

GENETIC STUDIES OF PROTEIN AND OIL IN SOYBEANS

[Glycine max (L.) Merr.]

By

MAHMOUD Y. SABBOUH

Bachelor of Science
Damascus University
Damascus, Syria
1977

Master of Science
Oklahoma State University
Stillwater, Oklahoma
1982

Submitted to the Faculty of the Graduate College
of the Oklahoma State University
in partial fulfillment of the requirements
for the Degree of
DOCTOR OF PHILOSOPHY
May, 1986

Thesis
1986D
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Thesis Approved:

Lewis H. Edwards

Thesis Adviser

Jewell Crahtree

Ronald W. McNew

James S. Kirby

Norman M. Dusham

Dean of the Graduate College

ACKNOWLEDGEMENTS

Sincere appreciation is expressed to my major adviser, Dr. Lewis H. Edwards, for his guidance, encouragement, and assistance throughout the course of this study. Special appreciation is also expressed to Dr. J.S. Kirby, Dr. R.J. Crabtree, and Dr. R.W. McNew for serving on my graduate committee and their help and valuable suggestions in preparation of this manuscript. Special gratitude is expressed to Dr. R.W. McNew for his assistance in conducting the statistical analyses of the data and to Dr.D.C. Abbott for his help in conducting the protein and oil analyses.

To my wife, Aiyda, my son, Nashat, my daughters, Shaza and Samah, I wish to express my deepest appreciation for their love, patience, understanding, and encouragement which made this study possible. Appreciation is expressed to my father and mother, Yousef and Tamrah, and my brothers, Ali, Souleiman, and Ahmed, for their love and support.

The author is indebted to Damascus University and the Agency for International Development for the financial assistance which made this study possible.

Gratitude is also expressed to the members of the Soybean Breeding Program for their assistance in this study.

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CHAPTER I

INTRODUCTION

Continuous crop improvement is one of the most important factors that has the potential to meet the world's increasing demand for food quantity and quality. Soybeans, Glycine max (L.) Merr., are probably the best candidate to meet these increasing demands. Soybeans are rich sources for protein (40%) and oil (20%). Soy oil accounts for about 83% of all vegetable oil consumed in the United States and is mainly used in food products, fuel, soap, and paints. Soy meal is widely used for feeding livestock. Soybean products are also used as carriers for antibiotics, vitamins, and drugs in animal feeds.

Soybean production in the United States, the major world producer, has increased steadily over the years. Research efforts have been extensively directed toward improving seed yield and other nonchemical traits. Less effort has been directed toward increasing percent protein and oil. Seed protein is affected by soil fertility, soil moisture, and may be increased by nitrogen application. However, the development and widespread use of soybeans higher in protein content would be more practical, especially in the developing countries where other methods of increasing seed protein are not available.

Genetic studies concerning heritability and correlations between protein, oil, seed yield, and seed size in soybeans have been conducted. Information related to the existence and magnitude of heterosis for

protein and oil has been limited. Information presented in Chapters II and III were obtained from a four-parent diallel cross. Chapter II discusses heterosis and combining ability for seed protein and oil contents. This study was carried out at one location for two consecutive years.

In the third chapter, estimates of heritability in the broad sense for protein and oil contents in the seed are presented. Phenotypic and genotypic relationships among protein, oil, seed size, and seed yield are also discussed.

In the fourth chapter, information concerning the genetic control of seed size and its relationship with protein, oil, and seed yield are presented. Estimates of heritability in the broad and narrow sense for the above four characters are also discussed.

Chapters II, III, and IV are presented in a form acceptable to the Crop Science Society of America¹. The fifth chapter is a general summary of the three studies. Additional data from the separate analyses as well as the combined analysis are presented in the Appendix.

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

CHAPTER II

Heterosis and Combining Ability for Protein and Oil in Soybeans¹

ABSTRACT

Little information is available about the existence and level of heterosis for protein and oil in soybean [Glycine max (L.) Merr.] hybrids. Four adapted cultivars 'Essex', 'Forrest', 'York', and 'Douglas' were hand-crossed in a diallel fashion with no reciprocals to derive six F₁ hybrids. Seeds from the six F₁'s, the six F₂'s and the four parents were space-planted in a randomized complete block design at the Agronomy Research Station, Perkins, Oklahoma in 1983 and 1984. This investigation was carried out to examine the existence and levels of heterosis for protein and oil, and to determine the relative magnitude of general and specific combining ability for the above two traits.

In 1983, three F₁ hybrids showed significant midparent heterosis of 2.3%, 5.8%, and 7.8% for percent oil. One of the three hybrids showed significant high-parent heterosis of 4.5%. In 1984, significant midparent (2.6%) and high-parent (1.8%) heterosis for percent protein were measured in one hybrid. Two hybrids showed significant midparent heterosis of 2.6% and 2.8% for percent oil. When averaged over years, midparent heterosis of 1.0% was measured for protein in one hybrid. Two

¹To be submitted for publication.

hybrids showed significant midparent (2.6% and 4.7%), and high-parent (2.1% and 2.3%) heterosis for oil.

General combining ability (GCA) mean squares were highly significant for protein in the 1983 F₁ and the 1983 and 1984 F₂ diallel analyses. Although significant specific combining ability (SCA) mean squares were observed in all but the 1983 analysis, GCA was more important than SCA for protein. The GCA mean square for oil was significant only in 1984. SCA mean squares were significant in both 1983 and 1984 but not in the combined data. Interactions of GCA and SCA with years were significant in both generations except for the F₁ in 1983. In all three analyses, Douglas was identified as having the highest positive GCA effect for protein. The results indicate that significant levels of both midparent and high-parent heterosis for both protein and oil exist in soybeans.

Additional index words: Protein, oil, heterosis, general, and specific combining ability.

Increasing percent protein and oil in soybeans [Glycine max (L.) Merr.] has become an urgent need, especially in the developing countries where nutritional sources are limited. The utilization of male sterility in soybeans (2) may provide the potential to produce hybrid seed economically. Sufficient levels of heterosis are required to justify commercial production of hybrid varieties.

Considerable evidence concerning midparent and high-parent heterosis for seed yield, plant height, maturity, seed size, and other agronomic characters in soybeans has accumulated (1,7,8,9,10,11,13,16,-19,21). However, less information is available about the existence and levels of heterosis for percent protein and oil (1,10,11,15,21). Weber et al. (21) evaluated heterotic performance of two-way F_1 soybean hybrids and reported no significant midparent heterosis for protein or oil. They also reported high-parent heterosis of -0.9% for protein and -1.5% to 0.14% for oil. Nelson and Bernard (11) found midparent heterosis to be in the ranges of -0.6% to 1.6% for percent oil, and -0.7% to 0.8% for percent protein. They concluded that neither midparent nor high-parent heterosis was statistically significant. Singh and Hadley (15) examined maternal and cytoplasmic effects on seed protein and found that F_1 seeds from one cross had higher percent protein than did selfed seeds from its corresponding high protein female parent. However, their conclusion was that little or no paternal effects existed for protein content of F_1 seeds.

Combining ability estimates are important in identifying superior parents and hybrids in early generations in a soybean breeding program. Information about combining ability estimates for protein and oil in soybeans is limited. Leffel and Weiss (10) found that neither general

combining ability (GCA) nor specific combining ability (SCA) effects were significant for protein. However, both types of combining ability were found to be important for percent oil. Weber et al.(21) estimated both GCA and SCA effects of five soybean varieties in 10 hybrid combinations. They found that only SCA effects were significant for percent oil.

This investigation was undertaken (1) to obtain more information on the magnitude of heterosis for percent protein and oil, and (2) to determine the relative magnitude of general and specific combining ability in soybeans grown under Oklahoma conditions.

MATERIALS AND METHODS

In this study, six hybrids were derived from hand-crossing four soybean cultivars, Essex (18), Forrest (6), York (17), and Douglas (12), in all possible combinations with no reciprocals. Douglas was used as a female parent only, York was used as a male parent only, while Essex and Forrest were used as male and female parents. The four parents were chosen because of genetic diversity in their pedigree, differences in seed protein and oil, and their adaptability to growing conditions in Oklahoma.

Seeds from the six F_1 's, and the six F_2 's along with the four parents were space-planted on a Teller Loam soil (Fine-Loamy, Mixed, Thermic Udic Argiustolls) at the Agronomy Research Station, Perkins, Oklahoma, in the crop seasons of 1983 and 1984. Soil tests indicated that amounts of nutrients for the growth of soybeans were adequate. Test plants were arranged in a randomized complete block design with eight blocks. Each block consisted of a total of 234 test plants distributed over 18 rows with 13 plants in each row. Each test plant was considered as an experimental unit. Each row was bordered by two discard plants and each block was bordered by two rows of discard plants. Plantings were made using a hill planter, and inoculum of Rhizobium japonicum was applied to the seed before planting. An equidistant planting of 75 X 75 cm between rows and plants was used. The total number of test plants was distributed as follows: 72 plants from each parent, 20 to 72 F_1 plants from each cross, and 218 to 227 F_2

plants from each cross. To minimize differential competition among plants, all dead plants were replaced with discard plants at the seedling stage. During the growing season, supplemental irrigation was provided in addition to rainfall to insure optimum growth conditions. All measurements were made on an individual plant basis. Seed protein and oil content were estimated on a dry weight basis from a 10 g sample by the Technicon InfraAnalyzer TM ⁴⁰⁰ (20) using the near infrared reflectance (NIR) of the sample.

In the analyses for this study, the block factor was considered random; therefore block within years was the appropriate error term to test for the significance of years. The factors years and entries were considered fixed and inferences are therefore valid only for the test materials in the study. Block X entry within years was used to test for the significance of entries and the interaction of years X entries. The data from the F_1 and F_2 generations were subjected to separate analyses utilizing method 4 (F_1 hybrids with no reciprocals) of Griffing (4). Heterosis values for the six F_1 hybrids were calculated as:

$$\% \text{ midparent heterosis} = [(F_1 - \text{midparent}) / \text{midparent}] \times 100$$

$$\% \text{ high-parent heterosis} = [(F_1 - \text{high-parent}) / \text{high-parent}] \times 100.$$

The Least Significant Difference (LSD) was used to test for the significance of the differences between the F_1 and high-parent. The significance of the differences between F_1 and midparent within each year and in the combined data was tested by orthogonal contrasts.

RESULTS AND DISCUSSION

The analyses of variance within years showed that differences among the six F_1 hybrids were highly significant for both protein and oil (Appendix Table 1). When averaged over the two years (Table 1), differences among the F_1 hybrids were highly significant for protein but not significant for oil. Differences among parents and the six F_1 hybrids in 1984 were smaller than those of 1983 for percent oil (Table 2). Also the six F_1 hybrids performed differently in the two years which resulted in highly significant interactions with years for this trait (Table 1). Essex/York had the highest oil percentage in 1983 but had the lowest in 1984 (Table 2). These factors could have contributed to the nonsignificant mean square for oil in the combined analysis. Significant differences among parents, years, parent X year, entry X year, and F_1 X year were observed for both traits (Table 1). The combined analysis indicated that neither the parents nor the F_1 hybrids were stable in performance over years for the two traits. The failure of parents and F_1 hybrids to perform the same in each year resulted in significant interactions with years in the combined analysis. This could be observed by examining Table 2 where, in general, hybrids with lowest protein content in 1983 had the highest protein content in 1984. Similar changes in performance of F_1 hybrids were observed for oil content. These changes in relative performance from one year to the next were the primary reasons for the indicated interactions with years for both traits.

Heterotic Performance

The analysis of variance of the combined two-years data revealed highly significant differences between generations for protein and oil contents (Table 1). This indicates the presence of nonadditivity required for heterosis. Gardner and Eberhart (3) indicated that the mean square of parents vs F_1 's generally reflects average midparent heterosis and it is totally caused by a type of gene action other than additive. Highly significant interactions of years with generations for both protein and oil indicates that both the parents and F_1 's acted differently over the two years. Significant interactions of midparent heterosis with years were observed for both protein and oil in Douglas/Forrest, Essex/York, and Forrest/York. Changes in direction and magnitude of the responses of the three hybrids in the two years were probably the main reasons for the indicated interactions.

Midparent and high-parent heterosis (%) of the six F_1 hybrids in 1983, 1984, and the combined two years are presented in Table 3. In 1983, the range of midparent heterosis for protein was from -1.2% to -6.6%, and the range of high-parent heterosis was from -1.9% to -8.8%. Three hybrids: Douglas/York, Forrest/York, and Essex/York had significantly lower protein percentage than the midparent. Essex/York had significantly lower protein percentage than its low parent. In 1984, the range of midparent heterosis for protein was from -2.0% to 2.6%, and the range of high-parent heterosis was from -2.6% to 1.8%. The hybrid of Douglas/Forrest showed significant midparent and high-parent heterosis of 2.6% and 1.8%, respectively. These values are larger than those reported by Weber et al.(21), Leffel and Weiss (10),

and Nelson and Bernard (11) from studies with adapted parents. The combined data (Table 3) showed that the range of midparent heterosis for percent protein was from -3.3% to 1.0%, and that the range of high-parent was from -5.4% to 0.2%. Only one hybrid, Douglas/Forrest, showed significant positive midparent heterosis.

The range of midparent heterosis for oil in 1983 was from 0.6% to 7.8%, and that of high-parent heterosis was from -2.1% to 4.5%. Significant midparent heterosis for oil was measured in three hybrids: Douglas/York (2.3%), Forrest/ York (5.8%), and Essex/York (7.8%). Essex/York also showed highly significant high-parent heterosis of 4.5% for oil. These values contrast with those reported by others (1,11,21) where no significant midparent or high-parent heterosis was reported for oil. In 1984, midparent heterosis for oil ranged from -3.4% to 2.8%, and high-parent heterosis ranged from -6.2% to 2.3%. The hybrids of Forrest/Essex and Forrest/York showed significant midparent heterosis of 2.6% and 2.8%, respectively. When averaged over the two years, significant positive midparent heterosis for oil was measured in Forrest/Essex (2.6%) and Forrest/ York (4.7%). The two hybrids also showed significant positive high-parent heterosis for oil of 2.1% and 2.3%, respectively (Table 3). Values of 2.6% and 4.7% for midparent heterosis, and 2.3% and 2.6% for high-parent heterosis for oil are generally larger than those previously reported for this trait (1,10,11,21).

These results provide additional evidence that nonadditive gene action may be important in controlling both protein and oil. The data suggest that partial and overdominance could be important in the expression of these two traits. The importance of additive X additive

epistasis and partial dominance in controlling protein and oil in soybeans has been reported by others (1,5,10,14). The results indicate that significant midparent and high-parent heterosis levels do exist for protein and oil in certain hybrids. If hybrid seed could be economically produced, hybrid cultivars of soybeans have a potential for producing higher percentages of protein or oil.

Combining Ability Analyses

Within years analyses of variance for general combining ability (GCA) and specific combining ability (SCA) from F_1 's and F_2 's are presented in Table 4. The F_1 data shows that, in 1983, the GCA mean square was highly significant for percent protein. The SCA mean square was highly significant for oil. However, in 1984, both GCA and SCA mean squares were highly significant for oil, but only the SCA mean square was significant for protein. This is in contrast with results reported by Weber et al.(21), who reported a zero estimate of GCA for oil. The ratio of GCA to SCA mean squares for oil in 1984 was 0.36, suggesting that SCA was more important than GCA. Selection of hybrids should be based on their performance rather than on their parents performance. Results also suggest that nonadditive gene action may be important in controlling the expression of oil, but additive gene action appears to be more involved in the expression of protein.

To further investigate the predominant type of gene action which controls protein and oil, diallel analyses were conducted for the F_2 generation. Within years (Appendix Table 2) showed that differences among the six F_2 hybrids were significant for protein and oil, with the exception of the mean square for oil in 1983. GCA mean squares for

protein were highly significant in both years, but significant for oil only in 1984 (Table 4). Significant SCA mean square for protein was detected in 1984. No significant SCA mean square was observed for oil. The ratio of GCA to SCA mean squares for protein in 1984 was 1.4, indicating that additive gene action is the predominant type of gene action that controls the expression of protein.

The combined analysis (Appendix Table 3) showed that differences among entries were significant for protein in both generations. Differences among entries were significant for oil only in the F_2 generation. The F_1 data showed that GCA mean square was significant for protein. SCA mean squares were not significant for either trait (Table 5). The interaction of GCA with years was highly significant for oil, and that of SCA with years was highly significant for both traits. These results contrast with those reported by Leffel and Weiss (10) who found that neither type of combining ability was significant for protein. Changes in direction and magnitude of responses of F_1 hybrids over years could be a primary reason for the indicated interactions with years. Significant interactions of GCA and SCA with years indicate that both types of combining ability were not stable in performance over the two years.

The F_2 data (Table 5) showed that both GCA and SCA mean squares were significant for protein but not for oil. The ratio of GCA to SCA mean squares for protein was 9.3, indicating that GCA was more important than SCA in determining the progeny performance for this trait. The nonsignificance of SCA mean square for oil also agrees with the theoretical assumptions that nonadditivity should be reduced in the F_2 in comparison to that in the F_1 . Additive gene action is also more

important than nonadditive in controlling oil. Significant interactions of GCA X years were observed for both protein and oil. SCA X years was significant only for protein in the F_2 analysis of the combined data (Table 5). This indicates that both types of combining ability were not stable in performance for both characters over the two years.

Estimates of GCA effects for protein from the 1984 F_1 's are not presented because of a nonsignificant GCA mean square for the above trait. Estimates of GCA effects of the four parents for protein in 1983, 1984, and the combined data are presented in Table 6. The F_1 data showed that Douglas had the highest positive GCA effect (0.65 and 0.40) in 1983 and the combined data, respectively. Forrest had the highest negative GCA effect (-0.49 and -0.39) in the two analyses, respectively. The F_2 data showed that Douglas also had the highest GCA effect (0.69, 0.36, and 0.52) in 1983, 1984, and the combined data, respectively. Forrest (1983) and York (1984 and 83-84) had the highest negative GCA effects for protein. Because of nonsignificant SCA mean squares for protein in the F_1 of 1983 and the combined data (Tables 4 and 5), only estimates of SCA effects from the 1984 F_1 's; and 1984 and the combined F_2 data are presented. In the F_1 , the highest positive SCA effect (0.68) was associated with the hybrids of Douglas/Forrest and Essex/ York. However, in the F_2 , Douglas/York and Forrest/ York had the highest positive SCA effect in both 1984 and the combined data (Table 7). Douglas/Forrest also showed significant midparent and high-parent heterosis for protein in 1984 (Table 3), indicating the importance of SCA estimates in selection and evaluation of performance of hybrids. The hybrids: Douglas/Essex and Forrest/York had the highest negative SCA effects for this trait in both generations and in all analyses.

Because of nonsignificant differences among F_1 hybrids for oil in the combined data, discussion is limited to within years results. Estimates of GCA (1984 only) for this trait are presented in Table 8. The F_1 data showed that Douglas had the highest positive GCA effect (0.27) followed by Forrest (0.16). York had the highest negative GCA effect (-0.23) for this trait. In the F_2 , York had the highest positive GCA effect (0.13) followed by Forrest (0.11). Both Douglas and Essex had an equal negative GCA effect of 0.12. Estimates of SCA effects from the 1984 F_1 's (Table 9) showed that Douglas/Forrest and Essex/York had the highest negative SCA effect (-0.50) for oil. Douglas/York and Forrest/Essex had the highest positive SCA effect (0.29). Forrest/Essex also exhibited significant midparent and high-parent heterosis for oil (Table 3). The 1983 F_1 data showed that the highest positive SCA effect (0.30) was associated with Douglas/Forrest and Essex/York. The highest negative SCA effect (-0.29) was associated with Douglas/York and Forrest/Essex. Essex/York also showed highly significant midparent and high-parent heterosis for oil in 1983. Douglas was stable in performance according to the within years and combined data and had the highest positive GCA effect for protein. This parent appears to transmit genes conditioning high protein to its progeny.

In conclusion, within years analyses showed that, in 1984, significant midparent (2.6%) and high-parent heterosis (1.8%) for protein were measured in one hybrid. When averaged over the two years, low but significant midparent heterosis of 1.0% was measured for protein in one hybrid. In 1983, three F_1 hybrids showed significant midparent heterosis for oil (2.3, 5.8, and 7.8%). One out of the three showed significant high-parent heterosis of 4.5% for oil. In 1984, two hybrids

had significantly higher oil percentages than the midparent (2.6 and 2.8%). When averaged over the two years, two hybrids exhibited significant midparent (2.6 and 4.7%) and high-parent (2.1 and 2.3%) heterosis for oil. Mean squares of GCA for protein were highly significant in all analyses. Although significant SCA mean squares were observed, GCA was always more important than SCA, indicating the predominance of additive gene action in controlling protein. Interactions of GCA and SCA with years were significant for protein and oil, indicating instability in performance of both types of combining ability over years. In most cases, hybrids with highest SCA effects showed significant midparent or high-parent heterosis, indicating that selection of hybrids based on their SCA effects and heterotic performance was practical.

These results contrast with previous studies (1,10, 11,21). Higher midparent and high-parent heterosis were measured for both protein and oil in hybrids involving adapted cultivars of soybeans. We conclude that significant levels of heterosis may exist for the two traits, and, if hybrid seed production could become more economical, the potential for hybrid cultivars does exist in soybeans.

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Table 1. Mean squares for protein and oil for parents
and F₁ hybrids averaged over two years.

Source	df	Protein	Oil
Years(Yr)	1	225.5*	1351.9**
Blocks(Yr)	14	56.4**	14.8**
Entry	9	26.8**	17.2**
Gen.	1	31.7**	19.9**
P	3	48.5**	44.2**
F	5	12.7**	0.5
Entry X Yr	9	23.9**	9.9**
Yr X Gen.	1	74.6**	19.9**
Yr X P	3	30.6**	10.6**
Yr X F	5	9.6*	7.5**
Block X Entry(Yr)	126	4.2**	1.3**
Error	603	2.0	0.9

*,** significant at p=.05 and p=.01 levels, respectively.

Table 2. Means of parents and F₁ hybrids for protein and oil in soybeans in 1983, 1984, and the combined data.

Entry	Protein			Oil		
	1983	1984	83-84	1983	1984	83-84
	%			%		
Essex	38.2	38.6	38.5	20.4	17.8	19.1
Forrest	36.3	38.2	37.2	20.8	17.7	19.3
York	39.4	38.7	39.0	19.2	17.5	18.4
Douglas	37.9	37.7	37.8	21.0	19.1	20.0
Douglas/Essex	37.5	38.5	38.4	20.8	18.2	19.4
Douglas/Forrest	36.7	39.0*	37.9 [†]	21.2	17.9 [‡]	19.5
Douglas/York	37.4 [‡]	38.2	38.1	20.6 [†]	18.3	19.3
Forrest/Essex	36.8	38.2	37.2 [‡]	20.9	18.2 [†]	19.7*
Forrest/York	36.0 [‡]	37.7	36.8 [‡]	21.2 [†]	18.1 [†]	19.7*
Essex/York	36.3 [‡]	39.2	38.1	21.4*	17.1 [‡]	19.0

* significantly larger than the high-parent at p=.05.

[†] significantly larger than the midparent at p=.05.

[‡] significantly smaller than the midparent at p=.05.

Table 3. Midparent and high-parent heterosis (%) for protein and oil in six F₁ hybrids of soybeans in 1983, 1984, and the combined data.

Hybrid	Protein			Oil			
	1983	1984	83-84	1983	1984	83-84	
Douglas/Essex	MP	-1.4	0.9	0.7	0.6	-1.1	-0.7
	HP	-1.9	-0.3	-0.2	-0.7	-4.4**	-2.9**
Douglas/Forrest	MP	-1.2	2.6**	1.0*	1.6	-2.5**	-0.5
	HP	-3.2**	1.8*	0.2	1.1	-6.2**	-2.3**
Douglas/York	MP	-3.3**	0.0	-0.8	2.3*	-0.1	0.5
	HP	-5.2**	-1.3	-2.3	-2.1	-4.2**	-3.6**
Forrest/Essex	MP	-1.3	-0.7	-1.7**	1.3	2.6*	2.6**
	HP	-3.8**	-1.2	-3.3	0.4	2.3	2.1**
Forrest/York	MP	-5.1**	-2.0*	-3.3**	5.8**	2.8*	4.7**
	HP	-8.8**	-2.6*	-5.4	1.7	2.3	2.3**
Essex/York	MP	-6.6**	1.5	-1.4	7.8**	-3.4**	1.5
	HP	-8.0**	1.4	-2.1	4.5**	-4.1**	-0.5

MP,HP= midparent and high-parent heterosis, respectively.

*,**significant at p=.05 and p=.01 levels, respectively.

Table 4. Mean squares for general(GCA) and specific(SCA) combining ability for protein and oil in six F₁ and six F₂ hybrids of soybeans in 1983 and 1984.

Character	Mean squares					
	1983			1984		
	GCA	SCA	Error	GCA	SCA	Error
	F ₁ †					
Protein	13.13**	5.19	2.61	3.56	20.30**	2.44
Oil	1.21	4.58**	0.74	4.04**	11.09**	1.13
	F ₂ ‡					
Protein	55.12**	3.43	3.55	24.27**	17.35**	2.14
Oil	1.65	0.54	1.43	7.17**	1.83	1.12

*,**significant at p=.05 and p=.01 levels, respectively.

†F₁ df for GCA, SCA, and Error are 3,2, and 162 for 1983, and 3,2, and 199 for 1984, respectively.

‡F₂ df for GCA, SCA, and Error are 3,2, and 764 for 1983, and 3,2, and 1127 for 1984, respectively.

Table 5. Mean squares for GCA and SCA for protein and oil from a four-parent diallel cross averaged over two years.

Source	df	Protein		Oil	
		F ₁	F ₂	F ₁	F ₂
GCA	3	13.73 ^{**}	77.49 ^{**}	1.65	1.63
SCA	2	3.83	8.30 [*]	1.10	1.86
GCA X Year	3	3.11	7.72 [*]	3.22 ^{**}	5.97 ^{**}
SCA X Year	2	20.80 ^{**}	10.05 [*]	14.19 ^{**}	0.22
Error	X	2.52	2.71	0.95	1.24

X= 361 for F₁ and 1891 for F₂.

^{*},^{**} significant at p=.05 and p=.01 levels, respectively.

Table 6. Estimates of GCA effects for protein in 1983, 1984, and the combined data from a four-parent diallel cross in soybeans.

Parent	1983		1984 [†]	83-84	
	F ₁	F ₂	F ₂	F ₁	F ₂
Douglas	0.65	0.69	0.36	0.40	0.52
Essex	0.18	-0.14	-0.01	0.24	-0.07
Forrest	-0.49	-0.29	-0.16	-0.39	-0.22
York	-0.34	-0.26	-0.19	-0.25	-0.23
Std.Error	0.20	0.10	0.07	0.13	0.06

[†] GCA mean square was not significant for protein, so no estimates of GCA effects are necessary.

Table 7. Estimates of SCA effects for protein from a four-parent diallel cross in soybeans (1984 and 83-84).

Hybrid	1984		83-84
	F_1	F_2	F_2
Douglas/Essex	-0.37	-0.22	-0.07
Douglas/Forrest	0.68	0.01	-0.06
Douglas/York	-0.31	0.21	0.13
Forrest/Essex	-0.31	0.21	0.13
Forrest/York	-0.37	-0.22	-0.07
Essex/York	0.68	0.01	-0.06
Std.Error	0.17	0.06	0.05

Table 8. Estimates of GCA effects for oil from a four-parent diallel cross in soybeans in 1984.

Parent	F ₁	F ₂
Douglas	0.27	-0.12
Essex	-0.20	-0.12
Forrest	0.16	0.11
York	-0.23	0.13
Std.Error	0.12	0.05

Table 9. Estimates of SCA effects for oil from a four-parent diallel cross in soybeans in 1983 and 1984.

Hybrid	F ₁ (1983)	F ₁ (1984)
Douglas/Essex	-0.01	0.21
Douglas/Forrest	0.30	-0.50
Douglas/York	-0.29	0.29
Forrest/Essex	-0.29	0.29
Forrest/York	-0.01	0.21
Essex/York	0.30	-0.50
Std.Error	0.09	0.12

CHAPTER III

Heritability of Protein and Oil and Their Relationships with Yield and Seed Size in Soybeans¹

ABSTRACT

Heritability estimates and knowledge of the genetic relationships between different attributes could be utilized by plant breeders for enhanced development of improved cultivars. Four adapted cultivars of soybeans [Glycine max (L.) Merr.] were hand-crossed in all possible combinations (except reciprocals) to originate six F₁ populations. The four parents ('Essex', 'Forrest', 'York', and 'Douglas'), the six F₁'s, and the six F₂'s were space-planted in a randomized complete block design at the Agronomy Research Station, Perkins, Oklahoma, during the 1983 and 1984 growing seasons. This study was conducted to provide estimates of heritability in the broad sense for protein and oil content, and to examine the relationship between these two traits and their association with yield and seed size.

Heritability estimates in 1983, averaged over all crosses were 0.33 and 0.38 for protein and oil, respectively. In 1984, much lower estimates of 0.12 and 0.05 were obtained for the two traits, respectively. When averaged over both years, estimates of 0.25 for

¹To be submitted for publication.

protein and 0.23 for oil were obtained. Forrest/Essex and Douglas/Essex should provide selections with desirable protein and oil content.

The direction as well as the magnitudes of phenotypic and genotypic correlations were quite variable. Seed yield was negatively correlated with seed protein in all but one cross. Both positive and negative associations were observed among seed weight, protein, and oil content. Similar relationships were observed between seed yield and oil content. Protein was negatively associated with oil in all crosses except Forrest/Essex. The results suggest that selection for both high seed yield and high protein may be possible in the Essex/York population. Forrest/Essex and Essex/York populations may provide good sources for simultaneous improvement of percent protein and seed size. Lines higher in seed yield and oil content may be selected from the Douglas/Forrest population. The Forrest/York population may provide selections for larger seed size and higher oil content. Development of lines high in protein and oil may be possible in the Forrest/Essex population.

Additional index words: Broad-sense heritability, % oil, % protein, phenotypic, and genotypic correlations.

Commonly grown soybean cultivars contain approximately 40.5% protein and 21.0% oil in the seed on a free moisture basis (7). Increasing demand for protein and oil in many areas of the world necessitates the inclusion of protein and oil objectives into soybean breeding programs. Selection of lines with high seed yield, high protein, and high oil content would be desirable in a research program leading to cultivar development. A knowledge of heritability estimates and the correlations between chemical and non-chemical traits would facilitate the development of such high-protein or high-oil cultivars with adequate seed yield.

Heritability estimates for seed protein and oil content in soybeans are generally high (2,3,5,11,14,15,17,20). However, lower estimates from some populations have been reported (4,9,12). Byth et al. (2) evaluated two soybean crosses in the F₆ and F₇ generations over three environments. Their estimates of heritability ranged from 0.71 to 0.90 for protein and from 0.63 to 0.91 for oil. Fehr and Weber (5) evaluated the effect of three cycles of mass selection on protein and oil in two soybean populations involving adapted varieties. They reported heritability estimates of 0.76 and 0.77 for protein and 0.72 and 0.74 for oil. Smith and Weber (14) reported estimates ranging from 0.71 to 0.92, and from 0.69 to 0.93 for protein and oil, respectively. Johnson et al. (9), utilizing two populations of F₃ lines over two years, reported heritability estimates of 0.39 and 0.83 for percent protein. Their heritability estimates for percent oil were 0.68 and 0.78. Utilizing 15 F₃ families selected from crosses between G. soja and G. max, Erickson et al. (4) found broad-sense heritability estimates on an individual plant basis to be 0.45 for percent protein. Kown and Torrie

(12) estimated heritability for protein and oil from populations derived from crossing adapted varieties. Their estimates were 0.57 and 0.51 for the two traits, respectively.

In soybean breeding, direct visual selection for chemical traits is not possible. Knowledge of how traits are genetically correlated is useful in planning for more efficient breeding programs. The magnitude as well as direction of correlations between seed yield, seed size, percent protein, and percent oil in the seed have been variable. With the exception of only a few populations evaluated, seed yield has been found to be negatively correlated with percent seed protein (1,2,8,10,11,12,13). Positive genotype correlations of 0.54 (13) and 0.47 (2) were found between the two traits. Positive phenotypic correlations ranging from 0.00 to 0.32 were also found (2). Johnson et al. (10) reported phenotypic correlations of -0.08 and -0.33; and genotypic correlations of -0.12 and -0.64 between yield and protein in two populations of soybeans. Both positive and negative correlations between seed yield and oil content have been reported (1,2,8,10,11). Phenotypic correlations of 0.05 (12), -0.02, to 0.26 (2), 0.07 (1), and 0.00 to 0.32 (10) between the two traits have been reported. Genotypic correlations of 0.07, -0.14 to 0.29, 0.11, and 0.02 to 0.44 were also reported in the above studies, respectively. Percent seed protein has been inversely associated with percent seed oil. Hartwig and Hinson (8) reported a negative correlation coefficient of -0.91 between protein and oil contents. Simpson and Wilcox (13) found negative genetic correlation coefficients between protein and oil to be in the range of -0.15 to -0.96 when evaluating progenies of four soybean crosses. Seed size was found to be both positively and negatively correlated with seed

protein and oil content depending on the reference populations utilized (1,10,12,13,17,19).

Information related to heritability estimates and correlations among protein and oil with agronomic traits of soybeans grown under Oklahoma conditions is limited. This study was conducted (1) to estimate heritability in the broad sense for seed protein and oil content, and (2) to examine the relationship among seed yield, seed size, seed protein, and oil content in six soybean crosses.

MATERIALS AND METHODS

In this study, all possible combinations of crosses, with no reciprocals, among four adapted soybean cultivars, 'Essex', 'Forrest', 'York', and 'Douglas' were made in the field and greenhouse to originate six F₁ populations. Douglas was used as a female parent only. York was used as male parent only, while Forrest and Essex were used as male and female parents. Seeds from selfed F₁ plants were used to initiate six F₂ populations. The six F₁'s, the six F₂'s, along with the four parents were space-planted on a Teller Loam soil (Fine-Loamy, Mixed, Thermic Udic Argiustolls) at the Agronomy Research Station, Perkins, Oklahoma, in the 1983 and 1984 growing seasons. Plantings were made using a hill planter. Rhizobium japonicum inoculum was applied to the seed before planting. Soil tests indicated that nutrient levels for the growth of soybeans were adequate. Test plants were arranged in a randomized complete block design with eight blocks. Each block consisted of a total of 234 test plants distributed over 18 rows with 13 plants in each row. Each test plant was an experimental unit. Each row was bordered by two discard plants and each block was bordered by two rows of discard plants. An equidistant planting of 75 x 75 cm between rows and plants was utilized. In this investigation, the total number of experimental units was distributed as follows: 72 plants from each parent, 20 to 70 plants from each F₁ population, and 218 to 227 plants from each F₂ population. Irrigation, when needed, was provided in addition to rainfall to insure optimum plant growth. All dead plants were replaced

by discard ones at the seedling stage to minimize unequal competition effects among plants. During the growing season, the experiment was continuously observed for disease, insects, and weeds. All measurements were made on an individual plant basis. Seed protein and oil content were estimated, on a moisture free basis of a 10g sample, by the Technicon InfraAnalyzer TM⁴⁰⁰ (16) using the near infrared reflectance (NIR) characteristics of the sample. Seed yield was the total weight in grams of the air-dried, cleaned seeds from each plant. Seed weight was the weight in grams of 100 whole, randomly selected seeds. Statistical analyses were carried out on the above four characters using the Statistical Analysis System.

Heritability estimates, in the broad sense (h_{bs}^2) were calculated as:

$$\frac{V(X)F_2 - [V(X)P_1 * dfP_1 + V(X)P_2 * dfP_2 + V(X)F_1 * dfF_1]}{dfP_1 + dfP_2 + dfF_1}$$

$$V(X)F_2$$

where $V(X)F_2$ denotes the F_2 variance; $V(X)P_1$, $V(X)P_2$, and $V(X)F_1$ represent the environmental variance, estimated from the corresponding error mean squares in the analyses of variances of character (X) in the P_1 , P_2 , and F_1 generations, respectively. The standard errors for the broad-sense heritability estimates were calculated as follows: $SE(h_{bs}^2) = \{1 - h_{bs}^2 [2 (df_2)^2 / (df_2 - 2)^2] (df_2 + df_E - 2) / (df_E)(df_2 - 4)\}^{1/2}$ where df_E = the pooled degree of freedom of the error mean squares of P_1 , P_2 , and F_1 . Df_2 = the degree of freedom of the error mean square of the F_2 .

The relationships among the four characters investigated in this study were evaluated by calculating correlations. Simple phenotypic correlations (r_p) were calculated as:

$$r_p = \frac{\text{Cov}(X,Y)F_2}{[V(X)F_2 * V(Y)F_2]^{1/2}}$$

Genotypic correlations (r_g) were calculated as:

$$r_g = \frac{\text{Cov}(X,Y)F_2 - \text{Cov}(X,Y)E}{[V(X)F_2 - V(X)E]^{1/2} * [V(Y)F_2 - V(Y)E]^{1/2}}$$

where $\text{Cov}(X,Y)F_2$ and $\text{Cov}(X,Y)E$ represent the covariances between the characters (X) and (Y) in the F_2 and the environment, respectively; $V(X)F_2$ and $V(Y)F_2$ represent the variances of characters (X) and (Y) in the F_2 ; $V(X)E$ and $V(Y)E$ represent the environmental variances of characters (X) and (Y) estimated as the pooled error mean squares of P_1 , P_2 , and F_1 generation. The covariances were estimated by the corresponding error mean products in the analyses of covariances. The standard errors for (r_g 's) were calculated as:

$$\begin{aligned} SE(r_g) = & \{1/df_2 [r^2/G (C^2XYF_2 + VXF_2 * VYF_2) \\ & - 2r^4/G^3 (CXF_2 * VXF_2 + CXYF_2 * VYF_2) \\ & + r^6/G^4 (C^2XYF_2 + 1/2 V^2XF_2 + 1/2 V^2YF_2)] \\ & + 1/df_E [r^2/G (C^2XYE + VX_E * VY_E) \\ & - 2r^4/G^3 (CXY_E * VX_E + CXY_E * VY_E) \\ & + r^6/G^4 (C^2XYE + 1/2 V^2X_E + 1/2 V^2Y_E)]\}^{1/2} \end{aligned}$$

where $CXYF_2$ and CXY_E denote the covariances between characters X and Y in the F_2 and environment, respectively. $G = \text{cov}(XY)F_2 - \text{cov}(XY)E$; $r =$ genetic correlation; df_E = the pooled degree of freedom of the error mean squares of P_1 , P_2 , and F_1 generations; VXF_2 and VYF_2 = the variances of characters X and Y in F_2 ; and VX_E and VY_E = the environmental variances of characters X and Y.

RESULTS AND DISCUSSION

In plant breeding, heritability estimates serve as a practical tool that is used by the breeder to estimate what portion of the total variability present in the F_2 is genetic. This information helps the breeder plan his selection program. The results showed that differences among all crosses were highly significant for percent protein in both years. However, differences among crosses for percent oil were significant only in 1984. When averaged over both years, significant differences among crosses were detected for both protein and oil contents in the F_2 generation.

Broad sense heritability estimates for protein and oil content in 1983 for the six crosses (Table 1) ranged from 0.00 to 0.66 for seed protein and from 0.00 to 0.84 for oil content. In general, these estimates were quite variable for both characters over all crosses. Forrest/Essex showed the highest heritability estimates for both percent protein (0.66) and percent oil (0.84) followed by Douglas/Essex. Negative heritability estimates were obtained in the Douglas/York cross for both characters. When averaged over all crosses, heritability estimates were 0.33 and 0.38 for protein and oil content, respectively. Heritability estimates for protein in 1983 obtained from Douglas/Essex (0.64), Douglas/Forrest (0.46), and Forrest/Essex (0.66) compare with estimates of 0.45 (4), 0.39 (9), 0.63 (11), and 0.57 (12) previously reported. Estimates of 0.63, 0.51, and 0.37 for oil obtained from Douglas/Essex, Douglas/Forrest, and Essex/York are similar to those of

0.64 and 0.51 reported by Weber (17) and Kown and Torrie (12) for this trait. Heritability estimate of 0.84 obtained from Forrest/Essex compares to estimates reported by Byth et al. (1 and 2), and Smith and Weber (14), but are larger than estimates obtained from other investigations (5,9,12) for oil.

Heritability estimates in 1984 (Table 2) ranged from 0.00 to 0.46 for percent protein, and from 0.00 to 0.40 for percent oil. Negative estimates for both characters were obtained in several crosses. When averaged over all crosses, heritability estimates were 0.12 for protein and 0.05 for oil. Heritability estimates of 0.46 for protein and 0.40 for oil obtained from Douglas/York in 1984 were similar to those reported by others (4,9) for protein, but lower than previous estimates for oil (9,11,12,17). In general, heritability estimates were much lower in 1984 than in 1983. The negative estimates could be primarily attributed to the larger magnitude of the environmental variances estimated from the corresponding mean squares of the non-segregating generations (P_1 , P_2 , and F_1) compared to that of the F_2 .

When averaged over two years (Table 3), heritability estimates for percent protein ranged from 0.06 to 0.50, and from 0.05 to 0.49 for percent oil. Douglas/Essex had the highest estimate for percent protein, and Forrest/Essex had the highest estimate for percent oil. These estimates, when averaged over all crosses were 0.25 for percent protein and 0.23 for percent oil. Heritability estimates for protein obtained from Douglas/Essex (0.50) and Forrest/Essex (0.35) compare to those obtained by others (4,9,12). The estimate of 0.49 obtained from Forrest/Essex for oil is similar to those obtained by Weber and Moorthy (18) and Kown and Torrie (12). Due to the large effect of the

environment, the combined estimates for protein, with the exception of those obtained from Douglas/Essex and Forrest/Essex, were much lower than estimates previously reported (2,3,5,14). Estimates for oil, with the exception of that obtained from Forrest/Essex, were also lower than previously published estimates (2,5,9,12). Results from this study suggest that genetic variability for protein and oil content was present with different magnitudes in the six crosses. Altering the level of protein and oil content by selection should be most effective in the crosses of Forrest/Essex and Douglas/Essex (Tables 1 and 3), and to a lesser extent in the cross of Douglas/York (Table 2). Our results confirmed that heritability estimates are subject to the environmental conditions of the test and inferences should be made only about the populations considered in the test.

Interrelationships Among Traits

Simple phenotypic correlation coefficients between seed yield, seed size, protein, and oil content estimated in 1983 are presented in Table 4. Phenotypic correlations between protein and yield were all negative ranging from -0.05 to -0.41. Seed weight and protein showed low but significant positive association in three crosses. The magnitude of the negative correlations observed in the other three crosses was generally small. A positive association between seed yield and percent oil was observed in all six crosses with different magnitude. Both positive and negative correlations were measured between oil and seed weight. A strong negative relationship was observed between protein and oil in five out of six crosses. However, a significant positive correlation coefficient of 0.39 was obtained between protein and oil in Forrest/Essex.

In 1984 (Table 5), percent protein was negatively correlated with both seed yield and seed weight. Phenotypic correlation coefficients between protein and yield ranged from -0.36 to -0.52 , and from -0.13 to -0.47 between protein and seed weight. Percent oil was positively correlated with both yield and seed weight. The magnitude of phenotypic correlations between oil and yield ranged from 0.15 to 0.49 , and from 0.26 to 0.49 between oil and seed weight. A strong negative relationship was observed between protein and oil in all crosses. When averaged over both years (Table 6), estimates of phenotypic correlations between seed yield and percent protein ranged from -0.19 to -0.41 . A low but significant negative correlation was observed between seed weight and protein. A positive correlation coefficient of 0.04 was obtained between the two traits in Essex/York. Estimates of phenotypic correlations were in the ranges of 0.20 to 0.47 between seed yield and oil, and -0.03 to 0.27 between seed weight and oil. Percent protein was negatively correlated with percent oil with a magnitude ranging from -0.17 to -0.80 .

Estimates of genotypic correlations obtained in 1983 are presented in Table 7. Due to the large magnitude of the environmental covariance estimated for Douglas/York, genotypic correlations among all five pairs of comparisons could not be estimated in this cross. With very few exceptions, genotypic correlations were higher than phenotypic correlations. This indicates that associations between the contrasted traits are mainly genetic. Seed yield was negatively correlated with protein. Estimates of genotypic correlations ranged from -0.11 to -0.76 , indicating that the strength of the negative relationship between the two traits varied with crosses. With the exception of Forrest/Essex

and Essex/York, seed weight was negatively correlated with percent protein with different magnitudes. Both positive and negative correlations were obtained between oil and yield, and between oil and seed weight. Estimates of genotypic correlations ranged from -0.82 to 1.00 between oil and yield, and from -0.30 to 1.00 between oil and seed weight. A strong inverse relationship was observed between protein and oil in all but the Forrest/Essex population where a genetic correlation of 0.65 was obtained between the two traits. Results from 1983 indicate that protein was negatively correlated, phenotypically and genotypically, with seed yield, but inconsistent in magnitude. Selection for high yield and high protein content may not be possible. An inconsistent relationship was observed between seed weight and protein content. The positive association, phenotypically and genotypically, between the two traits observed in Forrest/Essex and Essex/York indicates that selection for larger seed size and higher protein content should be possible in these crosses. In most crosses, a consistent positive relationship was observed between seed yield and oil content, indicating that simultaneous improvement of these two traits should be possible. The direction as well as the magnitude of the relationship between oil and seed weight were variable. However, desirable selections larger in seed size and higher in oil content may be obtained from Douglas/Forrest and Forrest/York. The strong inverse relationship observed between protein and oil in all but the Forrest/Essex population indicates that simultaneous improvement of the two traits may be possible only in this population.

Estimates of genotypic correlations among the four characters considered in this study in 1984 are presented in Table 8. Due to the

large magnitude of the environmental covariances estimated, genotypic correlations could not be estimated in Forrest/Essex and Essex/York. Seed yield was negatively correlated with protein except in the Douglas/Forrest population where a genotypic correlation of 0.26 was calculated between the two traits. Percent protein was found to be positively correlated with seed weight, but estimates of genotypic correlations were associated with large standard errors. Both positive and negative relationships were observed between oil and yield, and oil and seed weight. A strong negative association was observed between protein and oil. Results from 1984 indicate that seed yield and percent protein were inconsistently related. Both the direction and magnitude of the relationship between protein and seed weight were variable.

Nonsignificant negative phenotypic correlations coupled with large estimates of genotypic correlation (0.72) between protein and seed weight were observed in the Douglas/Forrest population. This indicates that simultaneous improvement of the two traits should be possible in this population. Douglas/York should provide good selections for high yield and high oil content. Desirable selections for large seed size and high oil content should be possible in Douglas/York and Forrest/York populations.

Estimates of genotypic correlations among the four characters, averaged over the two years, are presented in Table 9. Genotypic correlations between seed yield and protein content were higher than phenotypic correlations in three crosses. A positive genotypic association was observed between the two traits in the cross of Essex/York, which indicates that selection for high yield and high protein content should be possible in this cross. Similar findings have

been previously reported (2,4). Positive genetic associations were also observed between seed weight and protein content in the crosses of Forrest/Essex and Essex/York; and between seed weight and oil content in the crosses of Douglas/Forrest, Douglas/York, and Forrest/York. These results, which agree with those reported by others (1,10,12,13), suggest that simultaneous improvement of each contrasted pair of traits should be possible in these crosses. A strong negative genotypic correlation was observed between seed yield and oil content in Forrest/York and Essex/York. However, the positive association between the two traits in the crosses of Douglas/Essex and Douglas/Forrest suggests that selection for high yield and high oil content should be possible in these crosses. Excluding the cross of Forrest/Essex, a consistent inverse relationship was observed between protein and oil content in all crosses. The magnitude of correlation coefficients was quite variable. The range of genotypic correlations was between -0.10 and -1.00 (Table 9). In the cross of Forrest/Essex, the relationship between percent protein and percent oil deviated from the general pattern observed in all other crosses. A genotypic correlation coefficient of 0.61 and a phenotypic correlation coefficient of -0.17 were estimated in this cross. Phenotypic and genotypic correlations, negative but low in magnitude, between percent protein and percent oil have been reported by others (14,17,20) in some populations evaluated. However, a positive genotypic correlation of 0.61 coupled with a negative phenotypic correlation is rare. The reason for this positive correlation between the two traits is not known. The presence of different genetic systems for both traits and the competition between these systems for the outcomes of photosynthesis was proposed to be the reason for the negative

association between protein and oil content (6). When the competition between the two genetic systems is weak or absent, a positive genetic association between the two traits might occur.

Results from this study showed that sufficient genetic variability for protein and oil content was present in some crosses. Broad-sense heritability estimates of 0.50 for percent protein in Douglas/Essex and 0.49 for percent oil in Forrest/Essex indicate that altering these traits in the two crosses should be possible. Heritability estimates were quite variable between the two years, which resulted in somewhat low estimates for the two traits compared to those previously reported. Genotypic correlations were higher than phenotypic correlations for several comparisons in most crosses which emphasizes the genetic association between the contrasted traits. The combined data indicated that simultaneous improvement of seed yield and percent protein, seed weight and percent protein, seed yield and oil content, and seed weight and oil content should be most effective in the crosses of Essex/York, Douglas/Forrest, and Douglas/York, respectively. Selection for high protein and high oil content should be highly effective in the Forrest/Essex cross.

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Table 1. Broad sense heritability estimates for protein and oil content from six soybean crosses, 1983.

Hybrid	Protein	Oil
Douglas/Essex	0.64 ± 0.14	0.63 ± 0.14
Douglas/Forrest	0.46 ± 0.17	0.51 ± 0.16
Douglas/York	-0.13 ± 0.24 [†]	-0.13 ± 0.24 [†]
Forrest/Essex	0.66 ± 0.11	0.84 ± 0.08
Forrest/York	0.13 ± 0.19	0.05 ± 0.19
Essex/York	0.20 ± 0.18	0.37 ± 0.16

[†]values < 0 may be interpreted as 0.

Table 2. Broad sense heritability estimates for protein and oil content from six soybean crosses, 1984.

Hybrid	Protein	Oil
Douglas/Essex	0.30 ± 0.14	-0.05 ± 0.17 [†]
Douglas/Forrest	0.07 ± 0.16	0.17 ± 0.15
Douglas/York	0.46 ± 0.12	0.40 ± 0.13
Forrest/Essex	-0.03 ± 0.18 [†]	-0.07 ± 0.18 [†]
Forrest/York	-0.02 ± 0.18 [†]	0.06 ± 0.17
Essex/York	-0.08 ± 0.17 [†]	-0.22 ± 0.18 [†]

[†] values < 0 may be interpreted as 0.

Table 3. Broad sense heritability estimates for protein and oil from six soybean crosses averaged over two years.

Hybrid	Protein	Oil
Douglas/Essex	0.50 ± 0.09	0.22 ± 0.12
Douglas/Forrest	0.25 ± 0.11	0.27 ± 0.11
Douglas/York	0.25 ± 0.11	0.23 ± 0.11
Forrest/Essex	0.35 ± 0.10	0.49 ± 0.09
Forrest/York	0.06 ± 0.13	0.05 ± 0.13
Essex/York	0.07 ± 0.12	0.09 ± 0.12

Table 4. Phenotypic correlations among four characters in six soybean crosses, 1983.

Hybrid	Protein vs Yield	Protein vs Seed Weight	Oil vs Yield	Oil vs Seed Weight	Protein vs Oil
Douglas/Essex	-0.41 **	-0.09	0.33 **	0.13	-0.81 **
Douglas/Forrest	-0.28 **	-0.13	0.45 **	0.31 **	-0.72 **
Douglas/York	-0.29 **	-0.04	0.21 *	0.25 **	-0.70 **
Forrest/Essex	-0.05	0.18 *	0.17 *	-0.13	0.39 **
Forrest/York	-0.13	0.23 **	0.02	-0.13	-0.74 **
Essex/York	-0.18 *	0.34 **	0.11	-0.38 **	-0.80 **

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

Table 5. Phenotypic correlations among four characters in six soybean crosses, 1984.

Hybrid	Protein vs Yield	Protein vs Seed Weight	Oil vs Yield	Oil vs Seed Weight	Protein vs Oil
Douglas/Essex	-0.37**	-0.20**	0.15*	0.30**	-0.80**
Douglas/Forrest	-0.52**	-0.14	0.49**	0.26**	-0.86**
Douglas/York	-0.46**	-0.13	0.44**	0.29**	-0.87**
Forrest/Essex	-0.41**	-0.40**	0.46**	0.47**	-0.91**
Forrest/York	-0.41**	-0.47**	0.41**	0.49**	-0.84**
Essex/York	-0.36**	-0.37**	0.41**	0.41**	-0.81**

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

Table 6. Phenotypic correlations among four characters in six soybean crosses averaged over two years.

Hybrid	Protein vs Yield	Protein vs Seed Weight	Oil vs Yield	Oil vs Seed Weight	Protein vs Oil
Douglas/Essex	-0.38 **	-0.13 *	0.35 **	0.20 **	-0.79 **
Douglas/Forrest	-0.41 **	-0.13 *	0.47 **	0.27 **	-0.79 **
Douglas/York	-0.37 **	-0.09	0.33 **	0.27 **	-0.79 **
Forrest/Essex	-0.19 **	-0.12 *	0.27 **	0.17 **	-0.17 **
Forrest/York	-0.25 **	-0.14 *	0.20 **	0.23 **	-0.79 **
Essex/York	-0.25 **	0.04	0.23 **	-0.03	-0.80 **

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

Table 7. Genotypic correlations among four characters in five soybean crosses, 1983. †

Hybrid	Protein vs Yield	Protein vs Seed Weight	Oil vs Yield	Oil vs Seed Weight	Protein vs Oil
Douglas/Essex	-0.76	-0.14	0.59 ± .72	0.09 ± .07	-1.00
Douglas/Forrest	-0.57	-0.40	1.03 ± .99	0.56 ± .18	-0.94
Forrest/Essex	-0.31	0.14 ± .07	0.37 ± .62	-0.13	0.65 ± .13
Forrest/York	-0.28	-0.80 ± 1.0	-0.82 ± 4.0	1.79 ± 9.79 [‡]	-1.05 ± 14.8
Essex/York	-0.11 ± .43	0.26 ± .13	-0.01	-0.30	-1.2 ± .43

† No test is available for genetic correlation.

‡ values > 1 may be interpreted as 1.

Table 8. Genotypic correlations among four characters in four soybean crosses, 1984. †

Hybrid	Protein vs Yield	Protein vs Seed Weight	Oil vs Yield	Oil vs Seed Weight	Protein vs OIL
Douglas/Essex	-0.32	0.57 1.1	-- ‡	-- ‡	-- ‡
Douglas/Forrest	0.26±3.58	0.72±.88	-0.22±1.7	-0.15±.15	-0.97±6.9
Douglas/York	-0.31	0.04±.05	0.27±.58	0.18±.08	-0.90
Forrest/York	-- ‡	-- ‡	-- ‡	1.00±3.7	-- ‡

†No test is available for genetic correlations.
‡values are unestimatable.

Table 9. Genotypic correlations among four characters in six soybean crosses averaged over two years.[†]

Hybrid	Protein vs Yield	Protein vs Seed Weight	Oil vs Yield	Oil vs Seed Weight	Protein vs Oil
Douglas/Essex	-0.55	-0.02	0.37	-0.13	-1.00
Douglas/Forrest	-0.40	0.04	0.57	0.14	-0.88
Douglas/York	-0.08	-0.17	-0.01	0.49	-0.72
Forrest/Essex	--	0.43	--	-0.27	0.61
Forrest/York	-0.00	-1.00	-1.00	1.00	-0.73
Essex/York	0.30	0.72	-0.41	-0.91	-0.10

[†]No test is available for genetic correlation.

CHAPTER IV

Inheritance of Seed Size and Its Relationship with Protein, Oil, and Seed Yield in a Soybean Cross¹

ABSTRACT

Two cultivars of soybeans [Glycine max (L.) Merr.] 'Forrest' and 'Lancer' were crossed to derive F₁, F₂, BC₁, and BC₂ populations. These materials were space-planted in a randomized complete block design at the Agronomy Research Station, Perkins, Oklahoma during the growing season of 1984.

This investigation was conducted to determine the inheritance of seed size, to provide estimates of broad and narrow-sense heritability for yield, seed size, % protein and oil, and to examine the relationships between the above traits. All measurements were made on an individual plant basis.

The seed weight of the F₁ hybrid was not significantly different from that of the midparent, indicating the importance of additive gene action in controlling this trait. Transgressive segregation was also indicated for seed size.

Broad-sense heritability estimates were 0.57, 0.65, 0.71, and 0.49

¹To be submitted for publication.

for seed protein, oil, seed yield, and seed size, respectively. Narrow-sense heritability estimates were 0.56, 0.60, 0.66, and 0.58 for the above traits, respectively. Estimates of additive gene action were larger than nonadditive gene action for seed size. Based on the estimates of heritability and gene action, we concluded that there was sufficient genetic variability for effective selection for higher protein or larger seed size among the progenies derived from this cross.

Genotypic correlations were greater in magnitude than phenotypic correlations for all comparisons. Oil content was positively correlated with seed yield and seed size. Percent seed protein was negatively correlated with the other three traits evaluated. These results suggest that simultaneous improvement of seed yield and oil or seed size and oil should be feasible. However, development of high-yielding lines with high seed protein may not be possible.

Additional index words: Additive gene action, broad-sense heritability, narrow-sense heritability, genotypic and phenotypic correlation.

Heritability estimates generally vary depending on the reference populations, method of calculation, unit used, and environment of the test (5). Heritability estimates for seed size have been variable (1,7,12,22). Anand and Torrie (1) reported estimates ranging from 0.36 to 0.84 from three soybean crosses. Hanson and Weber (7) estimated heritability for seed size in F_3 and F_4 generations. Their estimates were 0.46 and 0.58 in the two generations, respectively. Studies have shown that protein and oil contents in soybeans have intermediate to high heritabilities (4,7,12,17,18,22). Shorter et al. (17) estimated heritability from F_4 variance components and F_3 - F_4 generations derived from three soybean crosses. They reported heritability estimates ranging from 0.54 to 0.60 for protein and 0.47 to 0.84 for oil. Weber and Moorthy (22) reported heritability estimates of 0.49 to 0.59 for oil percentage utilizing the variance among individual F_2 plants. Shannon et al. (16) utilized six populations of F_3 lines to estimate heritability for protein and found it to be in the range of 0.51 to 0.96. Recently, Openshaw and Hadley (15) reported heritability estimates of 0.75 to 0.90 for protein and 0.71 to 0.93 for oil. Several studies have shown that additive gene effects accounted for most of the genetic variance for seed size (3,7,8,10,22) which suggests that progress by selection for larger seed size is possible. However, partial and complete dominance were also found to be significant in controlling seed size (13,14).

The existence of negative correlations between protein and oil, and between protein and seed yield (4,12,16,17,18) have been major obstacles in the development of high-yielding soybean lines with high oil and protein. Positive phenotypic and genotypic correlations of different

magnitudes between seed yield and oil were found (12,16, 17,22).

Shorter et al. (17) reported an inconsistent relationship between seed size and protein. However, positive correlations between seed size and oil were found in most crosses evaluated.

The objectives of this study were (1) to investigate the inheritance of seed size in a 'Forrest' X 'Lancer' soybean cross, and (2) to evaluate the relationships among seed size, protein, oil and yield.

MATERIALS AND METHODS

The parents selected for this study were Forrest and Lancer. Forrest (11) originated as an F₅ line selected from a 'Dyer' x 'Bragg' cross. It is in maturity group V and is a small-seeded cultivar. Lancer is in maturity group VI and is a large-seeded cultivar. The two parents were chosen based on their differences in seed size. Both parents are adapted to Oklahoma and have average protein and oil contents.

Crosses between Forrest and Lancer were made in the summer of 1982 and backcrosses were made in the greenhouse during the following summer. P₁(Forrest), P₂(Lancer), F₁, F₂, BC₁, and BC₂ were grown at the Agronomy Research Station, Perkins, Oklahoma, in the 1984 growing season. Plantings were made using a hill planter on a Teller Loam soil (Fine-Loamy, Mixed, Thermic Udic Argiustolls) on June 4 and 5, 1984. Soil tests indicated that amounts of nutrients for the growth of soybeans were adequate. The planting arrangement was a randomized complete block design with six blocks and the experimental units were individual plants. Each block consisted of 120 plants grown in 15 rows with 8 plants in each row. An equidistant planting of 75 x 75 cm between rows and plants was used. Each row was bordered by two discard plants and each block was bordered by two rows of discard plants. The total number of test plants was as follows: 54 plants from each parent, 50 F₁ plants, 50 BC₁ plants to Forrest, 60 BC₂ plants to Lancer, and 452

F₂ plants. To minimize differential competition among plants, all dead plants were replaced with discard plants at the seedling stage. Supplemental irrigation was provided in addition to rainfall to insure optimum growth conditions. All measurements were made on an individual plant basis and the four characters in this study were evaluated as follows: Seed protein and oil content were estimated on the dry weight basis of a 10 g sample by the Technicon InFraAnalyzer TM⁴⁰⁰ (20) using the near infrared reflectance(NIR) characteristics of the sample. Seed yield was the total weight in grams of the cleaned, air-dried seeds from each plant. Seed size was the weight in grams of 100 whole, randomly selected seeds. Statistical analyses were carried out on the above four characters using the Statistical Analysis System.

Heritability estimates in the broad sense (h^2_{bs}) were calculated as:

$$\frac{V(X)F_2 - [V(X)P_1 \cdot dfP_1 + V(X)P_2 \cdot dfP_2 + V(X)F_1 \cdot dfF_1]}{(dfP_1 + dfP_2 + dfF_1)}$$

$$V(X)F_2$$

where $V(X)F_2$, $V(X)F_1$, $V(X)P_1$, and $V(X)P_2$ represent the variances estimated from the corresponding error mean squares in the analyses of variances of character(X) in the F₂, F₁, P₁, and P₂ generations, respectively; and dfP_1 , dfP_2 , and dfF_1 are the degrees of freedom of the error mean squares for P₁, P₂, and F₁. The standard errors for the broad-sense heritability estimates were calculated as follows:

$$SE(h^2_{bs}) = \{1 - h^2_{bs} [2(df_2)^2 / (df_2 - 2)^2] [(df_2 + df_E - 2) / (df_E)(df_2 - 4)]\}^{1/2}$$

where df_E is the pooled degrees of freedom of the error mean squares of P₁, P₂, and F₁; and df_2 = the degrees of freedom of the error mean square of the F₂.

Heritability estimates, in the narrow sense (h_{ns}^2) were calculated utilizing Warner's method (19) as:

$$h_{ns}^2 = \frac{2V_{x_{F_2}} - [V_{x_{BC_1}} + V_{x_{BC_2}}]}{V_{x_{F_2}}}$$

where $V_{x_{F_2}}$, $V_{x_{BC_1}}$, $V_{x_{BC_2}}$ represent the variances estimated from the corresponding error mean squares in the analyses of variances of character(x) in the F_2 , BC_1 , and BC_2 , respectively. The standard errors for the narrow-sense heritability estimates were calculated as:

$SE(h_{ns}^2) = (2)^{1/2} \{ [(V_{BC_1} + V_{BC_2})^2 / df_{F_2}] + (V_{BC_1})^2 / df_{BC_1} + (V_{BC_2})^2 / df_{BC_2} \}^{1/2} / V_{F_2}$ where df_{BC_1} and df_{BC_2} are the degrees of freedom of the error mean square of df_{BC_1} and df_{BC_2} . Additive and nonadditive variances for seed size were estimated as:

$$\hat{\sigma}_A^2 = 2V_{x_{F_2}} - [V_{x_{BC_1}} + V_{x_{BC_2}}]$$

$$\hat{\sigma}_{NA}^2 = V_{x_{F_2}} - \hat{\sigma}_A^2 \quad \text{where} \quad \hat{\sigma}_A^2 \quad \text{and} \quad \hat{\sigma}_{NA}^2$$

represent estimates of the additive and nonadditive genetic variances of character(X), respectively. Associations between seed size, protein, oil, and yield were evaluated by calculating correlations. Phenotypic correlations (r_p) were computed as:

$$r_p = \frac{\text{Cov}(X,Y)_{F_2}}{[V(X)_{F_2} * V(Y)_{F_2}]^{1/2}}$$

Genotypic correlations(r_g) were computed as:

$$r_g = \frac{[\text{Cov}(X,Y)_{F_2} - \text{Cov}(X,Y)_E]}{[V(X)_{F_2} - V(X)_E]^{1/2} * [V(Y)_{F_2} - V(Y)_E]^{1/2}}$$

where $\text{Cov}(X,Y)_{F_2}$ and $\text{Cov}(X,Y)_E$ represent the covariances between characters (X) and (Y) in the F_2 and environment, respectively; $V(X)_{F_2}$ and $V(Y)_{F_2}$ represent the variances of X and Y in the F_2 ; $V(X)_E$ and $V(Y)_E$

represent the environmental variance of X and Y estimated as the pooled error mean squares of P₁, P₂, and F₁ generations. The covariances were estimated by the corresponding error mean products in the analyses of covariances. The standard errors for (r_g's) were calculated as:

$$\begin{aligned}
 SE(r_g) = & \{1/df_2 [r^2/G(C^2_{XYF_2} + VX_{F_2} * VY_{F_2}) \\
 & - 2r^4/G^3(CXY_{F_2} * VX_{F_2} + CXY_{F_2} * VY_{F_2}) \\
 & + r^6/G^4 (C^2_{XYF_2} + 1/2 VX_{F_2} + 1/2 VY_{F_2})] \\
 & + 1/df_E [r^2/G(C^2_{XYE} + VX_E * VY_E) \\
 & - 2r^4/G^3(CXY_E * VX_E + CXY_E * VY_E) \\
 & + r^6/G^4(C^2_{XYE} + 1/2 VX_E + 1/2 VY_E)]\}^{1/2}
 \end{aligned}$$

where CXYF₂ and CXY_E denote the covariances between characters (X) and (Y) in the F₂ and environment, respectively; G= Cov(X,Y)_{F₂} - Cov(X,Y)_E; r= genetic correlation; df_E= the pooled degrees of freedom of the error mean squares of P₁,P₂, and F₁ generations; VX_{F₂} and VY_{F₂} = the variance of characters(X) and (Y) in the F₂; VX_E and VY_E = the environmental variances of (X) and (Y).

RESULTS AND DISCUSSION

Significant differences among all entries were detected for seed size and percent protein but not for oil or seed yield (Table 1). The lack of significance for yield and oil could be attributed to insufficient variability between the two parents for these traits. Number of plants, means, ranges and coefficient of variation of seed size for the populations derived from the Forrest x Lancer cross are presented in Table 2. Differences between the two parents were significant for seed size. The seed size of the F_1 hybrid was not significantly different from the midparental value. This indicates that additive gene action was important in controlling this trait. Since the deviation of the F_1 hybrid was not significantly different from the average of the two parents, additive genetic variance is considered to be more important than nonadditive genetic variance (3). However, the slight tendency of the F_1 hybrid to produce larger seed size than the midparent does provide some indication of nonadditive gene action involved in controlling seed size. Brim and Cockerham (3) and Gates et al.(6) also found that additive variance was the major component of genetic variance for seed size. However, Leffel and Hanson (13) and Leffel and Weiss (14) found that dominance was also important in controlling this trait.

Frequency distributions for seed size in the F_2 , F_1 , BCP_1 , BCP_2 , and the parental generations are presented in Table 3. Overlapping

between the two parents was observed for seed size. The segregation patterns in all generations showed greater variability for this trait in the segregating populations (F_2 , BCP_1 , and BCP_2) than in the non-segregating populations (parents and F_1). Both parental types were recovered in the F_2 generation, and the F_2 distribution appeared to be normal for this trait. The coverage of the entire range of parental types by that of the F_2 suggests a possible presence of transgressive segregation for seed size in both directions. The range of the F_2 and the recovery of the parental types in the F_2 indicate that the two parents used shared many genes that control this trait. This is in a close agreement with the findings reported from studies involved adapted varieties (22). The overall distribution of the F_2 for seed size did not fit discrete classes which suggests that this trait was quantitatively inherited. Quantitative inheritance of seed size has been reported by others (3,6,8,22,23).

Heritability and Gene Action

Estimates of broad and narrow sense heritability are presented in Table 4. Broad-sense estimates were 0.57, 0.65, 0.71, and 0.49 for percent protein, oil, yield, and seed size, respectively. Narrow-sense estimates were 0.56, 0.60, 0.66, and 0.58 for the above traits, respectively. Estimates of narrow sense heritability for traits other than seed weight were smaller than those of broad sense heritability. Heritability estimates have been found to be influenced by the method of estimate, unit of measurement, environmental conditions, and the reference population of genotypes for which they were estimated (5). Estimates of heritability for yield was considerably higher than most of

those previously reported (1,2,7,12,16,21), but similar to those obtained from certain populations in other investigations (16,22). Heritabilities for other traits were in close agreement with those obtained from other studies (1,7,12,17,22). Standard errors of the narrow-sense heritability estimates were larger than those of the broad sense for all traits evaluated. This indicates an overestimation of additive genetic variance and estimates of broad sense heritability were probably more accurate than narrow sense estimates. This could be attributed to larger sampling errors in the backcross generations in which numbers of plants were lower than those of the F₂ generation. Heritability estimates obtained from this study indicate the existence of genetic variability for seed size and protein in this population. Narrow-sense heritability estimates of 0.56 for percent protein and 0.58 for seed size indicate that selection for higher seed protein or larger seed size should be effective in this population. Estimates of additive and nonadditive variances for seed size were 1.74 and 1.26, respectively. This also suggests that selection for this trait should be effective in this population. The analysis of variance indicated no significant differences for seed yield or oil content among the progeny derived from this cross. However, broad and narrow sense heritability estimates were relatively high. This indicates that genetic variability did exist for these two traits. The genetic variance may have been over-estimated which resulted in larger estimates of heritability for these two traits. This study suggests that both additive, and to a lesser extent, nonadditive genetic variances are important in controlling seed size. Similar findings were also reported by other investigators (3,8,12,14).

Interrelationships Among Traits

Phenotypic and genotypic correlations among the characters evaluated are presented in Table 5. Genotypic correlations between all pairs of comparisons were found to be greater than the corresponding phenotypic correlations which emphasizes the importance of genetic relationships for the characters evaluated. Seed size was positively correlated, phenotypically and genotypically, with seed yield. However, a phenotypic correlation coefficient of 0.20, although significant, does not indicate a strong relationship between the two traits. Larger positive phenotypic (0.34) and genotypic (0.50) correlation coefficients were found between seed size and oil. Negative phenotypic (-0.21) and genotypic (-0.25) correlations were obtained between seed size and percent protein. The relationship between seed size and the above three traits have been found to be variable in both the direction and magnitude (1,12,17,22). Seed protein was negatively correlated, phenotypically and genotypically, with seed yield and oil. Phenotypic correlation coefficient of -0.42 and genotypic correlation coefficient of -0.58 were obtained between protein and oil. The reason for the strong inverse relationship between protein and oil appears to be due to the competition between different systems in soybeans. The existence of different genetic systems for the conversion of the outcomes of photosynthesis into protein and oil was proposed by Hanson et al.(9) who concluded that competition between these systems results in a negative correlation between these two traits. These results which are generally in agreement with those reported by others (1,12,16,17,18,22), suggest that selection for larger seed size and high oil content, and high seed

yield and high oil content should be possible in this population. The significant positive correlation between seed yield and seed size suggests that simultaneous improvement of these two traits may also be possible. The highly significant negative association of protein with the other three traits suggests that selection for high protein content and high seed yield, high protein and high oil content, or high protein and large seed size may not be possible in this population.

The results from this study show that the mean value for seed size of the F_1 hybrid was midway between the two parents with a slight tendency toward the parent larger in seed size. A probable presence of complementary genes conditioning seed size in both parents resulted in the wider range of F_2 and indicated transgressive segregation. Broad-sense heritability estimates were 0.57 and 0.49, and narrow-sense estimates were 0.56 and 0.58 for percent seed protein and seed size, respectively. These estimates and the presence of additive gene action indicate the feasibility of selection for protein and for seed size among the progeny derived from this cross. Genotypic correlations were larger in magnitude than phenotypic correlations. The positive correlations between seed yield and oil and seed size and oil suggest the feasibility of simultaneous improvement of the two contrasted traits. Percent seed protein was inversely associated with seed yield, seed size, and percent seed oil. This indicates that simultaneous improvement of these traits may not be possible in this population.

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Table 1. Mean squares of four characters in the cross of Forrest/
Lancer.

Source	df	Mean squares			
		Protein	Oil	Seed size	Yield
Blocks	5	94.16**	27.32**	16.60**	3866.03**
Entry	5	8.41**	2.84	43.33**	795.60
Block X Entry	25	2.88	1.58	1.67	518.51
Error	592	2.63	1.58	2.56	505.12
Pooled error †	617	2.64	1.58	2.52	505.66

**significant at P=0.01 level.

†Pooled error was used to test all AOV components because

Block*Entry mean squares were not significant for any characters.

Table 2. Ranges, means, and coefficient of variation for seed size in the populations obtained from Forrest/Lancer cross.

Population	N	Mean	Range	C.V
Forrest	36	11.6 ± 0.16	9.2-13.2	8.2
Lancer	49	14.4 ± 0.15	11.9-16.9	7.3
F ₁	37	13.2 ± 0.17	10.1-14.8	7.9
F ₂	423	13.0 ± 0.08	5.9-18.5	13.3
BC ₁	33	11.4 ± 0.24	7.7-14.4	11.9
BC ₂	50	13.4 ± 0.22	8.3-16.7	11.3
Midparent		13.0		

BC₁ and BC₂ backcrosses to Forrest and Lancer, respectively.

Table 3. Frequency distribution of seed size in the populations derived from Forrest/Lancer cross.

Population	Classes of seed size (g/100 seed)										N	C.V
	7.2	8.4	9.6	10.8	12.0	13.2	14.4	15.6	16.8	18.0		
Forrest			2	12	17	5					36	8.2
Lancer					4	9	17	18	1		49	7.3
F ₁			1	1	8	14	13				37	7.9
F ₂	7	4	11	33	86	143	98	28	9	4	423	13.3
BC ₁	1	1	3	5	12	7	4				33	11.9
BC ₂		1		4	11	10	16	7	1		50	11.3

BC₁ and BC₂ = backcrosses to Forrest and Lancer, respectively.

Table 4. Estimates of broad and narrow sense heritability for four characters in the cross of Forrest/Lancer.

Character	Broad sense(h^2)	Narrow sense(h^2)
Protein	0.57 ± 0.10	0.56 ± 0.27
Oil	0.65 ± 0.11	0.60 ± 0.26
Yield	0.71 ± 0.08	0.66 ± 0.25
Seed size	0.49 ± 0.09	0.58 ± 0.26

Table 5. Phenotypic (right of diagonal) and genotypic (left of diagonal)[†] correlations among four characters in the cross of forrest/Lancer.

Character	Protein	Oil	Yield	Seed size
Protein	--	-0.42 **	-0.36 **	-0.21 **
Oil	-0.58 ± --	--	0.42 **	0.34 **
Yield	-0.42 ± --	0.58 ± 0.37	--	0.20 **
Seed size	-0.25 ± --	0.50 ± 0.08	0.25 ± 0.23	--

** significant at the 0.01 level of probability.

[†]no test is available for significance of genotypic correlations.

CHAPTER V

SUMMARY

In this study, two separate experiments were conducted. They are referred to as experiments 1 and 2. Both of them were carried out at the Agronomy Research Station, Perkins, Oklahoma.

In experiment 1, four soybean cultivars: Essex, Forrest, York, and Douglas were crossed in all combinations (with no reciprocals) to derive six F₁ and six F₂ hybrids. The F₁'s, F₂'s, and parents were space-planted in a randomized complete block design with eight blocks in 1983 and 1984. This investigation was undertaken (1) to examine the existence and levels of heterosis for protein and oil, (2) to determine the relative magnitude of general and specific combining ability for the above two traits, (3) to estimate heritability for protein and oil, and (4) to examine the relationships among seed yield, seed weight, protein, and oil.

Within years analyses showed significant midparent (2.6%) and high-parent (1.8%) heterosis in 1984 for protein in the hybrid of Douglas/Forrest. When averaged over years, low but significant midparent heterosis of 1.0% was measured for protein in the above hybrid. In 1983, the hybrids of Douglas/York, Forrest/York, and Essex/York showed significant midparent heterosis for oil of 2.3, 5.8, and 7.8%, respectively. Essex/York also showed significant high-parent heterosis of 4.5% for oil. In 1984, the hybrids Forrest/Essex and

Forrest/York showed significant midparent (2.6 and 2.8%) heterosis for oil. When averaged over years, the hybrids of Forrest/Essex and Forrest/York exhibited midparent (2.6 and 4.7%) and high-parent (2.1 and 2.3%) heterosis for oil. Our results indicate higher midparent and high-parent heterosis for both protein and oil than previous reports with hybrids involving adapted cultivars of soybeans. This study suggests that significant levels of heterosis may exist for the two traits. If hybrid seed production could become more economical, the potential for hybrid cultivars does exist in soybeans.

Mean squares of GCA for protein were highly significant in all analyses except in the 1984 F₁. Although significant SCA mean squares were observed, GCA was always more important than SCA. This indicates that additive gene action was predominant in controlling protein. GCA mean squares for oil were significant only in 1984. SCA mean squares were significant in both 1983 and 1984, but not in the combined data. Interactions of GCA and SCA with years were significant for protein and oil, indicating instability in performance of both types of combining ability over years. In most cases, hybrids with highest SCA effects showed significant midparent or high-parent heterosis, indicating that selection of hybrids based on their SCA effects and heterotic performance was practical.

Estimates of broad sense heritability for protein ranged from 0.00 to 0.66 in 1983, 0.00 to 0.46 in 1984, and 0.06 to 0.50 in the combined data. Heritability estimates for oil ranged from 0.00 to 0.84, 0.00 to 0.40, and 0.05 to 0.49 in 1983, 1984, and the combined data, respectively. Heritability estimates were quite variable between years, which resulted in somewhat low estimates for the two traits compared to

those previously reported. Genotypic correlations were higher than phenotypic correlations for several comparisons in most crosses which emphasizes the genetic association between the contrasted traits. Protein was negatively correlated with seed yield and oil, with the exception of one hybrid where significant positive genotypic correlation was observed between protein and oil. Both positive and negative correlations were observed among seed weight, protein, and oil. Similar relationships were observed between oil and seed yield. Results from this study showed that sufficient genetic variability for protein and oil was present in some populations. This indicates that altering these traits should be possible in these populations. Simultaneous improvement of seed yield and protein, seed weight and protein, seed yield and oil, and seed weight and oil should be possible in several populations. Selection for high protein and high oil should also be possible in the Forrest/Essex population.

In experiment 2, the parental, F_1 , F_2 , BC_1 , and BC_2 populations originated from the cross of Forrest/Lancer were arranged in a randomized complete block design with six blocks in 1984. This experiment was conducted to examine the inheritance of seed weight and its relationship with seed yield, protein, and oil.

Results from this study showed that the seed weight of the F_1 hybrid was not significantly different from that of the midparent, indicating the importance of additive gene action in controlling this trait. A probable presence of transgressive segregation in both directions was also indicated for seed weight. The range of the F_2 population covered almost the entire ranges of both parents for this trait. Estimates of broad sense heritability were 0.57 and 0.49, and those of narrow sense were 0.56 and 0.58 for protein and seed size,

respectively. Estimates of additive genetic variance for the two traits were greater than those of nonadditive genetic variance. This indicates that selection for protein and seed weight among the progeny derived from this cross is feasible. Genotypic correlations were larger than phenotypic correlations. A positive association was observed between seed yield and oil suggesting the feasibility of simultaneous improvement of the two traits. Protein was negatively associated with oil, seed yield, and seed weight. This indicates that simultaneous improvement of these traits may not be possible in this population.

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Table 1. Mean squares for protein and oil in six F₁ hybrids of soybeans in 1983 and 1984.

Source	df	Protein		Oil	
		1983	1984	1983	1984
Block	7	10.68 **	44.51 **	1.08	16.81 **
Entry	5	9.98 **	8.97 **	2.49 **	5.79 **
block X Entry	35	3.54 *	5.06 **	1.02 *	1.67 *
Error	X	2.36	1.89	0.66	1.02

X= 127 for 1983 and 164 for 1984.

*,** significant at p=.05 and p=.01 levels, respectively.

Table 2. Mean squares for protein and oil in six F₂ hybrids of soybeans in 1983 and 1984.

Source	df	Protein		Oil	
		1983	1984	1983	1984
Block	7	78.92**	302.06**	16.26**	71.16*
Entry	5	34.44**	21.56**	1.29	5.02**
Block X Entry	35	4.88	3.77**	1.79	2.32**
Error	X	3.48	2.08	1.41	1.08

X= 729 in 1983 and 1092 in 1984.

*,** significant at p=.05 and p=.01 levels, respectively.

Table 3. Mean squares for protein and oil in six F₁ and six F₂ hybrids of soybeans averaged over two years.

Source	df	Protein		Oil	
		F ₁	F ₂	F ₁	F ₂
Year(Yr)	1	304.30**	439.94**	876.48**	4654.45**
Block(Yr)	14	27.60**	195.00**	8.94**	43.71**
Entry	5	8.48**	47.31**	0.58	2.68*
Entry(Yr)	5	10.48**	8.69**	7.60**	3.63**
Block X Entry(Yr)	70	4.30**	4.33**	1.35**	2.05**
Error	X	2.09	2.65	0.86	1.21

X= 291 for F₁ and 1821 for F₂.

*,** significant at p=.05 and p=.01 levels, respectively.

Table 4. Frequency distribution of percent seed protein in the populations derived from the Forrest x Lancer cross.

Population	N	Mean	C.V	Classes of % protein									
				31.2	32.4	33.6	34.8	36.0	37.2	38.4	39.6	40.8	42.0
Forrest	36	36.55	3.59			3	5	8	12	6	2		
Lancer	49	35.27	2.66	1		3	21	20	4				
F ₁	37	36.18	3.43			3	13	8	4	7	2		
F ₂	423	36.08	4.83	8	13	48	96	93	81	55	21	6	2
BcP ₁	33	36.54	4.17		1	3	6	7	10	1	4	1	
BcP ₂	50	36.21	3.97		1	2	11	19	7	9	1		
Mid-parent		35.91											

BcP₁ and BcP₂ are Backcrosses to Forrest and Lancer, respectively.

Table 5. Frequency distribution of percent seed oil in the populations derived from the FORREST x LANCER cross.

Population	N	Mean	C.V	Classes of % oil										
				13	14	15	16	17	18	19	20	21	22	
Forrest	36	17.01	6.11	1		4	9	5	12	5				
Lancer	49	17.22	4.71		1	1	4	24	15	4				
F ₁	37	17.28	6.09			4	4	12	14	3				
F ₂	423	17.09	7.85	9	7	33	79	132	109	41	10	1	2	
BcP ₁	33	16.78	6.34		1	4	7	12	7	1	1			
BcP ₂	50	16.76	7.01		2	5	14	17	9	1	1	1		
Mid-parent		17.12												

BcP₁ and BcP₂ are Backcrosses to Forrest and Lancer, respectively.

Table 6. Estimates of additive and non-additive variances for four characters in the cross of Forrest/Lancer.

Character	Additive variance	Nonadditive variance
Protein	1.70	1.33
oil	1.09	0.77
Seed Size	1.74	1.26
Yield	399.77	204.23

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VITA

Mahmoud Y. Sabbouh

Candidate for the Degree of

Doctor of Philosophy

Thesis: GENETIC STUDIES OF PROTEIN AND OIL IN SOYBEANS [Glycine max
(L.) Merr.]

Major Field: Crop Science

Biographical:

Personal Data: Born in Ra's Al Aein, Syria, January 1, 1954, the son of Yousef and Tamrah Sabbouh.

Education: Graduated from Bouka Agricultural High School, Lattakia, Syria, in 1972; received the Bachelor of Science degree in Agriculture from the University of Damascus in 1977; received the Master of Science degree in Agronomy from Oklahoma State University in May 1982; completed the requirements for the Doctor of Philosophy degree in Crop Science at Oklahoma State University in May 1986.

Professional Experience: Teaching Assistant in the College of Agriculture, Damascus University 1978-1980; worked in the soybean breeding program in the Department of Agronomy, Oklahoma State University 1980-1986

Professional Organizations: Member of the American Society of Agronomy and the Crop Science Society of America.