INHERITANCE OF YIELD AND AGRONOMIC CHARACTERS IN DIALLEL CROSSES OF SPRING FABABEANS (*Vicia faba* L.)

by

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ABSTRACT

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F1 and F2 complete diallels were used to study the heterosis and inheritance of yield and agronomic characters among inbred lines from five agronomically adapted fababean cultivars grown in Western Canada. The heterosis and performances of crosses were further studied in an F1 half diallel among the five cultivars themselves. The diallel crosses were grown in the field during 1982 and 1983.

Characters of more complexity and close association with vegetative and reproductive fitness appeared to express more heterosis, more dominance and lower narrow-sense heritabilities. Yield had the greatest extent of heterosis, most dominance and lowest narrow-sense heritability. Expression of heterosis for yield appeared to increase with heterozygosity at a genetically determined rate. Hybrid yield performances were related to that of their inbred line parents but not to their cultivar parents.

It was concluded that TDM and HI may be quite efficient as selection criteria for high yields. Protein content was generally independent of yield and controlled mainly by additive gene effects with some negative partial dominance.

Herz Freya, followed by Erfordia, were the better general combiners for yield, while Herz Freya x Erfordia was the best specific combina-

tion. Different growth and assimilate distribution patterns were displayed among all parents. It was concluded that specific hybrids with Herz Freya as a common parent, may produce a 35-40% yield advantage over open-pollinated cultivars.

CONTENTS

LIST OF TABLES

LIST OF FIGURES

Chapter I

INTRODUCTION

Fababeans are known botanically as Vicia faba L. Numerous English common names apply to the crop including Spanish, Egyptian, pigeon, winter, spring, garden, fava, vicia, common, horse, tick, broad and field beans. To eliminate the confusion resulting from this multiplicity of names, the term fababeans was adopted for the entire species in the early 1980s (Hawtin and Hebblethwaite 1983).

The species is diploid with 2n=12. It is not known to intercross with any other species and no wild ancestors have been identified (Lawes 1980). However, the species is classified by seed size into three botanical varieties, minor, equina and major. The minor and equina groups comprise the small and medium seeded varieties respectively, while the major group comprises the large garden broadbean varieties (Witcombe 1982). Great genetic variation exists between varieties as well as within varieties and intercrossing can occur freely (Lawes 1980).

Fababeans are a traditional crop in most areas of Europe, North and Central Africa, Central and South America and China, dating back to the origins of crop cultivation in the Middle East (Hawtin and Hebblethwaite 1983). In these regions, fababeans are an important protein source for human foods and livestock feeds.

Fababean cultivars from Western Europe were introduced into Western Canada in the early 1970s by scientists at the University of Manitoba (Furgal and Evans 1980). Fababeans showed immediate promise with a

high protein content (near 30%) and high seed yields averaging over 3000 kg/ha in plot scale yield trials (McVetty, personal communication).[1]

In contrast, yields on a commercial scale have averaged near 2000 kg/ha with wide fluctuations from 400 kg/ha to over 5000 kg/ha (Platford et al. 1981). These attributes of the crop have resulted in fababean breeders identifying increased yields and improved yield stability as two major breeding program objectives.

Fababeans are a partially cross-pollinated crop (Hanna and Lawes 1967) which display a considerable amount of heterosis and inbreeding depression (Poulsen 1979; Lawes et al. 1983). This heterosis is exploited by breeders via the production of open-pollinated populations and more recently, via the production of synthetics (Hawtin 1982). The development of F1 hybrids is on the horizon, since both genetic male sterility (Bond et al. 1964) and cytoplasmic male sterility systems (Bond et al. 1966a, 1966b) have been discovered. These pollen control systems are unsuitable for commercial production of F1 hybrid seed at present, but this may change in the future since research is presently being conducted into these pollen control systems (Picard et al. 1982).

Given the known heterotic response of the crop to genetic heterozygosity and the possible availability of pollen control systems, it seems logical for Canadian fababean breeders to pursue the production of synthetics and/or F1 hybrids as a potential solution to the low yields and poor yield stability of fababeans. Before this breeding approach can be effectively used, a considerable amount of information

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[1] McVetty, P. B. E. Unpublished data.

regarding the degree of heterosis for yield and related characters, the genetics for the characters of concern and the predictability of hybrid performance from parental performance is required.

The objectives of this research were to determine:

1. the degree of heterosis for yield and agronomic characters,
2. the relative agronomic performances of the parents in hybrid combinations,
3. the genetic control and heritability of yield and agronomic characters

in diallel crosses among genotypes from five agronomically adapted fababean cultivars grown in Western Canada.

Chapter II

LITERATURE REVIEW

2.1 CROP DESCRIPTION

Canadian grown fababeans belong to the small to medium seeded types since they must be handled with conventional cereal equipment. The plants are erect-stemmed annuals with an indeterminate flowering habit. They reach 1 - 1.5 metres tall and flower profusely at each node along the length of the stem starting about 20 cm from the ground. Only a few flowers produce pods and each pod contains three to four seeds. The seeds weigh 275 to 500 g per 1000, depending on the cultivar and environment. When fababeans mature, the leaves darken and drop, the pods blacken and dry progressively up the stem. Days from seeding to maturity depends on the cultivar and environment and ranges from 83 to 114 days (Platford et al. 1981).

2.2 BREEDING NATURE

Fababeans are a partially allogamous species with an average outcrossing frequency from 30 - 40%, although under different environments, frequencies from 5 - 80% have been reported (Hawtin 1982; Bond and Poulsen 1983). In Manitoba, a wide range from 8.5 - 58.8% outcrossing was reported (McVetty and Nugent-Rigby 1984). Pollinating bees trip (release the stigma and stamens from the keel) the flowers which can lead to cross- or self-pollination. Some plants are able to self-pollinate and self-fertilize without tripping and are referred to

as autofertile (Drayner 1959). Autofertility is a desired feature since it confers yield stability with variable bee populations. High autofertility is a general characteristic of cross-bred plants but can be genetically fixed in some inbred lines (Drayner 1959; Holden and Bond 1960; Siong and Knight 1980). Generally, autofertility decreases with inbreeding but after crossing, autofertility is fully restored. Inbreds tend to cross more and cross-breds tend to self, thus the intermediate breeding status of the crop is maintained (Drayner 1959).

As expected from its breeding nature, heterosis and inbreeding depression exist in fababeans. Cross-bred plants express hybrid vigor and high autofertility. Decreased yields, which usually reach a minimum after three generations of selfing occurred due to inbreeding depression and reduced autofertility (Poulsen 1975; Poulsen 1979; Monti and Frusciante 1982). With bee-pollination, inbreeding depression alone reduced yield 22% in one experiment (Monti and Frusciante 1982) and 11% in another experiment (Poulsen 1979). Yield reductions were even greater in undisturbed inbreds from the further effect of reduced autofertility (Poulsen 1979; Monti and Frusciante 1982). However, some inbred lines suffered little from inbreeding depression and yielded equally to open-pollinated populations (Lawes 1973; Poulsen 1979).

2.3 QUANTITATIVE GENETICS

The strategy for crop improvement by breeding depends on proper assessment of the genetic variation in relation to the environmental components of variation. The breeding methods depend on the type of genetic variation, that is, the action, interaction and linkage relationships of genes controlling the character.

Mendelian genetic principles have been most directly useful with the large recognizable effects of qualitative characters. Most economically important plant characters, however, are controlled by quantitative genes which display continuous variation. In these characters, discrete classes are not identifiable and classical Mendelian genetic analyses can not be used. Such characters are controlled by the joint action of many genes, each inherited in a Mendelian fashion and subject to environmental modification.

Quantitative or biometrical genetics allows these quantitative characters to be studied. This approach studies the genetic phenomena using statistical procedures. Statistical parameters such as means, variances and covariances are used to characterize families and populations. These statistics are then partitioned into genetic components, whose properties are derived from Mendelian principles. Various mating designs, such as diallel matings, were developed to allow these genetic components to be estimated (Breese 1972).

2.3.1 Components of Genetic Variation

Fisher (1918) was the first to partition genetic variation into its component parts. These are additive, dominance and epistatic effects.

The additive component describes genes either at the same locus or at different loci which act independently by increasing or decreasing the phenotypic expression. The dominance part describes the intra-allelic interaction between genes at the same locus such that one allele masks the effect of the other to varying degrees. Meanwhile, the epistatic part involves the inter-allelic interaction between genes at different loci such that expression at a gene locus is influenced by that of another gene locus (Allard 1960).

Additive and dominance gene effects are the more commonly partitioned components. Their relative importance can be implied from the dominance ratio. This is the ratio of the dominance effects over the additive effects. A ratio less than one implies partial dominance, a ratio equal to one implies complete dominance, while a ratio over one implies overdominance. However, this "average estimate" of relative dominance should be interpreted with caution. Since the individual genes controlling a quantitative character are not recognizable, biometrical genetics handles them as an overall effect. Most likely, in any one genotype not all its genes would be unidirectional but a balance of genes with some opposing effects. Crosses between genotypes with differing oppositional balances of genes, could produce under- or over-expressions of the genetic components (Mather and Jinks 1977).

2.3.2 Heritability

Heritability estimates provide a measure of the relative importance of genetic components to the phenotypic variation, the latter being the sum of the genotypic and environmental variations. There are two types of heritabilities, broad-sense and narrow-sense, of which the latter is more useful.

Broad-sense heritability is the ratio of genotypic variation over phenotypic variation. This expresses the degree of genetic determination or simply the amount of environmental influence on the character. Narrow-sense heritability is the ratio of additive genetic variation over phenotypic variation. It expresses the extent of resemblance between relatives and allows the determination of the response to selec-

tion and thus, is of great importance in breeding programs (Falconer 1981).

2.4 YIELD

2.4.1 Agronomic Considerations

Heterosis for yield in F1 hybrids is important in fababeans. Yields exceeding the top parent in crosses have been widely reported (Hayes and Hanna 1968; Samia 1977; Lawes and Newaz 1979). In diallel crosses of winter bean lines, F1 hybrids yielded 23% more than the best inbred parents and 18% more than the open-pollinated controls (Bond 1966). These superior yields were unique to the F1 since yields declined in subsequent generations (Hayes and Hanna 1968; Poulsen 1977; Kittlitz 1981).

2.4.2 Genetics and Heritabilities

Genetic analyses of several inbred line diallels indicated that overdominance was positively expressed for yield (Bond 1966; Lawes and Newaz 1979; Hobbs and Burnett 1982).

Yield generally had low heritability (Bond 1966; Dantuma et al. 1983). Broad-sense heritability estimates for yield per plant reported in several studies were 28.7% (Yassin 1973), 23% (Vries 1979) and 21.3% (El-Zahab et al. 1980). In contrast, a high broad-sense heritability estimate of 88.1% for yield per plot was reported by Yassin (1973). Thus, plot yields were less subject to environmental influence than yields per plant.

Narrow-sense heritability estimates varied. Poulsen (1977) reported a narrow-sense heritability for yield of 60% in an F1 diallel.

Hobbs and Burnett (1982) reported a mean narrow-sense heritability of 16.2% for three F2 diallels. Filippetti (1979) found a narrow-sense heritability of 18% obtained from regressions between parents and their progenies. Therefore, the genotypes under study, the estimation method used and the environmental effects seem to have a substantial effect on the narrow-sense heritability estimates for yield.

Thus, heterosis, positive overdominance and low to moderate narrow-sense heritabilities characterize the genetics and inheritance for yield in fababeans. All these attributes suggest that fababeans should be handled as synthetics or F1 hybrids to maximize the yield potential in this crop.

2.5 YIELD COMPONENTS

2.5.1 Agronomic Considerations

Low heritabilities for yield lead scientists to search for characters correlated with yield which had higher heritabilities. Rowlands (1955) partitioned yield into the product of the number of plants per unit area and the three primary yield components, number of pods per plant, number of seeds per pod and seed weight. The usefulness of these three primary yield components was shown when Kambal (1969) found they accounted for 95-98% of the variability in yield of three fababean cultivars.

Yield and yield components are frequently highly correlated. The literature stressed more than any other component, the role of pods per plant as the chief determinant of yield (Bond 1966; Sjodin 1977; Nassib et al. 1978; Lawes and Newaz 1979; Cubero and Martin 1981; Salih 1981). In different studies however, seeds per pod (Kambal 1969;

Salem 1982) and seed weight (Ishag 1973; Bianco et al. 1979; Pace 1979) were also important.

However, yield components are sometimes negatively correlated with yield. Yassin (1973) found yield was positively correlated with pods per plant but negatively correlated with seed weight. In other studies, yield components had no significant correlation with yield and thus were of no predictive value (Vries 1979; El-Zahab et al. 1980).

Positive correlations have occasionally occurred among yield components (El-Zahab et al. 1980; Salem 1982) suggesting that simultaneous selection for yield components could be successful. However, negative correlations are also widespread between yield components. For example, pods per plant was negatively correlated with seeds per pod (Ishag 1973; Pace 1979; El-Zahab et al. 1980) and with seed weight (Yassin 1973; Bianco et al. 1979). Negative correlations were also found for seeds per pod versus seed weight (Kambal 1969; Poulsen 1977; Bianco et al. 1979). These negative correlations can lead to yield component compensation which can severely limit the usefulness of yield components as selection criteria in breeding programs.

The particular yield components that showed F1 heterosis varied in different experiments, but generally, yield components displayed less heterosis than yield (Bond 1966; Lawes and Newaz 1979). Bond (1966) found the superiority of F1 yields was achieved through both more stems per plant resulting in more pods per plant and increased seed weight. Poulsen (1977) found increased seed weight alone was responsible for higher F1 yields. However, Samia (1977) found heterosis for yield depended mostly on increased pods per plant, while seed weight showed no significant heterosis. Lawes and Newaz (1979) reported neg-

ative F1 heterosis on a mid-parent basis for seed weight that was counteracted by positive heterosis for pods per plant and seeds per pod.

2.5.2 Genetics

Yield components generally exhibited less dominance and more additive gene action than yield (Lawes and Newaz 1979). Bond (1966) reported no overdominance in any yield component whereas yield exhibited considerable overdominance. In agreement, Hobbs and Burnett (1982) reported from a diallel using Afghanistany lines as well as from a diallel using European lines, that yield exhibited the greatest degree of overdominance even though some yield components also displayed overdominance.

Pods per plant generally expressed significant dominant gene action. In most studies, this was positively expressed as partial dominance (Bond 1966) or overdominance (Hayes and Hanna 1968; Martin and Cubero 1979). In other studies, dominant genes were ambidirectional (Poulsen 1977; Hobbs and Burnett 1982). There was evidence of interactions as well (Hayes and Hanna 1968; Martin and Cubero 1979).

Seeds per pod expressed a wide range of gene actions. Bond (1966) found more-or-less additive gene effects while some other studies indicated positive overdominance effects (Martin and Cubero 1979; Hobbs and Burnett 1982). In contrast, ambidirectional dominance (Poulsen 1977) and even negative partial dominance have been reported (Hobbs and Burnett 1982). Epistatic effects were also reported (Hobbs and Burnett 1982).

Similarly, for seed weight, increases in this character displayed partial dominance (Bond 1966; Poulsen 1977; Hobbs and Burnett 1982) or overdominance (Cubero-Salmeron 1976). However, in other studies, reduced seed weight displayed partial dominance (Martin and Cubero 1979; Hobbs and Burnett 1982).

2.5.3 Heritabilities

The yield components generally had high heritabilities exceeding that for yield (Bond 1966; Dantuma et al. 1983). Yassin (1973) found broad-sense heritability estimates of 93.7% and 54.7% for seed weight and pods per plant, respectively. El-Zahab et al. (1980) reported broad-sense heritability estimates of 84.3%, 99.9% and 98.4% for seed weight, seeds per pod and pods per plant, respectively.

Narrow-sense heritability estimates were generally highest for seed weight (Poulsen 1977; Filippetti 1979). Narrow-sense estimates were 95%, 79% and 73% for seed weight, seeds per pod and pods per plant respectively (Poulsen 1977). Filippetti (1979) obtained narrow-sense heritability estimates of 100%, 64% and 28% for seed weight, seeds per pod and pods per plant respectively, from regressions between parents and their progeny grown under open-pollination. In agreement, Vries (1979) reported high narrow-sense heritability for seed weight and intermediate narrow-sense heritability for pods per plant. In diallel crosses using Afghanistany lines, Hobbs and Burnett (1982) reported narrow-sense heritability estimates of 88.0%, 66.6% and 17.3% for seed weight, seeds per pod and pods per plant, respectively. However, in diallel crosses using European lines, seed weight had the highest narrow-sense heritability estimate of 85.9%, but pods per plant followed

with 67.8% and seeds per pod had the lowest estimate of 34.1% (Hobbs and Burnett 1982).

In summary, the genetic behavior for a particular yield component varied with different genotypes, estimation methods and environments. Yield components were frequently highly correlated with yield but yield component compensation was common. Yield components displayed less heterosis, less dominant and more additive gene action than yield. Yield components were generally highly heritable and seed weight had the highest narrow-sense heritability. Thus, selection for increased yields via selection for yield components would probably be unsuccessful, in spite of the high narrow-sense heritability of yield components due to yield component compensation.

2.6 TOTAL DRY MATTER AND HARVEST INDEX

2.6.1 Agronomic Considerations

A newer approach to examine yield in fababeans is through the concepts of total dry matter production (TDM) and harvest index (HI). TDM generally refers to the above ground portion of the plant, including the seeds. HI is defined as the ratio of seed yield to total dry matter produced expressed as a percentage (Hawtin 1978). The most economical determination is obtained from seed yield and TDM at maturity, although losses of senescent leaves give an apparent HI value higher than the actual defined HI (Dantuma and Thompson 1983). HI provides a crude measure of the efficiency in partitioning assimilates into the economical product, seed yield.

The relationships of TDM and HI to higher yields are variable. In F1 crosses, Neal (1982) observed the most heterosis for yield, followed by TDM and to a lesser extent, HI. From characterizing 535 fa-

babean accessions grown over two seasons, he also concluded that TDM was the best predictor of yield.

However,Thompson and Taylor (1981) observed higher TDM production in more fertile conditions but the increase in yield was not proportional, leading to a lower HI. Their controls, grown at lower levels of input, had lower TDM, similar yields and higher HI. They concluded that increased HI stability was important for increased yields. Similarly, Dantuma et al. (1983) found the highest HI values in a dry and sunny year with the lowest yields and lower HI values in an environment conducive to vegetative growth with the highest yields. In contrast, Keller and Burkhard (1981) reported that HI was relatively stable. With increasing plant densities, both TDM and yield per plant decreased progressively while HI decreased only slightly. Genotypic differences between cultivars in HI and HI stability over environments were evident (Keller and Burkhard 1981; Thompson and Taylor 1981; Dantuma et al. 1983).

2.6.2 Genetics and Heritabilities

Literature on the genetic control of TDM and HI is scarce. Cubero-Salmeron (1976) reported that weight per plant expressed positive overdominance in F1 diallel crosses.

Heritability estimates for TDM and HI are also rare. El-Zahab et al. (1980) reported a broad-sense heritability estimate of 70.2% for TDM after 170 days from planting. Vries (1979) found low broad-sense heritability estimates for HI of 42% and 40% for two different fababean populations. He also observed no significant genetic correlation for HI with yield. Thus, he concluded that HI offered no prospects as a criterion in yield selection.

To sum up, TDM and HI are relatively new and unexplored concepts as apparent from the scarcity of literature. The relationships of TDM and HI with yield as well as the genetics and inheritance for TDM and HI in fababeans require further elucidation. However, it is important to have both relatively high and stable TDM and HI to achieve maximum and stable yields in fababeans (Hawtin 1978).

2.7 PHENOLOGICAL CHARACTERS

2.7.1 Agronomic Considerations

The influence of different growth phases on yield was often studied as a possible selection criterion for yield as well as for early maturity (Poulsen 1977). Vries (1979) concluded the onset and duration for flowering as well as the onset, duration and end of grain filling could be useful as selection criteria for yield improvement.

Broadly, the total growth period for a crop is divided into the pre-anthesis and post-anthesis growth phases (Poulsen 1977). Most commonly studied are the total growth period or days to maturity and pre-anthesis growth phase or days to first flower.

Most studies found later maturity positively correlated with increased yields (Magyarosi and Sjodin 1976; Poulsen 1977; Vries 1979). In these studies, both later flowering and a longer post-anthesis phase were also positively correlated with yield (Poulsen 1977) or a longer post-anthesis phase alone was positively correlated with yield (Vries 1979). In contrast, some studies showed no correlation between days to maturity (Salem 1982) or days to flower (Bond 1966; Pace 1979) with yield.

2.7.2 Genetics

The genetic control of these characters was governed by additive genes with some dominant gene action, generally towards reduced expression of the character. Days to maturity exhibited either negative partial dominance (Poulsen 1977; Martin and Cubero 1979) or negative complete dominance (Cubero-Salmeron 1976). All studies reported days to flower expressed negative partial dominance (Bond 1966; Poulsen 1977; Martin and Cubero 1979; Hobbs and Burnett 1982). The post-anthesis phase displayed ambidirectional dominance (Poulsen 1977).

2.7.3 Heritabilities

Heritabilities for phenological characters were relatively high. Vries (1979) reported broad-sense heritability estimates of 90%, 99% and 85% for days to maturity, days to flower and post-anthesis growth phase respectively.

Narrow-sense heritability estimate for days to maturity was 85% in an F1 diallel (Poulsen 1977). Narrow-sense heritability estimates for days to flower were 65% in an F1 diallel (Poulsen 1977) and a range from 38.1% to 73.7% in F2 diallels (Hobbs and Burnett 1982). Post-anthesis phase had a narrow-sense heritability of 64% in an F1 diallel (Poulsen 1977).

Generally, shorter growth phases were negatively correlated with higher yields but these negative correlations were broken in a few cases. Additive gene effects with some dominance towards reduced expressions and high heritabilities generally characterize these phenological characters.

2.8 MORPHOLOGICAL CHARACTERS

2.8.1 Agronomic Considerations

Rapidly and easily measured morphological characters were frequently advocated as yield selection criteria. Rowlands (1955) stated the primary yield components were influenced by secondary components such as the position of the first podded node and plant height. Vries (1979) suggested number of stalks per plant and plant height as useful selection criteria.

The productivity of secondary stalks is generally lower than main stem productivity (Chapman and Peat 1978; Hawtin 1978). However, some studies found stalks per plant positively correlated with yield (Kambal 1969; Bianco et al. 1979; Pace 1979). In contrast, other studies found stalks per plant not correlated (Bond 1966; Salem 1982) or negatively correlated with yield (Vries 1979). Bond (1966) reported F1 heterosis for stalks per plant.

Similarly, several scientists found plant height positively correlated with yield (Sjodin 1977; Bianco et al. 1979; Vries 1979) while others reported no correlation between height and yield (Rowlands 1958; Bond 1966; Salem 1982). As in the case of stalks per plant, Bond (1966) found F1 heterosis for plant height.

Few studies noted the position of the first podded node in fababeans and its basic interest lies in its close association with early maturity, a desired feature with shorter growing seasons (Sjodin 1977). The first podded node is observed by height from ground level or by the number of nodes to the first podded node. The character expressed negative associations (Bianco et al. 1979) or slight positive associations (Kambal 1969) with yield but none were statistically significant.

2.8.2 Genetics

In F1 diallels, stalks per plant expressed positive partial dominance (Bond 1966) or additivity with considerable environmental effects (Martin and Cubero 1979). In F2 diallels, Hobbs and Burnett (1982) reported positive overdominance and epistasis for stalks per plant.

Plant height expressed partial positive dominance in some F1 diallel studies (Bond 1966; Martin and Cubero 1979). However, Cubero-Salmeron (1976) reported positive overdominance for height in F1 diallel crosses using Central-European lines. In F2 diallels, Hobbs and Burnett (1982) reported positive dominance ranging from partial to overdominance.

First podded node expressed complete negative dominance in F1 diallel crosses (Martin and Cubero 1979).

2.8.3 Heritabilities

The literature is meagre but what literature exists indicates intermediate heritabilities for these morphological characters. Vries (1979) found different broad-sense heritability estimates for two distinct populations of fababeans. For stalks per plant, the estimates were 55% and 59% whereas for plant height, the estimates were 46% and 75% respectively, for the two populations. These intermediate broad-sense heritabilities suggest a moderate influence of environment on these characters.

In F2 diallel crosses, Hobbs and Burnett (1982) found narrow-sense heritability estimates for stalks per plant ranging from 12.3% to 22.0% and for plant height ranging from 40.4% to 46.0%.

Thus, the usefulness of morphological characters depends greatly on the genotypes studied as well as the estimation method used and the environments in which they were grown. These characters are probably not too useful since they show moderate degrees of dominance and only intermediate heritabilities.

2.9 PROTEIN CONTENT

2.9.1 Agronomic Considerations

Fababeans are rich in seed protein, containing from 25 to 35% on a dry weight basis, depending on cultivar and environment. The amino acid composition, like other legumes, is high in lysine and low in the sulphur-containing amino acids, methionine and cystine (Chapman and Peat 1978).

Unlike most crops, the correlation between yield and protein content was not significant (Abdalla et al. 1976; Griffiths and Lawes 1978; Filippetti 1979) but a few non-significant negative correlations were reported (Chapman and Peat 1978; Sjodin et al. 1981). Protein content was not correlated with average seed weight (Frolich et al. 1974; Hanelt 1979; Sjodin et al. 1981).

2.9.2 Genetics and Heritabilities

Protein content was controlled by several genes expressing mainly additive gene effects (Chapman 1979), with some partial dominance towards lower values (Bond 1970; Haro et al. 1980).

Heritability is relatively high for protein content, but the literature is meagre on estimates. Direct evidence for high heritabilities comes from widely observed successes from selection for low or high protein contents (Griffiths and Lawes 1978; Sjodin et al. 1981).

Broad-sense heritability estimates for protein content were 70% (Griffiths and Lawes 1978) and 79% (Vries 1979). No report of narrow-sense heritability estimates was found. However, narrow-sense heritabilities are expected to be similar to broad-sense heritabilities since most of the genetic effects were additive.

Thus, polygenic control with largely additive effects and some dominance towards lower values and relatively high heritabilities characterize the genetics and inheritance for protein content in fababeans. These attributes along with the relative independence of protein content with yield suggest possible simultaneous improvement in both yield and protein content.

As a concluding remark, the literature has shown considerable variation in the genetics of certain characters with different experiments. Studies of different fababean populations in the same experiment found large genetic differences between them (Cubero-Salmeron 1976; Bianco et al. 1979; Pace 1979; Vries 1979; Cubero and Martin 1981; Hobbs and Burnett 1982). For these reasons, Lawes et al. (1983) concluded that studies using breeding material would be more valuable to the breeder than studies using a representative sample of fababean germplasm. Furthermore, the experimental design and estimation methods used, as well as the environment, have influence on the genetic estimates obtained. Thus, the genetic estimates should be interpreted relatively and cautiously.

Chapter III

MATERIALS AND METHODS

Diallel mating designs were used in this study. A diallel mating design is a set of all possible cross combinations among three or more parents. The parents are usually homozygous lines (Hayman 1954) but can also be heterozygous populations (Gardner and Eberhart 1966).

An F1 complete diallel and its selfed progeny forming the F2 complete diallel were studied. In addition, a smaller F1 cultivar diallel was studied.

3.1 THE F1 COMPLETE DIALLEL

3.1.1 Materials

The parental material consisted of five spring fababean lines selfed for four generations. The lines were not selected for the characters studied and were derived from the cultivars Ackerperle, Aladin, Diana, Erfordia and Herz Freya.

These cultivars are or were licensed for production in Canada. They are a genetically diverse group with both European and Canadian origins. They perform well in Western Canada and yield similarly when grown in Manitoba. On average however, Aladin, Erfordia and Herz Freya tend to outyield Diana and Ackerperle. Erfordia is the largest seeded cultivar while Ackerperle is the smallest seeded cultivar. Herz Freya and Diana are earlier maturing by a few days. Protein contents are very similar among the five cultivars with Diana slightly higher on average.

The experimental material was produced in the growthroom during the fall and winter 1981. The five S4 lines were crossed in all possible combinations including reciprocals to form the F1 complete diallel. Twenty-five S4 seeds from each parent were planted at four successive dates spaced two weeks apart. All 10 possible cross combinations and their 10 reciprocals were made among the lines. Selfed S5 parental seeds were obtained from uncrossed nodes and separately selfed plants. By April 1982, 104 to 193 seeds with an average 149 seeds for each F1 cross and over 250 S5 seeds for each parent were obtained.

The five controls used were the parent cultivars, Ackerperle, Aladin, Diana, Erfordia and Herz Freya.

3.1.2 Growthroom Conditions

Plants in the growthroom were given a 16-hour, 21°C day cycle and an 8-hour, 15°C night cycle. One plant was grown per 15 cm diameter clay pot with a 2 soil: 1 sand: 1 peat mix. The plants were watered daily and supplemented with 20-20-20 water soluble fertilizer at anthesis.

3.1.3 Crossing and Selfing Procedures

Crosses were attempted at one to three flowers per node on female parent plants. Excess flowers on the crossed nodes were removed. Emasculation was carried out on buds with intact immature anthers. Part of the inner keel petal and the 10 anthers were gently removed with forceps. Fresh pollen from male parents was placed on the stigma immediately after. The wing and standard petals were closed and the cross identified with colored thread (Bond et al. 1980).

Selfed seed production was ensured by manually tripping the flowers and removing excess flowers leaving three or four flower buds per node.

Crossed and selfed plants were decapitated after several flowering nodes to enhance seed set and pod fill. Mature pods were harvested, air dried and shelled by hand.

3.1.4 Field Study

On May 13, 1982, the F1 complete diallel was planted at the "Point" field lab at the University of Manitoba. The experimental design was a randomized complete block with six blocks. Each block had 30 plots that were randomly assigned to the 20 F1 crosses, five S5 parents and five control cultivars. Each plot consisted of a single three metre row spaced 60 cm apart. Using a corn planter, 15 to 17 seeds, along with Rhizobium leguminosarum inoculum, were planted 20 cm apart within each row. The entire experiment was bordered with Herz Freya guard material.

Plants were grown on Red River clay soil and received only natural precipitation throughout the growing season. Germination was generally quite uniform and transplanting was carried out where there were substantial gaps. The plots were weeded and monitored for pests. The experiment was sprayed four times with Pirimor insecticide during the growing season to control virus-bearing aphid populations. Disease was generally not severe and lodging was minimal.

Throughout the growing season, notes were taken on date of emergence, first flower and maturity as an average for each plot. The first podded node, determined by number of nodes from ground level,

was recorded as a mean from three random plants from each plot. Plant height was noted to the nearest five cm as a plot average at maturity. Seeds per pod were measured from a mean of ten random pods within each plot.

Just prior to harvest, diseased plants and plants at the end of each row or beside a gap within the row were rogued. Only representative plants remained while the number of plants and fertile stalks were counted for each plot. On August 25, 1982, the plots were cut at ground level, bagged, tagged and dried indoors at 30°C. When they reached 8-10% moisture, they were weighed for TDM, threshed and weighed for seed yield.

Plant numbers per plot ranged from 7 to 15 with an average of 11.6. Thus, the mean yield and TDM per plant were used to determine 10 plant plot means. Samples of 100 seeds were taken from each plot and weighed to estimate 1000 seed weight. Pods per plant were calculated indirectly from yield per plant, seeds per pod and seed weight.

To determine protein content, a 15 g bulk seed sample was taken from each plot and ground to flour. Each flour sample was oven dried at 110°C and a uniform 0.5 g analyzed by the micro-Kjeldahl procedure (N x 6.25) to determine percent crude protein on a dry weight basis.

3.2 THE F2 COMPLETE DIALLEL

3.2.1 Materials

The experimental material was produced in the field in 1982. Seeds from each cross in the F1 complete diallel were hand-planted in separate rows for the production of F2 families. The plants were caged prior to anthesis to ensure selfing by eliminating insect pollinators.

Similar to the F1 complete diallel, the five S5 parental lines and control cultivars of Ackerperle, Aladin, Diana, Erfordia and Herz Freya were used.

3.2.2 Field Study

On May 2, 1983, the F2 complete diallel was planted at the "Point" field lab at the University of Manitoba. A randomized complete block design with six blocks was used. Each block had 30 plots randomly assigned to the 20 F2 families, five S5 parents and five control cultivars. Each plot was a single three metre row with 60 cm between rows. Fifty seeds were planted per row using a seed drill planter. Inoculum was applied with the seed. The experiment was bordered with Herz Freya guard material.

Similar to the previous year, the experiment was grown on Red River clay soil and received only natural precipitation. Germination was quite uniform. The plots were weeded and pests were monitored. The level of virus was controlled by spraying Pirimor insecticide against aphids at regular 10 day intervals after emergence. Disease was minimal and lodging was not a problem.

Records taken throughout the growing season and at harvest were carried out similar to the previous year with the F1 complete diallel.

Plots were harvested on August 8, 1983. Plot yields and TDM were based on a random two metre sample within each row. An average 21.5 $\pm$ 4.2 plants was recorded per plot and an analysis of covariance (ANCOVA) conducted. Significant regressions for stand over yield and for stand over TDM were found. Therefore, ANCOVA correction of the data was used to correct for stand differences.

3.3 THE F1 CULTIVAR DIALLEL

3.3.1 Materials

The parental material consisted of the five spring fababean cultivars Ackerperle, Aladin, Diana, Erfordia and Herz Freya as described earlier. These cultivars were also used as controls.

The experimental material was produced in the growthroom in the summer, fall and winter of 1982. The five cultivars were crossed in all possible combinations excluding reciprocals to form an F1 half diallel. Ten seeds from each cultivar were planted at three successive dates spaced three weeks apart during the summer and fall. The female parent used in each cross combination was based on the crossing success of different parents used in the F1 complete diallel. A range of success rates from 24% to 47% was noted depending on female parent used. Herz Freya (HF) had the highest success rate, followed by Ackerperle (Ac), Aladin (Al), Diana (D) and Erfordia (E). Thus the ten crosses, female parent being designated first, were:

HF x Ac	Ac x Al	Al x D	D x E
HF x Al	Ac x D	Al x E	
HF x D	Ac x E		
HF x E			

By winter, approximately 80 seeds per F1 cross were obtained.

3.3.2 Field Study

On May 2, 1983, the F1 cultivar diallel was grown out at the "Point" field lab at the University of Manitoba. The field layout was a randomized complete block design with three blocks. Each block had

15 plots randomly assigned to the 10 F1 families amd five control parents. Each plot consisted of a single three metre row spaced 60 cm apart. A corn planter was used to plant 21 to 22 seeds, along with inoculum, into each row. Seeds were spaced approximately 15 cm apart in the row. Herz Freya guard material bordered the experiment.

Similar to the other diallels, this experiment was planted on Red River clay soil and received only natural precipitation. Germination was generally quite uniform. Weeds and pests were monitored. Virus infection was controlled by applying Pirimor insecticide against aphids at regular 10 day intervals. Plants harvested were minimally affected by disease and lodging. Notes taken were similar to the F1 and F2 complete diallels.

At harvest, the plots were rogued for diseased plants and plants at the end in each row or beside a gap in each row. On August 11, 1983, the plots were hand-harvested and handled as described for the other diallels. Plant numbers harvested per plot ranged 6 to 10 with a mean of 8.4. The mean yield and TDM per plant were used to determine 10 plant plot means.

3.4 CHARACTERS MEASURED

From direct determination or by calculation, the following characters were studied in the F1 and F2 complete diallels and the F1 cultivar diallel:

1. Seed yield per plot (YIELD)
2. Total dry matter per plot (TDM)
3. Harvest index (HI) = (YIELD/TDM) x 100.

Yield components

4. Pods per plant (PD/PLT)
5. Seeds per pod (S/PD)
6. 1000 seed weight (MSWT)

Phenological characters

7. Days from emergence to first flower (FLR)
8. Days from first flower to maturity (FMAT)
9. Days from emergence to maturity (MAT)

Morphological characters

10. Fertile stalks per plant (STK/PLT)
11. Plant height (HT)
12. First podded node (FPN)
13. Seed protein content (%) (PRO)

3.5 DATA ANALYSES

Basic statistics were calculated with the SAS computer programs (Helwig and Council 1979) available at the University of Manitoba computer terminals. Plots not planted due to insufficient seed quantity, diseased plots and technical handling errors were infrequently a cause for missing plots. Where these occurred, missing values were estimated using the SAS least squares program. The general linear models procedures were used for the analysis of variance (ANOVA) for unbalanced data and the analysis of covariance. Least squares means, paired comparisons using t-test and multiple comparison contrasts were also computed from these procedures. The correlation procedures were used to compute standard product-moment correlation coefficients. Statistical significance will be designated as *, **, ***, for P =

.05, .01, .001 respectively, and referred to as significant ($P > .05$) or highly significant ($P > .01$) in this study.

3.6 JINKS AND HAYMAN GENETIC ANALYSES

The F1 and F2 complete diallels were analyzed by the diallel method of Jinks (1954, 1956) and Hayman (1954, 1958, 1960) as described by Mather and Jinks (1982). The ANOVAs of diallel tables were based on a fixed effects model since the experimental material comprised a particular set of parents and crosses. Estimates of genetic variance components were calculated for all characters studied. The supplementary graphical analyses were conducted for yield, TDM and HI for the F1 and F2 complete diallels.

3.6.1 Genetic Model

The Jinks and Hayman analyses basically assumes an additive or an additive and dominance genetic model. The model is based on the following assumptions:

1. diploid nature of inheritance
2. homozygous parents
3. no reciprocal differences
4. no genotype by environment interactions
5. no multiple alleles
6. no epistasis
7. uncorrelated gene distribution

These assumptions were tested for as completely as possible. Vicia faba segregates in a diploid manner, the parents were selfed at least four generations and were assumed relatively homozygous and any recip-

rocal differences were removed by replacing entries in the diallel table with their mean reciprocals. Two basic tests were used to validate the assumptions, especially the latter four assumptions:

1. Test of the regression coefficient b, of array covariance (Wr) over array variances (Vr). (An array is defined as the set of progeny families with a common parent.) The t-tests must show that the regression coefficient is statistically equal to one, that is, significantly different from zero and non-significantly different from one.
2. Test for the homogeneity of Wr minus Vr among arrays over all blocks. The Wr-Vr ANOVA must show that variation of Wr-Vr among arrays is non-significant.

Failure to satisfy these validity tests implies that one or more of the assumptions are violated. Interactions are frequently the cause of violation and removing a block or an array from the experiment or transforming the data may eliminate the interaction.

3.6.2 Estimation of Genetic Components

The statistics measured and genetic components equated to them for the F1 complete diallel are:

1. variance of the parents (Vp) = D1 + E
2. mean variance of the arrays ($\bar{V}r$) =

$$1/4\ (D1 + H1 - F) + (n + 1)/2n\ E$$

3. mean covariance (between parent and progeny) of the arrays ($\bar{W}r$) =

$$1/2\ D1 - 1/4\ F + 1/n\ E$$

4. variance of the array means ($V\bar{r}$) =

$$1/4\ (D1 + H1 - H2 - F) + (n + 1)/2n^2\ E$$

5. the squared difference between parent and progeny means =

$$1/4\ h^2 + (n - 1)/n^2\ E$$

where n is the number of parents.

For the F2 complete diallel, the equations are similar except the coefficients of H1, H2 and h^2 terms are quartered, the coefficient of the F term halved and E proportionally changed depending on the statistic. These adjustments allow similar genetic component estimates to be determined from the different generations.

These statistics were calculated based on mean data values over replicates. The exact solution method solved the equations for the following genetic component estimates:

1. D1 : additive variance.
2. H1 : dominance variance.
3. H2 : dominance variance adjusted for assymmetric gene distribution among the parents. H1 equals H2 with equal gene frequencies.
4. F : covariance of additive and dominance effects which determines gene symmetry. A symmetric gene distribution is indicated by an F value non-significantly different from zero. A significant and positive F indicates a majority of dominant genes while a significant and negative F indicates a majority of recessive genes, regardless of whether dominance is toward higher or lower expressions.
5. h^2 : dominance variance over all heterozygous loci.
6. E : mean environmental variance.

Since the analyses were conducted on the means over replicates, the mean square error from the ANOVA of the diallel, which estimates E, was divided by the number of replicates. Standard errors for the ge-

netic components were calculated by the mean square deviation of the observed from expected values for Wr and Vr (Hayman 1954).

Genetic proportions derived from these genetic component estimates or from the statistics are:

1. D1 - H1 : mean difference between additive and dominance variances. A positive value indicates partial dominance, a value near zero indicates complete dominance while a negative value indicates overdominance. This proportion also estimates the y-intercept, equal to 1/4(D1 - H1), in the graphic analyses.
2. $\sqrt{H1/D1}$: average dominance ratio. With partial dominance, the ratio is less than one, with complete dominance, the ratio equals one and with overdominance, the ratio is greater than one. The ratio itself, measures the average relative expression of dominance and does not determine the true degree of dominance per se since particular combinations of positive and negative genes in the parents, complementary epistasis or correlated gene distributions could seriously alter this ratio (Hayman 1954).
3. $h^2/H2$: estimates the number of gene blocks that control the character and exhibit dominance to some degree. The ratio usually underestimates the number of gene blocks and provides no information about gene blocks exhibiting little or no dominance.
4. Wr + Vr for each array : determines the order of dominance of the parents. The correlation between parental order of dominance (from -(Wr + Vr) determination of low to high dominance values) and their corresponding array means (from low to high expressions) indicates the direction of dominance. A negative

correlation approaching -1 indicates that dominant genes decrease character expression, a positive correlation approaching +1 indicates that dominant genes increase character expression and a value approaching zero indicates ambidirectional dominance.

5. Broad-sense (BS) and narrow-sense (NS) heritability estimates were calculated by the formulae of Mather and Jinks (1982). For the F1 generation:

$$\text{BS heritability} = \frac{1/2\ D1 + 1/2\ H1 - 1/4\ H2 - 1/2\ F}{1/2\ D1 + 1/2\ H1 - 1/4\ H2 - 1/2\ F + E}$$

$$\text{NS heritability} = \frac{1/2\ D1 + 1/2\ H1 - 1/2\ H2 - 1/2\ F}{1/2\ D1 + 1/2\ H1 - 1/4\ H2 - 1/2\ F + E}$$

Similar formulae were used for the F2 generation with the coeffients of H1 and H2 terms quartered and the coefficient of the F term halved.

3.6.3 The Wr/Vr Graph

The graph of array covariances (Wr) versus array variances (Vr) has four features:

1. A validity test for the additive-dominance genetic model. As previously stated, a straight regression line with a slope of one indicates satisfactory fit to the model. With interactions, the slope deviates from one, while with no dominance, a regression line does not exist and all array points scatter around the mean values $\overline{Wr}$, $\overline{Vr}$.
2. An indication of the type of dominance. The y-intercept is 1/4 (D1 - H1), thus a significantly positive intercept indicates partial dominance, an intercept non-significant from zero indi-

cates complete dominance and a significantly negative intercept indicates overdominance.

3. An indication of the relative proportions of dominance and recessive genes present in the common parent of each array. Parents with more dominant genes have a lower array variance and covariance and lie near the origin. Highly recessive parents have large array variances and covariances and lie at the opposite end of the regression line.
4. The limiting parabola, defined as $Wr^2 = Vr \times Vp$, defines the theoretical range of the Wr/Vr line.

The Wr/Vr graphs for the F1 and F2 generations are similar except the regression line for the F2 would theoretically lie half-way between that for the F1 and the point for no dominance to allow for the halving of the heterozygote (Hayman 1958). These graphs were drawn on a relative scale from 1 to 12 by proportionally dividing variances and covariances by a common factor for each character. These statistics for F1 yield, F1 TDM and F1 HI were divided by 1000, 3000 and 3 respectively, while for F2 yield, F2 TDM and F2 HI, they were divided by 150, 400 and 1.5 respectively.

The WATFIV computer program by Lee and Kaltsikes (1971, 1972) was used to calculate the genetic component estimates and statistics for the Wr/Vr graph. Modifications were incorporated for these analyses to be carried out on the mean values over replicates. The ANOVA and heritability formulae according to Mather and Jinks (1982) were incorporated into the program.

Chapter IV

RESULTS AND DISCUSSION

4.1 CHARACTERIZATION OF 1982 AND 1983 GROWING SEASONS

The 1982 growing season was relatively dry with 240 mm precipitation compared to the normal 300 mm over the season. The spring was dry and warm with plants emerging around 14 days from planting. A dry, cool June followed and plants grew slowly with control plots flowering on the average 39 days from emergence. July had normal temperatures and the most precipitation that fell in an unusually large number of thunderstorms. Some lodging and flower drop occurred during these thunderstorms but there was minimal damage to the plant material. A cool, dry August followed and control plots matured on the average 90 days from emergence.

The 1983 growing season was generally characterized by unusually warm and dry conditions, although a near normal 280 mm precipitation fell over the season. Spring was dry but cooler than in 1982 and plants emerged about 10 days later than the previous year. June had warm temperatures and the most precipitation. Thus, plants grew rapidly and control plots flowered about 30 days from emergence. July had unusually dry and hot weather that reached record highs and this persisted into August. Plants halted growth early and matured about two weeks earlier than in 1982.

Plant development was not noticeably affected by disease, pest or environmental stress in either 1982 or 1983. Control plots at similar

planting densities yielded about 20% less in 1983 compared to 1982, due to the shorter growth duration.

4.2 DIALLEL AGRONOMIC PERFORMANCE

4.2.1 F1 Complete Diallel

4.2.1.1 General Comparisons

Mean raw data and analyses of variance for characters studied in the F1 complete diallel are set out in Appendix Tables 1 and 2. Coefficients of variation showed normal trends among the characters indicating relatively more environmental variation for yield, TDM and PD/PLT than for the other characters. Genotypic variation among diallel entries (crosses and parents) expressed high significance for all characters.

Table 1 shows a summary of cross, parent and control means. Variation among parents usually exceeded variation among crosses. However, variation between parents and crosses was most important for yield, TDM, HI, PD/PLT, STK/PLT and HT, perhaps from close association with vegetative and reproductive vigor. Variation between parents and crosses also showed significance for MSWT, FLR, FMAT and PRO.

Generally, variation among control cultivars was small attributed to a relatively large variation within them. The controls showed phenotypic similarity in yield, TDM and PD/PLT. In addition, the controls expressed mean values significantly beyond the range between the S5 parents and their crosses for some characters. This indicates possible gene differences between "gene pools" from these cultivars and that from the diallel.

TABLE 1. Summary of mean values, average % F_1 heterosis above top (+) or below bottom (-) parent and % comparison above (+) or below (-) control mean for characters studied in the F_1 complete diallel.

Character	Crosses	Parents	Controls	% Average Heterosis	% Above Control
YIELD (g)	476.6	329.6	427.7	+30.7***	+11.4***
TDM (g)	1014.7	798.5	909.9	+16.4***	+11.5***
HI (%)	47.3	41.4	47.6	+8.1***	-0.7
PD/PLT	31.1	24.3	29.6	+14.1***	+5.1*
S/PD	3.8	3.7	3.5	+0.8	+9.2***
MSWT (g)	408.4	374.4	417.0	+1.7	-2.1*
FLR (days)	39.3	40.3	39.1	-0.5	+0.5
FMAT (days)	47.6	47.0	48.5	+0.4	-1.8***
MAT (days)	87.0	87.2	87.7	-0.1	-0.8**
STK/PLT	2.7	2.6	2.4	+3.3	+15.7***
HT (cm)	118.8	113.8	111.3	+2.3*	+6.7***
FPN	7.1	7.2	6.5	-0.6	+8.1***
PRO (%)	31.2	31.9	30.9	-0.1	+1.3*

* ** *** Significant at P = .05, .01 and .001 respectively.

Average heterosis was computed as percent above top or below bottom parent for all characters (Table 1). Yield expressed the greatest extent of heterosis with a mean 30.7%*** above the higher parent. Similar findings were reported by Bond (1966) with F1 yields averaging 23% above their higher parent. Lesser degrees of positive heterosis for TDM and HI of 16.4%*** and 8.1%*** were also expressed, a trend parallel to that reported by Neal (1982).

Heterosis for yield thus resulted from both increased TDM and HI, which may be good estimators of vegetative and reproductive vigor respectively. Increased autofertility is postulated as the major contributing factor to reproductive vigor. When bee-pollination varies, especially with adverse weather, plants are forced to rely on their inherent autofertility to maximize pod set. Inbred plants are generally less capable of this than cross-bred plants (Drayner 1959). Monti and Frusciante (1982) reached a similar conclusion in inbreeding studies. They found that both inbreeding depression and reduced autofertility decreased yields of inbred plants.

PD/PLT was the only yield component to express heterosis (+14.1%***), in agreement with Bond (1966) and Samia (1977). Thus, heterosis for yield was probably achieved largely through more pods resulting from increased vegetative growth and increased autofertility. HT was the only other character to express some heterosis (+2.3%*), a finding in agreement with Bond (1966).

Hybrids also outyielded the control cultivars by 11.4%***. A higher TDM (+11.5%***) rather than HI was associated with this advantage. Hybrids also had more PD/PLT, more S/PD and a smaller MSWT than the controls.

4.2.1.2 Common Parent Comparisons

The average heterosis for different common parents in the F1 inbred line crosses is shown in Table 2. Interestingly, all common parents displayed similar extents of heterosis for yield, but they varied in actual performances relative to the control. Crosses with HF yielded best, followed by E crosses, averaging 20.8%*** and 14.1%*** over the control respectively. Crosses with A1 and Ac displayed intermediate performances, yielding 9.8%** and 7.5%* above the control respectively, while D crosses yielded only 5.1% above the control. Their respective S5 parents ranked likewise (Appendix Table 1). Thus, parental line performances were related to their general performances in hybrid combinations implying that good yield genes are necessary for high yields. Further evidence regarding this point was provided from correlations between mid-parents (mean of both parents) and their crosses. The correlation for yield in inbred line crosses was highly significant and positive ($r = +.79$***), thus good yielding S5 parents were associated with better hybrids. This was substantiated by the correlation between S5 mid-parents and their F2 families ($r = +.53$**), which was highly significant and positive but expectedly smaller in a segregating F2 generation. These findings agree well with Bond (1967). Therefore, hybrid performances probably can be predicted from parental line performances.

Heterosis for TDM and HI varied among common parents. For example, E crosses expressed +20.7% heterosis for TDM and +4.5% heterosis for HI. In contrast, D crosses expressed relatively less heterosis for TDM (+11.5%) and more heterosis for HI (+11.0%). These compensating components resulted in similar expressions of heterosis for yield over

TABLE 2. Average F_1 heterosis as % above top (+) or below bottom (-) parent and % comparison above (+) or below (-) control mean for crosses with a common parent in the F_1 complete diallel.

Character		Common parent				
		Ac	Al	D	E	HF
YIELD	% Heterosis	+33.3***	+28.2***	+30.8***	+31.2***	+29.8***
	% Above Control	+7.5*	+9.8**	+5.1	+14.1***	+20.8***
TDM		+19.7***	+13.8**	+11.5**	+20.7***	+16.5**
		+11.2***	+11.5***	+3.3	+16.8***	+14.8***
HI		+7.9***	+8.8***	+11.0***	+4.5	+8.4***
		-3.9**	-2.3	+1.5	-3.3*	+4.4***
PD/PLT		+20.5***	+11.6*	+13.1**	+11.8*	+13.3*
		+10.1***	+4.2	-3.2	-5.7*	+20.4***
S/PD		+0.9	+1.0	0.0	+1.6	+0.3
		+11.8***	+10.4***	+3.6	+13.6***	+5.7**
MSWT		0.0	+2.4	+1.8	+1.8	+2.4
		-12.5***	-4.0***	+4.9***	+6.5***	-5.3***
FLR		-0.5	-1.0	0.0	-0.9	-0.2
		+3.0***	+1.0*	-3.4***	+1.6***	+0.5
FMAT		+0.2	+0.4	+0.4	+0.6	+0.4
		-3.4***	-1.3*	+0.5	-2.0**	-3.2***
MAT		-0.1	-0.2	0.0	-0.1	0.0
		-0.5	-0.3	-1.2***	-0.3	-1.6***
STK/PLT		+5.7	+0.4	+3.9	+3.9	+2.4
		+20.7***	+19.7***	+14.9***	+14.9***	+14.3***
HT		+3.6***	+1.2	+1.3	+3.8***	+1.8
		+7.6***	+5.1***	+4.5***	+8.1***	+7.7***
FPN		-1.5	-1.5	-1.5	+1.0	+0.5
		+10.5***	+5.1	-3.1	+14.1***	+13.2***
PRO		-0.2	-0.1	0.0	0.0	0.0
		+1.4	-1.5	+6.3***	+2.9***	-3.1***

* ** *** Significant at P = .05, .01 and .001 respectively.

crosses. Thus, the parental genotypes differed in genes for vegetative and reproductive vigor.

Comparisons among common parents (relative to the control) revealed differences in patterns of assimilate distribution. Yields with HF ranked first associated with a high TDM and the highest HI. However, yields with E ranked second, accompanied by a TDM production greater than with HF but a relatively low HI. It is also interesting to note that comparatively low yield performances with D were associated with the lowest TDM values rather than with low HI values.

Comparisons using yield components likewise displayed different yield distribution patterns. Average performances of HF and E were the extremes among these parents. HF was associated with the highest PD/PLT but a low S/PD and MSWT. In contrast, E was associated with the highest S/PD and MSWT, but with the lowest PD/PLT. Similar observations have been frequently reported (Bond 1966; Kambal 1969; Neal 1982).

Other characters also reflected different genetic make-ups of these parents. For increased PRO, it is interesting to note that D performed best followed by E, Ac, Al and HF, thus ranking similar to their S5 parents (Appendix Table 1).

4.2.1.3 Individual Cross Comparisons

Heterosis for yield in specific F1 cross combinations between inbred lines ranged from +13.2% to +59.9% (Table 3). The cross expressing the most heterosis (Ac x D), however, did not yield highest. The higher yielding cross combinations (relative to the control) were HF x E, HF x Al, HF x Ac and their respective reciprocals. These crosses

TABLE 3. F_1 heterosis for yield as % above top (+) or below bottom (-) parent and % comparison above (+) or below (-) control mean for individual crosses in the F_1 complete diallel.

Cross (female x male)	% Heterosis	% Above Control
HFXAc	+29.0***	+19.9**
Reciprocal	+25.0**	+16.2**
HFXAI	+34.9***	+25.4***
Reciprocal	+31.3***	+22.1***
HFXD	+20.4*	+11.9*
Reciprocal	+13.2	+5.3
HFXE	+31.5***	+22.3***
Reciprocal	+53.3***	+42.6***
AcXAI	+23.3*	+1.3
Reciprocal	+23.1*	+1.1
AcXD	+59.9***	+5.0
Reciprocal	+47.6***	-3.1
AcXE	+25.0**	+5.9
Reciprocal	+33.5***	+13.1*
AIXD	+25.2**	+2.9
Reciprocal	+30.8**	+7.5
AIXE	+28.5**	+8.9
Reciprocal	+28.5**	+8.9
DXE	+22.5*	+3.8
Reciprocal	+26.9**	+7.5
LSD (.05)	--	+11.8

* ** *** Significant at P = .05, .01 and .001 respectively.

expressed about 30% heterosis and yielded 20% above the control with little reciprocal differences, except for E x HF. This particular cross, E x HF, was noticeably different from all other crosses including its reciprocal, yielding 53.3% above its higher parent and 42.6% above the control.

4.2.2 F2 Complete Diallel

4.2.2.1 General Comparisons

Mean raw data and analyses of variance for characters in the F2 complete diallel are set out in Appendix Tables 3 and 4. Genotypic variation among diallel entries showed significance for all characters except STK/PLT. Thus, further genetic analysis was not conducted for STK/PLT. Both STK/PLT and PD/PLT varied little, mainly due to the higher planting density used in this experiment compared with the F1 complete diallel.

A summary is shown of mean values and comparisons with top or bottom S5 parent and control for these characters (Table 4). Smaller differences existed between parents and crosses, as expected, since this is an F2 generation. Average F2 yields were only 14.9% above their top S5 parent, markedly lower than the 30.7% heterosis observed for F1 yields. Advantage above the top S5 parent for TDM (+5.8%) and HI (+3.3%) were also much reduced. These results suggest that the decline in F1 performance in subsequent generations is related to the halving of the average heterozygosity. Similar declines in F1 performance have been reported by Poulsen (1977) and Kittlitz (1981).

The F2 yields were slightly lower than the controls. Furthermore, controls are most probably less heterozygous (around 30%) than F2 families (theoretically 50% heterozygous). Thus, it seems that the dial-

TABLE 4. Summary of mean values, average % F_2 family difference above top (+) or below bottom (-) S_5 parent and % comparison above (+) or below (-) control mean for characters studied in the F_2 complete diallel.

Character	F_2 Families	S_5 Parents	Controls	% Difference	% Above Control
YIELD (g)	323.8	269.2	345.0	+14.9***	-6.4**
TDM (g)	703.7	635.1	729.9	+5.8*	-3.6
HI (%)	46.1	42.5	48.4	+3.3	-4.8***
PD/PLT	10.4	9.8	10.7	+3.9	-2.7
S/PD	3.7	3.4	3.6	+4.0	+0.8
MSWT (g)	399.1	381.6	416.7	+1.4	-4.2***
FLR (days)	32.0	33.0	30.8	-0.3	+3.8***
FMAT (days)	39.4	38.8	40.9	+0.3	-3.6***
MAT (days)	71.3	72.0	71.7	-0.6	-0.5
STK/PLT	1.3	1.3	1.3	-0.4	+3.1
HT (cm)	106.8	104.2	103.8	+1.3	+2.8**
FPN	7.1	7.3	6.5	-1.0	+9.1***
PRO (%)	31.2	31.5	30.6	-0.1	+1.9***

* ** *** Significant at P = .05, .01 and .001 respectively.

lel "gene pool" contained relatively inferior yield genes compared to the average genotypic value in the cultivars. It is likely, therefore, that prior selection for better genotypes would increase the advantage over open-pollinated cultivars, although heterosis per se may not necessarily increase.

As the basic objective was a comparison of hybrid performances, further comparisons for the F2 generation were of no practical interest.

4.2.3 F1 Cultivar Diallel

4.2.3.1 General Comparisons

Appendix Tables 5 and 6 tabulate the mean raw data and analyses of variance for characters in the F1 cultivar diallel. The characters showed less phenotypic differences among diallel entries compared with that observed in the inbred line diallels. This is attributed to the nature of a cultivar diallel and to less replication in this experiment resulting in slightly higher coefficients of variation. Cultivar parents showed little phenotypic differences. They are partially heterozygous and their crosses may not reach maximum heterozygosity when both parents have similar heterozygous loci. It follows that the increase in heterozygosity would be less than that for inbred line crosses. Thus, variation among crosses and parents would be relatively small, although considerable variation exists within crosses and parents.

A summary of mean values, heterosis and comparisons with the control mean (equivalent to parent mean in this experiment) is shown in Table 5. Contrary to the inbred line diallels, variation among crosses exceeded variation among parents for yield, TDM and HI. It seems

TABLE 5. Summary of mean values, average % F_1 heterosis above top (+) or below bottom (-) parental cultivar and % comparison above (+) or below (-) cultivar mean (control) for characters studied in the F_1 cultivar diallel.

Character	Crosses	Cultivars	% Average Heterosis	% Above Control
YIELD (g)	372.0	327.3	+12.7	+13.7*
TDM (g)	771.5	690.7	+9.0	+11.7*
HI (%)	48.2	47.5	+1.1	+1.6
PD/PLT	22.7	21.9	+1.5	+3.8
S/PD	3.7	3.5	+2.2	+4.2
MSWT (g)	447.9	427.1	+1.8	+4.9***
FLR (days)	29.7	30.2	-0.5	-1.6
FMAT (days)	42.4	42.9	-0.8	-1.2
MAT (days)	72.1	73.1	-0.8	-1.4
STK/PLT	2.2	2.0	+2.8	+9.4
HT (cm)	106.8	105.0	+0.1	+1.7
FPN	6.8	7.1	-1.4	-3.8
PRO (%)	30.4	30.8	-0.1	-1.2

* ** *** Significant at P = .05, .01 and .001 respectively.

that greater genotypic variation exists among these cultivars than would be expected based on their phenotypic similarity. Variation between parents and crosses was most important and significant for yield, TDM and MSWT only.

Heterosis for yield was the greatest, although values did not reach significance. Yields from F1 cultivar crosses averaged 12.7% above their top parent (compared with 30.7% for inbred line crosses) and were primarily associated with increased TDM or vegetative vigor. Average HI values were similar for parents and their crosses implying that parents and crosses contained heterozygous loci for autofertility that were expressed to similar extents in this environment.

The reduced heterosis for yield in this diallel probably resulted from the smaller increase in heterozygosity in cultivar crosses. In comparison with the control mean however, cultivar crosses (13.7% above control) yielded slightly more than inbred line crosses (11.4% above control). Furthermore, cultivar crosses may be less heterozygous than inbred line crosses since the possibility exists for similar heterozygotes to cross and produce some homozygotes. These findings provide further evidence that these inbred line crosses contained inferior genes and suggest that heterozygosity and good yielding genotypes are essential for high yields in fababeans.

4.2.3.2 Common Parent Comparisons

A similar comparison was made among the common parents of these cultivar crosses (Table 6). All common parents varied in extent of heterosis and actual performances (relative to the control) for yield. Likewise, HF performed best for yield among these cultivars, with an

TABLE 6. Average F_1 heterosis as % above top (+) or below bottom (-) parental cultivar and % comparison above (+) or below (-) cultivar mean (control) for crosses with a common parent in the F_1 cultivar diallel.

Character		Common parent				
		Ac	Al	D	E	HF
YIELD	% Heterosis	+8.3	+1.9	+13.2	+17.3	+22.8**
	% Above Control	+10.8	+6.9	+11.6	+14.4*	+24.7***
TDM		+9.6	+3.4	+8.8	+13.0*	+10.3
		+11.0	+9.7	+8.1	+14.5*	+15.1*
HI		+1.0	-3.6	-0.7	+1.7	+6.8**
		+0.4	-2.9	+2.5	-0.2	+8.1**
PD/PLT		-1.4	-4.5	-0.2	+3.7	+10.0
		+6.0	-7.4	+5.7	+0.5	+13.9*
S/PD		+2.0	+4.0	+3.2	+0.2	+1.7
		+1.9	+7.5	+4.7	+2.9	+3.7
MSWT		+1.1	+3.4	0.0	+3.6	+0.9
		+1.8	+6.9***	-0.3	+11.0***	+4.9**
FLR		+2.0	-0.3	-3.3	-1.1	+0.1
		+1.9	-1.2	-6.4**	-0.9	-0.8
FMAT		-2.7	-1.9	+0.4	+0.8	-0.4
		-2.5	-1.8	-0.2	-0.6	-1.0
MAT		-0.7	-1.2	-1.5	-0.2	-0.4
		-0.8	-1.6	-2.8**	-0.8	-1.0
STK/PLT		0.0	+1.0	+1.0	+5.9	+5.9
		+4.0	+16.3*	+16.3**	+2.7	+7.7
HT		+0.4	-0.4	0.0	+0.8	0.0
		+2.4	+1.6	-1.6	+3.6*	+2.8
FPN		0.0	-1.1	0.0	-2.1	-3.9
		-0.9	+2.0	-11.5**	-1.2	-8.3*
PRO		0.0	-0.9	-0.3	+0.1	+0.5
		-1.7	-1.6	-0.6	-1.3	-1.0

* ** *** Significant at P = .05, .01 and .001 respectively.

average 22.8%** heterosis above the higher parent and 24.7%*** advantage over the control. HF crosses were far superior to E crosses, which ranked second, with average yields 14.4% above the control. Yield performances for D, Ac and Al followed closely. Contrary to the inbred line crosses, HF was not the highest yielding parent (Appendix Table 5). Al yielded highest but expressed little heterosis in crosses. This indicates little relation between parent and average cross performance, also evidenced by the non-significant mid-parent versus cross correlation ($r = -.34$). This is thought to result from the extent of heterozygosity and similarity in potential cultivar parents. Similar heterozygous loci increase the proportion of homozygotes in the crossed progeny. The initial heterozygosity within a cultivar parent would determine the degree to which this occurs. However, different heterozygous loci are maintained heterozygous in the cross. Thus, genetic similarity and heterozygosity in parents would obscure potential heterosis in crosses. This indicates that good parental genotypes can be recognized only without the complications of heterogeneity.

Different assimilate distribution patterns were also displayed. Superior yields for crosses involving HF resulted from high TDM and unlike all other parents, high HI too. In contrast, E crosses achieved high yields primarily by high TDM.

Yield distribution patterns also varied such that HF crosses produced more pods while E crosses had higher MSWT. All parents performed similarly for PRO, regardless of yield performance, which suggests that one can obtain high yielding hybrids without sacrificing PRO.

4.2.3.3 Individual Cross Comparisons

Heterosis for yield among cultivar crosses ranged from -3.7% to +41.7%, a surprisingly wide range (Table 7). The two best crosses, HF x D and HF x E, expressed 41.7%** and 36.7%** heterosis for yield respectively, while they outyielded the control by 39.6%*** and 34.6%** respectively. This advantage is definitely worth exploiting in faba-bean breeding. These crosses "nicked" well, probably resulting from genetically divergent "gene pools" within these parents that maximized heterozygosity in crosses.

4.2.4 Summary and Discussion of Diallel Agronomic Performance

Genotypic variation showed significance for all characters in the F1 complete diallel and for all characters except STK/PLT in the F2 complete diallel. Relatively less genotypic variation was expressed in the F1 cultivar diallel. This may be largely attributed to heterogeneity within cultivars which obscured genetic differences and decreased expression of heterosis in crosses.

Heterosis was expressed greatest for yield, followed by TDM, HI, PD/PLT and HT in inbred line crosses and by TDM in cultivar crosses. This indicated heterosis for vegetative and reproductive fitness which increased with the complexity of the character.

Heterosis for TDM may represent vegetative vigor while heterosis for HI may represent reproductive vigor primarily as increased autofertility. Thus, heterosis for yield in inbred line crosses may have resulted through more pods from vegetative vigor and increased autofertility. Meanwhile, heterosis for yield in cultivar crosses may have resulted mainly from vegetative vigor with autofertility expressed by cultivar parents and their crosses to similar extents.

TABLE 7. F_1 heterosis for yield as % above top (+) or below bottom (-) parent and % comparison above (+) or below (-) control mean for individual crosses in the F_1 cultivar diallel.

Cross (female x male)	% Heterosis	% Above Control
HFXAc	+12.3	+13.3
HFXAI	+0.5	+11.3
HFXD	+41.7**	+39.6***
HFXE	+36.7**	+34.6**
AcXAI	+7.1	+18.6
AcXD	-3.7	-7.3
AcXE	+17.4	+18.6
AIXD	0.0	+3.7
AIXE	0.0	-6.7
DXE	+14.9	+10.6
LSD (.05)	--	+21.4

* ** *** Significant at P = .05, .01 and .001 respectively.

Yields from F1 inbred line crosses averaged 30.7% heterosis which declined by about half in the F2 generation. Yields from F1 cultivar crosses averaged 12.7% heterosis. The extent of heterosis also varied widely among crosses, independent of yield level. These results implied that expression of heterosis increased with heterozygosity at a genetically determined rate which was independent of genetic variation for yield performance.

S5 parent performance for yield ranked similar to their general performance in inbred line crosses. Correlation between mid-parents and crosses was significant and positive. This indicated that parental line performance was related to hybrid performance. In contrast, cultivar parent performance for yield showed little relation with average cross performance and no significant correlation was expressed between mid-parents and crosses. This suggested that genetic heterogeneity complicated identification of good parental genotypes. Thus, hybrid yield performances may be predicted from that of inbred line parents but not from cultivar parents.

It is further suggested that yields from cultivar crosses were not fully realized since genetic similarity and heterozygosity in cultivar parents, inevitable to some extent, would produce homozygotes in crosses. Therefore, genetic divergence and homozygosity in parents may maximize heterozygosity and thus, heterosis in crosses. It is suggested that selection of good yielding lines from genetically divergent and relatively homozygous material for use in hybrid breeding programs may maximize yields in fababeans.

Cultivar parents (controls) expressed mean values significantly beyond the range between the S5 parent and their cross values for some

characters. This suggested gene difference between "gene pools" of the S5 parents and that of the cultivar parents. Furthermore, yields from F1 inbred line crosses averaged 11.4% above the control while the following generation yielded slightly lower than the control. Yields from cultivar crosses averaged 13.7% over the control. These results suggest that the "gene pool" of the S5 parents contained inferior yield genes relative to the mean genotypic value of their original cultivars.

The ranking of common parent and specific cross performances varied somewhat between inbred line crosses and cultivar crosses. This may be attributed to complications from heterogeneity within cultivars, indications that S5 parents were not fully characteristic of these cultivars and the different seasons in which the studies were conducted.

Comparable results, especially for the identification of better parents and crosses were obtained. HF, followed by E, were the better general combiners for yield. All high yielding specific cross combinations involved HF as a parent. Only HF x E expressed high yields in both diallels.

Different growth and assimilate distribution patterns were displayed. HF and E expressed extreme yield distribution patterns among these parents suggesting that HF and E may have contained diverse gene combinations that combined well in crosses.

In conclusion, HF would most likely be a good parent for hybrid production, but precise testing for specific combinations is necessary for high yielding hybrids that may produce a 35-40% yield advantage over open-pollinated cultivars.

As a final remark, these comparisons indicate that inbred line crosses and cultivar crosses were both indispensable for a thorough examination of these parents in hybrid combination. Although less time and labor would be involved in studying cultivar crosses alone, complications from variability and heterozygosity occur which may obscure potential heterosis in such crosses. However, these crosses may detect heterosis resulting from genetic divergence which may be more useful and representative of better combining parents. The inbred line crosses were free from problems with heterogeneity, but their results pertain only to these particular lines. This is not very useful since these lines were not selected to represent the mean genotypic value of these cultivars nor were they potentially useful high yielding lines from these cultivars. These lines, nevertheless, may partly represent relative combining performances of their original cultivars. Thus, both sets of crosses complement each other and together, are more informative.

4.3 GENETIC ANALYSES (JINKS AND HAYMAN)

4.3.1 F1 Complete Diallel

4.3.1.1 Test of Assumptions

For unbiased genetic interpretation based on the Jinks and Hayman genetic model, the assumptions must be met as closely as possible. The assumptions of a diploid inheritance, homozygous parents and no reciprocal differences seemed reasonably satisfied. However, the assumptions of an uncorrelated gene distribution and no epistasis are least likely in actual practice (Baker 1978). Furthermore, the absence of genotype by environment interactions and multiple alleles are

unrealistic. These may not significantly bias genetic estimates or they may be undetected in a single generation. For the latter reason, the diallel crosses among inbred lines were analysed for two different generations and two different seasons, not for quantifying these effects per se, but rather to detect any great extent of bias in the genetic analyses.

In the F1 complete diallel, most characters satisfied the test for a Wr/Vr regression coefficient statistically equal to one (significantly different from zero but non-significant from one) and for a non-significant Wr minus Vr variation among arrays (Appendix Table 7). However, the tests were satisfied on only five of the six blocks for TDM (block 1 excluded) and STK/PLT (block 4 excluded), thus diallel analyses were conducted on the five remaining blocks only. The FPN failed to satisfy both tests, even after attempts to eliminate the interaction. In such a case, analysis can still be carried out, but the possibility of biased genetic estimates must be considered (Hayman 1954).

4.3.1.2 Parental Performance and Dominance

The relative performance and dominance of the parents, based on diallel combinations (crosses and parents), are shown in Table 8. The ranking of parental performances followed a similar trend to that discussed in the comparisons among common parents in F1 inbred line crosses (section 4.2.1.2).

Yield performance was highest with HF, followed by E, A1, Ac and D. Meanwhile, HF had the most dominant genes with A1, E, Ac and D progressively containing fewer dominant genes. Thus, the correlation be-

TABLE 8. Correlation (r) between mean parental performance and dominance of parents from F_1 complete diallel analyses.

Character	Mean parental performance (low --> high)					Dominance of parents (low --> high)					r
YIELD	D	Ac	Al	E	HF	D	Ac	E	Al	HF	+.98**
TDM	D	Ac	Al	HF	E	D	Ac	HF	E	Al	+.93*
HI	Ac	Al	E	D	HF	Ac	Al	E	D	HF	+.99**
PD/PLT	E	D	Al	Ac	HF	D	Ac	E	Al	HF	+.86
S/PD	D	HF	Al	Ac	E	D	HF	Al	E	Ac	+1.00***
MSWT	Ac	HF	Al	D	E	Al	Ac	HF	E	D	+.89*
FLR	D	HF	Al	E	Ac	E	Ac	Al	HF	D	-.85
FMAT	Ac	HF	E	Al	D	Al	Ac	E	HF	D	+.57
MAT	HF	D	Ac	E	Al	Ac	Al	D	E	HF	-.43
STK/PLT	D	E	HF	Ac	Al	D	HF	Ac	Al	E	+.35
HT	D	Al	Ac	E	HF	D	E	Ac	Al	HF	+.99**
FPN	D	Al	Ac	HF	E	Al	E	HF	Ac	D	+.07
PRO	HF	Al	E	Ac	D	D	Ac	E	HF	Al	-.92*

* ** *** Significant at P = .05, .01 and .001 respectively.

tween parental performance and dominance (r = +.98) was high and positive implying a unidirectional dominance towards increased yields.

HF was associated with high TDM and superior HI, while E was associated with high TDM and only average HI. High positive correlations between parental performance and dominance for TDM and HI implied dominance increased expressions for both characters.

For the yield components, it should be noted that HF performed best for PD/PLT while E performed highest for S/PD and MSWT but lowest for PD/PLT (Table 8). Dominance increased expression for all yield components.

D and HF arrays were earlier to FLR and MAT. Dominance decreased FLR, while for FMAT and MAT, some ambidirectional dominance was detected with dominance tending to increase FMAT and decrease MAT.

Dominance was partly ambidirectional but tended to increase STK/PLT, while dominance increased HT. Since FPN did not satisfy the model assumptions, one can only postulate that ambidirectional dominance or no dominance was involved. Dominance was unidirectional towards lower PRO.

4.3.1.3 Genetic Variance Estimates

Tables 9 and 10 summarize the estimates of genetic variance components and proportions from F1 diallel analyses. The following findings are presented for the characters studied.

Yield, TDM and HI. For yield, TDM and HI, both additive and dominance gene effects were highly significant, with dominance gene effects most important. There were equal proportions of dominance and recessive genes among the parents. These characters expressed positive overdo-

TABLE 9. Estimates of genetic variance components from F_1 complete diallel analyses.

Character	D_1	H_1	H_2	F	h^2	E
YIELD	3044.60***	17658.33***	17660.05***	-971.32	55034.21***	476.49*
TDM	14041.84***	40529.00***	40337.14***	113.03	118425.70***	2019.90*
HI	15.21***	35.86***	32.60***	2.60	87.96***	1.06
PD/PLT	26.02***	47.79***	43.66***	-18.30*	119.57***	1.86
S/PD	0.12***	0.01	0.01	-0.06	0.02**	0.01***
MSWT	5730.95***	1060.24***	1023.78***	-1017.90***	2941.60***	38.33
FLR	6.91***	0.92***	0.93***	0.43***	2.38***	0.08***
FMAT	2.55***	0.20	0.20	-0.98***	1.00***	0.26***
MAT	2.47***	0.19	0.22	0.48	0.03	0.24***
STK/PLT	0.01***	0.02*	0.02*	-0.01*	0.02***	0.01***
HT	19.20***	24.03**	20.66**	4.83	59.80***	3.26**
FPN	0.92***	0.28	0.21	-0.20	-0.03	0.09**
PRO	10.73***	1.91***	1.25**	2.11***	0.87**	0.14*

* ** *** Significant at P = .05, .01 and .001 respectively.

TABLE 10. Estimates of genetic variance proportions from F_1 complete diallel analyses.

Character	D_1-H_1	$\sqrt{H_1/D_1}$	h^2/H_2	Heritabilities (%) BS	Heritabilities (%) NS
YIELD	-14613.73***	2.41	3.1	93.1	29.1
TDM	-26487.15***	1.70	2.9	89.5	36.8
HI	-20.65**	1.54	2.7	93.8	46.3
PD/PLT	-21.77*	1.36	2.7	95.0	65.5
S/PD	0.12***	--	--	--	83.6
MSWT	4670.70***	.43	2.9	99.0	92.0
FLR	5.99***	.37	2.6	97.7	91.2
FMAT	2.35***	--	--	--	83.5
MAT	2.47***	--	--	--	83.5
STK/PLT	0.00	1.02	1.6	57.9	44.9
HT	-4.83	1.12	2.9	81.2	51.3
FPN	0.92***	--	--	--	83.1
PRO	8.82***	.42	.7	97.2	91.1

* ** *** Significant at P = .05, .01 and .001 respectively.

minance with dominance ratios highest for yield (2.41), followed by TDM (1.70) and HI (1.54).

Positive overdominance for yield has been extensively reported (Bond 1966; Lawes and Newaz 1979; Hobbs and Burnett 1982), whereas only one example of positive overdominance for TDM has been reported (Cubero-Salmeron 1976).

Estimates of the number of gene blocks controlling dominance were interpreted to the highest integer since they represent a minimum number and are most often underestimated (Mather and Jinks 1982). The gene blocks involved with dominance among these parents for yield, TDM and HI were four, three and three, respectively.

The environmental effects on yield, TDM and HI were relatively small and BS heritability estimates were high. The BS heritability estimates for yield, TDM and HI were 93.1%, 89.5% and 93.8%, respectively. The removal of block effects in the experimental design and collection of data as plot means, helped reduce the influence of the environment in this particular experiment. Yassin (1973) found plot yields were much less subject to environmental influence than yields per plant and reported similar high BS heritability estimates.

NS heritabilities however, are the more informative and useful estimates. Yield had the lowest NS heritability estimate of 29.1%. Similar low NS heritabilities for yield have been widely reported (Filippetti 1979; Hobbs and Burnett 1982). NS heritability was also low for TDM (36.8%) and was moderately low for HI (46.3%).

Yield Components. Yield components expressed less dominance and more additive gene effects than yield. S/PD expressed little variation among these parents and only additive gene effects showed signifi-

cance. For PD/PLT and MSWT, both additive and dominance gene effects were highly significant with recessive genes being more common among these parents. PD/PLT expressed positive overdominance (dominance ratio = 1.36), while MSWT expressed positive partial dominance (dominance ratio = .43). Three gene groups were involved with dominance for both characters.

Yield components were reported to express less dominance than yield, itself (Bond 1966; Lawes and Newaz 1979). Similarly, positive overdominance for PD/PLT (Hayes and Hanna 1968; Martin and Cubero 1979) and positive partial dominance for MSWT (Bond 1966; Poulsen 1977) have been widely reported.

Similarly, the environmental effects were relatively small and BS heritability estimates were high, especially for MSWT. BS heritability estimates for PD/PLT and MSWT were 95.0% and 99.0%, respectively. NS heritability estimates were much higher than that for yield. MSWT had the highest NS heritability estimate (92.0%), followed by S/PD (83.6%) and PD/PLT (65.5%). These results parallel those reported by Poulsen (1977) and Filippetti (1979).

Phenological Characters. All phenological characters expressed highly significant additive gene effects while dominance gene effects were significant only for FLR. Dominance genes for earlier FLR were more common among these parents. A partial dominance ratio (.37) was expressed with three gene blocks involved with dominance. Similar findings were reported by Bond (1966), Poulsen (1977) and Martin and Cubero (1979).

Phenological characters were influenced little by the environment. Thus, BS heritability estimates were high and in most cases, similar

to NS heritability estimates, since these characters were largely controlled by additive gene effects. NS heritability estimates were highest for FLR (91.2%), followed by similar estimates for FMAT (83.5%) and MAT (83.5%). Poulsen (1977) reported moderate to high NS heritabilities for these characters.

Morphological Characters. Significant additive and dominance gene effects were expressed for STK/PLT and HT. Recessive genes were in excess for STK/PLT, while gene distribution was symmetric for HT. STK/PLT expressed complete dominance with two gene blocks involved. This dominance was ambidirectional with a tendency to increase STK/PLT. Complete dominance for increased HT involved three gene blocks. Comparable results for STK/PLT and HT, but involving partial dominance were reported by Bond (1966).

The FPN did not satisfy the model assumptions, most probably because dominance gene effects were not significant. Thus, no definite relation existed between Wr and Vr among arrays which violated the tests of the assumptions. Only additive gene effects were highly significant for FPN.

BS heritability estimates for STK/PLT, HT and FPN were 57.9%, 81.2% and 83.1%, respectively. Environment affected HT and FPN little, but strongly influenced STK/PLT. This was expected since STK/PLT showed little genotypic variation compared to other characters and was thus subject to relatively higher environmental effects. NS heritability estimates for STK/PLT (44.9%) and HT (51.3%) were low to moderate, while for FPN (83.1%), it was relatively high. Moderately low NS heritabilities for STK/PLT and HT have also been reported (Hobbs and Burnett 1982).

Protein Content. PRO expressed highly significant additive and dominance gene effects with the additive gene effects being most important. Dominant genes were more common among these parents. Partial dominance (dominance ratio = .42) towards lower PRO involved a single gene group. Estimates of BS heritability (97.2%) and NS heritability (91.1%) were high. These results agree well with the literature (Bond 1970; Griffiths and Lawes 1978; Chapman 1979; Haro et al. 1980).

4.3.1.4 Wr/Vr Graphs

The Wr/Vr graph provides a supplementary overall picture of the genetic constitution among these parents. Wr/Vr graphs from F1 diallel analyses for yield, TDM and HI are presented in Figures 1-3. Regression lines for these characters had slopes (b) statistically equal to one which indicated a satisfactory fit to the additive-dominance genetic model. Their y-intercepts (1/4(D1 - H1)), were also significant and negative (Table 10), which indicated overdominance. Yield parental arrays were slightly clustered together over the theoretical range of the Wr/Vr line, as defined by the limiting parabola. However, for TDM and HI, the parental arrays were scattered quite uniformly over the range of the Wr/Vr line. Thus, genetic diversity contained among these parents was moderate for yield and considerable for TDM and HI. This reflects the greater variation in assimilate distribution patterns among these parents that results in comparatively less variation in yield, itself.

For yield and TDM, there was a tendency for parental arrays to cluster into two groups, with HF, E and Al containing more dominant genes while D and Ac contained more recessive genes. Although HF, E

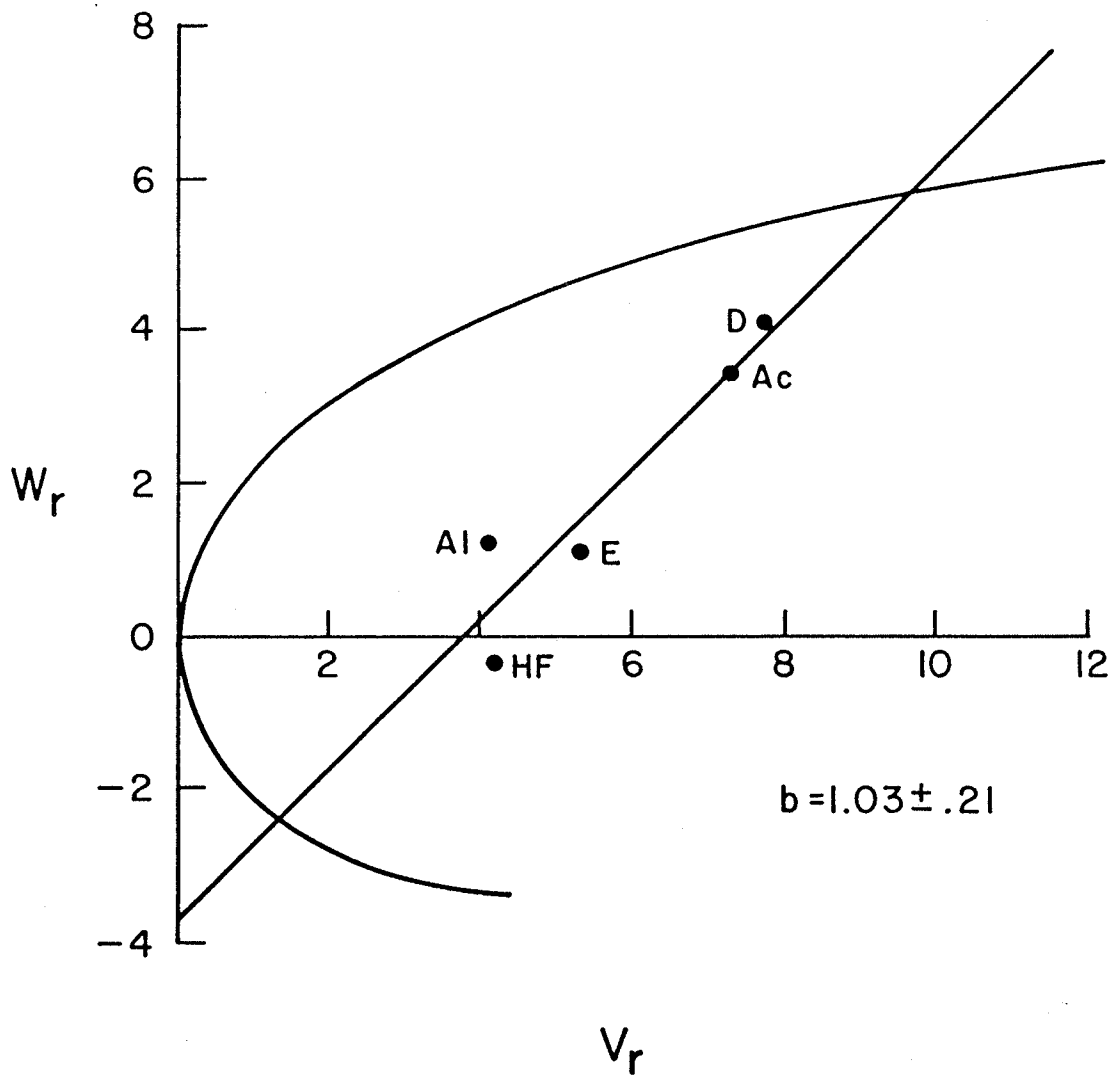

Figure 1. Wr/Vr graph for yield in the F_1 complete diallel.

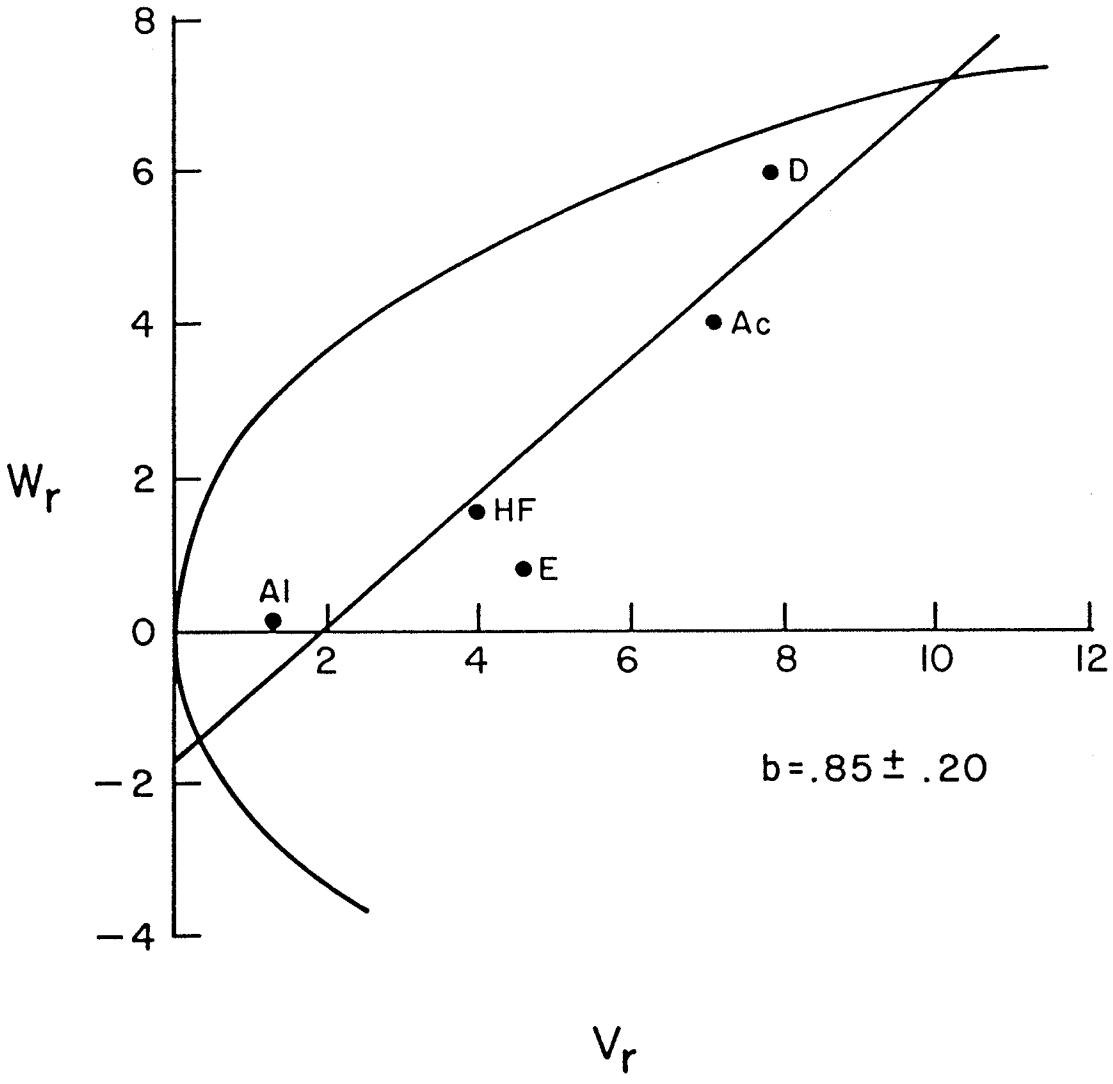

Figure 2. Wr/Vr graph for TDM in the F_1 complete diallel.

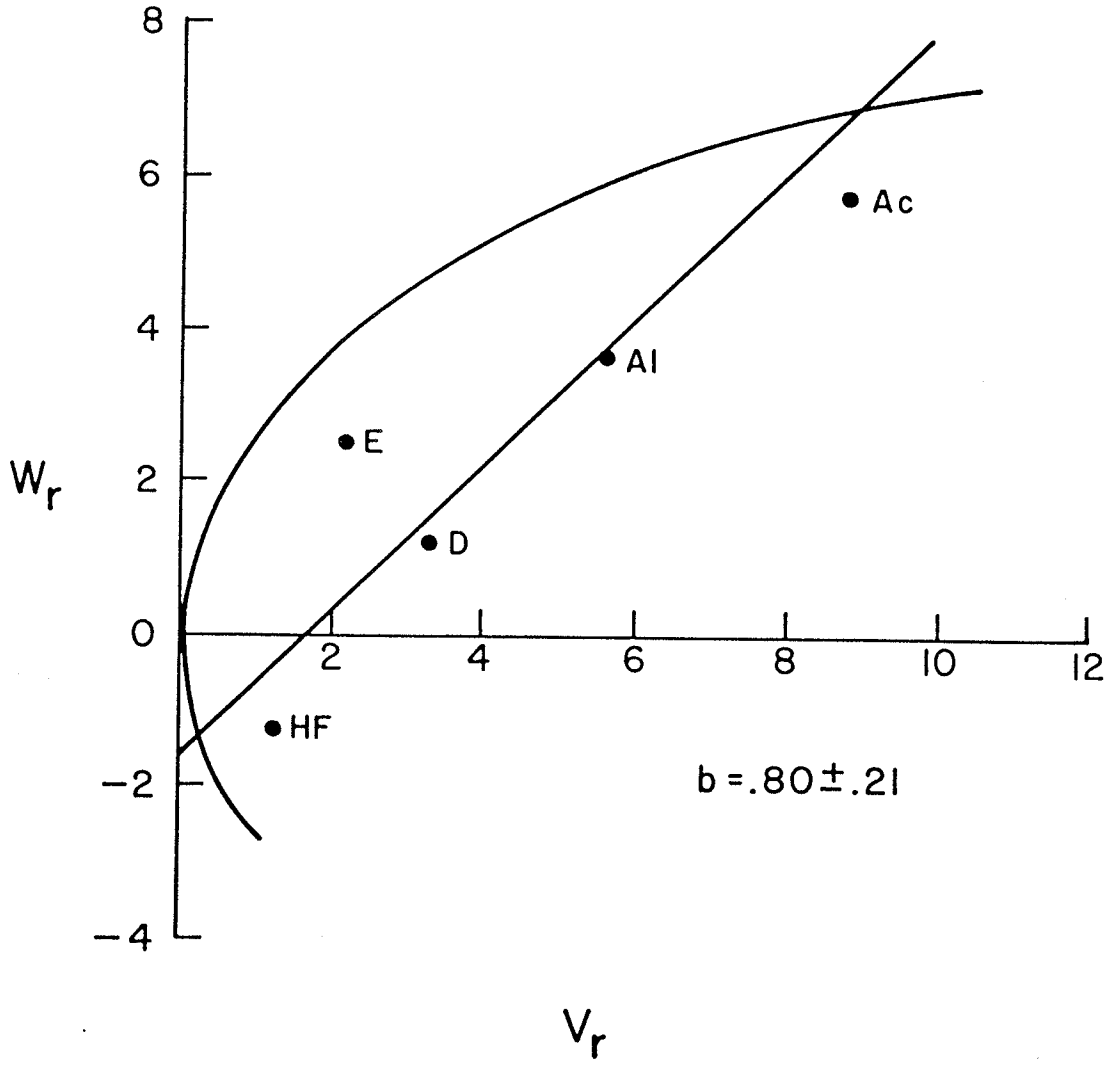

Figure 3. Wr/Vr graph for HI in the F_1 complete diallel.

and A1 contained more dominant genes for yield and TDM, only HF contained more dominant genes for HI, thus perhaps contributing to its superiority as a parent in hybrid combinations.

4.3.2 F2 Complete Diallel

4.3.2.1 Test of Assumptions

The Jinks and Hayman genetic model adequately fitted the data for most characters in the F2 complete diallel (Appendix Table 8). Block 5 was excluded from the analyses for S/PD to eliminate interactions. Meanwhile for MAT, attempts to remove the interactions failed and analyses were conducted considering the possibility of biased genetic estimates.

4.3.2.2 Parental Performance and Dominance

Relative performance and dominance among the common parents in the F2 complete diallel were, in large part, comparable to the F1 complete diallel grown out the previous year (Table 11).

Yield performance in the F2 ranked from highest to lowest, E, HF, A1, D and Ac. Although E and HF still ranked high, HF was less superior perhaps due to a differential response to inbreeding. For TDM and HI, similar patterns of assimilate partitioning were observed. E was associated with high TDM production while HF was associated with high HI. Unidirectional dominance increased yield, TDM and HI.

Similar yield distribution patterns were observed among the yield components. HF ranked highest for PD/PLT, while E ranked lowest for PD/PLT but highest for S/PD and MSWT. Dominance increased S/PD, while dominance with some ambidirection tended to increase PD/PLT and MSWT.

TABLE 11. Correlation (r) between mean parental performance and dominance of parents from F_2 complete diallel analyses.

Character	Mean parental performance (low --> high)					Dominance of parents (low --> high)					r
YIELD	Ac	D	Al	HF	E	Ac	D	Al	HF	E	+.99**
TDM	D	HF	Al	Ac	E	D	HF	Ac	Al	E	+.96**
HI	Ac	E	Al	HF	D	Ac	Al	E	D	HF	+.97**
PD/PLT	E	D	Al	Ac	HF	Ac	Al	HF	D	E	+.11
S/PD	D	HF	Ac	Al	E	D	Ac	HF	E	Al	+.87*
MSWT	Ac	HF	Al	D	E	HF	D	Ac	Al	E	+.55
FLR	D	HF	Al	E	Ac	Ac	E	HF	Al	D	-.90*
FMAT	Ac	E	HF	Al	D	E	Ac	HF	Al	D	+.86
MAT	HF	D	E	Al	Ac	HF	Ac	D	E	Al	+.44
HT	D	Al	Ac	E	HF	Ac	HF	E	D	Al	+.45
FPN	D	Al	HF	Ac	E	Ac	HF	E	Al	D	-.70
PRO	Al	HF	Ac	E	D	D	HF	Ac	E	Al	-.57

* ** *** Significant at P = .05, .01 and .001 respectively.

Ambidirectional dominance in segregating F2 generations have been reported (Martin and Cubero 1979; Hobbs and Burnett 1982).

Parental arrays for HF and D were earlier to FLR and MAT. Dominance decreased FLR and increased FMAT. However, dominance tended to increase MAT, in contrast to the 1982 F1 data where dominance tended to decrease MAT. This discrepancy may be attributed to the hot dry conditions that differentially forced an early maturity. Genotypes with more drought and heat tolerance perhaps prolonged their growth, thus complicated the genotypic expression for MAT and resulted in significant interactions with the model.

Genotypic expressions for STK/PLT were non-significant, ascribable mainly to a higher planting density. Dominance tended to increase HT. The genetic model fitted the data for FPN (unlike the 1982 F1 data), perhaps due to the higher planting density environment that led to significant dominance. Dominance decreased FPN, a result similar to that reported by Martin and Cubero (1979). Dominance tended to decrease PRO.

4.3.2.3 Genetic Variance Estimates

Summaries of genetic variance estimates from F2 diallel analyses are shown in Tables 12 and 13. Recall that the smaller contributions of dominance in the F2 were proportionally corrected, thus relative genetic estimates are theoretically similar for the F1 and F2 generations.

Generally, estimates of dominance and environmental effects were relatively more important in 1983. Additive and dominance gene effects were highly significant for all characters studied and BS heritability estimates were generally lower than in 1982. Slight differ-

TABLE 12. Estimates of genetic variance components from F_2 complete diallel analyses.

Character	D_1	H_1	H_2	F	h^2	E
YIELD	278.25**	9649.65***	9977.93***	-462.78*	29972.08***	218.38***
TDM	2484.72***	10376.25***	12300.54***	-2052.28**	46038.26***	849.53***
HI	14.87***	71.58***	64.60***	12.35***	124.82***	0.83*
PD/PLT	1.27***	4.88***	3.40***	-0.61	2.63***	0.24**
S/PD	0.11***	0.36***	0.32***	0.03	0.82***	0.01**
MSWT	3202.07***	1932.06***	1490.86***	534.28***	3046.49***	34.91**
FLR	9.43***	7.67***	6.10***	0.81***	10.05***	0.14***
FMAT	4.06***	3.23***	3.13***	-0.65	3.32***	0.27**
MAT	2.75***	8.49***	6.08***	2.50**	4.61***	0.16
HT	15.66***	96.43***	61.70***	23.87***	55.23***	3.89***
FPN	1.56***	1.99***	1.18***	-1.62***	0.30**	0.09**
PRO	10.65***	2.99***	1.96***	6.00***	0.81***	0.10*

* ** *** Significant at P = .05, .01 and .001 respectively.

TABLE 13. Estimates of genetic variance proportions from F_2 complete diallel analyses.

Character	D_1-H_1	$\sqrt{\frac{H_1}{D_1}}$	$\frac{h^2}{H_2}$	Heritabilities (%) BS	NS
YIELD	-9371.40***	5.89	3.0	79.3	20.3
TDM	-7891.54***	2.04	3.7	72.9	48.4
HI	-56.71***	2.19	1.9	91.8	51.8
PD/PLT	-3.61***	1.96	.8	83.2	68.2
S/PD	-0.25***	1.82	2.6	86.7	62.3
MSWT	1270.02***	.78	2.0	97.9	92.2
FLR	1.75***	.90	1.6	97.3	90.0
FMAT	0.83*	.89	1.1	89.7	82.4
MAT	-5.74***	1.76	.8	90.0	66.1
HT	-80.77***	2.48	.9	72.1	44.5
FPN	-0.43**	1.13	.3	94.0	89.0
PRO	7.66***	.53	.4	97.6	94.7

* ** *** Significant at P = .05, .01 and .001 respectively.

ences between experiments in gene symmetry and gene blocks involved with dominance existed, attributable to the different environment and generation (Tables 12 and 13).

For the most part however, the F2 diallel analyses paralleled results from the F1 diallel analyses. Highly significant overdominance was expressed for yield, TDM and HI, being most important for yield. Yield components displayed less dominance than yield. Some overdominance was expressed for PD/PLT and, in contrast to the 1982 F1 data, overdominance was also expressed for S/PD, perhaps primarily due to the different environment. MSWT expressed partial dominance (Table 13).

Phenological and morphological characters displayed relatively more additive gene effects than yield. The apparent overdominance expressed for MAT is most probably biased, since fit of the genetic model was not obtained. The dominance ratio was relatively large only for HT, perhaps from some association with TDM. PRO expressed partial dominance (Table 13).

Relative NS heritability estimates from the F2 analyses (Table 13) were also comparable with those from the F1 analyses. Yield had the lowest NS heritability (20.3%), followed by moderate NS heritabilities for TDM (48.4%) and HI (51.8%). NS heritabilities were higher for the yield components and was highest for MSWT (92.2%) while moderately high for S/PD (62.3%) and PD/PLT (68.2%). The other characters generally had relatively high NS heritabilities. FLR and FMAT had high NS heritabilities of 90.0% and 82.4%, respectively, while MAT had a moderately high NS heritability (66.1%) which may be biased from interactions with the genetic model. HT had a moderate NS heritability

(44.5%) while high NS heritabilities were expressed for FPN (89.0%) and PRO (94.7%).

4.3.2.4 Wr/Vr Graphs

Wr/Vr graphs for yield, TDM and HI in the F2 complete diallel resembled those in the F1 complete diallel (Figures 4-6). Regression slopes indicated satisfactory fit to the genetic model for these characters. Their y-intercepts were significant and negative (Table 13), indicating overdominance. The scatter of points over the range of the Wr/Vr line implied that genetic diversity among these parents was moderate for yield and considerable for TDM and HI. The relative proportions of dominant genes in these parents showed similar trends, except for TDM where HF contained relatively less dominant genes than in the F1 Wr/Vr graph. However, E, HF and A1 contained relatively more dominant genes for yield than Ac and D. HF also had relatively more dominant genes for HI.

4.3.3 Summary and Discussion of Genetic Analyses

Genetic analyses for the F1 and F2 complete diallels were largely comparable even though they represented different generations and were grown in different environments. Since the F2s were planted at plot density, one can imply that F1 results on "semi-spaced" plant density may probably relate well to commercial planting densities.

There were only slight differences in ranking of parental performance and few instances of less directed dominance, suggesting some ambidirectional or simply less dominance *per se*. These differences may be attributable to genotype by environment interactions such as dif-

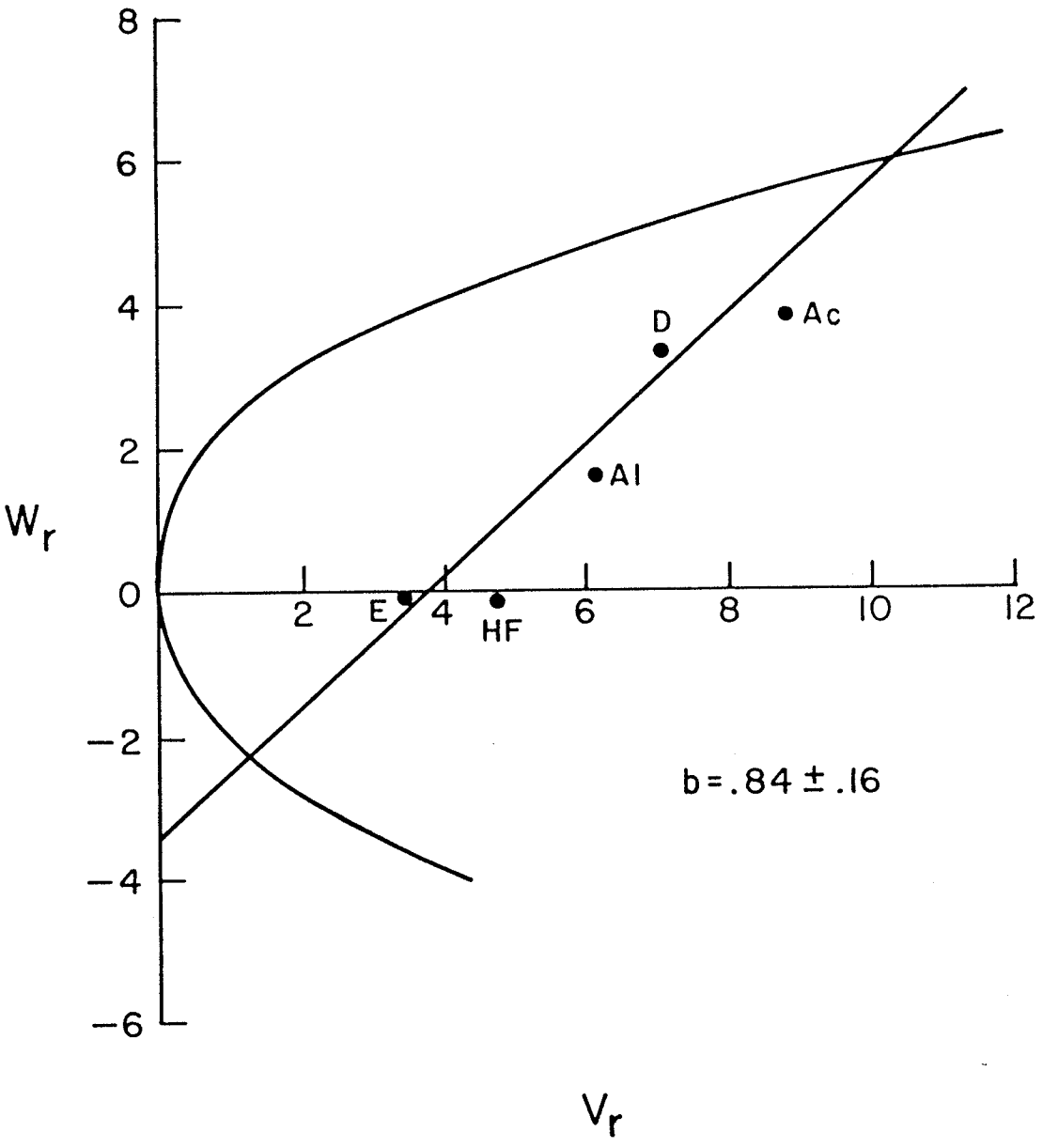

Figure 4. Wr/Vr graph for yield in the F_2 complete diallel.

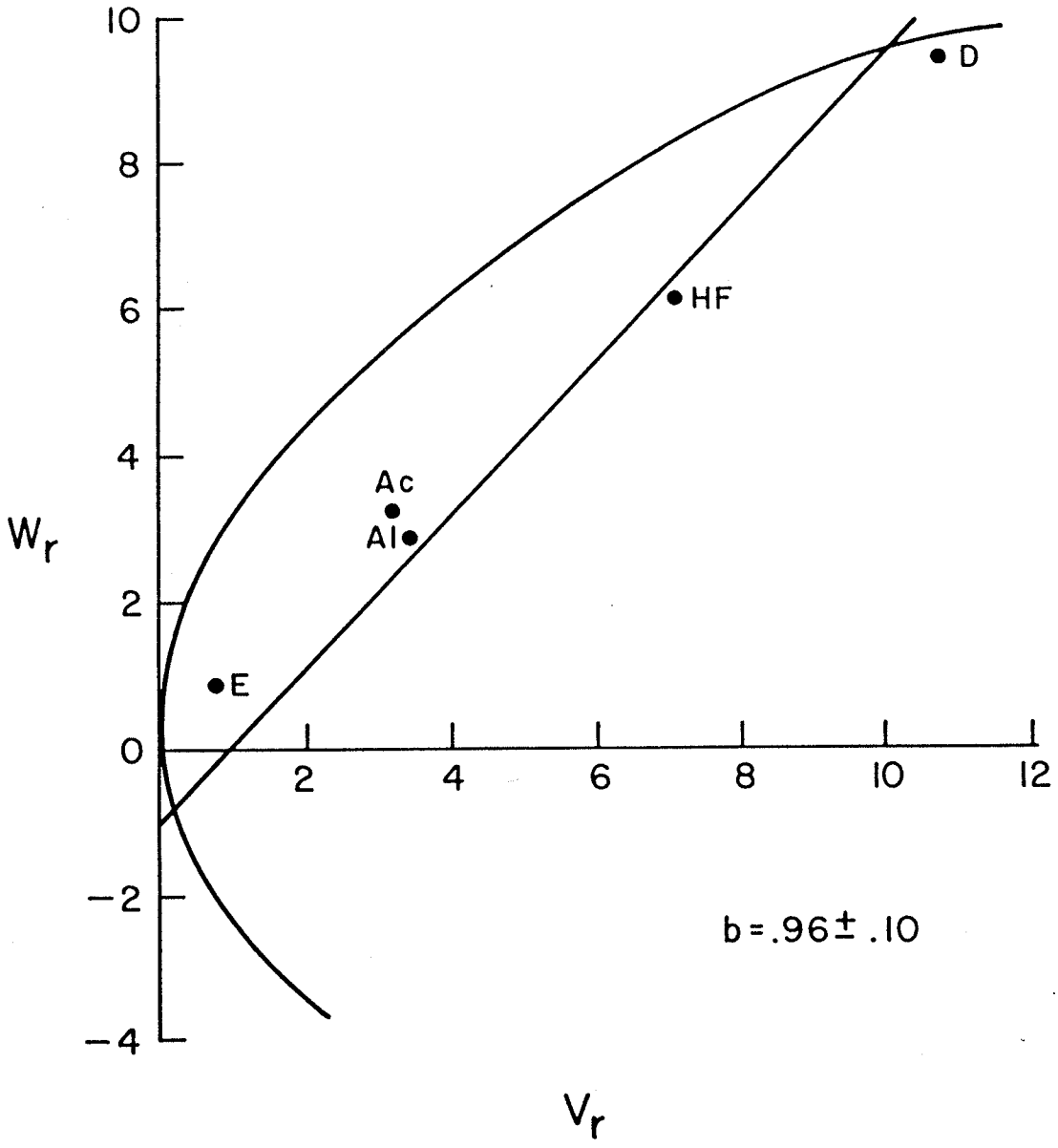

Figure 5. Wr/Vr graph for TDM in the F_2 complete diallel.

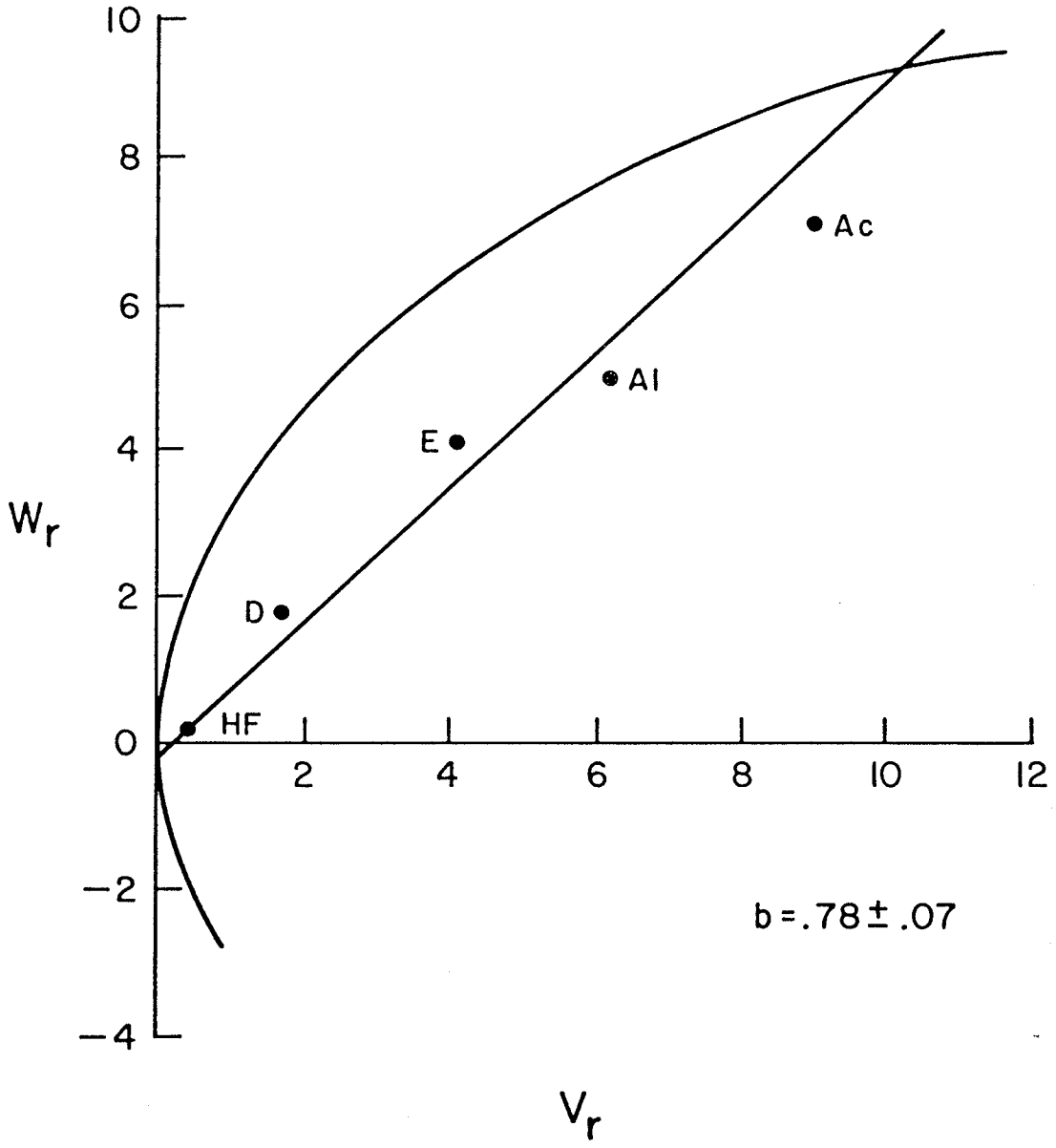

Figure 6. Wr/Vr graph for HI in the F_2 complete diallel.

ferential responses to the hot, dry and shorter growing season or higher planting density in 1983. In addition, intrinsic differences in the segregating F2 generation are inevitable such as differential responses to inbreeding and the segregation of possible epistatic or correlated gene effects undetectable in the F1. However, in general, differences were small and no great extent of bias was detected.

The genetic model assumptions were generally satisfied, except for FPN in the 1982 F1 data and MAT in the 1983 F2 data. This further indicates little bias in the genetic estimates.

Characters of greater complexity and closer association with vegetative and reproductive fitness expressed more dominance and lower NS heritabilities. Positive overdominance was expressed greatest for yield, followed by TDM and HI, while NS heritabilities were lowest for yield and low to moderate for TDM and HI. Three to four gene blocks controlled dominance for yield, TDM and HI among these parents.

Yield components expressed less dominance and had higher NS heritabilities than yield. Overdominance increased PD/PLT and NS heritabilities were moderate. Partial dominance increased MSWT while S/PD showed inconsistencies between experiments and generally expressed little genetic variation. MSWT and S/PD had high NS heritabilities. Where dominance was significant, two to three gene groups were involved.

Phenological characters displayed mostly additive gene effects and had high NS heritabilities. Negative partial dominance was expressed for FLR, while positive partial dominance tended to be expressed for FMAT (significant only in 1983). MAT expressed mainly additive gene effects in 1982 and showed inconsistencies with the model in 1983.

Vegetative characters, STK/PLT and HT, displayed moderate degrees of positive dominance and had moderate NS heritabilities. One to three gene groups controlled this dominance. FPN generally expressed additive gene effects and only in 1983, some negative dominance was also expressed. FPN had high NS heritabilities.

PRO exhibited mainly additive gene effects with a single gene group controlling partial dominance towards lower expressions. NS heritabilities were high for this character.

Thus, yield had the most dominance, lowest NS heritability as well as the most heterosis. It follows that high yields would be most difficult to select for and may be achieved only through hybrid breeding. As the breeding system in fababeans ranges from in- to out-breeding, the selection of good lines and production of hybrids would be quite adaptable to this crop species.

4.4 SIMPLE CORRELATION ANALYSES

The relationships of yield with other characters in the diallel crosses were studied using simple correlation analyses (Table 14).

Yield was most highly correlated with TDM in all diallel experiments (r ranged 0.78*** to 0.90***), a result similar to that reported by Neal (1982). TDM production may measure a genotype's ability to adapt to an environment. Since yield is contained within TDM, it follows that a greater adaptability or higher TDM would expectedly be correlated with higher yield. Yield was also highly correlated with HI (r ranged 0.61** to 0.72***), quite expected since HI represents a genotype's ability to partition assimilates into seed yield. Interestingly, the correlation between TDM and HI was non-significant and

TABLE 14. Phenotypic correlation coefficients among characters studied in (a) F_1 complete diallel (upper line), (b) F_2 complete diallel (middle line) and (c) F_1 cultivar diallel (lower line).

Character	TDM	HI	PD/PLT	S/PD	MSWT	FLR	FMAT	MAT	STK/PLT	HT	FPN	PRO
YIELD	0.90***	0.72***	0.70***	0.23	0.19	0.00	-0.09	-0.12	0.29	0.72***	0.29	-0.53**
	0.78***	0.61**	0.41*	0.44*	0.24	-0.07	0.01	-0.19	-0.01	0.45*	0.10	-0.34
	0.88***	0.63**	0.74**	0.23	0.15	0.19	-0.10	0.11	0.33	0.22	-0.32	0.06
TDM		0.38	0.60**	0.44*	0.09	0.27	-0.22	0.17	0.44*	0.75***	0.41*	-0.55**
		-0.02	0.08	0.76***	0.17	0.47*	-0.38	0.26	0.17	0.53**	0.53**	-0.39
		0.19	0.51	0.27	0.38	0.27	-0.11	0.19	0.23	0.44	-0.02	-0.23
HI			0.53**	-0.31	0.38	-0.52**	0.22	-0.60**	-0.07	0.31	-0.13	-0.27
			0.55**	-0.24	0.18	-0.71***	0.49*	-0.63***	-0.26	0.07	-0.49*	-0.05
			0.73**	-0.03	-0.31	0.00	-0.03	-0.03	0.30	-0.27	-0.62*	0.51
PD/PLT				-0.04	-0.47*	0.13	-0.39	-0.27	0.39	0.55**	0.25	-0.69***
				-0.16	-0.61**	-0.23	-0.06	-0.45*	0.17	0.05	-0.25	-0.50*
				-0.32	-0.42	0.03	0.05	0.06	0.31	-0.19	-0.68**	0.31
S/PD					-0.15	0.72***	-0.44*	0.65***	0.37	0.57**	0.59**	-0.30
					-0.03	0.56**	-0.43*	0.39	0.12	0.48*	0.55**	-0.49*
					0.23	0.12	-0.39	-0.22	0.29	0.12	0.30	-0.09
MSWT						-0.56**	0.63***	-0.13	-0.35	-0.12	-0.28	0.41*
						-0.24	0.39	0.05	-0.29	0.11	0.01	0.59**
						0.20	0.05	0.27	-0.27	0.71**	0.58*	-0.46
FLR							-0.80***	0.67***	0.29	0.42*	0.72***	-0.46*
							-0.83***	0.67***	0.31	0.17	0.83***	-0.34
							-0.55*	0.65**	-0.28	0.36	0.56*	-0.13
FMAT								-0.09	-0.08	-0.45*	-0.83***	0.54**
								-0.19	-0.16	-0.45*	-0.80***	0.38
								0.27	0.20	-0.12	-0.24	-0.08
MAT									0.37	0.13	0.17	-0.07
									0.38	-0.27	0.46*	-0.07
									-0.13	0.29	0.44	-0.23
STK/PLT										0.23	-0.02	-0.26
										-0.19	0.18	-0.17
										-0.56*	-0.46	0.40
HT											0.59**	-0.53**
											0.47*	-0.22
											0.65**	-0.68**
FPN												-0.44*
												-0.19
												-0.53*

* ** *** Significant at P = .05, .01 and .001 respectively.

even showed positive tendencies in the F1 complete and F1 cultivar diallels. Thus, higher yields in the diallels were associated with an increase in TDM and/or HI without a decrease in either.

Turning to yield components, PD/PLT was most closely correlated with yield (r ranged 0.41* to 0.74**). Associations of yield with S/PD and MSWT showed positive tendencies but was significant only for S/PD in the F2 complete diallel (r = 0.44*). These results agree well with the literature (Bond 1966; Kambal 1969; Sjodin 1977; Lawes and Newaz 1979).

Although all yield components showed some positive correlation with yield, yield component compensation was expressed. PD/PLT was negatively correlated with MSWT (r ranged -0.42 to -0.61**). Associations between the other yield components also displayed negative tendencies, but were not significant. Similar negative correlations were widely reported (Yassin 1973; Bianco et al. 1979).

The only other character to express some significant positive correlation with yield was HT, perhaps from some association with TDM. Similar findings have been reported (Sjodin 1977; Vries 1979).

Significant negative correlations between PRO and yield existed only in the F1 complete diallel (r = -0.53**). This negative correlation is not surprising nor does it pose any hindrance in a breeding program. In the F1 complete diallel, the S5 parents differed significantly in PRO (Appendix Table 2) and negative partial dominance controlled this character (Tables 8 and 10). Thus, hybrids would be expected to have slightly lower PRO than their parent mean (Table 1). This difference (-0.7%) is of no importance compared to the large heterosis for yield (Table 1). This negative relationship was non-

significant in the segregating F2 complete diallel as family means approached parent means. Meanwhile, no association existed between PRO and yield in the F1 cultivar diallel. This is attributed to the small variation among cultivars relative to within cultivars. Negative partial dominance is associated with the heterozygous genotypes. Cultivar parents and their crosses however, contain heterozygotes and homozygotes. This genotypic variation for PRO combined with genotypic variation for yield probably obscured the heterozygous PRO genotypes from the heterozygous higher yielding genotypes. Thus, PRO and yield are generally independent of each other. The literature is in close agreement with this conclusion (Chapman and Peat 1978; Griffiths and Lawes 1978; Sjodin et al. 1981). However, to maximize protein yield, it is suggested that recessive genes for high protein content be fixed into potential inbred lines prior to embarking on a hybrid breeding program.

Of interest, HI was significantly correlated with PD/PLT (r ranged 0.53** to 0.73**). This provides evidence that a higher HI may relate to increased autofertility to set more pods.

Interesting relationships also existed among the phenological characters, although variation was small. FLR was negatively correlated with FMAT, but positively correlated with MAT. Thus, the slightly earlier flowering hybrids were associated with a slightly longer flowering to maturity time, but they still matured a bit earlier than their parents. FPN was not very useful in relating to early maturity, although it was significantly correlated with FLR in these studies. Thus, hybrids seem to be an exception to the widely reported negative correlation between early maturity and higher yields (Magyarosi and Sjodin 1976; Poulsen 1977; Vries 1979).

In conclusion, selection for high yielding lines via TDM and HI may be more efficient. Although characterized with NS heritabilities only moderately higher than yield itself, TDM and HI were highly correlated with yield and displayed no compensatory relationship between them. It is presumed that HI may largely represent autofertility. Thus, selection for autofertility genes, possible under growthroom conditions, may result in increased HI.

Meanwhile, yield components had high NS heritabilities and were positively correlated with yield, but their use as selection criteria may be limited primarily due to yield component compensation. Other characters generally exhibited no high correlation with yield in this study.

Chapter V

CONCLUSIONS

1. Vegetative and reproductive characters of increasing complexity appeared to be characterized by more heterosis, more dominance and lower NS heritabilities. Yield had the most heterosis, most dominance and lowest NS heritability.
2. Extent of heterosis for yield seemed to increase with heterozygosity at a genetically determined rate which was independent of genetic variation for yield performance.
3. Relative hybrid yield performances may be predicted from that of inbred line parents but not from cultivar parents.
4. Evidence suggested that the "gene pool" of the S5 parents contained inferior yield genes relative to the mean genotypic value of their original cultivars.
5. It was suggested that selection of high yielding lines from relatively homozygous and perhaps genetically divergent material may maximize hybrid yields in fababeans.
6. HF, followed by E, had the higher common parent yield performances while HF x E was the best specific combination in this study. HF may be a good general combiner but it is important to test for specific combinations to maximize yield advantage over open-pollinated cultivars.
7. Selection for high yielding lines via TDM and HI may be more efficient. It was suggested that selection for autofertility may increase HI.

8. PRO exhibited mainly additive gene effects with a single gene group controlling partial negative dominance among the genotypes studied. PRO was usually independent of yield. To maximize protein yield, it was suggested that recessive genes for high protein content be fixed into potential hybrid material.

Chapter VI

SUGGESTIONS FOR FURTHER RESEARCH

This research study has clearly indicated that there is substantial potential in F1 hybrids of fababeans. Before this potential can be fully exploited, further research into the following areas should be pursued:

1. the development of a satisfactory pollen control system.
2. the identification of prospective parents using assessment of genetic distance.
3. early generation (i.e. S1 or S2) testing of potential inbred line parents.
4. the improvement of the evaluation of hybrid performance using multiple row plots as well as several locations and years.

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APPENDIX TABLE 1. Mean raw data from F_1 complete diallel.

Female parent	Male parent					Standard error
	Ac	Al	D	E	HF	
			Yield (g per plot)			
Ac	280.8	433.2	449.1	453.0	497.2	
Al	432.4	351.4	439.9	465.8	522.3	
D	414.5	459.6	255.4	443.8	450.5	
E	483.8	465.7	459.8	362.4	609.9	
HF	513.0	536.5	478.8	523.1	397.8	
Controls	388.0	465.0	376.1	453.6	455.7	23.2
			Total dry matter (g per plot)			
Ac	733.9	1028.1	913.9	992.6	1014.0	
Al	963.9	890.3	989.0	1027.5	1043.3	
D	884.1	975.9	605.1	937.6	901.7	
E	1227.2	1019.4	977.1	866.4	1239.9	
HF	1070.7	1070.5	937.7	1080.4	896.7	
Controls	916.4	978.1	796.3	877.0	981.6	47.3
			Harvest Index (%)			
Ac	35.7	43.3	47.9	44.1	49.2	
Al	44.6	39.1	46.5	45.0	50.0	
D	46.9	47.4	42.3	47.8	50.5	
E	41.3	44.9	48.3	43.9	48.9	
HF	48.8	50.5	51.7	48.3	45.9	
Controls	43.2	47.8	48.0	51.1	48.1	1.1
			Pods per plant			
Ac	24.8	32.4	29.8	27.0	39.1	
Al	32.5	26.6	30.1	25.5	37.8	
D	27.6	27.7	18.9	24.4	32.3	
E	31.2	25.5	23.9	19.5	35.4	
HF	41.2	35.4	33.5	30.5	31.6	
Controls	28.3	30.6	31.4	25.3	32.5	1.5
			Seeds per pod			
Ac	4.0	4.0	3.8	4.3	3.8	
Al	3.9	3.8	3.4	4.1	3.7	
D	3.8	3.8	3.1	3.7	3.3	
E	4.0	4.1	3.8	4.0	3.9	
HF	3.7	3.9	3.4	3.9	3.7	
Controls	3.9	3.4	3.1	3.8	3.3	0.1

APPENDIX TABLE 1. (continued)

Female parent	Male parent					Standard error
	Ac	Al	D	E	HF	
			1000 Seed weight (g)			
Ac	279.3	335.2	395.4	391.6	335.4	
Al	341.7	348.4	431.1	446.2	374.1	
D	396.3	437.7	438.1	491.4	421.8	
E	388.3	447.8	506.1	464.9	441.9	
HF	336.7	389.3	419.3	440.6	341.0	
Controls	351.9	446.3	388.2	474.3	424.2	6.6
			Emergence to flowering (days)			
Ac	42.8	40.3	39.0	41.0	39.8	
Al	41.8	41.0	37.5	40.3	40.2	
D	38.3	37.0	36.0	37.7	37.5	
E	41.8	39.7	37.7	41.8	40.2	
HF	40.2	39.2	37.7	39.7	39.8	
Controls	40.3	39.3	37.3	40.7	38.0	0.3
			Flowering to maturity (days)			
Ac	45.2	47.2	48.2	47.0	45.7	
Al	46.5	48.0	49.5	48.0	47.3	
D	48.5	50.3	49.2	49.3	48.0	
E	46.3	47.8	48.3	46.3	47.0	
HF	45.8	46.7	48.3	47.0	46.0	
Controls	48.0	49.5	49.0	47.5	48.7	0.5
			Emergence to maturity (days)			
Ac	88.0	87.5	87.2	88.0	85.5	
Al	88.3	89.0	87.0	88.3	87.5	
D	86.8	87.3	85.2	87.0	85.5	
E	88.2	87.5	86.0	88.2	87.2	
HF	86.0	85.8	86.0	86.7	85.8	
Controls	88.3	88.8	86.3	88.2	86.7	0.5
			Fertile stalks per plant			
Ac	2.6	2.9	2.9	2.6	2.8	
Al	3.0	2.9	2.7	2.5	2.8	
D	2.7	2.9	2.4	2.7	2.4	
E	2.9	2.8	2.7	2.5	2.7	
HF	2.8	2.8	2.5	2.6	2.6	
Controls	2.3	2.9	2.4	1.9	2.2	0.1

APPENDIX TABLE 1. (continued)

Female parent	Male parent					Standard error
	Ac	Al	D	E	HF	
			Height (cm)			
Ac	114.2	120.8	119.2	124.2	120.8	
Al	115.8	115.8	113.3	119.2	117.5	
D	115.8	113.3	105.8	119.2	116.7	
E	120.0	119.2	115.8	115.0	122.5	
HF	121.7	118.3	118.3	123.3	118.3	
Controls	114.2	109.2	103.3	112.5	117.5	1.8
			First podded node			
Ac	8.2	7.2	6.8	7.5	7.5	
Al	6.8	6.2	5.8	7.2	7.7	
D	6.7	5.5	6.0	6.5	6.5	
E	8.0	7.3	6.7	7.8	8.2	
HF	7.3	7.5	6.2	8.3	7.7	
Controls	7.2	6.5	6.0	7.2	5.8	0.3
			Protein (%)			
Ac	33.3	30.4	33.9	31.5	29.4	
Al	30.2	30.5	31.9	30.6	28.4	
D	33.7	32.2	36.6	33.8	31.5	
E	31.6	31.1	34.3	31.0	30.4	
HF	29.5	28.3	31.1	30.7	27.9	
Controls	30.8	31.1	31.8	31.2	29.4	0.4

APPENDIX TABLE 2. Analyses of variance for characters studied in the F_1 complete diallel.

Source of Variation	df	Mean squares					
		YIELD	TDM	HI	PD/PLT	S/PD	MSWT
Diallel entries	24	32761.66***	84126.30***	75.48***	188.10***	0.44***	17790.40***
Crosses	19	12750.89***	43849.47***	44.76***	145.70***	0.38***	14548.25***
Parents	4	21131.50***	80319.00***	97.67***	167.28***	0.79***	34615.75***
Crosses versus parents	1	518810.06***	935307.20***	830.96***	1132.18***	0.22	27807.96***
Blocks	5	18134.70***	141543.38***[b]	52.08***	107.87***	0.14	1436.27***
Error	120	2938.22[a]	10238.50[c]	6.62[a]	11.49[a]	0.07[d]	235.59[e]
Controls	4	10625.04	29776.21	48.27**	49.57	0.64**	13877.51***
Crosses versus controls	1	57414.47***	219732.07***	2.60	55.09*	2.46***	1758.91*
Parents versus controls	1	144403.20***	155224.78***	579.08***	429.87***	0.75**	27221.40***
Coefficient of variation (%)		12.08	10.44	5.56	11.38	7.05	3.81

Source of Variation	df	Mean squares						
		FLR	FMAT	MAT	STK/PLT	HT	FPN	PRO
Diallel entries	24	18.31***	10.40***	6.71***	0.13**	90.17***	3.68***	25.38***
Crosses	19	13.10***	9.01***	4.97***	0.13*	55.03***	3.36***	18.02***
Parents	4	41.95***	16.88***	16.22***	0.13	134.58***	6.08***	65.25***
Crosses versus parents	1	22.82***	12.04**	1.71	0.26*	580.17***	0.28	8.98**
Blocks	5	0.40	1.04	0.40	0.26**[b]	193.40***	10.26***	4.80***
Error	120	0.48	1.54	1.47	0.06[c]	19.55	0.56	0.85
Controls	4	12.53***	3.78**	7.25***	0.71*	174.17***	2.37**	4.79**
Crosses versus controls	1	0.88	19.08***	11.76**	2.84***	1320.17***	6.62***	3.56*
Parents versus controls	1	20.42***	38.40***	2.82	0.87**	93.75*	6.02**	14.90***
Coefficient of variation (%)		1.76	2.65	1.38	9.27	3.75	10.58	3.01

* ** *** Significant at P = .05, .01 and .001 respectively.
[a] With 117 df.
[b] With 4 df.
[c] With 95 df.
[d] With 119 df.
[e] With 118 df.

APPENDIX TABLE 3. Mean raw data from F_2 complete diallel.

Female parent	Male parent					Standard error
	Ac	Al	D	E	HF	
			Yield (g per plot)			
Ac	244.6	305.5	283.0	330.7	357.9	
Al	335.4	264.4	327.3	338.8	346.7	
D	303.6	318.5	253.0	347.5	294.6	
E	276.0	330.4	323.2	297.1	349.2	
HF	319.4	326.2	315.2	347.3	286.9	
Controls	377.3	355.1	282.7	364.5	346.0	14.6
			Total dry matter (g per plot)			
Ac	653.1	721.7	644.9	771.4	749.0	
Al	714.5	647.6	680.2	751.8	738.7	
D	675.1	646.0	540.8	751.4	603.3	
E	690.7	692.7	693.6	698.1	762.3	
HF	680.1	707.4	663.3	735.3	635.7	
Controls	801.8	821.3	571.4	752.6	714.8	29.2
			Harvest Index (%)			
Ac	37.1	42.4	43.9	42.7	47.6	
Al	47.1	40.2	48.2	45.8	46.7	
D	44.9	49.3	46.7	46.4	48.7	
E	39.7	47.6	46.5	42.6	45.8	
HF	47.0	46.0	47.5	47.3	46.1	
Controls	47.4	46.9	49.7	48.8	48.7	1.0
			Pods per plant			
Ac	9.5	9.6	10.1	9.7	13.0	
Al	11.6	9.1	10.7	9.7	12.2	
D	10.8	10.5	9.5	9.3	10.7	
E	8.0	9.6	9.0	9.1	10.2	
HF	11.5	11.0	11.0	10.0	12.0	
Controls	12.6	10.5	10.0	9.7	10.5	0.5
			Seeds per pod			
Ac	3.6	4.1	3.3	4.0	3.6	
Al	3.8	3.7	3.5	3.8	3.6	
D	3.4	3.6	2.8	3.9	3.4	
E	3.9	3.8	3.4	3.4	3.8	
HF	3.7	3.6	3.3	3.8	3.4	
Controls	3.7	3.5	3.4	3.9	3.6	0.1

APPENDIX TABLE 3. (continued)

Female parent	Male parent					Standard error
	Ac	Al	D	E	HF	
			1000 Seed weight (g)			
Ac	334.3	379.5	382.7	405.7	353.0	
Al	344.7	365.0	405.2	434.8	366.8	
D	384.2	402.2	436.6	471.2	384.8	
E	412.0	419.0	449.3	446.3	417.0	
HF	356.7	381.6	406.3	424.8	325.4	
Controls	377.3	451.7	384.8	447.7	422.5	5.9
			Emergence to flowering (days)			
Ac	36.7	34.2	31.2	34.0	33.2	
Al	33.7	32.8	30.2	32.5	32.5	
D	30.3	29.2	29.2	30.6	29.0	
E	35.2	32.8	30.8	35.3	33.3	
HF	32.8	32.7	29.0	32.7	31.2	
Controls	31.7	31.5	29.3	32.2	29.5	0.4
			Flowering to maturity (days)			
Ac	37.0	38.3	40.0	38.3	37.7	
Al	38.3	40.0	40.7	40.3	38.7	
D	40.7	41.0	41.8	41.3	40.3	
E	36.7	39.7	41.0	37.0	37.3	
HF	38.3	40.3	40.3	38.3	38.0	
Controls	41.5	41.7	40.3	40.0	40.7	0.5
			Emergence to maturity (days)			
Ac	73.7	72.5	70.8	73.0	70.8	
Al	72.0	72.8	70.5	72.8	71.2	
D	71.0	70.8	72.0	71.7	69.3	
E	71.8	71.8	70.7	72.3	70.7	
HF	71.2	73.0	69.3	71.0	69.2	
Controls	73.0	73.2	69.7	72.2	70.3	0.4
			Fertile stalks per plant			
Ac	1.4	1.4	1.4	1.3	1.5	
Al	1.2	1.4	1.3	1.5	1.4	
D	1.4	1.3	1.3	1.2	1.3	
E	1.3	1.3	1.2	1.3	1.4	
HF	1.4	1.4	1.2	1.2	1.2	
Controls	1.3	1.3	1.4	1.2	1.2	0.1

APPENDIX TABLE 3. (continued)

Female parent	Male parent					Standard error
	Ac	Al	D	E	HF	
			Height (cm)			
Ac	99.2	108.3	105.0	110.8	107.5	
Al	105.0	105.0	100.8	105.0	105.8	
D	105.8	103.3	101.0	107.5	105.0	
E	110.0	106.7	105.0	105.8	111.7	
HF	109.2	102.5	107.5	112.5	110.4	
Controls	107.5	108.3	91.7	106.7	105.0	1.9
			First podded node			
Ac	8.5	7.3	6.3	9.0	7.5	
Al	6.8	6.2	5.3	7.8	7.2	
D	5.8	5.8	5.9	7.0	6.0	
E	8.8	7.7	6.5	8.7	8.3	
HF	8.2	6.5	5.3	7.8	7.2	
Controls	7.0	6.8	5.5	7.0	6.0	0.3
			Protein (%)			
Ac	31.9	31.5	33.2	31.2	30.0	
Al	28.6	28.5	31.0	30.7	28.5	
D	33.1	31.3	36.4	33.1	32.0	
E	32.0	30.3	33.8	32.3	31.3	
HF	30.0	28.8	32.6	30.5	28.4	
Controls	30.3	30.7	31.3	30.2	30.5	0.3

APPENDIX TABLE 4. Analyses of variance for characters studied in the F_2 complete diallel.

Source of Variation	df	Mean squares					
		YIELD	TDM	HI	PD/PLT	S/PD	MSWT
Diallel entries	24	4913.79***	14079.06***	48.41***	7.91***	0.29***	7712.26***
Crosses	19	3030.18**	12156.32**	33.66***	8.09***	0.27***	6315.10***
Parents	4	2983.50	20016.75**	94.28***	9.05***	0.59***	19421.75***
Crosses versus parents	1	71557.50***	112978.70***	297.43***	7.59*	1.65***	7350.00***
Blocks	5	6490.64***	22749.37**	7.35	11.62***	0.11[c]	1437.83***
Error	116	1417.33[a]	5534.27[a]	5.42[b]	1.56[a]	0.06[d]	225.60[b]
Controls	4	8222.16***	58492.62***	7.58	7.44***	0.21*	7218.87***
Crosses versus controls	1	10407.81**	20452.20	108.75***	1.66	0.03	7428.68***
Parents versus controls	1	73114.80***	123710.61***	402.19***	8.93*	0.59**	15845.86***
Coefficient of variation (%)		11.97	10.74	5.12	12.12	6.64	3.79

Source of Variation	df	Mean squares						
		FLR	FMAT	MAT	STK/PLT	HT	FPN	PRO
Diallel entries	24	24.58***	13.08***	8.16***	0.03	65.43***	7.23***	18.05***
Crosses	19	20.03***	11.68***	6.58***	0.04	55.71**	7.23***	14.31***
Parents	4	57.42***	25.99***	17.41***	0.04	117.19***	9.85***	64.50***
Crosses versus parents	1	24.40***	9.43*	11.76***	0.00	152.80*	1.21	2.48*
Blocks	5	0.85	3.02	1.27	0.11*	129.94***	2.05**	2.14*
Error	116	0.92[e]	1.70[e]	1.03[e]	0.04[e]	24.17	0.53	0.67[b]
Controls	4	10.42***	2.93	14.20***	0.06	286.67***	2.78***	1.03
Crosses versus controls	1	31.41***	48.38***	3.02	0.04	204.17**	8.40***	7.98***
Parents versus controls	1	65.07***	56.81***	1.29	0.03	2.86	9.06***	10.24***
Coefficient of variation (%)		2.97	3.33	1.42	14.55	4.62	10.20	2.64

* ** ***Significant at P = .05, .01 and .001 respectively.
[a]With 110 df.
[b]With 112 df.
[c]With 4 df.
[d]With 91 df.
[e]With 111 df.

APPENDIX TABLE 5. Mean raw data from F_1 cultivar diallel.

Female parent	Male parent					Standard error
	E	D	Al	Ac	HF	
			Yield (g per plot)			
E	306.1					
D	361.8	314.9				
Al	306.8	339.3	362.5			
Ac	388.0	303.4	388.2	330.4		
HF	440.6	456.7	364.4	370.8	322.4	31.2
			Total dry matter (g per plot)			
E	664.0					
D	760.3	625.0				
Al	711.0	741.8	740.0			
Ac	862.8	624.8	833.2	709.1		
HF	829.2	860.7	746.1	744.8	715.5	56.6
			Harvest index (%)			
E	46.2					
D	47.6	50.3				
Al	43.5	45.0	49.0			
Ac	45.0	48.9	46.7	46.8		
HF	53.3	53.0	49.0	49.9	44.9	1.6
			Pods per plant			
E	18.0					
D	21.7	24.7				
Al	16.0	20.1	21.9			
Ac	25.0	21.7	22.7	24.0		
HF	25.2	28.9	22.2	23.3	20.7	1.8
			Seeds per pod			
E	3.7					
D	3.7	3.3				
Al	3.8	3.9	3.7			
Ac	3.3	3.5	4.0	3.4		
HF	3.8	3.7	3.5	3.6	3.6	0.2
			1000 Seed weight (g)			
E	459.3					
D	453.0	387.0				
Al	509.0	424.3	452.7			
Ac	475.0	397.0	428.3	402.3		
HF	459.0	429.7	465.3	438.0	434.3	9.2

APPENDIX TABLE 5. (continued)

Female parent	Male parent					Standard error
	E	D	AI	Ac	HF	
	Emergence to flowering (days)					
E	32.0					
D	29.0	29.3				
AI	29.3	27.0	30.3			
Ac	30.7	28.3	33.3	30.3		
HF	30.7	28.7	29.7	30.7	29.0	0.9
	Flowering to maturity (days)					
E	40.7					
D	44.0	42.7				
AI	42.7	42.7	44.7			
Ac	42.7	42.0	40.0	43.3		
HF	41.3	42.7	43.3	42.7	43.3	1.0
	Emergence to maturity (days)					
E	72.7					
D	73.0	72.0				
AI	72.0	69.7	75.0			
Ac	73.3	70.3	73.3	73.7		
HF	72.0	71.3	73.0	73.3	72.3	0.9
	Fertile stalks per plant					
E	1.5					
D	2.3	2.4				
AI	2.0	2.6	2.5			
Ac	1.9	2.1	2.5	2.0		
HF	2.1	2.4	2.3	1.9	1.7	0.2
	Height (cm)					
E	110.0					
D	101.7	93.3				
AI	109.9	103.3	106.7			
Ac	113.3	103.3	105.0	106.7		
HF	110.0	105.0	108.3	108.3	108.3	2.2
	First podded node					
E	8.1					
D	6.3	5.6				
AI	8.0	6.5	7.5			
Ac	7.1	6.4	7.6	7.0		
HF	6.5	5.8	6.7	6.9	7.1	0.3
	Protein (%)					
E	30.5					
D	30.4	32.3				
AI	29.9	30.7	31.0			
Ac	30.1	30.7	30.5	29.9		
HF	31.3	30.7	30.2	29.9	30.4	0.5

APPENDIX TABLE 6. Analyses of variance for characters studied in the F_1 cultivar diallel.

Source of Variation	df	Mean squares					
		YIELD	TDM	HI	PD/PLT	S/PD	MSWT
Diallel entries	14	6676.07*	17393.14	25.65**	29.30**	0.12	3059.57***
Crosses	9	7535.03*	17001.57	32.83**	34.96**	0.13	2959.59***
Parents	4	1409.25	6315.75	14.54	22.17	0.08	2974.75***
Crosses versus parents	1	20012.66*	65226.79*	5.48	6.89	0.22	4298.70***
Blocks	2	21502.00**	128536.00***	15.97	94.36***	0.00	112.00
Error	28	2913.07	9615.43	7.83	9.35	0.12	255.68
Coefficient of variation (%)		15.12	13.17	5.84	13.65	9.39	3.62

Source of Variation	df	Mean squares						
		FLR	FMAT	MAT	STK/PLT	HT	FPN	PRO
Diallel entries	14	7.08**	4.36	5.38*	0.31**	66.00***	1.61***	1.17
Crosses	9	8.95**	3.62	5.28	0.19	41.38*	1.31**	0.65
Parents	4	4.10	6.40	4.44	0.59***	133.33***	2.49***	2.48*
Crosses versus parents	1	2.18	2.84	10.00	0.36	33.12	0.77	1.39
Blocks	2	1.09	1.16	4.47	2.05***	2.26	0.43	0.89
Error	28	2.18	2.77	2.61	0.09	15.26[a]	0.32	0.65[a]
Coefficient of variation (%)		4.94	3.91	2.23	14.03	3.61	8.27	2.60

* ** ***Significant at P = .05, .01 and .001 respectively.
[a]With 27 df.

APPENDIX TABLE 7. Summary of Wr/Vr regression coefficients and mean squares from Wr-Vr analyses of variance for characters studied in the F_1 complete diallel.

Character	Wr/Vr Regression coefficient[a]	Source of variation and df from Wr-Vr ANOVA		
		Arrays 4	Blocks 5	Error 20
YIELD	1.03 ± 0.21**	2391744.00	9233715.00	4412211.00
TDM	0.85 ± 0.20*	63849600.00	98413310.00[b]	51726170.00[c]
HI	0.80 ± 0.21*	60.29	282.44+++	34.42
PD/PLT	1.14 ± 0.33*	115.64	137.01	63.34
S/PD	0.92 ± 0.12**	0.0001	0.0043+++	0.0007
MSWT	1.13 ± 0.07***	49712.00	543004.70+++	33425.59
FLR	1.00 ± 0.02***	0.02	1.43+++	0.07
FMAT	0.96 ± 0.09**	0.55	4.19+++	0.38
MAT	0.98 ± 0.34*	0.70	0.84+	0.30
STK/PLT	0.78 ± 0.16**	0.0007	0.0007[b]	0.0009[c]
HT	0.79 ± 0.18*	13.26	1070.91+++	84.83
FPN	0.53 ± 0.27	0.12++	0.68+++	0.02
PRO	1.06 ± 0.10***	0.22	6.07++	0.23

* ** *** Significantly different from zero at P = .05, .01 and .001 respectively.
\+ ++ +++ Significant at P = .05, .01 and .001 respectively.
[a]All regression coefficients were non-significantly different from one.
[b]With 4 df.
[c]With 16 df.

APPENDIX TABLE 8. Summary of Wr/Vr regression coefficients and mean squares from Wr-Vr analyses of variance for characters studied in the F_2 complete diallel.

Character	Wr/Vr Regression coefficient[a]	Source of variation and df from Wr-Vr ANOVA		
		Arrays 4	Blocks 5	Error 20
YIELD	0.84 ± 0.16**	242312.00	3995424.00+++	416264.70
TDM	0.96 ± 0.10**	10211910.00	29797130.00++	5787717.00
HI	0.78 ± 0.07**	9.44	11.71	14.76
PD/PLT	0.67 ± 0.16*	1.05	2.48	1.01
S/PD	0.86 ± 0.15**	0.0012	0.0026[b]	0.0012[c]
MSWT	0.98 ± 0.06***	9139.00	403822.30+++	4901.70
FLR	1.01 ± 0.04***	0.09	2.20+++	0.13
FMAT	0.97 ± 0.13**	1.72	5.19++	0.99
MAT	0.95 ± 0.49	1.91+++	1.27+++	0.18
HT	0.97 ± 0.14**	75.00	620.74++	117.48
FPN	0.88 ± 0.09**	0.04	0.59+++	0.06
PRO	1.01 ± 0.07***	0.23	0.41+	0.10

* ** *** Significantly different from zero at P = .05, .01 and .001 respectively.
+ ++ +++ Significant at P = .05, .01 and .001 respectively.
[a]All regression coefficients were non-significantly different from one.
[b]With 4 df.
[c]With 16 df.