THE EFFECT OF THE NARROW LEAF GENE ON YIELD AND OTHER CHARACTERS IN A SOYBEAN CROSS

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CHAPTER I

INTRODUCTION

Soybeans, Glycine max (L). Merrill, are an important agronomic crop due to the high levels of protein and oil in the seed. Decreasing farm land area and increasing world population demand a continued increase in yield per acre. Much of the increase in soybean yield has resulted from genetic improvement. This yield increase due to genetic improvement has been on the order of 0.7 to 0.9% per year (5,26). The search continues for methods to improve selection for yield and other desirable traits.

The yield components of soybeans are: seed weight, number of seeds per pod, number of pods per plant, and plants per unit area (39). The narrow leaf gene, present in some soybean cultivars, has a pleiotropic effect on number of seeds per pod (13). The narrow leaf character is inherited as a single gene (4,13,37). Thus the narrow leaf gene offers the opportunity to study characters, such as the yield components, which are normally under multigenic inheritance, through the manipulation of a single locus. Only narrow leaf and normal leaf lines have been compared. Results have not been published dealing with the effect of the narrow leaf gene in the heterozygous condition on yield either in the F_1 generation or succeeding generations. This is primarily due to the difficulty in distinguishing the heterozygote from the normal leaf homozygote.

The objectives of this study were to (a) evaluate F_1 heterosis for yield and yield components; (b) evaluate the reduction in heterosis in the F_2 generation and heterosis within the narrow, intermediate, and normal leaf types; and (c) to examine the relationships and inheritance of yield and yield components in the F_2 and backcross generations within narrow, intermediate, and normal leaf genotypes. The populations studied resulted from a cross between a normal leaf cultivar and a narrow leaf cultivar.

CHAPTER II

LITERATURE REVIEW

Narrow Leaf Gene

Most soybean cultivars grown in the United States have a broad or ovate leaflet. A few genotypes from the U.S. and Asia have distinctive narrow or lanceolate leaflets. A single recessive gene designated ln by Bernard and Weiss (4) controls the inheritance of the narrow leaf character. An association between narrow leaves and the yield component, number of seeds per pod, was first observed by Takahashi in 1934 (4,13). The narrow leaf genotypes tend to have a higher number of four seeded pods, compared to the usual two seeded pods produced by normal leaf cultivars. The yield component, number of seeds per pod, is very stable from cultivar to cultivar, and only slightly influenced by soil differences (40).

Domingo (13) tested the effect of the narrow leaf gene in crosses between normal and narrow leaf types. The expected frequencies were calculated for the proportion of narrow leaf plants which had high and low number of seeds per pod. These frequencies were compared to the proportion of normal leaf plants which had high and low number of seeds per pod. Domingo suggested that there was a crossover rate of 7.9 ± 0.8 between the narrow leaf gene and the gene for high number of seeds per pod. Weiss (37) found that selection for number of seeds per pod was possible within the narrow and normal leaf types. The number of seeds per pod produced by the lowest narrow leaf line remained higher than the high number of seeds per pod produced by the normal leaf lines. Weiss stated that the narrow leaf gene has a pleiotropic effect on the yield component, seeds per pod.

Jain and Singh (20) compared narrow leaf isolines of 'Clark' and 'Harosoy' developed through backcrossing to the normal cultivars. The T109 line, which is a line in the soybean germplasm collection, was the source of the narrow leaf gene (4). Plant height, number of pods per plant, seed weight, number of seeds per pod, and yield were compared. The authors reported that although the narrow leaf isolines were found to have more seeds per pod and lower seed weight no yield differences were found. None of the other yield components were found to be significantly different between the narrow leaf and normal leaf isolines.

Hartwig and Edwards (19) developed near isogenic lines with the narrow leaf trait through backcrossing. The recurrent parent was the line D49-2491 (a line closely related to the cultivar 'Lee'). The nonrecurrent parents providing the narrow leaf trait were the lines T109 and P. I. 181,537. A high number of seeds per pod was observed in the narrow leaf isolines in which the T109 germplasm was used. These narrow leaf lines also had lower seed weight than the normal leaf lines, but no yield differences were found. P.I. 181,527 was chosen because no differences in seed weight were observed in the selected isolines. Narrow leaf lines in which the P.I. 181,537 was used had a higher number of seeds per pod but the normal leaf lines had 28% more pods. Again, no differences in yield were observed.

Cooper (12) criticized the approach in which a single gene is incorporated into a line, suggesting that the introduced gene might not compliment the original genome of the plant.

Mandl and Buss (27) selected isolines from F_4 lines segregating for the leaf gene. These lines recieved the ln gene from D64-4731 which contains the gene from the T109 germplasm. Their results agreed with previous findings that the narrow leaf types were also associated with low seed weight, but no yield differences were found between isolines. Since the narrow leaf isolines had a higher number of seeds per pod, the authors concluded that the narrow leaf gene offered no yield advantages nor disadvantages.

The narrow leaf gene has an incomplete dominance effect (4), thus the heterozygote should be intermediate between the two leaf types but it is difficult to distinguish between the normal leaf type and the heterozygote. Domingo (13) first reported that the heterozygotes appeared to have an intermediate leaf shape. He used various leaf measuring techniques in his attempt to separate the normal leaf types from the heterozygotes but found no reliable index to use, however, he only measured a few plants from each cross. Consequently, all reported studies which have been conducted using the narrow leaf gene have only compared the normal and the narrow leaf types.

Heterosis

The extent of heterosis, ease of pollen transfer and a genetic-cytoplasmic male sterile system are some of the most important factors in determining the feasibility of commercial hybrids for a species. It is not presently economically feasible to produce hybrid soybeans due to the difficulty in cross pollination, and the lack of cytoplasmic male sterility. Normal outcrossing in soybeans ranges from 1 to 3% (15,41). Some genotypes which have the glabrous pubescence have been reported to have up to 10% outcrossing (2). A genetic male sterile exists for soybeans, but for efficient hybrid production an efficient method of pollen transfer has to be in effect (7).

Paschal and Wilcox (29) examined crosses among exotic germplasms for heterosis and reported 8% high parent heterosis for yield. They found significant (7.7%) high parent heterosis for plant weight. The number of pods per plant, however, was only 0.5% over the high parent, and a -4.6% high parent heterosis was observed for seed size. No heterosis was observed for number of seeds per pod, but plant weight showed 6.8% high parent heterosis. Yield exibited the highest amount of heterosis observed among all characters studied. The authors postulated that the wider than normal plant spacing conferred advantages that would not normally be present in rows. They concluded that the observed level of heterosis would not offset cost of seed production, and that breeding should be aimed at obtaining superior homozygous lines.

Weber et al. (36) found an average of 13.4% high parent heterosis for yield based on results from 85 combinations. High parent heterosis ranged from 90 to -39.1%, and 76% of the hybrids exceeded the high parent. They reported that heterosis was also observed for total plant weight, where 20.4% high parent heterosis was observed. Seed size was not found to differ significantly from the high parent the first year, but was significantly lower the second year. Plant height was observed to be intermediate.

Using adapted cultivars, Brim and Cockerham (6) reported significant mid-parent heterosis for yield, but no high parent heterosis. They found an average of 20% heterosis for yield in two crosses evaluated at two locations, in two years. The extent of inbreeding depression was measured for F_2 through F_6 . The data was not consistent over the two years that the study was conducted, however, the values did not vary significantly from the high parent. In one year the F_4 generation was found to be significantly higher than the high parent. The authors state that heterosis and inbreeding depression may not adequatly explain non-additive gene action for this self-fertilizing species.

Only a few instances have been observed where a single gene has had an effect on yield. Gustafsson (17) working with spontaneous chlorophyll mutants in barley reported two instances where the heterozygote produced more and larger seeds than the normal homozygous parents.

Heritability

Heritability in the broad sense is the fraction of the variance in the phenotype which is due to genetic effects. The genetic effects may be additive, dominant, or interactions, such as, additive X dominant, or additive X additive, termed as epistatic effects. The fraction of the phenotypic variance which is due to additive gene action is termed narrow sense heritability. Heritability estimates are based on the population of interest, thus a good estimate of the environmental variance is needed in order to accurately measure heritability. In self pollinating crops the parents are assumed to be homozygous, and the F_1 are assumed to be heterozygous at all loci. They are used to measure the environmental variance, since the observed variance within each class should be solely due to environment.

Weber and Moorthy (35) studied the inheritance of yield in three soybean crosses. They observed that their heritability estimates for yield in space planted soybean plants ranging from -0.78 to 0.60 were erratic due to large estimates of environmental variance. Heritability estimates for yield have generally been low (1,14,25).

Heritability estimates for plant height in soybeans range from 0.66 to 0.90 (10,25). Estimates of heritability for seed weight are generally considered to be high, ranging from 0.44 to 0.94 (14,25). Heritability for number of seeds per pod was found to be 0.59 (21). Heritability estimates for number of pods per plant were found to be between 0.22 to 0.56 (21).

Correlations

Grafius (16) stated that one must ultimatly change one or more of the yield components in order to improve yield. He suggested that in segregating populations of legumes and small grains correlations between yield components tend to be zero. This lack of correlation indicates that independent genetic systems govern the development of each particular yield component. Hansen (18) stated that yield components are genetically controlled but are secondary to the ability of the genotype to produce energy.

Yield components by definition, are correlated with yield. Phenotypic correlations for yield components with yield have been reported to be: number of pods per plant 0.15 (22) to 0.72 (30); seed weight 0.21 (10), 0.35 (30), 0.45 (22),and 0.46 (26); number of seeds per pod -0.17 (22) to 0.44 (30). Positive correlations have been observed between height and yield 0.25 (10), 0.31 (22), 0.32 and 0.44 (1), and 0.69 (30)

Negative phenotypic correlations were recorded among yield components. Correlations for number of pods per plant and seed weight range from -0.11 to -0.43. For number of pods per plant with number of seeds per pod, the range is from -0.57 to -0.68 (1). Correlations between seed weight and number of seeds per pod have been reported to be -0.06 to -0.28 (1).

Correlations are important in selection since a positive correlation between two economically important characters allows progress to be made on both characters simultaneously. However, if correlations between two desirable characters are negative, progress is hindered for one of the two characters.

CHAPTER III

MATERIALS AND METHODS

Cultivars

The parents chosen for this study were the cultivars 'Douglas', which is a normal leaf type, and the narrow leaf type 'Miles'. Both are maturity group IV and are well adapted to Oklahoma. Douglas was released in Kansas (28), originating as an F_4 selection from the cross 'Williams' X 'Calland'. The allele for white flowers, typical of Douglas, is recessive to the purple flower allele of Miles. Using Douglas as the female in crosses, flower color could be used as a marker gene to distinguish crossed seed from the selfed seed (40).

Miles was released in Maryland (24). It is the progeny of an F_6 plant selected from the cross 'Clark' X D64-4731. D64-4731 is a breeding line from the cross 'Lee' (2) X 'Clark' (2) X T109 . T109 is a narrow leaf line in the soybean germplasm collection which has been used in previous studies involving the narrow leaf type (19,20,27).

Original crosses were made in the field in 1981 and approximately 25 seeds were obtained. In 1982 the F_1's were grown in the field and some were backcrossed to each parent. Miles and Douglas were used as females for the backcrosses. These crosses resulted in 56 and 51 seeds backcrossed to

Douglas and Miles, respectively. The F_1's were selfed to produce the F_2 generation. Additional crosses were made between Douglas and Miles, and 130 seeds were obtained. The crossed seed was used to produce the F_1 generation.

Field Layout and Experimental Design

The study was conducted at the Perkins Agronomy Research Station Teller Loam Soil (Fine-Loamy, Mixed, Thermic Udic Argiustolls), Perkins, Oklahoma. The experiment was run as a Randomized Complete Block design consisting of ten replications. Experimental units were individual plants. Each replication was 7 X 9 m. consisting of 81 plants. A total of 130 crossed seed, 50 backcrossed seed to Douglas, 56 backcrossed seed to Miles, 110 seed from each parent, and 353 F_2 seed were planted at a spacing of 76 X 76 centimeters. The plants were spaced in order to minimize interplant competition. Each hill plot was individually planted. Three seeds were planted for each parent and F_2 hill which were thinned to one plant per hill following germination. Two cowpea (*Vigna unguiculata* (L.) Walp.) seed were planted with each F_1 and backcrossed seed to aid in breaking the soil, thus avoiding breaking the soybean coleoptyle. Each row was bordered by two similarly spaced discard plants. Discards were also planted in the cases where germination failed. Irrigation was provided throughout the summer as needed.

Characters Evaluated

The following characters were evaluated: leaf length, leaf width, height, plant biomass, number of pods per plant, seed weight, number of seeds per pod, and yield. The center leaflet, of the most recent fully expanded leaf was used for the leaf measurements. The leaf measurements were done on July 27 through July 29. All other measurements were done at harvest.

Leaf Length

Leaf length was measured in centimeters from the tip of the leaf to the beginning of the petiole.

Leaf Width

Leaf width was measured in centimeters at the widest part of the leaflet.

Height

Height was measured from the top of the last raceme of the plant to the ground, in centimeters, prior to harvest.

Plant Biomass

Total weight of air-dried above-ground biomass was measured in grams.

Seed weight

Weight of a random sample of 100 seed was measured in grams.

Seeds Per Pod

This character was indirectly calculated by dividing the total number of seed per plant by the number of pods per plant. The total number of seed was obtained by dividing yield by seed weight.

Pods Per Plant

The number of pods per plant was determined by counting all pods on harvested plants.

Yield

Total seed weight of each plant was weighed in grams.

Harvest Index

This character was calculated by dividing yield by plant biomass.

Comparisons Among Generations

Means over all generations were calculated and compared for all characters studied.

Heterosis

Heterosis was measured for the F_1 in relation to the mid-parent and high parent. An F test was used to determine the significance of differences between the F_1 and high parent, and the F_1 and midparent. Heterosis was calculated as follows:

$$(F_1 - MP)/MP \times 100 = \%\ \text{Mid-Parent Heterosis}$$

$$(F_1 - HP)/HP \times 100 = \%\ \text{High Parent Heterosis}$$

The average of the parents was used as the calculated mid-parent value.

Comparison Among Leaf Types

The ratio of leaf width to leaf length was used to classify each plant as narrow, intermediate, or normal leaf type. The ranges for leaf type were based on measurements obtained from the parents and F_1. A chi-square test was performed to test for homogeneity of the expected ratios for each genotype. The expected ratio for the F_2 was 1:2:1 narrow:intermediate:normal. Ratios for the backcrosses would be expected to be 1:1 intermediate:normal, and 1:1 narrow:intermediate, for backcrosses to Douglas and Miles, respectively.

Analyses were conducted to compare the narrow, intermediate and normal leaf types in the F_2 and backcrossed generations. The assumption was made that all other genes except for the leaf gene would be segregating independently. Thus any differences observed would be differences due to associations with the narrow leaf gene.

Heritabilities

Broad sense heritabilities were calculated using the method by Burton (9):

$$h^2_{bs} = \frac{var(x)_{F_2} - \left[(var(x)_{P_1} + var(x)_{P_2} + var(x)_{F_1})/3 \right]}{var(x)_{F_2}}$$

where $var(x)_{F_2}$, $var(x)_{F_1}$, $var(x)_{P_1}$, and $var(x)_{P_2}$, represent the variance of character 'x' in the F_2, F_1, and the parental generations, respectively. Heritabilities were estimated in the same way within each class using only the variance associated with the leaf type of interest in the F_2 variance term. Standard errors were calculated for all heritability estimates using an approach described by Kendall and Stuart (23).

Narrow sense heritability estimates were calculated using the method described by Warner (32).

$$h^2_{ns} = \frac{2var(x)_{F_2} - \left[var(x)_{BC_1} + var(x)_{BC_2} \right]}{var(x)_{F_2}}$$

where $var(x)_{F_2}$, $var(x)_{BC_1}$, and $var(x)_{BC_2}$ represent the variance of character 'x' in the F_2, backcross to Douglas, and backcross to Miles generations, respectively.

Narrow sense heritabilities were not calculated within leaf classes due to the low number of backcrossed plants in each leaf class.

Correlations

Relationships among the characters evaluated were studied by computing correlations. Phenotypic correlations were calculated using variances and covariances in the F_2 generation. using the following formula:

$$r_p = \frac{cov(x,y)_{F_2}}{\left[var(x)_{F_2} * var(y)_{F_2}\right]^{1/2}}$$

where $cov(x,y)_{F_2}$ represents the covariance between characters 'x' and 'y' in the F_2 generation, and $var(x)_{F_2}$ and $var(y)_{F_2}$ represent the variances of characters 'x' and 'y', respectively in the F_2 generation. Statistical significance was calculated in the usual way (31).

Phenotypic correlations were also calculated within each leaf type using the F_2 covariance and variances associated with characters 'x' and 'y' for a given leaf type.

Genotypic correlations were calculated using the following formula:

$$r_g = \frac{2cov(x,y)_{F_2} - \left[cov(x,y)_{BC_1} + cov(x,y)_{BC_2}\right]}{\left[\sigma^2_{A(x)} * \sigma^2_{A(y)}\right]^{1/2}}$$

where $cov(x,y)_{F_2}$, $cov(x,y)_{BC_1}$, and $cov(x,y)_{BC_2}$, represent the covariance between characters 'x' and 'y' for the F_2, BC_1, and BC_2 generations, respectively. $\sigma^2_{A(x)}$, and $\sigma^2_{A(y)}$ represent the additive variances for characters 'x' and 'y', respectively.

Genotypic correlations were not calculated within each leaf type due to the insufficient number of backcrosses.

CHAPTER IV

RESULTS AND DISCUSSION

Comparison of Means

Of the original 810 seeds planted, 530 plants survived and were used in the final analyses. Significant differences among generations for all characters were detected (Table I). Also, significant differences existed among leaf types for all characters except harvest index (Table II). The term entry was used to designate each generation, and leaf type refers to the narrow, intermediate, and normal leaf genotypes.

The leaf types are assumed to equate with genotypes as follows: the narrow leaf type is assumed to represent the _ln/ln_ genotype, the intermediate leaf type is assumed to have a _Ln/ln_ genotype, and the _Ln/Ln_ genotype is represented by the normal leaf type. Histograms of the number of plants in each leaf type for each generation are presented in Figures 1 and 2. The ranges for the ratio of leaf width to leaf length were 0.32 to 0.45, 0.52 to 0.65, and 0.65 to 0.87 for Miles, F_1, and Douglas, respectively (Figure 1). Although the ranges for Douglas and the F_1 ratios met at 0.65, there was no overlap. Based on the parental and F_1 ratios, the values 0.47 and 0.65 were used to differentiate between narrow to intermediate and intermediate to normal

TABLE I

ANALYSES OF VARIANCE FOR HEIGHT, PLANT BIOMASS, SEED WEIGHT, NUMBER OF SEEDS PER POD, NUMBER OF PODS PER PLANT, YIELD AND HARVEST INDEX

	df	Height	Plant Biomass	Seed Weight	Seeds Per Pod	Pods Per Plant	Yield	Harvest Index
Block	8	342.2**	18064**	19.89**	.2657**	15143**	3936**	.0193**
Entry	5	2111.5**	14138**	33.06**	.1092+	14845*	3745**	.0030*
Block * Entry	40	66.7	3665	1.83	.0364	5183	812	.0017
Error	447	69.38	3465	1.85	.0508	5243	726	.0016
C.V.		12.3	29.0	9.96	9.57	27.0	31.0	9.2

*,** Significant at the 0.05, and 0.01 levels of probability, respectively.
+ Significant at the 0.06 level of probability.

TABLE II

ANALYSES OF VARIANCE FOR HEIGHT, PLANT BIOMASS, SEED WEIGHT, NUMBER OF SEEDS PER POD, NUMBER OF PODS PER PLANT, YIELD AND HARVEST INDEX FOR COMPARISONS OF GENERATIONS, LEAF TYPE AND GENERATIONS IN LEAF TYPE

	df	Height	Plant Biomass	Seed Weight	Seeds Per Pod	Pods Per Plant	Yield	Harvest Index
Block	9	304.2**	19113**	21.92**	.3758**	16331**	5317**	.0278**
Leaf	2	3133.9**	66578**	93.39**	.4807**	75530**	13129**	.0019
Entry(Leaf)	9	608.8**	2689	3.38	.0480	2862	611	.0031
Block * Leaf	18	101.0	3655	1.97	.0579	5218	739	.0015
Bl * Ent(Leaf)	55	74.5	3349	2.04	.0473	4701	718	.0019
Error	436	69.7	3254	1.79	.0516	5067	679	.0015
C.V.		12.3	28.9	9.8	9.6	26.9	30.7	9.1

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

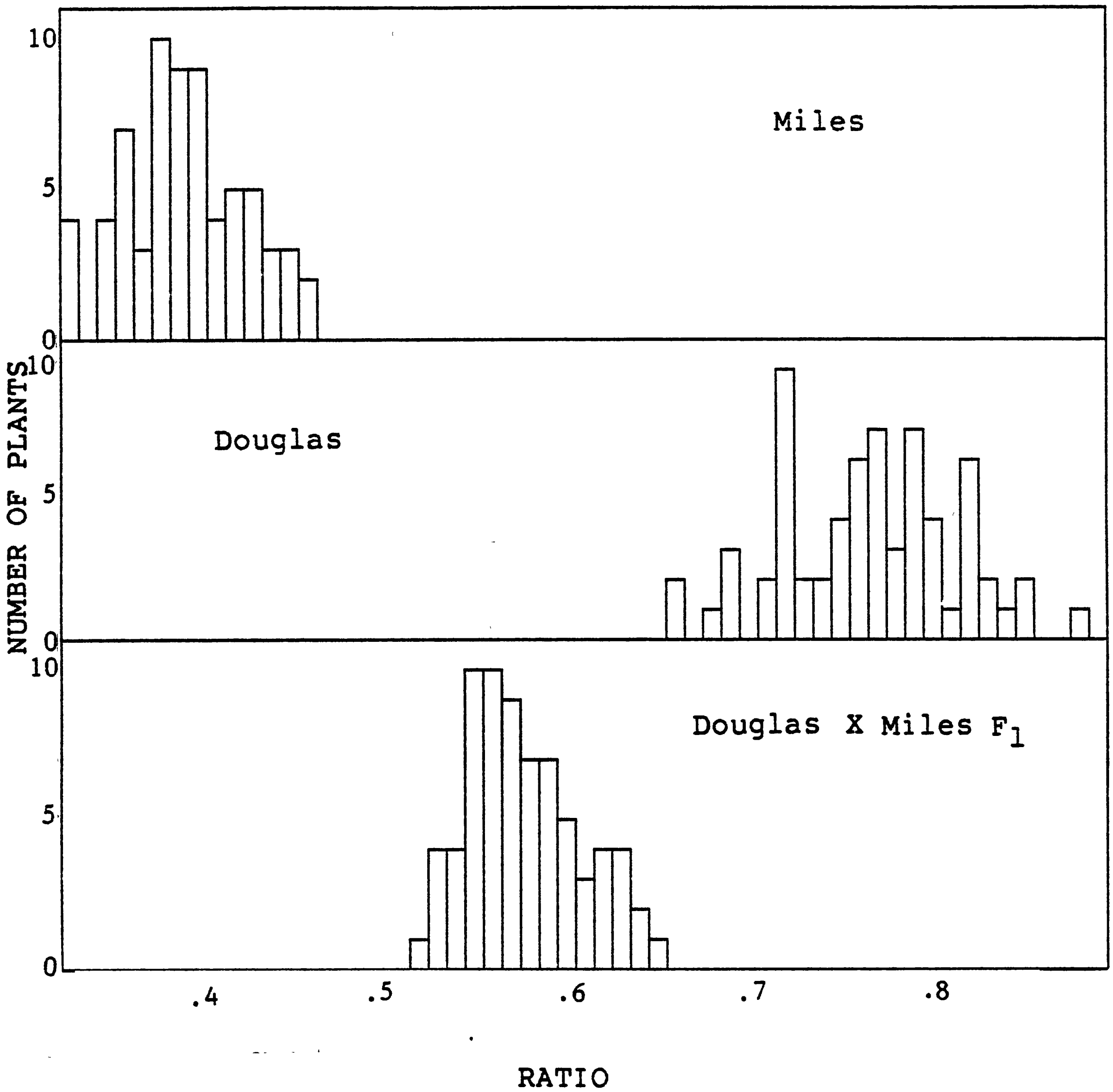

Figure 1. Distributions for the Parental and F_1 Generations for the Ratio of Leaf Width to Leaf Length.

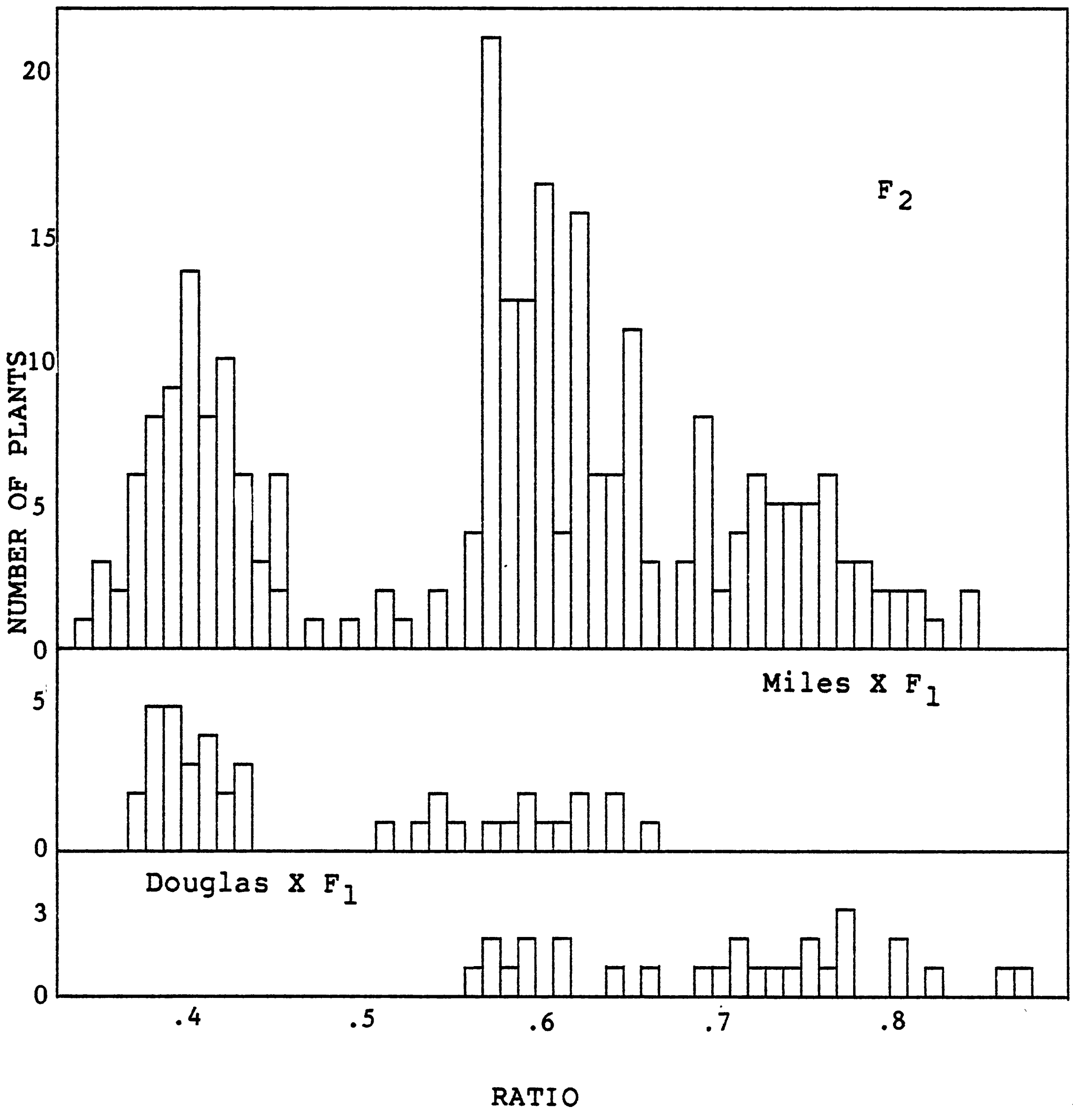

Figure 2. Distributions for the F_2 and Backcross Generations for the Ratio of Leaf Width to Leaf Length.

leaf types, respectively. The F_2 and backcrosses (Figure 2) were divided into narrow, intermediate, and normal leaf types by the above values.

There were 70, 126, and 58 plants classified as narrow, intermediate, and normal leaf type, respectively in the F_2 generation (Table III). Eleven plants were classified as intermediate and 18 as normal leaf types for the backcross to Douglas, and 24 and 16 plants were classified as narrow and intermediate, respectively, for the backcross to Miles. The numbers of plants in each leaf type were tested for the expected ratios assuming that the character is controlled by a single gene with incomplete dominance. For the F_2, the expected ratio was 1 narrow : 2 intermediate : 1 normal. The expected ratios for the backcrosses were 1 normal : 1 intermediate and 1 narrow : 1 intermediate for the backcrosses to Douglas and Miles, respectively. Chi square values of 1.15, 1.69, and 1.60 were calculated for the F_2, the backcrosses to Douglas, and the backcrosses to Miles, respectively. The probabilities that observed deviations will be as large as those actually obtained when the expected ratios are true are 0.5 to 0.7 for the F_2 generation and 0.2 to 0.3 for backcross to Miles, and 0.1 to 0.2 for backcross to Douglas. This indicates that the observed data show a good fit to the expected ratios of 1:2:1 and 1:1 for the F_2 and backcross generations, respectively.

Analyses of variance were conducted for height, plant biomass, seed weight, number of seeds per pod, number of

TABLE III

NUMBER OF PLANTS WITHIN LEAF TYPE FOR EACH GENERATION IN A DOUGLAS X MILES CROSS

	Leaf Type				
Generation	Narrow	Intermediate	Normal	X^2	Prob.
Douglas	0	0	58	--	--
Miles	72	0	0	--	--
F_1	0	71	0	--	--
F_2	70	126	58	1.15	.7-.5
Douglas X F_1	0	11	18	1.69	.2-.1
Miles X F_1	24	16	0	1.60	.3-.2

pods per plant, yield, and harvest index. Block four was omitted from the analyses among generations since no Douglas plants were included in that block due to an error in planting.

Comparison Among Generations

Overall means for each generation for height, plant biomass, seed weight, number of seeds per pod, number of pods per plant, yield, and harvest index are presented in Table IV.

Height. The parents were significantly different for height. Miles averaged 75.5 cm. while the Douglas mean was 57.8 cm. The F_1 mean was intermediate at 67.1 cm. and was significantly different from both parents. Mid-parent heterosis was calculated to be essentially zero (Table V). The distributions for height for the parents and F1 generations are presented in Figure 3. These results disagree with Caviness and Prongsirivathana (11) who found that the F_1 were as tall as the high parent. They suggested a single dominant gene was responsible for height. Paschal and Wilcox (29) found that three of the ten crosses they examined displayed significant mid-parent heterosis.

The F_2 and backcrosses were also intermediate to the two parental means and were not significantly different from the F_1. The F_2 were significantly different from both parents. The distribution of F_2 plants (Figure 4) show that possible additive gene action is responsible for the distri-

TABLE IV

MEANS FOR HEIGHT, PLANT BIOMASS, SEED WEIGHT, NUMBER OF SEEDS PER POD, NUMBER OF PODS PER PLANT, YIELD, AND HARVEST INDEX, FOR DOUGLAS, MILES, F_1, F_2 AND BACKCROSSES

Generation	Height (cm.)	Plant Biomass (grams)	Seed Weight (grams)	Seeds Per Pod (no.)	Pods Per Plant (no.)	Yield (grams)	Harvest Index
Douglas	57.8d*	188.5c	14.1ab	2.32c	249c	81.2cd	.4308ab
Miles	75.5a	181.7c	12.4c	2.44a	248c	76.3d	.4173b
F_1	67.1bc	211.3a	14.2b	2.35bc	278a	93.6a	.4429a
F_2	68.3b	205.5ab	13.8b	2.37bc	273ab	89.6ab	.4368ab
Douglas X F_1	63.8c	213.4abc	14.2ab	2.31bc	273abc	90.9abc	.4254ab
Miles X F_1	68.7b	185.0bc	12.9abc	2.42abc	260abc	81.7bc	.4416ab

*Means followed by the same letter do not differ at the 0.05 level of significance using the t test for each character.

TABLE V

PERCENT HIGH AND MID-PARENT HETEROSIS FOR SIX CHARACTERS FOR THE F_1 AND F_2 GENERATIONS IN A DOUGLAS X MILES CROSS

	F_1		F_2	
Character	Mid-Parent	High Parent	Mid-Parent	High Parent
Height	0.4	-11.6**	2.2	-10.0**
Plant Biomass	15.1**	11.9*	11.0**	9.0*
Seed Weight	7.2*	0.7	4.2**	-2.1
Seeds Per Pod	-1.3	-3.7*	0.4	-2.9*
Pods Per Plant	11.9*	11.6*	9.9**	9.6*
Yield	18.9**	15.3*	13.8**	10.3*
Harvest Index	4.4*	2.8	3.0**	1.4

*,** Significantly different at the 0.05 and 0.01 level of probability, respectively.

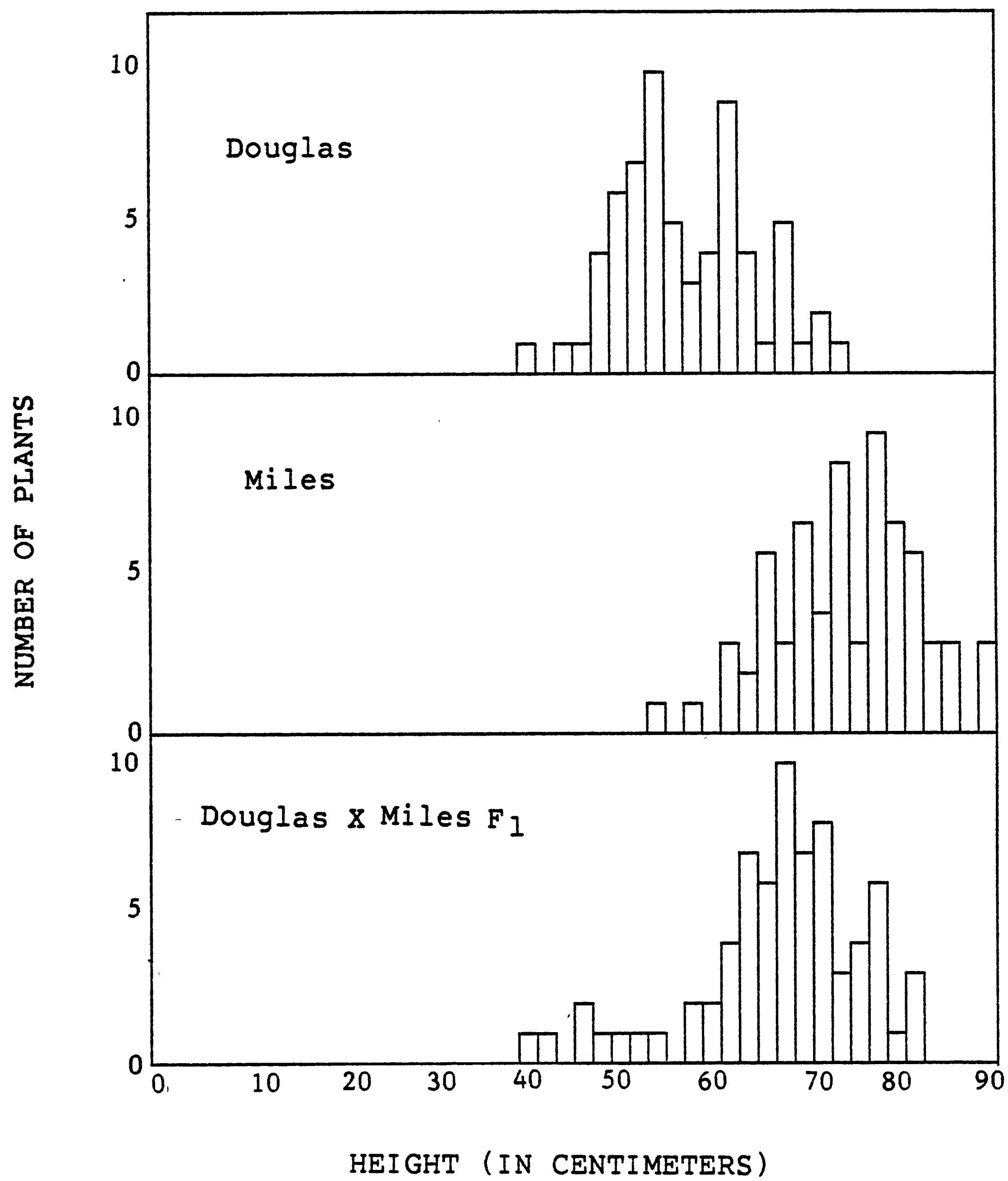

Figure 3. Distributions for the Parental and F_1 Generations for Height.

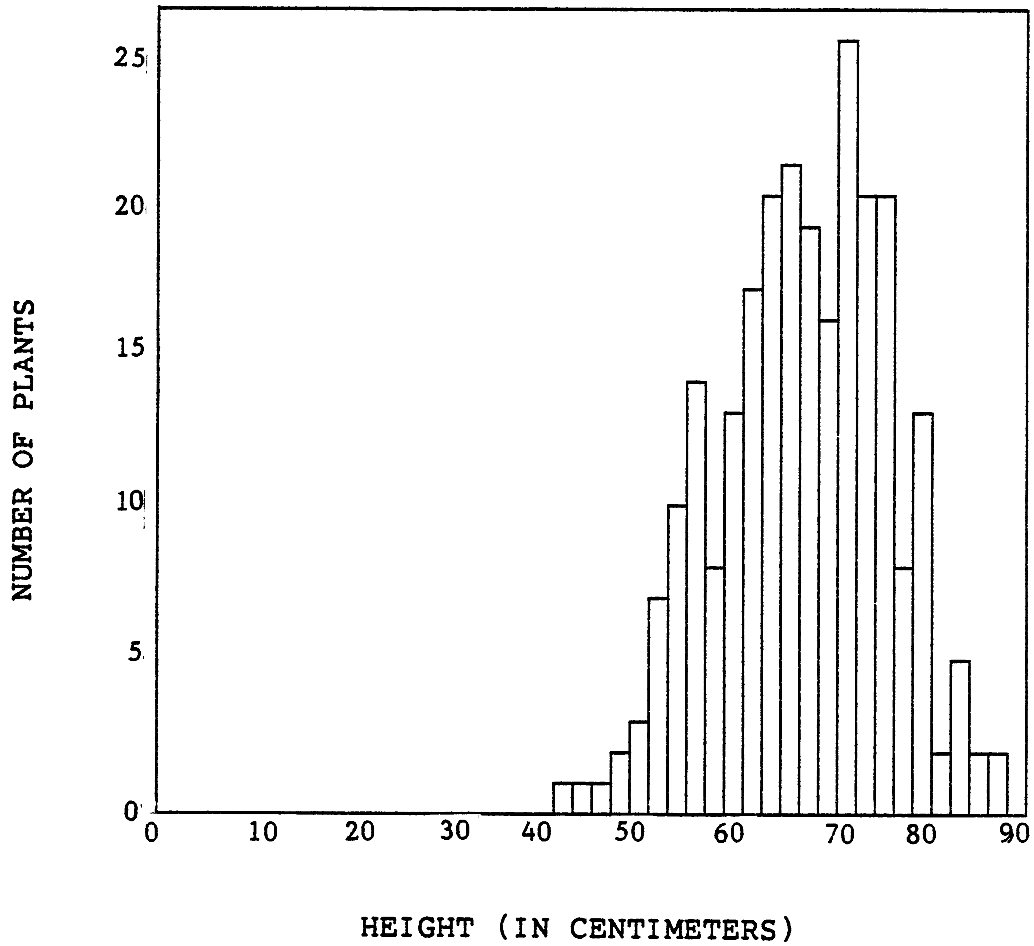

Figure 4. Distribution for the F_2 Generation for Height.

bution. Height may be influenced by few genes (11,18,40) however, from our results no discernable pattern emerged.

Plant Biomass. Both Miles (181.7 g.) and Douglas (188.5 g.) had low plant biomass weight (Table IV). The F_1 (211.3 g.) showed significant high parent heterosis (11.9%) (Table V). Weber *et al.* (34) found 20.4% high parent heterosis, and Paschal and Wilcox (29) found 6.8% high parent heterosis in soybeans. Brim and Cockerham (6) also found significant midparent heterosis in the F_1 generation, but later generations tended to regress toward the mid-parent suggesting additive gene action. The F_2 (205.5 g.) was significantly higher than either parent (Table IV), and continued to show high parent heterosis (9.0%) (Table V). The backcrosses were not significantly different from each other. The backcross to Douglas had the highest mean for all generations studied (213.4 g.). However, due to the low number of plants available it was not found to be significantly different from any of the generations studied. The backcross to Miles was low (185.0 g.) and was found to be different from the F_1 generation.

Seed Weight. There were significant differences between Douglas (14.1 g.) and Miles (12.4 g.) for seed weight (Table IV). Significant mid parent heterosis (7.2%) was observed, but high parent heterosis was close to zero (Table V). This observation is in agreement with previous results that some degree of mid-parent heterosis but no high parent heterosis is exhibited (38,38). The F_2 values did not differ from the F_1 values with an observed continued mid-parent heterosis (4.2%). These results are similar to those of Brim and Cockerham (6). They observed that from unselected F_2, the later generations tended toward the mid-parent value. Selection should be relatively easy for this character according to Hanson (18) since there are relatively few genes involved. This is not apparent, however, in the histogram of the F_2 population (Figure 5).

Means for the backcrosses to Douglas (14.2 g.) and the backcrosses to Miles (12.9 g.) did not differ from the respective recurrent parent values, but they were different from the non-recurrent parent values.

Seeds Per Pod. Entries were not significant at the 5% level in the analysis of variance, but they were found to be significant at the 6% level (Table I). However, when the interaction was pooled with the error term, entries were found to be significant. A probable reason for the low significance level for this character may be that an indirect method of obtaining number of seeds per pod was used. The narrow leaf parent had the highest mean number of seeds per pod (2.44) and the normal leaf parent had the lowest number of seeds per pod (2.32) (Table IV). The F_1 had an intermediate mean (2.35), and there was no difference observed from the mid-parent value. These results agree with Paschal and Wilcox (29) who reported that no significant mid-parent heterosis was detected for seeds per pod. The F_2 (2.37) was

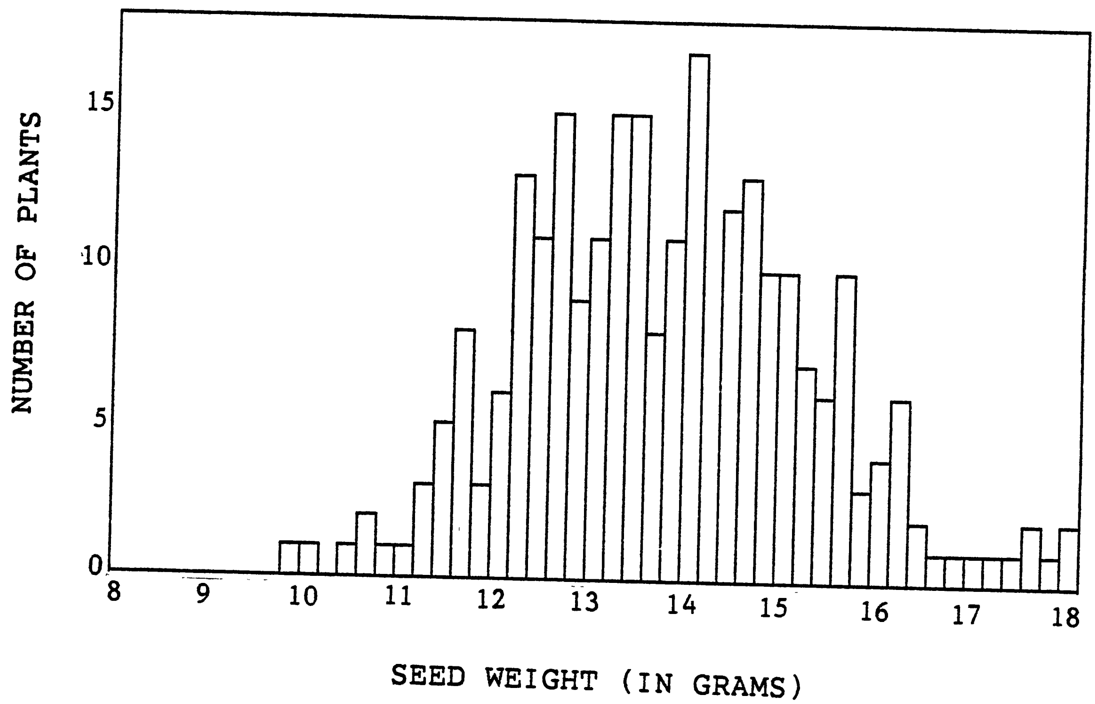

Figure 5. Distribution for the F_2 Generation for Seed Weight.

found to be intermediate and significantly different from Miles, but not Douglas, or the F_1 generation. The means for the backcrosses to Douglas (2.31) and to Miles (2.42) were significantly different from the non-recurrent parent but not from the recurrent parent.

Pods per Plant. Douglas and Miles both had a low number of pods per plant with means of 248 and 249 respectively (Table IV). The F_1 had a significantly higher mean number of pods per plant (278), displaying a 11.6% high parent heterosis (Table V). Paschal and Wilcox (29) stated that heterosis for number of pods per plant was negligible. Number of pods per plant has been shown to be the yield component character most closely associated with yield (38). The F_2 generation was not significantly different from the F_1 and displayed continuing high parent heterosis (9.6%). The means for the backcrosses to Douglas (273) and the backcrosses to Miles (260) were numerically higher than either parent but were not found to be significantly different from any generation.

Yield. Both Douglas and Miles had low mean yields of 81.2 g. and 76.3 g., respectively (Table IV). The F_1 mean yield of 93.6 g. exibited significant high parent heterosis (15.3%) (Table V). These results do not differ from previous estimates of 9.4%, 14.0%, and 13.4% for high parent heterosis for yield (29,36,38) in soybeans. The F_2 also showed a continuing high parent heterosis (10.3%). Brim and

Cockerham (6) reported some continued mid-parent heterosis in generations following the F_1. The means for the backcrosses to Douglas (90.9 g) and to Miles (81.7 g.) were not significantly different probably because of the small sample size. The mean yield for the backcrosses to Douglas was significantly higher than the yield of the high parent and equal to the yield of the F_1 and F_2.

Harvest Index. The mean harvest index values for Douglas (.4308) and Miles (.4173) were not significantly different (Table IV). The F_1 mean (.4429) was not significantly different from Douglas but was higher than Miles. A significant mid-parent heterosis (4.4%) was observed. The F_2 mean (.4368) was intermediate, and no differences were found with either parent. However, a mid-parent heterosis of 3.0% (Table V) was observed. The mean for the backcrosses to Douglas (.4254) did not differ significantly from the mean for any generation.

Comparison Among Genotypes

The F_2 and backcrosses were divided into narrow, intermediate, and normal leaf types and the means were compared among generations within leaf types. The analyses of variance did not detect any differences among generations within leaf types except for height (Table II). Means were also compared among leaf types within the F_2 and backcross generations. Leaf types were significantly different in the F_2 generation for most of the characters studied (Table VI).

TABLE VI.

ANALYSES OF VARIANCE FOR HEIGHT, PLANT BIOMASS, SEED WEIGHT, NUMBER OF SEEDS PER POD, NUMBER OF PODS PER PLANT, YIELD AND HARVEST INDEX WITHIN THE F_2 GENERATION

	df	Height	Plant Biomass	Seed Weight	Seeds Per Pod	Pods Per Plant	Yield	Harvest Index
Block	9	219.4**	11414**	10.3**	.1236*	12236*	2701**	.01451*
Leaf	2	12.2	38284**	22.7**	.1926*	51263**	6548**	.00043
Block * Leaf	18	105.4	3473	2.4	.0414	5435	797	.00202
Error	224	73.4	3326	1.8	.0548	5243	716	.00142
C.V.		12.6	28.7	9.9	10.0	26.8	30.6	8.7

*,** Significant at the 0.05, and 0.01 levels of probability, respectively.
+ Significant at the 0.06 level of probability.

The only difference detected among leaf types in the backcrosses for any character was number of seeds per pod in the backcross to Miles (Table VII). The reason no differences were detected for yield components may be due to sampling error because of the small number of backcrosses that were used, or it could be due to some interaction of the parental genotype on the backcrosses.

Means were compared for height, plant biomass, seed weight, number of seeds per pod, number of pods per plant, yield, and harvest index.

Height. Height was the only character in which differences were detected among generations within the same leaf type (Table II). Miles (75.5 cm.) was significantly higher than the F_2 narrow (68.0 cm.), and Douglas (57.8) was significantly shorter than F_2 normal (67.8 cm.) (Table VIII). No differences were observed between leaf types in the F_2 (Table VI) and backcross generation to Miles (Table VII). Differences were detected at the 0.06 level of significance between leaf types in the backcross to Douglas. The normal leaf was (62.9 cm.) and the intermediate leaf was (72.1 cm.) (Table VII). Height is reported to be under the control of few genes (18) and may be associated with the Douglas normal leaf genotype, however height and leaf type appear to segregate independently in the F_2 (Table VIII).

Plant Biomass. Differences were observed for plant biomass among leaf types in the F_2 generation (Table VI).

TABLE VII

ANALYSES OF VARIANCE FOR HEIGHT, PLANT BIOMASS, SEED WEIGHT, NUMBER OF SEEDS PER POD, NUMBER OF PODS PER PLANT, YIELD AND HARVEST INDEX FOR LEAF TYPES BACKCROSS TO DOUGLAS (TOP) AND BACKCROSS TO MILES (BOTTOM)

	df	Height	Plant Biomass	Seed Weight	Seeds Per Pod	Pods Per Plant	Yield	Harvest Index
Block	9	105.1	3529	1.18	.04013	4286	893	.00365
Leaf	2	221.2+	412	1.44	.00150	475	214	.00081
Block * Leaf	3	105.4	2988	0.38	.02566	1358	283	.00092
Error	22	44.7	4276	2.64	.04647	4217	958	.00122
C.V.		10.2	30.8	11.5	9.2	23.0	32.5	8.1
Block	9	84.1	1353	1.59	.07332	2745	337	.00206
Leaf	2	0.4	44	1.88	.22807*	14	46	.00277
Block * Leaf	6	53.4	1794	0.72	.05082	2412	201	.00292
Error	35	79.9	3299	2.27	.04344	5486	774	.00291
C.V.		13.1	31.5	11.7	8.6	28.8	34.8	7.8

*,+ Significant at the 0.05,and 0.06 levels of probability, respectively.

TABLE VIII

MEANS FOR HEIGHT (IN CENTIMETERS) WITHIN LEAF TYPE FOR EACH GENERATION IN A DOUGLAS X MILES CROSS

	Leaf Type		
Generation	Narrow	Intermediate	Normal
Douglas	--	--	57.8
Miles	75.5	--	--
F_1	--	67.1	--
F_2	68.0a*	68.7a	67.8a
Douglas X F_1	--	72.1	62.9
Miles X F_1	70.0	66.3	--

* Means followed by the same letter for the F_2 generation are not significantly different at the 0.05 level of probability using the LSD.

The intermediate F_2 (220.7 g.) had significantly higher plant biomass than F_2 narrow (182.3 g.) and F_2 normal (196.8 g.) (Table IX). Since all of the genes except the leaf gene are assumed to be segregating at random, no differences except those which are associated with the leaf gene would be expected. These results suggest that the genes governing the development of the plant biomass are asssociated with the narrow leaf gene. Continued heterosis was calculated and a 16.3% high parent heterosis was observed for the intermediate F_2 (Table X).

Seed Weight. Differences were observed for seed weight in the F_2 generation among leaf types (Table VI). The narrow leaf F_2 (13.1 g.) had smaller seed weight than either the intermediate (14.1 g.) or normal (14.1 g.) leaf types (Table XI). No differences were detected between normal and intermediate leaf types for the F_2. These results agree with previously published reports that the narrow leaf types had smaller seed weight than normal leaf types (20,27). The authors suggested that the lower seed weight observed in the narrow leaf types was due to the higher number of seeds per pod.

Seeds per Pod. Differences were observed for number of seeds per pod in the F_2 (Table VI) and backcross to Miles (Table VII) among leaf types. The narrow leaf types had a higher number of seeds per pod (2.43) than either the intermediate (2.34) or normal (2.31) leaf types (Table XII).

TABLE IX

MEANS FOR PLANT BIOMASS (IN GRAMS) WITHIN LEAF TYPE FOR EACH GENERATION IN A DOUGLAS X MILES CROSS

	Leaf Type		
Generation	Narrow	Intermediate	Normal
Douglas	--	--	188.5
Miles	181.7	--	--
F_1	--	211.3	--
F_2	182.3b*	220.7a	196.8b
Douglas X F_1	--	223.3	214.4
Miles X F_1	184.0	185.9	--

* Means followed by the same letter for the F_2 generation are not significantly different at the 0.05 level of probability using the LSD.

TABLE X

PERCENT HIGH AND MID-PARENT HETEROSIS FOR SIX CHARACTERS FOR THE F_2 INTERMEDIATE GENERATION IN A DOUGLAS X MILES CROSS

	F_2 Intermediate	
Character	Mid-Parent	High Parent
Height	3.1	-9.0
Plant Biomass	20.3**	16.3**
Seed Weight	6.4**	0.0
Seeds Per Pod	2.5	-4.1*
Pods Per Plant	17.5**	17.3**
Yield	22.1**	18.5**
Harvest Index	2.6**	1.0

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

TABLE XI

MEANS FOR SEED WEIGHT (IN GRAMS) WITHIN LEAF TYPE FOR EACH GENERATION IN A DOUGLAS X MILES CROSS

	Leaf Type		
Generation	Narrow	Intermediate	Normal
Douglas	--	--	14.1
Miles	12.4	--	--
F_1	--	14.2	--
F_2	13.1b*	14.1a	14.1a
Douglas X F_1	--	14.3	14.1
Miles X F_1	12.6	13.4	--

* Means followed by the same letter for the F_2 generation are not significantly different at the 0.05 level of probability using the LSD.

TABLE XII

MEANS FOR SEEDS PER POD (NUMBER) WITHIN LEAF TYPE FOR EACH GENERATION IN A DOUGLAS X MILES CROSS

	Leaf Type		
Generation	Narrow	Intermediate	Normal
Douglas	--	--	2.32
Miles	2.44	--	--
F_1	--	2.35	--
F_2	2.43a*	2.34b	2.31b
Douglas X F_1	--	2.35	2.33
Miles X F_1	2.47a	2.34b	--

*Means followed by the same letter for the F_2 and Miles X F_1 generations are not significantly different at the 0.05 level of probability using the LSD.

Published material regarding the narrow leaf gene indicate the presence of a pleiotropic effect of the narrow leaf gene on number of seeds per pod (19,20,27) The results of this study suggest that the narrow leaf gene must be in the homozygous condition for the association between the narrow leaf gene and number of seeds per pod to occur.

Pods per Plant. There were no differences detected among generations within each leaf type for number of pods per plant (Table II). Differences were detected among leaf types in the F_2 generation (Table VI). The intermediate F_2 had higher number of pods per plant (292) than the normal (262) or the narrow (250) (Table XIII). Continued high parent heterosis (14.2%) was observed for the intermediate F_2 (Table X). This suggests that there is an association between the narrow leaf gene in the heterozygous condition and the number of pods per plant.

Yield. Differences were detected for yield among leaf types in the F_2 generation. The intermediate leaf had significantly higher yield (96.2) than either the narrow (80.5 g.) or normal (85.6 g.) leaf types (Table XIV). Continued high parent heterosis for the intermediate F_2 was estimated to be 9.4% (Table X). This suggests that no heterosis was lost in the fraction of the F_2 generation that was heterozygous for leaf type and indicates that the narrow leaf gene present in the heterozygous condition has a favorable effect on yield (Table II).

TABLE XIII

MEANS FOR NUMBER OF PODS PER PLANT WITHIN LEAF TYPE FOR EACH GENERATION IN A DOUGLAS X MILES CROSS

	Leaf Type		
Generation	Narrow	Intermediate	Normal
Douglas	--	--	249
Miles	248	--	--
F_1	--	278	--
F_2	250b*	292a	262b
Douglas X F_1	--	289	277
Miles X F_1	261	258	--

* Means followed by the same letter for the F_2 generation are not significantly different at the 0.05 level of probability using the LSD.

TABLE XIV

MEANS FOR YIELD (IN GRAMS) WITHIN LEAF TYPE FOR EACH GENERATION IN A DOUGLAS X MILES CROSS

	Leaf Type		
Generation	Narrow	Intermediate	Normal
Douglas	--	--	81.2
Miles	76.3	--	--
F_1	--	93.6	--
F_2	80.5b*	96.2a	85.6b
Douglas X F_1	--	98.9	92.2
Miles X F_1	81.4	80.1	--

* Means followed by the same letter for the F_2 generation are not significantly different at the 0.05 level of probability using the LSD.

Harvest Index. No significant differences were observed for harvest index among leaf types within generations (Table II). The means among leaf types in the F_2 were very similar (Table XV). Differences were found in both components of harvest index, plant biomass (Table IX) and yield (Table XIV), but since the intermediate was high for both characters the effect was cancelled in the ratio.

Heritabilities

Over Generations

The mean squares for each generation for each character are presented in Table XVI. There were large differences in estimates of environmental variation among parents and the F_1. It is not known why the environment should affect one parent more than the other, but Douglas had higher variance estimates for five of the seven characters evaluated. The ratios of the phenotypic variances for Douglas and Miles were 0.74, 1.56, 1.82, 1.82, 1.4, 1.18, and 0.91 for height, number of pods per plant, yield, plant biomass, seed weight, number of seeds per pod and harvest index, respectively. When one of the parental estimates of the environmental variance is large, low heritability estimates occur.

Heritability estimates for all characters are presented in Table XVII.

Broad Sense Heritability Estimates. Heritability estimates were low for characters showing no significant differ-

TABLE XV

MEANS FOR HARVEST INDEX WITHIN LEAF TYPE FOR EACH GENERATION IN A DOUGLAS X MILES CROSS

	Leaf Type		
Generation	Narrow	Intermediate	Normal
Douglas	--	--	0.4308
Miles	0.4173	--	--
F_1	--	0.4429	--
F_2	0.4343	0.4350	0.4304
Douglas X F_1	--	0.4406	0.4297
Miles X F_1	0.4460	0.4262	--

* Means followed by the same letter for the F_2 generation are not significantly different at the 0.05 level of probability using the LSD.

TABLE XVI

MEANS SQUARE VALUES FOR HEIGHT, PLANT BIOMASS, SEED WEIGHT, NUMBER OF SEEDS PER POD, NUMBER OF PODS PER PLANT, YIELD AND HARVEST INDEX FOR EACH GENERATION IN A DOUGLAS X MILES CROSS

Generation	Height	Plant Biomass	Seed Weight	Seeds Per Pod	Pods Per Plant	Yield	Harvest Index
Douglas	48.4	3779	1.754	.0325	5581	816	.00168
Miles	65.1	2070	1.252	.0274	3564	448	.00185
F_1	77.4	3398	1.602	.0282	5584	617	.00152
F_2	75.2	3623	2.052	.0548	5634	770	.00145
Douglas X F_1	59.3	3759	1.890	.0339	4465	671	.00092
Miles X F_1	94.8	2667	2.803	.0665	4227	568	.00144

TABLE XVII

NARROW AND BROAD SENSE HERITABILITY ESTIMATES FOR SIX CHARACTERS FROM THE F_2 GENERATION IN A DOUGLAS X MILES CROSS

Character	Broad Sense	Narrow Sense
Height	0.15 ± 0.36	-0.05 ± 0.46
Plant Biomass	0.15 ± 0.36	0.23 ± 0.43
Seed Weight	0.25 ± 0.32	-0.29 ± 0.51
Seeds Per Pod	0.46 ± 0.22	0.17 ± 0.41
Pods Per Plant	0.13 ± 0.37	0.46 ± 0.36
Yield	0.18 ± 0.35	0.39 ± 0.38
Harvest Index	-0.16 ± 0.49	0.34 ± 0.36

ences between the parents . The heritabilities for yield, number of pods per plant and seed weight were estimated to be 0.18±0.35, 0.13±0.37 and 0.25±0.32, respectively (Table XVII). Although estimated heritabilities for yield are similar to previously published estimates (1,14,25), the estimates for the number of pods per plant and seed weight were lower than those previously published (14, 18, 21, 25). The variance for Douglas was almost as large as the F_2 variance for number of pods per plant and higher than the F_2 for yield (Table XVI).

The highest heritability estimate was for number of seeds per pod (0.46±0.22). This result should be expected due to the pleiotropic influence of the narrow leaf gene. Previously published results indicated that this character had an intermediate inheritance (1, 21). Heritability estimates for plant biomass and harvest index were 0.15±0.36 and -0.16±0.49, respectively.

Narrow Sense Heritabilities. Narrow sense heritability estimates were higher than the broad sense estimates for number of pods per plant (0.46±0.36 vs. 0.13±0.36), plant biomass (0.23±0.43 vs. 0.15±0.36), and yield (0.39±0.38 vs. 0.19±0.35) (Table XVII). The standard errors for the narrow and broad sense heritability estimates overlap however. Since the numerator in the broad sense heritability estimates is an estimate of the total genetic variance and the numerator in the narrow sense heritability estimates is only an estimate of additive genetic variance, broad sense estimates would be expected to be larger. However, the methods for obtaining the estimates use different sources in the estimation of the variances. Broad sense heritability was estimated using the F_2 variances, whereas the narrow sense estimates were based on the variance in the backcrosses. Since there were small numbers of backcrossed plants, the sampling error would be expected to be higher for the narrow sense estimates. The backcross to Miles had large mean squares for height and seed weight (Table XVI). This led to negative estimates for height (-0.05+0.46) and seed weight (-0.29+0.51), however both also had large standard errors so did not significantly differ from the broad sense estimates.

<u>Heritability Estmates Within Leaf Type</u>

Heritability estimates for each of the narrow, intermediate, and normal leaf types for all characters are presented on Table XVIII. Only broad sense heritability estimates were calculated for each leaf type due to the low number of backcrossed plants representing each leaf type. The estimated standard errors were high for all the characters evaluated. This was probably due to the low number of plants in each leaf type. Estimated heritabilities indicate that there may be differences among leaf types for height, seed weight, and number of seeds per pod, but they overlap due to the standard errors. Further studies utilizing a high number of plants in each leaf type would be needed to discern if there are any differences in heritabilities among

TABLE XVIII

BROAD SENSE HERITABILITY ESTIMATES FOR SIX CHARACTERS FROM WITHIN LEAF TYPE FOR F_2 GENERATION IN A DOUGLAS X MILES CROSS

	Leaf Type		
Character	Narrow	Intermediate	Normal
Height	-0.07±0.65	0.12±0.45	0.25±0.52
Plant Biomass	0.04±0.62	0.05±0.49	0.13±0.60
Seed Weight	-0.06±0.67	0.12±0.45	0.40±0.41
Seeds Per Pod	0.58±0.26	0.31±0.35	0.52±0.33
Pods Per Plant	0.11±0.57	0.04±0.49	0.03±0.67
Yield	0.19±0.52	0.07±0.51	0.20±0.55
Harvest Index	0.03±0.66	-0.27±0.65	-0.23±0.85

leaf types.

Correlations

Correlations In Generations

Phenotypic and genotypic correlations among all characters studied were calculated, and are presented in Table XIX.

Phenotypic Correlations. High positive phenotypic correlations were found between yield and plant biomass (0.95), and yield and number of pods per plant (0.91) (Table XIX). Positive correlations between yield and number of pods per plant have previously been reported (1). Since heritability estimates for both plant biomass and number of pods per plant were lower than heritability estimates for yield, and these characters were highly correlated, it may be easier to increase yield by selecting directly for yield than by selecting for individual yield components. Seed weight and number of seeds per pod were positively and significantly correlated to yield (0.28 and 0.38, respectively), but the correlations were low. Correlations among the yield components were all positive but some were very low. Anand (1) reported negative relationships among the yield components, however the plant spacing in the field was not as wide as in this study. The wider spacing may have reduced the amount of compensation among the yield components.

Genotypic Correlations. Genotypic correlation

TABLE XIX

PHENOTYPIC (TOP) AND GENOTYPIC (BOTTOM) CORRELATIONS BETWEEN HEIGHT, PLANT BIOMASS, SEED WEIGHT, NUMBER OF SEEDS PER POD, NUMBER OF PODS PER PLANT, YIELD AND HARVEST INDEX FOR A DOUGLAS X MILES CROSS.

Character	Height	Plant Biomass	Seed Weight	Seeds Per Pod	Pods Per Plant	Yield	Harvest Index
Height	--	0.38**	0.03	0.18**	0.33**	0.34**	-0.05
Plant Biomass	0.00	--	0.18**	0.32**	0.91**	0.95**	0.04
Seed Weight	0.00	0.00	--	-0.04	-0.01	0.28**	0.40**
Seeds Per Pod	0.00	0.32	0.00	--	0.12	0.38**	0.33**
Pods Per Plant	0.00	0.81	0.00	-0.32	--	0.91**	0.11
Yield	0.00	1.05	0.00	0.29	0.98	--	0.31**
Harvest Index	0.00	0.63	0.00	0.08	0.04	0.52	--

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

estimates were very similar to phenotypic correlations (Table XIX), except that estimates for height and seed weight were zero. This resulted from the fact that additive variances were greater for the backcrosses than for the F_2 due to high mean squares for the backcross to Miles (Table XVI). Correlations between yield and plant biomass, and between yield and number of pods per plant were 1.05 and 0.98, respectively. A high positive correlation was observed between plant biomass and number of pods per plant (r=0.81). It appears that the space planting favored large plants, which produced a high number of pods, and thus had high yield. Unfortunately, as was the case with the phenotypic correlations, the characters which showed a high correlation with yield had lower heritabilities than yield itself. Negative correlations were observed between the yield components, number of pods per plant and number of seeds per pod, (r=-0.32).

Correlations Within Leaf Types

Correlations within F_2 leaf types were calculated among yield, number of pods per plant, number of seeds per pod, seed weight, and plant biomass (Table XX). The correlation between yield and number of seeds per pod was highest for the narrow leaf type (.611) followed by the normal (.455) and intermediate (.271) leaf types. The positive correlation between yield and seed weight was not significant for the narrow leaf type (.038) but it was significant for the

TABLE XX

SIMPLE PHENOTYPIC CORRELATIONS BETWEEN SIX CHARACTERS FOR THE F_2 GENERATION IN THE NARROW, INTERMEDIATE AND NORMAL LEAF TYPES IN DOUGLAS X MILES.

Character	Genotype	Pods Per Plant	Seeds Per Pod	Seed Weight	Plant Biomass	Harvest Index
Yield	F_2 narrow	.923**	.611**	.038	.969**	.428**
	F_2 inter	.873**	.271**	.291**	.935**	.168
	F_2 normal	.912**	.455**	.375**	.963**	.438**
Pods Per Plant	F_2 narrow		.379**	-.220	.936**	.221
	F_2 inter		.056	.065	.875**	.042
	F_2 normal		.223	.125	.927**	.249*
Seeds Per Pod	F_2 narrow			.049	.548**	.387**
	F_2 inter			.004	.239**	.141
	F_2 normal			-.037	.400**	.500**
Seed Weight	F_2 narrow				-.052	.440**
	F_2 inter				.157	.437**
	F_2 normal				.303*	.460**
Plant Biomass	F_2 narrow					.188
	F_2 inter					.170
	F_2 normal					.231

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

intermediate (.291) and normal (.375). High positive correlations were found among yield, number of pods per plant, and plant biomass for all leaf types. But as was the case with the phenotypic correlations all heritability estimates were higher for yield than plant biomass or number of pods per plant for any leaf type (Table XVIII).

CHAPTER V

SUMMARY AND CONCLUSIONS

A single recessive gene designated ln by Bernard and Weiss (4) controls the inheritance of the lanceolate trifoliolate in soybeans. The ln gene has an incomplete dominance effect on leaf type with intermediate heterozygotes. Domingo (13) found that the lanceolate or narrow leaf condition was associated with a high number of four seeded pods. Other yield component characters that have been reported to be associated with the narrow leaf condition are low seed weight and fewer pods per plant (19,20). Only narrow leaf and normal leaf lines have been previously compared. No study has dealt with the effect of the narrow leaf gene in the heterozygous condition on yield either in the F_1 generation or succeeding generations. This is primarily due to the difficulty in distinguishing the heterozygote from the normal leaf homozygote.

The objectives of this study were to (a) evaluate F_1 heterosis for yield and yield components; (b) evaluate the reduction of heterosis in the F_2 generation in each leaf type, and (c) to examine the relationships and inheritance of yield and yield components in the F_2 and backcross generations within narrow, intermediate, and normal leaf genotypes. The populations studied resulted from a cross between a normal leaf cultivar and a narrow leaf cultivar.

The mean height for the F_1 generation was intermediate to both parents. There was significant heterosis for number of pods per plant, plant biomass, and plant yield. The character which displayed the highest amount of heterosis was yield. Number of pods per plant appeared to be the yield component which was responsible for the high yield heterosis. It appeared that the space planting favored larger plants which produced more pods and higher yields. There was no heterosis detected for seed weight or number of seeds per pod. Low number of seeds per pod appears to be dominant. Among the backcrosses the only character that was different was height.

The ranges for the ratio of leaf length to leaf width were 0.32 to 0.45, 0.52 to 0.65, and 0.65 to 0.87 for Miles, F_1, and Douglas, respectively. These ranges were used to classify the F_2 and backcrosses with respect to leaf type. There were 70, 126, and 58 plants classified as narrow, intermediate, and normal, respectively in the F_2 generation. These numbers fit the expected 1:2:1 ratio. The were 11, and 18 plants classified as intermediate and normal for the backcross to Douglas, and 24 and 16 plants classified as narrow and intermediate for the backcross to Miles. A Chi square test indicated no significant deviation from the expected 1:1 ratios.

There was an apparent compensatory effect in number of seeds per pod and seed weight for the narrow and normal leaf F_2 resulting in similar number of pods per plant and yield. The narrow leaf type had a high number of seeds per pod and low seed weight, while the normal leaf had low seeds per pod and high seed weight. The intermediate F_2 group had low seeds per pod, low seed weight, but had a high number of pods per plant resulting in high yield. The means for the intermediate F_2's were not significantly different from the F_1 means indicating that there is no apparent loss of heterosis among the intermediate leaf type.

Heritability estimates were low for characters showing no significant differences between the parents. For number of pods per plant, plant biomass, and yield, narrow sense heritability estimates were higher than broad sense estimates though the standard errors overlapped. The only character studied which did not agree with previous studies was the estimate for height which was lower than previous estimates. Heritability estimates within leaf types had high standard errors and thus were not declared significantly different from each other. A probable reason for the large standard errors was the low number of plants in each of the leaf classes. Further studies using larger numbers of F_2 plants would be required to achieve a more accurate estimate of heritabilities within leaf types.

High positive correlations were found among plant biomass, pods per plant and yield. Unfortunately, heritability estimates for both plant biomass and pods per plant are lower than heritability estimates for yield. Seed weight and pods per plant were positively and significantly correlated to yield, but correlations were low. Correlation estimates within leaf types were very similar for all three leaf types.

Continued generations should be tested to determine if the intermediate leaf types continue to produce higher yields. Also additional crosses should be made with different sources of the narrow and normal leaf genes, to see if the same results are obtained, or if these results are due to nicking in some manner of these parents. If the heterozygotes produce higher yields in general, incorporating the narrow leaf gene into hybrid combinations would be beneficial should soybean hybrid production become economically feasible.

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VITA 2

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