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ASSOCIATION AND HERITABILITY STUDIES OF OIL, PROTEIN AND AGRONOMIC CHARACTERS IN TWO SOYBEAN HYBRIDS

A Dissertation

Presented to

The Graduate Council of

The University of Tennessee

In Partial Fulfillment

of the Requirements for the Degree

Doctor of Philosophy

---

by

Raravi Parameswarappa

December 1971

DEDICATED TO THE MEMORY OF

MY PARENTS

THE LATE MR. MURUGAPPA AND MRS. PUTTAMMA RARAVI

1002632

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ABSTRACT

The study involved two soybean (Glycine max L. Merril) intervarietal hybrids--D54-2437 x D65-3054 and Hill x S-100. D54-2437 and S-100 are early flowering, indeterminate in growth habit and have gray pubescence color, while D65-3054 and Hill flower later, are determinate in growth habit and have tawny pubescence. The F_2 generation of the cross D54-2437 x D65-3054 was studied both in 1969 and 1970, while the cross Hill x S-100 was grown only in 1970. The parents and the F_1 hybrids were also included with the F_2 populations in 1970. The F_3 progenies of the cross D54-2437 x D65-3054 were studied in replicated trials at Knoxville and Jackson, Tennessee, in 1970. Correlation and heritability estimates were obtained from the data on each cross and each generation.

Correlations indicated significant positive associations of yield, genotypically and phenotypically, with date of flowering, date of maturity, length of fruiting period, plant height and, to some extent, seed size. Oil content was found to be correlated positively with height and seed size. Protein content was negatively correlated with oil content.

Broad sense heritability estimates were, in general, high in the F_2 and F_3 generations. Narrow sense estimates ranged from zero (for oil content) to 87 percent (for time of flowering) on a progeny basis. Regression of F_3 progenies on F_2 plants gave smaller estimates than the above broad sense estimates obtained in the F_2 and F_3 generations separately.

Mite infestation occurred in 1970 and indicated that the reaction of plants to mite incidence in the cross Hill x S-100 was monogenically controlled while in the cross D54-2437 x D65-3054 susceptibility was due to the complementary epistatic action of 2 pairs of genes, each present in a different parent. The gene symbol (Mtmt) has been proposed for resistance and susceptibility in the two crosses.

The number of genes differentiating the parents in each cross for each character studied varied from 3 to 5 pairs when estimated by Mendelian ratios. No satisfactory estimates were obtained by using the Castle-Wright and Burton formulae.

Predicted genetic advances for yield in different combinations of characters used in selection indices indicated that an index consisting of yield and maturity was more efficient than when selection was based on yield alone. The addition of seed weight and lodging did not improve the efficiency significantly.

Greenhouse tests on hypocotyl color indicated that a single gene controls both hypocotyl and pubescence color in the cross Hill x S-100. Studies pertaining to the mosaic virus disease, which causes leaf and seed-coat mottling, indicated the possibility of isolating genetically resistant types in the cross D54-2437 x D65-3054.

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CHAPTER I

INTRODUCTION

The ultimate aim in soybean (Glycine max L. Merril) improvement is to evolve high yielding types which have a desired level of oil and protein content. Yield is a complex character and is very much influenced by other genetic characters and environmental factors. Some quantitative genetic characters are very much influenced by environment, making the inheritance of seed yield highly complex. Results of previous studies on characters influencing yield have not been consistent. Varieties vary in their ability to react to diseases and pests. This necessitates that a breeder understand the inheritance of these characters and their influence on yield.

However, highly heritable characters, associated with yield and influenced to a lesser degree by environment, serve as indicators of yield in a selection program.

Correlation coefficients provide a measure of association of characters influencing yield. The measurements are more realistic when computed in terms of genotypic values.

The response of a character to selection is determined by its heritability which in practice is computed as a ratio of genetic variation to the pyenotypic variation. The additive component of the genetic variation is most important in obtaining true heritability values.

An indication of the relative importance of a character or combination of characters can be obtained from variance and covariance analyses from which one can obtain the necessary information for the construction of selection indices which combine two or more traits appropriately weighted in a selection formula which can be calculated from phenotypic information on plant materials for selection.

A knowledge of the nature of resistance to diseases and insect pests helps the breeder to develop resistant strains.

Estimates of gene numbers will help the breeder in determining the type of breeding procedure to follow.

The objectives of the present study were (1) to determine the association of different plant characters and yield, (2) to determine the association of characters in segregating populations between generations, (3) to estimate the heritability of yield and other characters, (4) to construct selection indices based on yield and some of the associated characters, (5) to estimate gene numbers that control each quantitative character and (6) to investigate the possibility of obtaining seed-coat mottling resistance in varieties.

A heavy infestation of spider mites (Tetranychus spp.) in F_2 segregating populations provided an opportunity to study the nature of inheritance of resistance to this pest.

CHAPTER II

REVIEW OF LITERATURE

Many of the genetic studies on soybeans reported in the literature pertain mainly to the improvement of yield, oil content and protein content, their relationships to one another, and with other characters such as plant height, flowering, maturity and lodging.

I. STUDIES ON HETEROSIS

Reports on heterosis in the F_1 generation for different characters studied have not been consistent.

Wentz and Stewart (1924) recognized vigor in some F_1 soybean hybrids for yield and plant height. Veatch (1930) and Woodworth (1933) found evidences of vigor for characters such as seed yield, plant height, total stem and branch length, number of pods and number of seeds. Weiss et al. (1947) conducted replicated trials under both greenhouse and field conditions and measured vigor in the F_1 crosses for seed yield. In the field the F_1 yields exceeded those of the high yielding parent in each cross, and in the greenhouse all but one of the 17 crosses studied exceeded the high yielding parent. The F_1 plants were intermediate between their respective parents for date of maturity, plant height, and lodging resistance.

In a study by Leffel and Weiss (1958) of the 45 possible F_1 hybrids from diallel crosses among ten varieties of soybeans, yield

and height were found to exhibit a considerable degree of heterosis. With respect to flowering, maturity, flowering to maturity, percent oil, percent protein, iodine number and seed size, the F_1 plants were near the midparental values. Brim and Cockerham (1961) evaluated the F_1 plants of two crosses in two locations over two years and found them significantly higher than the mean of the parents for maturity, unthreshed weight, seed weight and yield. One cross had higher average plant height. Yield, height and unthreshed weight in one population, and only yield in the other were significantly greater than their respective higher parent. It is interesting to note that the deviation of the F_1 performance from the mean of the parents was maintained through the F_5 generation of one of the crosses for maturity and height, and through the F_4 generation of the other for maturity. Caviness and Prongsirivathana (1968) observed vigor for height and number of nodes in the F_1 generation. Average length of the internode was intermediate between the parents.

Weber (1950), in a study of the interspecific hybrids between Glycine max and G. ussuriensis, observed distinct hybrid vigor in the F_1 for plant height. As regards seed size, maturity, percent oil and percent protein, the F_1 plants were lower than G. max, the high parent, and for iodine number the F_1 plants were lower than G. ussuriensis. Williams (1948), in a study of 15 different crosses involving the above species, observed the F_1 plants to be intermediate between their parents for maturity, seed size and oil content.

Weber et al. (1970) studied the heterotic performance of eight attributes measured in a number of spaced F_1 hybrids and their parents over many years. The F_1 plants exhibited an average of 13.4 percent heterosis for seed yield over their respective high parent in 85 crosses. The whole-plant dry weight was also larger in many crosses. Although other characters, such as seed size, maturity, plant height, protein and oil content exhibited heterosis, the values were inconsistent and, in some cases, nonsignificant.

II. CORRELATION STUDIES

Weiss (1949), and Johnson and Bernard (1962) summarized previous studies pertaining to the association of characters in segregating materials. Early studies on correlation did not differentiate the association between any two attributes as to genotypic association and phenotypic association. Until 1950 the correlations estimated were only phenotypic. An attempt to understand the masking effects of environmental factors on the heriditary expression was the basis for differentiating the associations as phenotypic and genotypic. These correlations have been determined for a number of characters both in intervarietal and interspecific crosses. In general, genotypic correlations have been observed to be higher than phenotypic correlations.

Stewart (1925), studying spaced F_2 soybean plants, found height of the plant significantly more associated with yield in determinate types than in indeterminate types.

Veatch (1930) postulated that a great number of nodes would increase the number of pod bearing positions, thereby increasing the potentiality for yield.

Woodworth (1933), in a study using 26 soybean varieties, indicated a significant negative association between percentage of aborted seeds and high unit seed weight and yield.

Weatherspoon and Wentz (1934) observed positive correlations of plant height, nodes per plant, pods per plant and pods per node with yield. Partial regression coefficients indicated that pods per plant, height and seed size were more important than other characters in yield improvement. Plant height and number of pods per plant were found to be negatively correlated with seed size.

In two experiments studied in successive years by Ma (1946), there was inconsistency of associations among characters although the experiments had ten varieties in common. In one of the experiments, yield was associated with only the percentage of developed pods and number of seeds per pod, whereas, in the other experiment, yield was associated only with seed size.

In a study of F_2 plants of 11 crosses, Yoshino (1955) found inconsistency in the association of the number of pods, plant height and flowering time with yield.

Kalton (1948), in a study of F_2 through F_4 populations of 25 soybean crosses, found seed yield measurements made on spaced F_2 plants to be of little value in predicting the yield potentialities of their F_3 and F_4 progenies. Although lateness of maturity and plant height

were positively associated with yield, the degree of relationship was not consistent. Association of lodging resistance with yield in the F_3 and F_4 generations of the pedigree study was not significant.

Bartley and Weber (1952), in a study of all cross combinations among three varieties, noted the association of a character in one generation with the same character in the succeeding generation. Characters studied were yield, maturity, height and lodging. Height and maturity showed higher correlations between generations, while those for yield and lodging were small.

Weber and Moorthy (1952), in a study of three F_2 populations, found that genotypic associations among characters were higher than phenotypic associations. Positive associations were found between yield and height, and between yield and lateness of maturity. Johnson et al. (1955b) studied 24 characters in two populations in the F_4 generation and found positive genotypic correlations of yield with length of fruiting period, lateness, seed size, resistance to shattering and lodging. Generally, a good agreement was observed between genotypic and phenotypic correlations. In a study of the F_3 and F_4 generations of three soybean crosses, Anand and Torrie (1963) obtained inconsistent associations among characters. Yield was more highly associated phenotypically with pods per plant and seeds per pod than with seed weight. Extent of lodging, tallness and lateness of maturity were inconsistent in their associations, both phenotypically and genotypically, with yield. In a study of two soybean crosses in F_3 through F_5 generations, measured over five environments, Kwon and Torrie (1964) found a positive

correlation of seed yield with plant height, lateness of maturity and increased lodging. Seed yield was to some extent correlated negatively with protein. Byth et al. (1969a) evaluated genotypic as well as phenotypic correlations of yield with other characters in similar studies in F_6 and F_7 generations over three years and obtained inconsistent values from environment to environment. Yield was positively associated with phenotypic score for maturity, and in some environments positively, and in others negatively, with maturity, lodging, height, seed size, protein content and oil content. In another study (1969b) they obtained average correlation values over eight F_3-F_5 generations tested over locations. The genotypic correlations of yield with maturity, height and seed size were positive and significant, with oil content positive but nonsignificant, and negative with lodging and protein content. Cooper (1971), in a yield trial over two locations, observed considerable yield reduction with increased early lodging.

Oil content and protein content in soybeans have been reported by several plant breeders to be negatively correlated (Bordakov, 1933; King and Wang, 1935; Viljoen, 1937; Weiss et al., 1950; Weber, 1950). Correlations obtained by these workers varied from -0.26 to -0.80. Weiss et al. (1950), in a variety-by-date-of-sowing experiment conducted over three locations obtained negative correlations both among the varieties and among the dates of planting. These correlations were, however, more pronounced and consistent among varieties than among dates of planting. Negative associations between oil content and protein content have been reported in terms of both genotypic and phenotypic values by Weber

and Moorthy (1952), Johnson et al. (1955b), Kwon and Torrie (1964), Hanson et al. (1961), and Byth et al. (1969b). Weber and Moorthy (1952) found a negative association of oil percentage with height and maturity, and its association with others varied from cross to cross. Johnson et al. (1955) observed that oil content was strongly associated negatively with time of flowering, positively with length of fruiting period and negatively with time of maturity, but Kwon and Torrie (1964) observed no association of oil content with these traits. Byth et al. (1969b) obtained a slight negative association of oil content only with time of maturity. Weber (1950), in his study of interspecific cross material, found oil percentage positively associated with seed size and negatively associated with both protein percent and iodine number of oil.

Protein content, as observed by Johnson et al. (1955) was negatively associated with yield, and resistance to shattering, and slightly positively associated with number of nodes. Kwon and Torrie (1964) indicated higher negative associations of protein content with yield. Protein content had low negative associations with late flowering and late maturity. Byth et al. (1969b) obtained a slight association of protein content with yield (negative) and seed size (positive).

Reports on the association of morphological characters with those of compositional characters are still more inconsistent. King and Wang (1935), in a study of 195 varieties, found size and weight of beans to have a slight positive association with oil content and a slight negative association with protein content. Viljoen (1937), in a study of F_2 segregates of three crosses, reported seed size to be negatively

associated with oil content and positively with protein content. Weiss et al. (1950), in their variety-by-time-of-planting trials observed seed size to be negatively associated with iodine number of oil, while there was no association with protein or oil content. Interspecific cross material studied by Weber (1950) indicated seed size to be positively associated with oil percent and negatively associated with iodine number of oil. Byth et al. (1969b) noted a slight positive association with protein content.

III. HERITABILITY STUDIES

Johnson and Bernard (1962) published a detailed summary of the literature pertaining to heritability estimates of various traits in soybeans. Heritability has been estimated from progeny on parent regression and from components of variance. In the components-of-variance method, the estimates reported were mostly of heritability in the broad sense.

Mahmud and Kramer (1951) studied the segregating material of the cross between Lincoln and Mandarin in different generations and estimated heritability using different methods. Estimates for yield, height and maturity were found to vary from method to method and generation to generation. The estimates were 43 percent and 41 percent for yield and height, respectively, in spaced plants of the F_2 generation. Regression of F_4 and F_3 produced estimates of 77, 91, and 100 percent for yield, height and maturity, respectively. Higher estimates of heritability were obtained for all characters when the estimates were based on

generations grown in the same year than when based on generations grown in different seasons. From this information they believed that F_3 lines should provide reliable estimates of the average yield potentialities of the F_4 segregates when the two generations are grown in similar environments. Bartley and Weber (1952), using the regression method, found the estimates based on the regression of F_4 on F_3 data provided better estimates than regression of F_3 on F_2. The estimates in the latter case were fairly high for maturity date and plant height. For yield, the estimates were between 15 and 30 percent and for lodging they varied from 17 to 75 percent. Anand and Torrie (1963) used the same procedures as Mahmud and Kramer (1951) and obtained smaller estimates for yield. The estimates for height and maturity were found to be similar by both pairs of workers. The estimates reported by Kwon and Torrie (1964), using only the components-of-variance method, agreed with the results of Anand and Torrie (1963), although the values were lower. The estimates for various characters based on spaced F_2 plants, by the components-of-variance method, were usually higher than the estimates obtained in later generations (Weber and Moorthy, 1952; Mahmud and Kramer, 1951; Yoshino et al., 1955; Nagata, 1960).

Heritability estimates obtained by Johnson et al. (1955a), using variance components for 24 characters in two populations of F_4 and F_5 generations grown over locations, were used to estimate the genetic advance when the top 5 percent of the lines in the sample were selected. Hanson and Weber (1962) obtained heritability estimates and estimated genetic progress for eight attributes in the F_3 and F_4 generations in

two replications over two locations. Time of flowering, length of time from flowering to maturity, time of maturity, height and oil content were found to be highly heritable. Byth et al. (1969a) obtained relatively consistent heritability estimates across environments in F_6-F_7 generations for all traits except seed yield. For yield the heritability estimates were highest under favorable conditions.

Weber (1950) estimated heritability by regressing F_3 progenies on F_2 plants of an interspecific cross. The regression coefficients in percentage were 55 for seed size, 70 for protein percentage, 64 for oil percentage, 47 for iodine number and 122 for maturity.

Heritability estimates for traits such as extent of shattering, number of branches, number of nodes, average number of seeds per pod and number of seeds per plant in addition to the economic traits of interest, were obtained by Johnson et al. (1955a), Yoshino et al. (1955), and van Shaik and Probst (1958). Caviness and Prongsirivathana (1968) estimated heritabilities for height, number of nodes and average length of internodes by the variance-component method in the F_2, and by regression of F_3 line values on F_2 plant values. Estimates obtained by the former method were very high. Caviness (1969) calculated heritability estimates from four crosses for pod dehiscence, date of flowering, date of maturity, days from flowering to maturity and seed size in their broad sense based on spaced F_2 plants. Estimates were very high for the first three attributes. Coefficients of regression of each character of F_3 progenies on values of F_2 plants estimated in all four crosses were inconsistent, but the values were significant for all the attributes.

IV. PARTITION OF GENETIC VARIANCE

Horner et al. (1955) developed an account of genetic variances and covariances in populations in different generations obtained by selfing a cross of homozygous lines, and presented also their expectations in terms of additive and dominance portions assuming an additive model with dominance. Horner and Weber (1956), utilizing the data on maturity from the F_2 through F_7 generations of a soybean cross evaluated the relationship of sample variance and covariance components to genotypic variances and covariances. Although they evaluated the additive x additive epistatic component in addition to additive and dominance portions, they found that a completely additive model explained 96 percent of the variation among sample variance and covariance components. The coefficients used by these workers were developed by Cockerham (1954).

Brim and Cockerham (1961), following the method of Horner and Weber (1956), obtained different variance and covariance component estimates for nine characters studied from the F_1 through F_5 generations in two populations. They fitted six different types of models involving additive, dominance, and additive x additive epistatic effects for each character with the results indicating additive variance to be the principal component of genetic variance for seed yield and seed weight. Other components were of minor importance. Studies by Gates et al. (1960) with hybrid material in F_2 through F_7 generations also agreed that the additive variance was the principal component of genetic variance for seed weight and seed yield, with little evidence of dominance

variance. Gates et al. (1960), however, differed from Brim and Cockerham (1961) in that linkage parameters were included in their model instead of the additive x additive component. Linkage was of significant importance for yield but not for seed weight. Hanson and Weber (1961, 1962) used the same source of material as Gates et al. (1960) and found evidence for an epistatic component for percent oil and suggested that the epistatic variability could be an important source of the genetic variability for seed yield and oil percentage. Components of additive variance for maturity, height, seed weight and percent oil were significant at the 0.01 level of probability.

Leffel and Weiss (1958) studied a diallel set of crosses among ten soybean varieties and observed a significant amount of dominance variance for seed yield and seed size using the diallel analysis. Leffel and Hanson (1961) evaluated the F_2 and F_3 bulks from this diallel set at two or three locations in two years, and F_3 progenies of randomly selected F_2 plants by the combining-ability and diallel-cross analysis methods to determine the average and specific contributions of parents to progenies, dominance and additive gene action and the presence or absence of epistasis. Average contributions of parents were large for seed yield and seed size.

V. MITE INFESTATION STUDIES

Little information is available concerning mite damage on soybeans. Baker and Connell (1961) noted a severe incidence of mites on soybean crops in areas where there were long periods of high temperatures without

rain. They also classified different species of mites feeding on soybeans. Rodriguez et al. (1957) studied the effects of different insecticides on mite populations on soybeans and other crops.

VI. GENE NUMBERS CONTROLLING QUANTITATIVE CHARACTERS

Castle (1921a) proposed a method, with certain assumptions, to estimate the number of genes that govern quantitative traits. Following Sewell Wright's correction, he modified the formula (Castle, 1921b) which utilizes the difference between the means of the two parents involved in the cross, the variation of the F_1 and the variation of the F_2 plants. This formula was used by Weber (1950) to estimate gene numbers affecting characters in a cross between Glycine max and G. ussuriensis. The formula was slightly modified to estimate the gene numbers based on data in backcross generations. He estimated the gene numbers for seed size, maturity date, protein percentage, oil percentage and iodine number of oil.

Burton (1951) utilized a slightly modified version of the formula, which was suggested to him by Sewell Wright, to estimate gene numbers for several traits in pearl millet.

VII. SELECTION INDICES STUDIES

Selection indices have been constructed to serve plant breeders as measuring scales in their task of identifying and selecting superior genotypes, giving consideration to more than one attribute.

Smith (1936) and Hazel (1943) constructed specific selection indices in selecting superior plants and animals, respectively. Although their methods of construction differed slightly, they arrived at the same method of index construction which gives maximum genetic advance from selection. They stated that the information necessary to construct such indices was (1) relative economic weight of each character, (2) genotypic and phenotypic variances, and (3) genotypic and phenotypic correlations between each pair of characters.

Robinson et al. (1951) illustrated the construction of selection indices for various combinations of characters in corn following the discriminant function theory proposed by Smith (1936) and determined the expected genetic advance in yield. They did not make use of the relative economic weights of each character.

Johnson et al. (1955b) estimated the effectiveness of selection in improving yield by constructing various indices including different combinations of characters. Selection based on the combination of fruiting period and seed weight was found just as effective as selecting for yield alone. There was slightly increased efficiency when resistance to lodging, oil percentage and protein percentage were included in the index.

Brim et al. (1959) constructed specific selection indices involving 15 combinations of six agronomic and chemical characters for expected advance in oil, protein and oil equivalent in soybeans. The economic weights assigned for oil content and protein content varied. Selection advance in oil equivalent from an index including yield,

oil and seed weight was 101 percent and that from an index based on oil, protein, and yield was 118 percent in two populations.

Hanson and Johnson (1957) reported a method of calculating a general selection index in soybeans. Utilizing an index including yield, oil content, and protein content, they estimated that a general index based on the data from two populations was 92 percent and 97 percent as effective in the two populations as a specific index calculated for each population.

Caldwell et al. (1966) constructed average selection indices and found that gain for yield was maximum when all attributes were used and when selection was for yield alone. Deleting any attribute other than yield did not affect the gain.

Caldwell and Weber (1965) compared the effectiveness of general, average and specific indices. They found that specific selection was superior to other procedures investigated in both predicted and actual selection advance. Selection based on yield performance alone was more efficient than average index selection, but was slightly inferior to specific index selection. Byth et al. (1969a) also evaluated the three indices for yield advance in two populations over three environments. In all environments, predicted genetic advance was greatest for the specific index from each population, but specific indices were generally less efficient for actual yield advance over environments.

Byth et al. (1969b) presented the estimates of predicted and actual yield advance for truncation selection of nine traits resulting from their use singly for yield selection in three environments,

individually and combined. Since the associations of all variables with yield varied over environments, predictions of yield advance from selection in any environment were inaccurate estimates of actual advance evaluated over environments. Selections of yield invariably resulted in maximum actual yield advance. Chemical composition was generally the best yield predictor for heterogeneous lines, while early lodging was the most effective trait for yield selection in genetically homogeneous lines.

VIII. SEED COAT MOTTLING

The appearance of irregular patches of dark brown to light brown pigments on the yellow or green seed coats of soybeans, a condition commonly referred to as mottling, was described by Woodsworth and Cole (1924). They reported that this trait was markedly affected by the environment. Owen (1927) observed that a rich loamy soil and thin planting favored the development of this trait whereas sandy soils and close planting did not. He observed also that in many instances, mottling was characteristic of plants having abnormal, crinkled and curled leaves or of plants delayed in maturity. Some of the selections, however, consistently developed fewer mottled seeds than others, which led him to believe that heridity played a major role in the expression of this character. Woodworth (1932) also reported mottling to be a genetic character with its expression readily influenced by environment. Conover (1949) found air temperature to have an influence on the severity of soybean mosaic and that the virus, which is responsible for the disease,

was transmitted through the seeds of inoculated and naturally infected plants. Ross (1963) found that there was significantly more seed mottling in plants inoculated with soybean mosaic. In a recent study Ross (1969) observed a differential influence of temperature on seed mottling in different genotypes. Kennedy and Cooper (1967) observed a higher frequency of seed mottling in the locations where there was a high frequency of natural infection. They also noted its frequency to be high in late planted crops. They further noted that the varieties differed in showing symptoms on leaves and on seeds and that the variety Merit did not show seed mottling. Wilcos and Laviolette (1968) observed that seeds differed in both color and extent of mottling depending upon the genotypes influencing the seed coat.

Owen (1928) reported that the dominant gene I, with a multiple allelic series, which prevents the normal development of brown or black seed coat had no effect on seed coat mottling.

Cooper (1966) found a major gene (Im) for resistance to seed mottling and that varieties having this gene were immune to mottling, regardless of environment. Varieties with the "im im" constitution showed variable mottling expression due to environmental effects.

Anand and Torrie (1964), while demonstrating the genetic control of seed mottling, also observed variation in the frequency of mottling in 1960 and 1961, whereas the intensity remained the same in both years. The heritability estimates for mottling frequency ranged from 58 to 118 percent and for intensity from 33 to 84 percent, depending upon the method of estimation and the cross evaluated.

CHAPTER III

MATERIALS AND METHODS

I. PARENT MATERIAL

The four soybean varieties and selections used in this study were received in 1969 from Dr. E. E. Hartwig, Research Agronomist, U. S. Department of Agriculture, located at Stoneville, Mississippi. Parentage of the selections and varieties is as follows:

Varieties or selections	Origin
1. D54-2437	Cross between N48-1394 and L6-5679. The former is a strain from North Carolina and the latter from Illinois.
2. D65-3054	Cross between Hill and PI 171442. The latter is an introduction from China.
3. Hill	Cultivated variety having the parentage D632-15 x D49-2525.
4. S-100	Off-type selected from the variety, Illini.

F_2 seeds derived from three F_1 plants from the cross D54-2437 x D65-3054 (hereafter abbreviated to D54 and D65, respectively) also were received.

D65 and Hill are determinate in growth habit and have tawny pubescence, while D54 and S-100 are indeterminate with gray pubescence.

II. 1969 EXPERIMENTS

The F_2 population of D54 x D65 and the parents were grown at Knoxville in 1969. Seeds obtained from each F_1 plant were sown separately in subgroups adjacent to each other. Varieties Hill and S-100 also were grown. The distance between rows was 36 inches, and that between plants was 12 inches.

The soil type was Etowah silty loam. The test area was fertilized at the rate of 200 lbs. of 0-20-20 per acre broadcast prior to planting. A total of 432 hills were planted with F_2 seeds. Two to three seeds were planted in each hill to facilitate emergence and provide a uniform stand of plants. The seedlings of both parent and F_2 plants were thinned 20 days after planting to one plant per hill.

The following observations were recorded on each of the parental and F_2 plants:

1. Flowering--Number of days from planting to the appearance of the first flower.
2. Growth habit--Determinate or indeterminate.
3. Pubescence--Tawny or gray.
4. Maturity--Number of days from planting to the time when near 95 percent of the pods were dry.
5. Fruiting period--Number of days from flowering to maturity.
6. Seed yield--Total weight in grams of seed from each plant.

7. Seed weight--Weight in grams of 100 seeds from each plant.

8. Oil percent--NMR rating on a 60-seed sample from each plant on a dry weight basis. Analyses were made at the U. S. Regional Soybean Laboratory, Urbana, Illinois.

Crosses were made between D54 and D65, and between Hill and S-100 when the parent plants commenced flowering. Thirty-nine and forty-one seeds were obtained from each cross, respectively. Twenty-two seeds from each cross were planted in the greenhouse along with their respective parents in November, 1969. Confirmation of crosses was based on growth habit and pubescence color of the putative F_1 hybrids. Additional day length was provided in order to prevent early flowering of plants due to short-day conditions that prevail during November and December. The pods were harvested when mature in late April, 1970.

III. 1970 EXPERIMENTS

The 1970 experiments were grown on the same area as the 1969 experiments. Fertilizer application and spacing details also were the same as in 1969.

F_2 Populations

Field planting. The two F_2 populations were each planted in ten-foot rows with a total of 165 hills of D54 x D65 and 180 hills of Hill x S-100. One row of the F_1 plants (11 hills) and two rows each of the parents (22 hills) of the cross D54 x D65 were grown, while ten hills each were grown of the F_1 and parents of the cross Hill x S-100.

For the F_2 populations, 2 to 3 seeds were planted per hill and later thinned to one seedling when they were about 25 days old.

A prolonged drought prevailed after planting and, although overhead sprinkler irrigation was provided, germination was slightly reduced. Shortly before flowering there was again an extended period of drought, which may have contributed to the mite damage.

In addition to the data recorded in 1969, the following observations were recorded on each parent, F_1 and F_2 plant in each cross:

1. Plant height--Total length of main stem.
2. Effective plant height--Total length of all branches, including the main stem.
3. Number of branches--Total number of main branches in addition to the main stem.

Greenhouse planting. The two F_2 populations along with their respective parents were grown also in pots in the greenhouse. The seed was sown during the first week of August. The F_1 plants of Hill x S-100 also were grown. As in 1969, F_1 hybrids were confirmed by dominant characters carried in the male parent. The cross was made with S-100 as the maternal plant which has gray pubescence which is recessive to tawny. Hill and S-100 seedlings can be differentiated by hypocotyl color also. Hypocotyl color in Hill is slightly yellowish-green, whereas, in S-100 it is light-green. All the F_1 plants were found to have a yellowish-green hypocotyl color, confirming them to be hybrids. F_2 seedlings also were observed for differences in hypocotyl color. Seedlings with light-green hypocotyl color were tagged for associations with other characters.

At maturity each hybrid plant of Hill x S-100 and the parents was observed also for its pubescence color.

Studies on hypocotyl color expression in the seedlings were made also in a separate laboratory experiment. Twenty F_2 seeds and 20 seeds of each of the parents of Hill x S-100 were germinated in three petri dishes exposed only to artificial light and moisture.

In the greenhouse the F_2 seeds of the D54 x D65 cross were grown in two groups. Group one included the parents, whereas, group two did not. The seedlings of the parents and F_2 plants were mechanically inoculated with common mosaic virus. The inoculum was prepared by grinding diseased leaves in cold water in a Waring blender. The ground material was filtered through cheese cloth after allowing for one hour in cool temperature; 600 mesh carborundum was dusted on the leaves of the plants to be inoculated to cause effective inoculation.

One month after the inoculation, the leaves of each plant were examined for the development of leaf mottling, and at maturity the seeds were observed for seed coat mottling.

Group two, which contained 90 F_2 seeds showing no seed coat mottling, was planted 20 days later than group one. The leaves of 45 seedlings were inoculated from the inoculum prepared from the leaves of the plants in group one, which developed no leaf-mottling. The other 45 seedlings were similarly inoculated with the inoculum prepared from the leaves which developed leaf mottling. The leaves of all seedlings in group two were observed for symptoms of leaf mottling, and at maturity the seeds were examined for seed coat mottling.

F_3 Progeny Trials

Field planting. Seeds from 120 F_2 plants from the cross D54 x D65 grown in 1969 were sown in the summer of 1970. Seeds were selected at random from 40 plants derived from each of three F_1 plants.

The F_3 progenies were grown at Knoxville, and Jackson, Tennessee, in randomized block designs with two replications at each location. The parents also were included in the experiments.

At Knoxville, 120 F_3 progenies and 4 entries of each parent were sown on May 19 in 8-foot rows with 80 seeds planted per row. The between-row distance was 36 inches.

The following information was recorded for each entry in each replication:

1. Flowering--Number of days from planting to 50 percent flowering of the plants.
2. Maturity--Number of days from planting to the time when nearly 95 percent of the pods were dry.
3. Mite damage--Percent of foliage in each row showing mite damage.
4. Plant height--Average total length of main stem of ten random plants.
5. Lodging score--Scored on a 1-5 basis of the total row, with 1 being complete erectness and 5 complete lodging.
6. Yield--Total weight in grams of seed from each row.
7. Seed weight--Weight in grams of 100 seeds taken at random from each row.

8. Oil percent--NMR rating on a sample from each row, on a dry-weight basis.

9. Protein percent--On a sample from each row, on a dry-weight basis.

The oil percent and protein percent data were obtained from analyses made at the U. S. Regional Soybean Laboratory, Urbana, Illinois.

At Jackson, 120 F_3 progenies and six entries of each parent were sown on May 18 in ten-foot rows, with 100 seeds planted per row. The distance between rows was 40 inches. At harvest the rows were reduced to 8 feet in length.

The test at this location was grown on the West Tennessee Experiment Station on a Memphis silty loam soil. The test area was fertilized at the rate of 200 lbs. of 0-20-20 per acre broadcast prior to planting.

The same information was obtained at Jackson as at Knoxville except for flowering, maturity and mite damage.

Greenhouse planting, 1971. Seeds from a plant inoculated with common mosaic virus in 1970 but which did not develop leaf or seed mottling, as well as seeds from a diseased plant, were planted in pots in the greenhouse during the latter part of June. The resulting plants from the first group were inoculated with inoculum from leaves of one of the diseased D65 plants found in the crop grown in the field during the summer of 1971. Plants from the second group were not inoculated since all the seedlings in these pots showed leaf mottling in early development.

Seedlings in both these groups were observed periodically for the development of leaf mottling.

IV. ANALYSIS OF DATA AND STATISTICAL METHODS

Heterosis

Heterosis for each character was estimated for the 1970 data as the deviation of the F_1 from the midparental value as:

$$H_1 = \overline{F}_1 - \frac{(\overline{P}_1 + \overline{P}_2)}{2}$$

and as the deviation of the F_1 from the high parent value as:

$$H_2 = \overline{F}_1 - \overline{H}_p$$

where

H_1 = heterosis,

$\overline{P}_1$ and $\overline{P}_2$ = mean of the parent 1 and parent 2, respectively,

$\overline{H}_p$ = mean of the high parent, and

$\overline{F}_1$ = mean of the F_1 plants.

The values were expressed as percentage increase or decrease.

Statistical Analysis

Analysis of variance of a single character in one location. A linear additive model of the following form with random effects was considered for the analysis:

$$X_{ij} = \mu + r_i + g_j + e_{ij}$$

where

X_{ij} = phenotypic value of the j^{th} progeny in the i^{th} replication,

μ = population mean,

r_i = effect of i^{th} replication,

g_j = effect of j^{th} F_3 progeny, and

e_{ij} = error associated with the effect of the i^{th} replication and the j^{th} F_3 progeny.

A general form of analysis of variance for a single character in one location is shown in Table 1.

Combined analysis of data over two locations. The following linear additive model with random effects was used:

$$X_{ijk} = \mu + \ell_i + r_{j(i)} + g_k + (\ell g)_{ik} + e_{ijk}$$

where

X_{ijk} = phenotypic value of the k^{th} F_3 progeny in the j^{th} replication in the i^{th} location,

μ = population mean,

ℓ_i = effect of the i^{th} location,

$r_{j(i)}$ = effect of the j^{th} replication within the i^{th} location,

g_k = effect of the k^{th} progeny,

$(\ell g)_{ik}$ = interaction effect of the i^{th} location and the k^{th} F_3 progeny, and

e_{ijk} = pooled error.

Table 1. General form of analysis of variance for a single location.

Source	d.f.	M.S.	Mean square expectations
Total	(rg-1)		
Replication	(r-1)		
Among F_3 progenies	(g-1)	MS1	$\sigma_e^2 + r\sigma_g^2$
Error (within F_3 progenies)	(r-1)(g-1)	MS2	σ_e^2

Where, r = number of replications, and

g = number of progenies.

Environmental variance $V_{e_1} = \hat{\sigma}_e^2$

Genotypic variance among F_3 progenies $V_{g_1} = \frac{MS1-MS2}{r} = \hat{\sigma}_g^2$

Phenotypic variance among F_3 progenies $V_{p_1} = \hat{\sigma}_e^2 + \hat{\sigma}_g^2$

The general form of the combined analysis of the data from the two locations is shown in Table 2.

Similarly the general form of covariance analysis between two traits is shown in Table 3.

In Table 3, when y is replaced by x, and x by y, the values become variances of x and y traits, respectively, i.e.

$\sigma_{e(xx)}$ and $\sigma_{e(yy)}$ become $\sigma_e^2{}_{(x)}$ and $\sigma_e^2{}_{(y)}$, respectively,

$\sigma_{g(xx)}$ and $\sigma_{g(yy)}$ become $\sigma_g^2{}_{(x)}$ and $\sigma_g^2{}_{(y)}$, respectively,

then

$\sigma_e^2{}_{(x)} + \sigma_g^2{}_{(x)}$ and $\sigma_e^2{}_{(y)} + \sigma_g^2{}_{(y)}$, respectively,

are the phenotypic variances among F_3 progenies of traits x and y.

Correlations Among Characters

Associations among yield and other characters were estimated for both phenotypic and genotypic correlation values for both the F_2 plant (1969 and 1970) and the F_3 progeny data.

From the F_2 plant data the correlation coefficients were calculated as follows:

$$\text{Phenotypic correlations, } r_{(p)xy} = \frac{\hat{\sigma}_{xy(F_2)}}{\sqrt{\hat{\sigma}_x^2{}_{(F_2)} \cdot \hat{\sigma}_y^2{}_{(F_2)}}}$$

where

σ_{xy} = phenotypic covariance between x and y in the F_2, and

Table 2. General form of combined analysis of data from two locations.

Source	d.f.	M.S.	Mean square expectations
Total	$(\ell rg-1)$		
Locations	$(\ell-1)$		
Replications/locations	$\ell(r-1)$		
Among F_3 progenies	$(g-1)$	MS1	$\sigma_e^2 + r\sigma_{\ell g}^2 + r\ell\sigma_g^2$
Progenies X locations	$(g-1)(\ell-1)$	MS2	$\sigma_e^2 + r\sigma_{\ell g}^2$
Error	$\ell(g-1)(r-1)$	MS3	σ_e^2

Where, ℓ = number of locations,

r = number of replications, and

g = number of F_3 progenies.

Interaction component, $\hat{\sigma}_{\ell g}^2 = \frac{MS2 - MS3}{r}$

Environmental variance, $V_{e2} = \hat{\sigma}_e^2 + \hat{\sigma}_{\ell g}^2$

Genotypic variance among F_3 progenies, $V_{g2} = \frac{MS1 - MS2}{r\ell} = \hat{\sigma}_g^2$

Phenotypic variance among F_3 progenies, $V_{p2} = \hat{\sigma}_e^2 + \hat{\sigma}_{\ell g}^2 + \hat{\sigma}_g^2$

Table 3. General form of covariance analysis for any two characters

Source	d.f.	M.P.	Mean product expectations xx	xy	yy
Total	(gr-1)				
Replications	(r-1)				
Among F_3 progenies	(g-1)	MP1	$\hat{\sigma}_{e}^{2}{}_{(x)} + r\hat{\sigma}_{g}^{2}{}_{(x)}$	$\hat{\sigma}_{e(xy)} + r\hat{\sigma}_{g(xy)}$	$\hat{\sigma}_{e}^{2}{}_{(y)} + r\hat{\sigma}_{g}^{2}{}_{(yy)}$
Error	(r-1)(g-1)	MP2	$\hat{\sigma}_{e}^{2}{}_{(x)}$	$\hat{\sigma}_{e(xy)}$	$\hat{\sigma}_{e}^{2}{}_{(y)}$

Where, r = number of replications, and

g = number of F_3 progenies.

Environmental covariance, $Cov_{e(xy)} = \hat{\sigma}_{e(xy)}$

Genotypic covariance, $Cov_{g(xy)} = \frac{MP1 - MP2}{r} = \hat{\sigma}_{g(xy)}$

Phenotypic covariance, $Cov_{p(xy)} = \hat{\sigma}_{e(xy)} + \hat{\sigma}_{g(xy)} = \hat{\sigma}_{p(xy)}$

$x^2(F_2)$ and $y^2(F_2)$ = phenotypic variance in characters x and y, respectively, in the F_2.

$$\text{Genotypic correlations, } r_{(g)xy} = \frac{\hat{\sigma}_{xy(g)}}{\sqrt{\hat{\sigma}_x 2(g) \cdot \hat{\sigma}_y 2(g)}}$$

where

$$\hat{\sigma}_{xy(g)} = \hat{\sigma}_{xy(F_2)} - \frac{\hat{\sigma}_{xy(P_1)} + \hat{\sigma}_{xy(P_2)}}{2},$$

$$\hat{\sigma}_x^2(g) = \hat{\sigma}_x^2(F_2) - \frac{\hat{\sigma}_x^2(P_1) + \hat{\sigma}_x^2(P_2)}{2},$$

$$\hat{\sigma}_y^2(g) = \hat{\sigma}_y^2(F_2) - \frac{\hat{\sigma}_y^2(P_1) + \hat{\sigma}_y^2(P_2)}{2}, \text{ and}$$

$\hat{\sigma}_x^2(P_1)$, $\hat{\sigma}_y^2(P_1)$, and $\hat{\sigma}_{xy}(P_1)$

are, respectively, variances of traits x and y, and covariance between x and y in parent P_1. Similarly, $\hat{\sigma}_x^2(P_2)$, $\hat{\sigma}_y^2(P_2)$, and $\hat{\sigma}_{xy}(P_2)$ correspond to the values in parent P_2.

Correlation coefficients (Genotypic) from the F_3 progeny data from both locations were calculated separately as follows:

$$r_{(g)xy} = \frac{\hat{\sigma}_{g(xy)}}{\sqrt{\hat{\sigma}^2_{g(x)} \cdot \hat{\sigma}_g^2(y)}}$$

$\sigma_g^2(x)$, $\sigma_g^2(y)$, $\sigma_e^2(x)$, $\sigma_e^2(y)$, $\sigma_{g(xy)}$, and $\sigma_{e(xy)}$

were already defined in Table 3, page 32.

Correlations of the same characters between generations also were calculated. In this case "x" refers to the trait in one generation and "y" to the same trait in another generation. The coefficients obtained for six characters were between the values of 120 F_2 plants grown in 1969 and the means of their respective F_3 progeny grown in 1970.

Partitioning of Variance and Covariance into Additive and Dominance Components

Genetic variance, environmental variance and genetic covariances were utilized in the estimation of additive and dominance components. Genetic and environmental variances from F_2 plant data, and F_3 progeny data (Table 1, page 29) were utilized. The covariance of the same character between F_2 plants and F_3 progeny means was obtained by dividing the corrected sum of products by the degrees of freedom. These covariances were assumed to estimate genetic variances on the assumption of no correlation of environmental errors in the two years (Gates et al., 1960).

The expectations of variances and covariances as presented by Horner et al. (1955) were considered for partitioning into additive and dominance components. According to these workers the expectations of the components are as follows:

Genetic variance among F_2 plants $\quad 1\ \hat{\sigma}_a^2 + 1\ \hat{\sigma}_d^2$

Genetic variance among F_3 progenies $\quad 1\ \hat{\sigma}_a^2 + 1/4\ \hat{\sigma}_d^2$

Covariance between F_2 plants and F_3 progenies	$1\ \hat{\sigma}_a 2 + 1/2\ \hat{\sigma}_d 2$

where $\hat{\sigma}_a 2$ and $\hat{\sigma}_d 2$ are estimates of additive and dominance components of variance or covariance, respectively.

Based on these expectations, estimates of $\sigma_a 2$ and $\sigma_d 2$ were obtained for each character by the least-squares method similar to that outlined by Mather (1949).

Heritability Estimates and Predicted Genetic Advance

Heritability estimates were calculated by both offspring-on-parent regression and the variance-components methods. In the offspring-on-parent regression method, the mean values of the F_3 progenies were regressed on the F_2 plant values. Heritability estimates were calculated as two-thirds of the regression coefficient (Smith and Kinman, 1965).

In the components of variance method, estimates of heritability were obtained in both the broad and narrow sense. To obtain estimates of narrow sense heritability, the estimated additive genetic variance ($\hat{\sigma}_a 2$) was divided by the phenotypic variance among the F_3 progenies. Heritability estimates in the F_3 generation were obtained by using the various values derived from the analysis of variance. Heritability was estimated as

$$\frac{\hat{\sigma}_g 2}{\hat{\sigma}_e 2 + \hat{\sigma}_g 2}$$ on the individual progeny basis, or

$$\frac{\hat{\sigma}_g^2}{\frac{\hat{\sigma}_e^2}{r} + \hat{\sigma}_g^2}$$ on a replication basis,

for the data in a single location (Table 1, page 29). When the data for both the locations (Table 2, page 31) were considered, heritability was estimated as

$$\frac{\hat{\sigma}_g^2}{\hat{\sigma}_e^2 + \hat{\sigma}_{\ell g}^2 + \hat{\sigma}_g^2}$$ on an individual progeny basis, or

$$\frac{\hat{\sigma}_g^2}{\frac{\hat{\sigma}_e^2}{r_\ell} + \frac{\hat{\sigma}_{\ell g}^2}{\ell} + \hat{\sigma}_g^2}$$ on a replication basis.

The estimates obtained from the F_3 progeny data were of the broad sense type.

Predicted genetic advance for each character in the F_3 progeny was calculated as follows:

$$\text{Genetic advance, } G_s = KH\hat{\sigma}_p$$

where

K = selection differential,

H = heritability, and

$\hat{\sigma}_p$ = phenotypic standard deviation.

Heritability estimates obtained at Knoxville on a progeny basis were utilized to obtain predicted genetic advance. The $\hat{\sigma}_p$ was taken from Table 1, page 29 (V_{pl}).

Inheritance of Mite Reaction

Ratios were tested for the inheritance of resistance or susceptibility of F_2 plants to damage by spider mites (Tetranychus spp.).

Gene Numbers Governing the Quantitative Characters

The following formula used by Burton (1951) was utilized to calculate gene numbers:

$$N = \frac{\cdot 25(\cdot 75 - h + h^2)D^2}{\sigma_{\overline{F}_1}^2 - \sigma_{\overline{F}_1}^2}$$

where

$$h = \frac{\overline{F}_1 - \overline{P}_1}{\overline{P}_2 - \overline{P}_1} ,$$

$$D = \overline{P}_2 - \overline{P}_1 ,$$

$\overline{P}_1$ = the mean of the smallest parent,

$\overline{P}_2$ = the mean of the highest parent,

$\overline{F}_1$ = the mean of the F_1 population, and

$\overline{F}_2$ = the mean of the F_2 population.

Gene numbers were also calculated by the Castle-Wright formula, 1921 as follows:

$$N = \frac{D^2}{8(\sigma_{F_2}^2 - \sigma_{F_1}^2)}$$

where

$\hat{\sigma}_{F_2}^2$ = the variance in the F_2 populations,

$\hat{\sigma}_{F_1}^2$ = the variance in the F_1 populations, and

D^2 = the squared difference between the parental means.

Different Mendelian ratios also were tested against segregating frequency ratios to find the gene numbers.

Construction of Selection Indices and Calculating Expected Genetic Advance

Selection indices including yield, oil content, protein content and lodging in various combinations and the genetic advance expected from selection based on these indices were computed by following the procedure described by Robinson et al. (1951) with the assumption of equal economic importance of all these traits. The formula,

$$I = b_1X_1 + b_2X^2 + b_3X_3 + \ldots + b_nX_n ,$$

was constructed so that the estimated "b" values would provide optimum weights for each of the various characters considered in selection to maximize the advance from selection.

In the above index, X_1, X_2, X_3, ..., X_n are the phenotypic values of the traits considered in selection, and b_1, b_2, b_3, ..., b_n are the relative weights applied to each character.

The "b" values were obtained by solving the following general form of simultaneous equations:

$$b_1P_{11} + b_2P_{12} + b_3P_{13} + \ldots + b_nP_{1n} = G_{1y}$$

$$b_1P_{21} + b_2P_{22} + b_3P_{23} + \ldots + b_nP_{2n} = G_{2y}$$

$$\vdots \qquad \vdots \qquad \vdots \qquad \vdots \qquad \vdots$$

$$b_1P_{n1} + b_2P_{n2} + b_3P_{n3} + \ldots + b_nP_{nn} = G_{ny}$$

where P_{ij} refers to phenotypic covariance (when $i = j$, $P_{ij} = P_{ii} = P_{jj}$ - phenotypic variance) and G_{iy} is the genotypic covariance.

Expected genetic advance was computed from the following formula:

$$\Delta_I = K \sqrt{b_1G_{1y} + b_2G_{2y} + b_3G_{3y} + \ldots + b_nG_{ny}}$$

where

K = selection differential in standard units.

It is assumed that in each case, the top 5 percent of the progenies would be selected.

The relative efficiency of each index was evaluated in comparison to yield alone considered as 100 percent efficient.

CHAPTER IV

EXPERIMENTAL RESULTS

Heterosis

The mean performance for different characters in the F_1 generation of two crosses grown in 1970 is presented in Tables 4 and 5. Since the number of crossed seeds was low in each cross, the F_1 rows were not replicated. The observations were based on ten plants spaced 12 inches apart. Many of the characters exhibited little heterosis in F_1 over their midparent values; however, height, effective height and yield expressed considerable heterosis over both midparent and high-parent values. Seed weight in the cross Hill x S-100 showed a fair amount of heterosis over the midparent value.

Partitioning Variance and Covariance Components in F_2 and F_3 Generations

The variances in the parental, F_1 and F_2 generations in the two crosses are presented in Appendix Table 17. Values of genetic variances estimated by equating average variances in the parents to environmental variances for the different characters are presented in Appendix Table 18. The covariance values for all pairs of characters in the F_2 generations of the two crosses are presented in Appendix Tables 19 to 21. Their genetic covariance values are presented in Appendix Table 22 for D54 x D65 grown in 1969 and 1970, and in Appendix Table 23 for Hill x S-100 grown in 1970.

Table 4. Heterosis in F_1 soybean cross D54 x D65, 1970

	D54	D65	Mid parent value	F_1	Heterosis	
					% from mid parent	% from high parent
Days to flower	54.2	66.8	60.5	64.9	7.3	-2.8
Days to maturity	127.2	133.9	130.5	132.8	1.7	-0.8
Fruiting period, days	73.0	67.1	70.0	67.9	-3.0	-7.0
Height, inches	25.9	18.2	22.1	40.9	85.4	57.8
Effective height, inches	121.8	102.8	112.3	222.4	98.1	82.6
Number of branches	5.9	7.5	6.7	6.5	-3.1	-13.7
Seed yield per plant, grams	73.8	87.9	80.8	145.4	79.9	65.5
100 seed weight, grams	13.9	14.3	14.1	14.9	6.0	4.4
Percent oil	22.8	24.1	23.5	23.8	1.5	-1.4

Table 5. Heterosis in F_1 soybean cross Hill x S-100, 1970.

	Hill	S-100	Mid parent value	F_1	Heterosis	
					% from mid parent	% from high parent
Days to flower	57.7	48.1	52.9	55.3	4.6	-4.1
Days to maturity	112.5	123.8	118.2	125.3	6.1	1.2
Fruiting period, days	54.8	75.7	65.2	70.0	7.3	-7.5
Height, inches	31.2	41.7	36.5	47.6	30.5	14.1
Effective height, inches	186.3	248.8	217.4	328.0	50.8	32.1
Number of branches	7.9	6.7	7.3	7.9	8.1	0.1
Seed yield per plant, grams	74.6	95.5	85.1	119.3	40.3	24.9
100 seed weight, grams	9.3	14.2	11.8	14.2	21.0	0.1
Percent oil	21.3	19.9	20.6	21.8	5.4	2.5

The analyses of variance for the different characters in the F_3 progeny trials of the cross D54 and D65 grown at Knoxville and Jackson and for the two locations combined are presented in Table 6. The variances among the F_3 progenies for all characters studied were significant in all cases. Location x progeny components of variance also were significant in all cases except for oil percent and seed weight. The estimated values of phenotypic and genetic variances for each of the characters are presented in Appendix Table 24. The mean products between the members of all pairs of characters obtained by the analyses of covariance for the Knoxville and Jackson data are presented in Appendix Tables 25 and 26, respectively. The values of genetic covariances between the members of pairs of characters estimated from these sums of products are presented in Appendix Tables 27 and 28.

Correlation Coefficients

The correlation coefficients, in terms of both genotypic and phenotypic values, were obtained for both crosses by utilizing the above variance and covariance values. The coefficients obtained for the F_2 generation of the cross D54 x D65 are presented in Tables 7 and 8, and those for the cross Hill x S-100 in Table 9. The genotypic values are shown in parentheses. The genotypic values were generally higher for most comparisons. In both crosses high seed yield was significantly associated, both genotypically and phenotypically, with tawny pubescence, growth habit, late flowering, late maturity, longer fruiting period, increased height, effective height, and greater number of branches. Although both were significantly associated positively with yield, the

Table 6. Mean squares for various characters from the analysis of variance of the replicated F_3 trials grown at Knoxville and Jackson and the combined locations, 1970.

Source	DF	Flowering	Maturity	Plant height	Lodging	Seed yield	Oil percent	Protein percent	100 seed weight
Knoxville									
Replications	1	101.02	46.05	2.15	4.91	39716.27	0.40	13.88	6.23
Among F_3 progenies	121	126.98**	104.94**	113.58**	0.93**	65935.19**	0.68**	1.09**	3.15**
Error	121	9.33	7.61	10.05	0.29	33284.02	0.28	0.59	1.03
Jackson									
Replications	1			91.35	0.01	117305.33	6.89	1.72	2.99
Among F_3 progenies	121			80.54**	1.45**	14123.94**	0.61**	1.85**	2.75**
Error	121			10.38	0.37	6072.16	0.17	0.55	0.68
Combined Analysis									
Locations	1			9802.95	26.44	923331.00	9.67	98.55	12.47
Replications x locations	2			46.75	2.45	78510.80	3.65	7.80	4.61
Among F_3 progenies	121			180.24**	1.91**	49452.45**	1.03**	2.12**	4.73**
Locations x progenies	121			13.88*	0.48**	30606.68**	0.26	0.82**	1.17
Error	242			10.22	0.33	19678.09	0.22	0.57	0.85

** indicates significance at P = .01

* indicates significance at P = .05

Table 7. Phenotypic and genotypic correlations among characters studied in the F_2 generation of the cross D54 x D65 grown in 1969.

Characters	Pubescence color	Growth habit	Flowering	Maturity	Fruiting period	Seed yield	100 seed weight
Growth habit	.027						
Flowering	-.768** (-.815)**	-.132** (-.143)**					
Maturity	-.681** (-.739)**	-.201** (-.220)**	.814 (.934)				
Fruiting period	-.431** (-.566)**	-.198** (-.262)**	.451** (.746)**	.875** (.919)**			
Seed yield	-.254** (-.361)**	-.221** (-.317)**	.291** (.539)**	.358** (.228)**	.321** (.221)**		
100 seed weight	-.065 (-.094)	-.049 (-.072)	.146** (.263)**	.338** (.438)**	.393** (.575)**	.234** (.092)	
Oil percent	-.071 (-.074)	-.344** (-.366)**	.193** (.217)**	.176** (.207)**	.120* (.049)	.338** (.107)*	.488** (.497)**

Genotypic values are shown in parentheses.

** indicates significance at P = 0.01

* indicates significance at P = 0.05

Table 8. Phenotypic and genotypic correlations among characters studied in the F_2 generation of the cross D54 x D65.

Characters	Pubescence color	Growth habit	Flowering	Maturity	Fruiting period	Height	Effective plant height	Number of branches	Seed yield	100 seed weight
Growth habit	.045									
Flowering	-.741** (-.778)**	-.144 (-.151)								
Maturity	-.629** (-.691)**	-.279** (-.307)	.746** (.827)**							
Fruiting period	-.344** (-.400)**	-.114 (-.133)	-.554** (-.598)**	.133** (.005)**						
Height	-.346** (-.366)**	-.694** (-.734)**	.339** (.449)**	.504** (.612)**	.109 (.047)					
Effective height	-.316** (-.336)**	-.509** (-.541)**	.304** (.408)**	.493** (.579)**	.148 (.088)	.870** (.811)**				
Number of branches	-.119 (-.146)	-.203** (-.248)**	.108 (.157)	.220** (.221)**	.090 (-.003)	.502** (.521)**	.751** (.768)**			
Seed yield	-.316** (-.368)**	-.411** (-.479)**	.248** (.364)**	.480** (.534)**	.199* (.082)	.735** (.785)**	.784** (.802)**	.622** (.579)**		
100 seed weight	-.059 (-.071)	-.274** (-.326)**	.098 (.193)*	.465** (.560)**	.431** (.401)**	.351** (.402)**	.333** (.352)**	.187* (.162)*	.447** (.411)**	
Oil percent	-.085 (-.121)	-.237** (-.309)**	.214** (.312)**	.198* (.313)**	-.083 (-.511)**	.246** (.219)**	.146 (.089)	-.039 (-.239)**	.132 (-.177)*	.217** (.351)**

Genotypic values are shown in parentheses.

**Indicates significance at P = 0.01

*Indicates significance at P = 0.05

Table 9. Phenotypic and genotypic correlations among characters studied in the F_2 generation of the cross Hill x S-100, 1970.

Characters	Pubescence color	Growth habit	Flowering	Maturity	Fruiting period	Height	Effective height	Number of branches	Seed yield	100 seed weight
Growth habit	-.055									
Flowering	-.497** (-.618)**	-.250** (-.311)**								
Maturity	-.373** (-.430)**	-.433** (-.499)**	.631** (.695)**							
Fruiting period	-.019 (-.025)	-.272** (-.347)**	-.199* (-.478)**	.611** (.654)**						
Height	-.185* (-.192)*	-.765** (-.797)**	.221** (.405)**	.479** (.598)**	.363** (.394)**					
Effective height	-.229** (-.242)**	-.635** (-.669)**	.215** (.216)**	.474** (.582)**	.371** (.440)**	.851** (.888)**				
Number of branches	.277** (-.313)**	-.175* (-.197)*	.217** (.218)**	.291** (.298)**	.159* (.203)**	.368** (.447)**	.728** (.745)**			
Seed yield	-.180* (-.218)**	-.261** (-.317)**	.065 (.172)*	.321** (.373)**	.347** (.353)**	.476** (.496)**	.644** (.685)**	.674** (.748)**		
100 seed weight	-.099 (-.136)	-.128 (.125)	-.117 (-.156)*	.223** (.135)	.402** (.342)**	.073 (.055)	.108 (.084)	.132 (.081)	.405** (.423)**	
Oil percent	-.237** (-.226)**	-.136 (-.380)**	.285** (.022)	.261** (-.073)	-.021 (.190)*	.254** (.333)**	.303** .439**	.194* (-.010)	.237** (-.156)*	.149* (-.203)**

Genotypic values are shown in parentheses.

**Indicates significance at P = 0.01

*Indicates significance at P = 0.05

the values for effective plant height were higher than those for height. Associations of yield with seed weight and oil content were inconsistent. Seed weight was positively associated with length of fruiting period in all experiments but was not always significant by association with other characters. Oil content was found to be associated with tawny pubescence only in the cross Hill x S-100. It was significantly associated both phenotypically and genotypically with indeterminate growth habit in the cross D54 x D65. Oil content was found to be positively associated also with height and seed size, but varied with other characters, both between years and between the two crosses.

The correlation coefficients calculated by utilizing genetic variance and covariance values for the F_3 progeny trials are presented in Tables 10 and 11. Yield was positively associated with flowering time and time of maturity at Knoxville. Information on flowering and maturity was not obtained at Jackson. Yield was also significantly associated positively with height, extent of lodging and seed weight at Knoxville, while at Jackson it was significantly associated only with seed weight. High yield was associated with low lodging at Jackson for some unknown reason. It might, however, be due to early lodging. Oil content was positively associated with plant height and seed size at Knoxville, but was not significantly associated with any character at Jackson. Protein content showed a highly significant negative association with time of flowering, time of maturity, plant height, extent of lodging, yield and oil content at Knoxville. At Jackson protein content was positively associated with seed size and negatively associated with oil content.

Table 10. Correlations among characters in the F_3 progeny trial grown at Knoxville, 1970.

Characters	Flowering	Maturity	Plant height	Lodging	Seed yield	100 seed weight	Oil percent
Maturity	.653**						
Plant height	.435**	.445**					
Lodging	.306**	.386**	.519**				
Seed yield	.647**	.916**	.384**	.237**			
100 seed weight	-.069**	.239**	.472**	-.136	.291**		
Oil percent	.019	.144	.457**	.035	.110	.441**	
Protein percent	-.328**	-.355**	-.360**	-.309**	.325**	.091	-.344**

** indicates significance at P = 0.01

* indicates significance at P = 0.05

Table 11. Correlations among characters in the F_3 progeny trial grown at Jackson, 1970

Characters	Plant height	Lodging	Seed yield	100 seed weight	Oil percent
Lodging	.493**				
Seed yield	.057	-.263**			
100 seed weight	.134	-.032	.204*		
Oil percent	-.024	-.079	.008	.065	
Protein percent	.155	.171	-.110	.416**	-.602**

** indicates significance at P = 0.01

* indicates significance at P = 0.05

Associations of characters between the F_2 and F_3 generations grown in 1969 and 1970, respectively, also were estimated. The correlations between F_2 plant and F_3 progeny mean values are presented in Table 12. Both the Knoxville and Jackson F_3 data were used for this purpose. Days to flowering, days to maturity, seed weight and oil percent had highly significant correlations between generations in the two locations. Between-generation associations for yield were not significant in either location.

Partitioning of Genetic Variances into Additive and Dominance Components

By using the variances of the F_2 and F_3 generations, and covariances between generations, the total genetic variance for five characters was partitioned into additive and dominance components. The expectations considered and the method followed were described in Chapter III. The total genetic variances for each character in the two generations and their estimated components are presented in Table 13. Genetic variances for flowering and seed yield were entirely of the additive type while those for maturity and seed weight were partly of additive and partly of dominance components. The genetic variance for oil content was found to be completely of the dominance type.

Estimates of Heritability

Heritability estimates were obtained in both the broad and narrow sense as described in Chapter III. The estimates based on the F_2 generation were generally high in all cases except for oil percent in 1970 (Table 14). The estimates based on F_3 progenies also were high. Those

Table 12. Correlations between characters of F_2 plants grown in 1969 and their corresponding F_3 progeny values obtained at Knoxville and Jackson in 1970.

Characters	F_3 progenies grown at	
	Knoxville	Jackson
Days to flower	.785**	
Days to maturity	.704**	
Seed yield	.157	.049
100 seed weight	.453**	.560**
Oil percent	.363**	.224*

** indicates significance at p = 0.01

* indicates significance at p = 0.05

Table 13. Total genetic variances and estimated additive and dominance variance components for five characters in the cross D54 x D65.

Characters	Flowering	Maturity	Seed yield	100 seed weight	Oil percent
Total genetic variance in F_2 (1969)	21.72	78.00	791.56	1.51	2.62
Total genetic variance in F_3 (Knoxville, 1970)	58.82	48.67	16325.58	1.06	0.20
Covariance between F_2 and F_3 generations	30.42	44.30	845.34	0.84	0.23
Additive component of genetic variance	59.37	28.48	13925.52	0.64	0.0
Dominance component of genetic variation	0.0	11.26	0.0	0.20	0.89

Table 14. Broad and narrow sense heritability estimates for the various characters in two crosses and predicted genetic advance in the F_3 generation of the cross D54 x D65.

Method of estimation and analyzed experiment	Flowering	Maturity	Fruiting period	Height	Effective height	Number of branches
BROAD SENSE						
(1) Variance components method						
F_2 - D54 x D65 - 1969	88.0	83.9	57.7	-	-	-
- D54 x D65 - 1970	90.7	82.7	74.0	89.4	88.4	66.6
- Hill x S-100 - 1970	64.6	75.4	61.5	92.1	90.1	78.6
F_3 - Replicated trial (D54 x D65)						
(a) Progeny basis						
1. Knoxville	86.3	86.5	-	83.8	-	-
2. Jackson	-	-	-	77.2	-	-
3. Combined	-	-	-	77.5	-	-
(b) Replication basis						
1. Knoxville	92.7	92.8	-	91.1	-	-
2. Jackson	-	-	-	87.1	-	-
3. Combined	-	-	-	92.3	-	-
(2) Regression method	31.9	56.3	-	-	-	-
NARROW SENSE						
(a) Progeny basis	87.1	50.6	-	-	-	-
(b) Replication basis	93.6	54.3	-	-	-	-
EXPECTED GENETIC ADVANCE						
(Progeny basis)	14.8	7.9	-	13.6†	-	-

Table 14 (continued)

Method of estimation and analyzed experiment	Lodging	Seed yield	100 seed weight	Oil percent	Protein percent
BROAD SENSE					
(1) Variance components method					
F_2 - D54 x D65 - 1969	-	49.1	47.3	89.1	-
- D54 x D65 - 1970	-	73.5	67.1	44.8	-
- Hill x S-100 - 1970	-	67.5	84.6	31.1	-
F_3 - Replicated trial (D54 x D65)					
(a) Progeny basis					
1. Knoxville	52.5	32.9	50.7	41.7	29.8
2. Jackson	59.3	39.9	60.5	56.4	54.2
3. Combined	47.4	15.8	46.9	44.2	32.3
(b) Replication basis					
1. Knoxville	68.1	49.5	67.1	58.8	45.5
2. Jackson	74.0	57.0	75.4	71.0	69.9
3. Combined	75.0	38.1	75.4	73.1	61.1
(2) Regression method	-	1.7	35.5	17.3	-
NARROW SENSE					
(a) Progeny basis	-	28.1	30.6	0	-
(b) Replication basis	-	42.2	40.5	0	-
EXPECTED GENETIC ADVANCE					
(progeny basis)	-	128.5	1.9	0.6†	0.6†

†Obtained by utilizing broad sense heritability in the F_3 generation.

estimated on the replication basis were higher than those estimated on the progeny basis. In the latter method the estimates for seed yield and protein content were generally low. Estimates obtained by the regression method were lower than those obtained by the other methods. Estimates for seed yield and oil percent were especially low by this method.

Narrow sense heritability estimates, using the additive portion of the genetic variation, were highest for flowering. The estimates for seed yield and seed weight on the progeny basis were low. Oil percent had zero heritability in the narrow sense since all the genetic variance was found to be of the dominance type.

Predicted Genetic Advance

Expected genetic progress for seven characters was calculated on the progeny basis, and the values are also presented in Table 14. In each case it was assumed that the top 5 percent of the progenies would be selected.

Mite Infestation on F_2 Plants and F_3 Progenies

It was observed during an infestation of spider mites (Tetranychus spp.) in the summer of 1970 that some plants and progenies were susceptible and others resistant. The incidence of mites on the F_3 progenies was recorded as the amount of foliage infected in each progeny. The variations in progeny yields caused by the mite damage could not be separated from the general environmental or genetic variation. It was considered as a confounded portion of the environmental variation.

Susceptible and resistant plants were recorded in both the D54 x D65 and Hill x S-100 F_2 populations. Mite incidence on all parental and F_1 plants also was noted. It was found that neither D54 nor D65 showed any mite damage, while all plants of the F_1 did. In the F_2 population 81 of 152 plants were found to be susceptible. This indicated a digenic complementary epistatic action between two pairs of genes each present in a different parent. The plant counts agreed with a ratio of 9:7 with a Chi-square value of 0.542 and a probability of 0.25-0.50.

In the other cross, all the Hill plants were found to be susceptible while all plants of S-100 and the F_1 were resistant. This indicated that the resistance to mites was dominant. Among 167 F_2 plants only 41 plants were found to be susceptible. A Chi-square value of 0.018 and a probability greater than 0.90 indicated a monogenic control of plant reaction to the incidence of mites in this cross.

The gene symbol (Mtmt) has been proposed for resistance and susceptibility in the two crosses.

Estimation of Gene Numbers

In each cross the minimum number of genes differentiating the parents for each character was estimated using the three methods described in Chapter III. The results are presented in Table 15.

The frequency distributions for the characters in the F_2 generation are shown in Appendix Table 29. When frequencies did not follow the normal distribution pattern, the characters were omitted for testing Mendelian ratios. Some characters showing normal distribution patterns

Table 15. Number of gene pairs differentiating the parents for various characters as estimated by three different methods.

Characters	Castle-Wright Formula		Burton Formula		Mendelian Ratios					
					D54 x D65			Hill x S-100		
	D54 x D65	Hill x S-100	D54 x D65	Hill x S-100	Number	X^2	P-level	Number	X^2	P-level
Flowering	0.3	0.6	83.5	-1081.7	-	-	-	4	11.56	.10-.20
Maturity	0.1	0.5	-18.4	-157.6	-	-	-	-	-	-
Fruiting period	0.1	3.5	-25.2	-131.7	-	-	-	4	7.10	.50-.70
Height	0.1	0.1	978.9	67.2	-	-	-	-	-	-
Effective height	0.1	0.1	-22.2	-10.7	-	-	-	-	-	-
Number of branches	0.1	0.1	-2.1	-1.3	3	11.72	.05-.10	4	14.19	.05-.10
Yield per plant	0.1	0.1	-7.1	-2.7	-	-	-	-	-	-
Seed weight	0.1	1.1	-1.2	-79.4	4	17.19	.02-.05	4	13.92	.05-.10
Oil percent	0.3	1.0	-37.3	-8.0	4	18.64	.02-.05	5	22.55	.01-.02

could be suspected as exhibiting the presence of a number of modifier genes. A few individuals which fell on the two ends of the distributions may also have had modifiers. These individuals also were omitted. Generally, the fitted Mendelian ratios indicated 3 to 5 pairs of genes differentiating the parents for the different characters. Although some frequency distributions indicated very low probabilities for the fitted Mendelian ratios, they were closer than other ratios tested.

Estimation of gene numbers by the Castle-Wright formula seemed to underestimate the actual gene numbers while the Burton formula overestimated the numbers. It was considered that these two formulae failed to give satisfactory estimates of gene numbers due to lower variances than expected in the F_2 and the limited number of F_1 plants grown.

Construction of Selection Indices and Estimation of Predicted Genetic Advance

The procedure adapted by Robinson et al. (1951) as described in Chapter III was utilized in constructing selection indices and estimating advance in yield following selection based on these indices. The details of the characters included in the different indices, and the relative efficiency of each index considering the advance expected on selecting for yield alone as 100 percent efficient, are presented in Table 16. It was assumed that in each case the top 5 percent of the progenies would be selected.

The addition of seed weight and lodging to yield in the index did not improve the predicted advance. The index consisting of yield and maturity resulted in an efficiency of 148 percent. The further

Table 16. Expected genetic advance using yield alone and from the use of selection indices based on different combinations of characters in the F_3 generation of the cross D54 x D65 and their relative efficiency.

Characters used in selection index	Genetic progress expected	Relative efficiency (in percent)
1. Yield alone	151	100
2. Yield + Seed weight	152	101
3. Yield + Maturity	224	148
4. Yield + Seed weight + Maturity	225	149
5. Yield + Seed weight + Lodging	159	105
6. Yield + Seed weight + Maturity + Lodging	226	149

addition of seed weight and lodging did not significantly improve the efficiency.

Greenhouse Experiments

Tests of hypocotyl color. Eight seedlings each of Hill and S-100, six seedlings of the F_1's and 108 seedlings of the F_2's were examined a few days after germination for their hypocotyl color. The hypocotyl colors of Hill and S-100 were described in Chapter III. On close examination the F_1 seedlings (obtained from the seeds produced on S-100 as female parent) were found to have yellowish-green hypotocyls, confirming them to be hybrid seedlings. Among the F_2 seedlings, 21 were light-green in color and 87 were yellowish-green. The 21 seedlings with light-green hypocotyls were identified and at maturity all were observed to have gray pubescence. All but one of the remaining 87 plants had tawny pubescence. This one was probably due to an error in classifying the seedlings for hypocotyl color.

Laboratory tests of Hill, S-100 and the F_2 seedlings grown in the presence of only artificial light and moisture failed to develop pigments in the hypocotyls.

Tests of leaf and seed-coat mottling. Parental and F_2 seeds of the cross D54 x D65 were planted in two groups as explained in Chapter III. Both leaf-mottling and no mottling were found in group 1. By identifying these plants as "susceptible" and resistant", 109 of 132 F_2 seedlings, 15 of 27 D65 seedlings, and 16 of 20 D54 seedlings were susceptible and the remainder resistant. When inoculum from the leaves

of susceptible seedlings was used to inoculate 45 seedlings in group 2, 39 seedlings developed leaf mottling, while inoculum prepared from the leaves of resistant seedlings did not cause leaf mottling on any of 45 seedlings in group 2. At maturity, all the parental plants which showed no leaf mottling earlier produced seeds free of seed coat mottling. Of 23 F_2 plants which did not show leaf mottling, 2 produced mottled seeds.

In group 2, of 45 seedlings tested 39 showed leaf mottling and produced mottled seeds at maturity. The other six seedlings had neither leaf mottling nor mottled seeds.

In the 1971 summer experiment, 20 seeds from resistant plants and 20 seeds from susceptible plants showing seed-coat mottling in the group 1 1970 experiment were planted in the greenhouse, and ten seedlings of the resistant class were artificially inoculated. It was observed that all of the 20 seedlings obtained from the seeds of the susceptible plants showed both leaf-mottling and seed coat mottling at maturity even though not inoculated. None of the seedlings, inoculated or otherwise, obtained from the seeds of the resistant plants showed leaf mottling, and none of the seeds produced were mottled.

CHAPTER V

DISCUSSION

The purpose of this study was to investigate the association of yield, oil content and protein content with various agronomic characters, to obtain heritability estimates for each character, to study the possibility of selection for leaf and seed-coat mottling resistance, to investigate the minimum number of genes differentiating the parents for each character and to investigate the importance of various characters in predicting the gain in yield when using them in selection indices. Considerable heterosis was observed in F_1 plants. Mite infestation which occurred in 1970 provided an opportunity to study the genetic basis of resistance to mite damage.

Heterosis

Heterosis for yield in F_1 plants is of interest. Although statistical tests could not be made, it is apparent from comparing the mean values of parents and F_1 hybrids that the latter exhibited a considerable amount of heterosis for yield in both crosses and for oil content, in the cross Hill x S-100. A fair amount of heterosis was observed in both crosses for seed size also. These results are in conformity with the observations of previous workers (Wentz and Stewart, 1924; Woodworth, 1933; Weiss et al., 1947; Leffel and Weiss, 1958; Brim and Cockerham, 1961). Heterosis for seed size and oil content could be attributed to the dominance type of gene action displayed in these

crosses (Table 13, page 53). Heterosis for seed yield is, perhaps, an accumulation of the effects of all the factors influencing yield in addition to its own gene effects. Although the present possibility of producing F_1 seeds on a large scale is meager, it would be very advantageous if an economical method of producing such seed could be found.

Variances, Covariances and Correlation Coefficients

In order to estimate genetic variances in each character in the F_2 generation, the average variance of the parents was equated to the environmental variance, even though data were available on F_1 plants grown in 1970. This was because it was assumed that the heterotic effects of many characters in F_1 plants tend to buffer the small environmental variations. In general, it was observed that the variances in F_1 plants were smaller than the average variances of the parents in many cases. In a segregating soybean population there is generally a great amount of interplant competition (Hinson and Hanson, 1962) which poses another difficulty for a satisfactory estimation of environmental variance. Under such conditions, even the average variance of the parents may underestimate the true environmental variance. Considering this fact, the estimated genetic variance may be an overestimate of its true value.

Similarly, it has been generally agreed that genetic variance estimated from a replicated trial at one location may be a biased one. The estimates obtained in the present study by the combined analyses of data were considered to be better. Any under- or over-estimation of

the environments may affect the reliability of the estimated genotypic correlation coefficients, and may serve also as one of the factors affecting the heritability estimates to be discussed later.

Yield showed significant, both genotypic and phenotypic, associations with time of flowering, time of maturity, length of fruiting period, plant height, number of branches and seed size in both F_2 plants and F_3 progenies. These results are in conformity with the results obtained by Kalton (1948), Weber and Moorthy (1952), and Johnson et al. (1955b). In the present study, the indications were that pubescence color is also important in obtaining high yields since tawny pubescence showed a significant association with high yield. Some indications are that genes for gray pubescence and early flowering are linked (Hartwig, personal communication). Early flowering, particularly in determinate types, retards growth, which in turn might affect the final yield.

Although seed size and yield showed positive correlations, both genotypically and phenotypically, the association in two F_2 populations of the same cross, D54 x D65, was inconsistent. Previous studies indicate such inconsistency also (Ma, 1946; Anand and Torrie, 1963). High oil content, in the cross Hill x S-100, was associated with tawny pubescence. It was positively associated also with seed size and plant height but was inconsistent with other characters in all F_2 material. The same was true in the F_3 material studied at Knoxville. At Jackson, oil content was not associated with any character. Earlier studies indicate inconsistency also in the association of oil content with other characters (Weber and Moorthy, 1952; Kwon and Torrie, 1964). Association

of protein content with seed yield and oil content was negative and consistent over locations. Inconsistent associations of protein content with other characters are in agreement with the findings of Viljoen (1937), Johnson et al. (1955b), Weiss et al. (1950), Kwon and Torrie (1964), and Byth et al. (1969b).

Among the other characters studied those that are more consistently associated genotypically with economic characters should serve as indicators in selection programs, assuming each one is highly heritable. Characters such as tawny pubescence, late flowering, late maturity, longer fruiting period, increased plant height, and, to some extent seed weight, might serve such purpose. Values of correlation of effective plant height with yield were slightly higher than those of plant height with yield. This may be due to effective plant height being a better indication of the total pod bearing area of the plant than is plant height. Since this information was obtained on spaced plants, it may not be of much practical value since, under general cultivation, the seeds are closely planted and there is less opportunity for the plants to branch heavily. Low protein content, larger seed size and, to some extent, increased plant height should serve as indicators of high oil content. Likewise, low oil content should serve as an indicator of high protein content. Since other characters were inconsistently correlated with both oil content and protein content they would not reliably serve as indicators.

Heritability Estimates and Partitioning of Genetic Variance into Component Parts

Broad sense heritability estimates obtained by the variance components method were generally higher than narrow sense heritabilities. Since the dominance component of the genetic variance in early segregating generations was generally greater, it is probable that the observed values may be over-estimates of actual values. The degree of over-estimation depends upon the expectations considered. The expected dominance portion, according to some workers, is higher (Horner et al., 1955), while other workers give lower expectations (Mather, 1949). The same is true for the additive component. The additive component is important in deciding how much of observed parental variation will be transmitted from parent to offspring. Hence, the removal of the dominance portion from the total genetic variance gives an estimate of narrow sense heritability. Because the expectations of the additive portion also vary, according to different workers, the reliability of the narrow sense heritability estimates is questionable.

The response obtained in the offspring should provide the best estimate of heritability. From this standpoint, the heritability estimates obtained by the regression method seem to be more reliable than others. The data in Table 14, page 54, indicate that some narrow sense heritability values are very close to the regression values. Although the dominance portion in the F_3 generation was higher, Smith and Kinman's (1965) suggestion to use two-thirds of the regression coefficient as an

estimate of heritability in self-pollinated crops may provide adjustments for the dominance component of the genetic variance.

The heritability values by the components-of-variance method, both in the narrow and broad sense, might be inflated by the over-estimate of environmental variance. In soybeans where there is a great deal of interplant competition, it is difficult to obtain reliable estimates of environmental variance.

In partitioning the genetic variance, it was assumed that the additive and dominance portions were the only components involved. Previous studies (Brim and Cockerham, 1961) have indicated that additive x additive, additive x dominance and other types of epistatic components and parameters that arise because of possible linkage between quantitative genes (Gates et al., 1960) also constitute a significant portion of the genetic variance. When these components are not separated, as in the present case, even the narrow sense estimates become unreliable over-estimates.

Mite Infestation in F_2 Populations

The Susceptibility of F_1 and F_2 plants in the cross D54 x D65 can be accounted for by the complementary epistatic action of two pairs of genes, one pair in each parent. The gene symbol (Mtmt) is proposed for reaction to mite damage. Assigning Mt_1Mt_1 to a locus in D54 and Mt_2Mt_2 to another locus in D65, the Mt_1 - Mt_2 - condition in hybrids makes the plant susceptible to the mite incidence, each locus complementing the action of the other; while Mt_1 - mt_2mt_2, $mt_1mt_1Mt_2$ - and

$mt_1mt_1mt_2mt_2$ conditions make the plants resistant.

In the cross Hill x S-100 where both S-100 and the F_1 plants were found to be resistant, S-100 is proposed as being of the genotype Mt_3Mt_3 and Hill of the genotype mt_3mt_3 at the corresponding locus. The Mt_3mt_3 condition that exists in the F_1 plants and the Mt_3Mt_3 and Mt_3mt_3 conditions that exist in F_2 plants confer resistance to the plants, while mt_3mt_3 plants are susceptible.

Gene Numbers

Possibly all the quantitative characters are governed by several pairs of genes. Mendelian ratios indicate that the number of genes that differentiate the parents for the various quantitative characters varies from 3 to 5 pairs. As mentioned in Chapter IV, the ratio tested in each case proved to be the best fit. Discrepancies observed in obtaining proper goodness of fit in Chi-square tests in some cases, and the appearance of a few extreme types in the segregating populations, were assumed to be the result of many minor genes which modify the effects of quantitative genes.

The Castle-Wright formula gave a very low estimation of gene numbers in almost every case. This may possibly be due to the underestimation of environmental variance. The F_1 variance equated to the environmental variance in the denominator was small. The difference $\hat{\sigma}^2_{F_2} - \hat{\sigma}^2_{F_1}$, therefore, remained larger in every case than the numerator. On the other hand, $\hat{\sigma}^2_{\bar{F}_2} - \hat{\sigma}^2_{\bar{F}_1}$ resulted in smaller values in the denominator often being negative since the $\hat{\sigma}^2_{\bar{F}_1}$ was based on a limited number of plants. This probably resulted in the overestimation of the number

of genes. It was, therefore, felt that the Castle-Wright and Burton formulae were not reliable at least in this study where the number of F_1 plants grown was limited.

Selection Indices and Predicted Genetic Advance

The objective in constructing these indices was to obtain information about the character or combination of characters, which would serve as the best indicator of yield in a selection program. In constructing selection indices, variance and covariance data on the F_3 progenies were used. Those characters which were found to be highly heritable, in addition to being highly associated with yield, were included in the selection indices.

The amount of genetic variance in each of the characters was found to decide the amount of genetic progress expected. Genetic variances for time of maturity and yield were higher than for other characters (Appendix Table 24). For the same reason, predicted advance was fairly high when selection was based on yield alone. The genetic variances for seed weight and extent of lodging were low, and the prediction of yield was not improved by adding either or both of these characters. On the other hand, the addition of time of maturity to the index improved the predicted advance considerably.

The extent to which these indices are reliable depends on three factors. Firstly, the relative economic importance of each character included in the index determines the reliability. Brim et al. (1959) assigned variable economic weights to each of the characters based on

importance of the character in deciding the economic worth of the predicted gain. Such economic weights for each character vary in both time and space. In the present study all characters considered were assumed to be of equal importance. Secondly, the heritability of each character is important. The higher the heritability of a character, the better it serves as an indicator in the selection program. Third and the most important is the accuracy with which the genetic variance is estimated as well as the size of the additive component. Any inaccuracy in their estimation will give biased values of the predicted advance and the discrepancy between the predicted and the actual gains becomes greater.

Relation of Hypocotyl Color to Pubescence Color

All the seedlings having light-green hypocotyl color developed plants bearing gray pubescence, while all seedlings having yellowish green hypocotyls, except for one, developed plants bearing tawny pubescence. This one discrepancy, as explained earlier, might be due to an error in identifying the hypocotyl color. This indicated that the gene that differentiated hypocotyl color and the gene that differentiated pubescence color were identical.

Hypocotyl tests in artificial light in the laboratory indicated that certain qualities of the light in nature are essential for the hypocotyl color to develop.

Reaction of Plants to Leaf and Seed-Coat Mottling

In 1969, field observations gave indications that D65 was more susceptible than D54 to leaf mottling. Greenhouse experiment group 1

indicated both D65 and D54 to be fairly susceptible. Since the parents were susceptible, a majority of the F_2 plants showed infection. Inoculations of group 2 plants with an inoculum prepared from plants in group 1 indicated that the leaf mottling was an indicator of the presence of the pathogen, that the causal organism was of an infectious nature and that the pathogen could be transmitted mechanically.

At maturity, all the plants with leaf mottling had seed-coat mottling also. In group 1, however, two plants not showing leaf mottling earlier did show seed-coat mottling which might be due to (1) a failure to recognize leaf mottling, (2) the slow rate of multiplication and development of the pathogen in some plants or (3) the symptoms which may appear in only leaves or only in seeds if leaf mottling and seed-coat mottling are independent phases affected by the pathogen. The remaining 21 plants could be inherently resistant types.

In group 2, the six plants in the "susceptible" class, which did not show leaf or seed-coat mottling, also could be ones which were genetically resistant.

In 1971, the absence of leaf or seed-coat mottling in any of the plants grown from the seeds of "resistant" class plants, even though artificially inoculated, further confirmed the possibility of isolating types resistant to this disease. Similarly, the appearance of both leaf and seed-coat mottling in all the plants grown from the seeds of "susceptible" class plants indicated that the pathogen was seed-transmitted which is in accordance with earlier findings (Conover, 1949).

CHAPTER VI

SUMMARY

Two intervarietal crosses of soybeans were involved in the study. The F_2 generation of the cross D54 x D65 was studied both in 1969 and 1970, while the F_2 of the cross Hill x S-100 was grown only in 1970. The F_3 generation of D54 x D65 was studied also in replicated tests in two locations in 1970. Yield, oil content, protein content, time of flowering, time of maturity, plant height and seed weight were the characters studied in the F_3 generation. Protein content was not included in the study of F_2 material, but fruiting, effective plant height and number of branches were studied in addition to the above characters.

Days to flowering, days to maturity, fruiting period, height and, to some extent, seed weight were found to be associated, both genotypically and phenotypically, with yield. Oil content was found to be associated with plant height and seed size. The only character with which protein content was consistently associated was oil content.

Both broad and narrow sense heritability estimates were obtained. Broad sense estimates obtained by the components-of-variance method in the F_2 and F_3 generations were, in general, higher than narrow sense heritability estimates. Estimates of narrow sense heritability, computed after partitioning the genetic variance and covariances, were high for time of flowering, medium for time of maturity and low for yield

and seed weight. Narrow sense estimates for oil content were zero. Estimates based on regression of F_3 on F_2 were smaller than those based on components-of-variance. The estimates obtained by the regression method are believed to be more reliable.

Mite damage occurred in the plantings in 1970 and afforded an opportunity to study its inheritance. Reaction of the plants appears to be monogenically controlled with resistance being dominant over susceptibility in the cross Hill x S-100. On the other hand, the susceptibility of the F_1 and F_2 plants in D54 x D65 appears to be due to the complementary action of two pairs of genes, each parent containing one of them. The gene symbol (Mtmt) has been proposed for resistance and susceptibility in the two crosses.

The number of genes differentiating the parents in each cross with respect to each character studied varied from 3 to 5 pairs when estimated by Mendelian ratios. The Castle-Wright formula and the one used by Burton failed to provide satisfactory estimates.

Selection indices and predicted genetic progress in yield were computed using maturity, seed weight and lodging in addition to yield. Considering the predicted gain when yield alone was included in the index as 100 percent efficient, the addition of seed weight and lodging to the index did not improve the predicted gain significantly, while the addition of maturity to yield improved the estimates considerably. This indicated that significantly higher yields could be obtained by using an index consisting of yield and maturity in the selection program.

Greenhouse tests with Hill x S-100 indicated that the gene controlling hypocotyl color controlled pubescence color also. S-100 had light-green hypocotyls and gray pubescence color, while Hill had slightly yellowish-green hypocotyls and tawny pubescence color. Studies pertaining to the mosaic virus disease which caused leaf and seed-coat mottling indicated that plants genetically resistant to this disease could be isolated in the cross D54 x D65.

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APPENDIX

Table 17. Variances of various characters in parental F_1 and F_2 generations of D54 and D65 grown in 1969 and 1970 and of Hill x S-100 grown in 1970.

Cross and generation	Pubescence color	Growth habit	Flowering	Maturity	Fruiting period
D54 x D65 (1969)					
P_1 (D54)	0.0	0.0	1.87	19.00	21.92
P_2 (D65)	0.0	0.0	4.05	10.90	11.67
F_1	-	-	-	-	-
F_2	0.19	0.18	24.68	92.95	39.69
D54 x D65 (1970)					
P_1 (D54)	0.0	0.0	12.64	18.14	16.50
P_2 (D65)	0.0	0.0	2.31	1.55	2.07
F_1	0.0	0.0	2.32	7.51	4.54
F_2	0.21	0.18	80.58	56.77	35.72
Hill x S-100 (1970)					
P_1 (Hill)	0.0	0.0	2.90	4.50	3.07
P_2 (S-100)	0.0	0.0	12.10	12.40	13.12
F_1	0.0	0.0	1.25	3.50	5.25
F_2	0.16	0.14	21.19	34.37	21.01

Table 17 (continued)

Cross and generation	Height	Effective height	Number of branches	Seed yield	100 seed weight	Oil percent
D54 x D65 (1969)						
P_1 (D54)				851.47	0.81	0.31
P_2 (D65)				786.25	2.55	0.33
F_1						
F_2				1610.42	3.19	2.94
D54 x D65 (1970)						
P_1 (D54)	24.58	1463.86	1.24	929.69	1.14	0.77
P_2 (D65)	15.46	1875.60	3.70	1301.27	1.07	0.22
F_1	11.43	2334.49	2.06	1792.60	1.88	0.11
F_2	188.72	14415.15	7.37	4206.11	3.34	0.89
H111 x S-100 (1970)						
P_1 (H111)	8.40	447.79	0.77	614.49	0.23	0.78
P_2 (S-100)	19.34	1852.71	0.90	503.61	0.84	0.34
F_1	3.53	3822.50	2.11	994.75	0.69	0.71
F_2	176.38	11564.12	3.90	1719.99	3.36	0.75

Table 18. Estimated genetic variances of various characters in the F_2 generations of D54 x D65 grown in 1969 and 1970 and of Hill x S-100 grown in 1970.

	CROSS		
	D54 x D65 (1969)	D54 x D65 (1970)	Hill x S-100 (1970)
Flowering	21.72	73.10	13.69
Maturity	78.00	46.93	25.92
Fruiting period	22.90	26.43	12.92
Height	-	168.70	162.51
Effective height	-	12745.42	10415.87
Number of branches	-	4.91	3.07
Seed yield	791.56	3090.63	1160.94
100 seed weight	1.51	2.24	2.84
Oil percent	2.62	0.40	0.23

Table 19. Covariances among characters in the parental and F_2 populations of the cross D54(P_1) x D65(P_2), 1969.

Characters		Flowering	Maturity	Fruiting period	Seed yield	100 seed weight	Oil percent
Pubescence color	F_2	-1.63	-2.81	-1.16	-4.37	-0.05	-0.05
	P_2^2	0.0	0.0	0.0	0.0	0.0	0.0
	P_2^1	0.0	0.0	0.0	0.0	0.0	0.0
Growth habit	F_2	-0.28	-0.84	-0.84	-3.83	-0.04	-0.26
	P_2^2	0.0	0.0	0.0	0.0	0.0	0.0
	P_2^1	0.0	0.0	0.0	0.0	0.0	0.0
Flowering	F_2		38.98	14.12	57.97	1.29	1.64
	P_2^2		-0.65	-2.58	-16.94	-0.19	0.01
	P_2^1		1.64	-2.40	-8.42	-0.23	0.06
Maturity	F_2			53.17	138.45	5.82	2.91
	P_2^2			19.45	69.96	0.65	-0.13
	P_2^1			9.26	93.42	1.47	0.04
Fruiting period	F_2				81.13	4.42	1.30
	P_2^2				84.76	0.85	1.86
	P_2^1				18.34	1.23	-0.02
Seed yield	F_2					16.74	23.24
	P_2^2					17.13	20.12
	P_2^1					10.00	16.61
100 seed weight	F_2						1.50
	P_2^2						-0.05
	P_2^1						-0.11

Table 20. Covariances among various characters in the parental and F_2 populations of the cross D54 (P_1) x D65(P_2), 1970.

Characters		Flowering	Maturity	Fruiting period	Height	Effective height	Number of branches	Seed yield	100 seed weight	Oil percent
Pubescence color	F_2	-2.84	-2.02	0.88	-2.03	-16.20	-0.14	-8.74	-0.05	-0.03
	P_2^2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	P_2^1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Growth habit	F_2	-0.59	-0.96	-0.31	-4.36	-27.99	-0.25	-12.20	-0.22	0.09
	P_2^2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	P_2^1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Flowering	F_2		50.44	-29.74	41.78	327.67	2.62	150.37	1.59	1.74
	P_2^2		7.14	-5.50	-13.32	-86.21	0.18	-36.46	-2.31	0.33
	P_2^1		0.90	-1.41	-2.89	-28.97	-0.89	-9.03	0.56	-0.21
Maturity	F_2			5.99	52.12	445.65	4.50	234.57	6.07	1.39
	P_2^2			11.00	-4.40	-16.80	1.26	34.04	-0.06	2.72
	P_2^1			0.65	-0.26	12.03	1.01	28.34	0.97	-2.65
Fruiting period	F_2				8.94	106.18	1.45	77.29	4.54	-0.35
	P_2^2				8.92	69.42	1.08	70.50	2.50	0.24
	P_2^1				2.63	41.01	1.89	37.37	0.41	0.24
Height	F_2					1345.47	18.70	654.52	8.59	2.75
	P_2^2					158.98	1.66	85.40	2.90	1.26
	P_2^1					154.64	5.67	89.46	-1.34	0.69
Effective height	F_2						244.88	6107.16	71.99	15.47
	P_2^2						27.56	858.86	27.30	9.89
	P_2^1						77.47	1291.54	-2.09	8.43
Number of branches	F_2							109.48	0.87	-0.09
	P_2^2							15.81	0.32	0.11
	P_2^1							60.72	0.35	0.38
Seed yield	F_2								51.58	7.12
	P_2^2								22.96	18.38
	P_2^1								11.90	8.27
100 seed weight	F_2									0.33
	P_2^2									0.12
	P_2^1									-0.13

Table 21. Covariances among characters in the parental and F_2 populations of the cross Hill(P_1) x S-100(P_2), 1970.

Characters		Flowering	Maturity	Fruiting period	Height	Effective height	Number of branches	Seed yield	100 seed weight	Oil percent
Pubescence color	F_2	-0.84	-0.81	0.03	-0.91	-9.11	-0.20	-2.75	-0.09	-0.04
	P_2^2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	P_2^1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Growth habit	F_2	-0.46	-1.01	-0.50	-4.06	-27.28	-0.14	-4.32	0.08	-0.07
	P_2^2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	P_2^1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Flowering	F_2		17.03	-4.20	13.53	106.42	1.97	12.31	-0.94	1.05
	P_2^2		2.17	-0.73	2.51	-13.57	-0.26	11.42	0.43	1.03
	P_2^1		5.69	-6.41	-13.63	-35.93	1.37	-30.17	-0.36	0.99
Maturity	F_2			16.43	37.26	298.81	3.37	78.06	2.49	1.23
	P_2^2			2.33	2.89	-0.39	0.28	22.44	0.72	1.46
	P_2^1			6.00	-5.96	-6.80	1.16	4.33	1.93	1.63
Fruiting period	F_2				22.09	182.67	1.44	65.99	3.36	-0.20
	P_2^2				0.37	13.18	0.53	11.02	0.29	0.42
	P_2^1				7.68	29.13	-0.21	34.51	2.29	0.65
Height	F_2					1214.85	9.66	262.03	1.73	2.57
	P_2^2					20.93	0.24	53.64	0.49	2.28
	P_2^1					97.13	-0.88	38.72	0.62	-1.25
Effective height	F_2						154.56	2873.05	20.98	25.47
	P_2^2						14.03	357.13	2.90	7.53
	P_2^1						28.47	621.67	10.13	0.05
Number of branches	F_2							55.17	0.46	0.28
	P_2^2							11.18	0.26	0.35
	P_2^1							9.94	0.18	0.22
Seed yield	F_2								29.92	6.91
	P_2^2								6.24	18.86
	P_2^1								5.00	0.12
100 seed weight	F_2									-0.22
	P_2^2									0.29
	P_2^1									-0.41

Table 22. Genetic covariances among various characters in the F_2 generation of the cross D54 x D65 grown in 1969 and 1970.

Characters	Year Grown	Flowering	Maturity	Fruiting period	Height	Effective height	Number of branches	Seed yield	100 seed weight	Oil percent
Pubescence color	1969	-1.63	-2.81	-1.16				-4.37	-0.05	-0.05
	1970	-2.84	-2.02	-0.88	-2.03	-16.20	-0.14	-8.74	-0.05	-0.03
Growth habit	1969	-0.28	-0.84	-0.54				-3.83	-0.38	-0.26
	1970	-0.59	-0.96	-0.31	-4.36	-27.98	-0.25	-12.20	-0.22	0.09
Flowering	1969		38.49	16.61				70.65	1.51	1.64
	1970		48.42	-26.28	49.88	393.36	2.97	173.12	2.46	1.68
Maturity	1969			38.82				56.76	4.76	2.96
	1970			0.16	54.45	448.03	3.36	203.38	5.62	1.35
Fruiting period	1969							29.72	3.38	0.38
	1970				3.17	50.96	-0.03	23.36	3.09	-1.66
Height	1969									
	1970					1188.65	15.03	567.09	7.81	1.78
Effective height	1969									
	1970						192.36	5031.96	59.38	6.31
Number of branches	1969									
	1970							71.21	0.54	-0.34
Seed yield	1969								3.17	4.88
	1970								34.16	-6.21
100 seed weight	1969									1.53
	1970									0.33

Table 23. Genetic covariances among various characters in the F_2 generation of the cross Hill x S-100 grown in 1970.

Characters	Flowering	Maturity	Fruiting period	Height	Effective height	Number of branches	Seed yield	100 seed weight	Oil percent
Pubescence color	-0.84	-0.81	-0.03	-0.91	-9.11	-0.202	-2.75	-0.09	-0.04
Growth habit	-0.46	-0.01	-0.50	-4.06	-27.28	-0.14	-4.32	0.08	-0.07
Flowering		13.10	-0.62	19.09	81.67	1.42	21.69	-0.9	0.04
Maturity			11.97	38.79	302.50	2.66	64.68	1.16	-0.32
Fruiting period				18.06	161.52	1.28	43.22	2.07	0.33
Height					1155.81	9.98	215.85	1.18	2.05
Effective height						133.31	2383.65	14.46	21.68
Number of branches							44.60	0.24	-0.01
Seed yield								24.30	-2.58
100 seed weight									-0.17

Table 24. Estimates of genetic and phenotypic variance values by the analysis of variance of the replicated F_3 trials grown at Knoxville and Jackson and the combined locations, 1970.

Component	Flowering	Maturity	Plant height	Lodging	Seed yield	Oil percent	Protein percent	100 seed weight
Knoxville								
Genetic ($\hat{V}g_1$)	58.82	48.67	51.77	0.32	16325.58	0.20	0.25	1.06
Phenotypic ($\hat{V}p_1$)								
Progeny basis	68.16	56.28	61.81	0.61	49609.60	0.48	0.84	2.09
Replication basis	63.43	52.47	56.80	0.47	32967.59	0.34	0.55	1.58
Jackson								
Genetic ($\hat{V}g_1$)			35.08	0.54	4025.89	0.22	0.65	1.04
Phenotypic ($\hat{V}p_1$)								
Progeny basis			45.46	0.91	10098.06	0.39	1.20	1.72
Replication basis			40.27	0.73	7061.97	0.31	0.93	1.38
Combined								
Genetic ($\hat{V}g_2$)			41.59	0.36	4711.44	0.19	0.33	0.89
Phenotypic ($\hat{V}p_2$)								
Progeny basis			53.64	0.76	29853.83	0.43	1.02	1.90
Replication basis			45.05	0.48	12363.11	0.26	0.54	1.18

Table 25. Mean products among characters by analysis of covariance of the replicated F_3 trial grown at Knoxville, 1970.

Character covariated	DF	Maturity	Plant height	Lodging	Seed yield	Oil percent	Protein percent	100 seed weight
Flowering								
Replications	1	68.20	-14.73	-22.26	2003.04	6.37	-37.45	-25.09
Progenies	121	69.85	49.58	2.77	1160.05	0.23	-2.61	-1.67
Error	121	-0.06	1.62	0.13	-108.81	0.10	-0.09	-0.58
Maturity								
Replications	1		-9.95	-15.03	1352.37	4.30	-25.28	-16.94
Progenies	121		47.05	3.13	1915.22	1.09	-2.57	5.04
Error	121		2.35	0.08	281.77	0.19	-0.10	1.60
Plant height								
Replications	1			3.25	-292.16	-0.93	5.46	3.66
Progenies	121			4.28	914.32	2.99	-2.74	7.92
Error	121			0.06	208.37	0.04	-0.16	0.93
Lodging								
Replications	1				-441.43	-1.403	8.25	5.53
Progenies	121				15.52	0.017	-0.12	-0.13
Error	121				-18.74	-0.001	0.05	0.03
Seed yield								
Replications	1					126.31	-742.53	-497.57
Progenies	121					22.83	-52.00	186.28
Error	121					10.25	-10.42	109.80
Oil percent								
Replications	1						-2.36	-1.58
Progenies	121						-0.34	0.42
Error	121						-0.29	0.02
Protein percent								
Replications	1							9.30
Progenies	121							0.17
Error	121							0.08

Table 26. Mean products among characters by the analysis of covariance of the replicated F_3 trial grown at Jackson, 1970.

Characters covariated	D.F.	Lodging	Seed yield	Oil percent	Protein percent	100 seed weight
Plant height						
Replications	1	0.25	3273.59	-25.09	12.54	16.52
Progenies	121	4.32	34.12	-0.55	1.84	1.91
Error	121	0.02	-7.71	-0.42	0.36	0.30
Lodging						
Replications	1		8.77	-0.07	0.03	0.04
Progenies	121		-19.08	-0.07	0.19	-0.10
Error	121		5.42	-0.02	-0.02	-0.05
Seed yield						
Replications	1			-898.98	449.49	592.01
Progenies	121			3.75	-9.27	39.08
Error	121			3.26	1.99	12.78
Oil percent						
Replications	1				-3.44	-4.54
Progenies	121				-0.62	-0.02
Error	121				-0.16	-0.08
Protein percent						
Replications	1					2.27
Progenies	121					0.92
Error	121					0.24

Table 27. Genetic covariances among characters estimated by the analysis of covariance of the replicated F_3 trials grown at Knoxville, 1970.

Characters	Flowering	Maturity	Plant height	Lodging	Seed yield	Oil percent	Protein percent
Maturity	34.95						
Plant height	23.98	22.35					
Lodging	1.32	1.52	2.11				
Seed yield	634.43	816.73	352.97	17.13			
Oil percent	0.06	0.45	1.47	0.01	6.29		
Protein percent	-1.26	-1.24	-1.29	-0.09	-20.79	-0.08	
100 seed weight	-0.55	1.72	3.49	-0.08	38.24	0.20	0.05

Table 28. Genetic covariances among characters estimated by the analysis of covariance of the replicated F_3 trials grown at Jackson, 1970

Characters	Plant height	Lodging	Seed yield	Oil percent	Protein percent
Lodging	2.15				
Seed yield	20.91	-12.25			
Oil percent	-0.06	-0.03	0.25		
Protein percent	0.74	0.10	-5.63	-0.23	
100 seed weight	0.81	-0.02	13.15	0.03	0.34

Table 29. Frequency distributions of various characters in the F_2 generations of D54 x D65 and Hill x S-100, 1970.

Class interval (days)	D54 x D65	Hill x S-100	Class interval (days)	D54 x D65	Hill x S-100	Class interval (days)	D54 x D65	Hill x S-100
	Flowering			Maturity			Fruiting Period	
35-37		1	101-103			51-53	2	1
38-40			104-106			54-56	3	1
41-43		2	107-109		2	57-59	5	2
44-46	7	2	110-112		2	60-62	20	7
47-49	4	5	113-115		6	63-65	30	18
50-52	9	14	116-118	10	15	66-68	23	36
53-55	10	41	119-121	4	15	69-61	27	46
56-58	4	54	122-124	13	25	72-74	31	40
59-61	7	33	125-127	18	30	75-77	6	11
62-64	12	9	128-130	11	34	78-80	3	4
65-67	26	4	131-133	24	32	81-83	1	1
68-70	29	1	134-136	7	6	84-86	1	
71-73	19	1	137-139	34				
74-76	11		140-142	23				
77-79	13		143-145	8				
80-82	1							

Table 29 (continued)

Class interval (inches)	D54 x D65	Hill x S-100	Class interval (inches)	D54 x D65	Hill x S-100	Class interval	D54 x D65	Hill x S-100
Height			Effective Height			Number of Branches		
1-5	5	1	1-25	15	3	1	5	1
6-10	13	4	26-50	14	10	2	3	4
11-15	15	9	51-75	7	8	3	5	2
16-20	8	7	76-100	14	10	4	13	12
21-25	15	11	101-125	11	7	5	22	18
26-30	21	11	126-150	9	11	6	33	32
31-35	22	11	151-175	14	10	7	24	43
26-40	21	33	176-200	15	13	8	15	29
41-45	17	37	201-225	18	10	9	4	14
46-50	9	20	226-250	5	23	10	12	8
51-55	4	7	251-275	2	13	11	6	1
56-60	2	12	276-300	8	14	12	3	3
61-65		3	301-335	7	6	13	4	
66-70		1	326-350	1	13	14	1	
			351-375		5			
			376-400	2	7			
			401-425	10	4			

TABLE 29 (continued)

Class interval (grams)	D54 x D65	Hill x S-100	Class interval (percent)	D54 x D65	Hill x S-100	Class interval (grams)	D54 x D65	Hill x S-100
Per Plant Yield			Oil Percent			Seed Weight		
1-20	21	10	18.0-18.5		1	8	1	
21-40	12	20	18.6-19.0			9	3	
41-60	21	17	19.1-19.5		1	10	8	3
61-80	15	25	19.6-20.0		3	11	13	8
81-100	16	27	20.1-20.5	2	9	12	25	16
101-120	12	34	20.6-21.0	1	26	13	36	36
121-140	13	18	21.1-21.5	1	25	14	30	34
141-160	12	12	21.6-22.0	6	40	15	17	37
161-180	13	4	22.1-22.5	9	18	16	7	20
181-200	6	1	22.6-23.0	24	11	17	1	6
201-220	4		23.1-23.5	20	6	18	2	1
221-240	6		23.6-24.0	32		19		2
241-260			24.1-24.5	22		20		
261-280	1		24.6-25.0	7		21		
			25.1-25.5	1		22		1
			25.6-26.0	2				

VITA

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He worked as a lecturer in the College of Agriculture, Dharwar, and also as a research worker in sorghum and cotton. Before his arrival in the United States for his graduate studies he held the post of Assistant Plant Scientist (cotton), Raichur, in the University of Agricultural Sciences, Bangalore.

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