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METHODS FOR EVALUATING PROTEIN AND OIL IN SOYBEANS AND MASS SELECTION BY SEED SIZE AND SPECIFIC GRAVITY IN SOYBEAN POPULATIONS

by

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TABLE OF CONTENTS

Page

LIST OF SYMBOLS ---------- iv

PART I. EVALUATION OF METHODS FOR PROTEIN AND OIL DETERMINATION IN SOYBEAN SEED ---------- 1

INTRODUCTION ---------- 2

REVIEW OF LITERATURE ---------- 4

MATERIALS AND METHODS ---------- 8

RESULTS AND DISCUSSION ---------- 12

SUMMARY AND CONCLUSIONS ---------- 22

PART II. MASS SELECTION BY SEED SIZE AND SPECIFIC GRAVITY FOR PROTEIN AND OIL COMPOSITION IN TWO SOYBEAN POPULATIONS ---------- 24

INTRODUCTION ---------- 25

REVIEW OF LITERATURE ---------- 27

Prerequisites for Success with Mass Selection ---------- 27

Fulfillment of Prerequisites in Soybeans ---------- 30

Genetic Advance ---------- 34

MATERIALS AND METHODS ---------- 36

Genetic Material and Character Evaluation ---------- 36

Experimental Design and Parameter Estimation ---------- 43

RESULTS AND DISCUSSION ---------- 49

Whole-plot Analyses ---------- 49

Sub-plot Analyses ---------- 49

Cycle Comparisons ---------- 54

Seed Size-Specific Gravity Comparisons ---------- 59

Genotypic Variance ---------- 64

TABLE OF CONTENTS
(Continued)

Page

Heritability ---------- 64

Phenotypic and Genotypic Correlations ---------- 68

Genetic Advance ---------- 70

Variety Development ---------- 76

SUMMARY AND CONCLUSIONS ---------- 78

BIBLIOGRAPHY ---------- 81

ACKNOWLEDGMENTS ---------- 84

LIST OF SYMBOLS

SS = Seed size

SD = Seed density

SG = Specific gravity

NMR = Nuclear magnetic resonance

Kj = Kjeldahl

SE = Solvent extraction

C0 = Control

C1 = Cycle 1

C2 = Cycle 2

C3 = Cycle 3

L = Large seed

S = Small seed

Lo = Low specific gravity

Hi = High specific gravity

E = Early maturity

M = Midseason maturity

Lt = Late maturity

EL = Early lodging

* = Exceeds the 5% probability level

** = Exceeds the 1% probability level

PART I. EVALUATION OF METHODS FOR PROTEIN AND OIL DETERMINATION IN SOYBEAN SEED

INTRODUCTION

Accurate determination of protein and oil content of soybean seed is essential for the development of superior varieties for these two attributes. A rapid, inexpensive, and accurate method of protein and oil determination would permit the evaluation of a large number of genotypes and result in more progress for protein and oil composition.

Five methods are presently available for evaluation of protein or oil composition of soybean seed: seed density (SD), specific gravity (SG), nuclear magnetic resonance (NMR), Kjeldahl (Kj), and solvent extraction (SE).

SD is defined as the ratio of the seed weight to seed volume. Weight is determined in the conventional manner and volume may be measured by liquid or gas displacement. SD is a measure of the relative amounts of oil and non-oil compounds in the seed. The density of soybean oil is approximately .93 gram per cubic centimeter and the density of the non-oil portion is 1.3 to 1.4 grams per cubic centimeter. High SD indicates a high protein to oil ratio and low SD indicates a lower protein to oil ratio.

SG is defined as the ratio of the weight of a given volume of a substance to that of an equal volume of another substance used as a standard. SG is based on the differential density of the oil and non-oil portions of a soybean seed. Low SG indicates a high oil to protein ratio and high SG indicates a lower oil to protein ratio. Low SG seed float in a given solution and high SG seed sink in the same solution.

NMR is the most recently developed method for determining oil composition of seed. It is a rapid, nondestructive method which can be used to analyze the oil content of a single soybean seed. NMR measures total hydrogen in the liquid oil fraction of seed independent of the hydrogen in the non-oil fraction (Conway and Earle, 1963; Dryer, 1965). Total hydrogen in the liquid oil fraction is used to calculate the oil concentration in soybean seed.

Kj is the standard chemical method for determining the protein content of soybean seed (Sallee, 1966). Kj determines as ammonia the total nitrogen content of a ground sample. Percent protein is equated to percent ammonia x 5.14 or percent nitrogen x 6.25.

SE is the standard chemical method for determining oil content of soybean seed (Sallee, 1966). Finely ground seed is extracted with petroleum ether for several hours. All of the extracted substances are considered a part of the oil fraction.

The objective herein was to evaluate SD, SG, NMR, Kj, and SE for use in developing superior soybean varieties.

REVIEW OF LITERATURE

SD has been used to a limited extent for determining protein and oil composition of soybean seed. Smith (1966) studied the relationship of SD with protein and oil in 300 F_4 and F_6 derived lines grown in two replications at two locations. Protein was determined for each plot by Kj, oil by SE, and SD with an analytical balance and an air comparison pycnometer. Heritability, defined as the ratio of genotypic variance to phenotypic variance, was .69 for SD. The phenotypic correlation of SD with protein was .57 and SD with oil was -.78. Both correlations exceeded the 5% probability level. Smith concluded that selection for protein and oil by SD was effective.

The first use of SG in soybean breeding was reported by Nitta (1952). SG was determined using a carbon tetrachloride and ethyl alcohol solution. He reported a correlation of SG with oil of -.93 and SG with protein of .70.

Yoshino et al. (1955) studied SG and its relationship with other soybean characters in lines from 10 soybean crosses. Heritability of SG ranged from .07 to .97 with an average of .47. They concluded that mass selection by SG was effective for increasing the frequency high oil lines in the population.

SG solutions were used by Hartwig and Collins (1962) to increase the frequency of high protein or high oil lines in two soybean crosses. Single plants in segregating populations were classified by counting the number of seed in a 60 or 100 seed sample which floated in a glycerol-water solution having a SG of 1.23. They found that selected plants with a

high percentage of seed which sank increased the frequency of high protein progenies while selection for low SD increased the frequency of high oil lines. They used a series of glycerol-water solutions with step-wise-increasing SG to isolate high and low density seed in a bulk F_4 population and found that selection of high SD increased the frequency of high protein lines and decreased the frequency of high oil lines. They concluded that SG separation could be utilized effectively by the soybean breeder as a coarse screen to increase the frequency of plant progenies having high oil.

Smith (1966) conducted two cycles of mass selection by SG in two hybrid soybean populations. High and low SG seed were selected using a series of step-wise-increasing glycerol-water solutions. A 25% selection pressure was used for each fraction in each cycle. He found that lines from high SG populations of cycle 1 had a higher mean protein content and a lower mean oil content than the unselected control populations. Low SG populations were above average in oil and below average in protein. The effects of cycle 2 varied among the populations studied. Continued selection for high SG resulted in increased protein and decreased oil in one cross with a decrease in protein observed in the second cross. In general, cycle 1 was more effective than cycle 2 for increasing the frequency of high protein or high oil lines.

The feasibility of using NMR to determine oil content of seed was investigated by Conway and Earle (1963). Using seed from 18 plant species, the correlation of oil content determined by NMR as compared with SE was .99. Oil content of 25 grams of soybean seed was 20.7% with NMR and 20.1% with SE.

Work by Collins indicated that NMR was a reliable method of oil analysis for corn, soybeans, safflower, sunflower, and oat seed. Correlations greater than .99 were observed between NMR and SE (Collins, F. I., U. S. Regional Soybean Laboratory, Urbana, Illinois. NMR analysis of oil in seed. Private communication. 1967.)

NMR for varietal development was used in corn (Zea mays L.) by Bauman et al. (1963) and indicated a highly significant correlation of .75 between the oil content of single kernels in a selfed ear of a single cross with that of their progeny. Eight kernels with the highest oil content produced progeny with an average of 16% more oil than the average of all 256 progeny.

Brim et al. (1966) reported that classification of soybean plants for high or low oil by NMR required proper seed sampling on the plant. They found that two pods, each containing two seed, selected at an intermediate node in the field and either the intermediate or basal node in the greenhouse were sufficient to distinguish high and low oil plants with 94% accuracy in the field and 86% in the greenhouse. They stated that sampling additional pods per plant should increase the classification accuracy.

Protein determinations by Kj have been used extensively for developing high protein varieties. Johnson and Bernard (1962) summarized soybean heritability values and interrelationships among characters. Heritability of protein ranged from .39 to .83 depending on the material used, the selection unit, and the method of calculation. Phenotypic correlations of protein and oil were between -.26 and -.92 while genotypic correlations ranged from -.48 to -.76.

SE has been used widely by soybean breeders to develop high oil lines. Heritability values for oil reported by Johnson and Bernard (1962) ranged from .49 to .78.

MATERIALS AND METHODS

Forty lines were selected for evaluation from each bulk population of two crosses, C1105 x A4-3159 and Lindarin x A4-3202. The parental lines were selected as having desirable agronomic and chemical characteristics. Bulk populations were obtained by growing 4,500 F_6 seed of each cross in 1963 at Ames, Iowa. At maturity, 400 plants, of Blackhawk maturity (September 15) were selected. Plants were threshed in bulk after cutting off the upper one-fourth of all plants to remove poorly developed seed. Bulk seed was truncated into large and small seed fractions using appropriate screens with a 25% selection pressure based on seed number. The large and small seed bulks were sub-divided for high and low SG using a glycerol-water solution with a 25% selection pressure based on seed number. In 1964, approximately 2,300 F_7 seed from each of the four SS-SG bulks of each cross were grown and at maturity 10 plants were randomly selected. A F_8 progeny row of each selection was grown in 1965. In 1966, each line was evaluated in a two replications at Ames, Iowa.

Samples of 100 seed were obtained from each of the 80 F_8 progeny rows grown in 1965 and from each replication of the same lines grown in 1966. The same sample was used for all methods of analysis to avoid sampling differences. A single determination was made on 1965 seed with each of the five methods listed previously. To obtain an estimate of the determination-to-determination variability associated with each method, two measurements were made on each of the 1966 samples. The first and second measurements for all methods were made approximately 24 hours apart.

SD was obtained from the ratio of seed weight in grams to seed volume in cubic centimeters. Weight and volume measurements were made during the same day to minimize error from temperature and humidity changes. An air comparison pycnometer was used to measure seed volume to the nearest .01 cubic centimeter.

SG measurements were made after the completion of SD determinations. The SG of a sample was equal to the number of floating seed in a glycerol-water solution. Ten samples were evaluated simultaneously to reduce the time required per sample. A sample of 100 seed was placed in a 500 cubic centimeter high form beaker containing approximately 475 cubic centimeters of a glycerol-water solution for approximately five minutes. SG of the solution was 1.202 for 1965 seed and 1.224 for 1966 seed. The SG selected was one in which an average of 50 seed would float. This minimized the possibility of having zero or 100% floating seed in a group of samples; such values would be of little worth in characterizing a line. After five minutes, floating seed and the seed which sank were collected separately by pouring the solution through tea strainers. Seed were washed with water and air dried for five minutes in screen pans with dimensions $3\frac{1}{2}$ x $3\frac{1}{2}$ x $1\frac{1}{2}$ inches. To prevent dilution of the glycerol-water solutions, water was removed from the tea strainers with forced air before the floating and sinking seed were removed from another solution.

Prior to NMR analysis, seed samples were oven dried for 96 hours in a forced draft oven at 130° C for three hours to lower seed moisture to three percent or less. Dried samples were weighed to the nearest .001

gram and a NMR analysis made using a Varian P7 analyzer. NMR readings were converted directly to oil percent by use of a standard linear graph of NMR score and oil composition. Oil percentages were expressed on a moisture-free basis.

Protein determinations were made with the modified Kj, A.O.C.S. Official Method Ac 4-41 (Sallee, 1966). One finely ground sample was prepared for all Kj and SE determinations. The two methods are destructive; therefore, part of the difference between two determinations on a single seed lot may be due to actual differences in the samples used. Fine grinding of a seed lot for all determinations should have provided a sample with maximum homogeneity and minimum sampling variation. The ground samples were preserved in capped glass bottles between determinations.

Moisture determinations were made on the ground samples using A.O.C.S. Official Method Ac 2-41 (Sallee, 1966). Protein and oil percent were expressed on a moisture-free basis.

SE was conducted according to the A.O.C.S. Official Method Ac 2-41 (Sallee, 1966). The procedure used to prepare the samples was described for the Kj method above.

The influence of seed moisture on SD and SG was evaluated for 60 samples of 1966 seed from certain replications of a number of lines. The samples were selected for seed weight in order to evaluate seed moisture over a more or less continuous range from 11.2 to 20.7 grams per 100 seed. Initial seed moisture was measured for each line with a Steinlite moisture

tester using 250 grams. One hundred random whole seed were obtained and their total dry weight calculated using the following equation: Dry weight = Seed weight - (Seed weight x Moisture percent). Subsequent moisture levels in the samples were calculated by the following relationship: Moisture percent = $\frac{\text{Seed weight - Dry weight}}{\text{Seed weight}}$.

The seed were dried to seven percent moisture at 40°C for the first SD and SG measurements. Subsequent moisture levels used were 9, 11, and 13%. The seed absorbed moisture while in the glycerol-water solution so that increasing the moisture level was not a problem. Drying at room temperature (22° C) and in an oven at 105° C were both used to remove excess moisture.

The effect of seed coat condition on SG was evaluated for 15 samples of 1966 seed using randomly selected lines and replications. For each sample, 50 seed with visibly cracked seed coats were compared with an equivalent number of seed with uncracked seed coats, as determined by soaking in a hypochlorite solution (Green et al., 1966).

Heritability estimates were calculated in standard units by correlating the 1965 performance of the 80 lines with their mean performance in 1966 (Frey and Horner, 1957). Correlations among characters were calculated using the mean performance of lines in 1966.

RESULTS AND DISCUSSION

The magnitude of measurement error, or determination-to-determination variability, for the 160 samples was expressed as the coefficient of variability (Table 1). The large coefficient of variability for SG was related to a mean difference between the first and second measurements of 7.2 floating seed. The higher values observed in the second measurement were due in part to increased seed moisture and modified seed coat conditions. Wrinkles in the seed coat and air trapped under cracked seed coats caused increased buoyancy and, therefore, a higher number of floating seed. Factors affecting SG measurements will be discussed in more detail later.

Measurement error was lowest for SD determinations. Errors in measurement were principally associated with seed volume determinations. The precision of the pycnometer was $\pm$ .05 cubic centimeters which could account for the major portion of the coefficient of variability observed. Consistently lower seed weight and volume were observed on the second measurement, but SD was not influenced appreciably because both factors varied concurrently. The average SD was 1.270 grams per cubic centimeter for the first determination and 1.271 grams per cubic centimeter for the second determination. Care should be taken to control temperature and relative humidity if samples are to be evaluated over a period of several weeks.

The coefficient of variability for Kj and SE may reflect errors in the analysis and actual differences in the two samples evaluated due to

lack of homogeneity in the ground sample. Sources of error in analysis for the two methods included varying fineness of the ground sample, incomplete extraction, foaming flasks during extraction, inaccurate sample weight measurements, chipped flasks, or incomplete removal of solvent.

Measurement error was lower for NMR than for SE indicating that the former method was a more precise method of oil determination. The principal errors in NMR measurements were temperature variation and incorrect readings by the machine operator. The mean and range observed for each method are presented in Table 1. One disadvantage of SD determinations was the limited range of values observed as compared to the other methods. The limited range reduced the ability to distinguish differences among soybean lines.

Consistently higher oil percentages were obtained with NMR than with SE. Similar results were obtained by Collins when large numbers of soybean lines were evaluated by NMR and SE. He made an attempt to determine the reason for the difference by re-extracting the SE samples. Oil was removed by the second extraction which suggested that the NMR value was a more accurate estimate of oil content in the seed (Collins, F. I., U. S. Regional Soybean Laboratory, Urbana, Illinois. Comparison of NMR and SE. Private communication. 1967.).

A major consideration in the selection of a procedure for chemical determination is the time and cost required per sample. SD, SG, and NMR were comparable in the time required per sample (Table 1). NMR had a higher cost per sample than the other two methods resulting from higher cost of equipment maintenance. The time and cost of Kj and SE determina-

Table 1. Coefficient of variability, mean, range, heritability, time per sample, and cost per sample for soybean lines evaluated by five methods of protein or oil determination

Method	Coefficient of variability (%)	Mean of 1966 data	Range of 1966 data	Heritability	Time per sample (min)	Cost per sample[a] ($)
SD (g/cc)	.31	1.271	1.258-1.284	.32	2.2	.12
SG[b]	10.39	61.0	36.0-86.0	.15	1.5[c]	.08
NMR (% oil)	.62	21.3	19.3-23.4	.84	1.0	.60
Kj (% protein)	.49	38.9	34.8-41.6	.75	6.0[c]	3.00
SE (% oil)	1.08	21.1	18.8-23.3	.89	6.0[c]	3.00

[a]Cost of labor ($3.00/hr) and expendable supplies or machine maintenance.

[b]Number of floating seed in a glycerol-water solution of 1.224 SG.

[c]Average time when 10 samples were run simultaneously.

tions are serious disadvantages of the two methods.

The initial equipment costs for the five methods are significantly different. As minimal estimates, the balance and pycnometer required for SD would cost $750 while an NMR analyzer would cost $25,000 to $40,000. Equipment required to run 10 samples concurrently for SG would cost approximately $32, while equipment to make 144 analyses per day would cost $780 for Kj and $400 for SE. The high cost of an NMR analyzer is a major disadvantage of the method.

The influence of seed moisture and seed coat condition on the accuracy

of SD and SG measurements was evaluated for 60 samples at four moisture levels (Table 2). SG increased rapidly from 7.0 to 9.1% moisture and at a slower rate from 9.1 to 13.1% moisture. The slower rate of increase at the higher moisture levels was attributable, in part, to a high frequency of lines with 90% floating seed at the 9.1% moisture level. This minimized the increase possible for higher moisture levels.

SD suggested that increased SG was due to modified seed coat conditions as well as higher moisture content (Table 2). SD decreased sharply from 7.0 to 9.1% moisture and increased to a constant value between 9.1 and 13.1% moisture. The sharp decline in SD was attributed to a disproportionate increase in volume. Percent increase of weight and volume should have been comparable with normal increases in seed moisture. Initial seed wetting during the first SG measurement at 7.0% moisture resulted in wrinkled seed coats and, therefore, a higher seed volume. Seed wetting during the SG test at 9.1% moisture caused rupturing of the wrinkles which permitted air to enter the cracks and allowed the pycnometer to record a more realistic volume. The results indicated that seed coat wrinkling can seriously effect SD measurements by its influence on volume measurements. Wrinkling could also influence SG by increasing seed buoyancy.

The influence of cracked seed coats on SG was estimated with 50 cracked and 50 whole seed in 15 random lines. The cracked samples had 15.6 more floating seed than the uncracked samples. Apparently, air bubbles were trapped under the seed coat giving the seed greater buoyancy.

Table 2. Average relationship of seed moisture to seed weight, volume, SD, and SG for 60 soybean lines

Moisture[a] (%)	Weight (g)	Weight increase[b] %	Volume (cc)	Volume increase[c] %	SD (g/cc)	SG[d]
7.0	15.944	-	12.68	-	1.257	51.1
9.1	16.314	2.32	13.21	4.01	1.235	85.7
11.0	16.651	2.11	13.41	1.58	1.242	92.4
13.1	17.061	2.57	13.74	2.60	1.242	95.1

[a]Seed moisture was increased from 7 to 13% by wetting.

[b]$\text{Weight increase (\%)} = \frac{\text{Weight at given moisture level} - \text{Weight at previous moisture level}}{15.944} \times 100.$

[c]$\text{Volume increase (\%)} = \frac{\text{Volume at given moisture level} - \text{Volume at previous moisture level}}{12.68} \times 100.$

[d]Number of floating seed in a glycerol-water solution of 1.224 SG.

SD should not be influenced by cracked seed coats since air can pass between the cracks and an accurate volume could be measured by the pycnometer.

In the development of soybean superior varieties, the value of a method for protein and oil determination depends on its ability to distinguish varietal differences for these two characters. Heritability estimates for the five methods indicated that SG and SD had far more environmental influence than the other three methods (Table 1). The estimates for SD and SG were considerably lower than those reported by other workers (Johnson and Bernard, 1962). This may be due in part to the different methods used in calculating the heritability estimates. NMR and SE had high heritability values of comparable magnitude indicating that they may be of comparable value for selecting high oil lines.

Selection effectiveness was evaluated also by the relative ability of a method to select the superior lines for protein and oil as determined by Kj and SE, respectively (Table 4). This criterion is based on the correlation of each method with protein and oil (Table 3). SD and SG had a low positive correlation with protein and a higher negative correlation with oil. NMR was highly correlated with SE and both methods displayed a high negative correlation with protein.

The correlation values indicated the ability to select high protein and high oil lines (Table 4). High protein lines were selected on the basis of high SD, high SG, low NMR, and low SE. SE was slightly superior to NMR in selection of high protein lines. Both of these methods were superior to SD and SG. In order to include all eight superior protein

Table 3. Correlation of five methods with Kj and SE determinations for 80 soybean lines[a]

	Kj	Probability (%)	SE	Probability (%)
SD	.134	30.0	-.342	.5
SG	.211	7.5	-.416	< .1
NMR	-.777	< .1	.967	< .1
SE	-.827	< .1	-	-

[a]Correlation coefficients were significant at the probability level given.

Table 4. Percent of eight superior lines for protein or oil present in the top 10, 20, and 30% of a population as determined by five selection methods[a]

Selection method	Character selected					
	Protein[b]			Oil[c]		
	10%	20%	30%	10%	20%	30%
SD	12.5	12.5	37.5	37.5	62.5	62.5
SG	0.0	12.5	25.0	50.0	62.5	75.0
NMR	12.5	50.0	75.0	62.5	87.5	100.0
Kj	-	-	-	37.5	62.5	87.5
SE	37.5	62.5	87.5	-	-	-

[a]Eight lines were 10% of the population.

[b]Determined by Kj.

[c]Determined by SE.

lines, 97.5% of population must be grown if SD is the selection method, 82.5% for SG, 42.5% for NMR and 31.3% for SE. The data clearly indicated that NMR and SE were superior for indirect protein selection.

High oil lines were selected on the basis of low SD, low SG, high NMR, and low Kj (Table 4). Selection by SD and SG was considerably more effective for oil than for protein. The two methods were comparable in effectiveness to Kj. NMR was the most effective of the four selection methods. In order to include all of the eight superior oil lines, 60.0% of the population must be grown if SD is the selection criterion, 72.5% for SG, 22.5% for NMR, and 42.5% for Kj.

A summary of the principal advantages and disadvantages of each method are present in Table 5. For protein evaluation, Kj was the only procedure which provided a direct measure of protein content. Selection of low oil lines by NMR was the most rapid, accurate method for indirect protein evaluation. SE was equally accurate but required appreciably more time and expense. SG was considered more practical than SD because of the low cost of equipment.

NMR was considered the most practical method for oil determination because of its low cost and nondestructive nature for seed analysis. SD and SG were more effective as an indirect method of oil analysis than they were for protein determination.

Table 5. Advantages and disadvantages of five methods used for evaluating protein or oil content of soybean seed

Method	Advantages	Disadvantages
SD	1. Nondestructive method of seed analysis. 2. Rapid and inexpensive determination. 3. Low measurement error under controlled conditions. 4. Possible to reanalyze a sample.	1. Does not provide an accurate measure of protein or oil content. 2. Low correlation with protein and oil content. 3. Low heritability. 4. Requires seed with unwrinkled seed coats for accurate volume. 5. Cannot be used readily for artificial mass selection of single seeds.
SG	1. Nondestructive method of seed analysis. 2. Rapid and inexpensive determination. 3. Readily used for artificial mass selection for single or many seed.	1. Does not provide an accurate measure of protein or oil content. 2. Low correlation with protein and oil content. 3. Low heritability. 4. Requires whole seed with uncracked or unwrinkled seed coats. 5. Difficult to reanalyze sample with accuracy.

Table 5. (Continued)

Method	Advantages	Disadvantages
NMR	1. Nondestructive method of seed analysis. 2. Rapid and inexpensive determination. 3. Low measurement error under controlled conditions. 4. Possible to reanalyze a sample. 5. Provides an accurate measure of oil content of one or many seed. 6. Moderately high negative correlation with protein content. 7. High heritability. 9. Not influenced by seed coat condition.	1. High cost of equipment.
Kj	1. Low measurement error under controlled conditions. 2. Provides an accurate measure of protein content. 3. High heritability. 4. Not influenced by seed coat condition.	1. Destructive method of seed analysis. 2. Expensive method of protein analysis. 3. Impossible to reanalyze a sample. 4. Cannot be used for selection of single seed.
SE	1. Low measurement error under controlled conditions. 2. Provides an accurate measure of oil content. 3. High heritability. 4. Not influenced by seed coat condition.	1. Destructive method of seed analysis. 2. Expensive method of oil analysis. 3. Impossible to reanalyze a sample. 4. Cannot be used for selection of single seed.

SUMMARY AND CONCLUSIONS

SD, SG, NMR, Kj, and SE were evaluated for their effectiveness in estimating protein or oil content of soybean seed. Estimates of measurement error were obtained by making duplicate determinations, approximately 24 hours apart, on each seed sample. SG had the largest measurement error due to incomplete drying of the samples and wrinkling and cracking of the seed coats between the first and second determinations. Measurement error was lowest for SD; the principal source of error being associated with seed volume determinations made with a pycnometer.

NMR had a lower measurement error than SE indicating that the former method was a more precise method of oil determination. The principal errors in NMR were temperature variation and incorrect readings by the machine operator. Measurement errors for Kj and SE reflected errors in the analyses and actual differences in the duplicate samples evaluated due to lack of homogeneity in the finely ground seed.

Cost of analysis per sample was approximately ten-fold higher for Kj and SE than for the other methods. Initial equipment costs ranged from $40,000 for an NMR analyzer to $32 for SG equipment.

Heritability estimates for the five methods indicated that selection for high protein or oil lines by SD or SG would be considerably less effective than the other methods. Selection effectiveness was evaluated also by the relative ability of a method to select lines with high protein or oil as determined by Kj and SE. It was concluded that the Kj was superior for direct measurement of protein while NMR was superior for indirect determinations. NMR was superior to SE as a rapid, accurate, inexpensive, non-

destructive method of oil analysis. SD and SG were comparable in effectiveness under most conditions.

PART II. MASS SELECTION BY SEED SIZE AND SPECIFIC GRAVITY FOR PROTEIN AND OIL COMPOSITION IN TWO SOYBEAN POPULATIONS

INTRODUCTION

The development of soybean varieties with a high yield and a high compromise of protein and oil is a major breeding objective. Protein shortages in underdeveloped countries, expanding markets for protein in the United States, and growing demands for plant oil throughout the world have stimulated the soybean breeder to evaluate plant breeding methods that may be useful in the development of varieties with higher protein and oil content.

One of the oldest methods of plant improvement is mass selection. This method is characterized by selection of phenotypically superior plants or seed from a genetically heterogeneous population and bulking the selected individuals to propagate the following generation. Selection is practiced to improve the gene frequency of a particular plant character in a genetically heterogeneous population. When a character is being improved directly, the effectiveness of mass selection is a function of the character's heritability. If one character is being improved by direct selection of another, mass selection effectiveness depends on the heritability of the selected character and the genetic relationship between the selected and the unselected characters.

The mass selection procedure used for truncating a population is dependent upon the character being manipulated. Visual selection may be adequate for characters such as maturity and heading date while mechanical devices may be useful for selection of large or small seed and tall or short plants.

Effective mass selection is a useful plant breeding tool because it is a rapid, simple, inexpensive method for improving segregating or non-segregating populations. It permits the simultaneous improvement of a larger number of populations than is possible with other breeding methods. Natural selection in populations may assist artificial techniques if the two selection forces do not counteract one another.

Lack of individual plant identity is the principal criticism of mass selection as a plant breeding tool. Mass selected populations are genetically heterogeneous and difficult to characterize in certification programs.

The objectives herein were to evaluate (1) the effectiveness of indirect mass selection for protein and oil by seed size (SS) and specific gravity (SG) truncation of heterogeneous soybean populations, (2) to determine the effect of selection on SS and SG per se, (3) to evaluate the relative effectiveness of three selection cycles for augmenting gene frequency of desirable attributes, (4) to investigate the interrelationship of SS and SG with agronomic and chemical characters, and (5) to improve and possibly release superior soybean varieties.

REVIEW OF LITERATURE

Prerequisites for Success with Mass Selection

Improvement of a character by direct mass selection is dependent on the following factors: (a) cost, speed, and objectivity of the selection procedure, (b) heritability of the selected attribute, (c) type of gene action operative, (d) magnitude and direction of natural selection, (e) interaction with correlated characters, and (f) the size of the population. Indirect improvement of one character by direct selection of another is also dependent on the genetic correlation between the selected and unselected characters.

Visual and mechanical devices have been used for mass selection depending on the character involved. Heading date, maturity, and seed coat color are characters which are amenable to visual mass selection. Numerous mechanical devices have been reported. Bennett (1959) selected for hard seed coat in crimson clover using a water-soaking technique. After soaking a bulk seed sample for three days in water, he discarded the swollen seed and retained the non-swollen seed that possessed hard seed coats. Hard seed coats in the bulk population were increased from 1.0 to 63.0% after eight mass selection cycles. Additional mechanical devices that have been reported include a lawn clipper for plant height selection in oats by Romero and Frey (1966), a set of sieves for discarding small kernels from crown rust infected plants in bulk populations of oats (Tiyawalee, Dumrong, Ames, Iowa. Mass selection for crown rust resistance

in oat populations. Private communication. 1967.), and glycerol-water solutions for selection of soybean seed with high protein or oil content by Hartwig and Collins (1962). All of the afore mentioned techniques are acceptable for mass selection in that they are inexpensive, rapid, and objective.

Heritability of a selected character is central to augmenting gene frequency in a bulk population. Heritability was defined by Lush (1937) as the portion of the observed variance for which differences in heredity are responsible. Narrow sense heritability may be defined by the equation:

$$\text{Heritability} = \frac{\text{Additive genetic variance}}{\text{Total genetic variance} + \text{Environmental variance}}$$

and broad sense heritability by the equation:

$$\text{Heritability} = \frac{\text{Total genetic variance}}{\text{Total genetic variance} + \text{Environmental variance}} .$$

Mass selection effectiveness is dependent on narrow sense heritability on a single plant or seed basis. From the above equation it is apparent that either low additive genetic variance, high environmental variance, or both can minimize heritability and progress from mass selection.

Mass selection for yield in barley was conducted by Atkins (1953) in 11 bulk hybrid populations. Selection was practiced in the F_2, F_3, and F_4 generations for vigorous plants with large, well-filled, disease-free heads. He compared lines from the selected and unselected bulk populations and found that selection was not effective in isolating appreciably higher yielding genotypes. Lack of success may be attributed to the low heritability of yield on a single plant basis. Romero and Frey (1966) studied

mass selection for plant height, a highly heritable character, in a bulk population of oats from F_3 to F_6. In each generation, panicles were clipped to a uniform height and the top four inches of the clipped population were harvested in bulk. They reported that the mass selection procedure was successful in reducing mean plant height by 2.7 inches after four cycles of selection.

Mass selection should increase the frequency of desirable genes if additive gene action predominates. Gardner (1961) reviewed the reasons for lack of success in improving corn yield by mass selection. He stated that a low amount of additive genetic variance for yield had been suggested as the cause of mass selection ineffectiveness. Subsequent studies by Lonnquist (1949) and Lonnquist and McGill (1956) have shown that adequate additive genetic variance was present for yield in corn and that proper selection methods resulted in yield advance.

Natural selection can enhance or retard artificial mass selection depending on the direction of the force. Natural selection is the basis of the evolutionary plant breeding method developed by Suneson (1956). He reported significant progress in improving barley yields with the method. Romero and Frey (1966) reported that mean plant height in an unselected oat population increased by .25 inch per generation. In this population, artificial selection for tall plants would be enhanced by natural selection, whereas, selection for short plants would be retarded. They indicated that the shift in plant height may be attributed to direct natural selection for the character or to indirect selection through a correlated character. For example, increased plant height in the unselected

population may have been due, in part, to natural selection for a later heading date as a result of the positive correlation of .77 between the two characters. The positive correlation would favor selection of tall plants and retard selection for short plants.

Florell (1929) stated that the number of individuals in a bulk population should be large enough to include all desired recombinants. Small populations would increase the probability of genetic drift with exclusion of favorable genotypes. He indicated that population size would be determined by the number of genetic factors involved.

The effectiveness of indirect mass selection has been reported by Romero and Frey (1966) to be dependent upon the following relationship: $H_d \times r_{gdi}$, where H_i is the heritability of the attribute selected directly and r_{gdi} is the genetic correlation between the attribute selected directly and indirectly. They reported that plant height was positively correlated with heading date and seed yield. Mass selection for short plant height in oats was found to result in earlier heading and higher yields.

Fulfillment of Prerequisites in Soybeans

Improvement of protein and oil by direct mass selection for SS and SG in soybeans depends on the degree to which the preceding mass selection prerequisites are met. SG is the only indirect mass selection procedure which has been reported for protein and oil improvement in soybeans. Hartwig and Collins (1962) reported that SG was a reliable, low cost, non-destructive method of mass selection for protein and oil improvement in

soybeans. They used a series of glycerol-water solutions with step-wise-increasing SG to separate high and low density seed in a bulk F_4 population. Selection of high density seed increased the frequency of high protein lines and decreased the frequency of high oil lines.

Use of SG is based on the density of soybean oil as approximating .93 gram per cubic centimeter and the density of the non-oil portion of the seed as 1.3 to 1.4 grams per cubic centimeter. Seed with a high density would have a higher protein to oil ratio than low density seed. In a solution of favorable SG, seed with a high protein content would sink while seed with a high oil content would float.

Smith (1966) conducted two cycles of mass selection by SG truncation in two hybrid soybean populations. A 25% selection pressure was used each cycle for high and low SG seed using a series of step-wise-increasing glycerol-water solutions. He found that lines from high SG populations of selection cycle 1 (C1) had a higher mean protein content and a lower mean oil content than the unselected control (C0) populations. Low SG populations were above average in oil and below average in protein. The effects of selection cycle 2 (C2) varied among the populations studied. Continued selection for high SG resulted in increased protein and decreased oil in one cross while a decrease in protein was observed in the second cross. In general, C1 was more effective than C2 for increasing the frequency of high protein or high oil lines.

The heritability of SS, SG, protein, and oil in soybeans has been reported by many workers. Johnson and Bernard (1962) reported that

heritability values for the above characters were as follows: SS = .35 to .92; SG = .07 to .97; protein = .39 to .83; and oil = .34 to .78. They indicated that the wide range in values for a given character were the result of differences in the genetic material studied, the selection unit, and the method of calculation.

Studies on gene action in soybeans have not been in complete agreement relative to the magnitude of additive and nonadditive genetic variances. Gates et al. (1960) reported the presence of additive genetic variance for SS and oil percent. They stated that the evidence is mounting for additive genetic variance in quantitatively inherited characters in soybeans. Using 45 diallel crosses in the F_2 and F_3 generations, Leffel and Hanson (1961) found prominent additive genetic variance for SS with lower amounts for protein and oil percent. Significant nonadditive variance was also observed for the three characters. Brim and Cockerham (1961) obtained estimates of additive, dominance, and additive x additive epistatic effects and concluded that additive variance was the principal component of variance for SS, protein, and oil. Estimates of additive genetic variance for SG have not been reported.

Hanson and Weber (1961) presented a model which demonstrated that additive gene variance predominates in advanced generations of selfing. These results indicated that mass selection in F_6 and later generations of soybeans, a self-pollinating species, should be effective if adequate genetic variance is present.

Estimates of phenotypic and genotypic correlations of SS, SG, protein, and oil with agronomic characters in soybeans have varied considerably

in the literature. Johnson et al. (1955) reported genotypic and phenotypic correlations between all pairs of 24 characters measured in two populations. SS was positively correlated with yield, maturity, height, and lodging. Protein was negatively correlated with yield, maturity, and height while lodging showed a positive correlation in one cross and a negative correlation in the other. Oil was positively correlated with yield and lodging, negatively correlated with maturity, and showed both positive and negative correlations for height. Correlations reported by Weber and Moorthy (1952), Weiss et al. (1952), and others showed general agreement with Johnson and Bernard's data for the positive correlation of SS with yield, but correlations among other characters were inconsistent. Johnson and Bernard stated that the extent to which correlations from various studies are comparable depends largely on how much the expression of various characters was influenced by environment for the different experimental units utilized. The only report of correlations of SG with agronomic characters was by Yoshino et al. (1955). They found the following range of correlation values in 11 crosses: yield = .01 to .43, maturity = .14 to .78, and height = -.08 to .56.

Natural selection was shown by Mumaw and Weber (1957) to alter the varietal percentages in three simulated soybean bulk populations grown for five years. They found that varieties with a branching growth habit increased in the composite while non-branching varieties decreased. High yielding ability of a variety grown singly was not an assurance of its ability to survive in the heterogeneous populations.

Smith (1966) measured the shift in population mean from F_4 to F_6 in

unselected bulk populations from two soybean crosses. He found a significant increase in maturity of three days and a significant decrease in oil of .3%. Significant alteration of the populations was not observed for SS, protein, and yield. The increase in maturity and decrease in oil may be due to natural selection, segregation in the hybrid populations, or inadequate sampling of lines from the populations.

Indirect mass selection for protein and oil was necessary due to the lack of a rapid, nondestructive method of single seed analysis for the two characters. Studies of the genetic interrelationships among SS, protein, and oil were reported by Johnson et al. (1955). SS gave a genetic correlation of .11 with protein and .12 with oil percent in one cross and a -.09 with protein and .15 with oil in the other cross. The genetic correlation of protein with oil had a range of -.48 to -.69. Weber and Moorthy (1955) reported a negative genetic correlation between SS and oil of -.1 to -.23. Johnson and Bernard (1962) found that the only consistent relationship reported in the literature was the negative correlation between protein and oil from -.48 to -.76.

Genetic Advance

The value of a selection procedure can be estimated by determination of expected and actual genetic advance. Allard (1960) stated that genetic advance for a selected character is a function of its selection differential, phenotypic standard deviation, and heritability. Deviations between predicted and actual advance would be expected when any of the components were improperly estimated. Expected change in an unselected character was

calculated by Johnson et al. (1955) as a function of the selection differential, the genetic covariance component between the selected and unselected character, and the phenotypic standard deviation of the selected character. They found that oil content of seed should be increased by selection for high yield, large seed, reduced plant lodging, and low protein.

Expected genetic advance for SS was found by Anand and Torrie (1963) to range from .9 to 1.8 grams per 100 seed in three soybean crosses. Kwon and Torrie (1964) reported expected genetic advance for SS in two soybean crosses of .9 to 1.9 grams per 100 seed. They stated that expected genetic advance in one of the crosses was 1.1% for protein and 0.4% for oil. Byth (1965) reported that estimates of predicted genetic advance varied among environments for soybean crosses. He stated that estimates of genetic advance were most reliable when an estimate of the genotype by environment interaction was available.

MATERIALS AND METHODS

Genetic Material and Character Evaluation

Populations used for the study were derived from two F_6 bulks from the crosses AX141 (C1105 x A4-3159) and AX144 (Lindarin x A4-3202). Parentage and general characteristics of the parental lines were as follows:

Parent	Parentage	Characteristics
C1105	Hawkeye x Mandarin (Ottawa)	Adapted; good protein and oil
A4-3159	Hawkeye x Capital	Fair adaptation; high protein and fair oil
Lindarin	Mandarin (Ottawa) x Lincoln	Adapted; good protein and oil
A4-3202	Hawkeye x Capital	Fair adaptation; good protein and oil

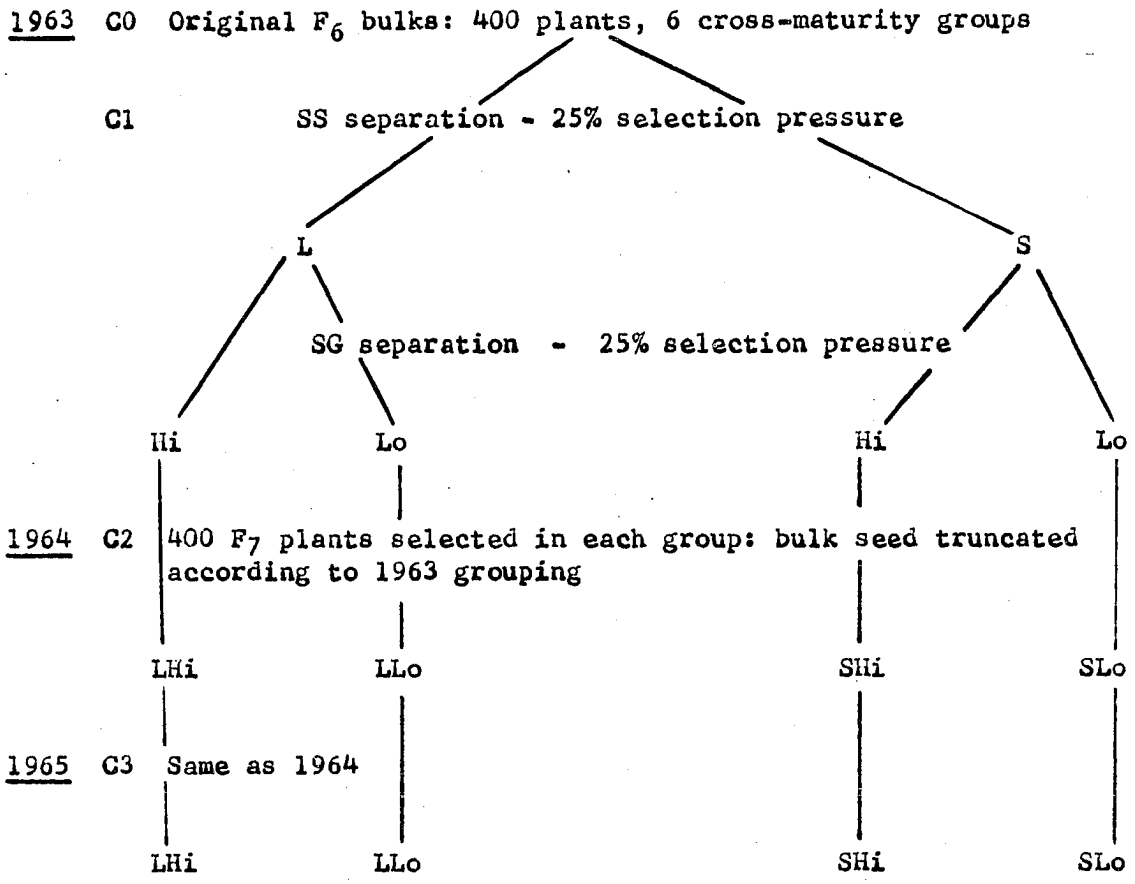
The two F_6 bulks were derived at Ames, Iowa, from 1957 to 1962. In 1957, crosses were made between parental strains. The F_1 populations were space planted in 1958 and bulked by cross at maturity. From 1959 to 1962, F_2-derived lines from the two crosses were grown as a part of a thesis study (Caldwell, 1963).

In the F_5 generation, grown in 1962, 30 random seed were bulked from 150 F_2-derived lines of each cross. In 1963, the 4,500 F_6 seed from each cross were grown as a bulk. At harvest, 400 plants were selected in each of three maturity groups: early (Blackhawk maturity, September 15), midseason (Hawkeye maturity, September 23), and late (Ford maturity, September 28). The upper one-fourth of all plants was cut off to remove

poorly developed seed and each maturity group was threshed as a bulk. Approximately 1,000 seed from each cross-maturity group were placed in cold storage to represent the C0 population. Remaining seed of each group was screened into large and small seed fractions using a 25% selection pressure based on seed number. Large and small seed fractions were sent to Urbana, Illinois, where each fraction was sub-divided for high and low SG using a series of step-wise-increasing glycerol-water solutions. A 25% selection pressure was used for each fraction based on seed number. The general selection procedure followed is outlined in Figure 1. SS and SG of each group after selection is presented in Table 6.

In 1964, approximately 2,300 F_7 seed from each SS-SG group were grown. At harvest, 400 plants in each group were selected on the basis of maturity, the upper one-fourth of the plants was removed and the remaining fraction threshed in bulk. The bulk seed was truncated according to its 1963 grouping with a 25% selection pressure for SS and SG (Figure 1). In addition to the 400 plants utilized for further mass selection, 40 plants from each SS-SG group were selected on the basis of maturity to represent C1. The single plant selections were increased in plant rows during 1965 and 10 random lines were selected from each classification for a replicated trial in 1966.

In 1965, approximately 1,000 F_8 seed from the second selection cycle were planted. At harvest, 400 random plants were selected and the seed truncated as in 1964. In addition to the material used for further mass selection, 100 seed from each SS-SG group of the second selection cycle and 625 seed from each of the F_6 C0 populations were space planted to



1966 Two replications grown of the following material for each cross-maturity group:

Cycle 1: 10 lines for each SS-SG group
Cycle 2: 10 lines for each SS-SG group
Cycle 3: 10 lines for each SS-SG group
Check varieties: Hark, Amsoy, and Ford
Total number of plots: 2016

Figure 1. Three mass selection cycles in bulk populations of two soybean crosses

Table 6. SS and SG of each population after each cycle of selection

Population		SS			SG		
		C1	C2	C3	C1	C2	C3
AX141 E	SLo	15.3	12.5	12.7	1.230	1.226	1.200
	SHi	15.3	12.6	13.0	1.248	1.248	1.245
	LLo	20.6	18.0	20.9	1.230	1.230	1.200
	LHi	20.6	18.7	21.9	1.248	1.248	1.240
M	SLo	15.2	13.3	13.5	1.235	1.230	1.200
	SHi	15.2	13.0	13.7	1.250	1.248	1.230
	LLo	20.6	19.0	22.1	1.230	1.220	1.205
	LHi	20.6	19.1	22.6	1.250	1.248	1.230
Lt	SLo	15.3	12.9	13.2	1.230	1.235	1.200
	SHi	15.3	12.8	12.9	1.248	1.250	1.220
	LLo	20.7	18.5	21.0	1.230	1.230	1.220
	LHi	20.7	18.5	20.9	1.250	1.250	1.240
AX144 E	SLo	12.0	11.2	11.5	1.212	1.220	1.200
	SHi	12.0	11.1	11.5	1.235	1.240	1.240
	LLo	17.2	16.6	18.7	1.220	1.222	1.200
	LHi	17.2	16.2	18.6	1.240	1.240	1.220
M	SLo	12.3	11.3	11.9	1.220	1.225	1.200
	SHi	12.3	11.3	11.9	1.240	1.246	1.230
	LLo	18.2	16.7	19.6	1.220	1.220	1.200
	LHi	18.2	16.5	19.9	1.235	1.238	1.220
Lt	SLo	13.1	11.5	12.1	1.230	1.220	1.200
	SHi	13.1	12.1	12.8	1.248	1.240	1.225
	LLo	18.8	18.5	21.7	1.230	1.226	1.200
	LHi	18.8	18.4	21.0	1.248	1.240	1.220

obtain adequate seed from single plants for the replicated trial in 1966. The space planted material was irrigated May 20 with 1.5 inches of water to facilitate germination and to activate the herbicide, Amiben, and on July 28 with 3.5 inches of water to enhance production. At maturity, 10 plants were selected in each SS-SG group to represent C2 and 40 plants were selected from each F_6 CO population.

After the third cycle of selection, a part of the resulting seed was sent to Chile, South America, during the winter of 1965-1966 under the auspices of the University of Minnesota and the Rockefeller Foundation. Seeds from each of the SS-SG groups were space planted and 10 single plant selections were made at maturity to represent C3.

In 1966, the experimental material was evaluated at Squaw Creek Bottom, Ames, Iowa. A total of 960 lines and three check varieties were planted on May 20 in two replications (Figure 1). Hark was the check variety for early, Amsoy for midseason, and Ford for late maturity groups. Check varieties were grown to serve as a guide for selecting superior lines that may be useful as future varietal releases. Each plot consisted of a 10-foot row with 40 inches between rows and 10 to 11 plants per foot of row. Each plot was trimmed to eight feet prior to harvest to minimize border effects. Due to droughty conditions after mid-June, the plots were irrigated with four inches of water on July 20 using overhead irrigation. All plots were kept weed-free throughout the growing season. The following attributes were evaluated on each plot:

Seed yield - kilograms per hectare; air dried to uniform moisture.

Maturity - days after August 31 when 95-100% of pods turned brown.

Lodging - scored at maturity; scale ranged from 1.0 (all plants erect) to 5.0 (most plants prostrate).

Height - centimeters from ground level to terminal bud; measured at maturity.

SS - grams per 100 seed; random sample of clean, whole seed.

Protein percent - Kj; measured on dry-weight basis.

Oil percent - NMR; measured on dry-weight basis.

SG - number of floating seed in a glycerol-water solution with a SG of 1.224.

Early lodging - scored at stage 7.0 on August 8; scale ranged from 1.0 (all plants erect) to 5.0 (most plants prostrate).

Monthly temperature and precipitation with departures from normal during the growing season at Ames, Iowa, from 1963 to 1966 are presented in Table 7. The 1966 growing season was influenced strongly by below normal rainfall from July to September and below normal temperatures during August and September.

Meteorological data from Santiago, Chile, South America, was not available for the 1965-1966 growing season. Average monthly data from the 1962 season was available (Table 8) and was considered to be typical of the locality (Lambert, Jean W., University of Minnesota, St. Paul, Minnesota. Meteorological data from Chile, South America. Private communication. 1967.) During the growing season, Santiago had warm days and cool nights, fair skies, and no rainfall. Irrigation water was applied at approximately 10-12 day intervals.

Table 7. Mean monthly temperature and precipitation with departures from normal for the growing season at Ames, Iowa, 1963 to 1966[a]

Temperature (°F)		Month				
		May	June	July	August	September
1963	Mean	60.2	73.5	74.2	70.1	65.1
	Departure	-.3	3.3	-.6	-2.6	.8
1964	Mean	65.8	69.1	75.6	68.3	65.6
	Departure	5.3	-1.1	.8	-4.4	1.3
1965	Mean	65.9	69.2	73.5	70.9	59.9
	Departure	5.4	-1.0	-1.3	-1.8	-4.4
1966	Mean	57.4	69.1	76.6	69.1	61.9
	Departure	-3.1	-1.1	1.8	-3.6	-2.4
Precipitation (inches)						
1963	Mean	5.66	2.45	4.17	5.06	2.33
	Departure	1.38	-2.76	.86	1.21	-.97
1964	Mean	4.07	7.71	4.34	3.14	3.07
	Departure	-.21	2.50	1.03	-.71	-.24
1965	Mean	4.68	4.80	1.62	2.68	7.23
	Departure	.40	-.41	-1.69	-1.17	3.92
1966	Mean	4.81	8.56	1.28	2.03	0.25
	Departure	.53	3.35	-2.03	-1.82	-3.05

[a]Data from the Weather Bureau, U.S. Department of Commerce.

Table 8. Meteorological data for the growing season at Santiago, Chile, South America, 1962[a]

Month	Temperature (°C)	Wind velocity[b] (mph)	Relative humidity[b] (%)
December	69.1	6.5	48
January	68.4	6.0	44
February	65.4	5.5	53
March	63.9	5.0	52
April	57.0	3.0	54

[a]Data from the meteorological station at Los Cerillos airport. Latitude: 33° 30' South; Longitude: 70° 42' West; Elevation: 1660 feet.

[b]Measurements made daily at 7 PM.

Experimental Design and Parameter Estimation

The experimental design was a split-split plot in two replications, with whole plots in a factorial arrangement. Each whole plot was a cross-maturity group containing two blocks as sub-plots. Each block consisted of 80 lines as sub-sub-plots, ie. five random lines from each of the four SS-SG groups in four selection cycles.

The effects of lines were considered random and the effects of crosses, maturity groups, cycles, and SS-SG groups were assumed fixed.

The following model was used for whole plots:

$$X_{ijk} = u + R_i + A_j + M_k + (MC)_{jk} + e_{ijk} .$$

The sub-plot model was as follows:

$$X_{ijklmno} = B_{ijkl} + D_{jklm} + E_{jklmn} + F_{jklmno} + e_{ijklmno}$$

where

R_i = i^{th} replication; i = 1 to 2

A_j = j^{th} cross; j = 1 to 2

M_k = k^{th} maturity group; k = 1 to 3

$(MC)_{jk}$ = Interaction of j^{th} cross with k^{th} maturity group

B_{ijkl} = l^{th} block in the k^{th} maturity group of the j^{th} cross in the i^{th} rep; l = 1 to 2

D_{jklm} = m^{th} cycle in the l^{th} block in the k^{th} maturity group of the j^{th} cross; m = 1 to 4

E_{jklmn} = n^{th} SS-SG group in the m^{th} cycle in the l^{th} block in the k^{th} maturity group of the j^{th} cross; n = 1 to 4

F_{jklmno} = o^{th} line in the n^{th} SS-SG group in the m^{th} cycle in the l^{th} block in the k^{th} maturity group of the j^{th} cross; o = 1 to 5

e_{ijk} and $e_{ijklmno}$ = higher order interactions, replication interactions, and random error.

Analyses of variance and expected mean squares for whole-plots and subplots are presented in Tables 9 and 10, respectively.

Variance components were obtained from the relationship:

$$\sigma_p^2 = (\sigma_e^2 + 2\sigma_g^2)/2 = \frac{\sigma_e^2}{2} + \sigma_g^2$$

$$\sigma_g^2 = [(\sigma_e^2 + 2\sigma_g^2) - \sigma_e^2]/2$$

where σ_p^2, σ_g^2, and σ_e^2 are the phenotypic, genotypic, and error variance components, respectively.

Table 9. Analysis of variance and expected mean squares for whole plots

Source of variation	d.f.	Expected mean squares
Total	11	
Replications (R)	1	
Crosses (Cr)	1	$\sigma^2_{ij} + 6\ \sigma^2_j$
Maturity Groups (MG)	2	$\sigma^2_{ik} + 4\ \sigma^2_k$
Cr x MG	2	$\sigma^2_{ijk} + 2\ \sigma^2_{jk}$
R x Cr	1	σ^2_{ij}
R x MG	2	σ^2_{ik}
R x Cr x MG	2	σ^2_{ijk}

Table 10. Analysis of variance and expected mean squares for a typical sub-plot

Source of variation	d.f.	Expected mean squares
Lines in block (B)	79	$\sigma^2_e + 2\ \sigma^2_B$
Lines in m^{th} cycle (D)	19	$\sigma^2_e + 2\ \sigma^2_D$
Lines in n^{th} SS-SG group (E)	4	$\sigma^2_e + 2\ \sigma^2_E$
E_I-E_{II} vs. E_{III}-E_{IV}	1	$\sigma^2_e + 2\ \sigma^2_{E_1}$
E_I vs. E_{II}	1	$\sigma^2_e + 2\ \sigma^2_{E_2}$
E_{III} vs. E_{IV}	1	$\sigma^2_e + 2\ \sigma^2_{E_3}$
D_0 vs. D_I-D_{II}-D_{III}	1	$\sigma^2_e + 2\ \sigma^2_{D_1}$
D_I vs. D_{II}-D_{III}	1	$\sigma^2_e + 2\ \sigma^2_{D_2}$
D_{II} vs. D_{III}	1	$\sigma^2_e + 2\ \sigma^2_{D_3}$
B_I vs. B_{II}	1	$\sigma^2_e + 2\ \sigma^2_{B_1}$
Replications x Lines in block	79	σ^2_e

Covariance analyses were calculated for all possible characters to obtain the components necessary for calculation of correlations and other pertinent information (Table 11). Covariance components were obtained by the following relationship:

$$Cov_{xy}P_{12} = (Cov_e + 2Cov_{xy}G_{12})/2 = \frac{Cov_e}{2} - Cov_{xy}G_{12}$$

$$Cov_{xy}G_{12} = [(Cov_e + 2Cov_{xy}G_{12}) - Cov_e]/2$$

Estimates of variance and covariance components were obtained by equating mean squares and cross products to their expectations and solving for the required components as indicated above. Estimates were made on a mean line basis.

Table 11. Partial analysis of covariance and expected mean squares for a typical sub-plot

Source of variation	d.f.	Expected mean squares
Lines in block (B)	79	$Cov_e + 2\ Cov_B$
Lines in m^{th} cycle (D)	19	$Cov_e + 2\ Cov_D$
Lines for n^{th} SS-SG group (E)	4	$Cov_e + 2\ Cov_E$
Replication x Lines in block	79	Cov_e

Broad sense heritability estimates were obtained for all characters from the ratio of genotypic to phenotypic variance. These estimates approximated narrow sense heritabilities since the additive genetic variance comprises 96% of the total genetic variance by the F_4 generation (Hanson and Weber, 1961).

Genotypic and phenotypic correlations of all possible pairs of characters were calculated using the relationship:

$$\text{Phenotypic } r_{xy} = \frac{Cov_{xyP_{12}}}{\sqrt{\sigma^2_{xP_1} \cdot \sigma^2_{yP_2}}} \qquad \text{Genotypic } r_{xy} = \frac{Cov_{xyG_{12}}}{\sqrt{\sigma^2_{xG_1} \cdot \sigma^2_{xG_2}}}$$

where $Cov_{xyP_{12}}$, $\sigma^2_{xP_1}$, $\sigma^2_{yP_2}$ = Estimates of the phenotypic covariance component between a given pair of characters and the phenotypic variance component of the characters, respectively.

$Cov_{xyG_{12}}$, $\sigma^2_{xG_1}$, $\sigma^2_{xG_2}$ = Estimates of the genotypic covariance component between a given pair of characters and the genotypic variance components of the characters, respectively.

Expected and actual genetic advance were evaluated for SS and SG. The expected and actual genetic change in protein and oil percent as a result of selecting for SS and SG was assessed. The following relationships were utilized:

Expected genetic advance = $k\sigma_A H$ (Allard, 1960)

Expected change in unselected character = $\frac{k\ cov_{G_{12}}}{\sqrt{\sigma^2_{P_1}}}$ (Johnson et al. 1955)

where

k = selection differential in standard units

σ_A = phenotypic standard deviation

H = heritability of selected character

Cov_{G12} = estimates of the genotypic covariance component between a given pair of characters.

$\sigma^2_{P_1}$ = phenotypic variance component of the selected character.

RESULTS AND DISCUSSION

Whole-plot Analyses

Significant differences were observed between crosses for SS, protein, and oil (Table 12). AX141 had larger SS, higher protein, and lower oil than AX144 (Table 13). Differences between the two crosses were desired in order to detect the effects of mass selection in diverse genetic backgrounds. Lack of significance between the crosses for SG was associated with a relatively large replication x crosses mean square.

Maturity groups differed significantly for yield, maturity, height, SS, and SG (Table 12). An increase in maturity and height from early to late maturity groups was expected; however, the decrease in yield and SS with maturity was unusual (Table 13). The decreased productiveness of the late lines was attributed to droughty conditions which began in late June and continued into September (Table 7).

Sub-plot Analyses

Sum of squares were pooled across blocks and maturity groups for all sub-plot analyses. Significant differences were observed among lines in most of the cycles and SS-SG groups for all nine characters (Table 12).

Blocks were different at the 1% level of probability for all characters. The deviations between blocks may be attributed to soil heterogeneity at the test site or differences in the genotypes assigned to the blocks due to sampling. Soil heterogeneity was a major factor at Squaw Creek Bottom due to the presence of a subsoil factor, perhaps a sand lense,

Table 12. Analysis of variance and coefficients of variability for nine characters in so

Source of variation	d.f.	Mean squares					
		Yield	Maturity	Lodging	Height	SS	Pr
Replications (R)	1	279150.42	2.48	2.837	1209.68	.23	2
Crosses (Cr)	1	1196252.93	103.14	14.214	1844.75	3435.24*	1
Maturity Groups (MG)	2	42233300.50*	11267.14**	6.610	50690.91**	455.92**	
Cr x MG	2	1425753.54	779.43	1.510	3453.03	230.98	
R x Cr	1	647131.65	149.08	5.208	43.20	4.96	
R x MG	2	1700154.79	21.10	3.235	210.18	3.48	
R x Cr x MG	2	409656.18	52.98	3.017	2383.33	18.11	
Lines in AX141-AX144	948	114558.10**	12.76**	.345**	167.79**	3.87**	
Lines in AX141	474	122366.78**	15.71**	.184**	69.92**	4.44**	
Lines in C0	114	114328.78**	14.38**	.185**	76.48**	5.01**	
Lines in SLo	24	105918.67	10.01**	.276**	65.03**	5.07**	
Lines in SHi	24	137796.74**	18.11**	.248**	110.09**	4.85**	
Lines in LLo	24	105975.57	12.01**	.155**	63.63**	5.22**	
Lines in LHi	24	94344.41	15.75**	.152**	60.75**	4.93**	
SLo-SHi vs.LLo-LHi	6	123959.18	10.97*	.074	32.05	4.06**	
SLo vs. SHi	6	132948.52	14.16**	.050	157.90**	5.76**	
LLo vs. LHi	6	139197.65	24.52**	.075	65.14*	5.03**	
Lines in C1	114	150740.47**	9.60**	.181**	55.27**	4.01**	
Lines in SLo	24	173167.24**	6.54*	.285**	40.75*	3.06**	
Lines in SHi	24	169940.85**	6.23*	.106	47.15**	3.00**	
Lines in LLo	24	114473.79*	9.44**	.233**	60.92**	2.71**	
Lines in LHi	24	130183.82*	6.99*	.124*	63.65**	5.13**	
SLo-SHi vs. LLo-LHi	6	154874.71	11.69**	.070	53.18*	9.60**	
SLo vs. SHi	6	99860.12	21.39**	.161*	39.84	5.31**	
LLo vs. LHi	6	258271.32**	32.41**	.224**	107.15**	5.72**	
Lines in C2	114	90854.82	13.89**	.131**	66.95**	3.62**	
Lines in SLo	24	54718.39	12.17**	.187**	79.34**	1.42**	
Lines in SHi	24	127407.04*	11.46**	.086	76.58**	2.99**	
Lines in LLo	24	119907.90*	22.09**	.145**	85.17**	3.14**	
Lines in LHi	24	53529.35	12.59**	.158**	41.46*	2.76**	
SLo-SHi vs. LLo-LHi	6	215686.41**	10.62*	.083	37.92	18.39**	
SLo vs. SHi	6	39260.22	9.38*	.064	20.57	3.77**	
LLo vs. LHi	6	49044.32	10.58*	.044	83.42**	5.50**	
Lines in C3	114	112571.44**	22.56**	.222**	76.50**	5.21**	
Lines in SLo	24	141717.49**	20.34**	.261**	68.67**	4.13**	
Lines in SHi	24	72850.52	11.02**	.279**	37.93*	1.69**	
Lines in LLo	24	84787.35	22.60**	.156**	145.09**	4.07**	
Lines in LHi	24	91096.29	28.78**	.164**	52.09**	1.87**	
SLo-SHi vs. LLo-LHi	6	162374.16*	12.52**	.356**	70.56**	35.58**	
SLo vs. SHi	6	265289.86**	35.06**	.275**	78.31**	10.62**	
LLo vs. LHi	6	149386.78	50.06**	.139	89.52**	5.82**	
C0 vs. C1-C2-C3	6	76186.47	16.76**	.239**	82.04**	1.83**	
C1 vs. C2-C3	6	508554.98**	51.68**	.364**	37.08	2.04**	
C2 vs. C3	6	180819.55*	25.16**	.294**	175.43**	7.22**	
Block 1 vs. Block 2	3	2060635.35**	71.82**	1.916**	1647.33**	5.97**	

y for nine characters in soybean lines derived from two crosses

	Mean squares					
ng	Height	SS	Protein	Oil	SG	EL
37	1209.68	.23	209.95**	42.99**	6329.27	.273
14	1844.75	3435.24*	1542.09*	1628.58**	12080.13	.537
10	50690.91**	455.92**	19.56	3.24	54983.18*	2.622
10	3453.03	230.98	113.31	2.10	3698.45	2.934
08	43.20	4.96	.39	.00	2443.52	1.031
35	210.18	3.48	15.80	1.93	831.76	.634
17	2383.33	18.11	12.02	2.76	504.85	1.395
45**	167.79**	3.87**	2.65**	.86**	379.00**	.172**
84**	69.92**	4.44**	2.31**	.78**	255.33**	.111**
85**	76.48**	5.01**	1.90**	.69**	246.94**	.104**
76**	65.03**	5.07**	1.45**	.75**	189.37**	.171**
48**	110.09**	4.85**	1.82**	.69**	321.19**	.113**
55**	63.63**	5.22**	1.41**	.50**	148.05**	.094*
52**	60.75**	4.93**	2.26**	.88**	331.08**	.082
74	32.05	4.06**	2.72**	.56*	214.81**	.046
50	157.90**	5.76**	3.21**	.58**	233.89**	.053
75	65.14*	5.03**	2.34**	.66**	284.38**	.043
81**	55.27**	4.01**	1.50**	.61**	227.77**	.109**
85**	40.75*	3.06**	2.04**	.86**	160.92**	.142**
06	47.15**	3.00**	.94*	.39**	216.58**	.110**
33**	60.92**	2.71**	1.77**	.54**	315.46**	.093*
24*	63.65**	5.13**	.84	.38**	246.90**	.117**
70	53.18*	9.60**	.44	.48*	246.48**	.086
61*	39.84	5.31**	3.30**	1.21**	176.39**	.038
24**	107.15**	5.72**	2.45**	1.14**	145.34**	.092
31**	66.95**	3.62**	1.53**	.62**	250.18**	.113**
87**	79.34**	1.42**	1.61**	.42**	189.91**	.141**
86	76.58**	2.99**	1.05**	.37**	280.46**	.095*
45**	85.17**	3.14**	1.24**	.70**	136.53**	.144**
58**	41.46*	2.76**	.60	.33*	225.00**	.119**
83	37.92	18.39**	2.02**	.66**	645.59**	.045
64	20.57	3.77**	2.77**	2.71**	464.85**	.054
44	83.42**	5.50**	6.31**	1.07**	315.37**	.054
22**	76.50**	5.21**	1.55**	.75**	280.75**	.109**
61**	68.67**	4.13**	2.08**	.72**	250.01**	.119**
79**	37.93*	1.69**	1.33**	.46**	188.03**	.116**
56**	145.09**	4.07**	1.12**	.37**	223.58**	.094*
64**	52.09**	1.87**	.63	.12	233.72**	.077
56**	70.56**	35.58**	1.16	.72**	314.39**	.173**
75**	78.31**	10.62**	2.68**	3.28**	619.16**	.198**
39	89.52**	5.82**	5.01**	3.62**	819.40**	.069
39**	82.04**	1.83**	5.33**	1.90**	495.85	.170**
64**	37.08	2.04**	16.91**	5.23**	275.94	.118
94**	175.43**	7.22**	37.16**	3.79**	292.30	.246**
16**	1647.33**	5.97**	111.03**	11.46**	748.29**	.274**

Table 12. (Continued)

Source of variation	d.f.	Yield	Maturity	Lodging	Height	Me SS
Lines in AX144	474	106749.42**	9.80**	.507**	265.67**	3.30
Lines in C0	114	87836.79**	7.74**	.370**	320.43**	2.12
Lines in SLo	24	101001.12	7.35**	.412**	295.23**	2.16
Lines in SHi	24	111082.92	8.45**	.319**	315.81**	2.28
Lines in LLo	24	79369.61	7.95**	.477**	271.25**	1.71
Lines in LHi	24	85217.64	4.90**	.397**	277.65**	2.10
SLo-SHi vs. LLo-LHi	6	28662.23	20.43**	.342*	491.00**	3.55
SLo vs. SHi	6	39578.38	3.62	.087	569.58**	1.82
LLo vs. LHi	6	93973.35	8.44**	.172	387.91**	1.93
Lines in C1	114	98792.07**	6.89**	.511**	221.74**	3.28
Lines in SLo	24	62706.45	8.02**	.694**	146.02**	2.41
Lines in SHi	24	132472.38*	5.81**	.548**	300.40**	1.58
Lines in LLo	24	91232.84	4.91**	.301**	170.29**	3.63
Lines in LHi	24	139815.15*	10.31**	.514**	258.86**	3.54
SLo-SHi vs. LLo-LHi	6	54425.31	7.70**	.616**	238.08**	14.65
SLo vs. SHi	6	70862.16	2.79	.563**	139.19**	1.14
LLo vs. LHi	6	46854.64	4.22	.309*	333.51**	1.93
Lines in C2	114	119769.91**	11.47**	.545**	255.72**	2.73
Lines in SLo	24	134415.64*	7.92**	.600**	261.13**	.95
Lines in SHi	24	130373.24*	14.52**	.266**	188.06**	1.16
Lines in LLo	24	160927.61**	9.16**	.746**	193.30**	2.60
Lines in LHi	24	43249.94	14.73**	.433**	320.32**	2.18
SLo-SHi vs. LLo-LHi	6	62401.36	12.59**	.716**	493.31**	21.83
SLo vs. SHi	6	87293.36	9.95**	.646**	299.32**	.80
LLo vs. LHi	6	250067.78**	10.01**	.802**	214.74**	1.72
Lines in C3	114	112782.06**	8.75**	.582**	246.12**	4.68
Lines in SLo	24	96573.92	5.13**	.306**	228.65**	2.53
Lines in SHi	24	132944.38*	10.23**	.429**	188.75**	1.09
Lines in LLo	24	80557.56	5.90**	.645**	119.79**	3.37
Lines in LHi	24	102349.10	7.78**	1.003**	274.25**	1.27
SLo-SHi vs. LLo-LHi	6	211302.98*	28.47**	.776**	714.74**	50.90
SLo vs. SHi	6	92373.28	7.97**	.340*	390.30**	1.60
LLo vs. LHi	6	189483.07*	13.73**	.404**	325.53**	3.31
C0 vs. C1-C2-C3	6	40762.47	15.98**	.604**	575.68**	6.47
C1 vs. C2-C3	6	193970.25*	91.46**	.510**	161.03**	6.12
C2 vs. C3	6	234035.61**	4.26**	.763**	414.69**	4.71
Block 1 vs. Block 2	3	306053.67**	38.58**	1.667**	1709.74**	5.62
Rx Lines in AX141-AX144	948	75427.97	3.20	.100	32.09	.27
Rx Lines in AX141	474	74203.87	3.97	.075	23.75	.35
Rx Lines in AX144	474	76652.06	2.44	.125	40.43	.19
Coefficient of variability (%)		10.6	8.7	12.4	5.1	3.5

Mean squares							
Maturity	Lodging	Height	SS	Protein	Oil	SG	EL
9.80**	.507**	265.67**	3.30**	2.98**	.94**	502.67**	.232**
7.74**	.370**	320.43**	2.12**	2.06**	.68**	315.44**	.228**
7.35**	.412**	295.23**	2.16**	1.24**	.85**	499.98**	.188**
8.45**	.319**	315.81**	2.28**	1.83**	.57**	421.23**	.259**
7.95**	.477**	271.25**	1.71**	1.96**	.36	176.01**	.355**
4.90**	.397**	277.65**	2.10**	1.47**	1.03**	183.76**	.129
20.43**	.342*	491.00**	3.55**	3.11**	.17	142.63*	.208*
3.62	.087	569.58**	1.82**	3.76**	.74**	434.95**	.283**
8.44**	.172	387.91**	1.93**	6.23**	.76**	291.85**	.112
6.89**	.511**	221.74**	3.28**	2.63**	.73**	327.62**	.235**
8.02**	.694**	146.02**	2.41**	1.03*	.31	297.31**	.264**
5.81**	.548**	300.40**	1.58**	1.80**	.28	179.45**	.277**
4.91**	.301**	170.29**	3.63**	3.20**	.63**	294.03**	.135
10.31**	.514**	258.86**	3.54**	3.58**	1.22**	273.02**	.263**
7.70**	.616**	238.08**	14.65**	5.27**	.36	981.10**	.304**
2.79	.563**	139.19**	1.14**	2.50**	.77**	382.12**	.168
4.22	.309*	333.51**	1.93**	3.72**	2.88**	686.28**	.240*
11.47**	.545**	255.72**	2.73**	2.16**	1.05**	693.67**	.211**
7.92**	.600**	261.13**	.95**	2.30**	1.23**	557.72**	.205**
14.52**	.266**	188.06**	1.16**	1.44**	.61**	371.09**	.111
9.16**	.746**	193.30**	2.60**	1.91**	1.42**	652.79**	.272**
14.73**	.433**	320.32**	2.18**	2.19**	.65**	369.04**	.257**
12.59**	.716**	493.31**	21.83**	4.39**	.68*	52.83	.397**
9.95**	.646**	299.32**	.80**	3.63**	2.10**	3625.22**	.082
10.01**	.802**	214.74**	1.72**	1.79*	1.52**	1699.13**	.152
8.75**	.582**	246.12**	4.68**	2.15**	1.03**	578.59**	.262**
5.13**	.306**	228.65**	2.53**	1.57**	.32	261.81**	.252**
10.23**	.429**	188.75**	1.09**	1.64**	.57**	139.82**	.138
5.90**	.645**	119.79**	3.37**	.60	.67**	298.38**	.161**
7.78**	1.003**	274.25**	1.27**	1.41**	.67**	137.04**	.297**
28.47**	.776**	714.74**	50.90**	10.98**	1.36**	1394.71**	1.039**
7.97**	.340*	390.30**	1.60**	3.62**	1.90**	1711.62**	.233*
13.73**	.404**	325.53**	3.31**	5.42**	7.33**	4538.68**	.325**
15.98**	.604**	575.68**	6.47**	8.59**	1.97**	140.86*	.134
91.46**	.510**	161.03**	6.12**	30.54**	2.07**	2553.73**	.112
4.26**	.763**	414.69**	4.71**	25.27**	3.65**	625.15**	.307**
38.58**	1.667**	1709.74**	5.62**	33.71**	1.49**	2430.46**	.459**
3.20	.100	32.09	.27	.62	.23	50.39	.076
3.97	.075	23.75	.35	.56	.20	42.29	.059
2.44	.125	40.43	.19	.67	.26	58.50	.093
8.7	12.4	5.1	3.5	2.0	2.3	16.8	10.8

Table 13. Mean agronomic and chemical performance of soybean lines in C0 and three selection cycles in three cross-maturity groups in two soybean crosses

Cross-maturity group	Yield	Maturity	Lodging	Height	SS	Protein	Oil	SG	EL
AX141 E									
C0	2830	16	2.3	106	17.2	40.4	19.9	45	2.5
C1	2784	16	2.4	104	17.1	40.2	20.5	53	2.5
C2	2914	16	2.4	105	17.4	40.5	20.0	48	2.6
C3	2978	15	2.5	102	17.5	41.9	19.6	50	2.6
Mean	2877	16	2.4	104	17.3	40.8	20.0	49	2.5
AX141 M									
C0	2708	20	2.5	108	16.8	40.9	20.2	47	2.5
C1	2638	20	2.5	108	16.6	41.0	20.3	42	2.5
C2	2663	19	2.4	106	16.4	41.0	20.2	41	2.5
C3	2773	18	2.6	106	17.1	42.0	19.9	44	2.6
Mean	2696	19	2.5	107	16.7	41.2	20.2	43	2.5
AX141 Lt									
C0	2313	25	2.4	119	14.7	40.1	20.2	26	2.5
C1	2243	27	2.4	119	14.6	39.8	20.2	28	2.5
C2	2266	26	2.6	121	14.3	39.7	20.2	26	2.5
C3	2339	25	2.6	119	14.7	41.3	19.7	28	2.5
Mean	2291	26	2.5	119	14.6	40.2	20.1	27	2.5
AX141 Overall									
C0	2617	20	2.4	111	16.3	40.5	20.1	39	2.5
C1	2555	21	2.4	111	16.1	40.3	20.3	41	2.5
C2	2615	20	2.5	111	16.0	40.4	20.1	38	2.5
C3	2697	19	2.5	109	16.4	41.7	19.7	40	2.6
Mean	2621	20	2.5	110	16.2	40.7	20.1	40	2.5
AX144 E									
C0	2688	18	2.4	103	13.3	38.1	22.1	52	2.4
C1	2695	17	2.4	100	13.4	37.7	22.2	62	2.4
C2	2761	17	2.4	102	13.9	38.7	22.0	52	2.4
C3	2757	17	2.6	100	14.4	40.0	21.6	44	2.5
Mean	2725	17	2.5	102	13.8	38.6	22.0	52	2.4
AX144 M									
C0	2653	21	2.6	118	13.4	38.5	22.1	46	2.6
C1	2602	22	2.8	112	13.6	38.8	21.9	41	2.7
C2	2652	20	2.7	113	13.5	38.5	22.1	46	2.7

Table 13. (Continued)

Cross-maturity group	Yield	Maturity	Lodging	Height	SS	Protein	Oil	SG	EL
AX144 M (continued)									
C3	2745	20	2.8	110	13.8	39.5	21.8	43	2.7
Mean	2663	21	2.7	114	13.6	38.8	22.0	44	2.7
AX144 Lt									
C0	2319	24	2.7	120	13.0	39.1	22.0	38	2.6
C1	2270	25	2.7	123	13.5	38.9	21.8	31	2.6
C2	2281	23	2.8	122	13.0	39.4	21.8	39	2.6
C3	2431	23	2.7	122	13.6	40.1	21.6	41	2.6
Mean	2325	24	2.7	122	13.3	39.4	21.8	37	2.6
AX144 Overall									
C0	2553	21	2.6	114	13.2	38.6	22.1	46	2.5
C1	2522	22	2.6	112	13.5	38.5	22.0	45	2.5
C2	2565	20	2.6	113	13.5	38.8	22.0	46	2.5
C3	2644	20	2.7	111	13.9	39.9	21.6	43	2.6
Mean	2571	21	2.6	112	13.5	38.9	21.9	45	2.6

which caused a marked decrease in plant growth. At planting, the soil appeared to be uniform, but when soil moisture became limiting in July, plants in a distinct 20-25 foot diagonal strip across the field exhibited decreased growth and earlier maturity than plants within two feet of them.

Deviations between blocks may be due also to differences in the genotypes each contained. For the C0 population, lines in SLo, SHi, LLo, and LHi were randomly selected from the same array of genotypes and mean differences among the four groups would be due to inadequate sampling of

the population. Highly significant differences were observed for the orthogonal comparisons involving these groups for all characters except yield, lodging, and early lodging (Table 12). These observations demonstrated the principal advantage and disadvantage of blocks in this experiment. The use of blocks reduced experimental error by decreasing soil heterogeneity within a whole plot, but they also reduced genotypic variance due to an unequal mean performance of lines in each block. Blocks were a valuable tool in this study because of the removal of a large amount of soil heterogeneity.

Cycle Comparisons

The mean of lines in C3 was significantly different than the combined mean of all other cycles for all characters except SG in AX141 (Table 14). In C3, yield, SS, and protein percent were consistently higher while oil percent was consistently lower than other cycles for the six cross-maturity groups (Table 13). This difference in cycle means may be due to (a) a seed source effect or (b) unequal mass selection effectiveness among the SS-SG groups in C3.

A seed source effect is defined as the dependence of a genotype's agronomic and chemical performance on the source of the seed used for propagation. Three methods of seed increase were used in the study. Seed for lines of C0 and C1 was obtained under irrigated conditions at Squaw Creek Bottom from plants spaced approximately one foot apart; lines in C1 were increased without irrigation at the Agronomy Farm in five-foot rows, 40 inches apart, with 9 to 10 plants per foot of row; and seed for lines

Table 14. Mean squares for non-orthogonal comparisons among selection cycles for nine characters in two crosses

Cross and comparison	Yield	Maturity	Lodging	Height	SS	Protein	Oil	SG	EL
AX141									
C3 vs. C0-C1-C2	1842143.84**	254.42**	1.610**	460.80**	15.07**	326.30**	33.52**	144.90	1.254**
C3 vs. C1	2401538.13**	330.01**	1.027**	231.02**	11.94**	238.15**	39.90**	33.60	.624**
C3 vs. C0-C2	1050084.02**	145.67**	1.463	465.81**	12.21**	276.76**	20.62**	414.95**	1.272**
C1 vs. C0-C2	584753.00**	79.34**	.002	16.26	.24	1.40	7.58**	732.45**	.047
C0 vs. C2	790.53	.41	.488*	.47	6.30**	.39	.17	183.77*	.331*
AX144									
C3 vs. C0-C1-C2	1719275.93**	107.72**	1.339**	762.61**	48.08**	275.10**	23.80**	1157.74**	1.058**
C3 vs. C1	1790474.70**	264.03**	.414	180.08*	21.25**	231.99**	11.78**	450.47**	.653**
C3 vs. C0-C2	1170267.08**	28.06**	1.600**	980.10**	51.04**	214.99**	24.18**	1286.33**	.976**
C1 vs. C0-C2	214646.92	181.33**	.272	250.00*	3.32**	8.56**	.91	129.00	.003
C0 vs. C2	15766.67	33.60**	.602*	185.01*	7.68**	9.35**	1.14*	1.52	.006

in C3 was obtained under irrigated conditions in Chile, South America, from plants spaced one foot apart.

Comparison of cycle means based on their method of increase are presented in Table 14. C3 was different than C1 at the 1% level of probability for all characters except SG in AX141 and lodging in AX144. The mean of C3 was significantly different than C0 and C2 combined for all characters, except lodging in AX141. For increases at Ames, differences between the mean of C1 and the combined mean for C0 and C2 were not consistently greater than the difference between C0 and C2. This indicated that if a seed source effect was present, it was more important in the comparison of C3 with the other cycles than comparisons among the cycles increased at Ames.

The possibility of a seed source effect imposed certain restrictions on the interpretation of experimental data in this study. Changes in the mean of a given SS-SG group from C0 to C3 could not be used as an index of mass selection effectiveness. For example, the mean protein percent of lines in LLo for AX141 should progressively decrease with selection (Table 15). The decrease was observed through C2, but in C3 the protein percent was 1.1% greater than in the C0 population. If the seed source effect was not considered, the interpretation would be that one adverse cycle of selection had eliminated all progress made in the preceding generations. A more accurate interpretation of the data was obtained by comparing the mean differences between SS-SG groups across cycles (Figure 1).

The occurrence of a seed source effect in soybeans would have strong implications in the preparation of seed for experiments conducted to

Table 15. Mean agronomic and chemical performance of soybean lines in SS-SG populations for two crosses

Population	Yield	Maturity	Lodging	Height	SS	Protein	Oil	SG	EL
AX141									
SLo									
C0	2617	20	2.4	111	16.3	40.4	20.1	39	2.5
C1	2534	22	2.5	110	15.6	40.0	20.6	41	2.5
C2	2598	20	2.5	111	15.1	40.1	20.4	39	2.5
C3	2639	19	2.5	110	15.4	41.4	20.1	40	2.5
SHi									
C0	2617	20	2.4	111	16.3	40.4	20.1	39	2.5
C1	2536	20	2.4	110	15.8	40.5	20.2	38	2.5
C2	2600	20	2.4	111	15.7	40.8	19.7	31	2.6
C3	2683	19	2.6	107	15.6	41.9	19.6	35	2.6
LLo									
C0	2617	20	2.4	111	16.3	40.4	20.1	39	2.5
C1	2507	22	2.4	110	16.6	40.1	20.5	44	2.5
C2	2632	20	2.4	111	16.7	39.9	20.4	44	2.5
C3	2754	20	2.5	111	17.5	41.5	20.0	43	2.6
LHi									
C0	2617	20	2.4	111	16.3	40.4	20.1	39	2.5
C1	2644	21	2.5	112	16.4	40.6	20.1	41	2.6
C2	2628	21	2.5	110	16.6	40.8	20.0	38	2.6
C3	2711	19	2.5	109	17.2	42.2	19.3	43	2.6
Overall mean	2621	20	2.5	110	16.2	40.7	20.1	40	2.5
AX144									
SLo									
C0	2553	21	2.6	114	13.2	38.6	22.1	46	2.5
C1	2529	22	2.7	112	13.1	38.0	22.1	45	2.6
C2	2604	21	2.8	116	12.7	38.4	22.3	58	2.6
C3	2623	20	2.8	118	12.7	39.2	21.9	47	2.8
SHi									
C0	2553	21	2.6	114	13.2	38.6	22.1	46	2.5
C1	2498	22	2.7	113	12.9	38.4	21.8	41	2.6
C2	2538	20	2.7	115	12.8	38.8	21.7	34	2.6
C3	2561	20	2.8	111	12.9	39.7	21.4	31	2.7
LLo									
C0	2553	21	2.6	114	13.2	38.6	22.1	46	2.5
C1	2528	21	2.5	109	14.2	38.4	22.2	50	2.4
C2	2522	20	2.6	108	14.4	39.0	22.2	54	2.5
C3	2744	21	2.6	111	15.2	39.9	22.2	62	2.4

Table 15. (Continued)

Population	Yield	Materials	Lodging	Height	SS	Protein	Oil	SG	EL
AX144 (Continued)									
LHi									
C0	2553	21	2.6	114	13.2	38.6	22.1	46	2.5
C1	2533	21	2.6	113	13.9	39.1	21.8	44	2.5
C2	2594	20	2.5	111	14.0	39.1	21.7	37	2.5
C3	2650	20	2.6	104	14.8	40.7	21.1	32	2.5
Overall mean	2571	21	2.6	112	13.5	38.9	21.9	45	2.6

evaluate the performance of a number of genotypes. The increasing availability of greenhouse space or winter nurseries has permitted plant breeders to increase seed of desirable genotypes during the winter months. To avoid a seed source effect, all genotypes to be evaluated should be increased at the same location rather than increasing only those which do not have adequate seed. Similarly, seed of genotypes developed at various states should be increased at a single site before a critical evaluation is made. The practice of using seed from wherever it can be acquired may lead to inaccurate experimental results, particularly if the locations have widely diverse environments during the growing season.

There has been no evidence reported for the occurrence of a seed source effect in soybeans. Recent work has shown that soybean seed of a given genotype grown at two locations in Iowa had differing degrees of seedling vigor when grown in the greenhouse. Seed quality differences in the seed lots were assumed to account for the seedling vigor response. (Metzler, Robert B., Ames, Iowa. Natural and induced variation in soybean

seed quality during maturation. Private communication. 1967.) Differences in seedling vigor may or may not result in differential agronomic and chemical performance.

Differences between cycle means could also be attributed to unequal mass selection effectiveness among the SS-SG groups, ie. unequal shifts in gene frequency. For example, if the third cycle of selection increased seed size .5 gram per 100 seed in the large seeded populations but decreased seed size .1 gram per 100 seed in the small seeded populations, the net change for the cycle would be an increase of .4 gram. Unequal progress from mass selection was observed among the SS-SG populations due to genetic interrelationships of SS and SG with the other characters (Tables 19, 20, and 21). Unequal progress was not considered to be of sufficient magnitude to cause the total disparity between the mean of C3 and the overall mean of the other cycles.

Seed Size-Specific Gravity Comparisons

Mass selection was effective in augmenting gene frequency for SS during three cycles of selection (Figure 2 and Table 16). Response to selection was approximately linear in both crosses, with C2 slightly less effective than the other cycles. The effectiveness of selection for SS was attributed to the high heritability of the character (Table 18).

Selection for SG was more effective in AX144 than in AX141. In both crosses, selection was effective for C1 and C2 while C3 was only effective in the large seeded populations of AX144. Similarities among the curves for SG, protein, and oil indicated that SG would be useful as an

Figure 2. Comparison of SS-SG population means for three selection cycles in two soybean crosses

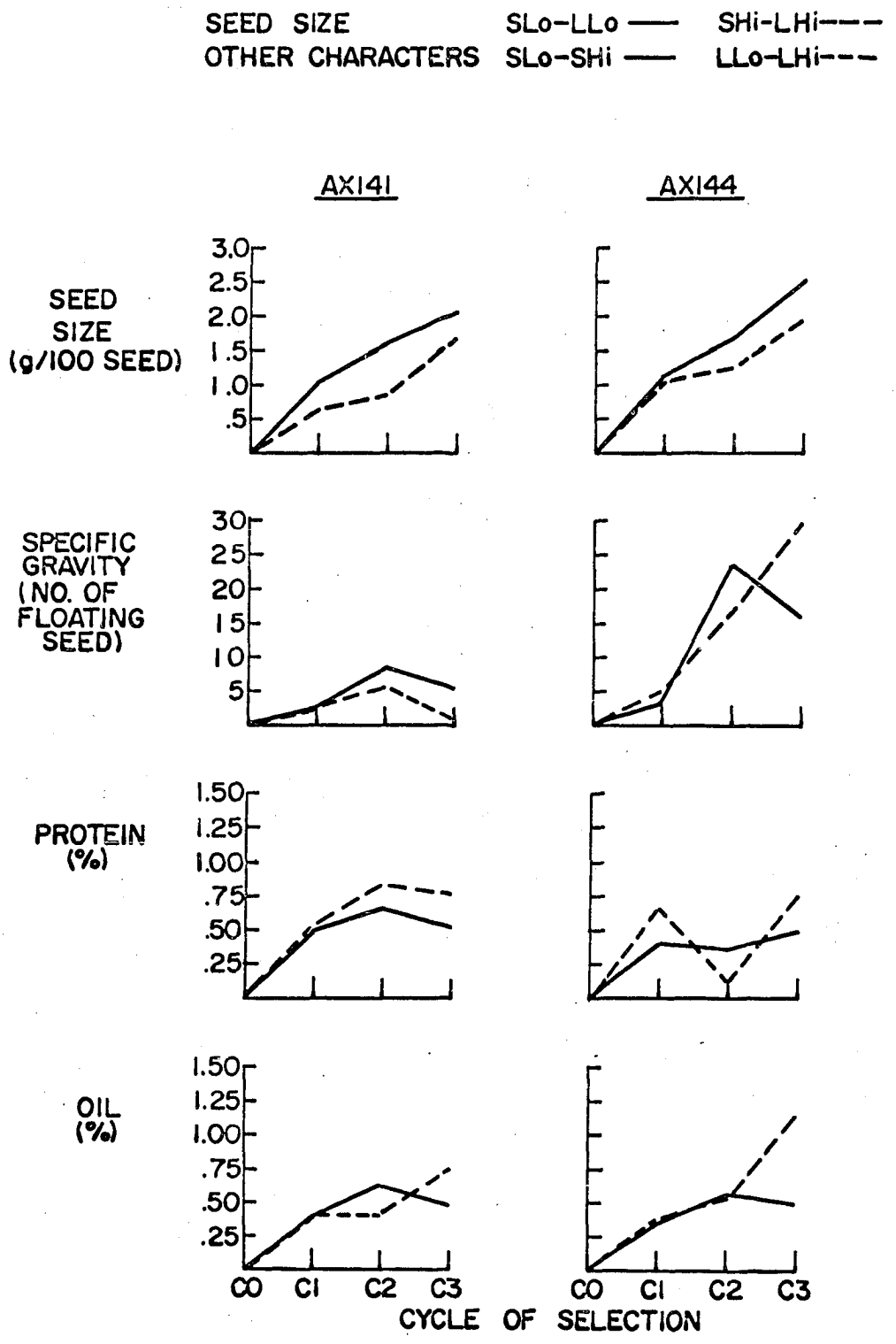

SEED SIZE SLo-LLo —— SHi-LHi---
OTHER CHARACTERS SLo-SHi —— LLo-LHi---
AX141
AX144
SEED SIZE (g/100 SEED)
3.0
2.5
2.0
1.5
1.0
.5
SPECIFIC GRAVITY (NO. OF FLOATING SEED)
30
25
20
15
10
5
PROTEIN (%)
1.50
1.25
1.00
.75
.50
.25
OIL (%)
1.50
1.25
1.00
.75
.50
.25
C0 C1 C2 C3
C0 C1 C2 C3
CYCLE OF SELECTION

Table 16. Mean squares for comparisons between SS-SG populations within cycles for SS, SG, protein, and oil

Characters and population	SLo vs. LLo		SHi vs. LHi	
	AX141	AX144	AX141	AX144
SS				
C1	32.21**	38.76**	12.10**	30.70**
C2	77.12**	83.83**	22.88**	45.14**
C3	128.96**	187.00**	84.34**	111.17**
	SLo vs. SHi		LLo vs. LHi	
	AX141	AX144	AX141	AX144
SG				
C1	195.08*	388.80*	205.41*	1116.30**
C2	2116.80**	17112.41**	907.50**	8333.33**
C3	891.08**	7664.01**	9.63	26940.03**
Protein				
C1	6.91**	5.08**	8.80**	13.60**
C2	13.07**	4.00*	20.92**	.51
C3	7.65**	7.45**	17.40**	17.71**
Oil				
C1	4.64**	3.60**	5.00**	4.33**
C2	12.03**	9.63**	5.04**	8.75**
C3	7.10**	7.25**	16.50**	39.79**

approximation for protein and oil content of soybean seed.

Effectiveness of selection on protein content of the seed was similar for both crosses if the C0 and C3 means were compared. Progress was observed in C1 and C2 of AX141 followed by a slight retrogression in C3. C1 was also effective in AX144, but C2 resulted in marked negative response followed by improvement in C3.

The effect of selection on oil content was different in the large and the small seeded populations. The large seeded populations of both

crosses showed marked progress in C1 and C3 but only slight improvement in C2 while the small seeded populations showed progress in C1 and C2 with a slight retrogression in C3.

The negative response from selection in certain populations, particularly during C3, may be due to (a) an error in SG truncation, (b) an error in classifying the lines of a given SS-SG population, (c) a seed source effect that may have suppressed actual differences among lines, and (d) failure to adequately sample the population. An error in SG separations, ie. selecting low in place of high and vice versa, was not confirmed by the curves for protein and oil (Figure 2). A negative response in protein was not accompanied by a similar response in oil, as would be anticipated if a truncation error had occurred.

Misclassification of lines between large and small seeded populations was not likely since continuous progress was observed for SS during all three selection cycles (Figure 2). Misclassification among SG groups was not probable since protein and oil did not show concurrent retrogression which would be expected with classification errors. The presence of a seed source effect, suggested earlier, may have suppressed the expression of genotypic differences among SS-SG groups. Lack of a negative response among all populations indicated that if a seed source effect was present it was not strong enough to suppress genotypic differences in some populations. The problem of inadequate sampling has been discussed with respect to block effects. Sampling must be listed as a possible reason for part of the apparent negative response, but it probably would not account for all of the observed retrogression.

Progress from selection was generally greater in the present study than that reported by Smith (1966). He stated that C1 was effective in altering gene frequency for protein and oil, but the slight increase realized between C1 and C2 would appear to have little practical utility relative to time and expense required to achieve this increase.

Genotypic Variance

Effective mass selection in homozygous populations should be associated with a decrease in genotypic variance. Genotypic variance estimates for a given SS-SG population were generally lower in C3 than in C0 (Table 17). Results for C1 and C2 were sporadic, nevertheless, there was a trend toward decreased genotypic variance with selection. The general increase in genotypic variance for cycles was consistent with the increasing deviation of the four SS-SG populations from their overall mean. Genotypic variances indicated that mass selection was effective in altering gene frequency for the desired characters.

The sporadic nature of the genotypic variances may reflect limited sampling of the populations. The use of 30 lines per population (10 per maturity group) may have been the minimum number required to obtain satisfactory estimates.

Heritability

Fluctuations in heritability for cycles and SS-SG populations tended to reflect changes in genotypic variance (Tables 17 and 18). This indicated that environmental variation was relatively consistent across the populations.

Table 17. Genotypic variance components of all characters for soybean lines in SS-SG populations from two crosses

Population	Yield	Maturity	Lodging	Height	SS	Protein	Oil	SG	EL
Lines in AX141	24081.46	5.87	.055	23.08	2.04	.87	.29	106.52	.026
C0	20062.45	5.20	.055	26.37	2.33	.67	.24	102.32	.023
C1	38268.30	2.81	.053	15.76	1.83	.47	.20	92.74	.025
SLo	49481.68	1.28	.105	8.50	1.35	.74	.33	59.32	.041
SHi	47868.49	1.13	.016	11.70	1.32	.19	.09	87.14	.025
LLo	20134.96	2.73	.079	18.58	1.18	.60	.17	136.58	.017
LHi	27989.98	1.51	.025	19.95	2.39	.14	.09	102.31	.029
C2	8325.48	4.96	.028	21.60	1.63	.48	.21	103.94	.027
SLo	.00	4.10	.056	27.80	.53	.52	.11	73.81	.041
SHi	26601.58	3.74	.006	26.41	1.32	.24	.08	119.08	.018
LLo	22852.01	9.06	.035	30.71	1.39	.34	.25	47.12	.042
LHi	.00	4.31	.042	8.85	1.20	.02	.06	91.36	.030
C3	19183.79	9.29	.073	26.38	2.43	.49	.27	119.23	.025
SLo	33756.81	8.18	.093	22.46	1.89	.76	.26	103.86	.030
SHi	.00	3.52	.102	7.09	.67	.38	.13	72.87	.028
LLo	5291.74	9.31	.040	60.67	1.86	.28	.09	90.64	.017
LHi	8446.21	12.40	.045	14.17	.76	.03	.00	95.72	.009
Lines in AX144	15048.68	3.68	.191	112.62	1.56	1.15	.34	222.08	.070
C0	5592.37	2.65	.122	140.00	.97	.69	.21	128.47	.068
C1	11070.01	2.23	.193	90.65	1.55	.98	.23	134.56	.071
SLo	.00	2.79	.284	52.79	1.11	.18	.03	119.40	.086
SHi	27910.16	1.69	.211	129.98	.70	.56	.01	60.48	.092
LLo	7290.39	1.24	.088	64.93	1.72	1.26	.19	117.77	.021
LHi	31581.55	3.94	.194	109.21	1.68	1.45	.48	107.26	.085

Table 17. (Continued)

Population	Yield	Maturity	Lodging	Height	SS	Protein	Oil	SG	EL
Lines in AX144 (continued)									
C2	21558.92	4.51	.210	107.64	1.27	.75	.40	317.59	.059
SLo	28881.79	2.74	.238	110.35	.38	.81	.49	249.61	.056
SHi	26860.59	6.04	.070	73.81	.49	.38	.18	156.30	.009
LLo	42137.77	3.36	.311	76.43	1.21	.62	.58	297.15	.090
LHi	.00	6.15	.154	139.95	1.00	.76	.20	155.27	.082
C3	18065.00	3.16	.228	102.85	2.24	.74	.39	260.04	.085
SLo	9960.93	1.35	.091	94.11	1.17	.45	.03	101.65	.079
SHi	28146.16	3.90	.152	74.16	.45	.48	.16	40.66	.023
LLo	1952.75	1.73	.260	39.68	1.59	.00	.21	119.94	.034
LHi	12848.52	2.67	.439	116.91	.54	.37	.21	39.27	.102
All lines in AX141-AX144	19565.07	4.78	.123	67.85	1.80	1.01	.31	164.30	.048

Table 18. Heritability of characters for soybean lines in SS-SG populations from two crosses

Population	Yield	Maturity	Lodging	Height	SS	Protein	Oil	SG	EL
Lines in AX141	.39	.75	.60	.66	.92	.76	.74	.83	.47
C0	.35	.72	.60	.69	.93	.70	.70	.83	.43
C1	.51	.59	.59	.57	.91	.62	.66	.81	.46
SLo	.57	.39	.74	.42	.88	.72	.76	.74	.58
SHi	.56	.36	.30	.50	.88	.40	.48	.80	.46
LLo	.35	.58	.68	.61	.87	.68	.62	.87	.36
LHi	.43	.43	.40	.63	.93	.32	.46	.83	.50
C2	.18	.71	.43	.65	.90	.63	.67	.83	.48
SLo	.00	.67	.60	.70	.75	.65	.52	.78	.58
SHi	.42	.65	.13	.69	.88	.46	.44	.85	.38
LLo	.38	.82	.48	.72	.89	.54	.71	.69	.59
LHi	.00	.68	.53	.43	.87	.06	.38	.81	.50
C3	.34	.82	.66	.69	.93	.64	.73	.85	.45
SLo	.48	.80	.71	.65	.91	.73	.72	.83	.50
SHi	.00	.64	.73	.37	.79	.58	.56	.78	.49
LLo	.12	.82	.52	.84	.91	.50	.46	.81	.37
LHi	.19	.86	.54	.54	.81	.10	.00	.82	.23
Lines in AX144	.28	.75	.75	.85	.94	.77	.72	.88	.60
C0	.13	.69	.66	.87	.91	.67	.62	.81	.59
C1	.22	.65	.76	.82	.94	.74	.65	.82	.61
SLo	.00	.70	.82	.72	.92	.35	.18	.80	.65
SHi	.42	.58	.77	.87	.88	.63	.09	.67	.67
LLo	.16	.50	.59	.76	.95	.79	.59	.80	.31
LHi	.45	.76	.76	.84	.95	.81	.79	.79	.65
C2	.36	.79	.77	.84	.93	.69	.76	.92	.56
SLo	.43	.69	.79	.85	.80	.71	.79	.90	.55
SHi	.41	.83	.53	.78	.84	.53	.58	.84	.16
LLo	.52	.73	.83	.79	.93	.65	.82	.91	.66
LHi	.00	.83	.71	.87	.91	.69	.60	.84	.64
C3	.32	.72	.79	.84	.96	.69	.75	.90	.65
SLo	.21	.53	.59	.82	.93	.57	.20	.78	.63
SHi	.42	.76	.71	.79	.83	.59	.55	.58	.33
LLo	.05	.59	.81	.66	.94	.00	.62	.80	.42
LHi	.25	.69	.88	.85	.85	.52	.62	.57	.69
All lines in AX141-AX144	.34	.75	.71	.81	.93	.77	.73	.87	.56

The high heritability of SS was consistent with the selection progress observed for each of the three cycles (Figure 2). The high heritability of SG was consistent with the general progress from selection in C1 and C2 but did not reflect the slight negative response in C3 for certain populations. Heritability values for protein and oil were similar in most of the populations.

Heritability estimates in this study were similar to the highest values reported by Johnson and Bernard (1962) and were approximately equal to those reported by Smith (1966).

Phenotypic and Genotypic Correlations

Phenotypic correlations of SS with other characters indicated a significant positive correlation with yield, protein, and SG and a significant negative correlation with the remaining attributes (Table 19). The positive correlation with protein and SG was considerably greater than the negative correlation with oil. Correlation coefficients were of similar magnitude between the two crosses except for early lodging which showed a positive correlation in AX141 and a negative correlation in AX144.

Genotypic correlations of SS with other characters were consistently larger than the respective phenotypic correlations (Table 19). This indicated the existence of a small environmental correlation opposite in sign to that of the genotypic correlation. The relationship between genotypic and phenotypic correlations can be represented by the following equation:

Phenotypic correlation = Genotypic correlation + Environmental correlation.

Table 19. Phenotypic and genotypic correlations of all characters with SS for soybean li two crosses

Population	Yield		Maturity		Lodging		Height		Protein		Oil	
	Pheno.	Geno.	Pheno.	Geno.	Pheno.	Geno.	Pheno.	Geno.	Pheno.	Geno.	Pheno.	G
Lines in AX141	.37**	.52	.00	-.07	-.07*	-.14	-.09**	-.17	.31**	.34	-.08**	-.
C0	.40**	.60	-.23**	-.35	-.16*	-.25	-.25**	-.36	.32**	.36	.01	.
C1	.37**	.46	.27**	.26	-.03	-.09	.09	.05	.28**	.32	-.02	-.
SLo	.42**	.51	.10	.00	-.01	-.06	-.11	-.30	.36**	.40	-.07	-.
SHi	.27*	.29	.52**	.73	-.34**	-.79	.09	.04	.51**	.76	-.01	-.
LLo	.11	.05	.09	.00	.21	.23	.37**	.43	.38**	.43	-.32*	-.
LHi	.50**	.71	.26*	.28	-.10	-.22	.01	-.04	-.03	-.14	.38**	.
C2	.30**	.56	-.03	-.12	-.08	-.21	-.14*	-.25	.30**	.34	.04	.
SLo	.39**	.00	-.50**	-.86	-.45**	-.76	-.45**	-.72	.25*	.27	.27*	.
SHi	.36**	.48	.30*	.29	.13	.20	-.05	-.13	.39**	.52	-.03	-.
LLo	.39**	.54	-.47**	-.62	-.13	-.28	-.08	-.15	.54**	.70	.10	.
LHi	.12	.00	.13	.06	-.05	-.15	-.27*	-.57	.23	.70	.03	.
C3	.34**	.51	.08	.04	-.07	-.13	-.01	-.06	.36**	.42	-.19**	-.
SLo	.38**	.49	.14	.10	-.23	-.32	-.09	-.18	.58**	.67	-.45**	-.
SHi	.11	.00	.18	.10	.19	.18	-.04	-.25	.32*	.38	-.17	-.
LLo	.42**	1.00	-.30*	-.40	-.25*	-.43	-.30*	-.38	.13	.13	.28*	.
LHi	-.10	-.53	.44**	.45	.07	.02	.34**	.39	.36**	.94	-.41**	.
Lines in AX144	.25**	.42	-.18**	-.26	-.33**	-.40	-.22**	-.27	.41**	.45	-.04	-.
C0	.34**	.89	-.24**	-.36	-.36**	-.48	-.23**	-.28	.22**	.24	-.02	-.
C1	.24**	.46	-.31**	-.44	-.34**	-.41	-.12	-.15	.37**	.41	.05	.
SLo	.39**	.00	-.50**	-.68	-.48**	-.56	.19	.20	.07	.05	.16	.
SHi	.12	.14	-.40**	-.65	-.07	-.10	-.32*	-.39	.40**	.49	-.09	-.
LLo	.31*	.71	-.06	-.14	-.37**	-.52	.30*	.34	.35**	.38	-.06	-.
LHi	.17	.22	-.38**	-.48	-.16	-.20	-.29*	-.34	.44**	.48	-.12	-.
C2	.04	.02	-.17**	-.23	-.39**	-.47	-.28**	-.33	.39**	.46	-.09	-.
SLo	.10	.09	.08	.03	-.14	-.20	-.05	-.10	.22	.24	-.40**	-.
SHi	.11	.11	-.29*	-.40	-.15	-.25	-.02	-.06	.13	.13	-.17	-.
LLo	-.05	-.11	-.09	-.15	-.72**	-.83	-.04	-.07	.58**	.71	-.08	-.
LHi	.27*	.00	-.04	-.09	-.19	-.24	-.43**	-.50	.31*	.36	-.04	-.
C3	.30**	.50	-.11	-.17	-.36**	-.42	-.30**	-.35	.48**	.56	.11	.
SLo	.33**	.67	-.28*	-.48	-.08	-.12	-.51**	-.61	.50**	.64	.21	.
SHi	.04	-.01	-.11	-.20	.04	.03	.14	.13	.43**	.54	-.20	-.
LLo	.26*	1.00	.07	.04	-.68**	-.79	.22	.24	.00	.00	-.44**	.
LHi	.07	.05	-.18	-.31	-.36**	-.42	-.44**	-.54	.13	.12	-.18	-.
All lines in AX141-AX144	.32**	.48	-.08**	-.15	-.21**	-.28	-.16**	-.21	.36**	.39	-.06*	-.

ions of all characters with SS for soybean lines in SS-SG populations from

odging		Height		Protein		Oil		SG		EL	
no.	Geno.	Pheno.	Geno.	Pheno.	Geno.	Pheno.	Geno.	Pheno.	Geno.	Pheno.	Geno.
*	-.14	-.09**	-.17	.31**	.34	-.08**	-.09	.27**	-.30	.06*	.02
*	-.25	-.25**	-.36	.32**	.36	.01	.02	.21**	.24	.00	-.07
	-.09	.09	.05	.28**	.32	-.02	-.02	.14*	.16	.11	.10
	-.06	-.11	-.30	.36**	.40	-.07	-.07	-.09	-.11	.18	.19
**	-.79	.09	.04	.51**	.76	-.01	-.01	-.14	-.17	-.26*	-.50
	.23	.37**	.43	.38**	.43	-.32*	-.42	.43**	.50	.20	.24
	-.22	.01	-.04	-.03	-.14	.38**	.59	.04	.05	.19	.22
	-.21	-.14*	-.25	.30**	.34	.04	.06	.30**	.35	-.03	-.13
**	-.76	-.45**	-.72	.25*	.27	.27*	.46	.51**	.67	-.42**	-.74
	.20	-.05	-.13	.39**	.52	-.03	-.04	.19	.23	-.07	-.22
	-.28	-.08	-.15	.54**	.70	.10	.14	.20	.26	-.11	-.23
	-.15	-.27*	-.57	.23	.70	.03	.06	.32*	.38	.02	-.06
	-.13	-.01	-.06	.36**	.42	-.19**	-.22	.43**	.49	.06	.03
	-.32	-.09	-.18	.58**	.67	-.45**	-.55	.24	.27	-.08	-.19
	.18	-.04	-.25	.32*	.38	-.17	-.24	-.10	-.12	.24	.27
*	-.43	-.30*	-.38	.13	.13	.28*	.44	.69**	.80	-.16	-.37
	.02	.34**	.39	.36**	.94	-.41**	.00	.49**	.61	.35**	.61
**	-.40	-.22**	-.27	.41**	.45	-.04	-.04	.08**	.10	-.29**	-.40
**	-.48	-.23**	-.28	.22**	.24	-.02	-.01	-.10	-.10	-.28**	-.39
**	-.41	-.12	-.15	.37**	.41	.05	.08	.26**	.30	-.28**	-.39
**	-.56	.19	.20	.07	.05	.16	.44	.19	.23	-.31*	-.41
	-.10	-.32*	-.39	.40**	.49	-.09	-.24	.23	.32	.03	.03
**	-.52	.30*	.34	.35**	.38	-.06	-.06	.11	.13	-.15	-.29
	-.20	-.29*	-.34	.44**	.48	-.12	-.13	.39**	.47	-.29*	-.38
**	-.47	-.28**	-.33	.39**	.46	-.09	-.10	.01	.02	-.29**	-.41
	-.20	-.05	-.10	.22	.24	-.40**	-.48	-.26*	-.30	-.11	-.20
	-.25	-.02	-.06	.13	.13	-.17	-.22	.29*	.35	.10	.21
**	-.83	-.04	-.07	.58**	.71	-.08	-.08	.15	.17	-.67**	-.87
	-.24	-.43**	-.50	.31*	.36	-.04	-.04	-.32*	-.35	-.09	-.14
**	-.42	-.30**	-.35	.48**	.56	.11	.14	.28**	.31	-.41**	-.53
	-.12	-.51**	-.61	.50**	.64	.21	.54	.10	.12	-.03	-.05
	.03	.14	.13	.43**	.54	-.20	-.27	.06	.12	.25*	.44
**	-.79	.22	.24	.00	.00	.44**	.59	.17	.21	-.46**	-.75
**	-.42	-.44**	-.54	.13	.12	-.18	-.22	-.16	-.20	-.37**	-.50
**	-.28	-.16**	-.21	.36**	.39	-.06*	-.07	.16**	.18	-.13**	-.22

Genotypic correlations represent the degree of genetic association between two characters while environmental correlations indicate the extent to which two characters are mutually influenced by environment.

SG had a significant positive phenotypic correlation with lodging, height, SS, oil, and early lodging and a significant negative correlation with maturity and protein (Table 20). The SG correlations were smaller than the corresponding correlations with SS, except for maturity and oil percent. Significant phenotypic correlations were the same sign in both crosses. The positive correlation of SG with oil indicated that lines with a higher than average oil content (low SG) had a high number of floating seed while the negative correlation with protein indicated that lines with a higher than average protein (high SG) had a low number of floating seed.

Genotypic correlations of SG with other characters were slightly greater than, or approximately equal to, the corresponding phenotypic correlations (Table 20). Genotypic correlations which were smaller than the phenotypic correlations suggested the presence of an environmental correlation which acted in the same direction as the genetic relationships.

The observed relationship between genotypic and phenotypic correlations was similar to that reported by Smith (1966). He reported that with few exceptions, genotypic correlations for SD with protein, oil, and all agronomic attributes were greater in magnitude than the phenotypic correlations.

Genetic Advance

Based on the genotypic interrelationships among SS, SG, protein, and

Table 20. Phenotypic and genotypic correlations of all characters with SG for soybean lines two crosses

Population	Yield		Maturity		Lodging		Height		SS		Pro
	Pheno.	Geno.	Pheno.	Geno.	Pheno.	Geno.	Pheno.	Geno.	Pheno.	Geno.	Pheno.
Lines in AX141	-.01	.00	-.14**	-.14	.15**	.24	-.03	-.01	.27**	.30	-.06*
C0	.03	.08	-.03	.00	.34**	.50	.11	.17	.21**	.24	-.06
C1	-.22**	-.33	-.07	-.05	.18**	.29	-.02	.01	.14*	.16	-.08
SLo	-.16	-.22	-.03	.05	.20	.29	-.05	-.02	-.09	-.11	-.32*
SHi	-.46**	-.66	-.26*	-.38	.17	.39	-.18	-.24	-.14	-.17	-.13
LLo	-.16	-.27	.04	.11	.37**	.50	-.03	-.02	.43**	.50	.17
LHi	-.28*	-.45	-.56**	-.86	.03	.08	.05	.10	.04	.05	-.13
C2	.10	.28	-.28**	-.32	-.02	-.01	-.26**	-.33	.30**	.35	-.28**
SLo	.29*	.00	-.57**	-.73	-.24	-.33	-.50**	-.64	.51**	.67	-.30*
SHi	-.09	-.13	-.47**	-.59	-.28*	-.78	-.34**	-.42	.19	.23	-.08
LLo	.12	.28	-.31*	-.36	-.03	.00	-.46**	-.61	.20	.26	-.38**
LHi	.38**	.00	-.21	-.23	.29*	.47	.11	.24	.32*	.38	.04
C3	.07	.15	-.19**	-.20	.13*	.19	.02	.05	.43**	.49	.10
SLo	.10	.19	-.29*	-.33	.25*	.34	-.08	-.08	.24	.27	-.16
SHi	.28*	.00	.25*	.42	.36**	.50	.31*	.65	-.10	-.12	-.03
LLo	.29*	.96	-.21	-.22	-.01	.02	-.16	-.17	.69**	.80	.25*
LHi	-.20	-.46	-.01	.02	.47**	.73	.20	.34	.49**	.61	.37**
Lines in AX144	.06*	.05	-.07*	-.08	.03	.02	.18**	.21	.08**	.10	-.28**
C0	-.03	-.24	-.02	-.02	.21**	.26	.08	.09	-.10	-.10	-.40**
C1	.10	.14	-.07	-.08	.21**	.25	.29**	.34	.26**	.30	-.15*
SLo	-.05	.00	.15	.21	.31*	.37	.32*	.42	.19	-.23	-.13
SHi	.21	.31	-.25*	-.37	.15	.18	.17	.21	.23	.32	.05
LLo	-.13	-.50	-.04	-.03	.14	.18	.34**	.43	.11	.13	-.04
LHi	.18	.23	.02	.04	.47**	.59	.35**	.43	.39**	.47	-.37**
C2	.06	.05	.02	.03	-.04	-.06	.22**	.25	.01	.02	-.35**
SLo	.36**	.54	.02	.04	-.44**	-.53	.35**	.40	-.26*	-.30	-.51**
SHi	.05	.03	-.15	-.17	.15	.20	.40**	.49	.29*	.35	-.28*
LLo	-.01	-.05	.01	.02	-.27*	-.32	.24	.28	.15	.17	-.40**
LHi	-.09	.00	-.18	-.21	.22	.26	.16	.19	-.32*	-.35	-.22
C3	.10	.13	-.04	-.04	-.03	-.05	.21**	.24	.28**	.31	-.13*
SLo	.03	-.04	.10	.18	.19	.25	.13	.16	.10	.12	.12
SHi	-.17	-.46	-.29*	-.42	.21	.28	-.08	-.12	.06	.12	.09
LLo	-.12	-.86	-.49**	-.68	-.45**	-.58	.45**	.61	.17	.21	-.23
LHi	-.42**	1.00	-.36**	-.54	-.05	-.09	-.07	-.11	-.16	-.20	.02
All lines in AX141-AX144	.03	.03	-.10**	-.10	.07*	.08	.12**	.15	.16**	.18	-.19**

ns of all characters with SG for soybean lines in SS-SG populations from

odging		Height		SS		Protein		Oil		EL	
no.	Geno.	Pheno.	Geno.	Pheno.	Geno.	Pheno.	Geno.	Pheno.	Geno.	Pheno.	Geno.
**	.24	-.03	-.01	.27**	.30	-.06*	-.06	.14**	.15	.11**	.19
**	.50	.11	.17	.21**	.24	-.06	-.06	.11	.11	.35**	.60
**	.29	-.02	.01	.14*	.16	-.08	-.10	.05	.03	.19**	.33
	.29	-.05	-.02	-.09	-.11	-.32*	-.42	-.01	-.04	.19	.31
	.39	-.18	-.24	-.14	-.17	-.13	-.19	.06	.04	.25*	.43
**	.50	-.03	-.02	.43**	.50	.17	.24	-.04	-.08	.34**	.62
	.08	.05	.10	.04	.05	-.13	-.22	.02	-.02	.01	.04
	-.01	-.26**	-.33	.30**	.35	-.28**	-.37	.40**	.50	-.17**	-.25
	-.33	-.50**	-.64	.51**	.67	-.30*	-.41	.43**	.63	-.38**	-.56
*	-.78	-.34**	-.42	.19	.23	-.08	-.10	.32*	.48	-.59**	-1.00
	.00	-.46**	-.61	.20	.26	-.38**	-.58	.45**	.60	-.07	-.09
*	.47	.11	.24	.32*	.38	.04	.28	.16	.23	.33**	.54
*	.19	.02	.05	.43**	.49	.10	.15	.04	.02	.10	.17
*	.34	-.08	-.08	.24	.27	-.16	-.19	.15	.17	.03	.06
**	.50	.31*	.65	-.10	-.12	-.03	-.02	.00	-.05	.21	.36
	.02	-.16	-.17	.69**	.80	.25*	.43	.20	.28	-.06	-.09
**	.73	.20	.34	.49**	.61	.37**	1.00	-.30*	.00	.49**	1.00
	.02	.18**	.21	.08**	.10	-.28**	-.29	.53**	.60	.03	.04
**	.26	.08	.09	-.10	-.10	-.40**	-.46	.44**	.53	.01	.02
**	.25	.29**	.34	.26**	.30	-.15*	-.12	.43**	.51	.20**	.28
*	.37	.32*	.42	.19	-.23	-.13	-.09	.08	-.06	.50**	.69
	.18	.17	.21	.23	.32	.05	.21	.14	.00	.39**	.57
	.18	.34**	.43	.11	.13	-.04	.01	.55**	.69	-.02	-.04
**	.59	.35**	.43	.39**	.47	-.37**	-.40	.37**	.41	.22	.30
	-.06	.22**	.25	.01	.02	-.35**	-.39	.55**	.62	.08	.11
**	-.53	.35**	.40	-.26*	-.30	-.51**	-.59	.73**	.82	-.16	-.24
	.20	.40**	.49	.29*	.35	-.28*	-.32	.07	.00	.34**	.92
*	-.32	.24	.28	.15	.17	-.40**	-.47	.59**	.64	-.16	-.20
	.26	.16	.19	-.32*	-.35	-.22	-.22	.10	.05	.52**	.71
	-.05	.21**	.24	.28**	.31	-.13*	-.11	.61**	.70	-.05	-.07
	.25	.13	.16	.10	.12	.12	.29	.01	-.24	.48**	.68
	.28	-.08	-.12	.06	.12	.09	.32	.16	.09	.17	.39
**	-.58	.45**	.61	.17	.21	-.23	.00	.56**	.70	-.16	-.28
	-.09	-.07	-.11	-.16	-.20	.02	.23	.19	.14	.09	.15
*	.08	.12**	.15	.16**	.18	-.19**	-.20	.37**	.42	.06*	.09

oil (Table 19 and 20) it was possible to predict in which SS-SG population maximum progress should be obtained for a given character. For example, low SG should favor high oil, low protein and large seed; whereas, high SG should favor low oil, high protein, and small seed. Populations with maximum predicted advance were compared with those populations in which maximum progress was observed after three selection cycles (Table 21). Predicted and actual advance were in complete agreement for all characters, except high oil in AX144. The results demonstrated that SS and SG could enhance or retard one another as mass selection techniques, depending on the direction of selection and the character being improved. Selection for large seed would be enhanced by concurrent selection for low SG and retarded by selection for high SG. Simultaneous selection for large seed and high SG in a given population would result in improvement of both characters, but at a lower rate than if each were selected independently in two different populations. On the other hand, large seeds and low SG could be improved more rapidly by simultaneous selection in one population than by independent selection in two populations.

Comparisons of predicted and actual advance for each selection cycle are presented in Table 22. Due to the possible presence of a seed source effect, genetic advance was calculated as the difference between SS-SG populations within a cycle. Predicted genetic advance for a character was the summation of advance based on SS and SG independently.

Predicted and actual advance were in much closer agreement for SS than for SG. Failure to estimate and remove genotype by environment interaction from the genotypic variance estimates may be the principal cause

Table 21. Comparison of populations with maximum predicted advance for a given character with populations in which actual advance was greatest after three selection cycles

Character desired	Predicted population	Actual population	
		AX141	AX144
Large seed	LLo	LLo	LLo
Small seed	SHi	SLo	SLo
High specific gravity	SHi	SHi	SHi
Low specific gravity	LLo	LLo	LLo
High protein	LHi	LHi	LHi
Low protein	SLo	SLo	SLo
High oil	SLo	SLo	LLo
Low oil	LHi	LHi	LHi

Table 22. Predicted and actual genetic advance for SS, SG, protein, and oil from selection for SS and SG in two crosses

	SLo vs. LLo		SHi vs. LHi		SLo-SHi vs. LLo-LHi	
	Predicted	Actual	Predicted	Actual	Predicted	Actual
SS						
AX141						
C1	4.56	1.02	4.56	.63	4.56	.82
C2	3.17	.58	3.13	.25	3.15	.42
C3	3.07	.47	3.44	.80	3.26	.64
AX144						
C1	2.16	1.14	2.16	1.01	2.16	1.08
C2	3.38	.53	3.55	.22	3.46	.38
C3	2.05	.83	1.90	.70	1.98	.76
	SLo vs. SHi		LLo vs. LHi		SLo-LLo vs. SHi-LHi	
	Predicted	Actual	Predicted	Actual	Predicted	Actual
SG						
AX141						
C1	29.2	2.5	29.2	2.6	29.2	2.6
C2	16.1	5.9	33.0	2.8	24.6	4.4
C3	31.5	-3.0	24.5	-4.9	28.0	-4.0
AX144						
C1	23.2	3.7	23.2	6.1	23.2	4.9
C2	26.5	20.2	31.6	10.6	29.1	15.4
C3	33.2	-7.9	33.6	13.3	33.4	2.7
Protein						
AX141						
C1	.82	.48	.82	.54	.82	.51
C2	.50	.18	-.58	.30	-.04	.24
C3	.30	-.15	-.06	-.08	.12	-.12
AX144						
C1	1.36	.41	1.36	.67	1.36	.54
C2	-.54	-.05	.71	-.54	.08	-.30
C3	1.02	.14	.36	.64	.69	.39
Oil						
AX141						
C1	.14	.39	.14	.40	.14	.40
C2	.03	.25	-.46	.01	-.22	.13
C3	.21	-.16	.44	.33	.32	.08

Table 22. (Continued)

	SLo vs. SHi		LLo vs. LHi		SLo-LLo vs. SHi-EHi	
	Predicted	Actual	Predicted	Actual	Predicted	Actual
Oil (Continued)						
AX144						
C1	.56	.35	.56	.38	.56	.36
C2	-.13	.21	.74	.16	.30	.18
C3	.96	-.07	.57	.61	.76	.27

of the deviation from predicted. Byth (1965) reported that genetic advance estimates were most reliable when an estimate of the genotype by environment interaction was available. Estimates of the interaction could not be obtained in this study since only a single environment was used.

Predicted advance was in closer agreement with actual advance for oil than for protein (Table 22). Both characters had much smaller deviations from predicted than SS and SG. The results indicated that predicted genetic advance for an unselected character may be more accurate than predicted advance of a selected character when there is no estimate of genotype by environment interaction.

Smith (1966) reported predicted and actual genetic advance for SD and correlated response for protein and oil. Estimates of the genotype by environment interaction were obtained by growing the experiment in three

environments. He found that actual advance across two environments were greater than predicted in the high SG population and less than predicted in the low SG populations. In general, the predicted and actual advance reported by Smith (1966) were in closer agreement than the values obtained in the present study. This may be due, in part, to the removal of genotype by environment interactions from genotypic variance and covariance estimates.

Variety Development

The number of lines in a cross-maturity group that exceeded the check mean for yield, protein, and oil is presented in Table 23. Hark (E), Amsoy (M), and Ford (Lt) were considered the best commercial varieties available to farmers.

Line means were compared to a check by the least-significant difference (LSD). The following equation was used to compute LSD at the 5% and 1% probability level:

$$LSD = t \sqrt{s^2(\frac{1}{32} + \frac{1}{2})}$$

The symbol t refers to Student's t for the chosen significance level with error degrees of freedom, s^2 is the error variance for the cross from which the line originated, and 32 and 2 are the replication numbers for a check and a line, respectively.

Five lines from AX144, representing .53% of the lines tested, were higher in yield than their respective check at the 5% probability level. Failure to obtain high yielding lines in AX141 was in agreement with the

Table 23. Number of experimental lines in a cross-maturity group that exceeded the check mean for yield, protein, and oil; checks were: Hark (E), Amsoy (M), and Ford (Lt)

	Yield		Protein		Oil	
	*	**	*	**	*	**
AX141 E	0	0	92	74	1	0
AX144 E	0	0	19	10	78	60
AX141 M	0	0	160	155	0	0
AX144 M	1	0	87	72	2	0
AX141 Lt	0	0	122	108	0	0
AX144 Lt	4	0	83	63	19	10

yield test results obtained by Caldwell (1963) using F_2-derived lines from the same cross.

A high proportion of lines from AX141 and AX144 exceeded the check in protein indicating that considerable improvement could be made for protein. The frequency of high oil lines was substantially smaller than for protein.

The relative value of AX141 and AX144 for the development of improved varieties would depend on the character desired. Selection of lines from AX141 would be suggested if the breeding objective was securing a high protein line. AX144 would be more useful for development of lines with high yield and high oil content.

SUMMARY AND CONCLUSIONS

Three cycles of mass selection for SS and SG were evaluated for their effect on protein and oil composition of two heterogeneous soybean populations. Large and small seed were selected with a set of screens after which each fraction was sub-divided for high and low SG using a series of step-wise-increasing glycerol-water solutions.

Nine characters were measured on 960 lines in two replications at Ames, Iowa, in 1966. Analyses of variance and covariance were obtained for each character in each SS-SG group, cycle, and cross.

Significant differences were observed between crosses for SS, protein, and oil. Differences between crosses were desired in order to observe the effects of mass selection in diverse genetic backgrounds. Maturity groups differed significantly for yield, maturity, height, SS, and SG. Decreased productiveness of late maturing lines was attributed to droughty conditions which began in late June and continued into September.

The mean of lines in C3 were significantly different than the combined mean of all other cycles for all characters except SG in AX141. The difference may have been due to a seed source effect since lines of C3 were increased in Chile, South America, in the winter of 1965-1966 and lines of the other cycles were increased at Ames in 1965. A seed source effect was defined as the dependence of a genotype's agronomic and chemical performance on the source of seed used for propagation. Implications of such an effect were discussed.

Selection for SS and SG was effective in altering the mean SS of the populations. Response to selection was approximately linear in both

crosses, with C2 slightly less effective than the other cycles. Selection for SG was more effective in AX144 than in AX141. In both crosses, selection was more effective in C1 and C2 than in C3.

Effective selection for protein content was observed in C1 of both crosses, but the effectiveness of the subsequent cycles differed between crosses. The effect of selection for oil content was different in the large and small seeded populations of both crosses. Large seeded populations showed marked progress in C1 and C3 but only slight improvement in C2. Small seeded populations showed progress in C1 and C2 and a slight negative response in C3.

Estimates of genotypic variance were obtained for all characters in each cross-maturity group. Genotypic variance within a SS-SG population tended to decrease with each cycle of selection.

A high heritability (.93) was observed for SS which was consistent with the selection progress obtained in each selection cycle. Average heritability estimates of .87 for SG, .77 for protein, and .73 for oil were observed.

Genotypes correlations of SS and SG with the other characters were generally greater than corresponding phenotypic correlations. SS was positively correlated with SG indicating that large seeds were associated with low SG and small seeds with high SG. SS was positively correlated with protein and negatively correlated with oil. SG was positively correlated with oil and negatively correlated with protein. Correlation values were similar in both crosses.

Predicted and actual genetic advance were evaluated for SS, SG,

protein, and oil. The results indicated that SS and SG could enhance or retard one another in mass selection depending on the direction of selection and the character being improved. Maximum advance for high protein and low oil was obtained by selection for large seed and high SG while selection for small seed and low SG resulted in maximum advance for high oil and low protein.

Mean performance of lines for yield, protein, and oil was compared to a check variety of similar maturity using the least-significant difference. Five of the 960 lines tested were higher in yield than the check at the 5% probability level. The high frequency of superior protein lines in AX141 and AX144 indicated that considerable progress could be made for the character. High oil lines were observed, but in a much lower frequency than high protein lines.

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