HETEROSIS IN PEAS
(*Pisum sativum* L.)

by

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Declaration

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Summary

This project sought to determine the level of heterosis in F_1 hybrids amongst a diverse set of genotypes to provide a measure of the potential for yield improvement in peas (*Pisum sativum* L.). The genetic diversity between parents was evaluated in various ways and its usefulness as a predictor of the levels of F_1 heterosis was tested. The proportion of the observed heterosis which could be fixed in pure-line derivatives of the better F_1 hybrids was determined as a means of estimating the potential yield increase in peas achievable by traditional breeding procedures.

To determine the levels of heterosis in F_1 hybrids, four current commercial varieties of pea from southern Australia were used as female parents and crossed with 18 introduced genotypes so 72 F_1 hybrids were produced. F_1 seeds of all crosses were grown in the glasshouse during summer 1989, but only 54 crosses produced sufficient seed for F_2 studies. Twenty-two parents, 72 F_1 hybrids and 54 F_2 families were grown in replicated plots in four environments. Grain yield, plant weight, harvest index, branches per plant, podded nodes per plant, pods per plant, seeds per pod, hundred seed weight, plant height, onset of flowering and flowering period were evaluated.

Most hybrids were higher yielding than their mid-parent but were less stable in yield across environments. Four hybrids were significantly higher yielding than the best parent, by up to 26%. There were significant correlations between F_1 and mid-parent value for plant height, podded nodes per plant, pods per plant and hundred seed weight but not for yield.

Overall, grain yield heterosis was mainly due to more pods per plant in the hybrids. The level of heterosis for yield in a poor yielding environment was higher than that in a high yielding one. Both additive and non-additive gene effects were important in the expression of all studied traits. The level of heterosis for grain yield and plant weight in F_2 was half of that in F_1. The level of inbreeding depression from F_1 to F_2 suggested that epistatic gene action also contributed to the expression of grain yield.

F_5 seeds from six highly heterotic F_1s were produced to determine the fixability of the superior performance of F_1 hybrids in pure-line derivatives. For each cross, 24-31 F_5 lines derived from single seed descent were compared with F_1 hybrids and their parents in two environments. The F_1s out-yielded the best parent by 1 to 11%. All crosses produced F_5 lines which were as high in yield as the F_1 indicating that pure-line derivatives equivalent in yield to the heterotic F_1 could be developed by conventional breeding.

To elucidate the relationship of the genetic distance between parental lines to the level of heterosis in their F_1s, the genetic distance between each pair of parents was estimated, using in turn isozyme markers, morphological polymorphisms, quantitative traits and finally a combination of isozyme markers and morphological polymorphisms. Genetic distance was moderately correlated with the level of heterosis for yield over mid-parent, but not significantly with heterosis over the better or best parent. It was, however, ~~highly~~ significantly correlated with all three measures of heterosis for pods per plant and hundred seed weight.

It is concluded that it is possible, although it may not be easy, to obtain F_1 hybrids showing superiority to outstanding commercial varieties. Highly heterotic hybrids can be used to derive pure lines with equally good yield. Genetic distance between lines can be estimated using quantitative traits, isozyme markers or the combination of isozyme markers and morphological characters, depending on the available facilities and preference of the breeders. The genetic distance separating parents, however, should not be the sole criterion for selection. Parental lines to be used in hybridization should perform well for yield and its components and also be genetically distant. There is considerable potential for optimising choice of parental combinations in the development of improved pea cultivars.

Chapter 1 Introduction

The field pea (*Pisum sativum* L.) is the most important grain legume crop in south eastern Australia (New South Wales, Victoria and South Australia). The area sown to peas has increased greatly over the last decade, from 33 000 ha in 1982 (BAE, 1987) to 445 500 ha in 1991-92 (ABARE, 1992).

Interest in field peas has increased for two reasons. First, they are a good source of cash income. In recent years the expansion in the intensive livestock industries, both in Australia and overseas, has stimulated demand for field peas as a cost-effective alternative to other sources of energy and protein. In addition, export markets for peas for human consumption have opened up in India, Europe and the Middle East.

Second, they are a useful break crop for cereals. Rotation of peas with cereals can reduce disease, and enhance the control of grassy weeds and thus help control root diseases in cereals (Ali, 1987). In addition, peas reduce the need for N fertilizers in the overall farming system.

Nevertheless, pea production is hampered by several problems. In particular

i) the yield of current pea cultivars is relatively low. In the Netherlands, it is estimated that dried peas have a yield potential of 7.5 to 8 t/ha (Dantuma, 1983) while the recommended cultivars in Australia have an average yield of less than 2 t/ha (ABARE, 1991). Furthermore, in Australia the average grain yield of peas is less than that of a range of other cereals and grain legumes including wheat, barley, peanut and soybean. However, the relative yield varies greatly with both locality and season.

ii) peas are susceptible to drought stress at flowering and pod filling stages and have a reputation for being "less reliable", in terms of yield variation from year to year and across sites, than cereals.

iii) all current cultivars are susceptible to the pea weevil and several fungal diseases such as black-spot complex (*Mycosphaerella pinodes* (Berk. and Blox.) Vestergr. and *Phoma medicaginis* var. *pinodella* (L.K. Jones) Boerema), downy mildew (*Peronospora viciae* (Berk.) Casp.) and powdery mildew (*Erysiphe pisi* DC.).

The major task facing pea breeders is to overcome these problems and to develop varieties that produce high and stable yields in the water-limited environments that constitute the major pea producing areas of southeastern Australia. Two principal approaches "traditional" and "ideotype", have been adopted in the past in pea breeding programmes. In the traditional approach, the basic philosophy is to cross amongst the best varieties, then select for the best segregants among the progenies, usually by pedigree or bulk selection. The main criterion used for selection is high yielding ability in the derived homozygous lines. This approach has been the mainstay of efforts to improve peas in South Australia. Alma and Wirrega, two important current commercial cultivars, were developed using this approach by the Department of Agriculture of South Australia.

The "ideotype" approach involves the definition, from a knowledge of the agronomy and physiology of a crop, of the idealized genotype for a given environment. The aim of defining an ideotype is to develop a plant which has high photosynthetic capacity and the ability to translate this into grain yield. Ideotype breeding in peas has been undertaken in Victoria and to a lesser extent in South Australia. Cultivars released by these programmes include Dinkum and Maitland, both semi-leafless cultivars. However, despite the efforts of breeders, varieties already in cultivation such as Early Dun, Dundale and Derrimut have continued to be widely grown because of their relatively high and consistent yields. This suggests that there is a pressing need for effective alternative breeding strategies to improve pea yields under Australian conditions.

One promising alternative approach is the exploitation of the fixable components of F_1 hybrid vigour or heterosis in pure-line cultivars. Heterosis can be exploited in crops using F_1 hybrid varieties. To date, the direct exploitation of heterosis in commercial hybrids is restricted to a very limited range of field crops (corn, sorghum, sunflower and rice and to a lesser extent canola and wheat). The major factor restricting the use of hybrid varieties to a few crops is the lack of the appropriate technologies for the production of hybrid seeds. This is especially true for self-pollinated crops. As an alternative, it is possible to exploit heterosis indirectly in breeding programmes by using the level of heterosis in F_1 hybrids as an indicator of crosses that are likely to generate elite transgressive lines.

It is now well established that the level of heterosis in F_1s depends on the combining ability of their parents (Gritton, 1975; Mak and Yap, 1977; Kaw and Menon, 1979; Venkateswarlu and Singh, 1981; Narula, 1984) and results from both additive and non-additive gene effects. Additive gene effects which are potentially fixable in segregants of heterotic F_1 plants are therefore worthy of study to determine what proportion of hybrid vigour can be fixed in pure-line varieties. Under this approach, the aim is to select F_1 hybrids which show high and stable yield in a range of environments. Once such hybrids are identified, the next step is to select those hybrids that generate superior lines at high frequency.

Field studies are required to obtain meaningful estimates of heterosis of relevance to the plant breeder. Such studies are expensive and time-consuming because of genotype-environment interactions and the need to use multiple sites and seasons. Nevertheless, a range of studies have shown that the level of heterosis of F_1 hybrids increases as the genetic distance between their parents increases (Murty and Anand, 1966; Moll *et al.*, 1965; Sriwatanapongse and Wilsie, 1968; Khanna and Misra, 1977; Ghaderi *et al.*, 1984; Singh and Ramanujam, 1981; Lefort-Buson *et al.*, 1986; Mittal *et al.*, 1987). This finding suggests that it may be possible to develop a preliminary screen for highly heterotic combinations by measuring the degree of genetic distance between parental lines. To do this requires a simple, reliable and inexpensive method of measuring genetic distance. The most reliable measure would be one based on a comparison of the DNA sequence of the entire genome amongst individuals, but this is not feasible at the present time. Analysis of specific DNA sequences is possible but is relatively difficult and expensive. A range of measures of genetic diversity have been developed based on different sorts of genetic loci which have potential in terms of estimating genetic distance between lines and hence combining ability.

A better understanding of heterosis and its underlying genetic control may lead to greater opportunities for its manipulation by plant breeders. In particular a better understanding of gene action of heterosis for yield and yield components may allow breeders of self-pollinated crops to identify those traits responsible for high yield in F_1 hybrids and to better exploit these traits in plant breeding.

In light of the above, this project was developed with the following aims:-

1. To determine the level of heterosis in F_1 hybrids amongst a diverse set of pea genotypes. These data will provide a measure of the potential for yield improvement in peas.

2. To investigate the relationship between F_1 heterosis and levels of genetic diversity between parents as well as to assess the values of various measures of genetic diversity between parents in predicting F_1 performance.
3. To estimate the proportion of the observed heterosis fixable in pure-line derivatives of the better F_1 hybrids. These data will provide an estimate of the fraction of the potential yield increase in peas which can be readily exploited by traditional breeding procedures.
4. To assess the genetic and morphological factors contributing to heterosis in peas. The results of this study will provide the information needed to improve predictions of which crosses would give highly heterotic F_1 hybrids and which progenies from these hybrids would give high yields.

Chapter 2 Literature review

2.1 The level of heterosis in inbreeding species

The level of heterosis has been studied in a wide range of crops. Emphasis has been given to studies of partially or predominantly out-breeding species, particularly those crops such as corn, sorghum, pearl millet and sunflower where heterosis is exploited commercially using F_1 hybrid varieties. Nevertheless, in recent years, increasing attention has been given to studies of heterosis in inbreeding species. Such studies have been motivated in part by the possibility of developing effective systems for the commercial exploitation of heterosis via F_1 hybrid varieties in such species. Obvious examples are rice and wheat. These studies have also been motivated in part by the potential for using yield data of F_1 hybrids and their progenies in selecting crosses. Breeders can then choose to give priority to deserving crosses from the usually very large number of potential crosses they can make.

2.1.1 Heterosis for yield

The level of heterosis has been found to vary widely both within and between crops. In this review, emphasis will be given to predominantly inbreeding species, and in particular, data from cereals and legume crops (Table 2.1) will be compared with the limited amount of data available for peas (Table 2.2).

The available reports indicate that heterosis is a widespread phenomenon in both cereals and legumes. Indeed, in terms of increased yields over the mid-parent value, heterotic F_1 hybrids have been found in every experiment. On average, approximately half of the hybrids showed heterosis over either their mid-parent and/or better parent. Further analysis of the data for cereals, legumes and peas showed that legumes in general, including peas, gave higher proportions of heterotic hybrids than cereals (Table 2.3). There were 59%, 82% and 88% of hybrids showing positive heterosis over mid-parent yields in cereals, grain legumes excluding peas, and peas, respectively. The low proportion of heterotic hybrids in cereals may be due to the fact that cereals have been

Table 2.1 Number of crosses showing heterosis and the amount of heterosis shown in F_1 hybrids of predominantly inbreeding cereals and legumes (other than peas)

Crop	Reference	Number of F_1s				Remarks
		Analysed	< MP	> MP	> BP/ BCC	(Heterosis levels)
Cereals						
Barley (*Hordeum vulgare* L.)	Gebrekidan and Rasmusson, 1970	27				-26 to 47% > BP, mean 11%
Oat (*Avena sativa* L.)	Murphy, 1966	72			49	to 133% > MP, to 114% > BP
Rice (*Oryza sativa* L.)	Virmani *et al.*, 1982	127			90	0.5 to 59% > BP
	Panwar *et al.*, 1983	45			19	34 to 50% > BP
	Peng *et al.*, 1988	75	44	31		-44 to 156% > MP, mean 34%
Wheat (*Triticum aestivum* (L.) emend Thell.)	Sikka *et al.*, 1959	12	0	12		119 to 231% > MP
	Fonseca and Patterson, 1968	21	0	21	19	Combined from two years
	Wells and Lay, 1970					
	1st year	44			33	to 63% > MP
	2nd year	44			27	to 61% > MP
	Sun *et al.*, 1972					
	1st year	5	0	5	1	1 to 31% > MP
	2nd year	5	0	5	1	2 to 14% > MP
	Mani and Rao, 1975	55			24	43 to 54% > BP
	Sindhu and Singh, 1975	15			8*	* > BCC -52 to 46% > MP
	Malik *et al.*, 1981	10	0	10	10	1 to 54% > MP, mean 33%; -9 to 42% > BP, mean 31 %
	Narula, 1984					
	High fertility	36	19	17	8	to 20% > MP, to 11% > BP
	Moderate fertility	36	20	16	4	to 29% > MP, to 13% > BP
	Low fertility	36	11	25	21	to 31% > MP, to 23% > BP
	Gautam and Jain, 1985	21	11	10	8	90 to 238% > BP for top 7 hybrids
	Uddin, 1991	8	1	7	7	-4.1 to 31.5% over MP 6.1 to 26.8% over BP
Legumes (other than peas)						
Long bean (*Vigna sesquipedalis* L.)	Mak and Yap, 1977	42				-21 to 18% > MP, mean 2%; -22 to 10% > BP
Common bean (*Phaseolus vulgaris* L.)	Foolad and Bassiri, 1983	12	0	12	10	-3 to 105% > BP, mean 37%
Mung bean (*Vigna radiata* L.)	Ramanujam *et al.*, 1974	25	7	18		
	Mittal *et al.*, 1987	28	1	27		-10 to 212% > MP
Peanut (*Arachis hypogaea* L.)	Parker *et al.*, 1970	15	0	15		96 to 140% > MP
	Isleib and Wynne, 1983	28	6	22		-2.7 to 58.3% > MP
Soybean (*Glycine max* L.)	Leffel and Weiss, 1958	45	19	26	14	
	Paschal and Wilcox, 1975	30	0	30	24	combined from 2 years mean 8% > BP
	Kaw and Menon, 1979	45	8	12	25	-33 to 57% > BP, mean 17%
	Nelson and Bernard, 1984	27	5	18	14	to 19% > BP

MP: Mid-parent, BP: Better parent, BCC: The best parent or best commercial cultivar.
Gaps indicate data not available.

Table 2.2 Number of crosses showing heterosis and the amount of heterosis shown in F_1 hybrids of peas

Reference	Number of F_1s				Levels of heterosis
	Analysed	< MP	> MP	> BP/ BCC	
Gritton, 1975	28			13	mean 55% > MP; mean 28% > BP
Singh *et al*., 1975	10	2	8	8	to 147% > MP; to 86% > BP
Singh *et al*., 1978	30	5	25	24	to 91% > MP; to 88% > BP
Narsinghani and Singh, 1979	36	7	29	19	to 215% > MP; to 108% > BP
Venkateswarlu and Singh, 1981	45	3	42	27	mean 47% > MP; mean 22% > BP
Rao and Narsinghani, 1987	23	0	23	23	10 to 126% > MP, mean 49% 1.3 to 91% > BP, mean 25%

MP: Mid-parent, BP: Better parent, BCC: The best parent or best commercial cultivar
Gaps indicate data not available.

bred more intensively for yield over a longer period of time than legumes. If so, the current pure-line varieties of these species would more closely approach the yield potential of heterotic hybrids.

The level of heterosis has also been found to differ in different studies within each species, presumably because of the differences in the genetic background of the parental lines and/or the test environments used. The level of heterosis in F_1 hybrids has been reported to depend upon both the general and specific combining ability of their parents but general combining ability has usually been found to be the more important (Gritton, 1975; Mak and Yap, 1977; Kaw and Menon, 1979; Venkateswarlu and Singh, 1983; Narula, 1984). It has also been shown to depend on both additive and non-additive gene effects but in inbreeding species additive gene action is predominant. For non-additive gene effects, dominance as well as epistasis was found to influence the expression of heterosis (Leffel and Weiss, 1958; Gritton, 1975; Narula, 1984). Maternal and reciprocal effects were found in a small proportion of hybrids. In some cases there was a positive association between performance *per se* of parents and heterosis (Singh *et al*., 1978; Narula, 1984).

However, Wells and Lay (1970) found no evidence that high yielding pure lines tended to produce high yielding hybrids.

F_1 hybrids which showed high levels of heterosis also generally exhibited high levels of inbreeding depression in F_2. Nevertheless there were notable exceptions to this rule and some highly heterotic hybrids showed only moderate inbreeding depression (Singh *et al.*, 1978). The reduction in heterosis in the F_2 generation is dependent on the level of non-additive rather than additive gene effects. The crosses which exhibit high heterosis but limited inbreeding depression in F_2 are obviously of more interest to the breeder of pure-line varieties of self-pollinated crops.

Table 2.3 Comparison of the proportion of heterotic and non-heterotic hybrids in cereals, grain legumes (other than peas), and peas

Crop	Number of F_1s		
	< MP	> MP	> BP
Cereals	75 (41%)	110 (59%)	NA
Legumes	46 (18%)	209 (82%)	NA
Peas	17 (12%)	127 (88%)	101 (70%)

MP = Mid-parent, BP = Better parent, NA = Not available

2.1.2 Heterosis for yield-related characters

Agronomic characters of grain legumes including peas, such as pods per plant, branches per plant, plant height and pod size showed significant differences in heterosis (Gritton, 1975; Singh *et al.*, 1975, 1978; Foolad and Bassiri, 1983). Most of the studies found that heterosis for pod number per plant was higher than for seed weight or seeds per plant (Mak and Yap, 1977; Isleib and Wynne, 1983; Foolad and Bassiri, 1983). The number of days from sowing to flowering and hundred seed weight showed negative heterosis (Foolad and Bassiri, 1983). A separate study of the components of heterosis in peas also found no heterosis for days to flowering, while the level of heterosis for pods per plant was higher than heterosis for seeds per pod and seed weight respectively (Gritton, 1975).

In contrast, Kaw and Menon (1979) reported that the level of heterosis in soybeans for seeds per pod (12.4%) was slightly higher than the levels for pods per plant (6.5%). Venkateswarlu and Singh (1981), who studied heterosis in 45 F_1 combinations, found that the level of heterosis for pods per plant based on mid-parent values (41%) was lower than that for hundred seed weight (76%).

In cereals, all yield components generally show heterosis, but different characters often manifest different levels (Gautam and Jain, 1985). For example, Fonseca and Patterson (1968) found that the levels of heterosis for spikes per hill and kernels per spike were low while heterosis for kernel weight was high. There was disagreement amongst authors with respect to the association between the level of heterosis for yield and those for its components. Murphy (1966), working with oats, found heterosis for yield was positively associated with heterosis for panicles per plant and seeds per panicle but negatively associated with weight per seed. Panwar *et al.* (1983) reported that heterosis for grain yield in rice was obviously due to an increase in one or more components of yield but that hybrids showing heterosis for grain yield were not heterotic for all characters. For example, plant height and onset of flowering of F_1 hybrids tended to be intermediate between their parental values. They concluded that the absence of desirable heterosis for grain yield in some of the crosses seemed to be due to the absence of desirable heterosis for important yield components such as grains per panicle.

2.1.3 Environmental effects on heterosis

A number of studies has shown that estimates of heterosis are influenced by the environment in which the hybrids are grown (Pederson, 1968; Griffing and Zsiros, 1971; Sun *et al.*, 1972; Jošt and Hayward, 1980; Hofmann *et al.*, 1984; Narula, 1984; Uddin, 1991). Griffing and Zsiros (1971) who studied the impact of genotype-environment interactions on levels of heterosis in *Arabidopsis thaliana* reported that the expression of heterosis was affected by temperature, nutrition and also by plant density. The level of heterosis can also be influenced by planting method. For example, Fonseca and Patterson (1968) found that the degree of hybrid vigour was greater for hill seeding than for normal seeding. Similarly, Severson and Rasmusson (1968) who conducted an experiment with barley hybrids sown at four rates (within-row spacings of 2.5, 7.5, 10.0 and 22.5 cm with 30.5 cm between rows) found that heterosis for yield and its components increased consistently with wider spacing.

Jošt and Hayward (1980) found that heterotic effects in common winter wheat F_1s were greater in a stress environment, mainly because of the poor winter hardiness. Narula (1984) also reported that the degree of heterosis in bread wheat hybrids was higher under stress conditions caused by low fertility and late sowing than under non-stress conditions. The average level of heterosis over mid-parent with a normal sowing date and high fertility was 20.0% while levels from a normal sowing date with low fertility and a late sowing date with moderate fertility were 31.8% and 29.2%, respectively.

Since heterosis is a relative measure, the magnitude of its expression depends not only on the performance of a hybrid but also on the performance of its parents. Therefore, differences in the level of heterosis across environments may result from the differences between hybrids and their parents in their responses to those environments. For example, Hofmann *et al.* (1984) reported that sorghum hybrids and their parents showed different responses to soil moisture stress. Similarly, Borghi *et al.*(1988) found in wheat a highly significant genotype x environment interaction for parental varieties but not for F_1 hybrids, concluding that the hybrids were more stable than their parents. Uddin (1991) found that when sown at different dates, wheat hybrids were generally more stable in yield than pure lines, and the highest level of heterosis for yield was observed at the optimum planting time in one year but not in the next.

In contrast, Guenzi *et al.* (1985) found that hybrids were less stable across environmental conditions in a study of three winter wheat hybrids and five pure lines at 59 locations across the USA over two years. Similarly, Johnson and Whittington (1977) compared 8 barley varieties and their 8 hybrids in 16 environments in England and found similar responses for hybrids and varieties to changing environments and little evidence of differences due to G x E interaction, while Zeven (1972) reported no effects of plant density on the expression of heterosis in wheat yield and its components. Finally, Carver *et al.* (1987) carried out an experiment with a large number of F_1 hybrids and pure lines of winter wheat genotypes between 1982 and 1985 to compare yield responses of hybrid and pure-line cultivars across a wide range of environments. They found plant type affected the differences in response between hybrids and pure lines across years.

The use of the F_1 generation as a means of determining the potential for the production of transgressive segregants in later generations has been limited, particularly in peas. If heterosis in the F_1 generation is indicative of the recombination potential of a cross in later generations and F_1 performance along with that of the parental lines can be used to predict the performance of crosses in later generations, then F_1 results would enable the desired ends to be obtained from a hybridization programme with minimum labour and cost. To do this it is important to understand the genetic basis of heterosis.

2.2 Genetic basis of heterosis

Despite many studies over several decades, the genetic basis of heterosis in crop plants remains unresolved and a focus of controversy and debate in the literature. Two main genetic models have been put forward to explain the phenomenon of heterosis (and its converse, inbreeding depression). The first is the "dominance" hypothesis which was first advocated in 1908 by Davenport and later supported by several authors (Gowen, 1952). It assumes that heterosis is caused by the combined action of dominant favourable genes in hybrids. It attributes heterosis to the covering of deleterious recessive genes by their dominant counterparts. Under this model the homozygous dominant genotype at each locus is phenotypically indistinguishable from the heterozygote; that is AA = Aa > aa. The average individual in a population of heterotic hybrids simply has more favourable dominant alleles than its parents. Evidence for the critical role of dominant genes in heterosis has been given by Emerson (1952), Robinson (1952) and Whaley (1952).

The second is the "overdominance" hypothesis which assumes that heterozygosity *per se* is responsible for heterosis. Heterozygotes are expected to be superior to both homozygotes, that is Aa > AA or aa, and this results in the superiority of F_1 hybrids. The overdominance hypothesis was advocated by East (1936). Evidence in support of the overdominance hypothesis has been provided by Robinson *et al.* (1949) and Crow (1952) from studies of grain yield in maize.

Both competing theories of heterosis have been set in the framework of classical Mendelian genetics. They both assume that heterosis results from the summed effects of interactions between alleles at individual loci. Support for each hypothesis has been found in different experimental systems, with the weight of evidence favouring the dominance theory. The absence of evidence of genuine overdominance has been described in detail by Gardner (1963), although he concluded that apparent overdominance due to non-allelic interaction and linkage disequilibrium was a common contributor to heterosis. Gallais (1988) suggested in a review of a range of biometrical analyses that the role of overdominance is likely to be small relative to that of dominance effects. Such analyses, however, may not be sufficiently powerful to identify the role of overdominance if it exists only for a limited set of the many loci governing the quantitative characters determining heterosis.

Stringfield (1950) studied the relationship between the level of heterosis for several traits including grain yield, days from planting to silking, height of ear node and level of heterozygosis in maize. Heterozygosis was assigned a value of zero in an inbred line, 100 for an F_1 cross between unrelated lines (including single crosses, three way crosses and double crosses), and 50 for backcrosses and F_2 populations. He found evidence of an interaction between genes at different loci. However, the expression of hybrid vigour did not follow a linear trend as equal increments of new dominants were added. The deviation from linearity was slight when yield was measured but for the other characters, the regression was curvilinear. Jinks and Jones (1958) concluded that heterosis was a genetically complex phenomenon depending on the balance of additivity, dominance and interaction components (particularly between homozygous/ homozygous and homozygous/ heterozygous gene combinations) of the generation means as well as on the distribution of the genes in the parental lines. It did not depend on the interaction between heterozygous/heterozygous combinations. Murty (1965) reported that epistatic interactions could result in the internal cancellation of some components of heterosis.

In terms of population genetics, Falconer (1964) reported that heterosis depended for its occurrence on dominance. Loci without dominance caused neither inbreeding depression nor heterosis. The amount of heterosis following a cross between two particular lines or populations depended on the square of the difference of gene frequency between the populations. If the populations crossed did not differ in gene frequency, heterosis would not be expected to occur. Heterosis would be greatest when one allele was fixed in one population and the other allele in the other population. Heterosis was defined as the joint effects of all the loci as the sum of their separate contributions:

$$HF_1 = \sum_i d_i y_i^2$$

where d_i is the deviation of heterozygote from the mean of the homozygotes due to dominance at the i^{th} locus, and y_i is the difference of allelic frequency between the two intermated populations at the i^{th} locus and summation is over all loci. Following this theory, the degree of genetic divergence between parents will strongly affect the level of heterosis.

2.2.1 Components of variance

Sprague and Tatum (1942) introduced the terms "general combining ability" (GCA) to designate the average performance of a line in a hybrid combination and "specific combining ability" (SCA) to designate the deviation in performance of a cross from that expected on the basis of the average performance of the parental lines. The hybrid value is the sum of the overall population mean, the GCA of the two parents and the SCA of the parental lines as follows:

$$Y_{ij} = M + g_i + g_j + s_{ij} + r_{ij}$$

where Y_{ij} is the hybrid value between parent i and j

M is the overall mean of the population.

g_i and g_j are the general combining abilities of parents i and j respectively,

s_{ij} is the specific combining ability between parent i and j, and

r_{ij} is the reciprocal effect involving the i^{th} and j^{th} parents.

These components were found to involve a range of genetic effects. Jinks and Jones (1958) suggested that wherever overdominance occurred, non-allelic interactions also occurred. They also concluded that SCA was always associated with the presence of non-allelic interaction while GCA was generally the outcome of simple dominance.

In experimental terms, Griffing (1956) partitioned the total genotypic variance into GCA and SCA components as follows:

$$\sigma^2_{bc} = \sigma^2_{gca} + \sigma^2_{sca}$$

where σ^2_{bc} is the variance between crosses or F_1 variance,

σ^2_{gca} is general combining ability variance and

σ^2_{sca} is specific combining ability variance

The total genotypic variance was partitioned into additive and nonadditive genetic components (Fisher *et al.*, 1932):

$\sigma^2_G = \sigma^2_A + \sigma^2_{NA}$

where σ^2_G is genotypic variance

σ^2_A is additive genetic variance

σ^2_{NA} is non-additive genetic variance

Non-additive genetic variance was partitioned into interaction between alleles at the same locus (σ^2_D) and interaction between alleles at different loci (σ^2_I). The estimation of additive and non-additive genetic components can be made from the experimental material in terms of general and specific combining ability variance (Griffing, 1956):

$\sigma^2_A = 2\sigma^2_{gca}$ and $\sigma^2_D = \sigma^2_{sca}$

The GCA variance contains not only all additive variance (σ^2_A) but also a portion of the epistatic variance (σ^2_I).

The expected level of heterosis can be expressed in terms of the genetic parameters of additivity and dominance (Mather, 1949) and the non-allelic interaction component (Hayman and Mather, 1955). These components of heterosis, or their derivatives, can be estimated using a variety of techniques including the diallel cross method (Griffing, 1956), the various forms of the triple test cross (Kearsy and Jinks, 1968; Jinks and Perkins, 1970) and the method of Chahal and Jinks (1978).

A number of studies in both inbreeding and outbreeding crops, have yielded evidence of the importance of combining ability together with additive and non-additive gene effects on heterosis for a range of characters. For example, Leffel and Weiss (1958) found that both GCA and SCA of parents affected yield per plant, maturity, height and seed size of F_1 hybrids of soybean.

Fasoulas and Allard (1962) studied the relative contributions of additive, dominant and epistatic gene action to the inheritance of eight quantitative characters by intercrossing four homozygous isogenic lines of barley. They found that the additive component was the largest, contributing 65% to the genetic variance in quantitative traits, followed by the epistatic component (32%) and a small dominance component (3%). Sprague *et al.* (1962) studied the effect of epistasis on grain yield in maize and concluded that epistasis may be an important factor for high average combining ability.

Miller and Marani (1963) found the extent of heterosis for yield in cotton was higher in interspecific crosses than in intraspecific crosses. In interspecific crosses, the effects of GCA were most important while the effects of SCA were significant in only a few cases and were not consistent from year to year. This suggested that the main component of genetic variance was the additive component.

Weber *et al.* (1970) studied heterosis, performance and combining ability in soybean and found GCA and SCA effects were significant for yield, maturity and height. Paschal and Wilcox (1975) also found significant differences of GCA effects for all characters in F_1s of soybean. SCA effects were significant for seed size, maturity and height. Mak and Yap (1977) found both GCA and SCA were important for all traits measured in long bean (*Vigna sesquipedalis*) except pod yield where only GCA was significant. They suggested that the main genetic variation was due to non-additive action for pod yield and additive gene action for other traits. Maternal and reciprocal effects were found associated with grain yield heterosis in long bean (Mak and Yap, 1977) and also in rice (Virmani *et al.*, 1982).

Isleib and Wynne (1983) studied heterosis in test crosses of exotic peanut cultivars. They found non-additive gene action expressed by peanut hybrids particularly for pod size and length in intersubspecific crosses. For pod yield all heterotic hybrids showed more dominance than epistasis, but epistasis was the predominant type of action determining heterosis for seed yield.

Combining ability in wheat was studied by Narula (1984) who demonstrated the importance of both additive and non-additive gene action in determining the level of heterosis in F_1 hybrids although additive gene action was predominant. Epistatic effects resulted in the internal cancellation of some components of heterosis in several crosses.

These data lead to the conclusion that the level of heterosis depends on the combining ability of parents. It is the result of both additive and non-additive gene effects, but additive effects are usually predominant. Additive gene effects can be estimated from the GCA variance and non-additive effects from the SCA variance. Non-additive gene effects are partitioned into dominance and epistatic effects.

Heterosis is generally estimated from the phenotypic values of the F_1 hybrids and their parents. The phenotypic value of each individual is a product of both genotypic and environmental effects. Consequently, the phenotypic expression of heterosis is the result of genotype x environment interactions. Jinks (1983) suggested that genotype x environment (G x E) interactions impinge on the study of heterosis at two levels:

1. If parents and hybrids respond differently to environmental change, the magnitude of heterosis will vary with the environment.
2. If genotypes differ in their sensitivity to environmental change because of G x E interaction, then that interaction becomes a character in its own right and may display heterosis.

In several studies the level of heterosis has been found to vary with environmental factors (eg. Narula, 1984) and crop management (eg. Fonseca and Patterson, 1968). The estimated combining ability of parents and genetic effects on heterosis thus may alter with environmental changes. Therefore it is important to grow crops over a range of environments for the estimation of the level of heterosis and genotype-environment interactions for combining ability.

2.3 The fixable proportion of heterosis

The theory and practice of plant breeding has generally developed separately for inbreeding *versus* outbreeding plants. In outbreeding plants, because of the high levels of heterosis and the frequent occurrence of mechanisms preventing self-pollination, breeders have concentrated on the development of hybrid or synthetic varieties. In inbreeding plants, in sharp contrast, emphasis has been given to development of pure-line varieties, in the presence of the restrictions imposed by the breeding system which make the commercial production of F_1 seed difficult. With predominantly self pollinated crops, breeders are therefore interested in identifying parental combinations that are likely to produce superior homozygous segregants.

The suggestion that heterosis may be fixable in pure lines has been based on the assumptions of the dominance and overdominance hypotheses (Jones, 1957). If the assumption is accepted that hybrid vigour results from the accumulation of dominant alleles, then heterosis could be accumulated *via* selection in homozygous genotypes. On the other hand, with overdominance, where heterosis occurs from the reaction of alleles at the same locus, the heterotic effects could only be accumulated in the heterozygous condition and could not be fixed in pure-line varieties.

A number of authors have critically examined the opportunities to fix heterosis in pure-line varieties. For example, Williams (1959) found that much of the superiority of two commercial F_1 hybrids over their parents could be fixed in pure-breeding lines. This supported the earlier work of Smith (1952) with tobacco, who showed that it was possible to develop pure-line varieties from highly heterotic hybrids which perform as well as or even better than the F_1. Later, Andrus (1963) suggested that the superior F_1 which results from concentration and interaction between favourable genes contributed by the two parents may produce highly productive transgressive segregants which approach the F_1 in yield. Singh and Malhotra (1971) studied heterosis for grain yield in interspecific crosses of *Pisum*. They suggested that in the development of high yielding pure lines it was possible to fix the heterosis which resulted from interspecific hybridization.

Hamblin and Evans (1976) studied the relationship between the yield potential of crosses for several generations in common bean (*Phaseolus vulgaris*). They found that when a cross proves to be low yielding in early generations it may safely be rejected without fear of losing potentially high yielding combinations. Paschal and Wilcox (1975) indicated that the predominance of additive genetic variance leads to the successful isolation of high-yielding homozygous lines in later generations.

Jinks (1983) concluded that heterosis arises in general from dominance of alleles of widely dispersed genes, so that it should be possible to extract pure-breeding lines equalling or out-performing the best F_1 hybrids, provided that linkage combinations could be broken. Nevertheless this may take many generations. He suggested that the relative performance of the F_1 and the better homozygous parent must then be one further factor to be considered in choosing between the alternative end products of a breeding programme. He also indicated that if there were incomplete dominance on average over all loci, masking the occurrence of overdominance at the same loci, pure breeding families superior to a heterotic F_1 would be extractable from that F_1.

Interactions between genes at different loci (epistasis) occur in the homozygous as well as in the heterozygous condition (Stringfield, 1950). Isleib and Wynne (1983) found that, if heterosis is due to epistatic gene action (particularly the additive by additive type of epistasis) or to repulsion phase linkage of loci exhibiting partial to complete dominance, it should be possible through selection to fix alleles at the interacting or linked loci to preserve the heterotic effect. Further, Narula (1984) noted that crosses between lines with good GCA are expected to produce desirable segregants in subsequent generations since these involve additive effects and additive x additive interactions. On the other hand, cross combinations between high x low general combiners, showing significant SCA effects, are likely to produce desirable transgressive segregants only if the additive genetic system present in the good combiner and the complementary epistatic effects in the F_1 act in the same direction to maximise the desirable plant attributes.

To date, few studies have been conducted to determine the proportion of hybrid vigour which can be retained in pure lines. Busch *et al*. (1971) compared the F_1 with 90 F_5 wheat lines from each of 3 crosses. They found several F_5 lines in each cross performed significantly better than the F_1, and F_6 lines derived from the best yielding F_5 still performed significantly better than their parental F_5 lines. Similarly, Cregan and Busch (1978) who studied heterosis and pure line performance in adapted spring wheats also found the best F_5 lines were equal to F_1 hybrids. Jošt and Hayward (1980) compared one highly heterotic hybrid and its derivatives in two locations. They found that in the more stressed environment the F_1 hybrid was significantly better than the best F_7 lines, but in the less stressed, two leading F_7 lines gave similar yields to the F_1 hybrids. More recently, Uddin (1991) investigated the potential to develop pure lines with similar yield to the heterotic F_1 hybrids using four hand-made hybrids and a commercial hybrid. Seventy-five F_7 lines derived by single seed descent were compared with their parents and F_1 hybrids in replicated hill plots. All crosses produced pure lines with similar yields to the F_1 hybrids, but there was no consistent pattern amongst the pure lines as to how they achieved their high yield in terms of physiological traits or yield components.

2.4 Measurement of genetic distance

Numerous studies, both theoretical and experimental, indicate that the level of heterosis in F_1 hybrids increases with the degree of genetic differentiation between the parental lines. These studies suggest that it may be possible to develop at least a preliminary screen for highly heterotic combinations by measuring the genetic distance between potential parents. To do this requires a rapid and reliable method of estimating the genetic distance using procedures normally available to plant breeders. The most appropriate measure of genetic difference would be a comparative analysis of the DNA sequence of the entire genome, but this is not feasible at the present time. Consequently, a range of measures of genetic diversity have been developed based on samples of different types of genetic loci.

In this section these measures will be outlined and their relative advantages and disadvantages discussed in relation to different classes of genetic markers (qualitative morphological traits, quantitative characters and enzyme and DNA markers).

2.4.1 Types of characters used in estimating genetic distance

Brown and Weir (1983) discussed the criteria required for an ideal set of marker loci in terms of estimating genetic variability in plant populations:-

1. Allelic expression should be distinguishable in individuals; in particular, heterozygotes should be distinguishable from both homozygotes.
2. The effect of each allelic substitution should be locus-specific and distinguishable from substitutions at other loci.
3. All base substitutions should be detectable.
4. Loci should be sampled at random, irrespective of their function or likely level of polymorphism.

Only the number of nucleotide or codon differences per unit length of DNA meets all these criteria, but this statistic cannot readily be measured at the present time even for a very limited sample of the genome of a species. Consequently scientists generally have to be satisfied with less than the defined ideal. For example, plant breeders have generally used traits of economic importance, other metrical traits, qualitative morphological characters and isozyme markers to measure genetic diversity (Moll *et al.*, 1965; Goodman, 1968; Jain *et al.*, 1975; Ghaderi *et al.*, 1984; Moore and Castle, 1988). Each of these has advantages as well as disadvantages. The best traits or markers to use for the present purposes will depend on their respective advantages and disadvantages and the effectiveness of the derived values in predicting the level of heterosis.

2.4.2 Advantages and disadvantages of each class of trait

a.) Quantitative traits

Measures of genetic diversity based on the variation of quantitative characters are commonly and widely used in biology and plant breeding (Goodman, 1968; Brown *et al.*, 1969; Bhatt, 1970; Khanna and Misra, 1977; Arunachalam, 1981; Shamsuddin, 1985; Souza and Sorrells, 1991a). The advantages of these measures are that (i) many traits are available for use and (ii) they are familiar to plant breeders (Marshall and Brown, 1975). Indeed improvement of such characters, for example yield and yield components, is a major aim of breeders. Genetic diversity can be quantified using multivariate statistical analysis of data from many different characters. Recently, commercially available computer programmes have been developed for this purpose.

Quantitative characters are often controlled by many genes. They are the result of the interaction of the genotype of an individual and the environment. The first disadvantage of measures based on quantitative characters is therefore that they yield only an indirect measure of genetic diversity. Such parameters measure only that portion of the genic variability which is expressed phenotypically. This portion varies markedly with the characters under consideration, their genetic background and the environmental conditions in which it is expressed. Therefore, measures based on quantitative characters may be unreliable indicators of the diversity in a population at the level of the individual gene (Marshall and Brown, 1975). A second disadvantage is that data collection is often a laborious and time-consuming task and requires access to substantial field facilities. A third is correlation between characters. To obtain useful information for estimating genetic diversity, all correlated variables must be transformed to uncorrelated variables.

b.) Qualitative morphological characters

Qualitative morphological characters have also been widely used in crop genetic studies and in measuring genetic distance (Allard and Hansche, 1964; Goodman,1968; Ashri, 1971; Jain *et al.*, 1975; Ghaderi *et al.*, 1984; Moore and Castle, 1988; Singh *et al.*, 1989; Souza and Sorrells, 1991b). Brown (1978) has observed the advantages of these characters: (i) they are usually controlled by a small number of genes and (ii) they are less affected by non-genetic factors than quantitative characters. These characters, such as flower colour, seed colour, leaf type, plant type, flowering habit, pod size and pod shape are easy to score. The obvious advantage of these characters is therefore a rapid classification of a large number of individuals.

Nevertheless such characters represent only a limited fraction of the genome and suffer from the technical problems caused by dominance. The recessive alleles of genes controlling these traits may be deleterious when homozygous. The number of markers may be limited by epistatic and/or pleiotropic effects.

c.) Isozyme markers

Isozymes are variant forms of an enzyme and have substantial advantages over morphological markers in measuring genetic diversity. The use of isozyme markers to estimate genetic distances or to assess genetic variation has been successful in maize (Hunter and Kannenberg, 1971; Heidrich-Sobrinho and Cordeiro, 1975; Price *et al.*, 1986; Frei *et al.*, 1986), soybeans (Gorman and Kiang, 1978), common beans (Bassiri and Adams, 1978), tomatoes (Tanksley *et al.*, 1981), oats and barley (Price *et al.*, 1984), peaches (Arulsekar *et al.*, 1986), green gram (Mittal *et al.*, 1987), citrus species (Moore and Castle, 1988), eucalyptus species (Jane *et al.*, 1988), peas (Przybylska, 1986; Weeden and Marx, 1987; Weeden *et al.*, 1988) and rice (Peng *et al.*, 1988). Isozymes are usually detected using electrophoretic techniques and this allows many individuals to be screened non-destructively and in a relatively short time. Further some properties of isozymes make them especially suitable as genetic markers. Brown and Weir (1983) have summarised their advantages as follows:-

1. They can be used to screen seedlings and this may save considerable time and field space.
2. The equipment and material needed for screening the isozyme banding patterns (zymograms) of plants is relatively inexpensive and it is possible to screen large numbers of plants rapidly.
3. Allelic expression is usually codominant and allows heterozygotes to be distinguished from homozygotes.
4. Each allelic difference is detected as a mobility difference which is independent of the functional role or the overall level of variation of the enzyme in question.

Despite these effective properties, isozyme-based genetic analyses also have a number of limitations. These are:-

1. Genetically or environmentally induced post-translational modification of electrophoretic mobility can occur leading to an over-estimation of genetic distance.
2. In polyploid species, multiple variants can arise through gene duplication and these can lead to difficulties in ascribing variants to single loci.

3. On average, only about 25% of base substitutions result in amino acid replacements which alter the nett charge on a protein and are therefore readily detectable by routine electrophoresis.
4. They consist of only a restricted class of proteins, so that some genetic variation may not be identifiable.
5. Some variants are present only in certain tissues or life stages of plants.
6. Large surveys of some particular enzymes can be time-consuming.

2.4.3 Measures of genetic distance

Several measures have been developed and proposed for quantifying genetic diversity (Rao, 1952; Sokal, 1961; Hanson and Casas, 1968; Hedrick, 1971 and 1975; Goodman, 1972; Rogers, 1972; Nei, 1973; Sneath and Sokal, 1973; Adams, 1977; Cervantes *et al.*, 1978; Rodgers *et al.*, 1983). These measures vary with the types of loci or characters under consideration, but they can be usefully subdivided into two groups - those applicable to quantitative or multigenically controlled traits and those applicable to individually scored marker loci. Each group is considered below.

a.) Multiple gene marker loci (quantitative traits)

A number of methods have been proposed for the estimation of the level of genetic diversity between two populations using quantitative characters. Mostly, such measures have been based on multivariate statistical analyses such as Pearson's coefficient of racial likeness (Pearson, 1926), Mahalanobis distance (Mahalanobis, 1936), Sokal distance (Sokal, 1961) and Euclidean distance (Goodman, 1972). Two examples will be discussed here.

a.1) Mahalanobis distance

Mahalanobis distance has been widely used for the quantitative assessment of genetic divergence in several crops. It has been shown to be particularly useful for grouping or classifying a number of accessions in germplasm collections into groups on the basis of their genetic diversity. Mahalanobis distance is an appropriate measure when traits are correlated. The main disadvantage of this technique is the need for a very large quantity of data if reliable groupings are to be developed (Goodman, 1968). The details of this technique and its application in evaluating genetic diversity have been given by Rao

(1952). Multivariate analysis is concerned with the relationship among sets of dependent variables and the individuals which bear them. To obtain useful information from this, the analysis of variance must first be obtained for all the characters under consideration. Then the variance-covariance (environmental) matrices are tested by Wilkes' criterion to establish whether there is a significant correlation between the variables. Normally no correlation is expected between the environmental portion of the variability unless these variables themselves are correlated. All correlated variables are then transformed to uncorrelated variables by the pivotal condensation method (Rao, 1952). Genetic distances are calculated from these uncorrelated variables by taking the sum of squares of the differences between the pairs of corresponding correlated variables for any of the two populations. The distance between any two groups is estimated from the equation

$$D^2 = (X_i - X_j)' S^{-1}(X_i - X_j)$$

where X_i and X_j are the vectors of means of the traits for the ith and jth groups respectively, and S^{-1} is the inverse of the pooled covariance matrix.

Goodman (1968) used Mahalanobis D^2 to measure the generalized distance between races of maize. Sixteen morphological characters were used in the analysis. Similarly, Prasad and Singh (1986) used this statistic to select 10 parents from 64 varieties of maize belonging to different geographical regions of the world. The observations were recorded on 12 morphological characters.

Lee and Kaltsikes (1973) measured genetic diversity in durum wheat using Mahalanobis distance. Characters used were days to flowering, days to physiological maturity, plant height, lodging and grain yield. The influence of the characters studied in assigning cultivars to particular groups varied from cultivar to cultivar.

Ghaderi *et al.* (1984) estimated genetic distance between common bean (*Phaseolus vulgaris*) and faba bean (*Vicia faba*) parents using 11 traits in dry edible bean and 14 characters in faba bean.

a.2) Euclidean distance

This method is an adaptation of the multivariate technique. Each cultivar may be identified on the basis of a large number of metrical traits as a single point in a standardised multi-dimensional space. The axes of this space are principal components obtained from the original data as orthogonal transformations of the original variates, each principal component being a linear combination of the varietal scores on the original variables. The Euclidean "distance" between any two points represents the degree of similarity or dissimilarity between the two cultivars whose scores on the principal axes determine their respective positions in the hyperspace. When two cultivars are highly related or genetically similar, they are expected to occupy the same region in the hyperspace, the distance between them being small. If they are more remotely related or genetically diverse, the Euclidean distance between their points will be correspondingly greater (Goodman, 1968; Adams, 1977). Adams (1977) used the method based upon the multivariate technique of principal components analysis to calculate a distance between any two cultivars in common bean. He found that such distances were highly inversely correlated with the genetic relationship estimated from a knowledge of breeding ancestry. Isleib and Wynne (1983) used Euclidean distance to determine the extent of the genetic basis for heterosis in crosses between 27 exotic peanut (*Arachis hypogaea* L.) cultivars and an adapted Virginia breeding line. The degree of genetic divergence was estimated from the vegetative and reproductive characters used in the principal component analysis.

b.) Single gene marker loci (qualitative morphological characters and isozyme markers)

Qualitative morphological characters and allele frequency data from isozyme markers can be analysed directly by multivariate analysis, for example principle component analysis (Goodman and Stuber, 1983; Doebley *et al.*, 1984; Smith, 1984; Smith *et al.*, 1984; Souza and Sorrells, 1991b). For inbreeding crops there are two simple measures which have been used to quantify genetic distance between parental lines based on single gene markers but more particularly, isozyme markers. These are the Diversity index of Hunter and Kannenberg (1971) and the Genetic Distance of Nei (1972).

b.1) Diversity index of Hunter and Kannenberg

Hunter and Kannenberg (1971) proposed a simple method to calculate a diversity index from isozyme markers. An isozyme system refers to the alternative isozymes produced within a given segment of a gel, this variation being considered to be controlled at a single locus. When any two inbred lines have different bands within the same system, the parents are said to be different for that system and given a rating of one. Inbreds with identical bands are rated zero for that system. For each pair of inbreds the ratings for all systems studied are totalled and termed the diversity index (DI). Heidrich-Sobrinho and Cordeiro (1975) and Mittal *et al.* (1987) used this method to study the relationship between genetic diversity and heterosis in maize and green gram respectively.

b.2) The genetic distance measure of Nei

Nei (1972) defined genetic distance as the extent of gene differences between cultivars, as measured by allele frequencies at a sample locus. He defined the genetic distance between two parents as

$$D = -\log_e I \text{ and}$$

$$I = \frac{J_{XY}}{\sqrt{J_X J_Y}}$$

where J_X, J_Y are the probability of identity of randomly chosen alleles in genotypes X and Y respectively and J_{XY} is the probability of identity of genes from X with that from Y. For a single locus with n alleles,

$J_{XY} = \sum P_i X P_i Y,$

$J_X = \sum P^2_i X,$

$J_Y = \sum P^2_i Y,$

where J_{XY} is the probability of identity of genes from X with that from Y, and

$P_i X$ and $P_i Y$ are the frequencies of the i^{th} allele in population X and Y.

For multiple loci, J_{XY}, J_X and J_Y values are calculated by summing over alleles at all loci and dividing by the number of loci.

Although a variety of measures of genetic diversity has been proposed and each measure is based on different biological or mathematical assumptions, in practice, many of the methods give similar values (Hedrick, 1975). Further, significant associations have often been found between single gene markers and quantitative traits (Stuber *et al.*, 1980; Tanksley *et al.*, 1981; Price *et al.*, 1986). In these circumstances, genetic distances estimated from isozyme or qualitative markers may correspond closely to those estimated from quantitative traits and morphological characters.

2.5 Correlation between genetic distance and heterosis

The association of genetic distance and heterosis has been investigated in many crop species. Predominantly outbreeding species and self-pollinated crops are considered in turn below.

2.5.1 Outbreeding species

Maize has undoubtedly been the most widely studied because of the widespread use of hybrids in commercial agriculture. The correlation of genetic distance between parents with F_1 heterosis has been reported to range from significantly positive to significantly negative values.

Moll *et al.* (1962) found that greater genetic diversity of the parental varieties was associated with greater heterosis in the variety crosses in maize (*Zea mays* L.). They suggested that crosses of widely divergent varieties from distant sources would have potential utility in yield improvement in spite of poor local adaptation of varieties. Moll *et al.* (1965) repeated this type of study using more geographically diverse races of maize. The result indicated that heterosis increased within a restricted range of divergence but extremely divergent crosses resulted in a decrease in heterosis. Sriwatanapongse and Wilsie (1968) compared the expression of heterosis between interspecific, intervariety and intravariety crosses in alfalfa (*Medicago sativa* L. and *Medicago falcata* L.) and found that highest yields were obtained from interspecific crosses followed by intervariety and finally by intravariety crosses.

Heterosis was associated with Mahalanobis genetic distance estimated from morphological (both qualitative and quantitative) traits in maize (Moll *et al.*, 1965; Prasad and Singh, 1986). The magnitude of heterosis for grain yield and its components was higher with moderate (intermediate) than with extreme parental diversity. They suggested that parental diversity should not be the sole criterion of selection. Parents that differed to a moderate degree but performed well could be more useful than those which were highly dissimilar genetically but poor performers. In common bean, Mahalanobis distance between parents was ~~highly~~ significantly correlated with the heterotic effect over mid-parent for yield, pods per plant and seeds per pod (Ghaderi *et al.*, 1984). No relationship was found for hundred seed weight. In faba bean, yield of seed *per se* was not associated with the Mahalanobis-D^2s, although both significantly positive and significantly negative correlations were found for an array of a number of traits in relation to yield (Ghaderi *et al.*, 1984). These contrasting results may be associated with the contrasting breeding systems of the two species, common bean being inbreeding and faba bean partially outbreeding.

Heterosis has been found to be associated with isozyme variability (Bruce and Kannenberg, 1971; Heidrich-Sobrinho and Cordeiro, 1975). Bruce and Kannenberg (1971) used isozyme variability as an indicator of genetic diversity related to single-cross hybrid performance in maize. Fifteen inbred lines were characterized electrophoretically for six isozyme systems which were used to calculate a diversity index (DI). The DI for an inbred pair represented the number of isozymes that were dissimilar in the two inbreds. Hybrids produced from inbred pairs with higher DI out-yielded those with low DI, but the correlation between grain yield performance of single-cross hybrids and DI was low and not significant. They concluded that the specific combining ability could be predicted reliably from DI based on isozymes. A similar experiment was conducted by Heidrich-Sobrinho and Cordeiro (1975) with other maize inbreds with similar results and they concluded that the poor correlation was because of the small number of inbreds (15 and 8 respectively) with relatively little isozyme diversity.

When more enzyme loci and more crosses were used, however, the correlation of genetic distance with heterosis of single-cross hybrids of maize remained poor and varied with the environments used for evaluation (Hadjinov *et al.*, 1982; Frei *et al.*, 1986; Price *et al.*, 1986; Lamkey *et al.*, 1987). Frei *et al.* (1986) suggested that there was a general association of allozyme diversity with higher yield but the reliability of the prediction depended on the pedigree background of lines. In addition, specific inbreds could deviate from the general allozyme-yield relationship, making predictive value questionable. They concluded that the predictive power of genotypes at allozyme loci does not appear to be markedly superior to the other characters such as flint-dent endosperm, chromosome knob and pedigrees.

Distances were measured in rapeseed (*Brassica napus* L.) by a function of kinship coefficient (Lefort-Buson *et al.*, 1986). Four classes of kinship coefficient values were defined and related to heterosis values and F_1 performance. Two different experiments were conducted over a 2-year period to examine the relationship between heterosis and genetic distance. The result showed a significant effect of the kinship class irrespective of the agronomic character and the year. The best hybrids showing the greatest heterosis were always obtained using unrelated parents coming from two different geographic pools.

2.5.2 Inbreeding species

In most predominantly self-pollinated crops, heterosis is not exploited directly in commercial F_1 varieties, but it has been extensively studied because of its potential for use as an indicator of the crosses that are likely to generate productive transgressive segregants in later generations. The relationship between genetic diversity of parents and the level of heterosis has been reported in several crops.

In cotton (*Gossypium* spp.), for example, Marani and Avieli (1973) found that interspecific hybrids showed significantly higher heterosis during early growth than their intraspecific counterparts. Murty and Anand (1966) reported that SCA effects were larger for a number of characters from crosses involving divergent parents than from crosses between more closely related parents in flax (*Linum usitatissimum* L.).

In tomatoes, Khanna and Misra (1977) studied the relationship between diversity and heterosis. The diversity between parents was estimated from multiple measurements on a number of characters including plant height, number of branches, days to flowering, locules per fruit, total soluble solids and yield per plant and classified into intraclass and interclass. There was a tendency for intercluster crosses to have greater heterosis than intracluster crosses.

In peanut, heterosis was correlated with geographical diversity (Parker *et al*., 1970) or morphological traits (Isleib and Wynne, 1983). Pod size, seed yield and other traits showed heterosis up to 19% above the higher parent. Heterosis deviations were partitioned into two components depending on the relative contributions of dominance and epistasis to non-additive genetic variation. Dominance was the more important source for pod yield, seed yield and pod length while epistasis was more important for pod number, seed number and percent shelling. The relationship between heterosis and genetic diversity of traits which exhibited more dominance was linear and the linear coefficients for these characters were all positive. For characters largely influenced by epistasis the relationship was curvilinear.

Arunachalam *et al.* (1984) found that heterosis in crosses between various diversity classes in peanut was related to parental divergence and/or the SCA of the parental combinations. The magnitude of heterosis for yield and its components was found to be higher in crosses involving parents which diverged only to an intermediate degree rather than the extreme ones. Arunachalam and Bandyopadhyay (1984) studied data from diallel crosses and divided genetic divergence among peanut parents into 4 classes. They found that the chances of high frequency and magnitude of heterosis were greater in crosses between parents within ±1 standard deviation of the mean than in crosses between parents with divergence outside this limit.

Heterosis was also found related to the differences in quantitative traits between parent lines in soybean (Chauhan and Singh, 1982) and mungbean (Ramanujam *et al.*, 1974). Ramanujam *et al.* (1974) studied genetic divergence and hybrid performance in mungbean using canonical analysis on quantitative characters viz. flowering time, maturity, pods per plant, seed size and seed density. On the other hand, the divergence between parents of each cross, estimated using generalized distance and canonical analysis, did not correspond to the level of heterosis in chickpea (*Cicer arietinum* L.) (Singh and Ramanujam, 1981).

Isozyme diversity index (DI) between parents was associated with the level of heterosis in eight varieties of green gram (*Vigna radiata*) (Mittal *et al.*, 1987). Hybrids obtained from a pair of inbreds having higher diversity index out-yielded those with lower DIs, but the correlation between DI and heterosis for seed yield was not consistent over seasons. It was concluded that isozymic diversity index may be of value in selecting pairs of parents for heterosis studies before an evaluation in the field. In contrast, Peng *et al.* (1988) found no relationship between the magnitude of yield heterosis in F_1 hybrids and isozyme patterns of the parents in Indica rice. The divergence between parents was classified from 6 isozyme systems. Most of the parental lines used in their study were elite rice cultivars bred from complex crosses involving parents of various geographic origin that allowed extensive recombination among genes. Consequently linkage disequilibrium between isozyme markers and gene blocks involved in heterosis for yield might have disappeared.

The relationship between genetic distance between parental lines and the level of heterosis in peas has been unclear. Singh and Malhotra (1971) studying grain yield in interspecific crosses of *Pisum* , found that heterosis appeared to be associated with genetic diversity among the parents. Gupta *et al.* (1984) and Rao and Narsinghani (1987), however, found that the most heterotic hybrids of field peas were between parents that were moderately divergent as determined from quantitative characters.

2.6 Summary

Detailed and extensive studies in a wide range of crop plants indicate that heterosis is a genetically complex phenomenon depending on the balance between allelic and non-allelic interactions. The components of variance of heterosis may include additive, dominance, epistatic and maternal effects, all of which may be fixed to varying degrees in pure-line varieties. However, applied research on the fixable proportion of components of heterosis in pure-line varieties of predominantly self-pollinated crops, which is a factor of critical importance in practical breeding programme, has been limited.

The level of yield heterosis in inbreeding crops has been found to vary markedly. Such variation reflects differences in the combining ability of their parents. Both general and specific combining ability are important for heterosis but GCA is predominant. Additive gene effects are nearly always larger than non-additive gene effects. Dominance as well as epistasis have been found to influence the expression of heterosis. The amount of heterosis varies with the environment in which the plants are grown. Genetic differences between parents influence the level of heterosis in F_1 hybrids.

A number of genetic distance measurements have been developed and tested for use in predicting heterotic response in the hybrids. Several measures suggested are highly correlated despite the fact that they are based on different markers or mathematical assumptions. The most appropriate method for any crop will depend on the objective of the breeding programme and the availability of facilities and resources. In recent years, the use of isozymes as single gene markers has proved to be a method for convenient detection of genetic differences close to the DNA level. Isozyme techniques have been developed for use in a wide range of crops. Further, in some instances estimates of genetic distance based on isozyme markers have been found to be clearly correlated with estimates based on quantitative traits.

Finally, while estimates of genetic diversity based on isozyme markers always closely correlate with F_1 heterosis, isozyme markers may be a useful tool to identify potential parents in screening for highly heterotic hybrids.

In the light of the above, and the problem facing Australian pea breeders in improving yield in water-limiting environments, it was postulated that a more effective approach may be to select F_1 hybrids which show high and stable yield in stress environments and ascertain if these desirable traits occur at high frequency in pure-line derivatives of such hybrids.

For an objective assessment of the potential of this breeding approach we need to know:-

i) The level of heterosis for yield and its components which can be obtained in field peas. Overseas studies indicate that F_1 pea hybrids may show significant heterosis. However, more information is required on the level of heterosis expected in a range of environments with optimal plant density.

ii) The proportion of hybrid vigour which is fixable in pure-line derivatives of heterotic hybrids. Clearly, if a large proportion of the observed heterosis is fixable then yield testing of F_1 hybrids to find highly heterotic combinations would be an attractive breeding strategy. Further, what studies have been done have yielded equivocal results. More experiments with a greater number and diversity of hybrids are required to answer this question.

Chapter 3 Materials and Methods

The project was conducted at the Waite Agricultural Research Institute, Urrbrae, South Australia (latitude 34°58' S, longitude 138°51' E) during 1988-1991. The project consisted of three experiments. The aim of the first experiment (experiment A) was to estimate (i) the level of heterosis exhibited by F_1 hybrids amongst a diverse set of pea genotypes, (ii) the level of heterosis and inbreeding depression in F_2 populations derived from these F_1 hybrids, (iii) the combining ability of each parent and (iv) the effect of genotype-environment interactions on grain yield and its components, both in parents and in their F_1 hybrids across four environments.

The aim of the second experiment (experiment B) was to determine the relationship between the performance of F_1s and the yield of their F_5 derivatives.

The third experiment (experiment C) explored the relationship between the genetic distance between parental lines and the level of heterosis in their progenies. The genetic distances between parental lines were estimated using isozyme markers, morphological characters and quantitative traits separately and in combination. Electrophoretic analyses of pea parental lines were undertaken in the Department of Plant Science laboratories, whereas morphological and quantitative characteristics were scored from the first experiment. The relationship between genetic distance between parents and the level of heterosis in their F_1 progenies was assessed by simple correlation analyses.

Monthly rainfall distribution at each site is presented in Figure 3.1. Annual rainfall at Urrbrae and Charlick in 1989 was higher than at Turretfield, but the distribution at all sites was suitable for growing peas. The annual rainfall in 1991 was slightly less than that in 1989, and the distribution was less suitable for peas with drought during flowering and pod filling stage and heavy rain during harvesting. The peas were infected with powdery mildew and consistently low seed weight and harvest index were recorded, especially at Northfield.

These sites are all in South Australia. Urrbrae and Northfield are suburbs of Adelaide, south east and north east of the city centre respectively. Charlick Experiment Station is 50 kilometers south east of Adelaide and Turretfield Research Centre 65 kilometres north east.

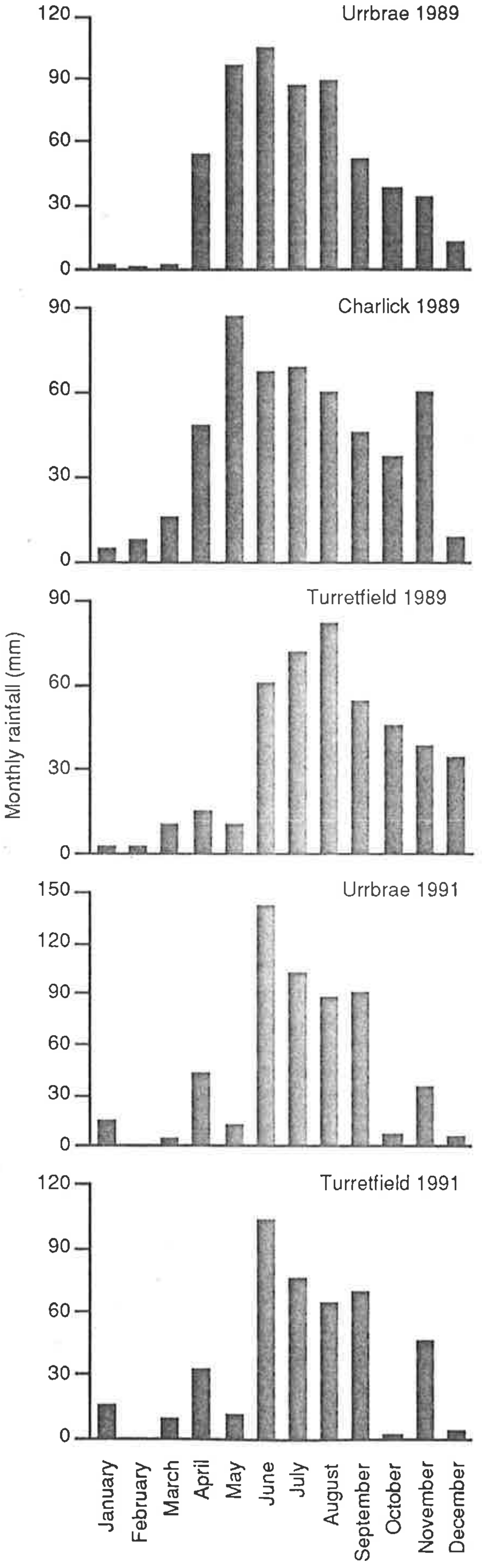

Figure 3.1 Monthly rainfall (mm) at the five experimental sites

3.1 Experiment A: The levels of heterosis in F1 hybrids and F2 progenies

3.1.1 Genetic materials

Four commercially available and widely grown pea cultivars, Alma, Derrimut, Dundale and Wirrega were used as female parents (Table 3.1). Alma was developed from White Brunswick x PI 173052 (SA 487) and was released in South Australia in 1986. White Brunswick was bred in South Australia and PI 173052 originated in Turkey. Alma is a Dun type of pea but its yield is more consistent and it outyields Dun in the presence of the fungal disease, black spot (Ali, 1986).

Derrimut was released by the Victorian Department of Agriculture in 1964. It is the earliest to flower among the commercial cultivars with mid-season maturity. Its seed is much smaller than that of Early Dun.

Dundale was selected from Early Dun by the SA Department of Agriculture and was released in 1970. It is similar in most respects to Early Dun but matures slightly earlier.

Table 3.1 Origins and characteristics of female parents

	Alma	Derrimut	Dundale	Wirrega
Year of release	1986	1964	1970	1986
Pedigree	White Brunswick x PI 173052	Unknown	selected from Early Dun	Derrimut x PI 1852
Flower colour	pink	pink	pink	white
Basal branches (number)	4	1-2	2-3	3-4
Onset of flowering (days after sowing)	93-95	80-83	82-85	94-98
Maturity	late	mid-season	mid-season	late
Seed type	dimpled	dimpled	dimpled	round
Seed coat	brown to green	green	brown to green	cream
Reaction to black-spot disease complex	tolerant	susceptible	moderately susceptible	moderately susceptible

Table 3.2 Origins and characteristics of male parents

Accession number	Species	Accession type	Origin
SA 15	*P. elatius*	Landrace	Hindukush
SA 24	*P. sativum*	Fixed breeding line	Sweden
SA 35	*P. sativum*	Fixed breeding line	Sweden
SA 51	*P. sativum*	Fixed breeding line	Poland
SA 54	*P. sativum* ssp.*transcausicum*	Landrace	USSR
SA 123	*P. sativum*	Landrace	Afghanistan
SA 129	*P. sativum*	Landrace	Afghanistan
SA 157	*P. sativum*	Mutation (Centrobscurum)	Sweden
SA 236	*P. sativum*	Landrace	Hindukush
SA 247	*P. sativum*	Landrace	Ethiopia
SA 248	*P. sativum*	Landrace	Ethiopia
SA 465	*P. sativum*	Fixed breeding line	Sweden
SA 483	*P. sativum*	Landrace (J1-181)	Nepal
SA 688	*P. sativum*	Landrace	Afghanistan
SA 828	*P. sativum*	Landrace	Ethiopia
SA 1041	*P. sativum*	cv. Garfield	USA
SA 1405	*P. sativum*	cv. Solara	Holland
SA 1423	*P. sativum*	cv. Whero	New Zealand

Wirrega was released in 1986 by the SA Department of Agriculture as a replacement for the cultivar Pennant. It is recommended for all areas of SA except for very early and drier districts. It was developed from the cross Derrimut x PI 1852 (SA 246). Variety PI 1852 originated in Ethiopia. Wirrega has rapid germination and seedling establishment, has consistently out-yielded Pennant and has shown some resistance to the black-spot disease complex (Ali, 1986). It produces white flowers and smooth, round seeds, in contrast to the other three varieties which have coloured flowers and dimpled seeds.

The 18 genotypes used as male parents were introduced from 10 different countries and represented a wide range of diversity in terms of origin, physiological traits and morphological characters (Table 3.2). Four were from Sweden, three from Ethiopia, five from the Hindukush region and one each from Poland, USSR, USA, Nepal, Holland and

New Zealand. Three were registered cultivars, four were fixed breeding lines, ten represented samples from landrace populations and one was an induced mutation.

Using the 4 females and 18 males, 72 F_1 hybrids were produced by manual emasculation and pollination according to the factorial mating design or design II of Comstock and Robinson (1952). The crossing was carried out in the growing season (May to November) of 1988. Eight seeds of each F_1 were grown in a glasshouse during the summer of 1989 to produce F_2 seed. The remainder of the F_1 seeds along with F_2 derivatives and the parental lines were used in field experiments.

3.1.2 Procedures

Experiment A was conducted during the growing seasons of 1989 and 1991. In 1989, it consisted of 148 genotypes which comprised of 22 parents, 72 F_1 hybrids and 54 F_2 families. There was insufficient seed of the other 18 remaining F_2 families for this trial. The genotypes were sown in plots in a randomized complete block design with three replications. Each plot consisted of 20 plants in four rows with 20 cm between rows and 10 cm between plants. A pathway of 50 cm x 80 cm was left between plots. Seeds were sown on 23, 27 and 29 May 1989 at Waite Agricultural Research Institute (Environment 1: Urrbrae clay loam, pH 6.5), Turretfield Research Station (Environment 2: sandy loam, pH 5.3) and Charlick Research Station (Environment 3: solonized brown soil, pH 6.4), respectively. In 1991, the experiment was repeated at the Waite Agricultural Research Institute with 166 genotypes which consisted of 22 parents, 72 F_1 and 72 F_2 families. Seeds were sown on 27 May 1991 with the same field layout as the 1989 experiment but in this year a pathway of 50 cm x 60 cm was left between plots and there were three replications. Double super phosphate (32%P) (150 kg/ha) was applied at Urrbrae (first year) and Charlick and triple super phosphate (48%P) (60 kg/ha) at Turretfield. Seeds were treated with a fungicide (triadimefon) before sowing and the recommended chemicals were used to control red-legged earth mite (methidathione), powdery mildew (triadimefon) and pea weevil (endosulfan) during the growing season. During land preparation a pre-emergence selective herbicide (Avadex®, diallate) was applied. Post-emergence grass weeds were controlled by a selective herbicide (Hoegrass®, diclofop methyl) and broadleaf weeds by hand weeding.

3.1.3 Data collection

At maturity, two plants were sampled at random from each plot at each site. Plant height, basal branches, pod-bearing nodes, pods and hundred seed weight were recorded from the two plants. Ten pods from the middle of the podded zone of each plant were chosen, the seeds from them were pooled and mean seeds per pod was estimated from this sub-sample. The days from planting to onset of flowering (1989, 1991) and the duration of flowering (1989) were recorded at Urrbrae.

At Charlick and Turretfield, the plots were damaged by birds shortly after emergence and this resulted in a reduction in the number of harvested plants in some treatments. Consequently, the data were analyzed on a single plant basis to minimize plot to plot variation due to bird damage.

3.1.4 Statistical analyses

The data recorded on parents and the F_1 hybrids were analysed together, while the F_2 data were analysed separately. The data from each environment were analyzed separately and then combined over environments. The form of the analysis of variance for the F_1 hybrids is given in Table 3.3 while that for the F_2 populations is given in Table 3.4.

The degrees of freedom for F_1 hybrids were subdivided into males, females and males x females, respectively, to provide tests for general combining (GCA) and specific combining abilities (SCA).

The levels of heterosis over (i) the mid-parent or parental average, (ii) better parent and (iii) the best parent were calculated as follows:

$$\text{Heterosis over mid-parent (Hmp)} \quad = \quad \frac{(F_1 - mp)}{mp} \times 100\ (\%)$$

$$\text{Heterosis over better parent (Hbp)} \quad = \quad \frac{(F_1 - bp)}{bp} \times 100\ (\%)$$

$$\text{Heterosis over the best parent (Hcm)} \quad = \quad \frac{(F_1 - cm)}{cm} \times 100\ (\%)$$

where F_1, mp, bp and cm are the means for F_1, mid-parent, better parent of each cross and the best parent of all crosses, respectively.

Table 3.3 Sources of variation and degrees of freedom for the analysis of variance of parents and F$_1$

Source	Degrees of freedom (df)	Expected Variance
Environments (E)	(e-1) = 3	$rg\sigma^2_s + g\sigma^2_r + \sigma^2_e$
Reps/Environments (R/E)	e(r-1) = 8	$g\sigma^2_r + \sigma^2_e$
Genotypes (G)	(g-1) = 93	$sr\sigma^2_g + r\sigma^2_{gs} + \sigma^2_e$
Parents (P)	(p-1) = 21	$sr\sigma^2_p + r\sigma^2_{ps} + \sigma^2_e$
F$_1$	(f$_1$-1) = 71	$sr\sigma^2_{f1} + r\sigma^2_{f1s} + \sigma^2_e$
Males (M)	(m-1) = 17	$srf\sigma^2_m + rf\sigma^2_{ms} + \sigma^2_e$
Females (F)	(f-1) = 3	$srm\sigma^2_f + rf\sigma^2_{fs} + \sigma^2_e$
Male x Female (M x F)	(m-1)(f-1) = 51	$sr\sigma^2_{mf} + rf\sigma^2_{fms} + \sigma^2_e$
E x G	(e-1)(g-1)= 279	$r\sigma^2_{sg} + \sigma^2_e$
E x P	(e-1)(p-1)= 63	$r\sigma^2_{sp} + \sigma^2_e$
E x F$_1$	(e-1)(f$_1$-1)= 213	$r\sigma^2_{sf1} + \sigma^2_e$
E x M	(e-1)(m-1)= 51	$rf\sigma^2_{sm} + \sigma^2_e$
E x F	(e-1)(f-1)= 9	$rm\sigma^2_{sf} + \sigma^2_e$
E x F x M	(e-1)(f-1)(m-1) = 153	$r\sigma^2_{smf} + \sigma^2_e$
Pooled Error	e(r-1)(g-1)= 744	σ^2_e

Table 3.4 Sources of variation and degrees of freedom for the analysis of variances of F$_2$

Source	Degrees of freedom (df)	Expected Variance
Environments (E)	(e-1) = 3	$gr\sigma^2_s + g\sigma^2_r + \sigma^2_e$
Reps/Environments (R/E)	e(r-1) = 4	$g\sigma^2_r + \sigma^2_e$
Genotypes (F$_2$)	(g-1) = 53	$sr\sigma^2_g + r\sigma^2_{gs} + \sigma^2_e$
G x E	(e-1)(g-1) = 159	$r\sigma^2_{gs} + \sigma^2_e$
Pooled Error	e(r-1)(g-1) = 212	σ^2_e

Inbreeding depression was estimated using values from F$_1$ and F$_2$ following equation:

$$\text{Inbreeding depression (Inb)} \quad = \quad \frac{(F_1 - F_2)}{F_2} \times 100\ (\%)$$

The GCA effect of any male line was estimated as the deviation of the mean performance of its F$_1$ hybrids with all female parents from the grand mean, and the GCA effect of any female line was computed similarly. The male x female interaction effect was used to estimate specific combining ability, SCA (Beil and Atkins, 1967). Thus the general effects for each line and specific effects for each hybrid were calculated as :

$$g_i = (Y_{i.} - Y_{..})$$

$$g_j = (Y_{.j} - Y_{..})$$

$$s_{ij} = (Y_{ij} - Y_{i.} - Y_{.j} + Y_{..})$$

where g_i is the general effect of female i

g_j is the general effect of male j

s_{ij} is the specific effect of the hybrid of female i and male j

$Y_{i.}$ is the mean performance of hybrids of female i over j males

$Y_{.j}$ is the mean performance of hybrids of male j over i females

Y_{ij} is the performance of hybrid ij

$Y_{..}$ is the grand mean

Standard errors for GCA (SE_{gi}) (SE_{gj}) and SCA (SE_{sij}) effects were calculated from the formulas described by Cox and Frey (1984)

$$SE_{gi} = \sqrt{MS_{fl}\frac{(f-1)}{mflr}}$$

$$SE_{gj} = \sqrt{MS_{ml}\frac{(m-1)}{mflr}}$$

$$SE_{sij} = \sqrt{MS_{fml}\frac{(m-1)(f-1)}{mflr}}$$

where SE_{gi} is standard error of general effects of female i

SE_{gj} is standard error of general effects of male j

SE_{sij} is standard error of specific effects of the cross of female i x male j

MS_{fl} is the female x environment mean square

MS_{ml} is the male x environment mean square

MS_{fml} is the male x female x environment mean square

m, f, l and r are the number of males, females, locations and replications respectively.

Two tailed t-tests were used to test the significance of the GCA and SCA effects, where $t = \frac{GCA}{SE_{GCA}}$ and $\frac{SCA}{SE_{SCA}}$ respectively.

3.2 Experiment B: Relative yield of pure-line derivatives of heterotic hybrids

3.2.1 Genetic materials

From experiment A, one F_3 seed was collected from each F_2 plant of 6 crosses: Alma x SA 24 (cross A), Alma x SA 828 (cross B), Derrimut x SA 129 (cross C), Dundale x SA 123 (cross D), Wirrega x SA 157 (cross E) and Wirrega x Whero (cross F). A single F_4 seed was taken from each F_3 plant to multiply the next generation which was raised in a birdcage at the Waite site during the growing season of 1990. At maturity, F_5 seeds were harvested from each plant and kept separately. Seeds were harvested from 26 plants for cross A, 31 each for crosses B and E, 27 for cross C and 28 each for crosses D and F. F_5 seeds originating from an F_2 plant were designated as an F_5 family.

3.2.2 Experimental design and management

The experiment was conducted at Urrbrae (site 1) and Northfield (site 2) with 3 replications at each site. Crosses were randomized as main plots and within each cross, F_5 families, F_1 and two parents were sown as randomized subplots. Each subplot consisted of 3 rows of 4 plants at a spacing of 20 x 10 cm. The spacing between plots was 60 x 50 cm. A selective post-emergence herbicide, Metribuzine was applied for weed control. Rotary hoes were used between plots and hand weeding was done inside plots when necessary. Plants were irrigated twice at both sites during pod setting. Aphids and powdery mildew were controlled by spraying Pirimor® and Benlate® respectively.

3.2.3 Data collection

Two plants were collected from each plot to determine the number of basal branches per plant, pods per plant, seeds per pod, hundred seed weight, plant weight and grain yield. The remaining plants were harvested as a whole plot to measure dry plant weight and grain yield. Plant weight and grain yield from the sample plants were added to those from the whole plot and results were then calculated on a single plant basis.

3.2.4 Statistical analyses

Separate analysis of variance was performed for each cross, then a combined analysis was performed for all crosses. The frequency distribution of line means was constructed for comparison with the mean performance of the F_1 and two parents. Broad sense heritability among random F_5 lines in each cross combined over two environments were calculated as follows:-

$$h^2 = \frac{\sigma^2_g}{(\sigma^2_e + \sigma^2_{gy} + \sigma^2_g)}$$

where σ^2_g = genetic variance component among lines, σ^2_{gy} = site x line interaction variance component, and σ^2_e = error variance component.

3.3 Experiment C: Genetic distance amongst parental lines and its relation to the level of heterosis

3.3.1 Isozyme markers

Electrophoretic analyses were carried out on the 4 female and 18 male parents from experiment A.

a.) Sample preparation

Seeds were used for 10 enzymes and leaves for the other two. Seeds were soaked over-night and dehulled. A small sample taken from a cotyledon was then crushed in 1-3 drops of extraction buffer. The extract was centrifuged at 2000 rpm for 1-2 min, then the supernatant was absorbed on chromatography paper wicks (6 mm x 3 mm) that were inserted into a vertical slit in the starch gel.

Leaflets from the first fully expanded leaves were cut into 1-cm square segments and crushed in 1-3 drops of extraction buffer. The rest of the protocol was identical to that for seeds.

The extraction buffer, depending on the enzyme assayed, was either phosphate buffer (0.05 M phosphate, pH 7.0) with DTT (DL Dithiothreitol) 10mg/ml solution, or Carlsons' extraction buffer (12.1 g tris, 7.44 g KCl, 1.86 g EDTA and 37.58 g sucrose, in 1000 ml H_2O) also with DTT (10mg/ml solution).(Table 3.5).

b.) Electrophoresis

The starch gel preparation and electrophoresis techniques were modifications of the procedures described by Shields *et al.* (1983). The gel and electrode buffer systems used for each enzyme are indicated by names and numbers in Table 3.5 and the buffer compositions are given Table 3.6.

Table 3.5 Criteria for extraction of samples for isozyme analysis

Enzyme		Sample material	Extraction buffer	Electrophoretic system
1	Alcohol dehydrogenase (ADH)	seeds	Carlson's	I
2	Aldolase (ADL)	seeds	Carlson's	II
3	Aminopeptidase (AMP)	seeds	Phosphate	III
4	Glutamate oxaloacetate transaminase (GOT)	seeds	Phosphate	II
5	Glucose 6 phosphate dehydrogenase (G6PD)	leaves	Phosphate	II
6	Isocitrate dehydrogenase (IDH)	leaves	Carlson's	I
7	Malate dehydrogenase (MDH)	seeds	Carlson's	I
8	Menadione reductase (MRD)	seeds	Phosphate	I
9	6-phosphogluconate dehydrogenase (6-PGD)	seeds	Carlson's	I
10	Phosphogluco-isomerase (PGI)	seeds	Carlson's	III
11	Phosphoglucomutase (PGM)	seeds	Carlson's	III
12	Shikimate dehydrogenase (SDH)	seeds	Carlson's	I

Table 3.6 Conditions for electrophoresis of isozymes (Shields *et al.* 1983)

System	Gel buffer	Electrode buffer	Electric current	Duration of electrophoresis
I	250 ml 0.025 M DL histidine pH 8; 8 mg NADP	0.4 M trisodium citrate pH 8; 8 mg NADP	25 Amperes ~ 100-150 V	5-5.5 h
II	16 ml 0.05 M citric acid; 19.5 ml 0.19 M tris added to 250 ml H_2O	0.3 M borate pH 7 (18.55 g boric acid + 4 g NaOH in 1 l H_2O)	200V (with wicks), 300V (without wicks)	3.5-4 h or until front at 9 cm
III	235 ml 0.65 M tris, add 0.091 M citric acid until pH 8.2; 15 ml electrode buffer	0.0787 M LiOH and 0.25 M boric acid pH 8.5	200V (with wicks), 300V (without wicks)	3.5-4 h or until front at 9 cm

Table 3.7 Composition of enzyme staining systems

Enzyme	Composition	Reference
1. ADH	50 ml 0.2 M tris-HCl buffer pH 8.0; 2 ml ethanol; 2 ml 0.5% NBT; 2 ml 0.5% β NAD; 1 ml 0.5% PMS.	2
2. ADL	50 ml 0.2 M tris-HCl buffer pH 8.0; 2 mg sodium arsenate; 165 mg fructose 1,6- diphosphate; 2 ml 0.5% NBT; 2 ml 0.5% MTT.	3
3. AMP	50 ml 0.2 M tris-maleate pH 6.0; 0.25 g PVP-40; 0.25 mg $MgCl_2$; 50 mg Fast Black KK; 5 ml 1% leucyl-β-naphthylamide in 50 ml acetone : 50 ml H_2O.	2
4. GOT	50 ml 0.2 M tris-HCl buffer pH 8.0; 50 mg α- ketoglutaric acid; 100 mg α-aspartic acid; 5 mg pyridoxal-5-phosphate; 75 mg fast blue BB salt.	3
5. G6PD	50 ml 0.2 M tris-HCl buffer pH 8.0; 100 mg $MgCl_2$; 100 mg Na_2 glucose-6-phosphate; 10 mg NADP; 2 ml 0.5% NBT; 0.5 ml 0.5% PMS.	3
6. IDH	50 ml 0.2 M tris-HCl buffer pH 8.0; 50 mg $MgCl_2$; 75 mg isocitric acid; 5 mg NADP; 2 ml 0.5% NBT; 0.5 ml 0.5% PMS.	3
7. MDH	2.5 ml 2 M malate pH 7.0; 47.5 ml 0.2 M tris-HCl buffer pH 8.0; 10 mg NADP; 2 ml 0.5% NBT; 0.5 ml 0.5% PMS.	3
8. MRD	45 ml H_2O; 5 ml 1.0 M phosphate buffer pH 7; 7.5 mg NADH; 25 mg Menadione; 2 ml 0.5% NBT.	1
9. 6PGD	50 ml 0.2 M tris-HCl buffer pH 8.0; 20 mg $MgCl_2$; 10 mg 6-phosphogluconic acid (trisodium); 5 mg NADP; 2 ml 0.5% NBT; 0.5 ml 0.5% PMS.	3
10. PGI	50 ml 0.2 M tris-HCl buffer pH 8.0; 100 mg $MgCl_2$; 20 mg fructose-6-phosphate; 40 units G6PD; 10 mg NADP; 2 ml 0.5% MTT; 0.5 ml 0.5% PMS.	3
11. PGM	50 ml 0.2 M tris-HCl buffer pH 8.0; 85 mg glucose-1-phosphate; 100 mg $MgCl_2$; 1 mg glucose-1,6-diphosphate; 0.04 mg G6PD; 5 mg NADP; 2 ml MTT; 0.5 ml 0.5% PMS.	3
12. SDH	50 ml 0.2 M tris-HCl buffer pH 8.0; 20 mg $MgCl_2$; 50 mg shikimic acid, titrate to pH 8; 10 mg NADP; 2.5 ml 0.5% NBT; 0.5 ml 0.5% PMS.	3

References: 1: Burdon *et al.*, 1980; 2: modification of Shaw and Prasad, 1970; 3: modification of Soltis *et al.*, 1983.

c.) Enzymatic assessment

Following electrophoresis, the gel was sliced into two to three pieces, and each slice was immersed in 50 ml of prepared staining solutions (see Table 3.7). Each gel slice was generally stained for a particular enzyme system.

After gels were sufficiently stained (30 min to overnight depending on the enzyme), they were washed with water and fixed with 50% ethanol, to allow ease of handling and photography.

The genotype of each accession for each enzyme system was scored from the gels. The isozyme marker data were used to estimate the genetic distance between each pair of parents.

3.3.2 Morphological polymorphisms

The 22 parental lines were characterised for 17 morphological traits and gene symbols were obtained (Blixt, 1974; M. Ali, Department of Agriculture South Australia, Pers. Comm.). The differences in morphological characters were used to estimate the genetic distance between each pair of parents.

3.3.3 Quantitative traits

Quantitative characteristics of parents from experiment A were used to calculate genetic distances between each pair of parents.

3.3.4 Genetic distance estimates from qualitative markers

Based on genetic information from isozyme genotypes and morphological characters, the Genetic Distance of Nei (1972) was calculated using the equations given in the literature review.

The allelic frequency was first transformed to 1s and 0s from isozyme genotypes and morphological characters. Where 2 cultivars carry different alleles, the allelic frequency in cultivar A is 1 and in B is 0. Where the same allele is present in both cultivars, the allelic frequencies are 1 for both. For example, the genetic distance between two cultivars may be calculated from 4 enzyme systems, three of which differed while the fourth was identical.

$$Jxy \quad = [(1x0)+(1x0)+(1x0)+(1x1)]/4 \qquad = 0.25$$

The probability of identity of two randomly chosen alleles in parent 1 (Jx) calculated following the equation is

$$Jx = [1^2+1^2+1^2+1^2]/4 = 1.00$$

The probability of identity of two randomly chosen alleles in parent 2 (Jy) calculated following the equation is

$$Jy = [0^2+0^2+0^2+1^2]/4 = 0.25$$

The genetic identity of the 2 parents calculated following the equation is

$$I = \frac{0.25}{\sqrt{1x0.25}} = 0.50$$

Genetic distance is

$$D = -\log_e 0.50 = 0.69$$

Thus the genetic distance of Nei between two parents differing at 3 of 4 alleles is 0.69.

Allelic frequencies at each locus for morphological traits were treated in the same way as isozyme markers. Furthermore, morphological and isozyme markers were pooled to calculate a combined estimate of genetic distance.

3.3.5 Genetic distance estimated from quantitative traits

Eleven quantitative traits of parental lines (basal branches per plant, plant height, podded nodes per plant, pods per plant, seeds per pod, hundred seed weight, grain yield, plant weight, harvest index, days to onset of flowering and duration of flowering) were recorded in four environments in experiment A and were used for the calculation of Euclidean distance

First, the 11 traits were orthogonally transformed to give principal components, each of which was a linear combination of varietal values of the original variables. These principal components were then used as the axes of a standardised multi dimensional space, in which each parent was characterised as a single point. The Euclidean distance was then be calculated from the coordinates of any two parents and represented the degree of dissimilarity between two parents. A GENSTAT statistical program was used to carry out the analysis.

3.3.6 Relationship between genetic distance and the level of heterosis

Four measures of genetic distance (GD) were calculated between all 72 parental combinations; GD_i, based on isozymes; GD_m, on morphological markers; GD_{i+m}, on isozymes and morphological markers; and GD_q, on quantitative traits. Three measures of the level of heterosis (Hmp, Hbp, Hcm) were calculated for F_1 and F_2. Simple correlation coefficients were then computed for all possible types of GD with all measures of heterosis.

Chapter 4 Results

4.1 Experiment A: Levels of heterosis in F_1 hybrids and in F_2 progenies

4.1.1 Yield of parents and F_1 s

a.) Analysis of variance

Separate analyses of variance showed that there were highly significant differences among varieties for each trait and in each environment (Table 4.1.1). Combined analyses of variance were carried out with the data from four environments for all traits except plant height, podded nodes per plant (for which data were available from only three environments), onset of flowering (two environments) and duration of flowering (one environment).

Significant differences were found among environments for all traits. The ratio of the estimates of the mean square for environments and the grand mean for each trait (coefficient of variation, cv), which provides a measure of the relative variability across environments, suggested that grain yield (cv = 6.84) was the most variable trait followed by podded nodes per plant (cv = 6.35), plant weight (cv = 5.31), pods per plant (cv = 5.26), harvest index (cv = 3.84), basal branches per plant (cv = 3.50), onset of flowering (cv = 3.16), seed weight (cv = 1.17), and plant height (cv = 1.15) and finally seeds per pod (cv = 1.04).

The variance due to genotypes was highly significant for all traits in both the F_1 and parental populations. The relative variability differed amongst characters and populations. For example, comparing the cv of genotype (ratios of mean squares from Tables 4.1.1 and the grand means of parents and F_1s from Tables 4.1.3 and 4.1.4) revealed that basal branches per plant, pods per plant, podded nodes per plant and hundred seed weight were highly variable in the parent population as well as in the F_1s. In contrast, onset of flowering and duration of flowering exhibited markedly less variation amongst genotypes than the other traits. This suggests that the variation pattern in F_1 populations

Table 4.1.1 Summary analyses of variance for 11 agronomic traits of parents and F_1 hybrids.

Source of variance	df	Mean square							df	Mean square		df	Mean square	
		Basal branches per plant (number)	Pods per plant (number)	Seeds per pod (number)	Hundred seed weight (g)	Grain yield (g)	Plant weight (g)	Harvest index		Plant height (cm)	Podded nodes per plant (number)		Onset of flowering (days after sowing)	Duration of flowering (days)
Environment (E)	3	96***	14493***	36.7*	545ns	10259***	37795*	2.6***	2	15426ns	10576**	1	127438***	
Replication / environment (R/ E)	8	5.5	845	4.5	161	113	5290	0.15	6	3684	448	3	1843	
Genotype (G)	93	16***	874***	5.8**	480***	115***	737***	0.039***	93	3527**	361**	93	502***	76**
Parent (P)	21	11***	294***	9.2***	706***	114	773***	0.043***	21	7221**	174**	21	938***	83**
F_1	71	16.8***	933***	4.8***	420***	57***	327**	0.039***	71	1597**	395**	71	349**	68**
Female (F)	3	1.3ns	127ns	1.3***	263***	66**	857***	0.072***	3	9993**	136**	3	2030***	179**
Male (M)	17	64***	3027***	6.4***	1668***	127***	615***	0.123***	17	2850**	1241**	17	856***	129**
F x M	51	105***	283***	2.1***	14***	34***	200*	0.009***	51	686**	128**	51	76ns	42**
G x E	279	2.1***	198**	1.1**	7.5***	26***	207***	0.007***	184	619**	81**	92	167***	
P x E	63	2.1***	171***	1.2***	4.6*	15***	153***	0.007*	42	358**	67**	21	306**	
F_1 x E	213	2.2***	213***	1.1***	8**	28**	214***	0.007***	142	701**	85**	71	126***	
F x E	9	2.8*	80ns	0.79ns	7.8*	28ns	290**	0.006*	6	38ns	39ns	3	286**	
M x E	51	2.1***	434***	1.7***	18***	40***	239***	0.008***	34	936**	150**	17	248***	
F x M x E	153	2.1***	149***	0.9***	4.9**	24***	205***	0.007***	102	662**	65**	51	75ns	
Pooled Error	744	0.89	70	0.58	3.4	14.6	106	0.003	558	346	29	372	52	19.5†
Mean		2.8	22.9	5.8	19.9	14.8	36.6	0.42		107.6	16.2		113	30

† 186 df.

ns, not significant; *, **, ***: $P < 0.05, 0.01, 0.001$ respectively simulated the variation for all these characters in parents except for grain yield and plant weight.

The degree of variation for grain yield, plant weight, harvest index, plant height and seed characteristics in the parental group was higher than in the F_1s, but for podded nodes per plant, pods per plant and basal branches, the coefficient of variability was higher in the F_1s than the parents.

The parent x environment (P x E) and the F_1 x environment (F_1 x E) interactions were highly significant for pods per plant, podded nodes per plant, and basal branches, and moderately significant for onset of flowering, hundred seed weight, seeds per pod and harvest index. The mean square for the F_1 x E interaction for grain yield was higher than that for P x E indicating that parental lines were more consistent in the yield across environments than F_1 hybrids. In contrast, the F_1 x E mean squares for pods per plant and seeds per pod were smaller than those for P x E interactions indicating that the F_1s were more consistent over environments with respect to those traits.

The mean squares for F_1s were partitioned into male, female and male x female components to estimate the general combining ability (GCA) of male and female parents and the specific combining ability (SCA) of crosses. The GCA effects of male and female parents were significant for all traits except for basal branches per plant and pods per plant in females. SCA effects were also significant for all traits except plant weight. This suggests that both GCA and SCA effects are important. The mean square of variance for male plus female exceeded the mean squares of variance for male x female in all traits indicating that additive gene effects were greater than non-additive gene effects.

The male x environment interactions were highly significant for all traits including grain yield but the female x environment interactions were significant only for plant weight, harvest index, basal branches per plant and hundred seed weight. Thus, the GCA effects for grain yield expressed by females are more consistent than those of male parents.

The highly significant male x female x environment interaction effects in all traits except onset of flowering suggests that the SCA effects are inconsistent and often markedly affected by environment.

Table 4.1.2 Environment means across genotypes for 11 agronomic traits

Environment	Basal branches per plant (number)	Plant height (cm)	Podded nodes per plant (number)	Pods per plant (number)	Seeds per pod (number)	Hundred seed weight (g)	Grain yield (g)	Plant weight (g)	Harvest index	Onset of flowering (days after sowing)
Urrbrae (E1)	2.1	104.6	10.5	14.4	5.3	19.9	9.2	19.9	0.47	98
Turretfield (E2)	2.9	113.4	23.4	30.7	6.1	19.8	18.4	41.0	0.45	NA
Charlick (E3)	2.8	119.1	17.3	26.4	6.0	21.5	21.4	45.1	0.48	NA
Urrbrae (E4)	3.5	NA	NA	20.1	5.7	18.1	10.2	42.4	0.28	130
LSD (0.01)	0.7	13.4	4.7	8.2	0.6	3.6	3.0	20.5	0.11	12.2

NA: Data not available

b.) Environments

Observations during plant growth in the experimental fields indicated that growth was best at Charlick (E3) followed by Urrbrae 1991 (E4), Turretfield (E2) and finally Urrbrae 1989 (E1). Average grain yields at E3 and E2 were higher than those at E1 and E4 (Table 4.1.2). Plant height, seeds per pod and seed weight were also highest at E3 but basal branches per plant, podded nodes per plant and pods per plant were highest at E2. At Urrbrae, parents and F_1s gave the lowest means for all traits except harvest index in 1989. These results suggest that Charlick (E3) and Turretfield (E2) were more suitable for growing peas than Urrbrae (E1 and E4). In the better conditions as found in E3, plants grew taller, weighed more, produced heavier seeds and gave higher yields. At E4, peas were grown early in the season but suffered from powdery mildew during flowering and pod filling. This disease resulted in poor pod filling, lower harvest index and subsequently poor grain yield.

c.) Parental performance

Female parents were moderate in the expression of agronomic characters and had higher grain yields (Table 4.1.3). They had the same number of basal branches per plant, podded nodes per plant, pods per plant, duration of flowering and grain yield, but varied

Table 4.1.3 Average performance of parents over 4 environments (except plant height and number of podded nodes perplant, 3 environment days to onset of flowering 2 environments, and duration of flowering, 1 environment)

Cultivar	Basal branches per plant (number)	Plant height	Podded nodes per plant (number)	Pods per plant (number)	Seeds per pod (number)	Hundred seed weight (g)	Grain yield (g)	Plant weight (g)	Harvest index	Onset of flowering (days after sowing)	Duration of flowering (days)
Females											
Alma	1.6	116	16.0	17.3	6.4	23.2	15.7	35.5	0.49	115	28
Derrimut	2.3	85	16.5	19.3	5.9	19.0	13.9	29.8	0.47	104	33
Dundale	2.0	116	14.1	17.9	5.8	23.6	16.0	37.1	0.46	111	32
Wirrega	1.8	100	16.8	21.1	6.4	18.4	15.7	43.7	0.37	112	31
Males											
Garfield	1.9	93	9.5	12.3	6.0	22.7	11.0	22.2	0.49	105	30
SA 15	2.6	82	13.6	16.8	3.5	32.2	10.4	21.6	0.47	91	30
SA 24	2.5	48	13.2	18.9	5.8	22.6	10.1	20.1	0.53	100	35
SA 35	1.5	89	7.0	9.4	4.8	22.9	8.6	22.5	0.39	119	37
SA 51	1.2	91	5.4	11.3	4.5	22.1	8.1	23.0	0.34	120	21
SA 54	4.5	67	17.2	24.7	6.3	5.6	5.7	21.2	0.29	134	26
SA 123	4.3	76	19.4	27.4	6.7	7.6	8.8	23.9	0.41	122	18
SA 129	4.0	64	14.3	19.1	6.1	8.3	6.4	15.7	0.40	130	18
SA 157	1.6	106	11.5	16.6	5.3	21.2	11.1	28.3	0.42	104	31
SA 236	1.9	121	9.6	13.6	5.7	33.6	14.5	36.0	0.41	115	23
SA 247	2.1	118	12.0	18.6	5.4	18.2	11.9	33.2	0.37	112	29
SA 248	2.8	121	19.4	23.5	5.0	20.0	13.1	42.2	0.38	123	29
SA 465	1.8	50	7.1	11.0	6.6	18.3	11.0	23.2	0.49	109	29
SA 483	4.0	58	20.4	27.4	5.5	7.3	7.9	17.8	0.46	129	21
SA 688	3.6	96	18.3	22.7	7.5	12.7	9.8	26.2	0.37	128	32
SA 828	2.2	141	15.1	19.9	6.6	14.8	10.8	27.1	0.40	127	26
Solara	2.2	45	8.2	16.8	4.8	29.2	11.6	24.2	0.51	104	29
Whero	1.8	120	12.8	19.9	5.4	24.9	16.0	39.1	0.41	114	22
Mean	2.5	92	13.5	18.5	5.7	19.3	11.1	28.6	0.41	115	28
LSD (0.01)	0.6	14	5.0	8.3	0.9	1.8	3.2	9.0	0.07	6	7

significantly in plant weight, harvest index, plant height, seeds per pod, seed weight and onset of flowering.

Among the female parents, Derrimut was the earliest and shortest and had the lowest yield as well as the lowest plant weight, but it had the most basal branches. Both Wirrega and Derrimut (a parent of Wirrega) had the same hundred seed weight and flowering period. Wirrega had more seeds per pod but was later in reaching maturity and it gave a higher yield and produced better vegetative growth; although Wirrega was the highest yielding female, with the highest plant weight, its yield and plant weight were not significantly different from those of Alma and Dundale. Alma and Dundale were similar in all characteristics except seeds per pod and they were taller and produced bigger seeds than Wirrega or Derrimut.

All traits were much more variable among the 18 exotic male parents than among the four locally adapted female parents. Whero, which gave the highest grain yield among the male parents (16.0 g per plant), had no outstandingly high yield component. It was taller and later in maturity than the female parents.

SA 236 produced heavier seeds (33.6 g per hundred seeds) but only a moderate number of seeds per pod (5.4). Although the number of pods per plant was low (12.4), its yield (14.5 g per plant) was as high as the females.

SA 54, SA 123, SA 129, SA 483 were low yielding although they had many pods per plant. They were similar in plant height, basal branches per plant, pods per plant and hundred seed weight. Among these males, SA 54 was the latest to mature, produced the smallest seeds and had the lowest harvest index. SA 123 and SA 483 had the equal most pods per plant.

SA 24, SA 465 and Solara were dwarf types with short internodes, a high harvest index, near average grain yield and relative earliness in the onset of flowering. The differences among them were that Solara was semi-leafless and had bigger seeds than SA 24 and SA 465, while SA 465 had more seeds per pod and fewer pods per plant than SA 24 and Solara.

SA 15 was the earliest parent, starting to flower 91 days after planting. It had larger seeds (32.2 g per hundred seeds), moderate pod numbers per plant (16.8) and the fewest seeds per pod (3.5) and consequently its yield was moderate.

Garfield, the introduced cultivar from the USA gave the same seed weight and the same number of seeds per pod as did the female parents but there were fewer pods per plant, therefore its yield was relatively low.

SA 35 started flowering at mid-season and had the longest flowering period of all parents. It had moderate hundred seed weight (22.6 g), fewest pods per plant (9.4), few seeds per pod (4.8) and a relatively low yield. Similarly, SA 51, a fasciated type, had moderate hundred seed weight (22.9), few pods per plant (11.3), few seeds per pod (4.5), and a low yield (8.1). Because of its low yield and more vegetative growth, its harvest index was also low (0.34).

SA 157 had moderate values for all agronomic traits including grain yield.

SA 247 and SA 248, accessions from Ethiopia, were similar in a number of morphological characteristics but SA 248 had more basal branches, a higher seed weight and initiated flowering eleven days after SA 247.

SA 688 and SA 828 were late maturing parents and had the same grain yield, plant weight and harvest index. SA 688 produced more basal branches, more seeds per pod and had a longer flowering period whereas SA 828 was taller and had bigger seeds.

d.) Parent x environment interaction

For most traits, the best parent was different in each environment (Table 4.1.4). SA 54 had the most basal branches at E1 and E3 while SA 123 had the most at E2 and SA 128 at E4. SA 236 was tallest at E2 while SA 828 was tallest at the other three sites. Hundred seed weight and seeds per pod were less variable over environments than the other traits. SA 688 had the most seeds per pod in three environments. SA 236 produced the biggest seeds at E1, E2 and E4 while SA 15 produced the biggest seeds at E3 and also the second biggest in the other three environments.

Table 4.1.4 The best parent for each character and its value in each environment

Character	Urrbrae (E1)		Turretfield (E2)		Charlick (E3)		Urrbrae (E4)	
Basal branches per plant (number)	SA 54	(5.0)	SA 123	(6.0)	SA 54	(5.1)	SA 128	(6.8)
Plant height (cm)	SA 828	(143)	SA 236	(136)	SA 828	(161)	NA	
Podded nodes per plant (number)	SA 54	(18)	SA 483	(36)	SA 248	(24)	NA	
Pods per plant (number)	SA 54	(31.8)	SA 483	(60.0)	SA 688	(44.1)	Solara	(33.0)
Seeds per pod (number)	SA 688	(7.6)	SA 688	(7.5)	SA 688	(7.9)	SA 123	(7.0)
Hundred seed weight (g)	SA 236	(33.5)	SA 236	(34.7)	SA 15	(35.7)	SA 236	(31.9)
Grain yield (g per plant)	SA 236	(10.7)	Wirrega	(22.3)	Whero	(26.8)	Dundale	(13.2)
Plant weight (g per plant)	SA 236	(23.9)	Wirrega	(51.0)	Whero	(55.1)	SA 248	(70.2)
Harvest index	SA 24	(0.63)	SA 24	(0.61)	SA 465	(0.60)	Solara	(0.41)

Environment

NA, data not available

e.) F_1 performance

In general, F_1s grew more vigorously than their parents, giving more basal branches, pods and podded nodes per plant as well as bigger seeds. They were taller with greater plant weight and higher yields than the average of their parents. The average performances of each cross across four environments are given in Table 4.1.5

The average grain yield of F_1s was 16.1 g per plant with a range from 9.1 (Alma x SA 123) to 20.3 g (Dundale x SA 123). Of the 72 crosses, 24 exceeded the yield of the best parent but only seven did so significantly ($P < 0.05$) and four of those highly significantly ($P < 0.01$).

The average for plant weight was 37.5 g per plant with the minimum of 29.4 and maximum of 50.3 g in crosses Derrimut x Solara and Dundale x SA 123 respectively. Nine crosses surpassed the highest parent for this trait.

The average harvest index in F_1s was 0.43 with the range from 0.27 (Alma x SA 54) to 0.55 (Derrimut x SA 465), the latter marginally exceeding the best parent value of 0.53.

The average number of basal branches per plant in F_1s was 2.9 with the minimum of 1.6 and maximum of 6.5 in Alma x SA 129 and Alma x SA 236 respectively. Seven crosses exceeded the best parent.

The majority of F_1s were taller than the mid-parent and more than half the F_1s exceeded the taller parent. However, no cross was taller than the tallest parent. The

Table 4.1.5 Average performance of F_1 over 4 environments (except plant height and number of podded nodes perplant, 3 environments; onset of flowering, 2 environments and duration of flowering, 1 environment)

Cross		Basal branches per plant (number)	Plant height (cm)	Podded nodes per plant (number)	Pods per plant (number)	Seeds per pod (number)	Hundred seed weight (g)	Grain yield (g)	Plant weight (g)	Harvest index	Onset of flowering (days after sowing)	Duration of flowering (days)
Alma x	Garfield	1.8	122	15.1	15.9	6.0	25.4	17.2	34.5	0.50	116	29
	SA 15	3.6	135	6.9	9.9	4.3	20.5	9.1	37.2	0.27	126	20
	SA 24	1.7	135	13.4	22.0	4.4	29.1	18.6†	43.9	0.44	109	32
	SA 35	1.8	125	11.1	17.6	5.5	25.6	16.9	39.6	0.45	108	35
	SA 51	1.8	117	11.9	19.0	5.7	27.0	15.7	38.6	0.44	108	38
	SA 54	5.6††	115	28.6††	48.8††	6.2	12.3	12.0	47.3	0.28	130	27
	SA 123	4.1	103	20.2	30.2	6.7	12.8	16.5	47.6	0.39	130	21
	SA 129	6.5††	113	33.7††	46.6††	6.5	9.4	14.4	47.9	0.31	129	16
	SA 157	1.7	101	12.9	17.3	6.0	23.5	14.4	32.3	0.46	110	28
	SA 236	1.6	135	9.4	15.9	5.7	30.3	17.6	46.5	0.43	112	30
	SA 247	2.6	124	17.5	22.6	6.0	21.0	16.2	42.2	0.41	115	27
	SA 248	2.6	108	16.0	22.4	6.1	21.8	15.9	36.0	0.44	118	28
	SA 465	1.8	128	10.7	14.7	6.6	22.3	15.0	31.0	0.48	113	32
	SA 483	4.9	101	24.7††	35.3††	6.4	11.9	17.6	43.9	0.41	124	19
	SA 655	3.7	109	18.1	27.3	6.8	14.1	15.0	41.6	0.37	122	39
	SA 828	2.0	143	19.0	25.9	6.4	18.1	18.4†	49.7	0.40	118	27
	Solara	2.0	119	11.1	18.3	6.1	26.3	18.0	39.0	0.47	104	32
	Whero	2.1	120	10.6	14.9	6.1	24.4	15.8	38.5	0.42	111	26
Mean		2.9	112	17.1	24.7	5.8	20.2	16.1	39.5	0.43	112	31
The best parent		4.5	141	20.4	27.4	7.5	33.6	16.0	43.7	0.53	91	37
LSD (0.01)		0.7	12	3.2	6.3	0.6	1.4	3.0	8.1	0.04	12	7

†, ††: Significantly better than the best parent at $P<0.05$, $P<0.01$ respectively

Table 4.1.5 continued

Cross		Basal branches per plant (number)	Plant height (cm)	Podded nodes per plant (number)	Pods per plant (number)	Seeds per pod (number)	Hundred seed weight (g)	Grain yield (g)	Plant weight (g)	Harvest index	Onset of flowering (days after sowing)	Duration of flowering (days)
Derrimut x	Garfield	2.8	106	19.3	21.5	5.8	21.2	16.9	36.1	0.47	105	37
	SA 15	3.8	95	19.7	29.4	4.2	20.0	13.1	36.1	0.37	112	42††
	SA 24	2.5	106	15.2	19.0	4.1	24.3	15.9	33.1	0.47	101	37
	SA 35	1.9	103	10.3	15.2	5.6	21.5	13.6	29.8	0.45	103	33
	SA 51	1.8	140	14.3	22.5	5.4	23.8	15.7	35.4	0.45	104	31
	SA 54	4.5	92	23.4	40.9††	4.9	10.5	15.5	40.4	0.40	111	35
	SA 123	5.0	95	32.9††	41.6††	5.4	10.8	16.6	47.0	0.39	111	31
	SA 129	5.1†	84	25.8††	32.5†	5.9	10.7	19.5††	40.0	0.48	119	25
	SA 157	1.8	114	14.0	17.3	5.4	22.2	15.7	35.3	0.46	112	40
	SA 236	2.2	114	14.4	19.9	5.9	28.8	17.8	39.5	0.46	104	28
	SA 247	2.1	107	18.3	23.5	5.8	19.8	19.5††	40.2	0.48	107	29
	SA 248	3.0	115	17.4	26.3	5.8	20.6	17.5	37.2	0.48	109	29
	SA 465	2.2	108	14.1	20.4	6.5	20.8	18.1	33.1	0.55	105	34
	SA 483	4.3	78	23.8†	30.4†	5.6	13.1	15.9	34.9	0.45	108	32
	SA 655	3.1	102	20.0	30.2†	6.3	15.5	16.8	39.1	0.43	114	28
	SA 828	2.8	122	22.7	26.8	6.1	17.7	15.9	37.0	0.42	112	30
	Solara	2.2	87	10.4	15.9	5.2	23.0	13.2	29.4	0.49	97	27
	Whero	2.3	111	14.1	19.3	5.9	23.3	16.8	38.9	0.45	103	29
Mean		2.9	112	17.1	24.7	5.8	20.2	16.1	39.5	0.43	112	31
The best parent		4.5	141	20.4	27.4	7.5	33.6	16.0	43.7	0.53	91	37
LSD (0.01)		0.7	15	4.2	6.3	0.6	1.4	3.0	8.1	0.04	12	7

†, ††: Significantly better than the best parent at P<0.05, P<0.01 respectively

Table 4.1.5 continued

Cross		Basal branches per plant (number)	Plant height (cm)	Podded nodes per plant (number)	Pods per plant (number)	Seeds per pod (number)	Hundred seed weight (g)	Grain yield (g)	Plant weight (g)	Harvest index	Onset of flowering (days after sowing)	Duration of flowering (days)
Dundale x	Garfield	2.1	117	13.2	17.1	6.0	25.5	17.2	39.2	0.46	109	38
	SA 15	3.6	114	18.5	23.8	4.3	23.3	14.3	36.8	0.40	117	38
	SA 24	2.0	110	13.7	21.0	4.2	28.9	15.0	38.7	0.43	105	34
	SA 35	1.6	121	12.6	16.2	6.5	24.6	15.9	34.4	0.46	93	36
	SA 51	1.9	139	11.5	17.7	6.0	26.8	16.4	37.7	0.45	104	33
	SA 54	4.3	117	32.7††	44.4††	5.4	11.7	11.5	35.8	0.33	118	37
	SA 123	4.2	107	21.5	33.6†	6.5	11.9	20.3††	52.9†	0.42	124	28
	SA 129	5.4††	115	41.9††	62.9††	6.5	8.0	11.3	35.7	0.34	117	27
	SA 157	1.8	125	11.9	18.4	5.1	23.6	15.3	39.7	0.42	107	35
	SA 236	2.2	115	12.0	16.8	5.9	31.0	16.5	45.6	0.45	102	30
	SA 247	2.5	126	15.9	19.8	5.9	21.2	17.1	38.1	0.46	109	30
	SA 248	2.7	118	13.6	22.0	5.8	21.8	17.3	41.9	0.44	117	32
	SA 465	2.0	107	10.4	16.6	6.7	22.2	16.0	33.9	0.50	106	29
	SA 483	3.8	96	20.4	27.4	5.9	12.4	17.5	40.1	0.44	111	27
	SA 655	3.0	125	16.5	27.5	5.7	17.4	14.9	41.2	0.38	113	36
	SA 828	2.7	134	17.5	27.0	6.3	19.2	17.0	44.1	0.41	117	28
	Solara	2.0	121	11.0	16.6	5.5	26.8	16.0	33.4	0.49	104	32
	Whero	2.5	119	11.6	18.2	5.7	25.7	16.3	37.9	0.44	107	28
Mean		2.9	112	17.1	24.7	5.8	20.2	16.1	39.5	0.43	112	31
The best parent		4.5	141	20.4	27.4	7.5	33.6	16.0	43.7	0.53	91	37
LSD (0.01)		0.7	15	4.2	6.3	0.6	1.4	3.0	8.1	0.04	12	7

†, ††: Significantly better than the best parent at $P<0.05$, $P<0.01$ respectively

Table 4.1.5 continued

Cross		Basal branches per plant (number)	Plant height (cm)	Podded nodes per plant (number)	Pods per plant (number)	Seeds per pod (number)	Hundred seed weight (g)	Grain yield (g)	Plant weight (g)	Harvest index	Onset of flowering (days after sowing)	Duration of flowering (days)
Wirrega x	Garfield	1.8	105	15.2	20.0	5.9	22.5	17.3	39.5	0.45	110	34
	SA 15	3.8	117	15.0	23.2	4.6	18.8	13.0	39.6	0.33	114	38
	SA 24	1.8	115	14.8	22.2	4.4	25.9	16.8	37.9	0.45	115	34
	SA 35	2.3	102	10.3	18.2	5.7	22.3	17.8	36.4	0.49	108	30
	SA 51	2.0	122	11.6	18.0	6.0	23.4	17.2	37.5	0.45	109	33
	SA 54	5.0	108	29.9††	43.2††	6.1	9.7	15.8	41.7	0.39	113	31
	SA 123	4.0	95	24.6†	33.1†	6.6	11.4	17.4	38.4	0.44	124	30
	SA 129	4.2	103	18.2	27.7	6.7	11.4	18.2	39.3	0.46	118	26
	SA 157	1.8	110	16.7	24.0	6.0	22.5	18.7†	41.9	0.46	112	31
	SA 236	2.1	103	12.6	16.6	6.0	27.4	17.6	42.3	0.45	106	29
	SA 247	2.1	99	13.6	19.2	5.8	19.0	16.5	40.3	0.43	110	30
	SA 248	2.6	105	12.5	25.8	5.3	19.8	18.1	39.5	0.46	113	30
	SA 465	1.8	97	12.1	17.9	6.5	18.9	17.9	38.8	0.47	115	31
	SA 483	5.2†	98	18.3	31.3	6.1	11.6	16.6	50.0†	0.39	114	23
	SA 655	3.9	111	25.0††	34.7†	6.5	14.3	16.0	46.1	0.37	124	30
	SA 828	2.5	127	22.1	27.8	6.3	16.9	17.2	42.6	0.42	111	31
	Solara	2.2	101	11.8	16.7	5.9	24.6	15.3	34.8	0.47	116	31
	Whero	3.0	105	18.5	25.4	6.0	21.6	19.9††	44.1	0.47	108	29
Mean		2.9	112	17.1	24.7	5.8	20.2	16.1	39.5	0.43	112	31
The best parent		4.5	141	20.4	27.4	7.5	33.6	16.0	43.7	0.53	91	37
LSD (0.01)		0.7	15	4.2	6.3	0.6	1.4	3.0	8.1	0.04	12	7

†, ††: Significantly better than the best parent at $P<0.05$, $P<0.01$ respectively

average plant height in F_1s was 112.4 cm with a range from 78.3 cm to 144.8 cm recorded on Derrimut x SA 483 and Alma x SA 828 respectively.

The number of podded nodes in the F_1 hybrids averaged 17.1 with a range from 6.9 to 41.9 recorded in Alma x SA 15 and Dundale x SA 129 respectively. There were 27.4 pods per plant on average with a range from 9.3 to 69.9 produced by these crosses respectively.

More than half the F_1s exceeded the number of seeds per pod and also the seed weight of the mid-parent but none surpassed the best parent. The number of seeds per pod was 5.8 on average with a range from 4.3 (Alma x SA 15) to 6.7 (Alma x SA 129, Dundale x SA 465 and Wirrega x SA 129). The average hundred seed weight was 20.2 g with a range from 8 to 31 g. In some crosses of SA 54, SA 15 and SA 129, seeds were aborted, therefore they had lower seed weight than expected and this may be a cause of lower yield. The aborted seeds were found in crosses which flowered late and had a long flowering period which coincided with an interval of limited soil moisture at the end of season.

F_1 plants started flowering 97-130 days after sowing (mean, 112) and continued for 31 days. None was earlier than the earliest parent. In 6 crosses, the duration of flowering was longer than in any parent. Derrimut x SA 35 had the longest flowering period (40 days) whereas Alma x SA 129 had the shortest (16 days).

f.) F_1 x environment interaction

The maximum for each characteristic was found in a different cross in each environment (Table 4.1.6) except for seed weight in which Dundale x SA 236 produced the heaviest seed in all environments. These crosses with maximum expression were derived from at least one parent which was high in the value for that character. SA 54, SA 123, SA 129 and SA 483 were high in basal branches, podded nodes and pods per plant and their progenies were also the best for these traits. Similarly in other characteristics, SA 51, SA 236 and Alma were tall, Alma and SA 688 had many seeds per pod, Dundale and SA 236 had big seeds, their F_1s were superior at least in one site. For grain yield, Alma x SA 248 was superior in E1, Alma x SA 828 in E2, Dundale x SA 123 in E3 and Derrimut x SA 465 (which was derived from dwarf parents) in E4.

g.) The correlation between agronomic traits in F_1

The correlation coefficients between 11 agronomic traits were calculated for the F_1s (Table 4.1.7). Highly significant coefficients (r = 0.82 to 0.95) were found between podded nodes, pods and basal branches per plant. Plant weight was significantly correlated with these traits (r = 0.35 to 0.42) and hundred seed weight showed high negative correlations with them (r = -0.81 to -0.86). Grain yield was significant correlated with only harvest index, plant weight and seeds per pod (r = 0.64, 0.34 and 0.33 respectively). There was a significant negative correlation between onset and duration of flowering (r = -0.43), indicating that crosses which started flowering early tended to have a greater duration of flowering.

The correlation between F_1 and mid-parent value was found to be highly significant (<0.01) for all agronomic traits except grain yield, plant weight and harvest index (Table 4.1.8).

Table 4.1.7 Correlation coefficients (r) between 11 agronomic traits of F_1

Agronomic trait	Correlation coefficient (r)									
	Plant height	Podded nodes per plant	Pods per plant	Seeds per pod	Hundred seed weight	Grain yield	Plant weight	Harvest index	Onset of flowering	Duration of flowering
Basal branches per plant	-0.39**	0.82**	0.85**	0.14	-0.86**	-0.26	0.42**	-0.64**	0.64**	-0.38**
Plant height		-0.27	-0.25	-0.04	0.43**	-0.10	0.11	-0.17	-0.03	0.06
Podded nodes per plant			0.95**	0.22	-0.81**	-0.15	0.35**	-0.51**	0.51**	-0.21
Pods per plant				0.20	-0.82**	-0.19	0.41**	-0.57**	0.54**	-0.22
Seeds per pod					-0.34**	0.33**	0.23	0.13	0.26	-0.40**
Hundred seed weight						0.13	-0.33**	0.49**	-0.63**	0.33**
Grain yield							0.34**	0.64**	-0.15	-0.09
Plant weight								-0.45**	0.51**	-0.37**
Harvest index									-0.63**	0.18
Onset of flowering										-0.43**

**: $P < 0.01$

Table 4.1.8 Correlation coefficients (r) between mid-parent and F_1 values for 11 agronomic traits

Agronomic trait	Correlation coefficient (r)
Basal branches per plant	0.86**
Plant height	0.54**
Podded nodes per plant	0.58**
Pods per plant	0.61**
Seeds per pod	0.58**
Hundred seed weight	0.88**
Grain yield	0.25
Plant weight	0.21
Harvest index	0.17
Onset of flowering	0.45**
Duration of flowering	0.57**

*, **: $P < 0.05, 0.01$ respectively

4.1.2 Estimation of heterosis in the F_1 hybrids.

a.) The levels of heterosis in the F_1 hybrids.

Heterotic effects were evident for all traits (Table 4.1.9). The average level of heterosis over the mid-parent was positive for all traits except seeds per pod and seed weight. Average heterosis over the best parent was negative for these characters and also for plant height, duration of flowering and harvest index.

No cross had high heterosis for all traits. Heterosis for yield over the mid-parent or the superior parent could always be attributed to heterosis in at least one of the yield components. The averages of the levels of heterosis for grain yield over the mid-parent (Hmp), over the better parent (Hbp) and over the best parent (Hcm) were 30.8%, 11.3% and -1.6% with ranges from -28% to 103%, -34% to 58% and -39% to 20% respectively. Of 72 crosses, 70 gave positive heterosis over mid-parent, 58 over the better parent and 36 over the best parent.

The levels of heterosis for plant weight over mid-parent, better parent and the best parent were 34%, 16% and -10% respectively with the range from -1.4% to 106%, -24% to 60% and -29% to 30% respectively. Sixty-seven crosses expressed positive heterosis over mid-parent, 59 crosses over the better parent and 35 crosses over the best parent.

The average levels of heterosis for harvest index were very low, 0.6%, -2.7% and -20% for Hmp, Hbp and Hcm respectively with the ranges from -45% to 37%, -43% to 37% and

Table 4.1.6 The best cross for each agronomic character and its value in each environment

Character	Environment							
	Urrbrae (E1)		Turretfield (E2)		Charlick (E3)		Urrbrae (E4)	
Basal branches per plant (number)	Derrimut x SA 54	(4.7)	Alma x SA 129	(9.0)	Alma x SA 54	(7.8)	Wirrega x SA 483	(9.0)
Plant height (cm)	Wirrega x SA 51	(132)	Alma x SA 236	(193)	Alma x SA 15	(172)	NA	
Podded nodes per plant (number)	Dundale x SA 123	(23.3)	Alma x SA 129	(60.0)	Dundale x SA 54	(42.5)	NA	
Pods per plant (number)	Wirrega x SA 54	(35.8)	Alma x SA 129	(79.0)	Dundale x SA 54	(77.0)	Dundale x SA 123	(37.0)
Seeds per pod (number)	Alma x SA 688	(6.7)	Alma x SA 157	(7.5)	Wirrega x SA 688	(7.9)	Derrimut x SA 688	(7.6)
Hundred seed weight (g)	Dundale x SA 236	(31.2)	Dundale x SA 236	(32.4)	Dundale x SA 236	(35.2)	Dundale x SA 236	(31.0)
Grain yield (g per plant)	Alma x SA 248	(12.7)	Alma x SA 828	(28.5)	Dundale x SA 123	(30.0)	Derrimut x SA 465	(22.5)
Plant weight (g per plant)	Alma x SA 54	(28.6)	Alma x Whero	(64.0)	Alma x SA 54	(72.0)	Dundale x SA 123	(86.5)
Harvest index	Derrimut x Solara	(0.59)	Alma x SA 157	(0.54)	Derrimut x SA 157	(0.57)	Derrimut x SA 465	(0.55)

-48% to 7%. There were one cross, 27 crosses and 40 crosses with positive value for Hmp, Hbp and Hcm respectively.

The average levels of heterosis for basal branches, podded nodes and pods per plant were high and their ranges were wide as well (the average Hmp was 36.6, 24.9 and 38.5% with a range from -16 to 130%, -32 to 193% and -23 to 242% respectively). The majority of F_1s were superior to the mid-parent, eleven crosses for basal branches per plant, 33 for podded nodes per plant and 32 for pods per plant had higher values than the best parent.

On average, heterotic values for seed characteristics were negative, although half of F_1s had positive heterosis over mid-parent. Thirteen F_1s were superior to the best parent for seeds per pod and none had positive heterosis over the best parent for hundred seed weight.

All crosses started to flower later than the earliest parent. The level of heterosis over mid-parent for the days to flower was 1.4% with a range from -15% to 29%. There were 57 ~~28~~ crosses, ~~20 and one~~ with negative heterosis 38 over the mid-parent, 20 over the earlier parent and one over the earliest parent, ~~respectively~~.

For flowering duration, 57 crosses had positive values for Hmp, 21 for Hbp and 7 for Hcm. The averages of Hmp, Hbp and Hcm were 6.7%, 4.5% and -18.4% with ranges from -32.0% to 57.4%, -44.4% to 36.4% and -59.3% to 5.3% respectively.

b.) Heterosis and environment

Hmp, Hbp and Hcm all varied significantly among environments for basal branches, podded nodes, yield, plant weight and harvest index (Table 4.1.10). Only Hmp and Hbp varied significantly among environments for onset of flowering.

The level of heterosis over mid-parent for yield in poor environmental conditions (42.9% and 34.6% at E1 and E4 respectively) was higher than that in good conditions (21.0% and 25.3% at E2 and E3 respectively). Similarly, the levels of heterosis over the better parent averaged 29.8%, 0.2%, 4.5% and 11% at E1, E2, E3 and E4 respectively. Similar results were obtained for plant weight and harvest index.

There were no significant differences among environments for the level of heterosis for plant height. The levels of heterosis for basal branches, podded nodes and pods per plant in the poorest environment, E3 were lower than that in E1, E2 and E4.

Table 4.1.9 Mean and range of heterosis over the mid-parent value (Hmp), over the better parent (Hbp), over the best parent (Hcm) and number of crosses superior to mid-parent (>MP), better parent (>BP), and the best parent (>CM)

Character	Hmp (%)		Hbp (%)		Hcm (%)		Numbers of crosses		
	Mean	Range	Mean	Range	Mean	Range	>MP	>BP	>CM
Basal branches per plant	36.6	-16 to 130	26.3	-15 to 154	-1.5	-61 to 52	67	62	11
Plant height	19.2	-15 to 66	0.9	-38 to 206	0.3	0 to 47	63	37	0
Podded nodes per plant	24.9	-32 to 193	16.0	-38 to 206	1.6	-50 to 140	56	39	33
Pods per plant	38.5	-23 to 242	33.0	-21 to 274	8.7	-50 to 191	66	61	32
Seeds perpod	-1.4	-33 to 25	-7.5	-36 to 15	-10.2	-37 to 8	37	22	13
Hundred seed weight	-2.1	-49 to 26	-14.7	-66 to 27	-39.1	-76 to -5	44	23	0
Grain yield	30.8	-28 to 103	11.3	-34 to 58	-1.6	-39 to 20	70	58	36
Plant weight	34.0	1 to 106	16.1	-24 to 61	0.7	-29 to 30	67	59	35
Harvest index	0.6	-45 to 37	-2.7	-43 to 37	-20.2	-48 to 7	40	27	1
Onset of flowering	1.4	-15 to 29	8.4	-12 to 40	19.7	-4 to 48	38*	20*	1*
Duration of flowering	6.7	-32 to 57	-4.6	-44 to 37	-18.4	-59 to 5	57	21	7

* number of crosses which started flowering earlier than mid-parent, earlier parent or earliest parent

Table 4.1.10 The mean of heterosis over mid-parent (Hmp), over better parent (Hbp), and over the best parent (Hcm) from 4 environments (Urrbrae 1989 (E1), Turretfield (E2), Charlick (E3) and Urrbrae 1991 (E4))

Heterosis	Environment	Basal branches per plant	Plant height	Podded nodes per plant	Pods per plant	Seeds per pod	Hundred seed weight	Grain yield	Plant weight	Harvest index	Onset of flowering
Hmp (%)	E1	39.1	17.9	33.8	49.0	-0.9	-2.0	42.9	41.2	2.6	1.2
	E2	50.4	20.5	32.6	52.0	3.7	-2.8	21.0	26.0	-2.8	NA
	E3	20.7	19.1	8.1	21.0	0.7	2.3	25.3	32.0	-3.2	NA
	E4	36.0	NA	NA	30.0	-9.1	-5.7	34.6	36.4	5.6	1.6
LSD (0.05)		16.2	NS	16.2	25.0	8.3	4.9	22.9	16.6	4.2	NS
Hbp(%)	E1	32.7	-2.5	26.6	40.1	-7.2	-15.5	29.8	26.2	3.9	5.5
	E2	33.3	4.5	20.0	39.2	-4.2	-15.9	-0.2	10.9	-6.0	NA
	E3	16.8	0.6	1.4	20.7	-6.4	-11.1	4.5	13.3	-5.9	NA
	E4	17.4	NA	NA	32.0	-12.3	-15.9	11.0	13.8	-2.9	11.3
LSD (0.05)		16.2	NS	21.1	28.2	6.9	4.9	25.4	19.2	4.4	4.6
Hcm (%)	E1	-55.1	-27.0	23.8	11.3	-18.8	-39.9	18.6	21.2	-13.3	6.5
	E2	-23.5	-16.2	-32.8	-34.7	-15.4	-39.6	-3.2	0.9	-12.8	NA
	E3	-41.8	-25.9	14.1	51.4	11.2	-35.6	-14.2	-10.8	-12.5	NA
	E4	-0.6	NA	NA	6.6	-13.7	-38.3	-5.5	-13.3	-38.6	32.9
LSD (0.05)		23.1	NS	34.7	NS	NS	NS	29.1	21.5	9.7	8.4

NS, not significant; NA, data not available

There was significant variation among environments for the levels of heterosis over mid-parent and better parent for seed characteristics. The levels of heterosis over the mid-parent for seeds per pod at E1, E2, E3 and E4 were 9%, 3.7%, 0.7% and -9.1% and over the better parent were -7.2%, -4.2%, -6.4% and -12.3% respectively. The levels of heterosis over the mid-parent for hundred seed weight at E1, E2, E3 and E4 were -2.0%, -2.8%, 2.3% and -5.7% respectively.

c.) The correlation between the levels of heterosis of agronomic traits in F_1

The correlation coefficients between the three types of heterosis for various agronomic traits of F_1s were calculated (Tables 4.1.11, 4.1.12, 4.1.13). Many of the corresponding coefficients were significant. As seen before, there were significant positive correlations among the levels of heterosis for basal branches per plant, podded nodes per plant, pods per plant and plant weight (r = 0.50 to 0.87 for heterosis over mid-parent). The levels of heterosis (Hmp, Hbp and Hcm) for basal branches, podded nodes per plant and pods per plant were negatively correlated with those for hundred seed weight

Table 4.1.11 Correlation coefficients (r) between the levels of heterosis over mid-parent of 11 agronomic traits of F_1

Agronomic trait	Correlation coefficient (r)									
	Plant height	Podded nodes per plant	Pods per plant	Seeds per pod	Hundred seed weight	Grain yield	Plant weight	Harvest index	Onset of flowering	Duration of flowering
Basal branches per plant	-0.07	0.50**	0.57**	-0.04	-0.80**	-0.04	0.56**	-0.54**	0.53**	-0.06
Plant height		0.09	0.09	-0.37**	0.11	0.09	0.23	-0.19	0.05	0.02
Podded nodes per plant			0.87**	0.03	-0.61**	0.29	0.62**	-0.29	0.11	0.08
Pods per plant				-0.05	-0.63**	0.33**	0.69**	-0.29	0.02	0.17
Seeds per pod					-0.08	0.13	-0.22	0.43**	-0.24	-0.04
Hundred seed weight						0.00	-0.58**	0.51**	-0.42**	0.13
Grain yield							0.51**	0.40**	-0.29	0.12
Plant weight								-0.53**	0.22	-0.01
Harvest index									-0.54**	0.06
Onset of flowering										-0.11

**: $P < 0.01$

Table 4.1.12 Correlation coefficients (r) between the levels of heterosis over the better parent of 11 agronomic traits of F_1

Agronomic trait	Correlation coefficient (r)									
	Plant height	Podded nodes per plant	Pods per plant	Seeds per pod	Hundred seed weight	Grain yield	Plant weight	Harvest index	Onset of flowering	Duration of flowering
Basal branches per plant	0.00	0.32**	0.40**	-0.18	-0.51**	-0.34	0.19	-0.40**	0.52**	-0.11
Plant height		-0.11	-0.07	-0.30	0.18	-0.08	0.06	-0.08	0.00	0.24
Podded nodes per plant			0.91	0.13	-0.69**	-0.12	0.46**	-0.51**	0.41**	-0.15
Pods per plant				0.11	-0.67**	-0.20	0.45**	-0.48**	0.40**	-0.22
Seeds per pod					-0.05	0.23	-0.14	0.27	-0.46**	-0.28
Hundred seed weight						0.31	-0.43**	0.56**	-0.53**	0.24
Grain yield							0.14	0.50**	-0.24	-0.10
Plant weight								-0.62**	0.38**	-0.09
Harvest index									-0.60**	-0.03
Onset of flowering										-0.17

**: $P < 0.01$

Table 4.1.13 Correlation coefficients (r) between the levels of heterosis over the best parent of 11 agronomic traits of F_1

Agronomic trait	Correlation coefficient (r)									
	Plant height	Podded nodes per plant	Pods per plant	Seeds per pod	Hundred seed weight	Grain yield	Plant weight	Harvest index	Onset of flowering	Duration of flowering
Basal branches per plant	-0.38**	0.29	0.83**	0.18	-0.86**	-0.28	0.62**	-0.62	0.68**	-0.32
Plant height		-0.15	-0.23	-0.02	0.41	-0.03	0.08	-0.19	-0.05	0.15
Podded nodes per plant			0.22	0.24	-0.31	0.10	0.24	-0.06	0.18	0.14
Pods per plant				0.20	-0.79**	-0.20	0.54**	-0.58**	0.54**	-0.16
Seeds per pod					-0.39**	0.30*	0.18	0.10	0.17	-0.27
Hundred seed weight						0.20	-0.51**	0.48**	-0.66**	0.27
Grain yield							0.14	0.61**	-0.31*	-0.09
Plant weight								-0.62**	0.63**	-0.16
Harvest index									-0.68**	0.04
Onset of flowering										-0.27

*, **: $P < 0.05$, 0.01 respectively

On average, heterosis for grain yield over mid-parent was mainly due to an increase in pods per plant rather than in hundred seed weight or seeds per pod. However, the correlation coefficient between the level of heterosis for grain yield and that for pods per plant was relatively low ($r = 0.33$). Plant weight was the only trait which showed a significant positive correlation with the levels of heterosis for grain yield ($r = 0.51$). There was no correlation between other agronomic traits and grain yield in terms of the levels of heterosis over the better or the best parents.

4.1.3 F_2 performance, inbreeding depression and heterosis

Separate analyses were done for each environment and a combined analysis was done using 54 F_2 families sown at all 4 environments. Significant differences among environments were found for grain yield (Table 4.1.14) but not for plant weight or harvest index. There were significant effects for cross and the cross x environment interaction for all 3 traits.

Table 4.1.14 Summary analysis of variance for grain yield, plant weight and harvest index of 54 F_2 families across 4 environments

Source of variance	df	Mean square		
		Grain yield (g)	Plant weight (g)	Harvest index
Environment (E)	3	4435**	13295ns	0.92ns
Replication / Environment (R/E)	4	205	2915	0.15
F_2	53	46***	238**	0.018***
F_2 x E	159	41***	218***	0.007**
Pooled error	212	16	87	0.005
Mean		14.4	33.6	0.45

ns, not significant; **, ***: $P < 0.01, 0.001$ respectively

Grain yield and plant weight were lower in the F_2 populations than in the F_1s while harvest index was marginally higher (Table 4.1.15). In the 54 families, the range of grain yield was 10.6 to 20.0 g per plant. One F_2 (Alma x SA 24) yielded more than the best parent and 27 F_2s were not significantly different from the best parent in yield. The range of plant weight in F_2 was from 22 to 48 g per plant and none exceeded the best parent. Thirty four F_2 families had as high harvest index as the highest parent but none surpassed the best parent.

The mean of inbreeding depression over four environments was 29.6%, 13% and 8.9% for grain yield, plant weight and harvest index respectively. The levels of heterosis (in the F_2) over mid-parent for grain yield, plant weight and harvest index were 16%, 27% and 2% respectively. There were negative values for the average of F_2 heterosis over the better and the best parent for all traits.

Table 4.1.15 Mean of F_2, F_1, inbreeding depression, the levels of heterosis over mid-parent, over better parent and over the best parent of F_2 in four environments

Environment	F_2 mean	F_1 mean	Inbreeding depression (%)	Hmp (F_2) (%)	Hbp (F_2) (%)	Hcm (F_2) (%)
Grain yield (g)						
E1	9.0	10.3	19.7	7.3	-2.6	-19.1
E2	18.8	20.6	36.3	17.1	-4.5	-7.9
E3	21.3	24.5	21.2	19.0	-5.8	-1.0
E4	9.6	12.1	41.3	21.3	-1.0	-9.6
Mean	14.7	16.9	29.6	16.1	-3.5	-9.4
LSD (0.05)						
Plant weight (g)						
E1	17.9	21.4	12.4	15.6	5.7	-6.0
E2	39.0	44.9	6.1	37.1	-3.2	-26.0
E3	43.1	50.0	9.2	39.1	-5.3	-7.9
E4	34.7	40.8	24.2	16.8	-4.0	-20.6
Mean	33.7	39.3	13.0	27.2	-1.7	-15.1
LSD (0.05)						
Harvest index						
E1	0.51	0.49	5.9	0.5	5.1	-47.9
E2	0.48	0.46	5.3	0.5	-1.0	-5.3
E3	0.50	0.49	2.5	0.5	-2.8	-12.6
E4	0.32	0.33	21.9	6.7	-5.9	-31.2
Mean	0.45	0.44	8.9	2.0	-1.1	-24.3
LSD (0.05)						

The expression of F_2 for grain yield, plant weight and harvest index were all also affected by environmental conditions (Table 4.1.15) together with the level of heterosis of F_2s over mid-parent.

4.1.4 Combining ability

General and specific combining ability for all traits varied significantly among parents, except SCA for plant weight (Tables 4.1.16 and 4.1.19). The significant GCA and SCA effects for onset and duration of flowering period could not be tested for significance because data were collected from only one location.

a.) General combining ability in female parents

Wirrega showed highly significant positive GCA effects for grain yield (0.80 g per plant) and seeds per pod (0.10) together with significant negative effects for plant height (-5.60 cm) and hundred seed weight (-1.1 g). Derrimut also had significant negative GCA effects for plant height and hundred seed weight as well as for onset of flowering, while Alma and Dundale which were the taller females with large seeds had significant positive GCA effects for plant height and seed weight. Alma expressed significant positive GCA effects for seeds per pod and onset of flowering but gave a negative GCA effect for the duration of flowering whereas Dundale gave the opposite results.

b.) General combining ability in male parents

None of the 18 males expressed significant positive GCA effects for yield, although the effects of SA 123, SA 236 and SA 247 approached significance (>1.0 g per plant). SA15 and SA 54 had highly significant negative effects for yield with values of -3.9 and -2.6 g per plant respectively. Both SA 15 and SA 54 had highly significant GCA effects for lateness in onset of flowering (5 and 6.1 days respectively), resulting in their F_1s being too late in setting seeds and low in yield. They also showed significantly negative GCA effects for harvest index.

SA 123 imparted significantly greater plant weight to its crosses (7.05 g) although this line was itself low in plant weight. On the other hand, the crosses of Solara, SA 465 and SA 35 had significantly reduced plant weights (4.35-5.43 g). Similarly, Garfield, SA 35, SA

Table 4.1.16 Estimates of general combining ability effects of parents for important agronomic traits

Parent	Basal branches per plant	Plant height	Podded nodes per plant	Pods per plant	Seeds per pod	Hundred seed weight	Grain yield	Plant weight	Harvest index	Onset of flowering	Duration of flowering
Females (gi)											
Alma	0.00	7.7**	-0.9	-1.0	0.17**	0.8**	-0.47**	1.56	-0.021	4.9**	-2.5
Derrimut	0.08**	-7.9**	1.3*	0.6*	-0.25**	-0.8**	0.06	-2.59**	0.022	-4.3**	1.4
Dundale	-0.09**	5.8**	-0.6	0.3	-0.03**	1.1**	-0.39**	-0.17	-0.004*	-2.0*	1.3
Wirrega	0.01	-5.6**	-0.3	0.1	0.10**	-1.1**	0.80**	1.20	0.004*	1.4	-0.2
Males (gj)											
Garfield	-0.73**	0.2	-1.4	-6.0*	0.15	3.6**	0.89	-2.08	0.038	-2.0	3.6
SA 15	0.81**	3.0	-2.1	-3.0	-1.46**	0.6	-3.91**	-1.96	-0.089*	5.0**	3.6
SA 24	-0.88**	4.2	-2.8	-3.5	-1.55**	6.9**	0.32	-0.98	0.015	-4.6**	3.6
SA 35	-0.97**	0.5	-6.0*	-7.8**	0.03	3.4**	-0.22	-4.35*	0.032	-8.9**	2.6
SA 51	-1.00**	16.9**	-4.8	-5.2	-0.04	5.1**	-0.01	-2.09	0.018	-5.7**	3.1
SA 54	1.96**	-4.2	11.6**	19.8**	-0.13	-9.1**	-2.55**	1.89	-0.083*	6.1**	1.9
SA 123	1.46*	-12.2	7.7**	10.1**	0.51**	-8.4**	1.42	7.05**	-0.019	10.5**	-3.0
SA 129	2.39**	-8.6	12.8**	17.9**	0.60**	-10.2**	-0.41	1.34	-0.036	8.8**	-7.4
SA 157	-1.09**	0.3	-3.2	-5.3	-0.17	2.9**	-0.26	-2.09	0.019	-1.7	2.6
SA 236	-0.85**	4.6	-5.0*	-7.3*	0.05	9.3**	1.07	4.09	0.018	-5.8**	-1.2
SA 247	-0.56*	1.7	-0.8	-3.3	0.09	0.2	1.04	0.82	0.011	-1.5	-1.4
SA 248	-0.17	-0.9	-2.1	-0.5	-0.07	0.9	0.91	-0.73	0.023	2.1	-0.9
SA 465	-0.95**	-2.2	-5.3*	-7.2*	0.79**	1.0	0.50	-5.43*	0.067	-2.4	0.8
SA 483	1.67**	-19.0**	4.7	6.5*	0.20	-7.8**	0.63	2.84	-0.008	2.5	-5.5
SA 688	0.55*	-0.4	2.8	5.3	0.49**	-4.8**	-0.60	2.57	-0.045	6.5**	2.4
SA 828	-0.39	19.3**	3.3	2.3	0.51**	-2.1**	0.87	3.95	-0.019	2.6	-1.9
Solara	-0.79**	-5.2	-6.0*	-7.7**	-0.11	5.1**	-0.62	-5.26*	0.050	-6.6**	-0.2
Whero	-0.44	1.7	-3.4	-5.1	0.11	3.6**	0.91	0.44	0.014	-4.6**	-2.8
t 0.05 (SEgi)	0.019	1.0	1.0	0.55	0.005	0.05	0.19	1.97	0.0004	1.95	NA
t 0.01 (SEgi)	0.025	1.3	3.1	0.72	0.007	0.07	0.25	2.60	0.0005	2.56	NA
t 0.05 (SEgj)	0.045	12.4	5.0	5.7	0.035	1.15	1.75	4.25	0.08	2.91	NA
t 0.01 (SEgj)	0.059	15.8	6.3	7.5	0.046	1.52	2.30	5.60	0.11	3.83	NA

NA, data not available; ns, not significant; *, **, ***: $P < 0.05, 0.01, 0.001$ respectively

157, SA 236 and Whero, all had moderate harvest indices whilst their crosses had higher harvest indices.

SA 54, SA 123, SA 129 and SA 483 showed many basal branches, podded nodes and pods per plant (Table 4.1.3) and also showed highly significant positive GCA effects for these characters (Table 4.1.16). In the same manner, SA 51 and SA 828 were tall parents with high GCA effects for plant height and SA 236, for high hundred seed weight.

Other parents showed a low value and also significant negative GCA for basal branches, podded nodes per plant, pods per plant, harvest index, plant height and seed weight. SA 483 had the highest negative GCA effect for plant height while Solara, SA 35, SA 465 and SA 236 had high negative GCA effects for podded nodes as well as for pod numbers. SA 54, SA 123, SA 129, SA 483, SA 688 and SA 828 gave highly negative GCA effects for seed weight.

Similarly, in flowering traits, SA 129 and SA 123 had short flowering duration and imparted this character to their crosses. SA 24, SA 35 and SA 157 which had long flowering duration, also imparted longer days of flowering to their crosses.

Solara, SA 24, SA 51 and SA 35 had significant positive GCA for earliness in their crosses. SA 123, SA 465, SA 688 and SA 828 had significant positive GCA for the seeds per pod and also produced many seeds per pod.

As mentioned above, the *per se* performance of parents was reflected in corresponding GCA effects in many traits. The correlation coefficient between the average performance and the GCA effects was highly significant for basal branches, podded nodes and pods per plant, hundred seed weight and duration of flowering (Table 4.1.17). However the correlations for other traits (grain yield, plant weight and harvest index) were positive but non-significant.

The correlation coefficients between the pooled general combining ability effects of parents (GCA female parent + GCA male parent) and all three level of heterosis were significant for all traits except Hbp and Hmp for plant height and were particularly high for Hcm (Table 4.1.18).

Table 4.1.17 Correlation coefficients between the *per se* performance of parents and their general combining ability effects for 11 agronomic traits

Agronomic trait	Correlation coefficient (r)
Basal branches per plant	0.89**
Plant height	0.56**
Podded nodes per plant	0.65**
Pods per plant	0.69**
Seeds per pod	0.59**
Hundred seed weight	0.89**
Grain yield	0.30*
Plant weight	0.14
Harvest index	0.25
Onset of flowering	0.45*
Duration of flowering	0.70**

*, **: $P < 0.05, 0.01$ respectively

Table 4.1.18 Correlation coefficients (r) between general combining ability and the level of heterosis over mid-parent, over the better parent and over the best parent

Agronomic trait	Correlation coefficients (r) between GCA and		
	Hmp	Hbp	Hcm
Basal branches per plant	0.74**	0.44**	0.95**
Plant height	0.02	0.12	0.82**
Podded nodes per plant	0.73**	0.84**	0.88**
Pods per plant	0.75**	0.76**	0.87**
Seeds per pod	0.54**	0.72**	0.92**
Hundred seed weight	0.75*	0.79**	0.99**
Grain yield	0.25*	0.60**	0.66**
Plant weight	0.30*	0.29*	0.71**
Harvest index	0.62**	0.74**	0.86**
Onset of flowering	0.46**	0.54**	0.84**
Duration of flowering	0.36**	0.57**	0.57**

*, **: $P < 0.05, 0.01$ respectively

c.) Specific combining ability

SCA effects were estimated for all traits in all 72 crosses (Table 4.1.19). Significant negative SCA effects were found for nine traits (all except onset and duration of

Table 4.1.19 Estimates of specific combining ability effects of 72 crosses for 11 important agronomic traits

Cross		Basal branches per plant	Plant height	Podded nodes per plant	Pods per plant	Seeds per pod	Hundred seed weight	Grain yield	Plant weight	Harvest index	Onset of flowering	Duration of flowering
Alma x	Garfield	-0.35	2.0	0.3	-1.7	-0.12	0.97	0.51	-4.4	0.053**	0.8	-3.1
	SA 15	-0.10	12.3	-7.2**	-10.7**	-0.21	-0.94	-2.79*	-1.8	-0.051*	3.9	-11.5
	SA 24	-0.30	11.0	0.1	1.9	-0.02	1.28*	2.48*	3.9	0.015	-2.8	0.5
	SA 35	-0.12	4.8	1.0	1.8	-0.50*	1.35*	1.32	3.0	0.009	0.2	3.9
	SA 51	-0.08	-20.1*	0.5	0.7	-0.22	0.98	-0.09	-0.3	0.013	-3.2	7.0
	SA 54	0.76*	0.0	0.9	5.5	0.37	0.48	-1.25	4.5	-0.046*	7.2**	-2.8
	SA 123	-0.25	-4.2	-3.7	-3.4	0.22	0.31	-0.71	-0.4	0.000	2.4	-3.9
	SA 129	1.23**	1.7	4.7	5.2	-0.07	-1.24*	-0.99	5.6	-0.063**	3.5	-5.1
	SA 157	-0.09	-19.0*	0.0	-1.0	0.20	-0.24	-1.13	-6.6	0.032	-4.8*	-2.5
	SA 236	-0.43	11.0	-1.8	-0.4	-0.32	0.16	0.73	1.5	0.003	0.8	3.0
	SA 247	0.27	2.6	2.1	2.3	-0.05	-0.03	-0.64	0.4	-0.010	-0.1	0.5
	SA 248	-0.12	-10.4	2.0	-0.7	0.21	0.01	-0.81	-4.2	0.008	-1.3	1.0
	SA 465	-0.13	10.4	-0.2	-1.7	-0.16	0.47	-1.29	-4.5	0.004	-1.6	3.0
	SA 483	0.35	0.4	3.9	5.2	0.23	-1.12*	1.17	0.1	0.008	5.1*	-4.0
	SA 655	0.27	-10.2	-0.8	-1.6	0.34	-1.96**	-0.20	-1.9	0.005	-0.9	8.1
	SA 828	-0.49	4.4	-0.4	0.0	-0.08	-0.63	1.73	4.8	0.009	-1.8	0.4
	Solara	-0.09	4.3	1.0	2.4	0.24	0.33	2.82*	3.3	0.011	-5.8*	4.3
	Whero	-0.34	-1.0	-2.2	-3.6	0.02	-0.09	-0.91	-2.9	-0.003	-1.5	0.6
t 0.05 (SEij)		0.68	17.6	5.5	5.8	0.46	1.05	2.32	6.8	0.039	4.1	NA
t 0.01 (SEij)		0.90	22.0	6.9	7.7	0.61	1.38	3.05	8.9	0.052	5.4	NA

NA: Data not available; *, **: P< 0.05, 0.01 respectively

Table 4.1.19 Continued

Cross		Basal branches per plant	Plant height	Podded nodes per plant	Pods per plant	Seeds per pod	Hundred seed weight	Grain yield	Plant weight	Harvest index	Onset of flowering	Duration of flowering
Derrimut x	Garfield	0.58	1.5	2.4	2.3	0.10	-1.67**	-0.32	1.4	-0.020	-0.2	1.1
	SA 15	0.03	-12.1	3.5	7.2*	0.11	0.12	0.68	1.3	0.006	-0.9	6.1
	SA 24	0.43	-2.6	-0.4	-2.6	0.10	-1.96**	-0.75	-2.7	0.002	-2.1	1.7
	SA 35	-0.09	-1.8	-2.0	-2.2	0.02	-1.20*	-2.51**	-2.7	-0.034	4.7*	-1.6
	SA 51	-0.15	18.1*	0.7	2.6	-0.10	-0.66	-0.62	0.7	-0.020	1.8	-4.4
	SA 54	-0.42	-8.1	-6.5*	-4.0	-0.52*	0.24	1.72	1.7	0.031	-2.7	1.4
	SA 123	0.58	2.8	6.8*	6.4*	-0.66**	-0.13	-1.14	3.1	-0.043*	-6.8**	2.0
	SA 129	-0.24	-11.8	-5.3	-10.5**	-0.25	1.61**	3.58**	1.9	0.064**	2.4	0.4
	SA 157	-0.06	9.3	-1.1	-2.5	0.02	0.02	-0.36	0.6	-0.011	5.9**	5.1
	SA 236	0.09	4.9	1.1	2.1	0.30	0.22	0.40	-1.4	-0.010	2.7	-2.5
	SA 247	-0.30	0.9	0.7	1.7	0.16	0.33	2.13	2.6	0.017	0.9	-1.3
	SA 248	0.21	11.5	1.3	1.6	0.32	0.37	0.26	1.1	0.005	-1.0	-1.8
	SA 465	0.20	5.8	1.1	2.5	0.16	0.53	1.28	1.7	0.031	-0.7	1.2
	SA 483	-0.32	-7.3	0.7	-1.3	-0.15	1.63**	-1.06	-4.7	0.005	-1.9	5.2
	SA 655	-0.41	-1.9	-1.2	-0.3	0.26	0.99	1.07	-0.3	0.022	0.1	-6.4
	SA 828	0.23	-1.6	1.1	-0.7	0.04	0.53	-1.30	-3.8	-0.014	1.7	-0.1
	Solara	0.04	-11.9	-2.0	-1.6	-0.24	-1.42**	-2.51*	-2.1	-0.012	-4.1*	-5.1
	Whero	-0.21	4.6	-0.8	-0.7	0.24	0.36	-0.44	1.7	-0.016	0.4	-0.2
t 0.05 (SEij)		0.68	17.6	5.5	5.8	0.46	1.05	2.32	6.8	0.039	4.1	NA
t 0.01 (SEij)		0.90	22.0	6.9	7.7	0.61	1.38	3.05	8.9	0.052	5.4	NA

NA: Data not available; *, **: P< 0.05, 0.01 respectively

Table 4.1.19 Continued

Cross		Basal branches per plant	Plant height	Podded nodes per plant	Pods per plant	Seeds per pod	Hundred seed weight	Grain yield	Plant weight	Harvest index	Onset of flowering	Duration of flowering
Dundale x	Garfield	0.04	-1.3	-2.5	-1.8	0.08	0.73	0.43	2.1	-0.005	0.6	2.4
	SA 15	0.00	-7.4	3.5	2.0	-0.01	1.52**	2.32*	-0.5	0.061**	1.8	2.1
	SA 24	0.09	-12.5	-0.5	-0.3	-0.02	0.74	-1.20	0.5	-0.012	-0.9	-1.6
	SA 35	-0.22	2.3	1.6	-0.9	0.70**	0.00	0.23	-0.5	0.001	-8.1**	1.4
	SA 51	0.12	3.6	-0.7	-1.9	0.28	0.44	0.52	0.6	0.005	0.0	-2.4
	SA 54	-0.45	3.2	4.1	-0.2	-0.23	-0.46	-1.83	-5.3	-0.014	2.2	2.8
	SA 123	-0.05	1.4	-3.2	-1.3	0.22	-0.93	3.00*	6.6	0.012	3.8	-1.0
	SA 129	0.22	5.7	12.1**	20.2**	0.13	-2.98**	-4.17**	-4.9	-0.051*	-1.6	2.1
	SA 157	0.10	6.4	-1.9	-1.1	-0.50*	-0.48	-0.32	2.6	-0.026	-1.8	0.1
	SA 236	0.26	-7.6	-0.1	-0.7	0.08	0.52	-0.46	2.3	0.005	-2.3	-0.5
	SA 247	0.27	5.7	-0.3	-1.7	0.05	-0.17	0.18	-1.9	0.022	0.7	-0.6
	SA 248	0.08	0.1	-1.2	-2.4	0.11	-0.33	0.50	3.4	-0.010	4.6*	0.9
	SA 465	0.16	-8.5	-1.4	-1.0	0.14	0.03	-0.38	-0.8	0.006	-1.4	-3.5
	SA 483	-0.66	-3.3	-1.3	-4.0	-0.07	-0.97	0.99	-2.0	0.020	-1.8	0.8
	SA 655	-0.34	7.3	-3.3	-2.7	-0.56*	0.99	-0.38	-0.6	-0.002	-2.9	1.3
	SA 828	0.30	-3.4	-2.8	-0.2	0.02	0.13	0.24	0.9	0.002	4.8*	-2.1
	Solara	0.00	8.5	0.0	-0.6	-0.15	0.48	0.74	-0.6	0.013	0.8	-0.1
	Whero	0.15	-0.4	-2.0	-1.5	-0.18	0.86	-0.50	-1.8	-0.001	1.4	-1.5
t 0.05 (SEij)		0.68	17.6	5.5	5.8	0.46	1.05	2.32	6.8	0.039	4.1	NA
t 0.01 (SEij)		0.90	22.0	6.9	7.7	0.61	1.38	3.05	8.9	0.052	5.4	NA

NA: Data not available; *, **: P< 0.05, 0.01 respectively

Table 4.1.19 Continued

Cross		Basal branches per plant	Plant height	Podded nodes per plant	Pods per plant	Seeds per pod	Hundred seed weight	Grain yield	Plant weight	Harvest index	Onset of flowering	Duration of flowering
Wirrega x	Garfield	-0.36	-2.2	-0.2	1.24	-0.15	-0.05	-0.66	1.0	-0.023	-1.2	-0.4
	SA 15	0.09	7.2	0.2	1.47	0.16	-0.76	-0.16	0.9	-0.017	-4.7*	3.6
	SA 24	-0.21	4.1	0.8	0.99	0.05	-0.04	-0.59	-1.7	0.000	5.8**	-0.4
	SA 35	0.37	-5.3	-0.5	1.26	-0.23	-0.07	0.95	0.2	0.023	3.3	-3.4
	SA 51	0.11	-1.6	-0.5	-1.47	0.14	-0.74	0.14	-1.0	-0.003	1.4	-0.3
	SA 54	0.15	4.9	1.5	-1.28	0.33	-0.24	1.29	-0.8	0.038	-6.7**	-1.4
	SA 123	-0.36	-0.1	0.1	-1.68	0.19	0.79	-1.08	-9.2**	0.024	0.7	2.8
	SA 129	-1.08**	4.4	-11.4**	-14.87**	0.20	2.64**	1.54	-2.6	0.061**	-4.3*	2.6
	SA 157	0.00	3.3	3.1	4.61	0.27	0.64	1.90	3.4	0.006	0.6	-2.4
	SA 236	0.05	-8.3	0.8	-0.83	0.05	-0.86	-0.54	-2.4	-0.003	-1.2	0.0
	SA 247	-0.24	-9.1	-2.5	-2.22	-0.19	-0.15	-1.61	-1.1	-0.016	-1.5	1.2
	SA 248	-0.13	-1.3	-2.1	1.55	-0.53*	-0.11	0.12	-0.4	0.002	-2.3	0.1
	SA 465	-0.14	-7.7	0.5	0.38	-0.19	-1.05*	0.34	3.6	-0.032	3.7	-0.6
	SA 483	0.64	10.2	-3.3	0.06	0.00	0.46	-1.10	6.6	-0.038	-1.4	-2.0
	SA 655	0.46	4.8	5.4	4.64	0.11	0.12	-0.47	2.9	-0.020	3.8	-2.9
	SA 828	0.00	0.6	2.1	0.76	-0.11	0.05	-0.74	-1.9	0.004	-4.7*	2.1
	Solara	0.10	-0.8	1.0	-0.34	0.11	0.51	-1.15	-0.5	-0.015	9.1**	1.0
	Whero	0.55	-3.2	5.1	5.80*	-0.01	-1.02	1.92	3.1	0.021	-0.3	1.3
t 0.05 (SEij)		0.68	17.6	5.5	5.8	0.46	1.05	2.32	6.8	0.039	4.1	NA
t 0.01 (SEij)		0.90	22.0	6.9	7.7	0.61	1.38	3.05	8.9	0.052	5.4	NA

NA: Data not available; *, **: P< 0.05, 0.01 respectively

flowering) and significant positive effects for eight of those nine (all except plant weight). Of 72 crosses, six gave significant positive SCA effects for hundred seed weight, five each for grain yield and onset of flowering, four for pods per plant and harvest index, two for basal branches and podded nodes per plant and one each for both seeds per pod and plant height.

The correlation coefficient between SCA effects and the level of heterosis was significant and positive for all traits except hundred seed weight (Table 4.1.20). Correlation coefficients for duration of flowering (0.78 with Hmp and 0.73 with Hbp and Hcm) and grain yield (0.65 with Hcm) were relatively high. For the other traits, the correlation coefficients were relatively low.

Table 4.1.20 Correlation coefficients (r) between specific combining ability (SCA) and the level of heterosis over mid-parent (Hmp), over the better parent (Hbp) and over the best parent (Hcm)

Character	Correlation coefficients (r)		
	SCA : Hmp	SCA : Hbp	SCA : Hcm
Basal branches per plant	0.30*	0.34**	0.33**
Plant height	0.41**	0.43**	0.56**
Podded nodes per plant	0.56**	0.45**	0.41**
Pods per plant	0.49**	0.47**	0.45**
Seeds per pod	0.45**	0.37**	0.34**
Hundred seed weight	0.31*	0.22	0.16
Grain yield	0.48**	0.57**	0.65**
Plant weight	0.32**	0.36**	0.47**
Harvest index	0.33**	0.34**	0.49**
Onset of flowering	0.36**	0.31*	0.39**
Duration of flowering	0.78**	0.73**	0.73**

*, **: $P < 0.05, 0.01$ respectively

4.1.5 The six promising crosses

Six crosses, F$_1$~~s~~ hybrids of which gave high yields with high heterotic effects over the best parent, were advanced to produce F$_5$ lines in order to examine the fixability of heterosis in pure lines (Table 4.1.21). The six crosses were Alma x SA 24, Alma x SA 828, Derrimut x SA

129, Dundale x SA 123, Wirrega x SA 157 and Wirrega x Whero (A to F respectively). Grain yield ranged from 18.4 to 20.3 g per plant, plant weight from 40.0 to 52.8 g per plant and heterosis over the best parent for yield from 0.2 % to 28.0 %.

Table 4.1.21 The details of 6 promising crosses which were selected to study the fixability of heterosis in pure lines

Character	Alma x SA 24 (A)	Alma x SA 828 (B)	Derrimut x SA 129 (C)	Dundale x SA123 (D)	Wirrega x SA 157 (E)	Wirrega x Whero (F)
Basal branches per plant (number)	1.7	2.0	5.1	4.2	1.8	3.0
Plant height (cm)	135.0	143.0	84.0	107.0	110.0	105.0
Podded nodes per plant (number)	13.4	19.0	25.8	21.5	16.7	18.5
Pods per plant (number)	22.0	25.9	32.5	33.6	24.0	25.4
Seeds per pod (number)	4.4	6.4	5.9	6.5	6.0	6.0
Hundred seed weight (g)	29.1	18.1	10.7	11.9	22.5	21.6
Grain yield (g per plant)	18.6	18.4	19.5	20.3	18.7	19.9
Plant weight (g per plant)	43.9	49.7	40.0	52.9	41.9	44.1
Harvest index	0.44	0.40	0.48	0.42	0.46	0.47
Onset of flowering (days after sowing)	109.0	118.0	119.0	124.0	112.0	108.0
Duration of flowering (days)	32.0	27.0	25.0	28.0	31.0	29.0
Yield Hmp in F_1 (%)	46.5	29.2	113.6	76.7	37.0	26.1
Yield Hbp in F_1 (%)	30.5	13.8	52.1	35.1	26.0	28.7
Yield Hcm in F_1 (%)	16.2	0.2	27.9	28.1	12.7	10.8
F_2 yield (g per plant)	20.0	15.9	12.8	13.7	13.5	17.6
Yield inbreeding depression in F_2 (%)	8.0	12.7	61.7	80.2	43.8	14.9
Yield Hmp in F_2 (%)	17.2	5.6	11.8	7.0	17.8	2.5
Yield GCA effect of female parent	-0.5	-0.5	0.1	-0.4	0.8	0.8
Yield GCA effect of male parent	0.3	0.8	-0.4	1.4	-0.3	0.9
Yield SCA effect of cross	2.5	1.7	3.6	3.0	1.9	1.9

Each cross gained much of its high yield from a different yield component. Alma x SA 24 had the heaviest seeds (39.1 g per hundred seeds) but had the fewest seeds per pod (4.4). Derrimut x SA 129 and Dundale x SA 123 had more basal branches, podded nodes and pods per plant but had very low seed weight. Alma x SA 828 and Dundale x SA 123 developed many seeds per pod (6.4 - 6.5).

The level of heterosis over the mid-parent for grain yield was highest in Dundale x SA 123 (76.7%), and lowest in Wirrega x Whero (26.1%). Correspondingly, the extremes of heterosis over the better parent were 52.1% in Derrimut x SA 129 and 13.8% in Alma x SA 828. The levels of heterosis for grain yield in these crosses were due to heterosis in a different yield component. The grain yield heterosis of Alma x SA 828, Derrimut x SA 129 and Dundale x SA 123 was mainly due to the heterosis in the pods per plant, while the yield heterosis of the Alma x SA 24 was due to heterosis for both pods per plant and seed weight. For Wirrega x SA 157 and Wirrega x Whero, the grain yield heterosis was derived from heterosis in all three important yield components (pods per plant, seeds per pod and hundred seed weight).

These crosses were produced from parents that tended to differ for their combining ability effects for grain yield. Alma x SA 24 and Derrimut x SA 129 were derived from parents which were low in GCA effects but were relatively high in SCA. Dundale x SA 123 was derived from a high GCA male parent, whereas Wirrega x SA 157 and Wirrega x Whero were derived from a high GCA female parent. Both the female and male parents of cross Alma x SA 828 had smaller GCA effects. All crosses had positive SCA effects for grain yield.

The six crosses were different in the level of inbreeding depression for grain yield at the F_2 generation. Inbreeding depression was over 60% in crosses Derrimut x SA 129 and Dundale x SA 123 and was less than 15% in crosses Alma x SA 24, Alma x SA 828 and Wirrega x Whero.

4.2 Experiment B: Relative yield of pure-line derivatives of heterotic hybrids

4.2.1 Performance of crosses

The analyses of variance of F_5 families over two locations (Table 4.2.1) indicated that the variation among crosses was significant for all traits. Cross A had the highest mean for hundred seed weight, grain yield and harvest index, and also started flowering earliest of all crosses (Table 4.2.2). Cross C produced the most basal branches per plant while cross D had the most pods per plant and seeds per pod. Cross B was the latest in maturity and had the highest plant weight but the lowest harvest index.

Table 4.2.1 Summary analyses of variance for eight agronomic traits of F$_5$ lines between and within 6 crosses of peas

Source of variance	df	Mean square							
		Basal branches per plant (number)	Pods per plant (number)	Seeds per pod (number)	Hundred seed weight (g)	Grain yield (g)	Plant weight (g)	Harvest index	Onset of flowering (days after sowing)
Between crosses	5	81.8***	6004.9***	17.9**	1878.4***	301.5**	13655***	0.578***	20733***
Within Cross A	28	1.7*	144.0***	1.3ns	33.5***	46.4***	860***	0.024***	1277***
Cross B	33	9.5***	579.4***	2.2**	33.2***	53.8***	2986***	0.025***	215***
Cross C	25	15.4***	336.6ns	2.9***	52.2***	80.7***	1465***	0.065***	1286***
Cross D	29	16.9***	986.4***	2.3***	46.6***	57.2**	2144***	0.082***	2845***
Cross E	33	1.7*	398.5***	3.9***	15.8***	64.8***	1823***	0.023***	581***
Cross F	30	2.8***	426.7***	2.9***	24.4***	39.0ns	4794***	0.028***	254***
pooled error	895	2.03	172	0.92	6.51	23.63	656	0.0095	234

ns, not significant; *, **, ***: $P < 0.05, 0.01, 0.001$ respectively

Table 4.2.2 Mean values and the least significant differences of grain yield and seven traits of F$_5$ lines in six crosses

Cross	Basal branches per plant (number)	Pods per plant (number)	Seeds per pod (number)	Hundred seed weight (g)	Grain yield (g)	Plant weight (g)	Harvest index	Onset of flowering (days after sowing)
Cross A	2.6	21.1	5.7	19.4	13.2	43	0.37	118
Cross B	3.1	27.1	5.8	14.9	10.0	60	0.22	142
Cross C	4.1	27.5	5.6	11.4	10.0	38	0.33	120
Cross D	3.8	36.6	6.4	11.8	11.8	45	0.34	121
Cross E	2.6	23.2	5.5	17.3	11.3	54	0.26	130
Cross F	2.5	21.6	5.9	17.7	12.5	56	0.28	139
Mean	3.1	26.1	5.8	15.5	11.4	50	0.30	129
LSD(0.05)	0.4	5.6	0.4	1.1	1.6	10	0.03	4
LSD(0.01)	0.6	7.6	0.6	1.4	2.2	14	0.04	5

Variation in basal branches per plant was high in crosses B, C and D (the mean squares were 9.5, 15.4 and 16.9 respectively) and low in crosses A, E and F (the mean squares were 1.7, 1.7 and 2.8 respectively). Cross D had the highest variation for pods per plant followed by crosses B, F and E while cross A had the least variation. The variation for seeds per pod was highest in cross E and lowest in cross A, while cross E had the lowest variation for hundred seed weight. Crosses C and D were highly variable in basal branches, harvest index and hundred seed weight. For grain yield, the variation was highest in cross C followed by crosses E, D, B, A and F. The variation for plant weight was greatest in cross F but least in cross A. Cross E had low variation for harvest index and cross B was lowest in the variation for days to onset of flowering.

4.2.2 Performance of lines within crosses

Frequency distributions of grain yield and seven agronomic traits for F_5 lines in comparison with their parents and their F_1 hybrids for each cross are given in Figures 4.2.1 to 4.2.8.

Basal branches per plant (Figure 4.2.1). The F_1s of crosses C and D were significantly higher than their parents for this trait. All crosses except C had some F_5 lines which exceeded their F_1s (2 lines for A, 6 for B, 1 for D, 5 for E and 4 for F). One line in cross C was superior to its F_1 (but not significantly) and this line had the most basal branches.

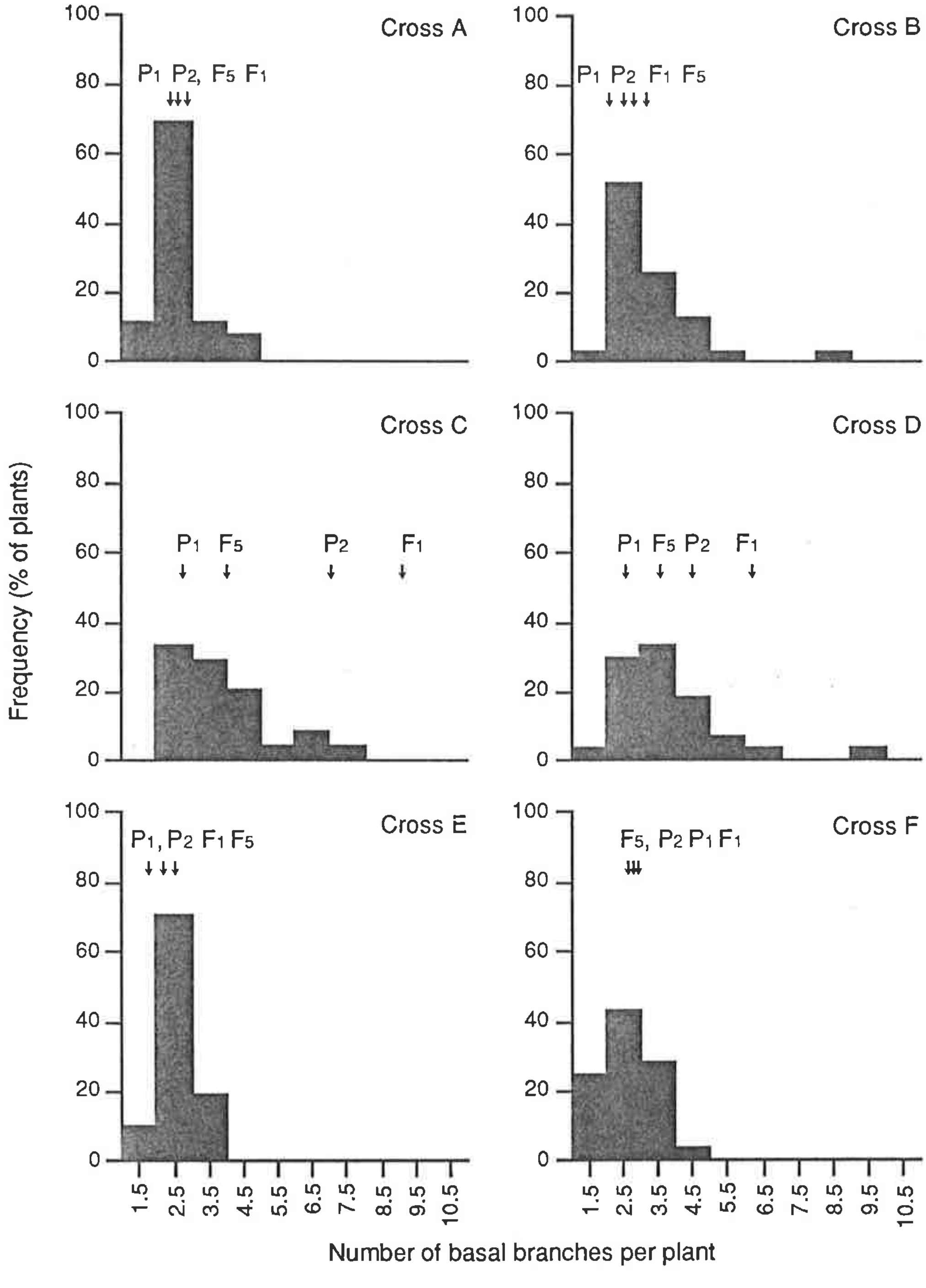

Figure 4.2.1 Frequency distribution of number of basal branches per plant in crosses A to F

key - for Figures 4.2.1 - 4.28 (p.84 - 91)
Vertical arrows indicate values of parents, F, hybrids and the mean of F_5 lines in the order indicated. Note in some case value overlap to show less than four arrows.

Pods per plant (Figure 4.2.2). F_1s were superior to their parents in crosses A, B, D and F. Among the F_5s, there were 2 lines in crosses A and D and 6 in E which had more pods per plant than their F_1s. Eight lines in cross C and 2 lines in cross F were not significantly different from their F_1s.

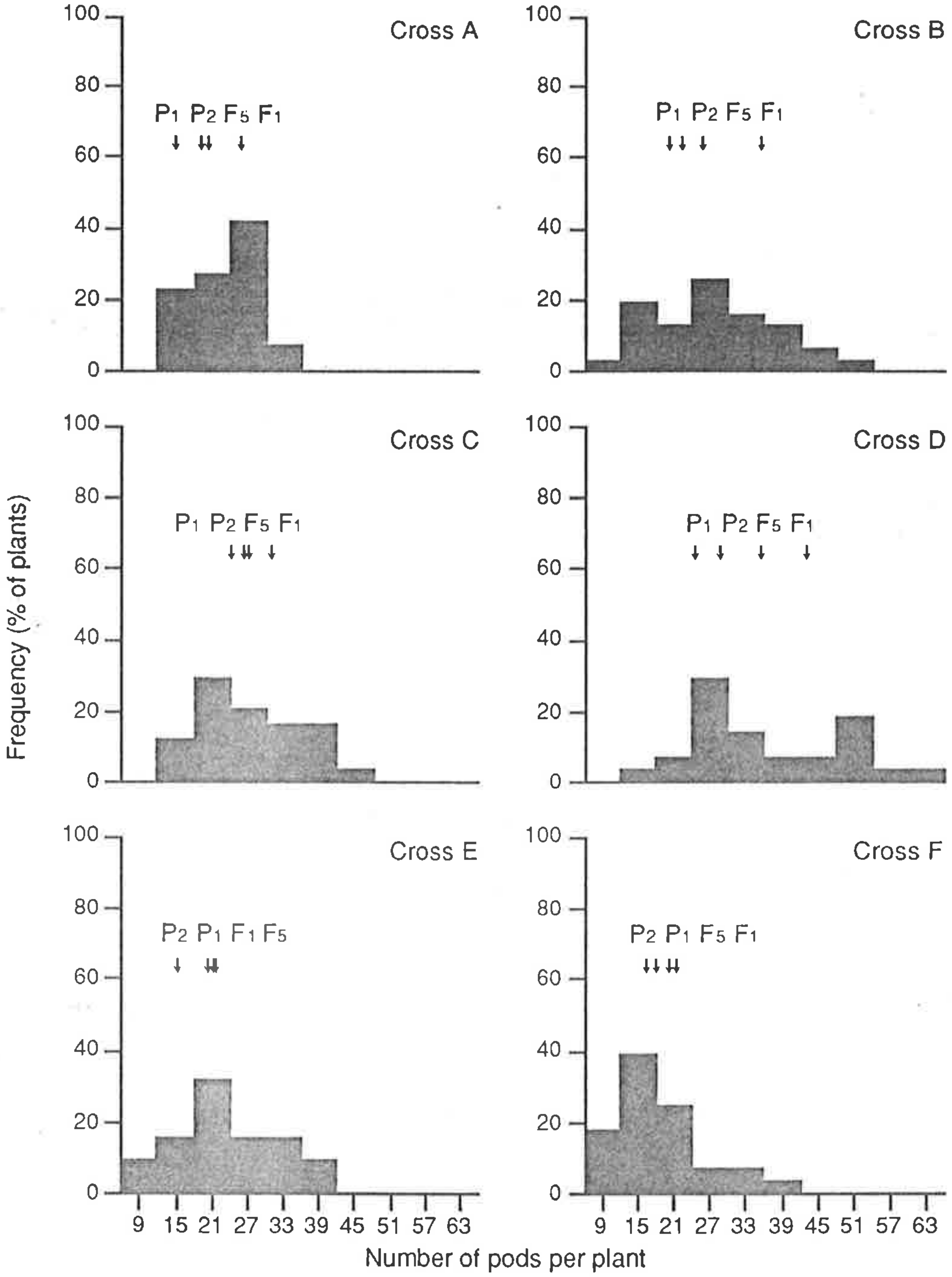

Figure 4.2.2 Frequency distribution of number of pods per plant in crosses A to F

<u>Seeds per pod</u> (Figure 4.2.3). F_1s of crosses B, D and E had similar values to their parents whereas those of crosses A and C were lower than their better parent and that of cross F was significantly higher. There were 7 F_5 lines in cross B, 6 in C, 4 in E and 1 in F which were superior to their F_1s.

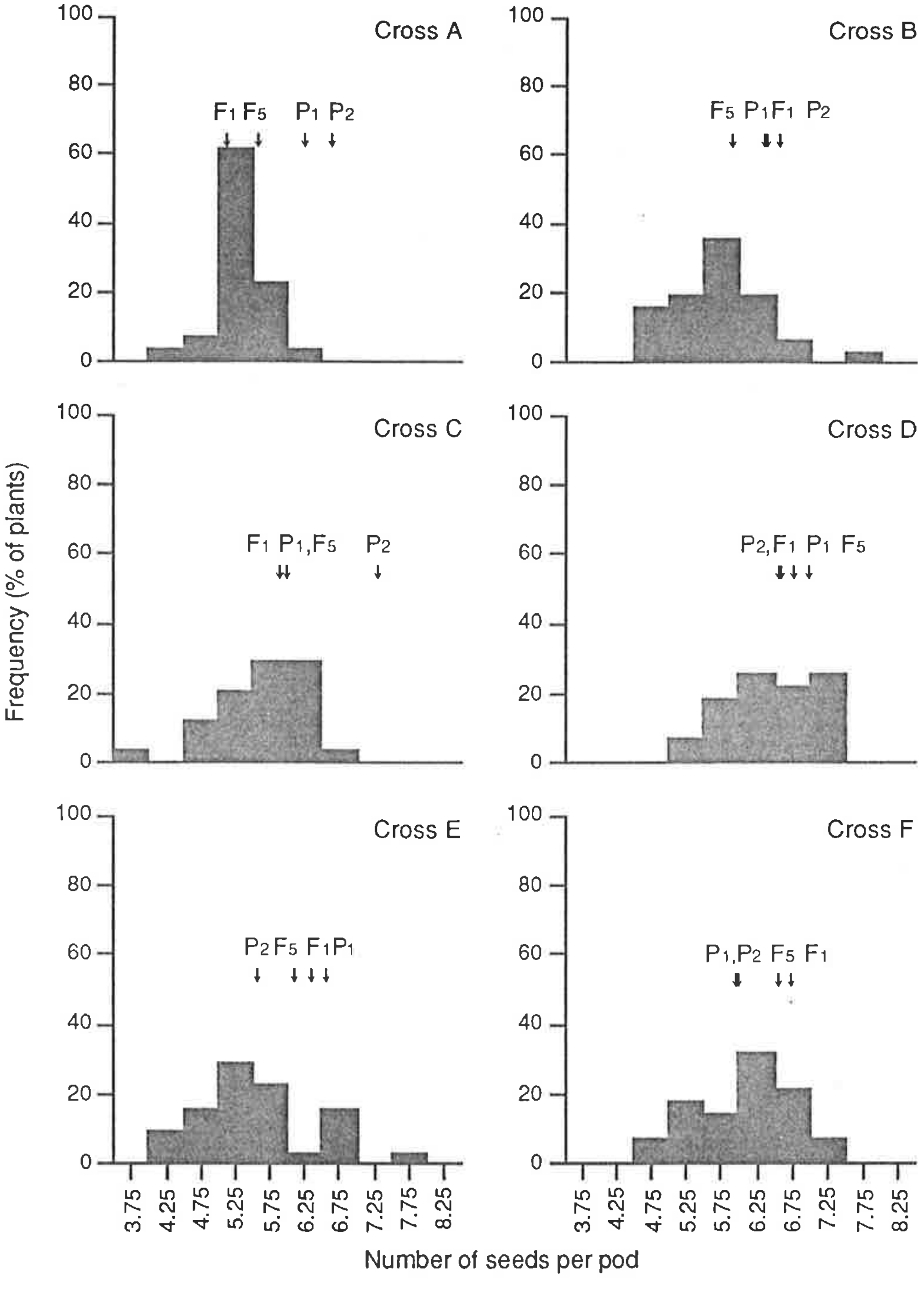

Figure 4.2.3 Frequency distribution of number of seeds per pod in crosses A to F

Hundred seed weight (Figure 4.2.4). The F_1 values of all crosses were not significantly higher than their better parents. There were 3 F_5 lines in cross A, 9 in B, 16 in C, 11 in D and 4 in E which exceeded their F_1s but none exceeded the better parent in crosses B, C and D. Most of the lines in cross E were equal to its F_1 but only 3 lines were significantly higher than the best parent. In cross F, there were 16 lines with as high seed weight as the

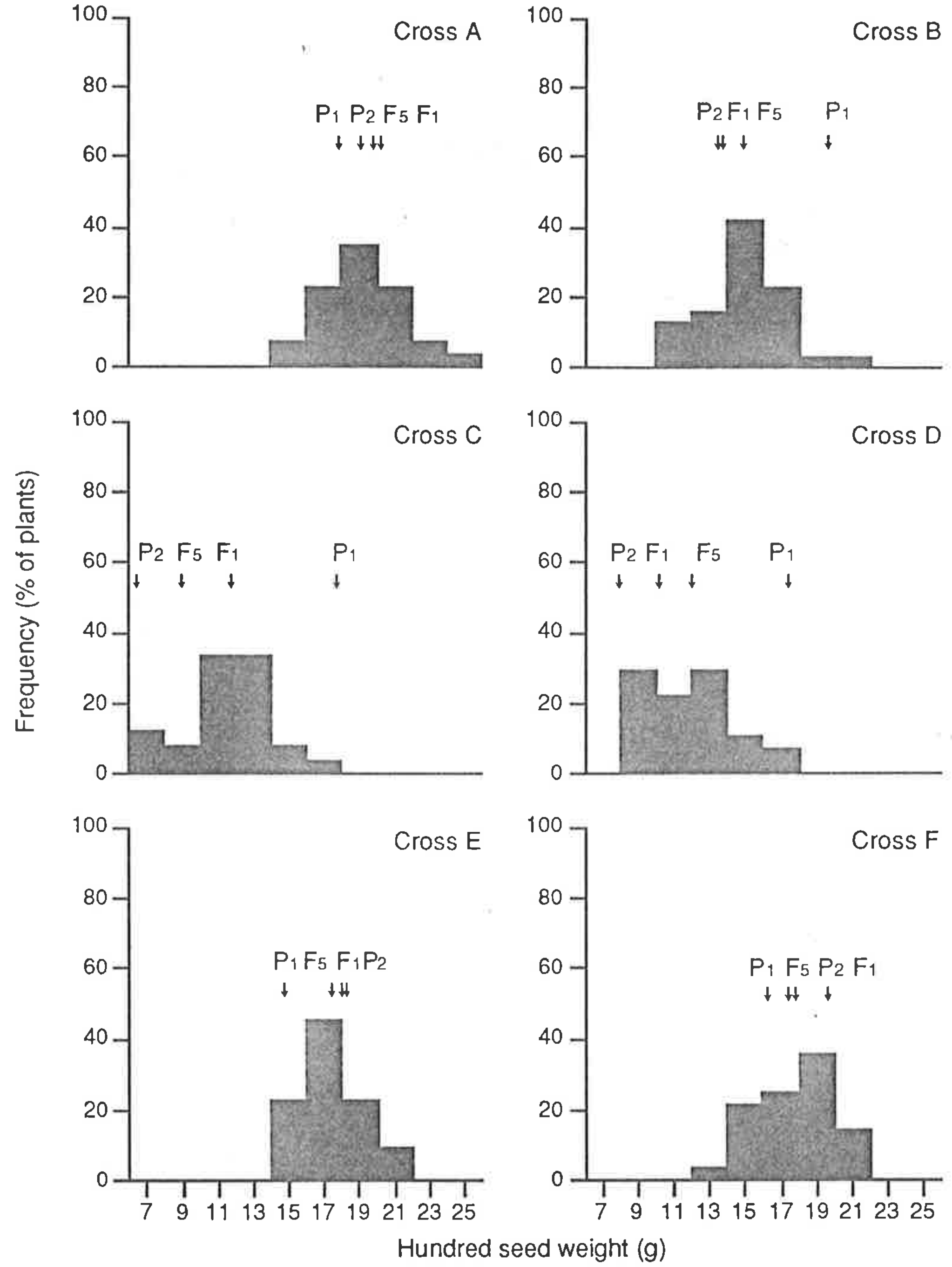

Figure 4.2.4 Frequency distribution of hundred seed weight in crosses A to F

F1 but only 4 lines were higher than the best parent and none significantly higher than the F1.

Grain yield (Figure 4.2.5). In all crosses, the F1 grain yields were higher than their better parent but not significantly. The yield heterosis of F1s over their better parents were 14.3%, 2.2%, 14.4%, 12.4%, 2.4% and 5.7% for crosses A to F. The yield heterosis of F1s over their mid-parent was in a range of 17.5 to 49.5%. No line was significantly higher

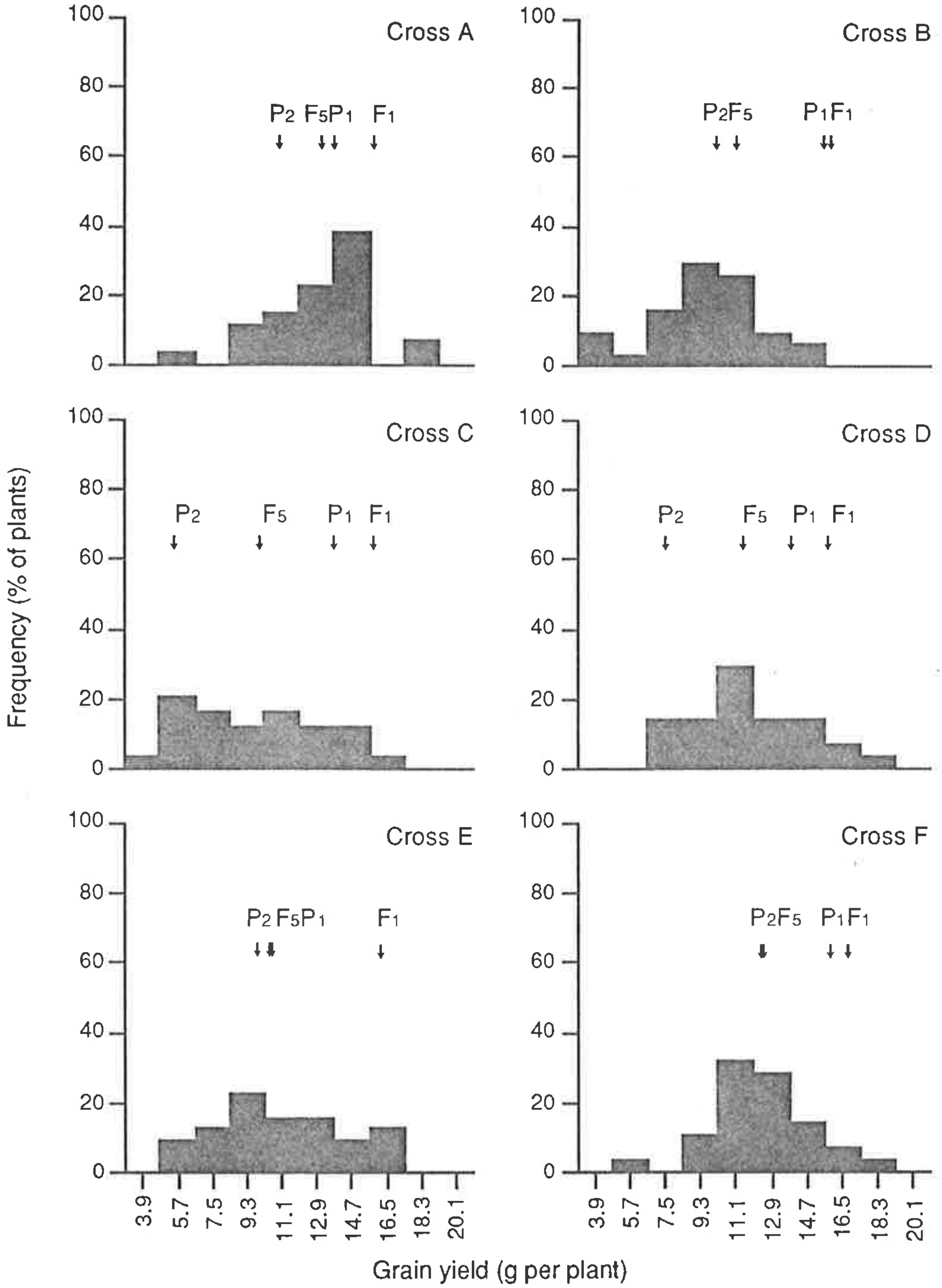

Figure 4.2.5 Frequency distribution of grain yield in crosses A to F

in yield than the best parent or its F1 although 4 lines in crosses D, 3 in E, 2 in A, 1 in C and 1 in F were arithmetically higher in yield than their F1s. The relative yield of the best line of each cross to its F1 was in a range of 93.6% (cross B) to 123.8% (cross D). Nine F5s in cross A, 7 in D and F, 6 in C and 5 in both B and E were as high in yield as their F1s.

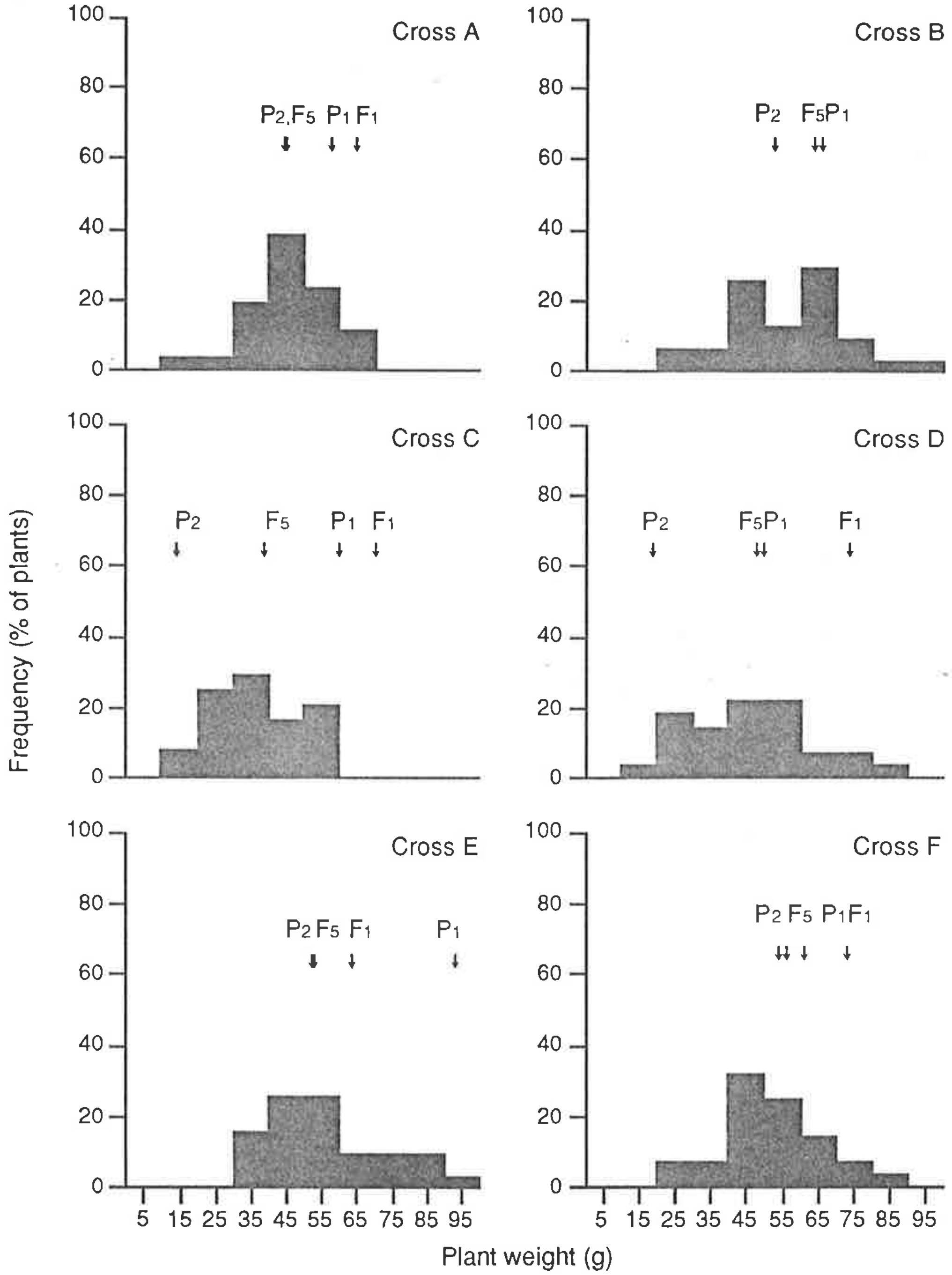

Figure 4.2.6 Frequency distribution of plant weight in crosses A to F

The relative yield of the best line of each cross to the best parent was 115.8%, 94.0%, 109.1%, 119.0%, 109.5% and 105.7% in crosses A to F respectively.

Plant weight (Figure 4.2.6). F$_1$s from crosses B and cross C were significantly higher than their better parents, and only one line from cross B exceeded the F$_1$. There were 12 lines in cross F, 10 in E, 7 in D, 6 in A, 5 in C and 1 in B which were as high as their F$_1$s.

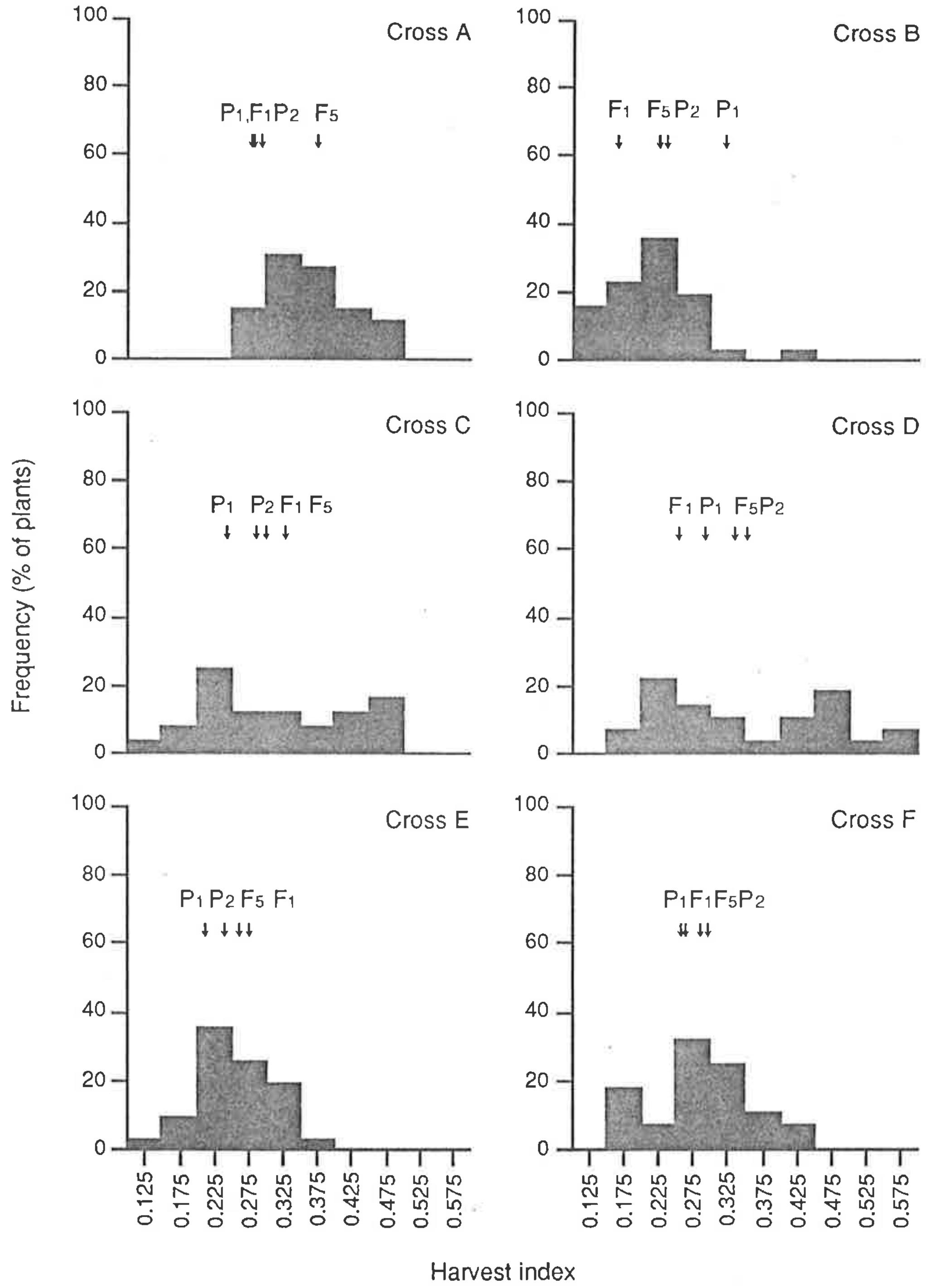

Figure 4.2.7 Frequency distribution of harvest index in crosses A to F

Harvest index (Figure 4.2.7). No F_1 of the six crosses was superior to its better parent. The values of most F_5 lines in all crosses were near to those of the F_1s. There were 14 lines in cross A, 13 in D, 8 in C, 7 in B and 1 in F which were significantly higher than their F_1s.

Onset of flowering (Figure 4.2.8). Most F_1s started flowering between their early and their late parents. F_5s of crosses A, C and D were earlier than their F_1 on average and *vice* *versa* for crosses B and E. In cross B no line was earlier than the F_1 whereas in cross C, 17 lines were earlier than F_1 and similar to the earliest parent. Seven lines in cross D started flowering earlier than the earliest parent. In cross E, three lines were as early as the earlier parent and 11 lines started flowering before the F_1. Four lines in cross F were earlier than the F_1 but none was earlier than the earliest parent.

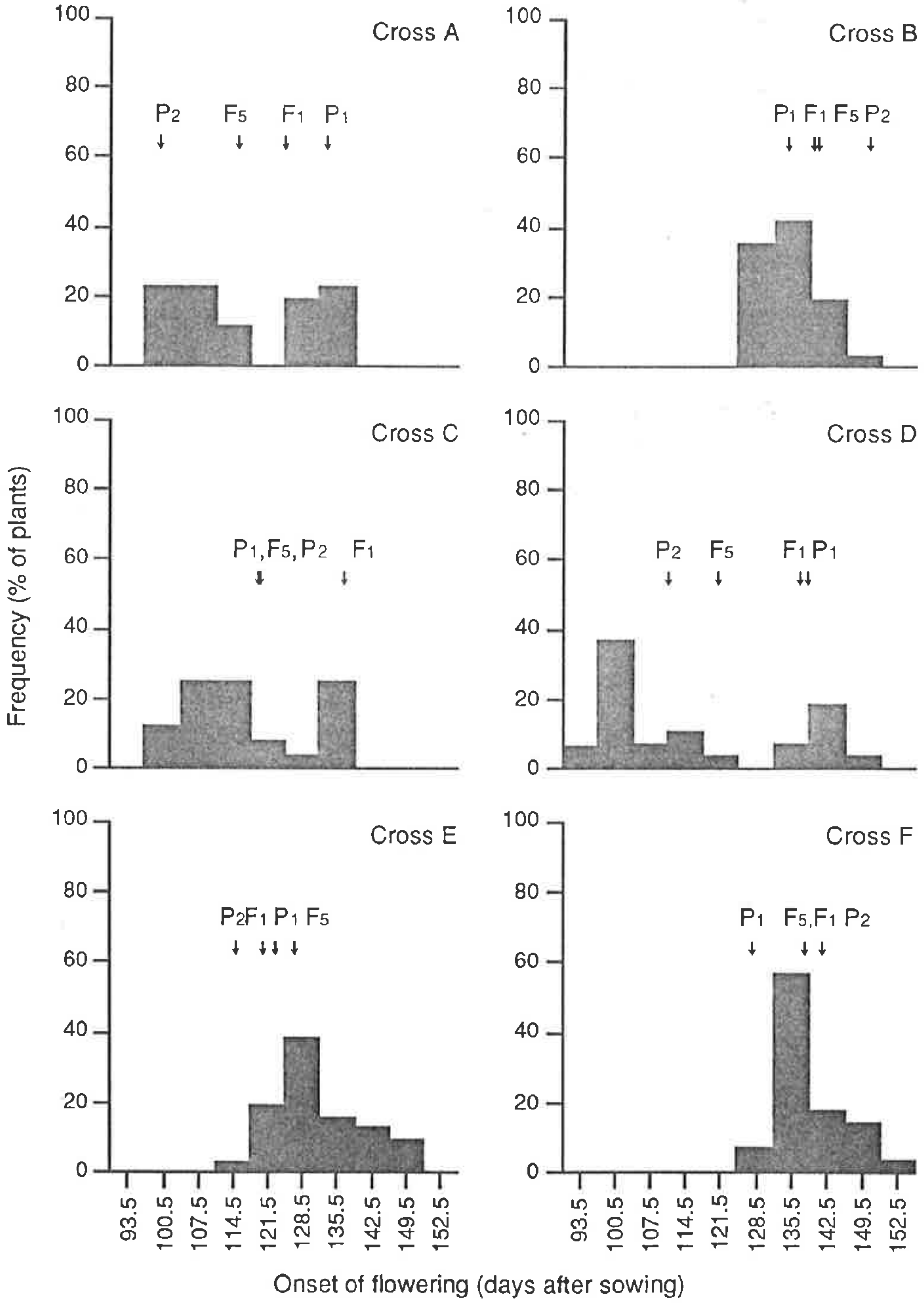

Figure 4.2.8 Frequency distribution of days to onset of flowering in crosses A to F

4.2.3 The relationship between yield and yield components in pure-line derivatives

The relationship between grain yield and the other agronomic traits within each cross was investigated and the significant correlation coefficients for each cross are summarised in Table 4.2.3. The number of pods per plant was significantly correlated with grain yield in crosses A, C, E and F whereas hundred seed weight was significantly correlated with grain yield in crosses B, C and D. Plant weight was found to be significantly correlated with grain yield only in cross A.

4.2.4 The relationship between parental lines and pure-line derivatives

Significant correlation coefficients were found between F_5 means and (a) mid-parent values, (b) GCA of parents and (c) F_1 values for both basal branches per plant and hundred seed weight. In addition, a significant correlation coefficient was found between F_1 and F_5 values for pods per plant (Table 4.2.4).

Table 4.2.3 Significant correlation coefficients between grain yield and related agronomic traits for F_5 lines of each of 6 crosses

Cross	Character		Correlation coefficient (r)
A	Grain yield vs.	Pods per plant	0.48*
		Plant weight	0.51*
B		Hundred seed weight	0.48*
C		Pods per plant	0.47*
		Hundred seed weight	0.58**
D		Hundred seed weight	0.47*
E		Pods per plant	0.53*
F		Pods per plant	0.45*

*, **: $P < 0.05, 0.01$ respectively

Table 4.2.4 Correlation coefficient between (A) mid-parent and means of F_5s (B) the general combining effects of parents and means of F_5s and (C) F_1 values and means of F_5s for 8 agronomic traits from 6 crosses

Agronomic trait	Correlation coefficient (r)		
	A	B	C
Basal branches per plant	0.92**	0.96**	0.87*
Pods per plant	0.31	0.69	0.86*
Seeds per pod	0.48	0.33	0.41
Hundred seed weight	0.97**	0.98**	0.98**
Grain yield	0.43	0.34	0.17
Plant weight	0.62	0.32	0.29
Harvest index	0.36	0.02	0.25
Onset of flowering	0.55	-0.15	-0.23

*, **: $P < 0.05, 0.01$ respectively

The difference between parents (P_1-P_2) for each of the agronomic traits was examined for its correlation with the mean square for (a) that same trait or (b) grain yield (Table 4.2.5). The difference in hundred seed weight between parents was significantly and linearly correlated with the variation of the same trait in F_5 progenies. The difference between parents in plant weight was highly correlated with the variation of grain yield in F_5 . The differences of basal branches per plant, seeds per pod and hundred seed weight also tended to be correlated with the variation in F_5 grain yield.

4.2.5 Heritability

Broad sense heritability values varied among traits and crosses (Table 4.2.6). Of all traits studied, onset of flowering had the greatest heritability (h^2= 56.6% from cross F to 93.6% from cross A) whereas pods per plant had the lowest (h^2= 38.0% from cross F to 61.0% from cross A). The heritability of grain yield was in a range from 36.7% from cross F to 65.5% from cross C.

Table 4.2.5 Correlation coefficients between parental differences for 8 agronomic traits and (A) mean square of F_5 for the same traits and (B) the mean square of F_5 yield

Agronomic trait	Correlation coefficient (r)	
	A	B
Basal branches per plant	0.83	0.79
Pods per plant	-0.16	0.48
Seeds per pod	0.54	0.83
Hundred seed weight	0.85*	0.76
Grain yield	0.54	0.54
Plant weight	-0.52	0.94**
Harvest index	0.30	0.04
Onset of flowering	0.74	0.50

*, **: $P < 0.05$, 0.01 respectively

Table 4.2.6 Percent heritability of grain yield and seven agronomic traits in crosses A to F estimated from F_5 lines

Character	Heritability (%)					
	Cross A	Cross B	Cross C	Cross D	Cross E	Cross F
Basal branches per plant	41.4	46.8	64.5	52.2	48.3	60.0
Pods per plant	46.5	61.0	38.0	49.6	47.6	40.1
Seeds per pod	42.2	47.8	57.7	59.6	65.8	49.7
Hundred seed weight	56.7	61.3	78.7	83.1	54.3	59.3
Grain yield	47.9	45.5	65.5	44.2	56.2	36.7
Plant weight	51.1	55.3	51.6	58.2	48.5	49.6
Harvest index	44.1	55.3	60.2	82.8	51.1	52.8
Onset of flowering	93.6	63.6	85.3	84.9	75.6	56.6

4.3 Experiment C part 1: Genetic distance amongst parental lines

4.3.1 Genetic distance based on isozyme genotypes (GD_i)

A single zone of isozyme activity on the stained gel was found and resolvable for each of the enzymes ADL, G6PD and MRD (Table 4.3.1). Double zones were found for AMP, GOT, IDH, 6-PGD, PGI and SDH but only one of them was resolvable in AMP, GOT, PGI

Table 4.3.1 Isozyme genotypes of pea parental lines

Cultivar	Enzyme system														
	ADH-1	ADL	AMP	GOT	G6PD	IDH-1	IDH-2	MDH-1	MDH-2	MDR	6PGD-1	6PGD-2	PGI	PGM	SDH
Females															
Alma	FF	FF	MM	FF	FF	FF	SS	FF	FF	SS	FF	FF	SS	SS	FF
Derrimut	FF	FF	MM	FF	FF	FF	SS	FF	FF	SS	FF	FF	SS	SS	SS
Dundale	FF	FF	MM	FF	FF	FF	SS	FF	FF	SS	FF	FF	SS	SS	FF
Wirrega	FF	FF	MM	FF	FF	FF	SS	FF	FF	SS	FF	FF	SS	SS	SS
Males															
Garfield	SS	FF	MM	FF	FF	FF	SS	SS	FF	SS	SS	FF	FF	SS	SS
SA 15	SS	FF	MM	FF	FF	FF	SS	SS	FF	SS	FF	SS	SS	SS	SS
SA 24	SS	FF	MM	FF	FF	FF	SS	SS	FF	SS	FF	FF	SS	FF	FF
SA 35	SS	FF	MM	FF	FF	FF	SS	SS	FF	SS	FF	FF	SS	SS	FF
SA 51	SS	FF	MM	FF	FF	FF	FF	SS	FF	SS	SS	FF	FF	FF	FF
SA 54	SS	SS	FF	SS	FF	SS	SS	SS	FF	SS	SS	FF	FF	FF	SS
SA 123	SS	SS	SS	SS	FF	SS	SS	SS	FF	FF	SS	SS	FF	FF	SS
SA 129	SS	SS	SS	SS	FF	SS	SS	SS	FF	FF	SS	FF	SS	SS	SS
SA 157	FF	FF	MM	FF	FF	FF	SS	SS	FF	SS	FF	FF	SS	SS	FF
SA 236	SS	FF	MM	FF	SS	FF	SS	FF	FF	SS	FF	FF	SS	SS	SS
SA 247	FF	FF	MM	FF	SS	FF	SS	SS	FF	SS	FF	SS	SS	FF	FF
SA 248	SS	SS	MM	FF	SS	FF	SS	SS	FF	SS	FF	FF	SS	FF	SS
SA 465	SS	FF	MM	FF	FF	FF	SS	SS	FF	SS	FF	FF	SS	FF	SS
SA 483	SS	SS	SS	SS	SS	FF	SS	SS	FF	SS	SS	FF	FF	FF	SS
SA 688	SS	SS	SS	SS	FF	SS	SS	SS	FF	SS	FF	SS	SS	FF	SS
SA 828	SS	FF	MM	FF	FF	FF	SS	FF	FF	SS	FF	FF	SS	SS	FF
Solara	SS	FF	MM	FF	FF	FF	SS	SS	FF	SS	FF	FF	SS	SS	FF
Whero	SS	FF	MM	FF	FF	FF	SS	FF	SS	FF	FF	FF	SS	FF	SS

FF = fast migrating band MM = medium migrating band SS = slow migrating band

and SDH. Three zones were found for enzymes ADH, MDH and PGM, but again only two zones were readable in MDH and one zone in ADH and PGM.

The genetic distance for 72 pairs of parents was in a range of 0.03 to 0.80 (Table 4.3.2). The male parent SA 123 was very divergent from the female parents. SA 54, SA 123, SA 129, SA 483 and SA 688 were high in distance from females (>0.38); SA 51, SA 248, SA 247, Garfield and Whero were moderate in distance from the females (0.16-0.38) while the remaining distances were low (<0.16). The smallest distance was found in the pair of Alma and SA 157 and also in the pair of Dundale and SA 157. Alma and Dundale were identical at every locus, as were Derrimut and Wirrega.

Table 4.3.2 Genetic distance of Nei. Estimates of genetic distance between each pair of parents, based on 15 isozyme markers (GD_i), 17 morphological markers (GD_m) and the combination of isozyme and morphological markers (GD_{i+m})

Male	GD_i between male and		GD_m between male and		GD_{i+m} between male and		
	Alma, Dundale	Derrimut, Wirrega	Alma, Derrimut, Dundale	Wirrega	Alma, Dundale	Derrimut	Wirrega
Garfield	0.20	0.16	0.13	0.10	0.17	0.14	0.12
SA 15	0.16	0.11	0.10	0.22	0.12	0.10	0.17
SA 24	0.11	0.16	0.17	0.22	0.14	0.17	0.19
SA 35	0.07	0.11	0.32	0.32	0.19	0.21	0.21
SA 51	0.26	0.31	0.27	0.32	0.26	0.29	0.32
SA 54	0.55	0.46	0.22	0.22	0.35	0.32	0.32
SA 123	0.80	0.66	0.13	0.17	0.35	0.32	0.35
SA 129	0.46	0.38	0.22	0.22	0.32	0.29	0.29
SA 157	0.03	0.07	0.10	0.10	0.07	0.08	0.08
SA 236	0.11	0.07	0.13	0.06	0.12	0.10	0.07
SA 247	0.16	0.20	0.13	0.00	0.14	0.12	0.08
SA 248	0.26	0.20	0.10	0.03	0.17	0.14	0.10
SA 465	0.16	0.11	0.17	0.13	0.17	0.14	0.12
SA 483	0.55	0.46	0.17	0.22	0.32	0.29	0.32
SA 688	0.46	0.38	0.10	0.13	0.26	0.24	0.24
SA 828	0.03	0.07	0.10	0.06	0.07	0.08	0.07
Solara	0.07	0.11	0.22	0.17	0.14	0.17	0.14
Whero	0.20	0.16	0.06	0.10	0.12	0.10	0.12

4.3.2 Genetic distance based on morphological polymorphisms (GD_m)

Seventeen morphological characteristics were observed (Table 4.3.3). Most of the parents were conventional plant types except SA 51 which was fasciated type, SA 35 had zigzag stems and SA 54 had hard stems (rms gene). The majority of parents had normal internode length, normal number of basal branches (1-4), normal number of upper branches and leaf types. Short internodes were found in SA 24, SA 123, SA 129, SA 483 and Solara; more basal branches in SA 123, SA 129 and SA 483; more upper branches in Wirrega, SA 247 and SA 828; semi-leaflessness in Solara and reduced lanceolate stipule in SA 35. In general, plants had wax over the whole plant, 1-2 flowers per node, young pods were green and dry pods had pointed apices, but there were exceptions in SA 157 and SA 688 which were without wax on their plants and SA 51 which was without wax on upper surface of leaflets and its young pods were yellow. SA 15, SA 54 and SA 35 had more flowers per node whereas SA 24, SA 35 and SA 465 had pods with a rounded apex. Flowers were pink, white or red in colour and most of the parents had normal flowers except SA 51 where peduncles were short and in SA 35 the petal was pressed to the keel petal. There was wide variation in seed colour; green, greenish blue, violet pattern on seed coat, creamy and marbled while seed shape was classified into dimpled and round. The cotyledon was yellow or green and hilum colour was black or white.

The genetic distance between each pair of parents estimated from 17 morphological characters was in a range of zero to 0.32. The highest distance was found between SA 35 and all female parents whereas SA 247 and Wirrega were almost identical (Table 4.3.2). The male parents SA 35, SA 51, SA 54 and SA 129 had high distance from female parents (>0.22) while Garfield, SA15, SA 24, SA 123, SA 157, SA 465, SA 483, SA 688 and Solara were moderate in distance from the females (0.10-0.22) and the distances of the remainders to female parents were relatively low (<0.10). Wirrega had a genetic distance of 0.10 from Alma, Dundale and Derrimut which were identical in all morphological characters.

4.3.3 Genetic distance based on the combination of isozyme markers and morphological polymorphisms (GD_{i+m})

The 15 isozyme and 17 morphological markers were pooled to give a GD based on 32 characteristics which ranged from 0.07 to 0.35 (Table 4.3.2). Equal highest distances were

Table 4.3.3 Morphological characters of parental lines

Cultivar	Plant type	Stem texture	Internode	Basal branching	Upper branching	Leaf type	Wax on plant	Flower colour	Peduncle	Wing shape	Flowers per node	Pod colour	Pod apex	Seed colour	Cotyledon colour	Seed shape	Hilum colour
Females																	
Alma	N	N	N	N	N	N	W	b	N	N	N	G	bt	G	I	R	w
Derrimut	N	N	N	N	N	N	W	b	N	N	N	G	bt	G	I	R	w
Dundale	N	N	N	N	N	N	W	b	N	N	N	G	bt	G	I	R	w
Wirrega	N	N	N	N	ram	N	W	a	N	N	N	G	bt	Cr	I	r	w
Males																	
Garfield	N	N	N	N	N	N	W	a	N	N	N	G	bt	GB	i	r	w
SA 15	N	N	N	N	N	N	W	b	N	N	fn	G	bt	M	I	R	pl
SA 24	N	N	le	N	N	N	W	b	N	N	N	G	N	obs	i	r	w
SA 35	Z	N	N	N	N	st	W	cr	N	k	fn	G	N	obs	I	r	w
SA 51	fa	N	N	N	N	N	wlo	cr	dt	N	N	gp	bt	M	I	r	w
SA 54	N	rms	N	N	N	N	W	cr	N	N	fn	G	bt	M	I	r	pl
SA 123	N	N	le	fr	N	N	W	b	N	N	N	G	bt	M	I	r	w
SA 129	N	N	le	fr	N	N	W	cr	N	N	N	G	bt	M	I	r	pl
SA 157	N	N	N	N	N	N	wa	b	N	N	N	G	bt	Cr	I	r	w
SA 236	N	N	N	N	N	N	W	a	N	N	N	G	bt	Cr	I	r	pl
SA 247	N	N	N	N	ram	N	W	a	N	N	N	G	bt	Cr	I	r	w
SA 248	N	N	N	N	N	N	W	a	N	N	N	G	bt	Cr	I	r	w
SA 465	N	N	le	N	N	N	W	a	N	N	N	G	N	GB	I	r	w
SA 483	N	N	le	fr	N	N	W	b	N	N	N	G	bt	M	I	r	pl
SA 688	N	N	N	N	N	N	wa	b	N	N	N	G	bt	M	I	r	w
SA 828	N	N	N	N	ram	N	W	b	N	N	N	G	bt	M	I	r	w
Solara	SL	N	le	N	N	af	W	a	N	N	N	G	bt	GB	I	r	w
Whero	N	N	N	N	N	N	W	b	N	N	N	G	bt	M	I	r	w

Abbreviations:: All characters: N = Normal; Plant type: fa = fasciated, SL = semi-leafless, Z = zig zag stems; Stem texture: rms = hard stems; Internode: le = short; Basal branches: fr = increased numbers; Upper branches: ram = increased numbers; Leaf type: af = leaflets converted to tendrils, st = stipule lanceolate and reduced; Wax on plants: W = whole plant with wax, wa = without wax, wlo = upper surface of leaflet without wax; Flower colour: b = deep rose pink, cr = crimson, a = white; Peduncle: dt = short peduncle; Wing: k = wing appressed to keel; Flowers pernode: fn = increased numbers; Pod colour: G = green, gp = yellow; Pod apex: bt = pod apex pointed; Seed coat colour: M = marbled, GB = greenish blue, G = green, Cr = creamy, obs = violet pattern; Cotyledon colour: I = yellow, i = green; Seed shape: D = dimpled seed, i = round and smooth seed; Hilum colour: w = white, pl = black found between the female parents and both SA 54 and SA 123 whereas the lowest distance was found between SA 157 and both Alma and Dundale. The genetic distances between female parents and SA 51, SA 54, SA 123, SA 129, SA 483 and SA 688 were high (>0.24), whereas those between females and Garfield, SA 24, SA 35, SA 465 and Solara were moderate (0.12-0.24) and those of the remainder were low.

4.3.4 Genetic distance based on quantitative traits (GD_q)

The Euclidean genetic distance between male and female parents was in a range from 2.2 to 33.1 (Table 4.3.4). The greatest distance was found between Dundale and SA 54 while the lowest distance was found between Whero and Alma. The male parents SA 54, SA 123, SA 129 and SA 483 were at relatively great distances from all females (>22), SA 15, SA 24, SA 465, SA 688, SA 828 and Solara were at moderate distance (9.0-22) and the remaining distances were low (<9.0). The genetic distances among the female parents were in a range of 4.6 to 7.4 (Table 4.3.5).

4.3.5 Correlations between four measures of genetic distances

Three of the four measures of GD, namely GD_i, GD_{i+m} and GD_q were highly correlated (0.76 to 0.89) (Table 4.3.6). GD_m was poorly correlated with the other measures, although its correlation with GD_{i+m}, of which it was a component, was significant at 0.57.

Table 4.3.4 The Euclidean genetic distance (GD_q) between each pair of parents estimated from 10 quantitative traits

Male	Female			
	Alma	Derrimut	Dundale	Wirrega
Garfield	3.3	4.8	5.2	5.9
SA 15	13.1	13.0	10.1	16.1
SA 24	12.2	9.3	12.6	12.4
SA 35	5.0	6.5	6.2	7.6
SA 51	7.8	5.4	8.3	6.3
SA 54	31.9	28.0	33.1	26.1
SA 123	27.8	23.7	29.1	23.2
SA 129	27.5	23.2	28.6	23.0
SA 157	4.2	4.4	6.1	3.2
SA 236	7.0	11.8	7.4	11.9
SA 247	7.1	6.1	9.2	4.9
SA 248	6.1	6.4	7.6	6.0
SA 465	12.9	10.0	14.9	11.2
SA 483	27.0	23.1	28.1	22.0
SA 688	15.4	13.3	17.6	11.0
SA 828	12.6	12.2	15.1	9.4
Solara	10.8	10.0	9.9	12.9
Whero	2.2	7.2	5.2	7.4

Table 4.3.5 Genetic distance estimated from quantitative characters (GD_q) for 4 female parents

	Alma	Derrimut	Dundale
Derrimut	6.7		
Dundale	4.6	6.0	
Wirrega	6.4	4.9	7.4

Table 4.3.6 Correlation matrix for genetic distance estimated from isozyme markers (GD_i), morphological polymorphisms (GD_m), isozyme markers and morphological polymorphisms (GD_{i+m}) and quantitative traits (GD_q)

	GD_i	GD_m	GD_{i+m}
GD_m	0.14		
GD_{i+m}	0.89**	0.57**	
GD_q	0.78**	0.23	0.76**

**: $P < 0.01$

4.4 Experiment C part 2: Relationship between parental genetic distance and heterosis

4.4.1 Correlation between parental genetic distance and the level of heterosis in F_1

The relationships between the level of heterosis and the highly correlated measures of genetic distance, GD_i, GD_{i+m} and GD_q, were similar. There were highly significant positive correlations between these three measures of distance and the levels of heterosis in basal branches per plant, podded nodes per plant, pods per plant and plant weight (Table 4.4.1). There were highly significant negative correlations between GD_i, GD_{i+m} as well as GD_q and the levels of heterosis for seed weight but there were no significant correlations between these three measures of distance and the level of heterosis for plant height, seeds per pod, harvest index, days to onset of flowering and duration of flowering.

The correlation coefficients between GD_m and the level of heterosis were low for all traits except plant height (r between GD_m and Hmp = 0.57). Although GD_m was different from GD_i, GD_{i+m} and GD_q in terms of its relationship to the levels of heterosis in agronomic traits, these four measures were comparable in predictability for grain yield.

The correlations between Hmp for yield and GD_i, GD_{i+m}, GD_m, and GD_q were 0.44, 0.53, 0.38 and 0.33 respectively. There were no significant correlations of any measure of genetic distance with either Hbp or Hcm for grain yield (Table 4.4.1).

Table 4.4.1 Correlations between heterosis and genetic distance. Correlation coefficients (r) between genetic distance estimates based on isozyme markers (GD_i), morphological polymorphisms (GD_m), isozyme markers and morphological polymorphisms (GD_{i+m}) and quantitative traits (GD_q); and the levels of heterosis over mid-parent (Hmp), better parent (Hbp) and the best parent (Hcm) for 11 agronomic traits in F_1

Agronomic trait		Correlation coefficient (r)			
		GD_i	GD_m	GD_{i+m}	GD_q
Basal branches per plant	Hmp	0.50**	0.07	0.47**	0.57**
	Hbp	0.10	0.04	0.12	0.26
	Hcm	0.76**	0.10	0.69**	0.84**
Plant height	Hmp	-0.02	0.52**	0.23	0.16
	Hbp	-0.06	0.45**	0.17	-0.14
	Hcm	-0.34**	0.00	-0.28	-0.33**
Podded nodes per plant	Hmp	0.51**	0.20	0.53**	0.63**
	Hbp	0.60**	0.06	0.54**	0.72**
	Hcm	0.68**	0.06	0.61**	0.77**
Pods per plant	Hmp	0.57**	0.27	0.61**	0.67**
	Hbp	0.56**	0.11	0.52**	0.68**
	Hcm	0.66**	0.10	0.61**	0.77**
Seeds per pod	Hmp	-0.02	0.09	0.00	-0.09
	Hbp	0.11	0.07	0.12	0.05
	Hcm	0.32**	0.01	0.26	0.20
Hundred seed weight	Hmp	-0.58**	-0.02	-0.50**	-0.73**
	Hbp	-0.68**	-0.07	-0.59**	-0.85**
	Hcm	-0.75**	-0.06	-0.65**	-0.80**
Grain yield	Hmp	0.44**	0.38**	0.53**	0.33**
	Hbp	-0.08	-0.13	-0.13	-0.20
	Hcm	-0.07	-0.18	-0.15	-0.24
Plant weight	Hmp	0.66**	0.30*	0.68**	0.74**
	Hbp	0.40**	-0.11	0.28	0.41**
	Hcm	0.53**	-0.15	0.38**	0.54**
Harvest index	Hmp	-0.25	0.12	-0.16	-0.43**
	Hbp	-0.39**	0.02	-0.33**	-0.49**
	Hcm	-0.39**	0.05	-0.31**	-0.53**
Onset of flowering	Hmp	0.13	-0.22	0.00	0.18
	Hbp	0.33**	-0.19	0.19	0.46**
	Hcm	0.57**	-0.19	0.39**	0.60**
Duration of flowering	Hmp	-0.06	0.11	0.10	-0.06
	Hbp	-0.20	0.04	-0.14	-0.24
	Hcm	-0.21	0.03	-0.15	-0.24

*, **: $P < 0.05$, 0.01 respectively

4.4.2 Correlation between parental genetic distance and the levels of heterosis in F_2

There was a significant positive correlation between the level of inbreeding depression and GD_i, GD_{i+m} and GD_q for grain yield and plant weight, but there was no correlation between the distance of parental lines and the levels of heterosis in F_2 for grain yield, plant weight and harvest index (Table 4.4.2).

Table 4.4.2 Prediction of F_2 performance from genetic distance. The correlation coefficient (r) between genetic distance estimated from isozyme markers (GD_i), morphological polymorphisms (GD_m), isozyme markers and morphological polymorphisms (GD_{i+m}) and quantitative traits (GD_q); and inbreeding depression (Inb) and the levels of heterosis over mid-parent (Hmp), over better parent (Hbp) and over the best parent (Hcm) for 3 agronomic traits in F_2

Agronomic trait		Correlation coefficient (r)			
		GD_i	GD_m	GD_{i+m}	GD_q
Grain yield	Inb	0.53**	-0.18	0.37**	0.42**
	Hmp	-0.13	0.17	0.01	-0.05
	Hbp	-0.37**	-0.07	-0.35**	-0.24
	Hcm	0.03	0.05	-0.31**	-0.29
Plant weight	Inb	0.52**	-0.17	0.36**	0.45**
	Hmp	-0.02	0.14	0.07	0.00
	Hbp	-0.31**	-0.06	-0.31**	-0.18
	Hcm	0.08	-0.02	0.05	0.05
Harvest index	Inb	-0.14	0.12	-0.08	-0.12
	Hmp	-0.05	0.00	-0.03	-0.01
	Hbp	-0.25	0.08	-0.17	-0.32**
	Hcm	-0.44**	0.06	-0.34**	-0.41

**: $P < 0.01$

4.4.3 Correlation between parental genetic distance and the genetic variance in F_5

The genetic distance between parents was significantly correlated with the mean square of their F_5 lines for basal branches per plant, hundred seed weight, harvest index and onset of flowering. GD_i, GD_{i+m} and GD_q were predictive for the variation of F_5 lines for these characters (r = 0.84 to 0.96; Table 4.4.3).

Table 4.4.3 Prediction of F_5 variability from genetic distance. The correlation coefficient (r) between the mean square for 8 agronomic traits in F_5 from 6 crosses and genetic distance estimated from isozyme markers (GD_i), morphological polymorphisms (GD_m), isozyme markers and morphological polymorphisms (GD_{i+m}) and quantitative traits (GD_q)

Agronomic trait	Correlation coefficient (r)			
	GD_i	GD_m	GD_{i+m}	GD_q
Basal branches per plant	0.80	0.42	0.81	0.92**
Podded nodes per plant	0.73	-0.36	0.48	0.58
Seeds per pod	-0.13	-0.28	-0.18	-0.35
Hundred seed weight	0.71	0.74	0.85*	0.94**
Grain yield	0.24	0.59	0.39	0.39
Plant weight	-0.13	-0.63	-0.27	-0.29
Harvest index	0.96**	0.56	0.97**	0.94**
Onset of flowering	0.91*	0.38	0.88*	0.84*

*, **: $P < 0.05, 0.01$ respectively

Chapter 5 Discussion

5.1 Experiment A: The levels of heterosis in F_1 hybrids and F_2 progenies

5.1.1 Hybrid and parental performances

Considerable genetic variation was found for all characters studied between and within all generations tested. Some traits were more variable than others in the parental generation and the breadth of variation in the F_1 was similar to that in the parents.

Among the traits studied, the more variable were basal branches per plant, pods per plant, podded nodes per plant and seed weight whereas the less variable traits were onset of flowering, duration of flowering and seeds per pod.

Hybrid performance was generally better than parental performance. A statistically significant correlation between hybrid performance and mid-parent value was found for many characters, which could generally be expected when hybrid vigour expression was predominantly contributed by additive and additive x additive gene effects. Such traits included plant height, podded nodes, pods per plant, seeds per pod and seed weight, and parental values for these traits were predictive of the means for populations derived from them. For yield, however, the correlation between GCA and *per se* performance of parents was not significant. Although additive gene effects are important, parental values alone would not be predictive for F_1 characteristics.

The only agronomic traits to show significant correlations with grain yield were plant weight and harvest index/ both of which have a substantial proportion of grain yield. ~~but~~ The correlation coefficient for plant weight was relatively low (r = 0.34). This means that in peas, grain yield is unlikely to be improved *via* selection for the individual components of yield. Numbers of basal branches, podded nodes and pods per plant were highly significantly correlated with each other, so all of these characteristics could be improved by increasing any one of them. The negative correlation between number of pods and hundred seed weight suggests that the maximum grain yield potential may depend upon the optimum agreement between these two characteristics. The strong negative correlation between pods per plant and hundred seed weight suggests that there is considerable compensation between these two yield components. The third component, seeds per pod, was independent of the other two, showing that combined selection of it with one of the other two could potentially result in increased yield.

In self-pollinating species where the cultivars grown are pure lines, any consideration of producing commercial hybrids would depend on their superiority over the best pure lines. The highest increase in grain yield of hybrids over the best pure lines was 26% and 4 of 72 crosses showed a significant superiority over the best line. The existence of considerable yield heterosis over 25% has been reported in peas (Gritton, 1975; Narsinghani and Singh, 1979) and 30% in wheat (Wells and Lay, 1970; Singh and Singh, 1971; Cregan and Busch, 1978; Malik *et al.*, 1981). The results from this study suggest that it is possible to obtain hybrids showing superiority to the outstanding commercial varieties but a large number of F_1s or parental combinations need to be screened.

All traits varied across environments. Pod characteristics such as podded nodes per plant and pods per plant were very strongly influenced by environment while seed characteristics such as seeds per pod and seed weight were influenced very little. Similarly, Khangildin (1970, quoted by Makasheva, 1975) found that the least variable characteristic in peas from 14 years of trials was seed size, followed by seeds per pod and the most variable yield component was pods per plant. Numerous studies in other legumes show pod number to be the yield component which is most sensitive to the environment, whereas number of seeds per pod and hundred seed weight are determined much more by the genotype. Significant genotype x environment interaction was evidence of the widely recognised need for multiple environments for testing lines, hybrids or populations.

The mean square for F_1 x environment interaction of yield was higher than that for parent x environment interaction indicating that parents produced more consistent grain yield than F_1s. This result was in agreement with the reports of Allan (1973) and Guenzi *et al*. (1985) that wheat hybrids were not as stable as the pure lines. In contrast, a number of authors have noted that hybrids were marginally more stable in yield than pure lines (Johnson and Whittington, 1977; Borghi *et al.*, 1988; Carver *et al.*, 1987; Uddin, 1991). The inferior adaptation of hybrids in the present study is attributable to the exotic origin and hence poor adaptation of their male parents.

One factor which affected the consistency of grain yield in F_1 was maturity or days to flowering. Crosses derived from different species or subspecies started flowering later than expected (mostly F_1s started flowering slightly earlier than mid-parent) and had a long flowering period. Many seeds of these crosses aborted, resulting in a lower than expected yield, and were more particularly affected when soil moisture was limited at the end of the growing season. These factors appeared to influence the stability of grain yield in F_1 and also affected the estimates of both combining ability and heterosis for grain yield and seed weight.

5.1.2 The levels of heterosis

Positive values of heterosis over the mid-parent and better parent were found in all the characteristics except harvest index, seeds per pod and seed weight. Grain yield heterosis was mainly due to increases in pods per plant of the hybrids. The contribution of pods per plant to heterosis for yield has also been reported by Gritton (1975). He reported that the average levels of heterosis of an 8 x 8 diallel cross of peas for pods per plant, seeds per pod and seed weight were 30.8, 8.0 and 0.8%, respectively. Similarly, in this experiment, the levels of heterosis obtained were 38, -1.4 and -2.1% for pods per plant, seeds per pod and seed weight respectively. The positive heterosis levels over the mid-parent and better parent for number of pods per plant suggested dominant or overdominant genes controlled the expression of this character. The lack of manifestation of heterosis for seed weight may be attributed to the presence of genes with oppositional dominance or no dominance. Hundred seed weight was the least heterotic of the yield components and no hybrid had significantly larger seeds than the high parent of the cross, although 23 F_1s showed significantly larger seeds than the mid-parent.

The level of Hmp for plant weight was equal to that for grain yield, therefore, Hmp for harvest index was close to zero.

The negative heterosis for days to onset of flowering is usually desirable because this will cause the hybrids to mature earlier than their parents, thereby increasing their productivity per day and per unit area. Most of the F_1s started flowering earlier than the mid-parent except F_1s from crosses between different subspecies, but no cross was earlier than the earliest parent. Thus genes controlling this trait would be partially dominant for lateness of flowering. This was in agreement with Johnson (1957, quoted by Gritton,

1975) who reported flowering time was probably determined by one or two major genes, plus partially dominant modifiers for late flowering.

For an individual cross, yield heterosis could often be attributed to significant heterosis in one or more components of yield. Often, however, component heterosis was small and non-significant and it was only the final yield heterosis which was significant. In other crosses, there was no detectable heterosis in yield and yield components. Since there was no consistent pattern, the only effective way to determine heterosis is on a comparative grain yield per plot basis.

Crosses which give high levels of heterosis for yield over the better parent or over the best parent are the most desirable for plant breeders. Very high levels of Hcm can be found in crosses between high x high yielding cultivars (e.g. Wirrega x Whero), high x moderate yielding cultivars (e.g. Wirrega x SA 157) and even between high x low yielding cultivars (e.g. Dundale x SA 123). The results from this study have not provided any clear cut strategies for consistently producing high-yielding, highly heterotic crosses.

5.1.3 Effects of environment on the levels of heterosis

The levels of heterosis for pods per plant, plant weight and grain yield were higher in poor yielding conditions than in high yielding conditions. Similarly, the levels of heterosis for wheat yield under stress conditions such as low fertility and late planting date were higher than those under non-stress condition such as high fertility and optimum planting date (Narula, 1984). Several other authors have reported that levels of heterosis were influenced by the environments in which the hybrids were grown (Pederson, 1968; Griffing and Zsiros, 1971; Sun *et al.*, 1972; Jošt and Hayward, 1980). They found the heterotic effects in common wheat were greater in a stress environment mainly due to poor winter hardiness of some parents. The expression of heterosis was affected not only by natural factors but also by crop management i.e. planting methods (Severson and Rasmusson, 1968; Fonseca and Patterson, 1968; Uddin, 1991).

The difference in the levels of heterosis across environments resulted from the different responses to the environment by the hybrids and their parents. Hybrids showed greater superiority to pure lines for pods per plant, grain yield and plant weight in inappropriate conditions than in appropriate conditions. This finding suggests that hybrids generally give greater advantages when growing in poor conditions than in good conditions. The significance of the heterosis x environment interaction for yield and other traits shows that to get valid heterosis estimates for each breeding programme, it is important to evaluate hybrids and parents in environments which correspond accurately to the target area.

5.1.4 F_2 performance, inbreeding depression and the level of heterosis in F_2

Yield and plant weight were lower in F_2s than in F_1s and the level of heterosis in F_2 was halved, which corresponds to the theory that the level of heterozygosity in F_2 is a half of that in F_1. The level of inbreeding depression for grain yield was higher than the decrease of Hmp from F_1 to F_2, which suggests that epistasis influenced grain yield in peas. Some F_2s still had grain yield as high as their F_1s whereas others were very much lower yielding. Crosses which maintain yield in F_2 as high as in F_1 may be affected mainly by additive or additive x additive gene effects. The segregation of elite lines from later generations of these crosses is worth attention.

5.1.5 Combining ability of parents

Both GCA and SCA have previously been shown in peas to be major contributing factors for pods per plant (Venkateswarlu and Singh, 1983), pods per plant and seeds per pod (Cervato *et al.*, 1977) and these two factors together with seed weight (Gritton, 1975).

GCA for males was larger than for females in all traits, which reflects the greater diversity among the male parents. No parental line was consistently a good general combiner for all the characteristics studied. Among the females, Wirrega was the best general combiner for grain yield *via* seeds per pod whereas among males SA 123 was the best combiner, by way of podding ability and plant weight, but this male line had negative GCA for seed weight.

Study of the relationship between *per se* performance of parents and GCA effects revealed a moderate to high correlation for several agronomic characters but not for yield, total plant weight and harvest index. This means that GCA for grain yield, total plant weight and harvest index cannot be predicted from the parental performance but that it could for the other characters. Similarly, it has been reported that *per se* performance of pea parents for days to onset of flowering, seed yield, pods per plant and seed weight in F_1 and F_2 was correlated with the GCA effects (Dubey and Lal, 1983).

The significant correlation between GCA and Hmp may suggest that additive gene effects were involved in the levels of heterosis for basal branches per plant, pods per plant, hundred seed weight and harvest index. The correlation coefficients were relatively low and therefore additive gene effects were less important for heterosis in grain yield, plant weight and both onset and duration of flowering.

Specific combining ability is a suitable index to determine the usefulness of a particular cross in the exploitation of heterosis. In this study five crosses showed significant positive SCA for grain yield and another five crosses showed a significant negative SCA effect, indicating some non-additive gene action. The highly significant correlation between SCA and Hmp showed that duration of flowering was also subject to considerable non-additive gene action. Other characters had moderate SCA so they were moderately affected by non-additive gene action.

5.2 Experiment B: Relative yield of pure-line derivatives of heterotic hybrids

5.2.1 Performance of crosses

The six crosses in this experiment were chosen on the basis of high estimates of heterosis over the best parent in experiment A. The results of the two experiments differed for the same genetic materials, with heterosis for yield in the F_1s in this experiment being less than in experiment A. This reduction in heterosis is probably attributable to environmental variation. F_5 means were lower than the corresponding F_1 values in the presence of reduced heterozygosity following four generations of inbreeding.

5.2.2 Performance of lines within crosses

F_5 lines which were at least as high in yield as the F_1 were recovered from every cross. Similarly, in wheat (Busch *et al.*, 1971; Cregan and Busch, 1978; Snape, 1982; Uddin, 1991) and in oats (Souza and Sorrells, 1991c), pure lines equal to the F_1 in yield have been recovered. This finding clearly shows that in peas, the yield advantage initially achieved with a hybrid could be recovered in the best pure breeding line of highly heterotic hybrids. This advantage could be obtained through any of the yield components.

The relationship between yield and yield components was investigated in each cross. Number of pods per plant was significantly correlated with grain yield in those crosses where seeds were larger (crosses A, E and F). Hundred seed weight was significantly correlated with grain yield in crosses which were obviously high in pods per plant but relatively low in hundred seed weight (crosses B, C and D). In addition, yield was significantly correlated with pods per plant in cross C. Thus in those crosses expressing a high mean number of pods per plant, selection of lines for high yield would be by preliminary screening for high hundred seed weight, whereas in crosses with large seeds, pods per plant would be used as a criterion for preliminary screening of lines for high yield. However, the correlation coefficients of these traits to yield were moderate and the correlation between hundred seed weight and pods per plant was significantly negative. Uddin (1991) found that for F_7 lines of wheat, kernel weight was significantly positively correlated with yield, but in both hybrids and pure lines, high yield was associated with intermediate kernel weight. He concluded on the basis of these data that selection for yield *via* its components was unlikely to be successful.

To determine which crosses are worth carrying on for selection, lines in each cross should be compared with a common standard which, in practice, is usually the best commercial cultivar. In this study, the comparison of lines from 6 crosses to the best commercial cultivars revealed that 11 lines were over 5% higher in yield than the best commercial parent, mostly from crosses D and E. Both these crosses ~~were~~ had a relatively moderate ~~in~~ mean and high ~~in~~ variation, whereas crosses A and F ~~were~~ had a high ~~in~~ mean but low ~~in~~ variation and contributed only 3 high yielding lines. Cross C which gave only 1 high yielding line was low in mean but high in variation. These relationships suggested that to obtain a high proportion of elite segregants, crosses should be high in variation and not too low for mean.

The mean of crosses in later generations should have been equal to the mid-parent value if the expression of genes were not affected by environment, lines were randomised and sample size were big enough to cover all possible genotypes. In this study, this relationship did not hold for the comparison of F_5 mean to the mid-parent value unless cross B was omitted from the calculation. Most lines in this cross were late in onset of flowering and severely infected by powdery mildew resulting in poor pod filling, so the exclusion of cross B is justifiable.

The variation among lines within crosses was expected to be correlated with genetic distance between parents because the greater the parental divergence, the greater the proportion of segregating loci in inbred generations. The genetic distance between parents was found to be significantly correlated with the variation within crosses for basal branches per plant, hundred seed weight and onset of flowering. The correlation for yield and pods per plant was significant for site 1 but not for site 2 or for the combined sites. In oats, in contrast, parental genetic distance (based on either parentage or morphological characters) was significantly correlated with the genetic component of the variance of yield, but poorly correlated for the yield components (Cowen and Frey, 1987). In another study, crosses between more distantly related oat lines produced larger variance among families than crosses between closely related parents for plant biomass, but for grain yield, heading date, grain filling period and maturity date, crosses between more closely related parents produced larger among-family variance than crosses of distantly related parents (Souza and Sorrells, 1991c).

The possibility to use genetic distance between parents in predicting variation of crosses would depend on the accuracy of the estimation of both GD and genetic variance. In this study, such prediction was possible for traits which were relatively insensitive to environment and for robust estimates of genetic distance such as GD_{i+m}. Yield, however, was very sensitive to environmental variation as well as to other factors e.g. epistasis, non-random sampling of progenies and genotype x environment interaction, all of which reduced its predictability.

Heritability is another criterion which is worth determining when choosing which crosses to make. The broad sense heritability of yield estimated in this study ranged from 36.7% (cross F) to 65.5% (cross C) which is comparable to that in F_5 of wheat (13.4% to 44.8%, Busch *et al.*, 1971) but much lower than that in F_7s of wheat ($h^2 = 92.9$ to 95.7%, Uddin, 1991). This discrepancy is not surprising, since early generations usually give lower estimates of heritability than later generations because the fixing of genetic components in later generation results in higher genotypic variance. Since this study was conducted in two different environments, the estimated heritability was also influenced by G x E interaction. The estimated heritability of yield in the 6 crosses suggests that selection for yield in crosses C and E would be more effective than in the others.

Among the studied traits, the heritabilities of onset of flowering (mean, 76.6%) and hundred seed weight (mean, 65.6%) were relatively high suggesting that selection of these traits in early generations would be possible.

From this study, it was difficult to determine how to maximise the choice of crosses which would give a high proportion of elite segregants. There was no consistent pattern of the performance and genetic distance between parents of crosses which gave high proportions of superior lines. For example, cross D was relatively high in SCA, GCA, inbreeding depression and genetic distance but moderate in mid-parent value and it produced as high a proportion of elite segregants as cross E which was similar in mid-parent value but lower in SCA, GCA, inbreeding depression, and GD between parents. Cross B was high in mid-parent value, low in inbreeding depression and moderate in SCA, GCA and GD between parents but produced no superior line.

5.3 Experiment C: Genetic distance amongst parental lines and its relation to the level of heterosis

5.3.1 The four measures of genetic distance

This experiment shows that it is possible to estimate genetic distance between pea varieties using quantitative traits (GD_q), isozyme markers (GD_i), morphological characteristics (GD_m) and the combination of isozyme markers and morphological polymorphisms (GD_{i+m}). Each method provided different estimate of genetic distance between parents and the ranges of GD_i and GD_q were greater than those of GD_m and GD_{i+m}. The significant linear correlation between GD_i and GD_q has also been reported in *Avena barbata* (Price *et al.*, 1984). Similarly, isozyme markers were recommended for use in improving quantitative characteristics in tomato (Tanksley *et al.*, 1981) and each isozyme locus in a set of 8 was strongly associated with at least one quantitative trait in F_2 of maize (Kahler and Wehrhahn, 1986). GD_m was found not to be correlated with either GD_i or GD_q which suggests that isozyme loci are more closely linked to quantitative than qualitative morphological loci.

5.3.2 The relationship between genetic distances and the levels of heterosis in F_1

The choice of class of traits or markers to estimate genetic distance should be based on its effectiveness in predicting the level of heterosis. All measures (GD_i, GD_m, GD_{i+m} and GD_q) were found to be positively correlated with heterosis over the mid-parent (Hmp) for yield in F_1 (r = 0.33 to 0.53). Similar findings have been obtained in mungbean (r not quoted; Ramanujam *et al.*, 1974) and in spring wheat (r = 0.45; Shamsuddin, 1985). Among these genetic distances, GD_{i+m} provided the highest correlation with heterosis and it remains to be seen whether this correlation is strong enough to allow prediction of Hmp for grain yield from GD_{i+m}. No GD had a significant correlation with the level of heterosis over better parent (Hbp), or over the best parent (Hcm), so none can be used to predict for the yield of F_1 relative to the better parent or the best variety, which is the most desirable use of GD by plant breeders.

Nevertheless, GD_i, GD_{i+m} and GD_q were good predictors of the levels of all three measures of heterosis for basal branches, podded nodes and pods per plant, hundred seed weight and total plant weight. All these agronomic characteristics showed high positive correlations with genetic distance, except that the correlation for hundred seed weight was negative. For this range of genetic material, the higher the genetic distance between parents the higher the level of heterosis for pods per plant but the lower for hundred seed weight.

The positive correlation between GD and the level of heterosis meant that dominant or overdominant genes determined such characteristics, that parents were different in the frequency of the alleles and also that the difference in the frequency of alleles of these characteristics corresponded to the difference of genetic markers which were used to estimate the genetic distance. The genes which control these characteristics may be dominant or overdominant.

The negative association for hundred seed weight may suggest that low seed weight was dominant to high seed weight. Number of seeds per pod, however, showed no association with any of the four genetic distances. Similarly, no association was found between GD and the level of heterosis for seeds per pod in faba bean (Ghaderi *et al.*, 1984). Theoretically the correlation for a completely additive characteristic is zero. The number of seeds per pod in F_1 was found to be highly correlated with the mid-parent value and the average heterosis over mid-parent was close to zero. This suggests that there is a predominantly additive effect for seeds per pod.

The significant positive correlation between all GDs and Hmp for yield may suggest that the difference of isozymes, morphological polymorphisms and quantitative traits corresponds to the difference of frequency of alleles for grain yield. The correlation coefficient between Hmp and GD_{i+m} was the highest, which indicated that the way GD_{i+m} was estimated more adequately covered the grain yield alleles than the other GDs, possibly because it was based on the most loci. The moderate correlation between GD and Hmp for grain yield shows yield heterosis is an output of genetically controlled biochemical, physiological and environmental interactions of the plant. These characters may be controlled and affected by a large number of genes which have epistatic effects, dominant effects and also additive effects. It is not clear why all GDs were significantly correlated with only Hmp but not Hbp and Hcm.

GD_m was the best predictor for plant height and, on the other hand, GD_i, GD_{i+m} and GD_q were all good predictors for basal stems per plant, podded nodes per plant, pods per plant, hundred seed weight and total plant weight.

5.3.3 The relationship between genetic distances and the level of inbreeding depression and heterosis in F_2

Following the occurrence of heterosis in F_1 for a given quantitatively inherited trait (Falconer, 1964), the same relationship between GD and Hmp should remain in F_2 if there were no epistatic effects on the expression of these traits. Ghaderi *et al.* (1984) found that the relationship between GD and the level of heterosis in F_2 was the same as that in F_1. In this study, there was no correlation between four genetic distances and the level of heterosis for yield, plant weight and harvest index in F_2 although the average level of Hmp in F_2 remained a half of that in F_1. GD_i, GD_{i+m} and GD_q were moderately correlated with the level of inbreeding depression for grain yield and plant weight.

Thus genetic distance was correlated not only with F_1 heterosis but also F_2 inbreeding depression. This high inbreeding depression from remote parents was from a high level of F_1 yield and it was evaluated over a population mean. As shown at the F_5 level, it is possible to select individual lines from these crosses which maintain the F_1 yield, even though the population mean shows considerable inbreeding depression. The correlation between genetic distance and F_2 inbreeding depression therefore does not mean that parents with high GD will give poor pure-line derivatives.

5.4 Implications in breeding peas for high yield

When improving yield in peas, the breeder may usefully start selection in the earliest possible generation. Heterosis of the F_1 over the best commercial cultivar is a useful indicator of future performance of the elite pure line derived from it. The 26% higher yield of the maximum F_1s over the best parent observed in this study suggests that there is relatively high potential for yield improvement in peas.

The ability accurately to identify parental combinations is crucial to the success of the breeding programme. This project was conducted to investigate what parental combinations would produce high proportions of elite lines in later generations, based on the hypotheses that heterosis in F_1 was fixable in pure lines and that genetic distance between parents was correlated with the level of heterosis of their hybrids and the variation among progenies in later generations. The choice of characters for determining genetic distance was based on their practicality to pea breeders.

The better predictive ability of GD_{i+m} than GD_i and GD_m showed that the ability of GD may be improved by increasing the number of genetic loci used for the estimation. Similarly, Souza and Sorrells (1991c) suggested that genetic distance between parents estimated from the combination of qualitative traits (isozyme markers and morphological characteristics) and quantitative traits was better a predictor than GD which was estimated from any single set of characteristics.

The combination of isozyme markers and morphological polymorphisms was considered to be a good genetic marker for estimating GD. Not only was GD_{i+m} predictive for the level of heterosis for yield and other agronomic traits, but also it was easy to obtain the data. The morphological description of lines or all germplasm usually being already in hand, isozyme markers may be characterised and added to the database for further use.

Genetic distance seemed to be predictive only for the proportion of the increased yield of hybrids which resulted from the effect of dominant genes. In fact, grain yield characteristics were complicated with additive, dominant and epistatic effects, together with the small number of genes controlling maturity. Therefore, the correlation coefficient between GD and the level of heterosis was only moderate. Among all estimated GDs, GD_{i+m} was considered to be the best predictor because the correlation coefficient for yield was highest and as good as GD_i in predicting other agronomic traits. The results showed that the greater the genetic distance between parents, the greater the level of heterosis. Thus, if we increase both the mid-parent value and the distance between the parents, the yield of hybrids would likely be increased.

Additive gene effects are inferred from high GCA levels. For some characters, such as hundred seed weight and onset of flowering, GCA effects were correlated with parental values. For these traits, one may select parents that perform well and predict that offspring will also perform well. Other characters, however, such as yield, while having high GCA and therefore significant additive gene effects, are also heavily influenced by environmental and GxE components, which impair their predictability. For these traits, a high additive gene component would be detected from well adapted lines.

It was possible to produce lines which were as high in yield as F_1 hybrids, but the proportion of superior lines potentially produced from each F_1 was different. It is desirable to predict which crosses will give a high proportion of elite pure-line derivatives. This prediction can be made if we know that the cross has a high mean together with a high variance. A high mean, in turn, can be predicted from a high mid-parent value, while high variance can be predicted from a high genetic distance between the parents. Nevertheless, the results show that we can not predict the production of elite lines from a high mid-parent value and a high genetic distance.

It is widely accepted that when improving crops for high yields the low potential crosses and/or genotypes are eliminated first, then the high potential ones are selected and after that are evaluated for the highest yield and the best adaptation. These results show that F_1 yield is not an effective means for eliminating low potential yield because yield in F_1 is much affected by environment and thus needs to be evaluated in replicates over a wide range of environments which is not feasible. Selecting for the good parental combination or culling low potential parents is however, more feasible for breeders. Although the genetic distance between parents in this study was not a clear predictor of the performance and genetic variance of crosses, it provided an additional and recommendable objective for efficient selection of parent combination.

Chapter 6 Conclusions

Experiment A: The levels of heterosis in F_1 hybrids and F_2 progenies

1. Most hybrids performed better than their respective parents for most of the traits. High yield in F_1 was usually achieved from a high value in only one component of yield. In comparison to the best parent, 4 out of 72 hybrids had significantly higher grain yield, by up to 26%.

2. The variation of each trait in F_1 obviously corresponded to that trait in the parental population. Both parents and F_1s showed greater variation in pod characteristics than in seed characteristics.

3. A high correlation was observed between hybrid performance and mid-parent value for plant height, podded nodes per plant, pods per plant and hundred seed weight, but it was low for grain yield.

4. Pod characteristics were negatively correlated with hundred seed weight. Plant weight and seeds per pod appeared to be more closely related to grain yield than the other yield components were, but no single yield component was consistently responsible for the higher yield of hybrids.

5. Environments affected the expression of all pod characteristics more than seed characteristics. Yield was marginally more stable across environments in parents than in F_1s.

6. The levels of heterosis for pod characteristics were higher than those for seed characteristics. Heterosis for grain yield was mainly due to heterosis for pods per plant. Very high levels of heterosis over the best parent were found regardless of the yield level of one parent as long as that of the other parent was high.

7. Differences in response of parents and hybrids to environments resulted in the difference in the level of heterosis across environments. F_1s were better adapted to poor yielding conditions than pure lines, therefore the levels of heterosis for grain yield, plant weight, and pods per plant were higher in a poor yielding condition than in a high yielding condition.

8. Both additive and non-additive gene effects were important to the expression of all traits. There was a high correlation between *per se* performance of parents and GCA effects for basal branches per plant, pods per plant, hundred seed weight, duration of flowering and seeds per pod. This means that gene effects were mainly additive for these traits and GCA effects of parents can be predicted from their *per se* performance.

9. The correlation between GCA effects and Hcm was highly significant for all traits. SCA effect was also highly significantly correlated with Hcm for grain yield and duration of flowering in F_1, suggesting that high yielding crosses comparable to the best parent can be obtained from parental lines which are high in GCA or in SCA effect.

10. The average performance of F_2s was less than that of F_1s. The level of heterosis for yield in F_2 was approximately half of that in F_1. The level of inbreeding depression was higher than the decreasing proportion of heterosis from F_1 indicating epistatic effects of genes on grain yield. Crosses which had a high level of Hmp always had a high level of inbreeding depression, but some F_2s maintained the high yield were found in their F_1s.

Experiment B: Relative yield of pure-line derivatives of heterotic hybrids

1. The relative yield of the best F_5 line of each cross to its F_1 was in a range of 93.6% (which was not significantly less than the F_1) to 123.8%. The relative yield of the best line of each cross to the best parent was in a range of 92.2% to 118.3%. These results indicated that the yield advantage initially achieved with a hybrid could be recovered in the best pure breeding lines of these crosses.

2. The higher the mid-parent value for basal branches per plant and hundred seed weight, the higher the F_5 line mean for the same trait. The greater the difference between parents for hundred seed weight, the greater the variation among the F_5 lines. When a high value for basal branches per plant, pods per plant and hundred seed weight was found in the F_1 it was also found in F_5.

3. There was an inconsistent pattern of the performance and genetic distance of crosses which gave high proportion of elite lines in later generations.

Experiment C: Genetic distance amongst parental lines and its relation to the level of heterosis

1. Genetic distance among pea lines can be estimated from isozyme markers, morphological polymorphisms, the combination of isozyme markers and morphological polymorphisms or quantitative traits.

2. The genetic distance estimated from quantitative traits (GD_q) was significantly correlated with those estimated from isozyme markers (GD_i) and from the combination of isozyme markers and morphological polymorphisms (GD_{i+m}). This may suggest that enzyme loci were associated with quantitative traits.

3. GD_i, GD_{i+m} and GD_q were equally good predictors for the level of heterosis in basal branches per plant, number of pods per plant and hundred seed weight whereas GD_m was the best predictor for the level of heterosis in plant height in F_1.

4. All measures of genetic distance proved moderately good predictors for Hmp for yield in the F_1, and GD_{i+m} was the best. None was predictive for yield in relation to the better (Hbp) or the best parent (Hcm).

5. There was no correlation between genetic distance and the level of heterosis for yield and plant weight in F_2, but GD_i, GD_{i+m} and GD_q were predictive for the level of inbreeding depression in grain yield and plant weight.

6. When parents were high in GD_i, GD_{i+m} and GD_q, crosses produced highly transgressive segregants for basal branches per plant, hundred seed weight, harvest index and onset of flowering.

Implications in pea breeding

1. There is considerable potential for improving yield in peas.

2. When choosing parents for a cross, consideration should be given to their genetic distance, their overall adaptation and their yield.

3. Selection for certain characters can be conducted in early generations. These traits include onset of flowering, which is important to general adaptation, and hundred seed weight.

4. Selection for yield should be conducted in the target (or similar) environment and should be based on yield *per se* rather than its components.

5. Genetic distance between cultivars can be estimated using quantitative traits, isozyme markers or the combination of isozyme markers and morphological characters, depending on the available facilities and preference of the breeders.

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Appendices

Appendix 1 Means across replicates for each genotype in each environment. Data from parents and F_1s for agronomic characters and yield.

Genotype	Basal branches per plant (number)				Plant height (cm)			
	E1	E2	E3	E4	E1	E2	E3	E4
Alma	1.167	1.000	2.100	2.167	118.7	122.7	122.2	
Derrimut	1.333	2.300	3.000	2.667	84.3	82.1	79.6	
Dundale	1.333	1.567	2.167	3.000	117.3	120.1	113.5	
Wirrega	1.833	1.667	2.000	1.833	96.7	107.5	102.5	
Garfield	1.167	1.167	2.333	3.000	81.0	87.5	99.8	
SA 15	1.500	2.333	2.500	4.000	64.3	76.3	92.0	
SA 24	1.000	2.567	3.300	3.000	33.3	46.1	50.4	
SA 35	1.000	1.300	1.333	2.333	79.2	88.0	88.6	
SA 51	1.000	1.567	1.167	1.167	78.7	89.1	89.1	
SA 54	5.000	4.067	5.100	3.667	63.3	66.7	70.7	
SA 123	2.167	6.033	3.500	5.333	57.3	65.7	81.2	
SA 129	2.833	2.567	3.667	6.833	51.3	55.9	57.6	
SA 157	2.167	1.067	1.000	2.000	103.0	121.0	119.3	
SA 236	1.500	1.833	2.167	1.933	106.7	125.7	135.7	
SA 247	1.833	1.500	2.000	3.167	98.8	116.2	114.8	
SA 248	2.000	2.033	3.000	4.000	109.7	115.0	114.7	
SA 465	1.167	1.500	2.000	2.333	42.0	44.0	52.5	
SA 483	2.167	5.500	3.000	5.333	53.2	59.5	56.8	
SA 688	2.000	4.933	4.600	2.667	83.0	92.7	101.0	
SA 828	1.833	2.167	2.833	1.923	143.7	136.3	134.7	
Solara	1.500	1.800	1.333	4.000	42.7	45.3	44.9	
Whero	1.333	1.500	2.167	2.250	114.8	128.5	132.7	
Alma x Garfield	1.333	1.833	2.333	2.777	115.7	123.2	125.0	
Alma x SA 15	4.000	3.567	2.833	4.539	120.5	127.2	118.6	
Alma x SA 24	1.467	1.333	2.100	1.890	134.2	144.9	133.2	
Alma x SA 35	1.500	1.833	1.667	2.333	120.7	130.5	131.0	
Alma x SA 51	1.667	1.667	1.667	2.167	131.0	115.0	120.0	
Alma x SA 54	3.833	5.800	7.800	3.713	121.3	137.8	142.8	
Alma x SA 123	3.733	3.500	3.600	5.500	72.2	81.9	105.9	
Alma x SA 129	3.333	9.000	6.333	7.699	98.3	110.5	139.2	
Alma x SA 157	1.167	1.033	2.300	2.333	101.7	92.8	90.3	
Alma x SA 236	1.467	1.000	1.333	2.890	113.2	146.1	169.3	
Alma x SA 247	1.733	3.400	2.100	3.333	118.2	126.8	121.0	
Alma x SA 248	2.333	2.067	2.500	3.500	109.7	111.9	95.9	
Alma x SA 465	1.000	2.000	2.333	3.162	121.0	118.3	110.0	
Alma x SA 483	3.333	6.167	5.367	4.114	94.3	103.7	117.5	
Alma x SA 688	2.500	4.400	3.833	5.206	97.8	111.0	104.3	
Alma x SA 828	1.233	2.033	2.367	2.640	126.2	115.9	128.7	
Alma x Solara	1.500	1.667	2.000	3.140	122.5	118.5	132.7	
Alma x Whero	2.000	2.167	1.500	2.667	104.3	110.7	107.3	
Derrimut x Garfield	1.667	4.067	2.833	2.667	104.0	100.3	101.1	

Appendix 1 continued

Genotype	Basal branches per plant (number)				Plant height (cm)			
	E1	E2	E3	E4	E1	E2	E3	E4
Derrimut x SA 15	3.333	4.800	2.833	5.206	91.0	72.5	100.5	
Derrimut x SA 24	1.833	2.833	2.567	2.333	110.3	96.2	107.2	
Derrimut x SA 35	1.467	1.633	1.833	2.833	109.2	105.4	111.7	
Derrimut x SA 51	1.500	1.500	1.667	2.500	121.0	137.0	150.2	
Derrimut x SA 54	4.667	5.500	3.333	5.444	80.7	87.8	100.2	
Derrimut x SA 123	3.500	7.333	4.500	4.833	83.0	101.3	112.0	
Derrimut x SA 129	4.167	6.667	4.333	6.890	73.7	75.7	82.3	
Derrimut x SA 157	1.833	1.333	1.600	2.333	91.7	110.7	130.7	
Derrimut x SA 236	1.333	2.300	2.500	2.912	115.0	111.0	105.4	
Derrimut x SA 247	1.500	2.567	1.667	3.662	99.7	113.2	119.9	
Derrimut x SA 248	2.000	3.333	2.833	4.162	94.8	104.8	107.2	
Derrimut x SA 465	1.333	2.500	2.000	3.333	92.2	87.2	94.2	
Derrimut x SA 483	3.833	5.167	4.167	3.174	75.7	76.7	70.0	
Derrimut x SA 688	3.000	3.300	2.833	3.912	81.7	93.8	104.0	
Derrimut x SA 828	3.300	2.500	2.667	2.667	118.8	133.8	120.7	
Derrimut x Solara	1.667	1.833	1.800	3.500	90.3	92.3	95.7	
Derrimut x Whero	1.667	2.333	1.833	3.167	112.3	128.2	130.8	
Dundale x Garfield	1.667	2.533	1.500	2.912	120.7	119.7	118.2	
Dundale x SA 15	3.833	4.167	3.533	1.892	93.0	115.5	121.5	
Dundale x SA 24	1.500	1.667	1.833	3.000	115.8	109.8	113.5	
Dundale x SA 35	1.433	1.900	1.300	1.833	114.5	107.3	119.0	
Dundale x SA 51	1.167	1.667	2.000	2.667	126.8	127.8	128.5	
Dundale x SA 54	4.167	4.167	5.067	3.949	95.2	120.2	134.2	
Dundale x SA 123	3.233	3.333	3.333	8.140	88.2	95.5	99.0	
Dundale x SA 129	4.333	6.333	6.100	4.412	99.0	108.3	121.5	
Dundale x SA 157	1.333	1.167	2.167	2.667	117.7	122.3	117.3	
Dundale x SA 236	1.500	2.800	1.600	2.833	123.8	126.9	132.1	
Dundale x SA 247	1.333	2.500	2.667	3.333	121.3	127.3	113.0	
Dundale x SA 248	1.467	2.900	2.600	3.833	104.2	119.2	118.5	
Dundale x SA 465	1.467	2.067	1.333	3.000	116.0	107.5	99.0	
Dundale x SA 483	2.733	4.067	4.167	4.699	84.5	89.9	96.4	
Dundale x SA 688	3.167	2.300	3.333	4.169	99.0	115.0	142.0	
Dundale x SA 828	1.833	1.900	2.833	4.640	130.0	135.8	127.2	
Dundale x Solara	2.167	1.833	1.833	2.000	120.0	138.0	137.3	
Dundale x Whero	1.333	1.200	2.000	5.333	122.5	119.8	114.4	
Wirrega x Garfield	1.000	1.500	2.167	2.723	109.0	104.8	90.8	
Wirrega x SA 15	4.167	4.667	2.567	4.744	99.3	110.7	105.0	
Wirrega x SA 24	1.333	1.667	2.167	2.449	106.3	112.7	112.0	
Wirrega x SA 35	1.233	2.133	3.100	2.949	102.2	127.2	104.7	
Wirrega x SA 51	1.333	2.000	2.333	2.662	131.7	126.7	114.0	
Wirrega x SA 54	4.333	6.333	4.333	4.949	85.7	87.7	96.0	
Wirrega x SA 123	2.833	5.333	4.500	3.449	82.3	102.3	95.3	

Appendix 1 continued

Genotype	Basal branches per plant (number)				Plant height (cm)			
	E1	E2	E3	E4	E1	E2	E3	E4
Wirrega x SA 129	3.000	4.000	4.167	5.500	97.0	114.0	103.7	
Wirrega x SA 157	1.167	1.667	2.333	2.167	100.5	119.5	118.7	
Wirrega x SA 236	1.667	2.033	2.167	2.890	95.0	109.8	122.5	
Wirrega x SA 247	1.333	1.667	2.333	3.167	96.0	92.3	94.0	
Wirrega x SA 248	1.167	2.900	2.500	3.667	106.0	105.3	120.7	
Wirrega x SA 465	1.167	1.700	2.333	1.833	106.0	105.7	99.9	
Wirrega x SA 483	3.000	2.533	6.333	9.000	78.7	87.2	94.0	
Wirrega x SA 688	3.000	5.000	3.833	3.667	97.3	102.7	102.5	
Wirrega x SA 828	1.333	1.800	2.833	4.000	84.6	91.0	97.3	
Wirrega x Solara	1.333	2.167	2.367	3.167	93.0	82.2	90.8	
Wirrega x Whero	1.500	2.833	2.833	5.390	102.3	107.3	120.7	

Genotype	Podded nodes per plant (number)				Pods per plant (number)			
	E1	E2	E3	E4	E1	E2	E3	E4
Alma	5.7	11.7	16.0		8.00	18.77	26.43	15.94
Derrimut	8.5	12.8	15.5		10.17	20.63	25.17	21.17
Dundale	8.7	13.3	19.3		9.00	19.63	22.33	20.55
Wirrega	10.7	16.0	18.7		12.00	27.33	23.33	21.67
Garfield	5.5	7.8	9.7		6.83	12.67	17.67	12.17
SA 15	5.3	7.5	14.5		5.40	23.17	23.50	15.00
SA 24	5.5	10.4	11.3		8.17	23.23	30.13	14.11
SA 35	3.5	7.1	9.4		4.83	11.63	12.83	8.17
SA 51	5.0	7.0	7.3		6.83	17.87	11.33	9.25
SA 54	18.5	15.3	15.3		31.83	22.37	31.10	13.33
SA 123	9.2	18.2	26.8		14.67	51.00	25.33	18.50
SA 129	9.8	13.1	13.9		15.27	16.63	28.83	15.67
SA 157	9.5	13.8	12.2		12.83	22.17	17.83	13.39
SA 236	7.2	9.3	8.5		9.33	12.00	16.00	16.95
SA 247	8.0	12.2	13.5		12.33	22.67	20.50	18.72
SA 248	8.2	13.8	19.5		13.83	30.50	30.83	18.79
SA 465	4.3	7.2	8.3		7.83	13.50	14.67	8.11
SA 483	10.5	22.8	28.5		9.17	60.67	21.33	18.28
SA 688	9.0	15.7	18.5		11.83	25.97	44.13	8.67
SA 828	10.2	20.5	23.5		16.67	34.33	15.60	13.17
Solara	5.7	8.8	10.7		7.50	13.50	13.33	33.01
Whero	6.2	13.8	16.7		10.00	29.17	23.03	17.56
Alma x Garfield	19.7	24.5	14.6		10.50	21.67	15.50	16.02
Alma x SA 15	7.3	8.0	6.0		11.33	10.77	8.83	12.55
Alma x SA 24	8.5	9.6	14.6		13.57	22.17	26.93	24.26

Appendix 1 continued

Genotype	Podded nodes per plant (number)				Pods per plant (number)			
	E1	E2	E3	E4	E1	E2	E3	E4
Alma x SA 35	6.0	12.8	15.0		9.83	27.17	15.17	18.11
Alma x SA 51	7.7	10.8	15.5		12.00	21.50	19.33	23.33
Alma x SA 54	17.8	27.0	35.2		31.17	58.37	67.13	23.27
Alma x SA 123	9.7	15.1	17.9		16.57	40.33	35.33	28.55
Alma x SA 129	13.2	35.8	53.2		20.00	79.00	50.00	33.98
Alma x SA 157	6.2	9.7	11.2		11.17	18.00	27.40	12.45
Alma x SA 236	8.2	11.2	13.1		9.57	24.97	10.83	16.26
Alma x SA 247	7.0	15.5	21.3		12.33	35.97	29.10	13.06
Alma x SA 248	10.0	13.9	15.1		17.17	18.63	30.67	23.06
Alma x SA 465	5.5	8.5	11.0		8.67	17.50	20.50	8.68
Alma x SA 483	14.0	22.3	35.1		15.37	60.33	36.17	14.42
Alma x SA 688	9.2	20.2	22.8		16.00	40.00	28.17	25.75
Alma x SA 828	6.5	12.5	21.2		9.07	40.00	27.93	24.26
Alma x Solara	8.2	13.3	16.2		12.50	19.67	14.83	27.42
Alma x Whero	7.2	9.2	11.2		11.67	15.00	17.00	15.89
Derrimut x Garfield	8.8	18.8	24.8		11.17	35.63	23.33	15.83
Derrimut x SA 15	17.3	23.9	24.8		25.17	44.63	23.33	20.30
Derrimut x SA 24	9.5	14.5	21.5		11.50	29.00	19.17	14.00
Derrimut x SA 35	7.5	9.6	12.3		10.33	20.10	14.83	15.61
Derrimut x SA 51	9.3	14.8	14.3		13.63	30.67	22.00	23.83
Derrimut x SA 54	19.8	23.8	29.7		34.00	45.33	43.50	37.22
Derrimut x SA 123	15.8	30.3	40.3		24.83	79.50	35.00	27.23
Derrimut x SA 129	18.2	26.8	35.0		25.50	46.17	31.33	46.92
Derrimut x SA 157	10.8	11.8	18.2		13.00	17.83	23.93	14.28
Derrimut x SA 236	7.8	14.7	19.2		9.33	28.00	16.50	30.02
Derrimut x SA 247	8.3	15.7	18.2		11.83	28.37	30.67	39.35
Derrimut x SA 248	10.3	16.3	18.0		15.33	33.17	26.33	33.68
Derrimut x SA 465	8.7	11.3	13.7		11.67	30.67	18.83	23.06
Derrimut x SA 483	15.0	15.2	20.2		20.50	32.00	44.67	9.47
Derrimut x SA 688	11.0	17.8	23.8		17.17	49.60	31.33	11.85
Derrimut x SA 828	13.8	21.8	30.7		22.17	39.83	32.33	13.00
Derrimut x Solara	8.8	8.3	12.2		12.00	15.83	14.00	21.61
Derrimut x Whero	11.3	14.5	19.0		14.50	22.83	16.67	23.22
Dundale x Garfield	8.5	15.0	19.2		10.83	25.27	15.00	18.77
Dundale x SA 15	16.0	17.5	19.7		19.67	31.83	25.83	12.21
Dundale x SA 24	9.5	13.7	16.7		14.17	22.67	23.67	23.56
Dundale x SA 35	7.4	8.8	15.1		13.17	19.60	21.13	10.72
Dundale x SA 51	6.2	11.7	15.2		10.00	22.33	21.83	16.78
Dundale x SA 54	18.8	28.0	43.0		31.33	66.83	54.73	16.39
Dundale x SA 123	14.7	22.9	28.2		20.33	47.00	31.00	34.42
Dundale x SA 129	23.3	38.3	51.7		35.00	95.67	77.67	35.10
Dundale x SA 157	6.7	11.2	13.0		9.67	18.00	21.00	25.11

Appendix 1 continued

Genotype	Podded nodes per plant (number)				Pods per plant (number)			
	E1	E2	E3	E4	E1	E2	E3	E4
Dundale x SA 236	6.2	12.0	15.7		8.50	22.13	17.83	18.61
Dundale x SA 247	12.8	15.7	14.0		18.83	22.67	27.33	10.39
Dundale x SA 248	5.2	11.1	14.6		8.07	23.37	30.10	26.28
Dundale x SA 465	8.5	11.7	12.6		10.83	20.37	13.00	22.06
Dundale x SA 483	14.7	17.2	21.0		21.07	35.63	32.50	18.06
Dundale x SA 688	12.5	14.8	17.3		19.00	33.87	29.67	24.00
Dundale x SA 828	9.5	16.5	20.0		13.67	30.37	31.10	32.75
Dundale x Solara	7.2	11.7	13.3		10.50	21.33	18.33	16.39
Dundale x Whero	6.2	10.5	13.5		9.83	19.27	22.00	21.83
Wirrega x Garfield	6.7	15.5	18.0		8.50	26.67	25.50	19.24
Wirrega x SA 15	11.5	17.7	16.7		19.33	24.33	25.83	19.44
Wirrega x SA 24	9.7	11.2	16.0		14.00	32.33	24.33	17.31
Wirrega x SA 35	5.5	11.0	11.8		7.57	23.37	24.03	19.23
Wirrega x SA 51	7.2	10.8	14.2		11.17	22.83	21.83	16.60
Wirrega x SA 54	21.5	33.2	39.8		35.83	63.50	40.50	10.89
Wirrega x SA 123	15.3	23.2	27.5		21.00	39.00	46.33	23.81
Wirrega x SA 129	11.5	19.8	26.7		18.33	39.33	32.33	18.89
Wirrega x SA 157	10.8	17.3	18.2		14.67	27.33	27.17	26.83
Wirrega x SA 236	7.0	12.8	17.2		8.83	23.00	17.00	15.26
Wirrega x SA 247	8.5	16.8	17.5		11.50	23.00	20.33	22.00
Wirrega x SA 248	7.8	8.8	13.2		12.17	34.87	25.17	31.06
Wirrega x SA 465	7.0	9.5	11.3		11.17	13.80	28.17	18.28
Wirrega x SA 483	13.0	13.2	13.2		20.33	26.27	42.67	36.06
Wirrega x SA 688	12.3	24.0	26.8		21.33	50.83	48.60	18.11
Wirrega x SA 828	10.3	21.8	30.5		15.00	45.87	32.50	17.89
Wirrega x Solara	6.2	8.8	11.3		8.07	20.00	19.30	17.22
Wirrega x Whero	7.2	13.7	21.7		9.33	41.83	24.17	23.59

Genotype	Seeds per pod (number)				Hundred seed weight (g)			
	E1	E2	E3	E4	E1	E2	E3	E4
Alma	5.867	6.000	7.500	6.200	24.33	22.84	24.39	21.22
Derrimut	5.133	7.033	5.533	6.050	19.33	18.96	20.41	17.45
Dundale	4.600	6.700	5.933	5.967	24.14	24.51	23.77	22.02
Wirrega	6.133	6.067	6.867	6.517	18.81	18.35	19.27	17.19
Garfield	5.700	6.600	6.133	5.683	23.31	22.21	24.08	21.24
SA 15	2.467	3.733	2.867	4.967	31.96	33.51	35.67	27.83
SA 24	4.800	5.533	6.567	6.167	23.41	22.23	22.96	21.63
SA 35	5.467	4.033	5.400	4.200	23.18	21.64	24.79	21.98
SA 51	3.933	5.533	4.333	4.250	18.96	21.79	24.71	22.78

Appendix 1 continued

Genotype	Seeds per pod (number)				Hundred seed weight (g)			
	E1	E2	E3	E4	E1	E2	E3	E4
SA 54	5.800	6.033	6.633	6.700	5.13	5.48	5.37	6.61
SA 123	6.667	6.400	6.800	6.867	6.60	7.72	7.96	7.99
SA 129	6.200	5.833	5.733	6.467	6.77	10.66	7.33	8.57
SA 157	6.000	4.667	5.133	5.283	20.39	21.72	22.38	20.35
SA 236	5.400	5.667	5.200	6.533	33.53	34.72	34.09	31.89
SA 247	5.200	5.467	5.667	5.367	18.11	18.53	19.16	16.97
SA 248	3.800	6.400	5.133	4.500	20.68	19.57	21.35	18.59
SA 465	7.133	7.333	5.867	5.917	17.84	18.27	19.39	17.82
SA 483	5.667	5.333	5.100	5.733	6.95	6.84	9.02	6.57
SA 688	7.600	7.467	7.967	6.800	12.46	12.77	11.97	13.42
SA 828	6.667	6.667	6.667	6.500	14.31	14.89	15.59	14.55
Solara	4.000	5.500	5.400	4.267	29.29	30.07	32.36	25.26
Whero	5.067	5.667	5.067	5.933	25.15	26.08	26.26	22.26
Alma x Garfield	5.467	6.800	5.867	5.936	25.34	25.15	25.73	21.99
Alma x SA 15	3.533	3.200	5.233	6.139	19.26	20.57	20.47	21.37
Alma x SA 24	4.300	4.467	4.800	4.031	29.65	28.94	32.09	25.45
Alma x SA 35	5.067	6.067	6.000	4.983	25.77	27.64	28.19	20.74
Alma x SA 51	5.400	5.367	6.067	5.800	28.10	25.64	29.53	24.69
Alma x SA 54	6.067	6.333	5.767	6.736	11.51	14.23	10.87	9.76
Alma x SA 123	6.300	7.067	6.833	6.667	11.76	11.64	12.80	14.91
Alma x SA 129	6.000	7.533	6.333	6.013	8.53	8.11	9.31	11.48
Alma x SA 157	5.133	6.800	5.167	6.800	26.13	23.22	24.14	20.59
Alma x SA 236	4.800	6.600	5.833	5.531	30.62	31.27	34.81	23.06
Alma x SA 247	5.600	5.600	6.533	6.200	20.60	21.02	21.39	20.85
Alma x SA 248	5.033	7.033	6.467	5.933	22.39	21.41	23.95	19.61
Alma x SA 465	6.433	7.333	6.733	4.406	21.78	21.98	23.45	18.21
Alma x SA 483	6.500	6.933	6.900	4.663	11.97	12.15	12.19	11.00
Alma x SA 688	6.733	6.133	7.067	7.006	14.36	12.95	14.26	12.18
Alma x SA 828	6.000	6.700	6.667	6.531	19.10	17.60	20.40	15.41
Alma x Solara	5.467	6.000	7.000	5.931	26.30	26.33	28.95	23.85
Alma x Whero	5.000	6.933	6.533	5.917	25.16	23.23	28.07	21.02
Derrimut x Garfield	5.533	6.833	5.267	5.533	22.11	20.30	22.62	19.78
Derrimut x SA 15	3.800	3.833	4.833	4.546	21.71	19.56	18.72	19.20
Derrimut x SA 24	3.467	4.867	3.600	4.717	24.19	24.82	26.04	21.00
Derrimut x SA 35	6.000	6.267	5.133	5.100	20.86	24.06	23.30	17.69
Derrimut x SA 51	4.533	4.733	6.533	5.833	23.33	24.59	26.03	21.40
Derrimut x SA 54	4.667	4.933	5.133	4.802	10.56	9.59	11.34	8.19
Derrimut x SA 123	5.733	5.533	4.667	5.800	10.49	10.14	12.06	10.67
Derrimut x SA 129	5.400	6.267	5.833	6.930	10.54	10.92	11.17	11.11
Derrimut x SA 157	5.267	6.067	6.200	4.233	22.42	21.80	25.45	19.13
Derrimut x SA 236	5.733	7.100	5.667	4.506	29.24	27.30	31.22	26.45
Derrimut x SA 247	5.733	6.133	5.333	5.940	18.88	19.05	21.03	17.62

Appendix 1 continued

Genotype	Seeds per pod (number)				Hundred seed weight (g)			
	E1	E2	E3	E4	E1	E2	E3	E4
Derrimut x SA 248	5.533	6.333	5.733	5.206	20.13	21.30	21.75	18.31
Derrimut x SA 465	5.600	6.800	7.133	6.563	18.71	20.20	23.85	19.48
Derrimut x SA 483	5.667	5.933	5.667	5.131	10.74	14.47	16.00	8.02
Derrimut x SA 688	5.067	7.100	6.133	6.206	14.72	14.28	16.22	16.22
Derrimut x SA 828	5.467	5.867	5.733	7.490	17.68	16.62	19.46	16.85
Derrimut x Solara	4.733	6.133	5.467	4.533	22.63	22.37	25.10	21.94
Derrimut x Whero	5.700	6.000	6.733	5.050	23.75	23.85	25.44	20.07
Dundale x Garfield	5.067	6.400	6.200	6.606	24.42	25.17	28.85	22.27
Dundale x SA 15	3.533	4.467	4.833	3.949	23.42	20.29	24.70	24.84
Dundale x SA 24	4.467	4.200	4.533	3.467	29.91	29.50	31.81	24.31
Dundale x SA 35	6.267	6.167	7.767	5.600	23.60	24.62	29.16	21.01
Dundale x SA 51	4.600	6.533	7.333	5.367	27.47	26.85	29.61	23.08
Dundale x SA 54	4.400	5.800	5.567	6.128	10.95	9.86	17.39	5.85
Dundale x SA 123	6.500	6.800	6.333	6.467	12.04	11.22	13.26	11.46
Dundale x SA 129	5.400	6.800	7.300	6.206	6.43	8.79	8.07	8.53
Dundale x SA 157	4.133	5.600	5.000	5.767	24.70	22.96	25.24	21.63
Dundale x SA 236	5.300	6.633	5.933	5.600	31.20	32.36	35.25	25.13
Dundale x SA 247	5.333	6.867	6.333	5.200	22.51	20.05	22.74	19.53
Dundale x SA 248	5.100	6.767	6.133	5.000	23.39	19.66	23.90	20.40
Dundale x SA 465	6.200	6.733	7.467	6.467	22.08	21.07	23.69	22.08
Dundale x SA 483	5.400	6.433	6.133	5.588	11.98	12.21	13.20	11.11
Dundale x SA 688	5.400	5.333	6.467	5.189	16.45	14.65	22.25	14.47
Dundale x SA 828	5.467	6.967	6.433	6.831	19.17	19.32	21.49	17.04
Dundale x Solara	4.533	5.667	6.200	5.600	26.27	27.55	27.77	25.67
Dundale x Whero	5.800	6.500	5.467	5.000	26.18	27.34	28.96	20.21
Wirrega x Garfield	5.400	7.067	5.867	5.367	22.62	20.18	26.59	20.74
Wirrega x SA 15	4.067	4.867	4.767	6.383	19.43	17.69	19.34	22.97
Wirrega x SA 24	4.000	3.800	4.467	5.463	25.72	26.71	26.81	22.65
Wirrega x SA 35	5.200	5.767	5.833	5.533	22.00	22.52	22.41	21.33
Wirrega x SA 51	4.333	6.667	6.533	6.067	23.22	24.08	25.39	19.92
Wirrega x SA 54	5.967	6.400	5.867	6.139	9.80	10.52	9.03	7.60
Wirrega x SA 123	6.333	7.000	6.467	6.463	11.22	10.64	10.99	12.27
Wirrega x SA 129	6.400	7.467	6.733	5.663	10.95	11.06	12.05	10.66
Wirrega x SA 157	5.400	6.200	6.267	6.000	22.96	21.48	24.69	20.88
Wirrega x SA 236	5.533	6.700	5.800	6.031	29.01	28.44	29.84	21.02
Wirrega x SA 247	6.067	6.667	5.533	5.000	19.07	18.92	21.02	17.11
Wirrega x SA 248	4.667	5.967	5.000	5.400	19.05	19.80	21.91	18.33
Wirrega x SA 465	6.200	6.100	6.867	6.767	19.00	16.96	21.29	18.24
Wirrega x SA 483	5.733	6.500	6.000	6.067	10.83	14.01	12.29	9.35
Wirrega x SA 688	5.667	6.333	7.933	5.933	15.14	13.75	15.58	12.53
Wirrega x SA 828	6.200	6.633	6.133	6.267	17.75	16.97	16.03	16.68
Wirrega x Solara	5.533	6.867	6.200	5.031	23.94	24.05	27.72	22.51
Wirrega x Whero	5.600	6.467	6.333	5.456	22.68	22.24	23.86	16.83

Appendix 1 continued

Genotype	Grain yield (g)				Plant weight (g)			
	E1	E2	E3	E4	E1	E2	E3	E4
Alma	9.19	21.90	20.95	10.85	19.16	46.37	39.91	36.68
Derrimut	7.31	16.71	21.11	10.30	15.35	33.04	40.63	29.98
Dundale	7.58	20.18	22.86	13.22	15.87	40.00	44.36	48.00
Wirrega	8.80	22.28	22.97	8.83	22.02	51.03	48.26	53.44
Garfield	7.06	13.04	17.10	6.67	13.92	27.29	33.58	13.82
SA 15	6.58	13.90	15.70	5.24	12.53	27.39	30.45	16.05
SA 24	7.10	12.45	13.50	7.53	11.24	21.08	23.04	25.03
SA 35	3.52	12.05	14.73	3.94	8.83	25.58	33.71	21.90
SA 51	4.32	9.10	15.02	3.86	11.10	25.27	35.55	20.28
SA 54	3.79	4.95	8.77	5.47	10.57	21.14	22.70	30.37
SA 123	4.11	14.33	11.30	5.47	8.88	43.80	22.56	20.41
SA 129	2.60	8.51	11.15	3.31	5.81	19.34	22.25	15.58
SA 157	7.96	12.87	15.01	8.57	17.98	27.30	30.93	36.86
SA 236	10.70	16.08	21.77	9.55	23.89	32.66	43.64	43.81
SA 247	6.63	15.83	17.83	7.22	15.19	36.21	41.83	39.45
SA 248	10.31	14.95	16.52	10.45	22.70	31.41	43.61	70.91
SA 465	6.68	13.33	18.21	5.77	11.46	25.11	30.54	25.79
SA 483	4.42	8.82	11.75	6.41	10.50	17.43	22.54	20.81
SA 688	5.87	13.61	15.13	4.56	14.20	43.83	30.26	16.66
SA 828	8.55	17.74	10.62	6.13	20.57	38.86	28.07	21.00
Solara	7.83	14.16	14.95	9.59	14.26	27.60	27.70	27.29
Whero	8.39	20.40	26.76	8.62	17.75	44.14	55.07	39.56
Alma x Garfield	11.20	16.61	23.83	13.58	22.86	34.28	46.21	41.45
Alma x SA 15	8.05	10.19	9.62	7.76	28.51	26.18	53.26	63.23
Alma x SA 24	11.29	21.17	25.39	15.47	25.01	44.73	50.09	54.16
Alma x SA 35	10.21	20.30	26.23	10.91	20.31	41.59	60.68	35.92
Alma x SA 51	11.21	18.20	21.28	12.27	23.15	37.88	42.48	50.95
Alma x SA 54	9.91	12.24	13.91	9.42	28.55	47.71	72.35	42.59
Alma x SA 123	9.19	20.93	26.61	9.29	19.95	46.99	61.85	61.45
Alma x SA 129	7.57	16.45	22.82	8.91	24.02	51.77	61.26	59.61
Alma x SA 157	9.25	14.86	23.55	9.84	18.13	26.78	47.97	36.31
Alma x SA 236	9.13	25.23	23.73	9.20	17.97	52.55	45.24	74.36
Alma x SA 247	10.21	17.80	29.12	7.58	21.77	37.10	61.60	48.48
Alma x SA 248	12.74	14.42	22.48	13.82	26.02	32.85	45.38	39.80
Alma x SA 465	9.35	17.34	21.36	8.65	18.43	35.83	43.56	40.60
Alma x SA 483	11.23	24.14	20.62	8.59	25.23	54.03	46.34	52.76
Alma x SA 688	9.01	14.42	21.11	10.71	22.14	43.71	52.47	75.87
Alma x SA 828	8.46	28.45	25.12	8.12	19.17	63.95	51.12	64.20
Alma x Solara	11.02	20.18	24.28	15.66	22.77	48.51	45.01	32.51
Alma x Whero	8.88	15.41	24.78	14.03	18.58	36.99	53.92	44.54
Derrimut x Garfield	10.80	24.01	23.99	8.84	18.18	45.96	48.01	32.43
Derrimut x SA 15	7.93	15.34	17.59	12.35	19.80	44.45	46.59	44.02

Appendix 1 continued

Genotype	Grain yield (g)				Plant weight (g)			
	E1	E2	E3	E4	E1	E2	E3	E4
Derrimut x SA 24	9.43	19.60	24.39	7.79	18.83	40.86	47.52	27.09
Derrimut x SA 35	8.62	15.87	22.11	7.94	18.12	30.98	39.20	30.81
Derrimut x SA 51	8.79	16.56	23.57	13.78	18.88	32.91	45.69	44.23
Derrimut x SA 54	11.98	17.05	17.57	9.39	27.96	44.69	48.43	47.36
Derrimut x SA 123	10.20	24.73	22.36	8.95	21.51	57.67	47.48	61.20
Derrimut x SA 129	10.25	22.38	26.24	20.84	21.90	49.18	50.71	44.15
Derrimut x SA 157	7.48	23.29	22.12	9.79	17.38	48.55	39.19	36.09
Derrimut x SA 236	10.80	19.54	22.58	18.57	22.88	47.28	41.56	55.73
Derrimut x SA 247	10.81	20.73	28.51	17.91	22.80	42.90	56.06	57.82
Derrimut x SA 248	9.99	21.21	23.27	13.70	19.96	42.45	46.23	47.74
Derrimut x SA 465	8.93	21.85	20.69	18.94	16.80	42.25	37.73	38.38
Derrimut x SA 483	9.93	14.70	25.54	6.22	20.88	32.04	52.28	21.98
Derrimut x SA 688	9.70	23.90	20.32	5.39	21.60	54.73	47.21	35.44
Derrimut x SA 828	10.66	17.44	29.87	5.76	23.99	35.97	56.32	31.54
Derrimut x Solara	8.44	15.70	17.84	11.00	14.68	31.51	31.73	39.50
Derrimut x Whero	12.09	21.61	22.48	10.99	24.00	45.06	41.83	44.85
Dundale x Garfield	10.91	21.51	21.39	14.42	23.35	56.43	39.23	42.85
Dundale x SA 15	9.79	17.18	18.97	5.80	23.75	46.15	47.95	29.77
Dundale x SA 24	8.34	18.16	21.58	11.96	17.80	39.72	38.43	58.84
Dundale x SA 35	10.63	15.22	28.65	9.05	20.59	29.01	57.38	30.72
Dundale x SA 51	8.74	20.63	23.72	12.44	17.21	43.05	46.28	44.24
Dundale x SA 54	10.02	15.63	14.91	1.80	25.10	56.75	34.27	15.64
Dundale x SA 123	11.03	21.64	29.97	19.12	23.97	43.93	68.30	73.56
Dundale x SA 129	7.91	14.94	12.66	7.73	21.65	50.42	43.17	29.50
Dundale x SA 157	8.93	21.18	21.85	9.24	18.87	45.10	44.26	50.74
Dundale x SA 236	11.02	19.47	23.71	11.79	23.15	37.93	45.32	76.14
Dundale x SA 247	9.62	18.57	24.36	16.01	20.24	38.47	53.11	40.46
Dundale x SA 248	11.63	16.47	25.77	15.41	24.93	34.63	50.15	57.92
Dundale x SA 465	11.47	15.35	22.53	14.73	23.68	30.33	41.12	36.73
Dundale x SA 483	10.79	22.02	25.58	7.17	23.43	47.57	55.77	31.92
Dundale x SA 688	10.00	21.18	17.15	2.26	24.83	54.29	39.45	44.11
Dundale x SA 828	9.27	21.32	19.77	17.51	23.46	45.32	40.82	70.75
Dundale x Solara	11.01	23.81	17.04	12.33	21.44	45.24	30.82	35.94
Dundale x Whero	9.67	18.21	26.05	11.29	20.14	37.89	48.74	44.68
Wirrega x Garfield	10.72	18.50	29.26	10.85	20.69	42.10	57.69	37.44
Wirrega x SA 15	9.07	15.31	14.62	4.72	25.48	45.08	48.22	24.46
Wirrega x SA 24	9.13	23.32	21.85	10.79	18.78	51.28	43.58	39.94
Wirrega x SA 35	8.84	21.86	26.26	11.82	17.51	44.35	46.51	35.22
Wirrega x SA 51	10.03	20.39	25.12	12.09	22.18	42.60	48.54	42.17
Wirrega x SA 54	12.49	19.75	17.53	8.41	26.88	57.02	44.73	77.25
Wirrega x SA 123	9.18	21.82	26.32	8.37	19.75	41.57	54.13	39.77
Wirrega x SA 129	11.82	20.38	26.34	10.74	25.94	43.91	50.92	34.10

Appendix 1 continued

Genotype	Grain yield (g)				Plant weight (g)			
	E1	E2	E3	E4	E1	E2	E3	E4
Wirrega x SA 157	10.37	23.55	28.81	11.95	20.01	48.60	55.87	43.01
Wirrega x SA 236	11.95	21.07	23.39	11.69	24.03	43.74	45.95	54.41
Wirrega x SA 247	8.59	21.12	22.81	13.34	17.56	40.22	48.61	54.79
Wirrega x SA 248	10.18	24.70	24.33	13.15	20.96	49.17	46.58	41.27
Wirrega x SA 465	11.24	18.55	29.71	12.03	21.97	38.60	53.34	41.40
Wirrega x SA 483	8.00	22.63	27.58	8.33	16.92	53.76	56.21	73.27
Wirrega x SA 688	12.48	18.57	23.53	9.26	28.04	47.62	56.33	52.24
Wirrega x SA 828	10.41	25.07	23.50	9.99	18.58	54.72	51.25	45.95
Wirrega x Solara	8.02	18.96	18.63	12.98	15.53	39.03	35.43	43.96
Wirrega x Whero	8.33	27.06	28.26	13.51	16.43	52.47	52.54	52.47

Genotype	Harvest index				Onset of flowering (days after sowing)			
	E1	E2	E3	E4	E1	E2	E3	E4
Alma	0.4800	0.4733	0.5300	0.3100	97.67			132.00
Derrimut	0.4767	0.5200	0.5233	0.3500	89.00			108.67
Dundale	0.4767	0.5100	0.5167	0.3233	91.33			118.00
Wirrega	0.3967	0.4367	0.4767	0.1800	95.33			124.67
Garfield	0.5067	0.4767	0.5133	0.4667	95.67			114.33
SA 15	0.5267	0.5067	0.5167	0.3300	84.33			94.67
SA 24	0.6300	0.6133	0.5800	0.3133	89.00			99.00
SA 35	0.4000	0.4633	0.4300	0.1800	96.67			137.67
SA 51	0.3900	0.3433	0.3933	0.2267	98.00			143.33
SA 54	0.3500	0.2300	0.3900	0.1800	106.00			164.00
SA 123	0.4600	0.3633	0.5033	0.2933	100.67			144.00
SA 129	0.4400	0.4333	0.5000	0.2333	102.33			161.44
SA 157	0.4500	0.4733	0.4833	0.2800	96.67			110.00
SA 236	0.4533	0.4900	0.5000	0.2067	98.33			132.33
SA 247	0.4400	0.4333	0.4300	0.1633	102.33			121.33
SA 248	0.4567	0.4900	0.3967	0.1833	104.33			142.67
SA 465	0.5867	0.5233	0.6000	0.2533	94.33			123.00
SA 483	0.4400	0.5400	0.5200	0.3200	104.00			155.00
SA 688	0.4100	0.3167	0.4933	0.2633	106.00			151.33
SA 828	0.4200	0.4667	0.4067	0.3200	108.00			147.67
Solara	0.5433	0.5200	0.5467	0.4100	89.67			117.33
Whero	0.4733	0.4667	0.5200	0.2567	100.67			127.67
Alma x Garfield	0.4933	0.4933	0.5267	0.2546	98.67			132.33
Alma x SA 15	0.2800	0.3833	0.1900	0.0648	127.33			133.21
Alma x SA 24	0.4533	0.4733	0.5100	0.3030	92.00			128.35

Appendix 1 continued

Genotype	Harvest index				Onset of flowering (days after sowing)			
	E1	E2	E3	E4	E1	E2	E3	E4
Alma x SA 35	0.5067	0.4867	0.4400	0.3567	91.33			126.35
Alma x SA 51	0.4833	0.4900	0.5033	0.2933	96.33			130.85
Alma x SA 54	0.3500	0.2433	0.2000	0.3544	117.33			144.53
Alma x SA 123	0.4733	0.4533	0.4333	0.1967	105.33			152.94
Alma x SA 129	0.3133	0.3167	0.3733	0.1687	113.33			146.53
Alma x SA 157	0.5133	0.5367	0.4900	0.3000	95.33			126.85
Alma x SA 236	0.5100	0.4833	0.5233	0.1530	96.33			128.35
Alma x SA 247	0.4700	0.4833	0.4733	0.1967	99.33			131.35
Alma x SA 248	0.4900	0.4433	0.4933	0.3400	96.33			140.35
Alma x SA 465	0.5100	0.4833	0.4933	0.1983	92.67			127.85
Alma x SA 483	0.4433	0.4433	0.4400	0.2287	110.67			140.72
Alma x SA 688	0.4067	0.3300	0.4000	0.1846	102.33			143.85
Alma x SA 828	0.4433	0.4433	0.4933	0.1580	99.33			137.35
Alma x Solara	0.4867	0.4433	0.5400	0.4330	91.33			118.85
Alma x Whero	0.4900	0.4200	0.4567	0.3033	98.67			124.35
Derrimut x Garfield	0.5933	0.5333	0.5000	0.2633	96.67			112.35
Derrimut x SA 15	0.4133	0.3400	0.3800	0.1946	100.33			123.00
Derrimut x SA 24	0.4967	0.4867	0.5133	0.2983	86.67			115.00
Derrimut x SA 35	0.4800	0.4933	0.5600	0.2733	94.00			112.67
Derrimut x SA 51	0.4633	0.5033	0.5133	0.3233	91.00			117.85
Derrimut x SA 54	0.4300	0.3867	0.3700	0.0928	100.67			121.33
Derrimut x SA 123	0.4767	0.4367	0.4700	0.1933	99.00			124.85
Derrimut x SA 129	0.4667	0.4500	0.5200	0.4780	100.67			138.53
Derrimut x SA 157	0.4333	0.4700	0.5667	0.3633	86.67			127.00
Derrimut x SA 236	0.4767	0.4400	0.5433	0.3333	94.67			113.44
Derrimut x SA 247	0.4767	0.4833	0.5067	0.3233	97.00			117.00
Derrimut x SA 248	0.5000	0.5033	0.5100	0.3183	95.00			123.85
Derrimut x SA 465	0.5333	0.5167	0.5500	0.5987	89.33			119.67
Derrimut x SA 483	0.4800	0.4567	0.4900	0.2934	96.00			121.85
Derrimut x SA 688	0.4567	0.4400	0.4300	0.2346	109.67			123.54
Derrimut x SA 828	0.4400	0.4900	0.5300	0.2000	98.67			125.00
Derrimut x Solara	0.5900	0.4933	0.5700	0.3167	88.33			105.33
Derrimut x Whero	0.5000	0.4833	0.5333	0.2933	94.00			114.35
Dundale x Garfield	0.4700	0.4000	0.5467	0.3533	91.67			125.33
Dundale x SA 15	0.4133	0.3900	0.4000	0.2745	106.33			128.85
Dundale x SA 24	0.4667	0.4567	0.5600	0.2267	90.67			111.67
Dundale x SA 35	0.5167	0.5167	0.5000	0.3100	80.67			97.55
Dundale x SA 51	0.5133	0.4800	0.5100	0.2933	90.67			119.35
Dundale x SA 54	0.4000	0.2733	0.4300	0.1167	105.33			132.85
Dundale x SA 123	0.4667	0.4967	0.4400	0.3000	98.33			151.35
Dundale x SA 129	0.3733	0.2967	0.2933	0.3733	100.33			134.00

Appendix 1 continued

Genotype	Harvest index				Onset of flowering (days after sowing)			
	E1	E2	E3	E4	E1	E2	E3	E4
Dundale x SA 157	0.4700	0.4700	0.5000	0.2367	90.00			123.00
Dundale x SA 236	0.4767	0.5233	0.5233	0.2867	95.33			109.85
Dundale x SA 247	0.4767	0.4767	0.4600	0.4067	94.33			124.00
Dundale x SA 248	0.4633	0.4733	0.5133	0.3100	94.33			125.35
Dundale x SA 465	0.4967	0.4933	0.5500	0.4400	94.33			118.00
Dundale x SA 483	0.4567	0.4700	0.4633	0.3137	99.67			121.67
Dundale x SA 688	0.4033	0.3900	0.4367	0.1236	96.67			131.85
Dundale x SA 828	0.4067	0.4733	0.4833	0.2730	98.33			137.85
Dundale x Solara	0.5167	0.5333	0.5533	0.3700	90.33			118.00
Dundale x Whero	0.4800	0.4867	0.5333	0.2567	95.67			119.35
Wirrega x Garfield	0.5267	0.4500	0.5067	0.2967	91.33			130.54
Wirrega x SA 15	0.3567	0.3367	0.3100	0.1937	105.00			123.85
Wirrega x SA 24	0.4833	0.4600	0.5033	0.2987	91.67			127.33
Wirrega x SA 35	0.5133	0.4867	0.5633	0.3533	95.67			120.35
Wirrega x SA 51	0.4500	0.4800	0.5200	0.2883	91.00			127.00
Wirrega x SA 54	0.4600	0.3500	0.3933	0.1837	106.67			120.54
Wirrega x SA 123	0.4700	0.4733	0.4967	0.2537	100.33			149.85
Wirrega x SA 129	0.4533	0.4667	0.5167	0.3100	99.67			137.53
Wirrega x SA 157	0.5133	0.4900	0.5133	0.3267	94.33			130.00
Wirrega x SA 236	0.4967	0.4900	0.5067	0.2530	92.33			121.85
Wirrega x SA 247	0.4900	0.5200	0.4767	0.2233	95.00			125.67
Wirrega x SA 248	0.4867	0.5067	0.5233	0.3167	97.00			130.85
Wirrega x SA 465	0.5100	0.4867	0.5533	0.3100	103.33			127.35
Wirrega x SA 483	0.4767	0.4133	0.4933	0.1833	107.00			123.35
Wirrega x SA 688	0.4500	0.3967	0.4200	0.2167	104.33			144.35
Wirrega x SA 828	0.5300	0.4600	0.4667	0.2367	102.33			130.00
Wirrega x Solara	0.5167	0.4867	0.5133	0.3200	92.00			129.67
Wirrega x Whero	0.5100	0.5233	0.5400	0.2680	94.67			123.85

Appendix 2 F2 results. Means for grain yield, plant weight and harvest index at each of the four environments E1 to E4

Cross	Yield (g/plant)				Plant weight (g/plant)				Harvest index			
	E1	E2	E3	E4	E1	E2	E3	E4	E1	E2	E3	E4
Alma x Garfield	9.37	20.53	11.49	11.93	20.88	42.16	22.64	47.00	0.46	0.49	0.53	0.26
Alma x SA 24	11.33	17.42	33.63	13.24	23.16	34.45	64.26	43.28	0.50	0.51	0.53	0.32
Alma x SA 35	8.70	27.60	19.03	11.22	16.35	54.12	36.26	36.76	0.54	0.51	0.53	0.30
Alma x SA 51	8.95	17.53	23.46	7.55	18.76	32.75	49.91	30.61	0.48	0.54	0.47	0.29
Alma x SA 123	12.40	15.61	18.72	7.10	28.55	45.29	45.20	20.85	0.44	0.40	0.41	0.34
Alma x SA 157	7.00	22.89	21.92	8.18	13.24	45.50	44.98	37.80	0.53	0.50	0.50	0.22
Alma x SA 247	8.05	24.71	22.63	9.85	15.05	53.63	46.56	30.83	0.54	0.45	0.49	0.35
Alma x SA 248	9.89	15.55	17.62	16.75	21.57	29.62	39.08	61.29	0.47	0.51	0.45	0.32
Alma x SA 483	7.55	13.48	17.20	9.70	16.51	28.52	40.90	47.84	0.46	0.47	0.42	0.24
Alma x SA 828	8.76	25.61	22.40	7.80	16.77	51.75	45.61	42.60	0.53	0.49	0.50	0.24
Alma x Solara	8.87	26.57	26.76	11.30	16.65	49.91	56.69	27.19	0.54	0.53	0.47	0.42
Alma x Whero	9.07	25.84	28.33	5.86	19.76	50.99	59.41	20.28	0.46	0.50	0.48	0.39
Derrimut x Garfield	10.22	23.48	29.65	9.20	15.25	47.78	52.96	20.29	0.69	0.49	0.60	0.46
Derrimut x SA 35	8.72	19.24	21.86	9.42	15.97	36.72	42.13	32.26	0.55	0.54	0.52	0.35
Derrimut x SA 51	6.85	15.96	19.88	10.62	14.49	25.20	42.45	45.31	0.48	0.64	0.47	0.26
Derrimut x SA 54	8.77	8.65	23.59	8.35	21.73	22.07	60.28	57.47	0.41	0.36	0.39	0.11
Derrimut x SA 123	7.33	19.72	23.66	3.86	14.94	40.15	51.67	26.66	0.50	0.50	0.46	0.25
Derrimut x SA 129	8.26	13.66	18.49	8.21	18.64	28.96	40.25	31.43	0.45	0.47	0.46	0.32
Derrimut x SA 157	7.88	33.22	14.31	7.12	15.53	62.85	27.82	28.90	0.51	0.53	0.52	0.30
Derrimut x SA 236	11.78	19.54	31.49	11.54	21.44	37.27	60.22	34.28	0.56	0.53	0.53	0.35
Derrimut x SA 247	8.85	23.82	19.77	9.01	18.90	47.52	26.94	45.05	0.47	0.50	0.48	0.20
Derrimut x SA 248	9.16	14.74	25.59	10.97	17.86	29.92	50.87	39.83	0.51	0.52	0.51	0.30

Appendix 2 continued

Cross	Yield (g/plant)				Plant weight (g/plant)				Harvest index			
	E1	E2	E3	E4	E1	E2	E3	E4	E1	E2	E3	E4
Derrimut x SA 465	8.72	17.27	22.15	7.76	16.54	29.20	45.29	17.90	0.53	0.57	0.49	0.44
Derrimut x SA 688	8.60	10.91	22.08	3.69	17.82	28.20	53.05	4.49	0.48	0.36	0.41	0.32
Derrimut x SA 828	10.64	11.22	19.88	7.28	21.79	26.32	42.21	17.43	0.49	0.41	0.47	0.42
Derrimut x Solara	8.71	22.27	17.24	11.82	15.93	39.24	34.21	25.55	0.55	0.57	0.51	0.32
Derrimut x Whero	8.82	19.12	19.64	10.55	18.35	38.89	37.69	25.45	0.65	0.49	0.53	0.42
Dundale x Garfield	8.55	15.20	13.87	7.36	18.64	29.75	26.97	25.18	0.46	0.52	0.53	0.31
Dundale x SA 24	8.84	19.49	17.88	15.53	16.07	37.91	31.17	51.90	0.55	0.52	0.59	0.37
Dundale x SA 35	10.79	26.57	21.87	8.17	18.74	48.95	44.46	32.95	0.58	0.55	0.50	0.28
Dundale x SA 51	8.43	13.16	22.45	8.48	18.43	25.18	46.36	27.22	0.45	0.51	0.49	0.31
Dundale x SA 123	9.80	20.31	17.69	7.14	17.29	48.17	37.86	45.53	0.56	0.43	0.47	0.20
Dundale x SA 157	8.34	8.62	16.98	9.22	17.70	26.65	32.66	41.61	0.48	0.54	0.52	0.25
Dundale x SA 247	8.06	47.14	17.64	13.17	15.50	101.95	35.86	36.15	0.54	0.46	0.50	0.37
Dundale x SA 248	8.43	16.63	21.70	7.73	17.12	38.27	48.36	36.42	0.50	0.43	0.45	0.27
Dundale x SA 465	10.26	6.70	18.17	11.56	19.23	15.78	34.01	33.26	0.54	0.43	0.55	0.47
Dundale x SA 483	7.52	15.50	16.94	7.23	15.05	34.08	36.08	29.05	0.50	0.46	0.48	0.30
Dundale x SA 688	10.07	4.50	16.53	3.92	23.01	40.85	37.42	30.86	0.45	0.11	0.45	0.20
Dundale x Solara	7.43	18.11	21.69	15.73	14.74	35.10	40.39	24.88	0.50	0.51	0.54	0.53
Wirrega x Garfield	8.76	19.67	21.14	7.13	16.50	39.85	39.14	23.61	0.54	0.49	0.53	0.31
Wirrega x SA 24	9.15	7.70	22.44	7.04	17.84	16.64	41.86	23.92	0.52	0.47	0.54	0.30
Wirrega x SA 35	9.25	21.29	22.93	3.85	17.51	40.57	43.87	29.00	0.53	0.53	0.52	0.14
Wirrega x SA 51	7.68	17.14	20.63	11.16	13.97	33.96	43.60	27.59	0.59	0.51	0.47	0.43
Wirrega x SA 123	9.35	9.14	17.74	8.61	17.77	20.40	39.68	44.92	0.53	0.45	0.45	0.34

Appendix 2 continued

Cross	Yield (g/plant)				Plant weight (g/plant)				Harvest index			
	E1	E2	E3	E4	E1	E2	E3	E4	E1	E2	E3	E4
Wirrega x SA 129	10.47	23.47	26.24	7.59	23.68	56.07	55.89	57.54	0.45	0.41	0.48	0.21
Wirrega x SA 157	11.03	16.31	19.51	9.91	22.31	32.43	36.40	42.19	0.50	0.50	0.53	0.24
Wirrega x SA 236	8.41	14.12	32.30	12.46	15.23	33.35	59.39	28.52	0.56	0.43	0.54	0.44
Wirrega x SA 247	7.61	23.09	18.51	8.04	17.00	49.05	36.01	31.69	0.45	0.42	0.52	0.29
Wirrega x SA 465	8.22	9.41	28.78	10.27	15.12	19.98	55.86	26.03	0.54	0.46	0.52	0.39
Wirrega x SA 483	6.22	15.05	17.83	6.60	11.81	35.49	35.11	13.55	0.53	0.44	0.51	0.54
Wirrega x SA 688	9.79	21.83	26.73	6.79	22.48	66.08	54.61	45.95	0.46	0.33	0.49	0.21
Wirrega x SA 828	9.56	14.81	20.55	7.76	17.73	31.32	43.80	36.98	0.55	0.47	0.47	0.21
Wirrega x Solara	8.04	20.31	17.42	13.74	16.22	37.87	31.30	44.78	0.50	0.54	0.56	0.35
Wirrega x Whero	10.66	27.75	25.45	4.79	18.87	52.35	50.24	49.47	0.57	0.54	0.51	0.17

Appendix 3 F5 results. Mean values across replicates for each agronomic trait of each F5 line derived from crosses A to F in each environment, E1 and E2.

Cross	Line	Basal branches per plant (number) E1	Basal branches per plant (number) E2	Pods per plant (number) E1	Pods per plant (number) E2	Seeds per pod (number) E1	Seeds per pod (number) E2	Hundred seed weight (g) E1	Hundred seed weight (g) E2	Grain yield (g) E1	Grain yield (g) E2	Plant weight (g) E1	Plant weight (g) E2	Harvest index E1	Harvest index E2	Onset of flowering (days after sowing) E1	Onset of flowering (days after sowing) E2
A	1	2.0	3.2	15.1	34.3	5.7	5.9	22.2	18.0	9.0	15.3	22.3	41.5	0.41	0.36	99	96
A	2	2.0	1.8	22.9	39.0	4.1	4.6	26.6	24.2	10.3	19.0	34.7	76.6	0.36	0.31	100	102
A	3	3.0	1.8	17.6	32.5	4.9	6.3	20.0	17.1	12.7	16.5	36.0	51.4	0.38	0.40	104	99
A	4	2.6	2.6	25.6	24.8	5.5	6.8	26.3	15.5	19.5	9.3	58.7	56.8	0.39	0.37	133	125
A	5	3.0	1.1	18.2	10.8	5.7	5.0	23.7	16.6	10.5	9.4	24.1	50.5	0.43	0.20	111	108
A	6	2.7	2.8	21.2	29.5	5.9	5.8	20.2	19.0	19.9	17.5	56.0	52.2	0.34	0.39	138	132
A	7	2.2	2.5	17.1	25.0	5.5	5.8	21.2	15.7	8.1	11.7	19.7	43.0	0.41	0.39	134	133
A	8	2.6	2.6	15.7	46.8	5.2	6.7	19.9	14.8	8.7	14.6	16.2	50.6	0.60	0.33	131	132
A	9	2.9	2.5	19.0	28.2	6.0	6.4	17.4	13.7	10.6	13.0	39.2	100.0	0.32	0.17	111	117
A	10	2.2	2.6	10.4	21.1	6.3	5.6	22.3	18.5	9.3	12.2	27.8	53.7	0.33	0.25	137	136
A	11	2.3	1.5	19.2	18.0	5.9	5.5	23.3	20.4	10.1	9.6	31.9	49.2	0.33	0.23	139	135
A	12	2.5	2.0	24.0	29.5	5.3	6.0	26.5	20.4	14.1	16.6	31.4	61.7	0.44	0.41	102	95
A	13	3.2	2.7	15.5	15.3	5.3	5.8	21.2	17.3	11.2	10.7	24.0	80.2	0.49	0.17	105	108
A	14	3.2	5.0	16.6	32.2	6.3	5.5	18.4	16.3	10.6	15.0	38.2	83.6	0.28	0.28	137	125
A	15	2.3	3.7	12.2	23.2	5.2	5.9	22.6	9.9	5.3	4.4	10.4	27.9	0.54	0.33	110	101
A	16	2.8	2.3	19.4	21.8	4.9	5.8	26.2	20.3	14.9	22.4	42.0	51.9	0.35	0.45	115	97
A	17	3.2	3.8	11.8	35.5	5.0	6.4	21.7	17.7	8.1	16.1	20.3	36.0	0.42	0.51	107	101
A	18	2.8	3.3	24.0	33.2	6.4	5.9	21.0	12.1	15.9	13.3	39.7	91.4	0.41	0.19	125	111
A	19	2.2	2.3	13.9	19.3	6.3	5.6	20.3	11.2	12.1	13.0	35.1	64.0	0.36	0.28	135	136
A	20	1.4	3.0	13.7	39.2	5.6	6.4	14.7	19.4	12.3	17.4	17.8	58.4	0.39	0.37	104	97
A	21	2.5	2.7	15.5	41.2	5.4	6.2	18.7	14.5	12.7	15.5	39.9	75.7	0.31	0.34	118	117
A	22	2.2	2.5	12.6	32.2	6.0	5.5	19.1	19.9	14.0	16.5	28.0	57.6	0.54	0.42	130	132
A	23	3.0	5.0	23.0	34.2	5.3	6.1	20.0	19.1	13.7	14.6	46.3	40.5	0.30	0.38	111	100
A	24	2.5	1.3	19.7	23.3	6.0	6.7	23.7	14.9	16.9	9.7	39.7	49.9	0.42	0.34	126	133

Appendix 3 F_5 results continued

Cross		Basal branches per plant (number)		Pods per plant (number)		Seeds per pod (number)		Hundred seed weight (g)		Grain yield (g)		Plant weight (g)		Harvest index		Onset of flowering (days after sowing)	
	Line	E1	E2	E1	E2	E1	E2	E1	E2	E1	E2	E1	E2	E1	E2	E1	E2
A	25	1.8	3.3	20.5	30.2	6.7	6.9	23.9	19.2	15.1	14.1	43.9	42.8	0.37	0.29	134	132
A	26	2.9	2.7	14.0	17.6	5.9	5.2	20.8	17.3	15.0	9.5	27.3	87.3	0.55	0.20	103	101
A	F_1	2.2	3.3	19.2	34.5	3.7	5.5	23.3	17.5	15.1	16.8	53.2	71.8	0.30	0.26	125	125
A	P_1	2.8	2.1	13.0	19.8	6.0	5.7	20.2	15.9	14.6	13.4	52.0	63.4	0.30	0.25	132	133
A	P_2	3.0	2.2	17.2	24.0	6.2	6.3	21.6	18.7	7.5	15.0	25.0	60.0	0.31	0.28	99	101
B	1	3.5	2.3	15.4	14.8	6.7	8.3	19.8	12.5	8.8	10.1	36.7	45.2	0.31	0.22	141	139
B	2	4.2	3.2	28.3	39.4	5.9	4.9	12.0	8.9	6.8	8.4	46.1	70.8	0.17	0.07	156	148
B	3	4.0	4.5	34.2	24.9	6.8	6.3	11.3	13.1	5.7	12.1	65.4	88.8	0.22	0.18	140	150
B	4	2.7	2.5	17.8	24.6	4.3	6.2	14.3	6.0	4.7	2.0	37.7	66.5	0.21	0.02	158	158
B	5	2.7	3.5	26.0	12.1	5.1	5.4	18.1	9.4	11.8	5.4	46.5	79.5	0.28	0.10	142	153
B	6	3.2	1.5	11.4	14.4	4.2	5.6	25.2	15.9	6.5	14.8	42.0	123.1	0.17	0.17	128	144
B	7	2.3	2.5	19.7	38.1	5.5	6.7	17.6	14.1	11.7	13.7	31.7	45.8	0.28	0.26	136	134
B	8	3.0	4.2	38.3	64.4	5.9	6.3	15.1	11.1	11.4	6.3	44.4	101.8	0.25	0.13	142	145
B	9	2.7	2.1	13.0	16.9	5.5	5.0	17.1	12.6	5.1	10.3	25.1	61.8	0.21	0.15	141	134
B	10	2.5	4.2	26.7	43.9	5.6	5.3	16.8	13.5	8.6	11.2	23.3	23.7	0.38	0.21	149	142
B	11	2.4	2.2	32.7	40.4	5.7	5.8	14.5	15.1	10.5	12.3	45.0	85.8	0.22	0.22	141	141
B	12	5.3	4.3	35.3	37.8	5.8	5.3	15.9	15.3	14.7	5.0	46.3	82.5	0.39	0.07	144	134
B	13	2.0	2.8	23.0	28.6	5.0	4.6	19.6	19.3	10.7	4.0	59.6	63.1	0.25	0.11	138	137
B	14	2.1	6.8	19.0	60.9	6.0	6.5	21.3	12.1	8.3	18.8	53.1	134.7	0.23	0.16	141	134
B	15	2.9	3.3	19.3	23.9	5.9	5.4	18.4	11.5	9.7	10.7	30.1	54.9	0.31	0.21	140	138
B	16	1.8	3.3	14.5	8.8	4.8	6.2	15.8	12.1	7.5	0.8	29.7	58.2	0.17	0.04	150	141
B	17	2.0	2.8	14.0	39.6	5.8	6.2	15.2	13.8	4.4	15.2	14.7	31.4	0.43	0.38	137	136
B	18	4.1	4.5	31.7	53.7	4.8	6.5	15.7	10.4	7.2	10.6	20.8	118.3	0.33	0.12	141	149
B	19	2.6	1.6	15.9	15.4	6.1	4.9	16.8	10.2	5.7	4.1	33.0	62.8	0.15	0.10	156	147

Appendix 3 F_5 results continued

Cross		Basal branches per plant (number)		Pods per plant (number)		Seeds per pod (number)		Hundred seed weight (g)		Grain yield (g)		Plant weight (g)		Harvest index		Onset of flowering (days after sowing)	
	Line	E1	E2	E1	E2	E1	E2	E1	E2	E1	E2	E1	E2	E1	E2	E1	E2
B	20	3.3	7.8	28.2	37.8	6.1	5.7	14.1	8.0	9.4	7.0	39.9	86.9	0.25	0.09	139	139
B	21	2.7	13.8	28.2	61.7	5.8	6.1	17.4	14.9	12.2	16.1	31.6	69.2	0.30	0.19	136	135
B	22	3.0	2.0	32.7	34.1	5.3	6.0	18.4	13.4	14.0	8.5	54.9	42.1	0.25	0.26	142	140
B	23	2.8	3.5	23.8	30.8	5.2	4.8	18.2	11.4	8.0	12.9	29.4	101.0	0.23	0.20	142	143
B	24	3.5	1.3	38.8	16.8	5.6	3.5	18.4	11.4	11.1	3.8	34.5	99.1	0.23	0.02	146	144
B	25	1.8	5.8	26.7	45.8	5.2	5.5	19.3	13.8	12.1	8.8	31.1	90.3	0.27	0.13	137	150
B	26	1.7	2.4	20.9	27.8	5.6	4.1	15.8	8.0	8.4	1.0	34.4	75.2	0.25	0.15	137	160
B	27	1.9	2.3	25.4	19.6	6.8	6.2	18.6	15.6	8.9	13.1	35.9	59.2	0.26	0.22	137	134
B	28	2.6	2.3	13.9	18.3	6.6	6.3	20.5	12.8	7.1	13.0	20.0	40.5	0.27	0.31	137	136
B	29	2.0	2.8	20.0	15.8	4.3	5.2	18.6	10.3	12.5	12.1	51.3	191.4	0.28	0.04	146	152
B	30	3.7	3.5	34.7	31.4	6.1	5.3	20.5	9.3	16.2	12.7	56.4	92.9	0.28	0.15	135	141
B	31	1.7	2.0	21.1	37.4	5.7	6.6	18.3	15.6	7.2	16.2	31.6	65.2	0.23	0.24	140	135
B	F_1	3.2	2.2	40.7	31.9	5.9	5.9	14.4	12.9	14.0	16.9	85.1	161.6	0.19	0.12	139	140
B	P_1	2.0	2.4	17.0	22.4	6.3	5.5	13.6	13.3	6.8	15.6	23.2	105.4	0.30	0.18	148	159
B	P_2	2.8	3.3	18.2	27.6	6.0	6.0	20.2	18.4	14.6	15.7	52.0	51.5	0.30	0.36	132	136
C	1	3.1	5.7	18.6	29.8	5.7	5.6	13.4	9.2	4.5	7.7	13.4	62.5	0.34	0.15	111	99
C	2	3.7	1.7	34.5	27.9	5.8	6.0	11.2	10.6	13.6	16.1	37.1	51.7	0.37	0.40	104	106
C	3	3.2	2.7	25.4	18.0	5.9	5.2	14.4	12.2	8.6	14.4	24.8	15.7	0.32	0.53	122	101
C	4	4.7	0.9	19.0	15.5	5.7	6.9	11.7	13.1	10.6	12.8	34.4	49.7	0.43	0.26	127	117
C	5	3.6	4.3	29.1	20.0	5.4	4.8	8.7	5.0	11.9	4.3	41.5	39.9	0.21	0.09	133	132
C	6	2.5	2.2	26.3	26.3	4.3	4.8	11.8	10.2	7.4	6.3	40.5	48.9	0.18	0.17	131	136
C	7	4.5	2.7	27.0	38.6	6.3	6.3	13.6	11.4	7.3	12.3	18.4	19.2	0.42	0.49	107	98
C	8	4.1	3.9	27.7	26.0	5.3	2.4	15.6	10.9	9.8	17.5	32.9	46.7	0.32	0.29	109	120
C	9	3.3	2.2	15.5	34.2	5.3	6.3	13.6	11.6	16.3	11.4	43.1	32.9	0.38	0.42	101	99

Appendix 3 F5 results continued

Cross		Basal branches per plant (number)		Pods per plant (number)		Seeds per pod (number)		Hundred seed weight (g)		Grain yield (g)		Plant weight (g)		Harvest index		Onset of flowering (days after sowing)	
	Line	E1	E2	E1	E2	E1	E2	E1	E2	E1	E2	E1	E2	E1	E2	E1	E2
C	10	4.0	1.9	41.0	29.7	6.7	6.9	16.2	11.9	14.8	19.6	34.0	43.4	0.45	0.47	125	104
C	11	2.4	1.9	21.2	21.4	5.9	4.7	11.6	11.4	10.3	15.8	22.2	36.6	0.42	0.52	113	105
C	12	2.8	3.9	16.3	12.4	5.8	5.3	9.1	7.9	4.5	4.7	16.7	19.4	0.28	0.17	146	129
C	13	3.3	3.4	28.5	44.2	5.7	6.3	13.3	11.2	11.3	10.8	29.0	26.0	0.39	0.52	111	100
C	14	2.8	1.7	19.0	19.4	5.6	5.1	13.5	13.6	5.0	10.2	28.7	27.1	0.16	0.42	110	102
C	15	6.8	7.5	26.3	47.8	4.9	4.8	11.4	9.4	5.2	8.6	22.4	45.3	0.23	0.22	110	113
C	16	5.9	6.0	50.9	21.6	6.6	6.1	12.0	10.8	15.0	7.9	57.9	50.7	0.30	0.20	138	126
C	17	4.7	7.8	39.8	45.6	6.1	6.5	13.0	12.0	7.0	12.1	21.1	84.1	0.41	0.22	103	103
C	18	5.6	1.8	31.8	15.7	5.3	4.5	11.1	10.1	4.9	6.7	33.2	19.6	0.18	0.30	140	130
C	19	4.3	3.9	27.9	10.5	5.8	6.6	9.3	11.3	6.7	5.8	49.5	23.1	0.24	0.24	112	122
C	20	3.0	2.9	37.0	35.3	5.8	4.5	19.7	9.8	14.5	13.1	44.5	72.7	0.33	0.22	127	137
C	21	4.2	5.8	25.3	13.4	5.2	4.9	9.8	8.1	6.4	5.6	21.6	50.3	0.29	0.11	122	108
C	22	2.4	5.9	12.1	22.4	6.4	5.4	8.0	6.2	3.1	7.0	31.3	84.1	0.13	0.10	126	142
C	23	5.5	3.5	39.8	6.9	5.8	7.0	10.6	5.2	6.7	10.9	21.4	35.5	0.45	0.42	105	107
C	24	3.0	3.0	40.2	22.3	5.9	5.4	17.8	17.2	11.3	14.9	22.1	91.5	0.55	0.20	119	131
C	F_1	7.2	9.5	34.1	27.9	6.2	4.7	10.0	7.6	17.8	12.6	53.7	76.6	0.36	0.21	141	133
C	P_1	2.3	3.5	17.6	37.3	6.2	5.0	23.1	14.9	12.6	14.0	72.8	86.9	0.25	0.23	128	112
C	P_2	6.8	5.4	15.7	31.9	6.5	7.2	8.6	5.2	3.5	7.6	16.3	23.8	0.23	0.33	157	160
D	1	1.8	3.8	25.0	18.5	7.2	6.0	11.0	7.5	9.8	12.0	32.9	56.9	0.33	0.29	118	113
D	2	2.5	2.8	34.3	51.8	6.9	6.6	14.9	13.3	14.1	13.2	41.5	35.7	0.39	0.48	121	103
D	3	3.8	3.5	51.2	48.8	7.0	6.1	10.9	9.1	13.9	11.0	50.7	46.9	0.28	0.33	142	141
D	4	3.1	3.3	32.6	21.8	6.1	5.8	13.3	12.9	19.3	18.3	56.5	53.0	0.46	0.45	108	100
D	5	1.7	3.7	13.5	26.6	7.7	6.7	18.0	16.3	7.7	13.9	22.4	41.7	0.33	0.37	100	95
D	6	2.1	2.2	13.9	34.6	5.8	5.0	13.0	10.7	7.9	9.4	15.6	32.4	0.47	0.42	102	94

Appendix 3 F_5 results continued

Cross		Basal branches per plant (number)		Pods per plant (number)		Seeds per pod (number)		Hundred seed weight (g)		Grain yield (g)		Plant weight (g)		Harvest index		Onset of flowering (days after sowing)	
	Line	E1	E2	E1	E2	E1	E2	E1	E2	E1	E2	E1	E2	E1	E2	E1	E2
D	7	2.7	3.0	26.3	70.6	6.0	5.8	15.9	13.9	10.8	19.0	19.9	41.8	0.54	0.53	101	83
D	8	3.5	2.8	35.8	32.5	6.5	6.5	13.6	13.7	15.2	13.8	31.6	30.0	0.49	0.43	107	87
D	9	2.5	2.6	15.7	18.7	6.9	7.9	15.3	8.9	14.7	7.9	37.5	67.8	0.24	0.15	149	150
D	10	2.5	3.2	21.0	50.8	7.7	7.1	15.1	12.4	7.7	16.7	13.6	28.2	0.57	0.53	108	93
D	11	4.3	3.8	27.8	29.8	6.3	5.9	9.6	9.2	6.3	11.0	37.0	49.1	0.22	0.20	136	107
D	12	3.3	3.8	23.0	76.5	6.5	5.6	9.8	6.7	8.2	13.1	26.1	5.5	0.31	0.25	139	158
D	13	3.0	6.3	30.2	47.8	7.1	7.7	16.2	17.4	17.8	14.3	32.9	50.9	0.54	0.40	104	106
D	14	2.5	3.5	11.1	87.1	6.2	6.8	12.8	13.5	4.0	14.6	10.7	44.0	0.37	0.43	111	88
D	15	3.2	2.5	31.7	39.8	6.4	5.9	12.7	13.5	16.7	15.9	32.9	22.9	0.61	0.52	113	90
D	16	3.6	5.0	36.6	50.8	6.8	6.2	11.5	12.9	15.8	13.0	88.6	88.9	0.21	0.23	146	151
D	17	4.5	7.7	30.3	68.8	6.8	5.7	11.6	5.8	5.3	10.0	23.9	75.7	0.23	0.20	154	161
D	18	4.0	3.2	28.3	31.1	6.1	6.2	12.9	10.1	7.2	8.5	26.8	90.8	0.28	0.16	125	92
D	19	3.0	3.0	18.3	45.3	6.2	6.1	13.5	13.3	5.9	17.1	15.6	37.8	0.38	0.53	113	80
D	20	1.5	2.3	20.7	28.1	4.9	5.2	11.9	9.5	6.1	9.9	25.3	113.7	0.28	0.13	141	142
D	21	3.2	4.2	25.8	31.0	7.2	7.3	10.2	8.1	9.0	13.7	30.8	86.1	0.31	0.20	135	116
D	22	6.0	4.1	72.0	37.5	6.1	5.6	11.5	10.5	17.3	5.2	64.3	73.9	0.26	0.12	105	91
D	23	4.0	4.2	40.3	85.2	6.8	7.2	11.6	8.8	12.8	13.4	41.6	109.0	0.31	0.20	121	110
D	24	6.6	4.5	27.4	23.8	6.9	4.9	11.2	6.6	6.9	11.6	24.5	64.1	0.29	0.28	137	165
D	25	3.2	18.0	52.0	82.3	5.5	5.6	9.3	7.4	10.8	20.3	35.0	67.1	0.31	0.37	100	107
D	26	2.7	3.9	22.5	57.3	6.6	6.1	14.9	13.2	7.8	15.8	27.6	73.2	0.51	0.33	102	97
D	27	4.5	4.2	36.7	20.3	6.9	7.8	9.6	6.9	9.4	4.0	32.1	113.7	0.30	0.12	127	172
D	F_1	5.2	7.2	30.2	57.3	6.1	6.1	11.2	9.8	16.3	14.1	61.6	88.2	0.29	0.21	154	132
D	P_1	4.3	4.9	24.5	32.8	6.6	5.8	9.0	6.1	6.5	7.6	19.0	19.5	0.35	0.37	119	102
D	P_2	4.3	1.2	27.0	23.7	5.8	6.3	20.3	15.0	13.6	13.4	52.7	43.3	0.25	0.32	144	146

Appendix 3 F5 results continued

Cross		Basal branches per plant (number)		Pods per plant (number)		Seeds per pod (number)		Hundred seed weight (g)		Grain yield (g)		Plant weight (g)		Harvest index		Onset of flowering (days after sowing)	
	Line	E1	E2	E1	E2	E1	E2	E1	E2	E1	E2	E1	E2	E1	E2	E1	E2
E	1	3.0	2.1	8.1	13.0	5.9	5.5	19.4	12.6	6.8	5.6	32.7	69.4	0.10	0.02	133	129
E	2	3.3	4.4	19.5	8.0	6.3	5.2	20.3	9.5	10.7	5.9	38.4	111.2	0.28	0.07	139	144
E	3	2.6	2.1	23.2	22.3	4.6	3.6	21.2	13.1	5.0	7.2	21.1	77.2	0.23	0.11	132	125
E	4	2.3	2.0	17.9	21.2	7.5	6.0	18.5	14.6	12.0	8.4	38.9	53.8	0.27	0.25	150	146
E	5	2.5	2.3	18.3	25.5	5.3	4.7	18.1	14.4	10.2	6.8	33.1	45.2	0.32	0.13	127	118
E	6	2.5	2.4	27.6	22.5	5.2	4.6	16.8	14.4	8.7	8.0	32.8	57.2	0.27	0.17	137	132
E	7	2.7	4.0	29.7	37.5	5.5	4.8	18.6	14.6	11.9	12.5	44.0	51.7	0.29	0.26	138	131
E	8	2.1	2.9	32.1	33.2	5.6	4.8	22.1	14.9	9.9	10.3	36.3	115.2	0.30	0.13	134	129
E	9	3.8	3.7	22.1	23.8	5.2	4.3	18.3	19.1	8.9	9.6	39.8	64.2	0.22	0.19	137	126
E	10	3.3	2.8	23.1	21.6	5.5	4.8	20.5	14.2	18.5	16.1	83.7	105.4	0.25	0.18	135	125
E	11	2.1	2.3	26.9	33.2	4.8	4.0	17.2	13.5	8.5	13.9	23.1	44.1	0.44	0.24	134	121
E	12	3.7	1.7	32.3	16.3	4.9	5.1	17.2	16.2	13.4	9.9	39.3	77.6	0.34	0.17	132	122
E	13	3.3	3.6	24.8	47.2	6.2	5.6	20.1	14.9	12.4	17.6	44.9	57.9	0.27	0.29	138	128
E	14	2.3	2.0	6.7	6.9	5.6	6.5	18.2	15.4	4.3	5.6	24.5	59.4	0.18	0.08	142	158
E	15	2.0	2.9	13.8	49.2	4.6	5.7	21.9	16.8	4.9	17.2	17.7	60.6	0.30	0.28	135	121
E	16	2.0	3.2	13.1	32.9	4.6	4.3	20.7	19.2	7.5	21.7	39.9	125.4	0.23	0.19	137	116
E	17	2.5	2.7	16.0	23.3	5.7	3.8	21.3	15.5	11.2	11.0	35.3	101.7	0.33	0.12	123	116
E	18	2.2	3.7	14.3	15.2	5.9	5.4	18.3	12.7	6.7	13.0	23.6	113.4	0.28	0.13	152	135
E	19	2.5	1.4	25.9	17.0	5.7	4.3	16.9	14.6	10.4	15.3	41.6	133.9	0.25	0.16	128	109
E	20	2.1	2.0	22.9	22.8	6.1	6.9	19.2	14.5	14.7	18.8	39.6	41.3	0.37	0.25	128	112
E	21	2.9	2.0	32.0	2.5	5.8	5.4	18.8	13.2	9.0	8.9	29.2	51.3	0.31	0.22	131	119
E	22	2.3	2.1	14.9	16.8	6.9	6.9	17.7	16.9	7.9	10.7	35.0	40.5	0.27	0.34	145	139
E	23	1.6	2.0	10.2	6.0	7.9	7.4	23.2	17.5	6.6	8.4	26.9	46.5	0.34	0.20	150	153
E	24	3.0	2.7	24.3	41.8	5.1	4.5	18.5	13.2	8.9	16.5	41.6	88.6	0.21	0.22	136	130

Appendix 3 F_5 results continued

Cross	Line	Basal branches per plant (number)		Pods per plant (number)		Seeds per pod (number)		Hundred seed weight (g)		Grain yield (g)		Plant weight (g)		Harvest index		Onset of flowering (days after sowing)	
		E1	E2	E1	E2	E1	E2	E1	E2	E1	E2	E1	E2	E1	E2	E1	E2
E	25	2.2	2.3	14.8	21.4	5.3	5.6	21.8	18.8	13.8	19.6	39.5	76.0	0.35	0.28	138	136
E	26	2.5	3.0	27.7	50.3	4.8	5.8	17.2	15.9	9.5	16.4	33.7	53.5	0.28	0.42	118	112
E	27	4.0	3.0	28.3	29.1	5.7	4.9	21.6	18.8	12.2	13.8	44.0	58.0	0.32	0.32	125	116
E	28	1.7	2.0	18.8	13.7	6.9	6.1	20.9	18.2	7.9	8.8	73.4	85.5	0.18	0.13	132	158
E	29	3.2	2.3	20.7	55.2	5.3	6.1	19.6	15.0	12.1	21.1	36.9	132.5	0.38	0.16	131	124
E	30	3.0	2.6	25.6	33.8	6.2	7.6	20.6	16.2	10.3	18.2	28.7	71.2	0.33	0.28	127	123
E	31	2.3	2.9	12.8	39.0	4.3	5.0	17.9	13.3	6.5	13.0	52.3	63.0	0.17	0.26	129	113
E	F_1	2.7	2.2	23.0	21.2	5.7	5.9	20.5	15.1	15.7	17.0	68.9	60.5	0.28	0.27	130	112
E	P_1	2.0	1.8	10.7	29.6	5.3	4.6	20.4	15.8	8.6	12.2	36.9	69.0	0.28	0.20	110	118
E	P_2	1.7	2.2	20.0	13.4	6.5	5.4	17.2	11.9	12.2	10.7	60.0	122.7	0.21	0.20	125	131
F	1	3.2	3.3	20.0	22.1	5.5	7.1	16.2	14.3	8.7	14.7	33.2	59.5	0.27	0.27	135	143
F	2	2.3	1.8	17.5	25.1	6.1	5.9	20.6	17.2	13.0	9.7	38.3	51.5	0.32	0.28	138	133
F	3	1.5	0.8	12.3	-10.9	7.1	5.1	17.7	16.1	11.1	7.1	41.5	70.4	0.28	0.24	140	157
F	4	3.2	2.7	20.3	9.3	4.9	4.1	20.1	12.1	12.5	22.6	30.3	84.7	0.41	0.28	141	131
F	5	3.3	3.6	15.6	52.1	4.7	6.4	21.5	16.3	9.6	15.3	30.2	10.5	0.33	0.54	139	128
F	6	2.8	3.0	16.6	16.7	6.4	7.4	23.3	16.5	11.1	14.2	30.0	51.0	0.37	0.29	138	139
F	7	2.8	3.3	30.3	30.4	6.3	6.4	22.6	17.1	15.0	16.7	42.8	104.3	0.36	0.30	134	136
F	8	2.3	1.8	25.0	7.3	7.1	6.9	16.9	14.2	18.7	12.9	63.3	71.1	0.30	0.24	143	138
F	9	2.0	1.7	10.8	18.2	6.3	7.0	22.4	14.1	10.9	13.1	32.0	67.1	0.36	0.23	141	146
F	10	2.7	3.5	14.0	25.3	4.9	5.2	20.6	14.8	7.9	15.0	29.3	82.8	0.31	0.23	137	135
F	11	3.0	2.0	19.4	12.2	6.3	7.0	14.0	13.3	10.7	14.9	43.8	34.3	0.26	0.39	139	139
F	12	2.0	1.5	16.9	10.9	6.4	8.4	18.2	17.9	11.5	16.3	55.2	88.7	0.26	0.23	122	146
F	13	1.2	1.4	13.5	7.3	6.3	6.5	18.2	12.4	7.4	4.5	37.9	73.6	0.21	0.11	148	155
F	14	2.9	2.5	12.1	37.5	5.4	5.5	25.0	17.1	11.4	12.1	31.0	53.8	0.34	0.22	135	128

Appendix 3 F_5 results continued

Cross		Basal branches per plant (number)		Pods per plant (number)		Seeds per pod (number)		Hundred seed weight (g)		Grain yield (g)		Plant weight (g)		Harvest index		Onset of flowering (days after sowing)	
	Line	E1	E2	E1	E2	E1	E2	E1	E2	E1	E2	E1	E2	E1	E2	E1	E2
F	15	1.7	1.3	23.1	26.6	5.0	5.4	21.4	16.8	17.0	10.4	37.5	18.8	0.44	0.35	134	128
F	16	3.0	2.9	19.5	27.0	5.9	4.7	18.9	15.9	13.3	13.0	33.8	55.4	0.40	0.25	136	133
F	17	2.5	2.2	15.7	7.9	6.1	6.3	19.5	18.1	10.8	13.9	52.8	72.0	0.22	0.14	138	148
F	18	1.7	2.2	13.6	19.0	5.4	5.3	19.3	14.4	8.1	12.3	26.6	61.2	0.34	0.22	134	131
F	19	2.3	3.0	14.5	4.1	6.4	7.2	16.3	14.2	12.7	7.6	64.3	60.6	0.20	0.17	136	132
F	20	2.3	4.7	16.0	27.6	5.8	6.4	24.4	16.7	12.2	9.8	42.1	50.6	0.33	0.28	136	134
F	21	3.0	2.2	20.8	5.3	5.6	4.2	17.2	14.7	12.2	15.5	54.5	327.6	0.25	0.07	143	133
F	22	2.5	3.7	11.0	18.1	5.0	6.7	19.2	13.9	9.9	10.2	48.9	71.2	0.23	0.28	137	138
F	23	3.1	1.5	13.3	25.5	5.9	7.6	22.0	19.2	7.8	11.6	28.0	139.6	0.29	0.07	145	132
F	24	2.6	2.3	15.5	4.9	5.8	6.4	20.9	21.5	16.7	4.9	66.9	45.2	0.32	0.10	159	154
F	25	3.4	4.7	21.8	24.8	4.9	5.6	21.2	15.9	15.7	15.2	50.2	51.6	0.34	0.42	136	133
F	26	2.7	1.3	24.1	7.1	5.2	5.9	17.7	11.2	9.7	10.7	37.5	45.8	0.27	0.23	138	139
F	27	2.7	0.8	14.5	20.6	6.5	6.8	17.8	18.6	13.4	17.2	45.3	59.1	0.29	0.37	144	153
F	28	3.0	3.8	12.3	60.6	5.7	6.9	17.6	14.6	7.4	19.7	28.9	49.2	0.32	0.43	136	160
F	F_1	2.6	2.8	13.6	71.8	6.2	6.1	21.3	17.6	12.6	21.1	47.6	96.9	0.29	0.24	128	157
F	P_1	3.2	1.8	23.5	10.9	5.4	5.6	19.3	15.6	18.0	13.9	60.2	45.2	0.31	0.27	138	139
F	P_2	2.0	3.2	17.5	19.8	7.0	4.1	18.2	14.5	10.3	14.5	56.4	61.1	0.23	0.27	126	129