HETEROSIS AND COMBINING ABILITY IN MUNGBEAN (*VIGNA RADIATA* (L.) WILCZEK)

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by

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CHAPTER I

INTRODUCTION

This paper is a study of a diallel cross involving five high yielding lines of mungbean (*Vigna radiata* (L.) Wilczek). The purposes of this study were (a) to study heterosis for several quantitative characters in F_1 hybrids produced, (b) to determine the general and specific combining ability of the parent lines involved, (c) to assess the narrow sense heritability for the characters studied, and (d) to calculate coefficients of correlation among characters. Information gained in this study would be useful in identifying high yielding parent varieties which could be utilized in a breeding program to obtain superior transgressive segregants.

The breeding of hybrid mungbeans is not a practical procedure at this time since neither genetic nor cytoplasmic sterility has been reported in this crop species. However, it has been established (Singh, 60) that good yielding recombinants may be selected from segregating generations of crosses showing heterosis for yield. Furthermore, knowledge about the inheritance of specific characters, which are components of yield or which may be correlated with yield, is useful in determining the best selection procedure to use.

CHAPTER II

LITERATURE REVIEW

The Concept of Heterosis

The concept of heterosis was first distinctly recognized in work with hybrid corn carried out by G. H. Shull in the early years of this century (55, 56). Shull stated that self-fertilization served to purify strains and that comparisons between self- and cross-fertilized strains were more properly to be considered comparisons between pure strains and their hybrids. His definition of heterosis was first stated in 1914 (57) as "the physiological vigor of an organism, as manifested in its rapidity of growth, its height and general robustness . . . positively correlated with the degree of dissimilarity in the gametes by whose union the organism has been formed." Dr. Shull tended to attribute heterosis to heterozygosis from which he obtained the term.

Theories of Heterosis

Davenport (14) first suggested the possibility that "degeneration" in characters resulting from inbreeding might be attributable to a combination of "minus" genetic factors. Bruce (9) took the next step in attributing

heterosis to the combined action of favorable dominant or partially dominant factors and was the first to point out that dominant characters tend to be beneficial while recessive factors have a weakening effect. Keeble and Pellew (38) cited an example in peas of how dominance factors might be responsible for hybrid vigor. Jones (36, 37) presented the notion of dominance of linked genes to explain the fact that an inbred superior to the parent lines could not readily be obtained as the dominance theory might suggest. Desirable dominant characters are linked with undesirable recessive characters in such a way as to make homozygous dominant inbreds virtually impossible, at least in a manageable population size.

The concept of physiological stimulation caused by heterozygosis *per se* as the basis for hybrid vigor has found support in work by Gustafsson (27), Hull (33), Jones (38), and Castle (11). Hull (33) suggested the term overdominance to describe this phenomenon. According to Crow (13) it has been called superdominance, hyperdominance, single gene heterosis, cumulative action of divergent alleles, and heterosis. Dobzhansky (15) has suggested that recessive genes might be preserved in a population because of overdominance. Crow (13) and Emerson (18) have attempted to reconcile the concept of overdominance with the one gene one enzyme hypothesis, claiming that an intermediate enzyme level might be the optimum level. Flor (21) cited an

example of rust resistance in flax in which each of two homozygotes was resistant to a certain rust, but the hybrid was resistant to both.

Richey (50) and Richey and Sprague (51) designed a test to determine which hypothesis was correct, the dominance theory or the overdominance hypothesis. Two inbreds were crossed and the hybrid was backcrossed to both parents. When the backcross was made to parent A, selection was made for characters of parent B and vice versa. It was intended that inbred A should have some dominant genes from line B and that inbred B would have some dominant genes from line A. These inbreds would be more productive than the original inbreds according to the dominance theory, but the A x B crosses from recovered inbreds should be equal to the original A x B crosses. The recovered inbreds were more vigorous, lending support to the dominance hypothesis, but the cross between them was superior to the A x B cross.

Brewbaker (8) has pointed out that it is not reasonable to assume one cause for such a complex phenomenon as heterosis. The dominance theory is presently more in favor than the overdominance hypothesis, but both are reported to be involved in heterosis as is interallelic action or epistasis. The notion of epistasis originated with A. J. Manglesdorf (cited by Brewbaker, 8) and found support in the work of W. J. Robbins (52). It is a bottleneck type of theory which states that the excellence of a

genotype depends not upon its strongest link but upon its weakest link. Emphasis is placed upon the inferiority of parents rather than upon superiority of a hybrid. If two dominant alleles, A_1 and B_1 were required for the completion of a particular synthetic pathway, the homozygotes $A_1A_1B_0B_0$ and $A_0A_0B_1B_1$ would fail to complete this synthesis. Mather (41) discusses the phenomenon of nonallelic interaction. He concludes that genes producing heterosis are not the same kind as those between a fully efficient allele on the one hand and a lethal or semi-lethal on the other, but should be considered as "environmental alleles", i.e. alleles which initiate the same synthesis but with different optima of pH or temperature or substrate affinity.

Williams (77) gave an explanation for inbreeding depression of a complex trait based on the multiplicative relationships among the components. Duarte and Adams (16) analyzed the expression of leaf area in a bean (Phaseolus vulgaris) cross by dividing the trait into two components, number of leaflets and size of leaflets. They concluded that heterosis for certain complex characters could be interpreted as resulting from multiplicative (number of leaves x size of leaves) relationships among the components controlled by genes causing additive effects or partial to complete dominance. Such heterosis, being due to component interaction, is potentially fixable in true breeding genotypes, as opposed to heterosis due to genic heterozygosity.

Grafius (22) analyzed the components of yield in oats.

Jinks (34) and Jinks and Jones (35) report that the presence or absence of heterosis is not in itself indicative of the presence or absence of any particular type of gene action or interaction. It can result from a whole range of combinations of gene effects. A correlation exists between the presence or absence of heterosis and the presence or absence of epistasis and, while heterosis can arise in the absence of nonallelic interactions, it arises less frequently and with a lower mean expression according to their interpretation.

Heterosis in Self-Pollinated Crops

Hayes (28) has determined that the first step in the utilization of heterosis in self-pollinated crops should be the selection of available parental varieties that in themselves produce the best combination of characters. This conclusion was supported by the work of Carnahan (10) in flax, Powers (48) in tomatoes, and Moore and Currence (46) in tomatoes. However, these studies demonstrated that the only means of selecting the most desirable F_1 cross was by actual trial.

Hayes also concluded that it is important to continue breeding self-fertilized crops for the best combination of characters which can be obtained in relatively homozygous varieties. Smith (71) in tobacco and Williams (76) in

tomato have shown in these crops, which exhibit high heterosis, that it is possible to develop pure lines which perform better than or as well as hybrids. Busch and his associates (7) have reached the same conclusion with spring wheat. Three heterotic crosses of hard red spring wheat were made and 90 F_5 lines were derived from a bulk population of F_3's. F_5 lines were found which performed significantly better than the F_1 hybrid in each cross. Only one F_1 hybrid failed to outyield its high parent. F_6 lines performance was similar to that of the respective F_5 parents. In a study in tomatoes by Williams (76) desirable recombinants were isolated at a frequency of one in every one thousand to fifteen hundred individuals.

Grafius (23), working with a diallel cross involving six barley varieties, concluded that yield is an artifact of interaction among the uncorrelated yield components which were shown to be controlled by additive gene effects. According to his view there are no genes for yield *per se*.

Heterosis in Pulse Crops Other than Mungbeans

Solomon, Argikar, Salanki, and Morbad (72) reported hybrid vigor up to 24.5% for grain yield in pigeon pea (*Cajanus cajan*). The best yielding hybrid did not outyield the best parent. Bond, Fyfe, and Toynbee (6) observed significantly higher yields with field bean hybrids than were found in pure lines. Ramanujam, Rohewal, and Singh (49) studied nine crosses of gram (*Cicer arietinum* L.)

involving seven varieties as parental lines. Two crosses gave significantly higher yield than the best parent included in the study.

Singh and Singh (69) performed a diallel cross in field pea (Pisum sativum) involving six parents. Significant differences were in evidence for days to flower, branch number, length of main branch, number of pods per plant, seeds per pod, grain yield, and 100-grain weight. Heterosis up to 162% was in evidence for grain yield. The increase in yield was determined to be influenced most by branches per plant and pods per plant. Days to flower and length of main stem did not correlate with increased yields. The notion was presented that hybrid varieties might not merit consideration unless they exceeded the highest yielding pure line by at least 25%. In peas, as in mungbean, flowers do not open until pollen is shed, and no source of male sterility is available.

A study by Singh and Singh (68) on heterosis in black gram or urid bean demonstrated heterosis of F_1's over the midparents for yield, cluster number, pod number, and branch number, but negative values were observed for seed size and pod length. Maximum heterosis for grain yield was 52% over the midparent and 21% over the high parent. Six of the eighteen crosses outyielded the outstanding tester variety, three by a significant margin. Heterosis in yield was associated with the expression of heterosis

in the yield components, cluster number and pod number, but was not necessarily correlated with any other character.

In a heterosis study by Singh and Jain referred to by Singh (60), involving fifteen crosses of cowpeas, 70% of the crosses outyielded their respective midparents and 60% outyielded their respective high parents. The largest heterotic increase over midparent was 39%. Yield was positively correlated with pod length and seeds per pod.

A study on heterosis in lentil involving ten crosses from eleven parents was conducted by Singh and Jain (65). Three crosses significantly outyielded their high parent and the best variety in the region. Heterosis over the high parent was observed for branches per plant, clusters per plant, and pods per plant. Heterosis for yield was reflected through heterosis of the yield components. In this study genetic diversity among parents apparently made some contribution to heterosis.

Singh (60) concluded that high yielding and genetically diverse genotypes with a high number of pods per palnt would be the best parents to use in a pulse breeding program. Singh concludes that presently emphasis should be placed on development of high yielding pure lines, but that cytoplasmic male sterility and restorer genes might be sought to develop hybrid varieties of the future. Bond, et al. (6) reported cytoplasmic male sterility to be present in field beans.

Singh (60) summarized the approach to heterosis breeding in pulse crops as consisting of:

1. selecting high yielding, genetically diverse, widely adapted and disease resistant parents for crosses,

2. studying heterosis in F_1 hybrids over the standard variety in the area, and

3. selecting elite crosses for development of pure lines, following the pedigree method of breeding.

Heterosis in Mungbean

The first study of heterosis in mungbean was conducted by Bhatnagar and Singh (3). The F_1's exceeded their respective midparents for the eight characters studied in three crosses. Four characters, number of branches, number of pods, yield of pods, and seed yield, showed a high degree of heterosis. Heterosis for seed yield ranged from 108 to 252% of midparent.

Misra and Sahu (45) concluded that hybrid vigor was present for plant height, number of primary branches, leaf size, total number of pods per plant, and plant yield. In a cross involving Nayagarh 2-4 as the female parent and Kopergaon as the male parent, the yield of the F_1 showed a 79.44% increase over the midparent and a 57.88% increase over the high parent.

In more extensive study Singh and Jain (64) concluded that with increased yield there was a corresponding increase in one or more of the yield components. Although the

overall F_2 mean yield was less than that of the F_1 hybrids; the differences were not statistically significant. This suggests that part of the increase in the F_1 over the superior parent is due to epistasis and is therefore potentially fixable. If pure lines are to be generated following hybridization, crosses which manifest only a slight reduction in yield in the F_2 might tend to produce high yielding transgressive segregants in later generations.

Singh (60) reported that mungbean crosses were selected until the F_5 or F_6 generations and that the selections were retained on the basis of disease resistance and good agronomic qualities. Good segregants were obtained from the crosses which had the highest heterosis in the F_1. In another study discussed in the same paper; the cross Hyb 45 x P23-67 showed maximum heterosis. The exception to the principle of highly heterotic crosses giving rise to the best transgressive segregants occurred in lines with high susceptibility to bean yellow mosaic virus. Singh's study in mungbean supports the notion that crosses which show a high degree of heterosis in the F_1 will give rise to good segregants and that the crosses which perform poorly can be discarded.

Combining Ability Studies

General and specific combining ability have been defined by Sprague and Tatum (74). General combining ability implies "the average performance of a line in hybrid combinations" the specific combining ability designates "cases in which certain combinations do relatively better or worse than would be expected on the basis of the average performance of the lines involved." Hayman (29, 30, 31) presented a series of papers on diallel crosses and a review (32) of theories and methods used in the analysis of diallel crosses.

Griffing (25) describes four possible experimental methods which can be employed in the analysis of diallel crosses as follows:

1. Parent, one set of F_1's and reciprocal F_1's included (all p^2 combinations).

2. Parents and one set of F_1's are included but reciprocal F_1's are not (1/2(p+1).

3. One set of F_1's and reciprocals are included but not the parents (p(p-1) combinations).

4. One set of F_1's but neither parents nor reciprocal F_1's are included (1/2p(p-1) combinations).

Each method requires a different form of analysis. With regard to sampling, two situations are considered as follows:

1. The situation in which the parental lines or the experimental material as a whole are assumed to be a random sample from some population about which inferences can be made.

2. The situation in which the lines are deliberately chosen and cannot be regarded as a random sample from any population, i.e. the experimental material constitutes the entire population about which inferences can be made.

The first assumption characterizes a Model II experiment in which variety effects are considered random variables and block effects are constants. The second assumption fits a Model I experiment in which variety and block effects are constants.

In single crosses of corn involving lines previously tested, Sprague and Tatum (74) found that genes conditioning specific combining ability had the most effect in determining yield. Since differences in additive effects (implied by general combining ability) had been largely eliminated, epistasis and dominance effects became relatively more important. In crosses involving untested inbred lines the variance for general combining ability was much greater than that for specific combining ability.

In the previously cited study in black gram by Singh and Singh (68), it was suggested that those lines which had significant general combining ability effects for yield, pod number, and cluster number should make good parents in

crossing programs. In this experiment the crosses which had significant specific combining ability effects for yield also had significant combining ability effects for cluster number and pod number. In a five parent diallel cross with mungbeans Singh and Jain (63) estimated combining ability and gene action for grain yield, seeds per pod, and pods per plant. Their study indicated that both general combining ability and specific combining ability effects were important and significant for all three traits. Greater general combining ability values than specific combining ability values were found. For seeds per pod, the mean square for general combining ability was about equal to the mean square for specific combining ability. General combining ability mean squares were roughly double specific combining ability mean squares for yield and for pods per plant. The cross between Hybrid 45, the best general combiner, and No. 305, the second best general combiner, gave the highest specific combining ability for yield and for pods per plant. Crosses involving 'high x high' general combiners gave high specific combining ability effects.

Singh and Malhotra (66) determined that pod length and seed size are two major components of yield in mungbean. In a study by Singh and Jain (63) on combining ability for these characters, the variances due to general combining ability and specific combining ability were significant at

the one and five percent levels, respectively. Their study indicated that general combining ability was most important for pod length. Both general and specific combining ability were important for seed size.

Heritability

Dudley and Moll (17) define heritability in the broad sense as "the ratio of total genetic variance to phenotypic variance" and heritability in the narrow sense as "the ratio of additive genetic variance to phenotypic variance."

Lush (40) calls attention to the fact that regression of offspring on midparent gives an estimate of heritability "a little larger than the narrow one but distinctly smaller than the broad one." It does not include dominance effects or random environmental effects.

Falconer (20) describes a technique for calculation narrow sense heritability by regression of offspring on midparent. He points out that the concept of additive genetic variance does not imply additive gene action. Additive genetic variance can arise from genes with any degree of dominance or epistasis.

A paper by Warner (75) includes a review of literature concerning heritability. Three main methods of estimating heritability in crop plants are described as follows: (1) parent-offspring regressions, (2) variance

components from the analysis of variance, and (3) non-heritable variance approximations from genetically uniform populations. Nei (47) describes a test of significance for heritability estimates.

Matzinger, Sprague, and Cockerham (42), Matzinger, Mann and Robinson (43), and Matzinger (44) have described methods of estimating genetic components (and hence heritability) from diallel crossing systems.

Sandha and Chandra (53), working with bengal gram, found high narrow sense heritability values for number of primary and secondary branches. Chandra (12), referenced by Sandha and Chandra (53), had shown that number of primary and secondary branches are among the most important contributors to yield in gram.

A broad sense heritability study in mungbean was conducted by Empig, Lantican, and Escuro (19). Estimates of broad sense heritability for nine characters were as follows: days to flower 62%, days to maturity 71.2%, plant height 27.0%, maturity range (days from second to last ripe pod) 42.8%, pods per plant 24.6%, seeds per pod 10.0%, seed weight 51.2%, seeds per plant 27.6%, and seed yield 8.6%. The lowest heritability was for seed yield. There was low genetic variability for seed yield among the lines crossed. This study described the phenomenon of mungbeans setting pods in flushes and stated that yield is reduced if pods are not picked as they mature since

flowering is inhibited and senescence is encouraged. They reported considerable genetic variability for maturity range which also had a high heritability value.

Correlation Studies

Singh and Malhotra (66) reported on a comprehensive correlation study in mungbean. Yield was found to be positively associated with bunches per plant, pods per plant, seeds per pod, and pod length. Length of pod and 100-seed weight were positively correlated with each other. It appeared that yield and pod length might be increased by selection for 100-seed weight. However, a substantial negative association existed between seed size, seeds per pod, and pods per plant. Multiple regression analysis showed seed size, seeds per pod, and pods per plant to be the most important yield determining characters. It was concluded that if an increase in yield is to be obtained a compromise had to be reached between those characters so that progress in one might not be nullified by deterioration in another.

Genetic Variability in the Mungbean

The genetic variability in the mungbean has been studied by Yohe and Poehlman (78). Three hundred and twenty-one strains originating in eighteen countries were evaluated for yield, days to first ripe pod, plant height, length of first branch, pods per plant, number seeds per

pod, 1000-seed weight, virus resistance, mildew resistance, percent protein, percent lysine, and percent methionine. A wide range in genetic variability was identified for each character. The 10% high yielding strains tended to be large, moderately early, plants as measured by height and branch length, having large numbers of pods per plant and seeds per pod, high seed weight and virus resistance. Protein, lysine and methionine varied widely among the high yielding strains.

Gupta and Singh (26) have conducted a study of thirty-six "elite" strains involving sixteeen pure lines and the progenitors of eight crosses. The strains utilized were from Uttar Predesh, Gujarat, Bihar, and twenty were from Punjab, where the study was conducted. An analysis of variance of plot means for the different characters showed significant differences among the varieties for all nine characters studied. Weight of fifty seed and pod length together contributed 61.93% of the divergence in this material. The clustering pattern of the varieties revealed that geographic diversity was not always associated with genetic diversity.

Banks (1), and Bharagave, Johri, Sharma, and Bhatt (2) have written papers relating to genetic variability in mungbean and a collection possessed by K. B. Singh (61) has been described.

Inheritance of Quantitative Characteristics in Mungbean

Bose (5) discovered early flowering to be dominant to late flowering in mungbeans, but described early flowering as a quantitative character. Singh and Malhotra (65) reported days to flower to be closely correlated with days to maturity. The same relationship has been noted by Yohe and Poehlman (76) in mungbeans and by Singh and Mehndiratta (66) in cowpeas.

In a study by Sen and Murty (53) on the inheritance of seed weight in mungbean, small, medium, and large seeded varieties were crossed with each other. The range of the F_2 and F_3 means of the 'small x medium' crosses extended beyond the range of the small parent, but seed as large as the largest seed of the medium parent were not recovered. In the 'small x large' crosses, the mean seed weight of the two parents was about five times greater than in the 'small x medium' crosses, but the F_1 mean remained very close to that of the small-seeded parent. However, the F_2 mean shifted toward the large-seeded parent. The F_3 mean was about midway between the small seeded parent and the midparent. In 'medium x large' seeded crosses the F_1 and F_2 means were close to that of the small parent. Seed bigger than the seed of the larger parent were obtained among segregants in the F_2 and the F_3. It was concluded that small seed character is more or less completely

dominant to large seed; however, the results indicated that seed size inheritance is a complex affair and that the large seed are probably the result of an accumulation of recessive genes. Singh and Jain (64) also obtained seed weights lower than the midparent in a study on heterosis.

Singh and Singh (70) have described a possible mechanism for the inheritance of clusters per node in mungbean.

CHAPTER III

MATERIALS AND METHODS

This study compares five parent lines of mungbean (*Vigna radiata* (L.) Wilczek) and all nonreciprocal single crosses between them.

Parents and F_1's

Five parent lines were grown along with the ten possible nonreciprocal F_1 hybrids. Four of the parent lines, M90, M101, M203, and M232 originated in India and had been received from the United States Department of Agriculture plant introduction collection. The fifth line, M472, is an apparent reselection from M118. M118 originated in India and was received from the United States Department of Agriculture, also. Crosses were made using progenies of single plants to avoid possible genetic differences within the original parent stocks. Subsequent progeny tests have shown that the plant from M118 used in crossing differs from the original M118. Data on performance of the four parents, M90, M101, M203, and M232, grown at Columbia during 1970 and 1971 are given in Table 1. Comparable data for M472 are not available.

The crossing procedure employed was similar to that of Boling, Sander, and Matlock (4), and Yohe (unpublished).

Table 1. Comparative data on parent lines grown at Columbia, Missouri, two-year average, 1970, 1971.

Mo. acc. no.	P.I. no.	Origin	Yield kg/ha	Leaf size	Days to flower	Days to ripe	Height cm	Branch length cm	Pods per plant	Seeds per pod	1000-seed weight mg
M90	223711	India	2336	7.5	59	81	77	83	167	11	63
M101	271401	India	1982	7.5	52	73	45	45	85	12	75
M203	183136	India	2068	7.4	58	79	81	73	112	12	54
M232	212907	India	2029	7.6	53	76	69	64	110	12	53

Boling et al. obtained about 20% seed set and Yohe obtained about 25% set. The writer obtained less than either, the probable cause being reduced night temperatures in the greenhouse. The night temperature was reduced below 16°C to arrest high respiration, but this resulted in the mungbean stigmas being almost altogether unreceptive to pollen.

Plants were emasculated about two to three hours before sunset when the anthers are almost ripe but before they have opened. Care must be taken when emasculations are performed late in the evening, as pollen may have already begun to be shed and selfs are than almost inevitable. Care must be taken during emasculation not to injure the pedicle or to remove the style and stigma along with the keel petal. Cross pollinations are made the following morning, shortly after sunrise.

Field Procedure

This study was conducted at the Bradford Farm in the vicinity of Columbia, Missouri in the summer of 1972. Five parents and ten F_1's were planted in a randomized complete block design with four replications. Planting was done in peat pots on June 1, and the plants were transferred to the field one week later. Plots consisted of ten plants, spaced eighteen inches apart, with rows (plots) spaced thirty-nine inches apart. A row of each parent was grown

on either side of each F_1. Only one parent row was harvested for yield in each replication.

The plants were harvested and threshed as a plot, with the exception of two plants from each plot which were used to sample for pods per plant, seeds per pod, and 1,000-seed weight. All notes other than yield were taken on a per plant basis. The data subjected to analysis were the plot means for the characters analyzed.

Characters Analyzed

The F_1 and parent data from each replication were subjected to an analysis of variance for the following characters:

Number of plants--Number of plants were recorded for all plots. In some F_1 plots there were fewer plants than in the corresponding parent rows. Some seedling plants were destroyed by cutworms after the seedlings were transplanted to the field. While there were sufficient parent seedling plants to replace those destroyed, this was not the case for all of the F_1's. Since all data is presented on a per plant basis this would suggest that the plants might have an advantage in the rows with fewer plants. However, since the original spacing between plants within the rows was quite large, the extra space from missing plants probably did not significantly affect individual

plant performance. Furthermore, an analysis of variance did not indicate a significant variation in number of plants among entries over the entire experiment.

Yield per plant--Yield per plant was obtained by dividing the total yield of the plot by the number of plants in the plot. Only the two sample plants were threshed on an individual basis. The yields of these two plants and the yield of the remainder of the plot were added together and the sum divided by the total number of plants.

Leaf size--Leaf size was scored from 1 to 8 by comparing with a chart on which sample leaves of varying sizes had been traced. Two typical leaves were sampled for each plant and the average taken. A leaf score of six represents 8.49 square inches, a leaf score of seven represents 10.64 square inches, and a leaf score of eight represents 22.50 square inches.

Days to flower--Days to flower is the number of days from planting until the day the first flower on the plant opened.

Days to ripe--Days to ripe is the number of days from planting to the first mature pod.

Plant height--Plant height is the length of the main stem of the plant in centimeters.

Branch length--Branch length is the length of the lowest branch in centimeters.

Pods per plant--Pods per plant is the average number of mature pods from a sample of two plants from each plot.

Seeds per pod--Five pods which appeared to be typical in length were selected from each of two plants in a plot and the seed counted. Seeds per pod is the average number of based on this sample of ten pods per plot.

1000-seed weight--A sample of 100 seeds were counted and weighed from each of the two sample plants from every plot. The average of these eight samples was then multiplied by ten.

Analysis of Data

An analysis of variance was performed on all available data utilizing plot means. The F_1 was compared with the midparent and the high parent for all crosses. In addition to the analysis of variance a coefficient of variation was calculated for each character. Heterosis is expressed as percent of midparent and as percent of high parent.

An LSD was calculated for the difference between the midparent and the F_1 and, also, for the difference between the F_1 and the parent lines for each of the characters studied. The formulas for calculating the LSD were

$t \times \sqrt{\frac{3EMS}{2n}}$ for comparing differences between the F_1 and its midparent and $t \times \sqrt{\frac{2EMS}{n}}$ for comparing differences between the F_1 and the high parent, where t is the t value at the .05 or .01 level with forty-two (error or within group) degrees of freedom, EMS is the error mean square, and n is the number of replications.

General specific combining ability effects were calculated according to Griffing (25), Model I, method 4. Griffing's paper is set up as if there were only one replication in the experiment. Consequently, it was necessary to substitute $\frac{\sigma^2}{r}$ when the formula called for σ^2. The error mean square is the best estimate of σ^2. The same revision also needed to be made in the calculation of the variances. In Griffing's paper x_{ii} represents a plot mean and $x_{i.}$ represents the sum for all crosses involving a particular parent, in this case, whether as male or female. The reader might hereby avoid some confusion over the conventional connotation of $x_{i.}$, being the sum for a particular treatment.

Narrow sense heritability estimates were calculated by regression of offspring on midparent as described by Falconer (18). For the regression of offspring on midparent, $b = h^2$. Correlation coefficients were calculated as described by Snedecor (73).

The FORTRAN program for calculation of parent and F_1 means, analysis of variance, heritability values,

coefficients of variability, and correlation was written by Dr. Ernest Hilderbrand, University of Missouri.

CHAPTER IV

EXPERIMENTAL RESULTS

Mean squares obtained from an analysis of variance for each of the nine characters studied in a five parent diallel cross with mungbeans are presented in Table 2. There were no differences among replications except for the characters leaf size, days to first flower, and days to first ripe pod. Entries differed significantly for all characters except branch length and pods per plant and F_1's differed significantly for all characters except leaf size and pods per plant. The comparisons of parents and F_1's showed significant differences for all characters including pods per plant.

Since this experiment is concerned primarily with an evaluation of heterosis it is of interest to look at the differences among parents and among F_1's. Yield differences among parents were significant at the .05 level but among F_1's the significance reached the .01 level. Differences among parents and among F_1's were highly significant for days to first flower, days to first ripe pod, plant height, seeds per pod, and 1,000-seed weight. For leaf size parents differed at the .05 level, but F_1's did not differ significantly among themselves. The opposite was observed for branch length where only differences

Table 2. Mean squares from an analysis of variance for each of the nine characters studied in a five parent diallel cross with mungbeans.

Source of variation	D.F.	Yield per plant	Leaf size	Days to first flower	Days to first ripe pod	Plant height	Branch length	Pods per plant	Seeds per pod	1,000-seed weight
Replications	3	156.95	0.2304**	82.54**	82.55**	25.80	78.99	2856.82	0.436	4.98
Entries	14	2058.91**	0.0601*	84.93**	85.50**	361.52**	299.84**	3694.09	3.046**	224.24**
Parents	4	930.04*	0.0758*	130.67**	136.62**	283.45**	110.57	4005.58	5.233**	447.12**
F_1's	9	1730.89**	0.0297	56.40**	54.89**	321.66**	240.45**	1530.10	2.402**	137.49**
Parents vs. F_1's	1	9525.65**	0.2662**	158.39**	156.00*	1032.21**	1591.13**	21924.03**	8.890**	113.11*
Error	42	304.05	0.0242	14.60	14.09	31.62	54.05	2356.75	0.267	18.14
Coefficient of variation		0.1705	0.0207	0.0588	0.0448	0.0925	0.1164	0.2151	0.0415	0.0705

*, **Significant at .05 and .01 levels of probability, respectively.

F_1's were significant. No significant F ratio was found for parents or F_1's for pods per plant, so no LSD's could be calculated. Actual data for each of these characters are given in Tables 3 through 11.

The coefficient of variation for each character is given in Table 2. Highest C. V. was for pods per plant (21.51%) which probably explains the failure of the F ratio for pods per plant to be significant. Next highest coefficient of variation was for yield (17.05%). For all other characters the coefficient of variation was in the acceptable range of 11.64% for branch length to 2.07% for leaf size.

Heterosis

Tables 3 to 11 give the mean of the parents (mid-parent) for each cross and the F_1 as a percent of the midparent and as a percent of the high parent except for the characters days to flower, days to first ripe pod, and seed weight. For each of these characters the F_1 is expressed as percent of the low parent. For days to flower and days to first ripe pod this means that the F_1 is compared with the early parent and for 1,000-seed weight the F_1 is compared with the smaller seeded parent.

Over all crosses the F_1's averaged 26.6 grams seed per plant more than the parents (Table 3), a difference which was highly significant (Table 2). All of the F_1's

Table 3. Yield of parents, F_1's, and midparents (MP), and F_1's as a percent of midparent and of high parent (HP).

	Yield, g per plant			F_1 as a percent of	
	Parent	F_1	MP	MP	HP
Parent:					
M90	84.9				
M101	108.9				
M203	67.0				
M232	80.9				
M472	80.5				
Mean	84.6				
Cross:					
M101 x M90		149.5	96.6	154**	137**
M203 x M90		103.1	76.0	136*	121
M232 x M90		106.6	82.9	129*	126
M472 x M90		91.1	82.7	110	107
M203 x M101		129.9	88.0	148**	119
M232 x M101		129.0	94.9	136**	118
M472 x M101		121.4	94.7	128*	111
M203 x M232		99.0	73.9	133*	122
M472 x M232		80.8	80.7	100	100
M203 x M472		101.3	73.7	137*	125
Mean		111.2	84.4	131	119

LSD for comparison of F_1 with parent = 24.88 (.05), 33.27 (.01). LSD for comparison of F_1 with midparent = 21.548 (.05), 28.820 (.01).

*, **Significantly different from midparent and high parent at .05 and .01 levels of probability, respectively.

Table 4. Leaf size for parents, F_1's, and midparents (MP), and F_1's as a percent of midparent and of high parent (HP).

Parent or cross	Leaf size score, 1 to 8			F_1 as a percent of	
	Parent	F_1	MP	MP	HP
Parent:					
M90	7.45				
M101	7.58				
M203	7.38				
M232	7.45				
M472	7.20				
Mean	7.41				
Cross:					
M101 x M90		7.65	7.52	102	101
M203 x M90		7.65	7.42	103*	103
M232 x M90		7.40	7.45	99	99
M472 x M90		7.50	7.33	102	101
M203 x M101		7.65	7.48	102	101
M232 x M101		7.57	7.52	101	100
M472 x M101		7.55	7.33	102*	100
M203 x M232		7.58	7.41	102	102
M472 x M232		7.45	7.33	102	100
M203 x M472		7.53	7.29	103*	102
Mean		7.55		102	101

LSD for comparison of F_1 with parent (.05) = 0.2220.
LSD for comparison of F_1 with midparent (.05) = 0.1925.

*Significantly different from its midparent or high parent at the 5 percent level, based on LSD. No comparisons were significant for leaf size at the 1 percent level.

Table 5. Days to first flower for parents, F_1's, and midparents (MP), and F_1's as a percent of midparent and of early parent (EP).

Parent or cross	Days to first flower			F_1 as a percent of	
	Parent	F_1	MP	MP	EP
Parent:					
M90	71.8				
M101	60.8				
M203	73.5				
M232	62.0				
M472	68.5				
Mean	67.3				
Cross:					
M101 x M90		63.8	66.3	96	105
M203 x M90		68.3	72.7	94	95
M232 x M90		64.5	66.9	96	104
M472 x M90		68.3	70.2	97	100
M203 x M101		62.8	67.2	93	103
M232 x M101		57.5	61.4	94	95
M472 x M101		58.0	64.7	90**	95
M203 x M232		64.5	67.8	95	104
M472 x M232		63.8	65.3	98	103
M203 x M472		67.3	71.0	95	98
Mean		63.9		95	100

LSD for comparison of F_1 with parent = 5.453 (.05), 7.293 (.01). LSD for comparison of F_1 with midparent = 4.7225 (.05), 6.3162 (.01).

*,**Significantly different from midparent and early parent at .05 and .01 levels of probability, respectively.

Table 6. Days to first ripe pod for parents, F_1's, and and midparents (MP), and F_1's as a percent of midparent and early parent (EP).

Parent or cross	Days to first ripe pod			F_1 as a percent of	
	Parent	F_1	MP	MP	EP
Parent:					
M90	90.8				
M101	79.3				
M203	92.0				
M232	80.5				
M472	87.5				
Mean	86.0				
Cross:					
M101 x M90		82.2	85.1	97	104
M203 x M90		87.3	91.4	96	96
M232 x M90		82.8	85.7	97	103
M472 x M90		87.0	89.2	98	99
M203 x M101		81.5	85.7	95	103
M232 x M101		76.8	79.9	96	97
M472 x M101		76.8	83.4	92**	97
M203 x M232		83.5	86.3	97	104
M472 x M232		82.0	84.0	98	102
M203 x M472		86.0	89.7	96	98
Mean		82.6		96	100

LSD for comparison of F_1 with parent = 5.3553 (.05), 7.1626 (.01)
LSD for comparison of F_1 with midparent = 4.6379 (.05), 6.2030 (.01).

**Significantly different from midparent and early parent at the .01 level of probability, respectively.

Table 7. Plant height for parents, F_1's, and midparents (MP), and F_1's as a percent of midparent and of high parent (HP)

Parent or cross	Plant height, cm			F_1 as a percent of	
	Parent	F_1	MP	MP	HP
Parent:					
M90	52.8				
M101	42.3				
M203	61.3				
M232	63.8				
M472	54.5				
Mean	54.9				
Cross:					
M101 x M90		51.5	47.5	108	98
M203 x M90		73.3	57.1	128**	126**
M232 x M90		77.3	58.3	133**	121**
M472 x M90		69.3	53.6	129**	127**
M203 x M101		58.8	51.8	114*	96
M232 x M101		60.0	53.1	113*	94
M472 x M101		49.5	48.4	102	91
M203 x M232		68.3	62.6	109	107
M472 x M232		62.3	59.2	105	98
M203 x M472		66.5	57.9	115*	108
Mean		63.7		116	107

LSD for comparison of F_1 with parent = 8.024 (.05), 10.731 (.01)
LSD for comparison of F_1 with midparent = 6.949 (.05), 924 (.01)

*, **Significantly different from midparent and high parent at the .05 and .01 levels of probability, respectively.

Table 8. Branch length for parents, F_1's, and midparents (MP), and F_1's as a percent of midparent and of high parent (HP)

Parent or cross	Branch length, cm			F_1 as a percent of	
	Parent	F_1	MP	MP	HP
Parents:					
M90	49.5				
M101	58.3				
M203	60.3				
M232	60.5				
M472	51.0				
Mean	55.9				
Cross:					
M101 x M90		62.5	53.9	116	107
M203 x M90		72.3	54.9	132**	120*
M232 x M90		75.5	55.0	137**	125**
M472 x M90		65.3	50.3	130**	128**
M203 x M101		77.0	59.3	130**	128**
M232 x M101		70.8	59.4	119*	117
M472 x M101		54.0	54.7	99	93
M203 x M232		67.0	60.4	111	111
M472 x M232		58.3	55.8	104	96
M203 x M472		62.8	55.7	113	104
Mean		66.6		119	113

LSD for comparison of F_1 with parent = 10.49 (.05), 14.03 (.01). LSD for comparison of F_1 with midparent = 9.085 (.05), 12.15 (.01).

*, **Significantly different from midparent ahd high parent at .05 and .01 levels of probability, respectively.

Table 9. Pods per plant for parents, F_1's, and midparents (MP), and F_1's as a percent of midparent and of high parent (HP).

Parent or cross	Number pods per plant			F_1 as a percent of	
	Parent	F_1	MP	MP	HP
Parent:					
M90	160.8				
M101	199.5				
M203	236.8				
M232	221.8				
M472	174.5				
Mean	198.6				
Cross:					
M101 x M90		283.5	180.1	157	142
M203 x M90		236.5	198.8	119	100
M232 x M90		248.0	191.3	130	112
M472 x M90		222.8	167.7	133	128
M203 x M101		228.5	218.2	105	96
M232 x M101		243.5	210.7	116	110
M472 x M101		212.5	187.0	114	107
M203 x M232		250.0	229.3	109	106
M472 x M232		226.5	198.2	114	102
M203 x M472		240.3	205.7	117	101
Mean		239.2		121	110

No LSD's were calculated because the F ratio for entries was not significant.

Table 10. Seeds per pod for parents, F_1's and midparents (MP), and F_1's as a percent of midparent and of high parent (HP).

Parent or cross	Number, seeds per pod			F_1 as a percent of	
	Parent	F_1	MP	MP	HP
Parents:					
M90	11.98				
M101	12.23				
M203	11.18				
M232	12.33				
M472	14.28				
Mean	12.40				
Cross:					
M101 x M90		12.38	12.11	102	101
M203 x M90		11.65	11.58	101	97
M232 x M90		11.68	12.16	96	95
M472 x M90		13.93	13.13	106*	93
M203 x M101		11.90	11.71	102	97
M232 x M101		12.38	12.28	101	100
M472 x M101		13.13	13.26	99	92
M203 x M232		11.80	11.76	100	96
M472 x M232		13.33	13.31	100	93
M203 x M472		12.65	12.73	99	89
Mean		12.48		101	96

LSD for comparison of F_1 with parent = .7373 (.05), .9861 (.01).
LSD for comparison of F_1 with midparent = .6385 (.05), .8539 (.01).

*, **Significantly different from midparent and high parent at .05 and .01 levels of probability, respectively.

Table 11. 1,000-seed weight for parents, F_1's, and midparents (MP), and F_1's as a percent of midparent and of low parent (LP).

Parent or cross	1,000-seed weight, g			F_1 as a percent of	
	Parent	F_1	MP	MP	LP
Parent:					
M90	66.28				
M101	77.83				
M203	61.55				
M232	56.05				
M472	50.03				
Mean	62.35				
Cross:					
M101 x M90		68.88	72.06	96	104
M203 x M90		64.83	63.92	101	105
M232 x M90		59.35	61.17	97	106
M472 x M90		55.28	58.16	95	110
M203 x M101		63.85	69.69	92	104
M232 x M101		63.08	66.94	94	113*
M472 x M101		61.08	63.93	96	122**
M203 x M232		53.10	58.80	90	95
M472 x M232		52.55	53.04	99	105
M203 x M472		52.30	55.79	94	105
Mean		59.43		95	107

LSD for comparison of F_1 with parent = 6.077 (.05), 8.127 (.01)
LSD for comparison of F_1 with midparent - 5.262 (.05), 7.038 (.01).

*, **Significantly different from midparent and low parent at .05 and .01 levels of probability, respectively.

exceeded the midparent with the difference being significant in eight of the ten crosses. All of the F_1's equaled or exceeded the yield of the high yielding parent but the difference was significant in only one cross, M101 x M90. These results indicate a large amount of heterosis for yield to be present in the hybrids among parents included in this study. M101 x M90, the only cross exhibiting heterosis over high parent, produced a 37% yield increase over M101, which was the highest yielding parent in the study and one of the highest yielding lines in previous yield trials at Columbia. Average F_1 heterosis for yield was 31% over midparent and 19% over high parent.

Mean leaf size (Table 4) was greater over all crosses than over all parent lines with significance at the .01 level. Significant midparent heterosis for leaf size at the .05 level was in evidence for three crosses, M203 x M90, M472 x M101, and M203 x M472. None of the crosses significantly exceeded the high parent for this character.

The character days to first flower was compared to the midparent and the early parent (Table 5). Five F_1's were earlier than the early parent in this study and all F_1's were earlier than the midparent. However, no cross was significantly earlier than the early parent and only one was significantly earlier than the midparent. F_1's were, on the average, about 3.4 days earlier than the parents.

Data for days to first ripe pod precisely paralleled data for days to first flower with regard to which crosses were earlier than midparent and high parent (Table 6). Once again, no crosses were significantly earlier than the midparent. F_1's were 3.4 days earlier than parents, overall.

Plant height (Table 7) was measured as the length of the central axis. All crosses had greater plant height than their midparents and five were greater than their high parents. Six crosses showed significant heterosis over midparent and three (all M90 crosses except M101 x M90) were significantly superior to the high parent, all at the .01 level. The F_1's were 8.8 centimeters longer than the parents on the average. The F_1's averaged 116% of the midparent and 107% of the high parent.

Nine crosses were longer-branched than their midparent and eight were longer-branched than their high parent (Table 8). Significant midparent heterosis was present in five crosses, with four at the .01 level of probability. Significant heterosis over high parent was present in four crosses with three at the .01 level of probability.

The lowest branches, which were the ones measured for branch length, of the F_1's were 10.7 centimeters longer on the average, than those of the parent lines. F_1's

averaged 119% of midparent and 113% of high parent for branch length.

For pods per plant, the F_1 averaged 239.2 pods whereas the parents averaged 198.6 pods. The comparison, parents vs. F_1's, was significant at the .01 level (Table 2), however, none of the F_1's from specific crosses was significantly higher than its respective midparent or high parent (Table 9). LSD's were not calculated for pods per plant because the F ratio for entries was not significant.

Except for M472, the range in number of seeds per pod was not large among the parents in this study (Table 10). Only one cross, M472 x M90, demonstrated significant heterosis over midparent for this character at the .05 level of probability. The F_1's averaged 101% of midparents and 96% of high parents.

The average 1,000-seed weight over all F_1's was 3.42 g less than the average of the parents (Table 11). This difference was significant at the .05 level (Table 12). Except for the cross, M203 x M90, all F_1's had lower 1,000-seed weight than their respective midparents. Because the F_1's were below the midparent they have been compared to the low parent rather than the high parent. The F_1 of the one cross, M203 x M232, was less than the low parent but the difference is not significant.

Diallel Analysis

Data on all characters studied were subjected to diallel analysis as described by Griffing (25). The results of the analysis of variance for general and specific combining ability are reported in Table 12. All characters showed significant general combining ability mean squares except pods per plant. Specific combining ability effects were significant for two of the characters studied, plant height and branch length. General combining ability mean squares were larger than specific combining ability mean squares for all characters studied.

General Combining Ability

General combining ability values appear in Table 13. M101 clearly demonstrated the best general combining ability for yield in the study and was significantly superior to the only other positive general combining ability effect, that of M90. The gca effects for M90 and M203 did not differ significantly from zero. The performance of M472 was significantly lower than the performance of M90 at the .05 level.

M101 had the highest and M232 the lowest calculated general combining ability effect. No general combining ability effects for leaf size were statistically different from zero. M101 was different from M232 and M472 at the

Table 12. Gca and sca mean squares for nine characters in a five-parent diallel cross of mungbean varieties.

Character	Source of variation		
	GCA	SCA	Error
Yield	3585.667**	247.5073	304.0449
Leaf size	0.06299*	0.0064	0.0242
Days to flower	118.0553**	7.3867	14.6043
Days to ripe	115.9541**	6.4580	14.0853
Plant height	623.8047**	80.1741*	31.6209
Branch length	367.9943**	138.8097*	54.0536
Pods per plant	1469.7083	1578.3333	2356.7451
Seeds per pod	4.6977**	0.5765	0.2670
1000-seed weight	286.2891**	18.5701	18.1351

*, **Significant at the .05 and .01 levels of probability, respectively.

Table 13. Estimates of general combining ability effects for nine characters in a five parent diallel cross of mungbeans.

Character	Parents					LSD between effect and 0		LSD between two effects	
	M90	M101	M203	M232	M472	(.05)	(.01)	(.05)	(.01)
Yield	1.8685	28.3518	-3.8065	-9.7232	-16.6898	9.0852	12.1514	14.3653	19.2131
Leaf Size	-0.0033	0.0717	0.0634	-0.0700	- 0.0616	0.0807	0.1080	0.1281	0.1714
Days to flower	3.1171	-4.4662	2.4504	-1.7163	0.6171	1.9912	2.6632	3.1483	4.2104
Days to ripe	2.9837	-4.3496	2.6504	-1.7663	0.4837	1.9554	2.6153	3.0918	4.1351
Plant height	5.4836	-11.6830	3.9836	4.4836	-2.2664	2.9299	3.9187	4.6327	6.1961
Branch length	3.7338	-1.0162	4.9005	1.4005	-9.0162	3.8308	5.1235	6.0570	8.1010
Pods per plant	11.3167	3.7333	-0.5167	3.7333	-18.2667	ns	ns	ns	ns
Seeds per pod	-0.0983	-0.0483	-0.6399	-0.2483	1.0351	0.2692	0.3600	0.4256	0.5692
1000-seed weight	3.5383	5.3883	-1.2117	-3.2117	- 5.5033	2.2188	2.9676	3.5083	4.6922

.05 level and M203 was significantly different from M232. No parents were different from each other at the .01 level. M232 has the lowest calculated general combining ability for this character.

M101 had the lowest general combining ability effect with regard to days to flower. This is desirable since a low gca signifies early maturity. Therefore, M101 would be the best general combiner for this character. It is significantly superior at the .01 level to M90, M203, and M472. M101 is not statistically superior to M232, however, the gca of M232 is not statistically different from zero, and that of M101 is different from zero at the .01 level. M90 is significantly different from zero at the .01 level in general combining ability effect for lateness. M203 is significantly different from zero at the .05 level with a positive effect, implying lateness.

Data for days to first ripe pod exactly parallel that for days to flower, M101 being superior at the .01 level to M90, M203, and M472. The only difference in effects of days to first ripe pod from days to flower is that M203 is significantly different from zero at the .05 level, being positive.

M90, M203, and M232 all have general combining ability effects for plant height which are different from zero at the .01 level and are positive. M472 has a negative effect which is not significantly different from zero.

M101 has a high negative general combining ability effect for plant height. It is significantly lower than the only other negative plant height effect, that of M472, at the .01 level. All three parents with positive general combining ability effects are significantly superior to M472 at the .01 level, and none are significantly different in effect from each other.

M203 exhibited significant positive general combining ability effects for branch length at the .05 level. M472 demonstrated negative effects which were significant at the .01 level. The remaining three parents, M90, M101, and M232 did not differ significantly from zero, from each other, or from M203. M472 differed from M101 at the .05 level. M472, as stated, exhibited a highly negative general combining ability and was different from the remaining parents at the .01 level for this character.

No significant F test was found for pods per plant, so LSD values were not calculated for the general combining ability effects for this character. This implies that no significant differences in general combining ability effects can be said to exist between parents for this character on the basis of the sample taken.

M472 exhibited significant positive general combining ability effects for seeds per pod, differing from zero at the .01 level. M472 was the only parent which showed positive general combining ability effects for seeds per

pod. M90, M101, and M232 did not differ significantly from zero in their effects while M203 differed significantly from zero at the .01 level. M232 had the lowest calculated general combining ability value for seeds per pod. M203 and M232 do not differ significantly from each other. M203 is significantly different from M90 at the .05 level and significantly different from M101 at the .01 level, the calculated gca for M101 varying from zero by less than .05.

M101 was the best general combiner for 1,000-seed weight, showing positive effect different from zero at the .01 level. M90 was also different from zero at the .01 level with a positive effect. M472 and M232 were significantly different from zero at the .01 level and were negative. M203 did not differ significantly from zero in its effect. M101 and M90 were both positive and significantly different from all other gca's at the .01 level. They were not significantly different from each other. M472, the worst general combiner for this character, was significantly different from M203 at the .05 level. M472 and M232 were not significantly different from each other.

Specific Combining Ability

No significant F ratios were found for specific combining ability except for plant height and branch length (Table 12). Therefore, LSD's were calculated for the two characters only and they are given in Tables 14 and 15.

Table 14. Estimates of specific combining ability for plant height from all single crosses in a five parent diallel with mungbeans

Parent	M90	M101	M472	M203
M101	-6.000			
M472	2.333	-0.250		
M203	0.083	2.750	1.083	
M232	3.583	3.500	-3.170	-3.917

LSD among crosses having one parent in common = 6.5516 (.05), and 8.7626 (.01).
LSD among effects which have no parents in common = 4.6327 (.05) and 6.1961 (.01).

Table 15. Estimates of specific combining ability for branch length from all single crosses in a five parent diallel with mungbeans.

Parents	M90	M101	M472	M203
M101	-7.042			
M472	3.708	-2.792		
M203	-0.209	6.291	0.041	
M232	3.541	3.541	-0.959	-6.126

LSD among crosses having one parent in common - 8.5658 (.05), and 11.45645 (.01).
LSD among crosses having no parents in common = 6.0570 (.05), and 8.1010 (.01).

M232 x M90 was the cross which exhibited the highest specific combining ability for plant height. It did not differ significantly from the sca for crosses involving the other parents. However, it was superior statistically to the sca for M101 x M90, M472 x M232, and M203 x M232. Superiority to the sca for the M101 x M90 cross was at the .01 level of significance. The sca of M232 x M101 was also superior to that of M101 x M90 at the .01 level and to that of M472 x M232 and M203 x M232 at the .05 level. SCA of M203 x M101 was significantly superior to that of M101 x M90 for plant height at the .05 level, as was the sca of M472 x M90.

Crosses having no parent in common which were statistically different in specific combining ability for plant height were M203 x M472, superior to M101 x M90, and M472 x M90, superior to M203 x M232, both at the .05 level of significance.

The M203 x M101 cross had the highest specific combining ability for branch length and M101 x M90 had the lowest specific combining ability for this character. M203 x M101 was superior to M101 x M90 in sca for branch length at the .01 level. If higher values imply superiority, M232 x M90, M472 x M90, and M232 x M101, all had superior sca to M101 x M90 at the .05 level. M203 x M101, the best specific combination for branch length was superior in sca to M203 x M232 at the .01 level and to

M203 x M90 at the .05 level. Other crosses having one parent in common which were statistically different in sca from each other at the .05 level were M232 x M90, superior to M203 x M232, M232 x M101 superior to M203 x M232, and M472 x M90, superior to M203 x M232. M232 x M90, M232, M101, and M472 x M90 were all superior sca for branch length to M203 x M232 at the .05 level.

Crosses having no parents in common which were statistically different from one another in sca were M203 x M101, superior to M472 x M232 at the .05 level, M472 x M90, superior to M203 x M232 at the .01 level, M232 x M90, superior to M472 x M101 at the .05 level, and M203 x M472, superior to M101 x M90 at the .05 level.

Heritability Study

Narrow sense heritability values were calculated for each character by regression of offspring on midparent. The results appear in Table 16. Regression values less than one indicate a large additive component of genetic variance. Regression values greater than one would indicate nonadditive effects. Significant heritability values were obtained for yield, 0.9488, days to flower, 0.7624, days to ripe, 0.7326, seeds per pod, 0.3820, and 1000-seed weight, 0.5201.

Table 16. Narrow sense heritability estimates for characters in a five parent diallel cross of mungbeans

	Heritability value
Yield	0.9488 ± 0.3664*
Leaf size	0.2132 ± 0.1810
Days to flower	0.7624 ± 0.2306*
Days to ripe	0.7326 ± 0.2210*
Plant height	0.3080 ± 0.1834
Branch length	0.0000 ± 0.2119
Pods per plant	0.3230 ± 0.2177
Seeds per pod	0.3820 ± 0.1812*
1000-seed weight	0.5201 ± 0.1543*

*Significant at the 5 percent level.

Correlations

Correlation coefficients were calculated and are presented in Table 17. Yield was significantly and positively correlated with leaf size, branch length, pods per plant, and 1,000-seed weight. It was negatively correlated with days to flower and days to ripe. Leaf size was positively correlated with branch length, pods per plant, and 1000-seed weight. Branch length and pods per plant were positively correlated. Branch length and seeds per pod were negatively correlated, and seed weight and seeds per pod were negatively correlated at a high level. Seeds per pod was the only yield component not significantly correlated with yield in this study.

Days to flower was correlated with days to ripe with a coefficient of correlation of 0.9907, one following the other almost precisely. Days to flower and days to ripe were negatively correlated with branch length. Plant height was closely correlated with branch length and negatively correlated with 1000-seed weight.

Table 17. Correlation coefficients among characters in a five-parent diallel cross of mungbeans

	Yield	Leaf size	Days to flower	Days to ripe	Plant height	Branch length	Pods per plant	Seeds per pod	1000-seed weight
Yield	1.000								
Leaf size	0.456*	1.000							
Days to flower	-0.398*	0.075	1.000						
Days to ripe	-0.397*	0.087	0.991*	1.000					
Plant height	-0.148	0.043	0.093	0.087	1.000				
Branch length	0.305*	0.344*	-0.294*	-0.294*	0.663*	1.000			
Pods per plant	0.355*	0.274*	-0.087	-0.113	0.216	0.381*	1.000		
Seeds per pod	-0.119	-0.237	-0.173	-0.163	-0.119	-0.286*	-0.225	1.000	
1000-seed weight	0.378*	0.302*	0.010	-0.006	-0.473*	-0.032	0.048	-0.476*	1.000

$r_{.05,58} = \pm .255$ (Significant correlation at the 5 percent level).

CHAPTER V

DISCUSSION

Heterosis Analysis

The principal objective of this study was to determine if significant heterosis could be observed for the characters being studied. Yield was of particular significance because the lines utilized were chosen primarily on the basis of yield. Although it is unlikely that heterosis can be commercially exploited in mungbean, the information derived from heterosis studies could be used as an indication of which crosses are most likely to generate the most productive transgressive segregants in succeeding generations (60). In mungbean breeding in the Punjab (62) only those hybrids which exceed the best varieties available by 20% or more are carried into further generations.

The results of the analysis of variance appear in Table 2. Replication mean squares were significant only for leaf size, days to flower, and days to first ripe pod. This indicates that replications, or blocks, did not eliminate gross environmental effects which might have been present. The small error mean square for yield tends

indicate that gross environmental variations did not exist among the plots.

Entry mean squares were highly significant for all characters except leaf size and pods per plant. The leaf size entry mean square was significant at the .05 level of probability. The pods per plant mean square was not significant. This is partly because of high variation within entries as reflected in the high error mean square and the high coefficient of variation. Also, the total sample size per entry was only eight plants.

The analysis of variance showed a difference between at least two parent lines for all characters except branch length and pods per plant. A significant difference existed between at least two F_1's for all characters except leaf size and pods per plant.

The grand mean for parents was highly significantly different from the grand mean for F_1's for all characters studied except 1000-seed weight in which the F_1 mean was superior to the parent mean at the .05 level of probability. This shows the F_1's in general to be superior to the parents for all characters with the possible exception of branch length. Even though branch length was significantly correlated with yield, short branches might ultimately be desired in breeding for plant type. The data indicates that the difference between the parents and the F_1's in days to flower and days to first ripe pod was due to the

F_1's being earlier than the parents. Earliness is a desirable characteristic in the mungbean for most production areas if there is no corresponding loss in yield.

Heterosis Analysis

Highly significant heterosis for yield was found in this study, particularly in those crosses involving M101. Eight crosses were significantly superior to their respective midparents including all crosses involving M101. The M101 x M90 cross yielded 37% more than M101, the high yielding line in the study. M101 outyielded the next lowest parent line by 24 grams per plant or 28% of the lower line.

The four crosses involving M203 outyielded their high parent by 25, 22, 21, and 19%, respectively. Unfortunately, M203 was the low yielding line in this study, but it performed well in preceding years at Columbia and these crosses may have some promise.

M232 x M90 yielded 125% of the yield of M90, the second highest yielding line in the study and the second highest yielding line among all strains planted in Columbia in 1970 and 1971 (Table 2).

More differences might have been detected between high parents and F_1 lines had it not been for the high coefficient of variation for yield (17.05%). F_1's overall outyielded parents overall by an average of 26.6 grams per plant.

The only crosses which showed significant increases in leaf size over their respective midparents were M101 x M90, M203 x M90, and M203 x M101, all at the .05 level of probability. The leaf size readings were inevitably somewhat subjective in that the plant contained a whole range of leaf sizes and no leaves precisely fit the sketches against which leaves were compared to obtain leaf size scores. It is likely that these values were somewhat stabilized since the data subjected to analysis were plot means. All of the lines were large leafed compared to many other varieties in the U.S.D.A. world collection. Leaf size in F_1's overall averaged 102% of midparent and 101% of high parent.

Earliness of flowering is desirable if it can be achieved without significant loss in yield. Earliness tends to be dominant in character, although only one F_1 was significantly earlier than its midparent for days to flower and days to first ripe pod. No F_1's were significantly different from their early parent although five F_1's were earlier than their earliest parents. Variations in days to first flower may have influenced yield in this experiment due to drought conditions in the field. M101 and M101 derivatives tended to escape damage due to low soil moisture, at least in the earlier flushes of flowers and pods. An average advantage of 3.4 days for F_1's over

parents was found for days to flower and days to first ripe pod.

Significant increases in plant height over high parent were discovered in three of the crosses involving M90. The M101 x M90 cross did not show significant heterosis for this character over midparent. The high parent heterosis in these three crosses was over 20% in each case. This could be quite promising if the taller F_1's are more upright. These lines, M90 and M101, are semiprostrate with long branches and a short main stem, and tend to lay closely along the ground. The F_1's were, on the average, 16% taller than the midparent and 7% taller than the high parent.

Significant heterosis for branch length may or may not be desirable. While the longer branches would provide a greater capacity for the plant to hold pods, unless they are held upright, the pods may lay on the ground and spoil. The three crosses involving M90 which showed significant high parent heterosis for plant height also showed significant high parent heterosis for branch length, as did one other cross, M203 x M101. The increase in branch length of F_1's over the midparent averaged 19% and over the high parent averaged 13%.

Only two of the F_1's were significantly superior to the low parent for 1000-seed weight and none were superior statistically to the midparent. This is consistent with

the findings of two other studies concerned with seed size by Sen and Murty (54) and Singh and Jain (64). Sen and Murty suggest that a large number of recessive genes condition large seed size in mungbean. The parent average in the present study was about three grams per 1000-seed higher than the F_1 average. F_1's manifested about 107% of the early parent and about 95% of the midparent and seed weight.

Diallel Analysis

General Combining Ability

The best general combiner for yield in this study proved to be M101. The general combining ability effect for yield for M101 was significantly superior to the only other positive general combining ability effect, that of M90. M101 was a large-seeded, prostrate, early maturing variety. M472 was the poorest general combiner for yield. M232 also performed poorly. The gca effect of M203 was not different statistically from zero.

It is difficult to say that any of the general combining ability effects for leaf size have any meaning since none differ significantly from zero. However, M101 is the best general combiner, followed closely by M232 according to calculated values. M101 is statistically superior to M472 at the .05 level of probability.

M101 had the lowest general combining ability effect with regard to days to flower and is therefore the best general combiner for this character. M232 is next in line as a progenitor of earliness, while M472 is a progenitor of lateness. Data for days to flower closely parallel that for days to ripe.

M90 has the highest general combining ability effect for plant height, followed closely by M232. M101 conditions short central axis in hybrids at a very high level of significance.

Even though branch length was significantly correlated with yield in this study, heterosis and high general combining ability for branch length might ultimately be deleterious in breeding programs. Long branches tend to lie along the ground, and since there is no seed dormancy in mungbean the seeds tend to germinate in the pods during wet weather. This not only destroys the seed involved but reduces the total seed quality. M203 showed the highest general combining ability effect for branch length, closely followed by M90. M472 had the lowest general combining ability effect for branch length but other characters would make this a poor line for use in breeding programs.

There was too much variation within treatments for pods per plant so that the F test for general combining ability was not significant. LSD's are not calculated unless a significant F test is obtained.

M472 had the best general combining ability effects for seeds per pod, all other calculated values being negative. Only M203 demonstrated a negative general combining ability effect for seeds per pod which was significantly different from zero.

Seed weight has been shown to be an important character in determining yield in mungbean by Singh and Malhotra (66). Crosses involving M101 did not show heterosis for seed weight because all crosses produced seed smaller than the midparent. However, a high positive general combining ability value shows M101 to be a good contributor to seed weight in crosses. M232 and M472 are both poor general combiners for seed weight. M203, gca effects do not differ significantly from zero.

Specific Combining Ability

The only F ratios which were significant with regard to specific combining ability were those for plant height and branch length. Consequently, these were the only effects for which LSD's were calculated. The best single cross as far as specific combining ability is concerned was M232 x M90.

M232 x M101 was a good cross also for specific combining ability, as was M203 x M101. Specific combining ability is related to the performance of the two lines involved in the cross and not directly to the performance

of all lines involved. It happens that the tallest cross is the same as the cross which had the highest specific combining ability. However, the mean for the cross which exhibited the second highest sca for plant height (M232 x M101) was below average plant height for all crosses. M101 x M90 exhibited the lowest sca effect for plant height and the second lowest mean for plant height. The second lowest sca effect was for M203 x M232 and the third lowest was for M472 x M232.

The highest sca effect for branch length was exhibited by the cross, M203 x M101. The M472 x M90 had the second highest sca effect for this character. The crosses M232 x M90 and M232 x M101 had high sca effects for branch length and were equal to each other. The cross exhibiting the lowest sca effect for branch length was M101 x M90 and the second lowest was for M203 x M232. Other sca effects were relatively close to zero.

Heritability Analysis

Narrow sense heritability is defined as the percent of total phenotypic variation which has its base in additive gene effects passed from parent to offspring. A narrow sense heritability value of .95 was calculated for yield in this study. This implies that 95% of the total variation in the F_1 is derived from additive gene effects, or that yield in these crosses was 95% heritable as

additive gene effects, which is a highly desirable situation. Values greater than one are possible in this kind of analysis which would imply a greater percentage of dominance and epistatic effects.

Lower heritabilities were calculated for days to flower and days to ripe, but heritability as additive fraction is still quite high at 76 and 73%, respectively.

Seed weight had the next highest heritability value, being 52 percent heritable by additive effects. This is consistent with the theory of Sen and Murty that seed size is conditioned by a large number of recessive genes. Such a group of genes would act additively, the seed weight increasing as more genes accumulated.

Seeds per pod was the only other significantly heritable character for this study at a level of 38%.

Correlations

The fact that yield was closely correlated with leaf size in this study implies that yield is correlated highly with general health and vigor, healthy vigorous plants tending to have large leaves. Leaf size was also correlated with two yield components, pods per plant and 1000-seed weight.

The negative association between yield and days to flower probably implies that earlier plants had a longer time to produce pods and profited by it. It may be that

drought escape might have had something to do with the higher yield of earlier plants, the soil having become progressively drier after the last half of July.

A high correlation existed between seed size and yield. This is consistent with the findings of Singh and Malhotra (66) in multiple regression analysis. The Singh and Malhotra study also showed seed size to be correlated with pod length which was correlated with seed yield.

Days to first flower was so closely correlated with days to ripe that one can be used to predict the other, as described by Bhatnagar and Singh (3) and Singh and Malhotra (66).

Branch length was correlated with yield, leaf size, and plant height and was negatively associated with days to flower and days to ripe. The correlation with yield, leaf size, plant height, and branch length was clearly an association with general health and vigor. The negative association with days to flower and days to ripe might not have existed by the end of the season. Late maturing plants tended to grow more slowly and to be smaller when measurements were taken. Long branches might ultimately be deleterious when breeding is designed to improve plant type, as discussed earlier.

Pods per plant was positively correlated with leaf size and branch length. It is reasonable that longer

branches should bear more pods. Leaf size and branch length are both indications of general vigor.

Seeds per pod was the only yield component not associated with high yield in this study. The probable reason for the negative association between yield and seeds per pod is that M472, an overall poor line, was the only line in the study that had an obviously higher number of seeds per pod than the other lines involved. Among the other lines, range in seeds per pod was very small. Seeds per pod were negatively correlated with branch length, probably because of the contribution of M472, also.

Seed weight was positively associated with leaf size and plant height and was negatively associated with seeds per pod. This is strictly consistent with the findings of Singh and Malhotra (66).

CHAPTER VI

SUMMARY AND CONCLUSIONS

This study compares five parent lines of mungbeans and all possible nonreciprocal crosses between them.

Significant heterosis of F_1's over parents overall was present for all characters studied except days to flower, days to first ripe pod, and 1000-seed weight.

Eight hybrids significantly outyielded their respective midparents and one outyielded its high parent, the highest yielding parent in the study by 37% of the parent. Highest heterosis over midparent for yield was 154% of midparent. Average heterosis over midparent was 31% and over high parent was 19%.

Heterosis for leaf size averaged 102% of midparent and 101% of midparent. F_1 lines were on the average, 3.4 days earlier in flowering and ripening than the parent lines. Plant height in F_1's averaged 116% of midparents and 107% of high parents. Branch length averaged 119% of midparents and 113% of high parents. Pods per plant averaged 121% of midparents and 110% of high parents. Seeds per pod averaged 101% of midparents and 96% of high parents. F_1 seeds were smaller than parent seed in general, averaging 95% of midparents and 107% of small seeded parents.

General combining ability mean squares were much larger than specific combining ability mean squares over all characters except pods per plant. Neither gca nor sca F ratios were significant for pods per plant. Gca F ratios were highly significant for all characters except leaf size, for which the F ratio was significant at the .05 level of probability, and pods per plant, for which there was no significance. Sca F ratios were significant only for plant height and branch length.

Yield was shown to be highly heritable by the narrow sense heritability estimate. Additive gene effects conditioning yield accounted for 95% of the total phenotypic variation in the F_1's. Days to flower and days to first ripe pod were highly heritable by additive gene effects, as was 1000-seed weight and high seed weight. Apparently 1000-seed weight is conditioned by a large number of recessive genes. Seeds per pod was also significantly heritable via additive effects according to the narrow sense heritability estimate.

Yield was significantly correlated with leaf size, branch length, pods per plant, and 1000-seed weight, and was negatively correlated with days to flower and days to ripe. Days to flower was correlated with days to first ripe pod at the .991 level, one following almost precisely from the other. Pods per plant and 1000-seed weight were

not significantly correlated. 1000-seed weight was highly negatively correlated with seeds per pod.

The best performing parent in this study was M101. It was the earliest and the highest yielding strain and had the highest general combining ability for yield, leaf size, days to flower, days to first ripe pod, and 1000-seed weight. It had the second (equal to M232) highest gca effect for pods per plant. M90 was probably the next best parent, with the second highest yield, the best gca for pods per plant and plant height, and the second best gca for yield and 1000-seed weight. The cross M101 x M90 was the outstanding single cross in the study. Unfortunately M90 was the latest parent and the one most significantly conditioning lateness. M472 performed most poorly in crosses with regard to yield, leaf size, plant height, branch length, pods per plant, and 1000-seed weight.

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