length of internodes on the main stem. Veatch (13) postulated that an increase in the number of nodes would result in an increase in the production of pods and seeds since flowers are located at the nodes. In addition, a plant with a short internode length would be expected to lodge less than one with a long internode length. A better understanding of the inheritance of plant height and its components should be useful for a soybean breeding program especially under highly a production environment such as irrigation.

Plant height is usually quantitatively inherited (2,3,7,12), but one (4,8,15) or two (1,10) major gene pairs determine stem termination thereby influence plant height. Information on the inheritance of height components is limited. However, studies (4,11) reported that a single recessive gene appeared to control short internodes on the main stem. Continuous variation was detected for average internode length.

Canivess and Prongsirivanthana (4) reported that heritability estimates were relatively high for both plant height and node number but somewhat low for average internode length. A high correlation between node number and plant height was also found.

The objectives of this study were: (i) to determine the inheritance of plant height and its components following a soybeans cross, and (ii) to investigate phenotypic and genotypic associations between plant height and its components.

MATERIALS AND METHODS

Crosses between 'Douglas' (P_1) and 'Essex' (P_2) were made in the field in the summer of 1981. In 1982, the F_1 was backcrossed in the field and greenhouse to each of the two parents to produce BC_1 (P_1 x F_1) and BC_2 (P_2 x F_1) populations. The parents, F_1, F_2, BC_1 and BC_2 populations were grown at the Agronomy Research Station, Perkins, Oklahoma, in the summer of 1983. The field layout was a randomized complete block design with six blocks. Plantings were made using a hand planter with an adjusted depth of 3.5 cm on 8 June on a Teller Loam soil (fine-loamy, mixed, thermic Udic Argiustolls) with a pH of 6.5. Based on soil tests, these were sufficient nutrients for the growth of soybeans. The space between plants and rows was 76 x 76 cm. Each row consisted of 12 experimental plants. In each block, all plants were randomly planted; therefore, each plant was an experimental unit. Each block consisted of 204 experimental plants and was bordered by two rows of similarly spaced discard plants. A total of 60 plants from each parent, 60 F_1 plants, 102 BC_1 plants to Douglas, 83 BC_2 plants to Essex, and 859 F_2 plants were grown. When a plant died, it was replaced with a discard plant to minimize competition effects on surrounding plants. Sprinkle irrigation was provided throughout the growing season as needed. Measurements for the following characters were made on individual plants:

Height. The distance in cm from the cotyledonary node to the tip of the main stem at maturity.

Number of nodes on the main stem. The number of the true leaf nodes including the tip of the main stem, but not the cotyledonary node.

Internode length. Obtained by dividing plant height (cm) by number of nodes on the main stem.

An analysis of variance was conducted for each character to determine whether significant differences existed among generations. Significant differences between generation means was determined by the F-LSD (protected LSD) (6,9). Orthogonal contrasts were used to test for significances between the F_1 and the midparental values.

Broad-sense heritability estimates (h^2_{bs}), on a plant basis, were computed as: $h^2_{bs} = (V_{F_2} - V_E) / V_{F_2}$ where V_{F_2} = the F_2 variance and V_E = environmental variance. $V_E = [df_{P_1}(V_{P_1}) + df_{P_2}(V_{P_2}) + df_{F_1}(V_{P_1})]/(df_{P_1} + df_{P_2} + df_{F_2})$. V_{P_1}, V_{P_2} and V_{F_1} = the variances of the two parents and F_1, respectively; and df_{P_1}, df_{P_2}, and df_{F_1} = the degree of freedom of the error mean squares for the two parents and F_1, respectively. The variances were estimated by the corresponding error mean squares in the analyses of variances. A standard error for the broad-sense heritability estimate was computed as: $SE(h^2_{bs}) = V_E\{[2(df_{F_2})^2(df_{F_1} + df_{F_2} - 4)/ df_E(df_{F_2} - 2)^2(df_{F_2} - 4)]\}^{1/2} / V_{F_2}$.

Narrow-sense heritability estimates (h^2_{ns}) was computed following Warner's method (14) as: $h^2_{ns} = [2V_{F_2} - (V_{BC_1} + V_{BC_2})] / V_{F_2}$ where V_{F_2}, V_{BC_1}, V_{BC_2} are the variances of the F_2, BC_1, and BC_2 generations, respectively, and were estimated by the corresponding error mean squares in the analyses of variances. A standard error for h^2_{ns} was computed as $SE(h^2_{ns}) = (2)^{1/2}\{[(V_{BC_1} + V_{BC_2})^2/df_{F_2}] + (V_{BC_1}^2/df_{BC_1}) + (V_{BC_2}^2/df_{BC_2}\}^{1/2}/V_{F_2}$ In this formula df_{F_2}, df_{BC_1}, df_{BC_2} are the degrees of freedoms associated with V_{F_2}, V_{BC_1}, and V_{BC_2}, respectively.

The phenotypic correlation coefficient (rp), on a plant basis, was computed as: $r_p = Cov\ (x,y)_{F_2} / [(V_{xF_2})(V_{yF_2})]^{1/2}$. The genotypic corr-

elation coefficient (r_g), on a plant basis, was computed as:

$r_g=[Cov(x,y)_{F_2}-Cov(x,y)_E]/[(Vx_{F_2}-Vx_E)^{1/2}(Vy_{F_2}-Vy_E)^{1/2}]$ where $Cov(x,y)_{F_2}$

and $Cov(x,y)_E$ represent the covariances between character x and y of the

F_2 and environment, respectively; $Cov(x,y)_E = [df_{P_1}(Cov(x,y)_{P_1})+$

$df_{P_2}(Cov(x,y)_{P_2}+df_{F_1}(Cov(x,y)_{F_1})]/(df_{P_1}+df_{P_2}+df_{F_2})$; Vx_{F_2} and Vy_{F_2} denote

the variances of x and y of the F_2; Vx_E and Vy_E denote the environmental

variances and were calculated similarly to that in the heritability

estimates. The covariances were estimated by the corresponding error

mean products in the analyses of covariances. A standard error for the

genotypic correlation (r_g) was calculated as :

$$SE(r_g)=r_g\left\{ \frac{[(Cov(x,y)_{F_2})^2+Vx_{F_2}Vy_{F_2})]/df_{F_2}+[(Cov(x,y)^2_E+Vx_EVy_E)]/df_E}{[Cov(x,y)_{F_2}-Cov(x,y)_E]^2} \right.$$

$$+ \frac{(Vx_{F_2})^2/df_{F_2}+(Vx_E)^2/df_E}{2(Vx_{F_2}-Vx_E)^2} + \frac{(Vy_{F_2})^2/df_{F_2}+(Vy_E)^2/df_E}{2(Vy_{F_2}-Vy_E)^2}$$

$$- \frac{2[Cov(x,y)_{F_2}(Vx_{F_2})]/df_{F_2}+2[Cov(x,y)_E(Vx_E)]}{[Cov(x,y)_{F_2}-Cov(x,y)_E](Vx_{F_2}-Vx_E)}$$

$$- \frac{2[Cov(x,y)_{F_2}(Vy_{F_2})]/df_{F_2}+2[Cov(x,y)_E(Vy_E)]}{[Cov(x,y)_{F_2}-Cov(x,y)_E](Vy_{F_2}-Vy_E)}$$

$$+ \left. \frac{[Cov(x,y)_{F_2}]^2/df_{F_2} + [Cov(x,y)_E]^2/df_E}{[Cov(x,y)_{F_2}-Vx_E][Vy_{F_2}-Vy_E]} \right\}^{1/2}$$

RESULTS AND DISCUSSION

Plant Height and Number of Nodes

Significant differences were detected among the six generations for plant height and number of nodes. Ranges, means, and coefficients of variations (CV) of plant height and number of nodes on the main stems for the populations studied are presented in Table 1. Plant height and the number of nodes followed the same pattern of inheritance, thus these two characters will be discussed together. The two parents differed significantly with respect to plant height and number of nodes. The F_1 hybrid was significantly taller and had significantly greater number of nodes than the average of the two parents, indicating that a sizable amount of non-additive gene action was present for these two characters.

There was some overlapping for plant height and number of nodes of the two parents, and the F_2 plants were distributed over the entire range of the parents. These results indicate the presence of transgressive segregation for these two characters. The segregating generations (F_2 and backcross) were more variable than the non-segregating generations (F_1, P_2, and F_2) for plant height and number of nodes (Table 1). The frequency distribution of the F_2 plants was approximately unimodal for plant height and number of nodes. The data on plant height and number of nodes did not fit discrete classes. Therefore, these two characters appeared to be quantitatively inherited. Quantitative variability for plant height has been reported by others (3,7,12).

Average internode length

No significant difference was detected among the six generations for average internode length. The failure to detect a significant difference for this character could be due to large sampling error, but more likely was the result of the nearly equal means of the two parents (Table 2). Douglas plants were distributed over the entire range of Essex plants and the F_2 plants were also distributed over the range of the two parents, indicating transgressive segregation for this character. The distribution of the F_2 plant was approximately normal for internode length. It was not possible to classify internode length into discrete classes. Therefore, this character appeared to be quantitatively inherited.

Heritability

Heritability estimates in the broad-sense and narrow-sense are given in Table 3. The broad-sense heritability estimates were high for plant height (0.82) and number of nodes (0.81) and moderate for average length of internodes (0.40). The narrow-sense heritability estimates were 0.21 for number of nodes, 0.15 for plant height, and -0.37 for internode length. Standard errors of the narrow-sense estimates were larger than those of the broad-sense estimates for all characters studied. Numbers of backcross plants were relatively low compared to numbers of F_2 plants. Therefore, high standard errors might be attributable to larger sampling errors in the backcross generation. The negative narrow-sense heritability estimate for internode length resulted from larger estimates for backcross variances than for F_2

variances (Table 2). Based on the heritability estimates, number of nodes would be slightly more responsive to direct selection pressure than plant height, but internode length would be the least responsive.

Associations among Characters

Correlation coefficients for plant height and its components are shown in Table 4. Significant positive phenotypic correlation coefficients were found for plant height versus number of nodes and plant height versus internode length, which is in agreement with other workers (4). Phenotypic and genotypic correlation correlations agreed both in magnitude and sign. Genotypic correlations were greater than the phenotypic correlations for all cases which indicated that the association of the two characters contrasted was primarily genetic. Genetic correlations for plant height versus number of nodes (r_g=0.90) and plant height versus internode length (r_g=0.86) were slightly different. Genetic correlation for number of nodes and internode length was 0.60. These results indicated that a taller plant tended to have larger number of nodes and longer internode length. Also, an increase in number of nodes might result in increasing internode length.

In conclusion, the F_1 hybrid was significantly taller and had significantly greater number of nodes than the midparental value, indicating that a sizable amount of non-additive gene action was involved for these three characters. Plant height, number of nodes on the main stem, and internode length appeared to be quantitatively inherited. A large amount of transgressive segregation was observed for plant height and number of nodes as shown by the distribution of the F_2 plants over the entire range of the two parents for these two

characters. The F_2 population was also distributed over the entire range of the two parents for internode length. Broad-sense heritability estimates were high for plant height and number of nodes and moderate for internode length. Narrow-sense heritability estimates were considerably lower than the broad-sense estimates with the values of 0.15 for plant height, 0.21 for number of nodes and 0 for internode length. Significant positive correlations were observed for plant height versus number of nodes, plant height versus internode length, number of nodes versus internode length suggesting that the two characters being contrasted were probably not inherited independent of each other. Genotypic correlations were greater than phenotypic correlations, indicating that the associations of plant height and its components were primarily genetic.

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Table 1. Ranges, means, and coefficients of variations (CV) for plant
height and number of nodes at maturity in populations obtained from
the cross of Douglas/Essex.

Population	No. of Plants	Range	Mean with its standard error	CV (%)
Plant height (cm)†				
P_1 (Douglas)	23	40 - 72	58.1$\pm$1.9	16.2
P_2 (Essex)	27	32 - 54	44.6$\pm$1.9	11.7
F_1	10	53 - 80	68.7$\pm$2.5	11.3
F_2	558	5 -103	55.1$\pm$0.7	32.0
$BC_1(F_1xP_1)$	22	21 - 80	55.9$\pm$3.2	26.9
$BC_2(F_1xP_2)$	39	15 - 80	51.4$\pm$2.8	33.8
Number of nodes‡				
P_1 (Douglas)	23	13 - 25	20.1$\pm$0.6	13.7
P_2 (Essex)	27	13 - 18	16.1$\pm$0.3	9.2
F_1	10	20 - 26	23.3$\pm$0.7	8.9
F_2	558	2 - 51	19.2$\pm$0.2	26.7
$BC_1(F_1xP_1)$	22	7 - 27	19.0$\pm$1.0	24.1
$BC_2(F_1xP_2)$	39	9 - 25	18.2$\pm$0.7	24.6

†LSD (0.05) for plant height of P_1 vs. P_2=9.5 and of F_1 vs. P_1=12.6.

‡LSD (0.05) for number of nodes of P_1 vs. P_2=2.7 and of F_1 vs. P_1=3.6.

Table 2. Ranges, means, variances, and coefficients of variations for internode length at maturity in populations obtained from the cross of Douglas/Essex.

Population	No. of plants	Range	Mean with its standard error	CV
		cm	cm	%
P_1(Douglas)	23	1.95 - 4.92	2.82 ± 0.12	19.57
P_2(Essex)	27	2.13 - 3.33	2.74 ± 0.05	10.15
F_1	10	2.30 - 3.19	2.95 ± 0.03	4.01
F_2	558	1.00 - 5.08	2.84 ± 0.02	18.32
$BC_1(F_1 \times P_1)$	22	1.62 - 4.21	2.96 ± 0.12	18.78
$BC_2(F_1 \times P_2)$	39	1.36 - 4.21	2.79 ± 0.11	23.47

Table 3. Estimates of broad-sense and narrow-sense heritabilities and their standard errors for plant height and height components in the cross of Douglas/Essex.

Character	Broad-sense heritability estimates	Narrow-sense heritability estimates
Plant height	0.82±0.04	0.15±0.37
Number of nodes	0.81±0.04	0.21±0.35
Internode length	0.40±0.14	-0.37±0.59

Table 4. Phenotypic (r_p) and genotypic (r_g) correlation coefficient

for plant height and its components in the cross of Douglas/Essex.

Correlations	Phenotypic	Genotypic†
Plant height vs. number of nodes	0.83**	0.90 ± 0.03
Plant height vs. internode length	0.68**	0.86 ± 0.11
Number of nodes vs. internode length	0.22**	0.60 ± 0.19

**Significant at the P=0.01 levels.

† No test for significance is available for gentoypic correlations.

CHAPTER VI

SUMMARY

Two experiments were performed to investigate the inheritance of
agronomic characters in soybeans. The experiments were conducted at the
Agronomy Research Station, Perkins, Oklahoma.

In the first experiment, six F_1 hybrids (all combinations except
reciprocals) of the cultivars Douglas, Essex, Forrest, and York were
space-planted along with the parents in the summer of 1982 and 1983.
The 1983 experiments also included six F_2 hybrids. The objectives of
this experiment were: (i) to determine the magnitude of heterosis,
inbreeding depression, and combining ability for agronomic characters,
and (ii) to determine the magnitude of heritability estimates and the
association of yield with other agronomic characters. The characters
evaluated include seed yield, number of pods/plant, number of seeds/pod,
seed weight, plant height, plant weight and harvest index.

Heterosis and inbreeding depression were greater for yield than for
any other character. Number of pods/plant expressed the greatest
heterotic response and inbreeding depression of the yield components.
Significances of average heterosis, inbreeding depression, and F_2
deviations were observed for yield, pods/plant, and harvest index,
suggesting that both dominance and epistatic effects could be involved
for these three characters. When averaged over years and crosses,
midparent heterosis for yield, pods/plant, seeds/pod, seed weight,

height, plant weight, and harvest index were 25.4, 18.9, 0.2, 3.2, 14.6, 21.5 and 3.8 %, respectively.

Average high-parent heterosis for yield, pods/plant, seeds/pod, seed weight, height, plant weight, and harvest index were 20.9, 9.0, -3.5, -6.5, 9.5, 15.6, and 1.1 %, respectively. The relatively high level of high-parent heterosis for yield found in this study suggests that if an economical large-scale method of producing F_1 seed could be found, the commercial production of hybrid soybeans should be favorable.

General combining ability (GCA) estimates were significant for pods/plant, seeds/pod, seed weight, and height. Specific combining ability (SCA) estimates were significant for yield, pods/plant, seed weight, and plant weight. The interactions of year x GCA and of year x SCA were not significant for yield, yield components, height, and plant weight. The year x GCA interaction was significant for harvest index, whereas the year x SCA was not significant suggesting that SCA was more stable over years than GCA.

When averaged over all crosses, the magnitude of broad-sense heritability estimates were as follows: 0.66 (height), 0.64 (days to flowering), 0.56 (harvest index), 0.54 (seed yield), 0.53 (pods/plant), 0.51 (seed weight), 0.49 (plant weight), and 0.10 (seeds/pod). High yield was positively associated with greater number of pods/plant and with increases in plant weight and plant height. Number of pods/plant and plant weight was closely related to yield. Significant positive correlations for yield with seeds/pod, seed weight, and harvest index were found in three populations while the correlations in the other three populations were not significant. Both positive and negative correlation were observed between yield and days to flowering.

In the second experiment, parental, F_1, F_2 and backcross (BC_1 and BC_2) generations of a Douglas/Essex cross were spaced planted in the summer of 1983. The objectives of this experiment were: (i) to determine the inheritance of plant height and its components and (ii) to investigate the correlations between plant height and its components.

The F_1 was significantly taller and had significantly greater number of nodes on the main stem than the midparental value, indicating that a sizable amount of non-additive gene action was involved for these two characters. A large amount of transgressive segregation was observed for plant height and number of nodes. The F_2 population was distributed over the entire range of the two parents for internode length.

Broad-sense heritability estimates for height, number of nodes, and internode length were 0.82, 0.81 and 0.40, respectively. Narrow-sense heritability estimates for height, number of nodes, and internode length were 0.15, 0.21, and 0, respectively. Significant positive associations were observed for plant height versus number of nodes, plant height versus internode length, and number of nodes versus internode length suggesting that the characters contrasted were probably not inherited independent of each other. Genotypic correlations were greater than phenotypic correlations for all cases indicating that the associations of height and its components were primarily genetic.

APPENDIXES

LIST OF APPENDIX TABLES

Table 1. Means of parents and F_1's for height and other characters in soybeans in 1982 and 1983.

Entry	Year	Height	Days to flowering	Plant Wt	Harvest index
		cm		g/plants	
Douglas	1982	62.2	34.3	252.5	0.406
	1983	64.3	38.5	215.6	0.410
Essex	1982	59.6	46.8	192.0	0.434
	1983	49.5	54.0	230.7	0.467
Forrest	1982	60.5	48.4	255.3	0.391
	1983	59.5	56.0	235.7	0.459
York	1982	54.4	46.4	281.2	0.405
	1983	54.3	55.3	250.0	0.414
Douglas/Essex	1982	75.9*	43.3†	305.7*	0.431
	1983	72.4*	50.2†	291.1*	0.454
Douglas/Forrest	1982	90.2*	44.7†	321.2*	0.358‡
	1983	74.0*	52.4†	225.6	0.468†
Douglas/York	1982	76.6*	44.7†	305.5	0.419
	1983	69.5†	51.4†	262.2	0.485*
Essex/York	1982	55.1	48.9*	286.6†	0.436
	1983	51.8	56.5	273.0	0.465
Forrest/Essex	1982	58.4	48.0	293.5†	0.423
	1983	54.9	55.7	273.9†	0.470
Forrest/York	1982	63.6†	48.4†	355.6*	0.400
	1983	59,2	57.9†	287.1*	0.465†
CV.,%	1982	5.3	1.7	12.0	4.8
	1983	10.2	4.4	15.6	5.2

*Significantly larger than the high-parent at the 0.05 probability level.

†Significantly larger than the midparent-value at the 0.05 probability level.

‡Significantly smaller than the midparent-value at the 0.05 probability level.

Table 2. Midparent heterosis, inbreeding depression, and F_2 deviations for yield and yield components in six soybean hybrids, 1983.

Hybrids	Criteria (%)	Yield	No. of pods/plant	No. of seeds/pod	Seed Weight
Douglas/	Midparent heterosis	35.2**	24.4**	-1.1	7.7*
Essex	Inbreeding depression	27.4**	28.5*	-1.6	-0.9
	F_2 deviations	-16.5**	-20.7**	1.0	4.6
Douglas/	Midparent heterosis	6.6	1.7	-3.4	6.5
Forrest	Inbreeding depression	13.2	14.7*	-2.7	2.4
	F_2 deviations	-10.4	-14.0*	-0.9	0.7
Douglas/	Midparent heterosis	32.2**	20.1*	4.6*	3.3
York	Inbreeding depression	-22.0**	17.1*	1.5	4.7
	F_2 deviations	-11.1	-9.5	0.7	-3.1
Essex/	Midparent heterosis	20.2**	18.3**	2.5	-5.3
York	Inbreeding depression	2.8	4.2	0.2	-1.0
	F_2 deviations	6.1	3.9	1.1	-1.8
Forrest/	Midparent heterosis	19.5**	14.8*	-1.7	3.2
Essex	Inbreeding depression	15.2*	13.4*	-1.4	1.6
	F_2 deviations	-7.7	-7.5	0.5	0.4
Forrest/	Midparent heterosis	25.0**	19.5**	4.2	-6.3*
York	Inbreeding depression	18.8*	10.2	1.8	0.5
	F_2 deviations	-4.8	-2.2	0.2	-3.7

*,**Significant at the P=0.05 and 0.01 levels, respectively.

Table 3. Midparent heterosis, inbreeding depression, and F_2 deviations for four characters in six soybean hybrids, 1983.

Hybrids	Criteria (%)	Ht wt	Plant wt	Harvest index	days to flowering
Douglas/	Midparent heterosis	27.2	30.5**	3.6	8.5**
Essex	Inbreeding depression	21.1**	24.8**	2.8	1.9
	F_2 deviations	-12.0**	-14.9**	-1.1	2.1
Douglas/	Midparent heterosis	19.5**	-0.0	7.7**	10.8**
Forrest	Inbreeding depression	10.2**	5.2	8.3**	2.4
	F_2 deviations	-2.2	-5.2	-4.8**	2.6
Douglas/	Midparent heterosis	17.1**	12.6	17.6**	1.3**
York	Inbreeding depression	15.3**	10.0	13.5**	1.2
	F_2 deviations	-8.7**	-4.7	-6.4**	3.3
Essex/	Midparent heterosis	-0.3	14.1	5.6*	9.4*
York	Inbreeding depression	-9.0	-0.5	4.1	1.0
	F_2 deviations	8.9	6.8	-1.5	0.8
Forrest/	Midparent heterosis	0.7	17.5*	1.5	3.3
Essex	Inbreeding depression	-2.4	13.6*	1.5	3.3
	F_2 deviation	2.7	-6.6	-0.7	0.9
Forrest/	Midparent heterosis	4.1	7.5**	6.4*	4.0*
York	Inbreeding depression	3.8	9.1	5.8*	2.4
	F_2 deviation	-1.8	-1.5	-2.9	-0.5

*,**Significant at the p=0.05 and 0.01 levels, respectively.

Table 4. Midparent and High-parent heterosis for seven characters in six F_1 hybrids in soybeans averaged over two years.

Hybrids	Criteria† (%)	Yield	No. of pods/plant	No. of seeds/pod	Seed weight	Ht	Plant wt	Harvest index
Douglas/Essex	MP	38.1**	24.2**	2.0	7.1**	25.9**	34.0**	3.0
	HP	38.0**	14.7*	−4.1*	6.4**	17.2**	27.5**	−1.8
Douglas/Forrest	MP	10.0	0.2	−2.6	11.7**	33.2**	14.0*	−1.0
	HP	5.4	−13.8*	−5.0*	1.9	29.8**	11.4	−2.9
Douglas/York	MP	24.7**	12.3*	2.4	7.3**	24.2**	13.6*	10.5**
	HP	17.3**	11.7	−3.6	−4.6	15.4**	6.8	10.3**
Essex/York	MP	23.8**	24.4**	2.0	−4.9*	−1.8	17.3**	4.8*
	HP	16.6*	15.5*	1.9	−16.0**	−2.0	5.3	0.1
Forrest/Essex	MP	26.6**	22.5**	−2.0	2.3	−1.1	24.2**	1.9
	HP	21.4**	14.3*	−5.7**	−6.0	−5.6	15.6*	−0.9
Forrest/York	MP	29.4**	28.9**	−1.0	−3.7	7.4*	25.7**	3.5
	HP	27.0**	11.5*	−4.6*	−21.0**	2.4	21.0**	1.6

†MP = midparent heterosis and HP = high-parent heterosis.

*,**significant at the P = 0.05 and 0.01 levels, respectively.

Table 5. Means squares for general (GCA) and specific combining ability (SCA) for seven characters in six F_1 hybrids of soybeans in 1982 and 1983.

| | Mean squares[1] | | | | | |
| | 1982 | | | 1983 | | |
Character	GCA	SCA	Error	GCA	SCA	Error
Yield	173.0	558.2	307.1	660.6	1 158.0†	429.8
No. of pods/plant	14 921.4*	5 031.4	2 794.4	20 989.9**	5 181.0	3 337.1
No. of seeds/pods	0.103*	0.001	0.023	0.028	0.012	0.021
Seed weight	12.2**	0.7	0.7	31.4**	1.2	1.4
Height	1 143.8**	54.3*	13.4	1 172.9**	59.5	37.5
Plant wt	2 550.3	2 272.9	1 844.9	3 205.0	6 338.0†	2 091.5
Harvest index	0.005**	0.001	0.001	0.004	0.001	0.001
Days to flowering	35.9**	1.6	0.8	127.8**	3.2	7.5

†,*,**Significant at the P = 0.10, 0.05, and 0.01 levels, respectively.

[1]Degrees of freedom for GCA, SCA, and error mean squares are 3,2, and 15 for 1982, and 3,2, and 35 for 1983, respectively.

Table 6. Mean squares for general (GCA) and specific combining ability (SCA) for seven characters in six F_2 hybrids of soybeans, 1983.

	Mean squares[1]		
Characters	GCA	SCA	Error
Yield	1 918.2**	40.4	101.4
No. of pods/plant	30 029.3**	78.9	850.9
No. of seeds/pod	0.047**	0.386	0.005
Seed weight	26.1**	0.1	0.5
Height	142.5**	96.0	19.2
Plant wt	7 230.0**	243.61	519.3
Harvest index	0.003**	0.001	0.0004
Days to flowering	136.9**	1.7	3.2

**Significant at the P = 0.01 level.

[1]Degrees of freedom for GCA, SCA, and error mean squares are 3,2, and 35, respectively.

Table 7. Estimates of general combining ability effects for seven characters form a four-parent diallel cross in soybeans averaged over two years.

Parent	Yield	No. of pods/plant	No. of seeds/pod	Seed weight	Height	Plant weight	Harvest index
Douglas	-5.57	-47.38	0.094	0.97	13.80	-9.48	-0.003
Essex	3.84	30.89	-0.043	-0.71	-7.36	2.50	0.005
Forrest	-3.54	27.01	-0.036	-1.52	-0.54	-0.57	-0.009
York	5.27	-10.51	-0.015	1.25	-5.89	7.55	0.007
Standard error	3.5	10.00	0.026	0.20	0.97	7.9	0.004

Table 8. Estimates of specific combining ability effects for seven characters from a four-parent diallel cross in soybeans averaged over two years.

Hybrids	Yield	No. of pods/plant	No. of seeds/pod	Seed weight	Height	Plant weight	Harvest index
Douglas/Essex	7.79	20.23	0.012	-0.20	1.39	19.94	-0.004
Douglas/Forrest	-8.78	-20.15	-0.020	-0.11	0.41	-15.50	-0.005
Douglas/York	0.99	-0.08	0.007	0.31	-1.80	-4.45	0.010
Essex/York	-8.78	-20.15	-0.020	-0.11	0.41	-15.50	-0.005
Forrest/Essex	0.99	-0.08	0.007	0.31	-1.80	-4.5	0.010
Forrest/York	7.79	20.23	0.012	-0.20	1.39	19.94	-0.004
Standard error†	3.30	9.39	0.024	0.18	0.92	7.49	0.004

†For comparison of F_1's having one common parent.

Table 9. Means squares of plant height and height components in a cross of Douglas/Essex, 1983.

Source of variation	df	Height	No. of nodes	internode length
Replication	5	603.29	20.51*	1.226*
Entry	5	1 072.86**	99.60*	0.155
Pooled error†	668	288.17	24.03	0.275
Entry * Block	25	177.27	12.77	0.259
Error	643	292.48	24.47	0.273
Corrected Total	678	296.28	24.56	0.281

† The entry * block mean squares were not significant at the

P = 0.25 for any characters; therefore, entry * block mean square

for each character was pooled with the error mean square to obtain

the pooled error mean square.

Table 10. Frequency distributions for plant height of parental, hybrid, and segregating populations in a cross of Douglas/Essex, 1983.

Population	Height classes designated by upper limits, cm																				n†	CV (%)
	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90	95	100		
Douglas(P_1)								3	1	2	5	6	3	3							23	16.7
Essex(P_2)					2	5	3	11	6												27	11.7
F_1										1	1	1	2	2	2	1					10	11.3
F_2	8	8	7	11	4	24	34	61	46	44	55	81	50	53	33	24	5	7	2	1	558	32.0
F_1xP_1(BC$_1$)				2				3	3		5	1	4	2	1	1					22	26.9
F_1xP_2(BC$_2$)			1	3	1	3	2	4	2	4	5	3	4	4	2	1					39	33.8

† Number of plants for each population.

Table 11. Frequency distributions for number of nodes on the main stem of parental, hybrid, and

segregating populations in a cross of Douglas/Essex, 1983.

| | Number of nodes classes designated by upper limits | | | | | | | | | | | | | | | | CV |
Population	2	4	6	8	10	12	14	16	18	20	22	24	26	28	30	n†	(%)
Douglas (P$_1$)						1	1	2	1	7	5	6				23	13.6
Essex (P$_2$)						1	8	11	7							27	9.2
F$_1$										2	4	2	2			10	8.9
F$_2$	1	5	11	12	8	29	53	67	78	97	86	83	22	4	2	558	26.7
F$_1$xP$_1$ (BC$_1$)			1		1	1	1	2	4	4	7		1			22	24.2
F$_1$xP$_2$ (BC$_2$)				1	3	2	7	4	4	7	6	5				39	24.6

† Number of plants for each population.

Table 12. Frequency distributions for internode length of parental, hybrids, and segregating populations in a cross of Douglas/Essex, 1983.

Population	Internode length classes designated by upper limits, cm																	n†	CV (%)
	1	1.25	1.5	1.75	2	2.25	2.5	2.75	3	3.25	3.5	3.75	4	4.25	4.75	5	5.25		
Douglas(P_1)				1	2	2	4	8	3	2					1			23	20.0
Essex(P_2)					1	4	6	11	4	1								27	10.2
F_1					1			3	6									10	4.0
F_2	4	7	5	9	34	53	111	125	104	57	30	10	3	2	1	3		558	18.3
$F_1 \times P_1$ (BC$_1$)		1		3			1	6	4	4	1	1	1					22	18.8
$F_1 \times P_2$ (BC$_2$)		1		1	4	4	8	7	8	5						1		39	23.5

† Number of plants for each population.

Table 13. Phenotypic correlation coefficients (r_p) for height and height components with other agronomic characters in a cross of Douglas/Essex, 1983.

	Yield	No. of pods/plant	No. of seeds/pod	Seed size	Plant wt	Harvest index	Days to flowering
Height	0.51**	0.48**	0.23**	−0.22**	0.59**	−0.06	0.30**
No. of nodes	0.48**	0.47*	0.21**	−0.23**	0.53*	0.01	0.20**
Internode length	0.27**	0.26**	0.13**	−0.19**	0.33**	−0.06	0.28**

*,** Significant difference from zero at the P = 0.05 and 0.01, respectively.

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