THE INTERACTION OF HETEROSIS AND ENVIRONMENT IN WHEAT

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Statement

This thesis contains no material which has been accepted for the award of any other degree or diploma in any University and, to the best of my knowledge and belief contains no material previously published or written by another person, except when due reference is made in the text.

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SUMMARY

Three experiments were conducted to examine the interaction of heterosis and environment in wheat. In the first, eight hybrids and their parents were grown in a wide range of plant densities in the field. The responses would have been influenced by a complex set of environmental factors and it was realised that a greater degree of control of the environment was necessary for a simpler interpretation of interactions. This was obtained by conducting the second and third experiments in the glasshouse and by varying nitrogen and phosphorus over a range from sub- to super-optimal levels.

With some exceptions the general result in all experiments was that significant changes in heterosis percentage for grain weight did not occur. However, in view of other results presented it is believed that it is likely that heterosis for grain weight does change with the environment and the occurrence of a non-significant change was related to the necessary restrictions in the size of the experiments.

Where the parents were found to have different responses and optima for grain weight the hybrid had a response and an optimum intermediate between the parents.

A multiple regression procedure was employed to examine this relationship in more detail. This analysis proved of value in explaining differences in the relative performance of hybrids and parents in environments where heterosis did and did not occur.

Hybrids and parents were compared for the variabilities between and within sets of environments and a consistent feature was that the hybrids were more variable across environments than their parents.

The variability between plants within an environment was found to be associated with the slope of the response. A genotype which is more responsive to change in the environment is expected to have a

larger variation between plants. The hybrids, however, were found to be less variable than the parents in certain environments, while being more responsive to the environment. It was not possible in this study to accurately identify the reason for this discrepancy.

The use of transformations to eliminate interactions is inappropriate since no simple transformation will eliminate interactions between genotypes which have overlapping responses with different optima. Further, they may conceal important features of the response.

Examination of the grain yield components revealed no evidence to suggest that heterosis for grain yield was due to the multiplicative action of additively inherited components where the parents displayed a reciprocal high expression of the components. As well, selection for grain yield on the basis of selection for the components is believed to be ineffective because the contribution of the components to heterosis for grain yield changed with the environment.

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1.0.0. INTRODUCTION

Heterosis or hybrid vigour is said to occur when the hybrid between two genetically different lines shows an increased expression of a character relative to the parental lines. The phenomenon is usually defined by comparing the hybrid with the mean value of both parents or the value for the high-parent.

The exploitation of heterosis is of great practical importance for modern agricultural production. The development and use of this phenomenon in maize alone has been considered to be the most important practical achievement of genetics (Gardner, 1968). With increasing pressures being placed on world food production there is little doubt that heterosis will be more extensively used to increase production of other food crops. Well developed systems for producing hybrid varieties are now available for wheat and sorghum and studies designed to develop hybrid rice are being conducted.

The manifestation of heterosis, however, has been found to change with environment. As early as 1931, Bredeman and Heuser noted fluctuations in heterosis in rye from season to season, recognising "good and bad heterosis years" and Bulsonov (1936) working with tobacco found that soil drought sharply diminished heterosis, and other factors, such as rainfall, influenced its manifestation. In wheat, Rosenquist (1931) observed that heterosis decreased as plant density increased and recently Parodi and Patterson (1973) found that heterosis was low in a favourable environment but increased greatly under unfavourable conditions at a different site.

It was believed that a better knowledge of the reasons for the interaction of heterosis and environment should be obtained because the results of such a study may have implications not only for understanding the occurrence of heterosis but also for the analysis of genotype-environment interactions and the utility of genetic analyses performed in restricted sets of environments.

2.0.0. LITERATURE REVIEW

Since heterosis needs to be considered in relation to the environment and is a measure of the relative performance of related genotypes it is a form of genotype-environment interaction. The study of such interactions in field environments is complex because of the difficulty encountered in identifying those factors influencing plant growth and assessing the effects of these on each genotype.

Section 2.1.0. examines some methods employed to study genotype-environment interactions. It was commonly concluded from these analyses that more meaningful results would be obtained if the genotypes were grown in series of quantitatively related environments.

Theoretical considerations of hybrid and parental responses to sets of known environments are presented in Section 2.2.0. Genotypic differences between the mean and variability of such responses are examined. Sections 2.3.0. and 2.4.0. review the relevance of such considerations in the published literature.

Change in the variability of response with environment also has significance for the use of transformations in genetic analyses. This feature is examined in Section 2.5.0.

The importance of the components of grain yield in determining heterosis for this character and changes in the relationships between components in different environments have been considered in Section 2.6.0. Other plant characters and their significance in relation to grain production are presented in Section 2.7.0.

Section 2.8.0. examines the environmental variables used in this study and the effects of these on plant growth.

In this review, examples of species other than wheat (*T. aestivum* L. are used to illustrate principles where there is a paucity of information on wheat.

2.1.0. Analysis of Genotype-Environment Interactions

A number of methods have been developed to analyse such interactions. One, the analysis of variance, developed by Fisher (1926, 1932) has been adapted and used to study varietal performance over sites and seasons. (Yates and Cochran, 1938; Horner and Frey, 1957; Plaisted and Peterson, 1959; Wricke, 1962). Initially one of the main purposes of the analysis was to identify varieties with an atypical response, for example high or low yield.

The analysis has been extended subsequently. Regressions of the performance of an individual genotype on some index of the environment, such as the mean performance of all genotypes, has been utilised to account for differences in performance between that genotype and the remaining genotypes (Yates and Cochran, 1938; Finlay and Wilkinson, 1963; Eberhart and Russell, 1966; Bucio Alanis and Hill, 1966; Perkins and Jinks, 1968a; Tai, 1971). Where responses are not linear this procedure does not account for much of the interaction observed (Perkins and Jinks, 1968a,b; Paroda and Hayes, 1971). Further, regression coefficients derived in a particular study for each genotype may be more an artifact of the environments and genotypes sampled rather than a predictive description of the genotype (Knight, 1970; Whitcombe and Whittington, 1971; Easton and Clements, 1973).

Procedures designed to investigate the absolute and relative sensitivity of genetic effects such as additivity, dominance and epistasis to environmental change have not been capable of reaching consistent conclusions (Chapman and McNeal, 1971). On the one hand, additive genetic effects have been shown to be more stable over environments than dominance effects (Gamble, 1962; Paroda and Hayes, 1971), while on the other hand, the relative sensitivity of additive and dominance effects has been found to vary between characters under study (Allard, 1956). Situations in which the dominance component was more, equally and less sensitive than the additive component to changes in the environment have also been observed utilising regression analyses (Bucio Alanis, Perkins and Jinks, 1969; Jinks and Perkins, 1969; Breese, 1969).

Since most of these experiments have been grown in different sites and seasons, many environmental factors are likely to have varied and influenced the interactions between genotypes and environment. No attempt has been made to develop procedures which relate changes in plant growth to specific changes in the environment.

It has been suggested that genotype-environment interactions are most simply understood when the response of individual genotypes to specifically defined and controlled environmental factors is known (Griffing, 1954; Hardwick and Wood, 1972).

The mathematical treatment of environmental response was initially considered by Mitscherlich who developed logarithmic response functions to describe plant response in the sub-optimal and optimal ranges of the environment (Russell, 1972). More general equations are necessary to describe responses which also sample super-optimal environments. Multiple regression equations with linear and non-linear components have been used to describe such responses (Hader et. al., 1957; Heady and Dillon, 1961; Gross and Rust, 1972; Prior and Russell, 1975). If a large part of the variation remains unexplained, further parameters of the environment may need to be analysed (Dowker, 1971; Dowker and Fennell, 1974).

However, it is difficult to develop equations which accurately describe genotypic response. Equations involving simple linear and quadratic components may not account for a great deal of the observed variability (Gardener and Rathjen, 1975). Further, where the equations are complex, interpretation of differences between these will also be difficult.

A multiple regression procedure has been developed for the analysis of differences between F_1 hybrid and parental responses (Knight, 1971). This procedure estimates the hybrid value as a multiple linear function of parental values. It has been found to account for a large proportion of the environmental variation of a number of hybrids, including situations in which the hybrid was intermediate or exceeded both parents.

2.2.0. An Environmental Response Approach

In order to accurately define genotypic response a wide range of levels of each environmental factor must be studied. When this is attempted a curvilinear relationship with the environment is often obtained involving sub-optimal, optimal and super-optimal responses (Bradshaw *et al.*, 1964; Asher and Loneragan, 1967; Eagles, 1967; Loneragan *et al.*, 1968; Westerman, 1971).

There is evidence to indicate that genotypes within a species may differ in their response to specific environmental factors depending on the environments under which they evolved (Bradshaw, 1965; Antonovics *et al.*, 1967; Marks, 1973). Also, it has been found that the response of parents and their hybrids to various environmental factors may be different. They may differ by having optima at different levels of the environment (Parsons, 1959), different yields at the optima (Griffing and Langridge, 1963) and differences in the range over which they will grow (Hiesey, 1963). It was suggested by Knight (1973) that conceptually it was more reasonable to expect the hybrid to have a response to the environment intermediate between the parental responses, rather than to have a yield which was intermediate.

Recognising such situations, Knight (1973) examined hypothetical responses of two parents and their hybrid. The parents were specified as having identical response surfaces but reaching an optimum at different levels of one environmental factor. The hybrid had a similarly shaped response surface with an optimum intermediate between the parental optima. An examination of the three surfaces revealed that the genetic situations of no dominance, positive dominance and overdominance occurred in different environments. If the hybrid response has an optimum closer to one parent than the other, negative dominance will occur in certain environments.

Knight pointed out some other aspects of response curves and surfaces that have genetic relevance. Phenotypic stability is a term used variously to describe the variation in means over a range of environments or variation within a single environment. The stability of response between individuals of a genotype grown over a range of environments may be defined as macro-environmental variability. Where a hybrid and its parents have identical spherical or ellipsoidal response surfaces normal to the axes, the macro-environmental variability of the parents and hybrid for any response curve would be identical. If the surfaces are not of this nature then the macro-environmental variability of a hybrid response curve making up the surface will always be smaller than the mean macro-environmental variability of its parents and may be smaller than that of both parents.

Micro-environmental variability is the variation in performance of genetically identical individuals grown as far as possible under the same environmental conditions. It has been found that micro-environmental variability is lowest in optimal environments and increases with displacement from the optimum (Went, 1953; Gustafsson and Dormling, 1972). Such variability is due partly to minor fluctuations in the availability of environmental factors to the individuals. Knight suggested that these fluctuations will occur proportionally to the slope of the response surface. At the optimum, fluctuations in availability will result in little change in response, while elsewhere variations in availability will result in larger fluctuations in response. As a result, a series of genotypes which have different response surfaces and optima may have different levels of micro-environmental variability at any one level of an environmental factor.

The variability of a response surface will in fact increase curvilinearly with displacement from the optimum. Consequently, if a hybrid response surface lies between its parents then its micro-environmental variability must always be less than the mean variability of its two parents and may be less than the variability of both parents.

2.3.0. Environmental Response and Heterosis

The response of parents and hybrids to various environmental factors have been investigated in many studies. Some of the results are reviewed in the following sections.

2.3.1. Temperature

The environmental factor that has been most widely studied has been temperature with *Drosophila* as the experimental organism. The response curves for viability of two parental stocks grown in a range of temperatures from 15 to 30°C had the same optimum temperature, but the Oregon strain had a narrower range of survival (Thoday, 1953). The hybrid displayed an intermediate type of response, but since no change in rank occurred between the parents at high temperature, heterosis relative to the mid-parent was increased in this range.

Recent studies of *Drosophila* have confirmed that heterosis is more usually expressed at high temperature. Heterosis relative to the mid-parent was observed for larval viability and egg production at 25°C but not at 22°C in strains of *D. melanogaster* maintained for many years at 15°C (Vetukhiv and Beardmore, 1953). Such an increase in heterosis at high temperature has been attributed to the greater susceptibility of one parent to exposure to high temperatures (Parsons, 1959; Tantawy, 1961; Parsons, 1966).

Increased heterosis relative to the mid-parent at high temperature has also been observed in some plant species including maize (*Zea mays* L.) (McWilliam and Griffing, 1965) and *Phalaris* (McWilliam *et al*., 1969). Studies in a self-pollinated species over a sufficiently wide range of temperatures have been made only in *Arabidopsis thaliana*. An F_1 hybrid between parental lines from different geographic locations displayed heterosis relative to the high-parent at all temperatures. More particularly, the hybrid was not as severely depressed as the parents by high temperature resulting in an enhanced heterosis relative to the mid-parent in this range (Griffing and Langridge, 1963). Investigations of F_2 hybrids have shown the same phenomenon (Pederson, 1968; Griffing and Zsiros, 1971).

An explanation of high temperature-dependent heterosis at the molecular level has been proposed which suggests that heat-sensitive enzymes are the most common consequence of mutations that do not inactivate the enzyme. Some of these mutations are expressed in the organism only at high temperatures and complete dominance of the normal phenotype is expected in the heterozygote (Langridge, 1962, 1968). Further, it has been suggested that such alleles occur randomly between and within genotypes producing an array of responses for different genotypes (McWilliam *et al*., 1969).

The occurrence of heterosis relative to the mid-parent is not restricted, however, to high temperatures and has been observed in the sub-optimal temperature range for viability in *Drosophila melanogaster* (Fontdevila, 1970), longevity in *D. pseudoobscura* (Heuts, 1948), viability in *D. pseudoobscura* (Marinkovic *et al*., 1969; Jefferson *et al*., 1974) and growth rate in maize (McWilliam and Griffing, 1965). Some mechanism other than that suggested by Langridge (1962) must be operative for heterosis observed at low temperatures (Spiess, 1950;

Spiess, 1967). The low temperature heterosis observed in maize has been largely attributed to the presence of mutant genes in the homozygote restricting the formation of chlorophyll, and, in extreme cases, of the chloroplasts.

Other workers have shown heterosis relative to the mid-parent to occur in a more general range of temperatures. Young (1971) observed heterosis in both sub- and super-optimal temperatures, while Li and Redei (1969) reported heterosis in a wide range of temperatures.

2.3.2. Fluctuating Temperature

If these results on the response of genotypes to temperature are to help explain interactions between heterosis and the environment, they must also account for heterosis in natural conditions, where individuals are subjected to widely fluctuating temperatures.

The results from a number of studies suggest that the level of heterosis may depend on the magnitude of fluctuations in temperature. No heterosis was observed in Drosophila where temperatures fluctuated around the optimum temperature (Vetukhiv and Beardmore, 1959) but where temperature varied over a wide range, heterosis relative to the mid-parent was high and almost as great as that expressed at the high temperature (Tantawy, 1961). Further, it has been shown that heterosis expressed in fluctuating temperatures depended on the mean temperature and not on the magnitude of the fluctuation (Parsons, 1959). High temperature shocks of long or short duration were also found to equally induce high levels of heterosis in maize, while repeated shocks were cumulative in their effect when applied over a wide range of growth stages (McWilliam and Griffing, 1965).

Hybrids have been shown to maintain their growth rate when shifted from one environment to another, whereas the parents exhibited a lag phase (Lewis, 1954). This result suggests that these hybrids not only grew better at high temperatures, but that they also recovered from heat shock more quickly than their parents. Similarly, for *Arabidopsis*, pronounced heterosis was observed under high temperature shock treatments, but no greater heterosis was expressed by cold temperature shock than at an optimum constant temperature.

2.3.3. Nutrients

In a study of barley parents and hybrids under conditions of nitrogen and phosphorus deficiency and optimal nutrition, the hybrid was found to yield less than one or both parents. Only under conditions of potassium deficiency did the hybrid grow better than both parents (Gregory and Crowther, 1931).

A more complete series of nitrogen treatments ranging from deficient to toxic levels was used to study the responses of two maize inbreds and their hybrid (Burkholder and McVeigh, 1940). Heterosis relative to the high-parent occurred at all rates of nitrogen but was relatively higher about the optimum. However, in a further series of experiments heterosis was greatest at the intermediate levels of nitrogen. The hybrids did not show greater efficiency in the utilisation of low rates of nitrogen.

A study of the phosphorus nutrition of four inbred lines of maize and their hybrids gave a similar result, however, it also indicated that differences may occur between the responses of the hybrids (Smith, 1934). Lines were selected for their efficiency at low levels of phosphorus and tested at various rates of applied phosphorus rising to an optimum. Heterosis relative to the high-parent was greatest at intermediate rates (20% and 50% optimum P supply). Hybrids between efficient or between efficient and inefficient lines gave high levels of heterosis, while crosses between inefficient lines produced relatively little heterosis. Low levels of heterosis were observed for all crosses under extremely deficient conditions. The inheritance of phosphorus responsiveness as a dominant character has also been reported (Lyness, 1936).

Hybrids of inbred lines of maize have been found to be relatively more tolerant of high soil acidity (Lutz et al., 1971). Heterosis was expressed at all levels of pH (3.9 to 6.1), but was higher at the lower pH.

Studies with Drosophila have also found that under more or less optimal protein supply, survival, development rate and weight of the hybrids were generally superior to those of inbred lines (Sang, 1964). However, as protein (casein) supply was decreased, the relative efficiency of the hybrids declined, no heterosis being expressed at low levels. The increased efficiency of protein utilisation at optimal levels also led to a reduction in the requirement for pyridoxine and choline.

In Arabidopsis, heterosis expressed by F_2 hybrids has been shown to be greater under optimal nutritional conditions than at 1/36 optimum (Pederson, 1968) or 1/16 optimum (Griffing and Zsiros, 1971). The latter workers also found that nutrient-dependent heterosis was influenced by developmental time and temperature, but not by plant density and suggested that if hybrids were to be expected to contribute to agricultural production they would perform best under conditions of optimum nutrition.

However, in a study of Japanese quail lines selected on optimum and deficient protein diets, heterosis was only observed on the low protein diet (Marks, 1973). This evidence suggests that heterosis is associated with nutritional status in a more complex manner than was suggested by Griffing and Zsiros (1971) and is related to the nutritional status of the environments under which the genotypes evolved and their consequent responses to variation in nutritional status

(Robertson, 1960; Sang, 1962).

2.3.4. Light

Inbred lines of maize and their hybrids have been shown to have markedly different reactions to varying light conditions. At low light intensities the hybrids showed no superiority over their parents (Whaley, 1944). Variations in heterosis in snapdragons (*Antirrhinum majus* L.), observed at different sowing times, has also been attributed to changes in light intensity (Haney *et al*., 1953; Gartner *et al*., 1953). A high correlation was found between solar radiation and heterosis.

Similarly, heterosis expressed by a particular *Phaseolus* hybrid responded dramatically to changes in photoperiod. In a normal day-length the hybrid continued to grow for a longer period and produce a much larger plant than the parental lines, while under a restricted day-length, no heterosis was displayed (Malinowski, 1935).

A similar result was obtained in a study of *Lycopersicon* hybrids (Lewis, 1956). It was found that the hybrids were fully fertile at light intensities of 600 and 400 foot-candles at 18 - 19°C and also at 200 foot-candles at 14 - 15°C. However, the parents were sterile under all conditions indicating that the limiting light intensity for fertility in the inbreds must be at least three times as high as that for the hybrids.

2.3.5. Plant Density

Since heterosis was first observed in wheat (Freeman, 1919) many studies have been made on its interaction with plant density. Some have shown that heterosis decreased with density and others that it increased with density. Other workers have failed to find any evidence for an effect of density on heterosis or have obtained inconsistent results.

The first such study of a range of hybrids indicated that heterosis relative to the mid-parent declined as plant density increased from 33 to 133 plants m^{-2} (Rosenquist, 1931). In a more comprehensive study involving variation in sowing time and density, higher levels of heterosis relative to the high-parent were recorded in the more favourable conditions for plant growth, that is with early sowing and wide spacing (Pal and Nek Alam, 1938). Heterosis decreased with density not only for yield, but also for the yield components, number of fertile spikelets, number of grains per head, average grain weight and head length.

A decline in heterosis with density as found by Singh and Tashi Dawa (1968) and Dhindsa and Anand (1973) is not necessarily a general phenomenon. Others have found that a decline occurred only with some hybrids (Zeven, 1972; Barabas et al., 1973).

An example of heterosis increasing with density is provided by an investigation of a nine parent diallel cross in which the parents and F_1's were grown under widely spaced and drill plantings (Khekra and Sandhu, 1971). A similar result was observed for a large number of hybrids grown at 100 and 400 plants m^{-2}, although a few hybrid combinations did show reduced levels of heterosis at high density or no effect of plant density on heterosis (Barabas et al., 1973). If the best hybrids were selected, levels of heterosis relative to the high-parent were 70% and 156%, and 40% and 69% respectively at the low and high density when compared with the highest yielding parent in the trial. At the high seed rate most of the yield component values of the hybrids compared favourably with those of the better parents, while at the low density few yield components of the hybrids were equivalent to the better parent.

A number of studies have failed to observe an effect of plant density on heterosis. A spring and a winter wheat hybrid were grown by Briggle et al. (1967a,b) over the range of densities, 27 - 324 plants m^{-2}, achieved by decreasing intra-row spacing. They did not comment on heterosis in their results, but it can be calculated that for the spring wheat hybrid there was little change in the expression of heterosis relative to one parent, for yield per plot, and number of ears per plant (Zeven, 1972). For number of grains per ear and average grain weight there was no effect of density on heterosis, despite great changes in plant performance with density. Results for the winter wheat hybrid varied markedly over densities and no consistent effect of density on heterosis was apparent.

Similar instances of the failure to detect a consistent effect of density on heterosis have been reported by Clement (1972) and Zeven (1972). The latter study revealed that heterosis for the yield components did not change with density. Comparable results were obtained by Knott and Sindagai (1969), Bitzer et al. (1971) and Sage (1973).

From the literature, reviewed above, it is concluded that heterosis may change with the environment and that hybrids may be distinguished which show maximal expression of heterosis in either sub-optimal, optimal or super-optimal environments. The existence of such contrasts has been attributed to differences in the environmental conditions under which the parental genotypes evolved.

The phenomenon of heterosis continues therefore to be unpredictable requiring new approaches and the accumulation of further data before any generalisations can be made.

2.4.0. Phenotypic Stability

This term is used to describe the stability of performance of individual genotypes both between and within a set of micro-environments.

The term micro-environment is used synonymously with the term environmental level. For example, plants growing at one temperature level, in an experiment involving a range of temperatures, are said to be in a micro-environment.

Macro-environmental variability will be defined in this thesis as being a measure of the variation in means across the range of micro-environments. The variation between genetically identical individuals grown in a common micro-environment, on the other hand, is defined as micro-environmental variability.

2.4.1. Macro-environmental Variability

Many comparisons have been made between the macro-environmental variation shown by homozygous and heterozygous genotypes. One compared inbred lines of maize and their crosses grown in solutions differing in nutrient content (Harvey, 1939). Although these data provided no information on the response to specific factors, the heterozygotes were found, in general, to be more stable in their response to nutrient changes.

In other cross-fertilised species the heterozygotes consistently have had lower variabilities than the homozygotes. Heterozygotes of *Drosophila* species (Robertson and Reeve, 1952; Dobzhansky and Wallace, 1953) and *Primula sinensis* (Mather, 1950) were better able to cope with a wide range and changes in the environment.

For self-fertilised species the evidence is less clear. It has been postulated that a breakdown of the normal breeding system leads to a loss of internal physiological buffering and to an increase in environmental variance (Lerner, 1954). If this is true the expectation for self-fertilised species is that the variance of the F_1 will be higher than that of the parents. However, hybrids of the self-pollinated species *Nicotiana* appeared to have variabilities comparable to those of the parents (Jinks and Mather, 1955) while tomato hybrids were more stable than their parents (Lewis, 1953, 1956).

Not only has it been observed that inbred parents differ in phenotypic stability, but also that hybrids having the same level of heterozygosity may have different phenotypic stabilities, sometimes called homeostasis (Adams and Shank, 1959; Shank and Adams, 1960; Williams, 1960; Allard, 1961; McWilliam _et al._, 1969). Heterozygosity _per se_ is not then the only hypothesis required to account for homeostasi

The macro-environmental variability of _Aradidopsis_ hybrids has been found to be lower than that of their parents when these were grown over the temperature range 16° to 31°C (Griffing and Langridge, 1963). They suggested this was due to the relative insensitivity of the hybrids to extreme temperatures, particularly high temperatures. Pederson (1968) arrived at the same conclusion but he also observed greater phenotypic stability in the hybrids under conditions of low light intensity and high moisture stress, but lower stability with a sub-optimal nutrient status. Major changes in specific nutritional status may affect the hybrids as greatly as they do their parental inbreds (Sang, 1964) while some inbreds may even be more resistant to particular nutritional changes than the hybrids (Prahbu and Robertson, 1961; Sang, 1964).

2.4.2. Micro-environmental Variability

It has been commonly observed in outbreeding species such as _Drosophila_ and mice that heterozygotes show less variation between genetically identical individuals in a particular environment than do homozygotes (Gowen and Johnson, 1946; Robertson and Reeve, 1952; Vetukhiv and Beardmore, 1953; Gruneberg, 1956). Even where heterosis has occurred hybrid variability was often less than inbred variability (Gowen and Johnson, 1946; Vetukhiv and Beardmore, 1953).

For the cross-pollinated species Zea mays L. and Primula sinensis hybrid variabilities have been found to range from a level intermediate between that of the parental inbreds (Jones, 1918, 1920; Emerson and Smith, 1950) to a level much lower than either parent (Jones, 1922, 1939; Mather, 1946, 1948, 1950).

Similarly for self-pollinated species the evidence on relative micro-environmental variability of parents and hybrids is inconsistent. Results in the literature can be grouped into three categories. Hybrid variability is:

(a) less than parental variability: for Phaseolus (Malinowski, 1935) and wheat (Granhall, 1946; Palmer, 1952).

(b) intermediate between that of the parents: for tomatoes (Powers, 1941; Lewis, 1953), Nicotiana (Jinks and Mather, 1955; Paxman, 1956) and Galeopsis (Hagberg, 1952).

(c) greater than parental variability: for barley (Gustafsson, 1946), wheat (Copp and Wright, 1952) and Nicotiana (Smith, 1952).

It may be suggested that the differences between these results are due to the fact that they were obtained in different environments. As was pointed out, micro-environmental variability is expected to be greater in sub- and super-optimal environments than in more optimal environments. It is possible that a different ranking of the variabilities of parents and hybrids may occur in different environments.

Examination of the micro-environmental variabilities of parents and hybrids grown in a range of known environments has been undertaken by a number of workers. Comparison of micro-environmental variabilities of inbred and hybrid mice grown at optimal (21°C) and sub-optimal (-3°C) temperatures indicated that the hybrids were very much more uniform than the inbreds and that this feature was accentuated at the sub-optimal temperature (Barnett and Coleman, 1960). From an examination of means and coefficients of variation it is obvious that there is no simple relation between these, since where hybrid performance at -3°C is reduced to the level of the parental inbred mice at 21°C, the hybrid coefficient of variation remained much lower than those of the parents. Similar results have been obtained by Lewis (1954) using tomatoes and McWilliam _et al_. (1969) using _Phalaris_ parental and hybrid populations. However, in the latter study the hybrids were relatively more stable and displayed considerably enhanced heterosis under high temperature stress.

This lower variability of the hybrids relative to the parents is not necessarily related to the occurrence of heterosis. In a study of a _Phaseolus_ hybrid grown in two daylengths, the hybrid coefficient of variation was less than that of the inbreds under the optimal conditions of long daylength where heterosis was expressed. In the sub-optimal short daylength environment the coefficient of variation of the hybrid was lower than that of the inbreds despite the absence of heterosis (Malinowski, 1935).

It was not possible to determine from any of these studies whether the micro-environmental variability of a genotype was related to the slope of its response or to explain differences between parental and hybrid variabilities in terms of the slopes of their responses.

2.5.0. Transformations

Following any biological experiment the question arises as to whether an analysis should be attempted on the raw data or some transformation of the data. It is known that transformations may increase, decrease or eliminate statistical interactions (Bartlett, 1947) and that the interpretation of the analysis may change with the transformation used. Mather and Jinks (1971) have suggested that genotype-environment interactions should be eliminated and additivity induced in data if at all possible.

If the range of environments considered is limited, then interactions between genotypes and environment may be linear and be eliminated by transformations. However, if a sufficiently wide range of environments is sampled, genotypes will have a curvilinear response and no simple transformation will eliminate interactions (Knight, 1973). A number of authors have found no transformation that would induce additivity (Powers, 1950; Smith, 1952; Mather and Vines, 1952; Copp and Wright, 1952; Lewis, 1954).

Homogeneity of error variation (micro-environmental variation) is required in genetic analyses dependent on least square procedures in tests of significance. However, when curvilinear responses to the environment are considered, error variation may be expected to vary between genotypes and environments. Differences in error variation have been observed between homozygous genotypes (Williams, 1960) and between heterozygous and homozygous genotypes (Mather, 1953; Lerner, 1954). Further, error variation has been shown to change in a consistent manner with changes in the environment. Went (1953), Barnett and Coleman (1960), Griffing and Langridge (1963), Sang (1964), McWilliam _et al_. (1969) and Gustafsson and Dormling (1972) all produced evidence that error variation was low in optimal environments, increasing in more sub- and super-optimal environments.

The use of transformations in these situations may conceal important features of the data. It is believed that it is more appropriate to develop new approaches which account for interactions and changes in error variation in terms of genotypic responses to the environment.

2.6.0. Yield Component Interaction and Heterosis

Attempts have been made to explain heterosis for a character such as yield in terms of the components of the character. For instance yield in a cereal is the product of head number, grain number per head and average grain weight. If these components are inherited additively and the parents display reciprocally high expression of the components then heterosis for yield is expected to occur due to the multiplicative relationship between the components and yield. Other workers have studied components in the belief that they are more basic to an understanding of yield, and of heterosis for yield.

Higher levels of yield heterosis at low density has been attributed to heterosis for head number (Grafius, 1959; Suneson, 1962; Rajki and Rajki, 1968). Similarly, heterosis for grain yield in a densely seeded trial was relatively higher than at a lower plant density, this difference being due primarily to the tillering ability of the hybrids (Yap and Harvey, 1971). In the dense stands most hybrids were able to produce more heads per unit area than the parents, whereas in the spaced stands the hybrids produced fewer heads than the parents. An increasing contribution by head number to yield heterosis with increasing density, as well as relatively constant contributions by grain number per ear and average grain weight were also reported by Briggle *et al*. (1967a).

In one study, heterosis at low density was due to contributions by head number, grain number per ear and 1000 grain weight and at high density to 1000 grain weight only (Dhindsa and Anand, 1973), while in other studies heterosis at both high and low densities has been shown to be due to moderate contributions by all the yield components (Rasmusson, 1968; Barabas *et al*., 1973).

One school of thought believes that it is more appropriate to study the inheritance of the yield components since these are supposedly more closely related to the primary effects of genes influencing yield (Grafius, 1956, 1959). Heterosis may then be attributed to the reciprocal high expression of components in the parents (Hagberg, 1952; Williams, 1959; Williams and Gilbert, 1960) and the fact that yield is the multiplicative product of these components (Powers, 1941, 1944, 1945; Grafius, 1960).

An alternative hypothesis suggests that yield itself is more closely controlled by the primary effects of genes as it depends on the total energy absorbed by the plant minus structural and chemical energy (Moll _et al_., 1962). It is possible that the components of yield cited by Powers (1941), Williams and Gilbert (1960) and Grafius (1960) may not control the level of yield. Genetic control of the component traits may only be related to the distribution of the stored food and not to the system influencing production and storage of energy (Leng, 1963). Further, because of the compensatory nature of yield components (Leng, 1963), variations in environment may drastically alter their phenotypic and estimates of their genetic control without greatly affecting the yield level (Nickell and Grafius, 1969).

Heterosis has been observed in crosses where the parental varieties did not differ reciprocally for the components while, alternatively, other hybrids have been identified which exhibited no heterosis even though the parents differed reciprocally for the component traits (Upadhaya and Rasmusson, 1967). It has also been pointed out that rarely are the components transmitted from parent to hybrid in a consistent manner (Shebeski, 1966).

Given such results it is appropriate to examine the relationships between the responses by parents and hybrids for the yield components in a range of environments. Such an approach would determine whether changes occurred between environments in the relative contribution by each of the components to heterosis for yield. Further, the generality of the hypothesis relating heterosis for grain yield to the additive inheritance and multiplicative nature of the components could be tested where the relative expression of the parental components changes between environments.

2.7.0. Other Plant Characters

A number of other plant characters such as height and heading date may influence grain yield and for this reason were measured in this study.

1. Total dry weight

It has been suggested that the total dry matter yields of modern cereal varieties are no higher than those of older varieties and that breeding has brought about a shift in the distribution of dry matter between the straw and the grain (Cannell, 1968; Russell, 1973).

A number of workers have advocated the measurement of total dry matter yield in order to calculate the ratio of grain to total dry matter referred to as harvest index (Donald, 1968; Syme, 1972).

These authors have suggested that it will be more efficient to improve grain yield by selecting for higher harvest index. However, this does not appear to be the case (Rosielle and Frey, 1975).

2. Height and Head length

In those environmental conditions in which there is a possibility of lodging, such as high levels of N fertiliser, short plants may have an advantage because they are less prone to lodging. On the other hand, taller plants may have an advantage in hot dry conditions where the leaves have died before anthesis. The greater green stem area may result in a larger supply of photosynthate during the grain-filling period. Plants with longer heads may have a similar advantage.

3. Heading and Anthesis date

The time at which plants reach heading and anthesis is important in the Mediterranean environment of South Australia. Genotypes which mature early may have low yields because the cool wet conditions prevailing during the middle of the season are more conducive to lodging or the low temperatures restrict the accumulation of sugars in the grain (A.J. Rathjen, pers. comm.). The grain production of those which mature late will be limited by the hot dry conditions which prevail at the end of the season. An optimum heading and anthesis date is therefore believed to occur, probably in early October for most seasons.

2.8.0. Experimental Environmental Variables

In the experiments to be described some control and variation of the environment was achieved by varying plant density in a field experiment and levels of nitrogen and phosphorus fertiliser in glasshouse experiments.

2.8.1. Plant Density

The availability of environmental resources to individual plants may change in a complex manner when the plants are grown at different densities. However, plant density is worthy of study in an investigation of heterosis in a cereal since it is easily varied by crop management. Furthermore, information may be obtained on individual plants as well as the community. Because of the difficulty encountered in producing hybrid seed in crops such as wheat and barley, and the consequent higher cost of seed, it is important to determine the optimum density for grain yield by studying hybrids in a range of densities. Other workers have employed different densities to determine the contribution of physiological attributes to yield.

Results on the effect of density on different genotypes have been conflicting. Some have found that relative performance changed with density. This has been reported for wheat (Engledow, 1925;

Rosenquist, 1931; Pendleton and Dungan, 1960; Siemens, 1963; Fawcett, 1964; Sinha and Singh, 1970; Zeidan, 1974), barley (Sakai, 1965; Kirby, 1967; Severson and Rasmusson, 1968; Blum, 1970; Gardner, 1972), maize (Termunde, 1963; Giesbrecht, 1969), Lolium perenne (Lazenby and Rogers, 1964) and Dactylis glomerata (Knight, 1960, 1961).

Other experimenters have found that the ranking of genotypes was consistent across different densities (Rennie, 1957; Lazenby, 1957; Guitard et al., 1961; Demirlicakmak et al., 1963; Stickler et al., 1964). Many studies, no doubt, have failed to achieve significant interactions due to the physiological similarity of genotypes being tested or to the narrow range of plant densities employed.

Increasing density increases competition and reduced the environmental resources available to the plant. Responses to density occur when the phenotype changes in response to this reduced availability. The different conclusions arrived at in the studies referred to previously may have arisen from different responses to limiting factors (Knight, 1960; Donald, 1963). The occurrence or non-occurrence of interactions with density will depend on the environmental factors that are limiting to growth and the existence of differences in the response of genotypes to these factors.

Where the major factor determining growth affects spaced and dense stands equally, as temperature might, there is less likelihood of any interaction between genotypes at different densities. However, it has been established that factors expected to have no differential effect over density may in fact have an indirect effect. Temperature has been found to have a differential effect on light utilisation in different densities (Fukai, 1974).

Differences in response due to plant density have been explained as being due to genotypic differences in:

(i) Tillering ability:

Lupton (1961), Kirby (1967), Yap and Harvey (1971).

(ii) Water use:

Lazenby and Rogers (1962), Blum (1970).

(iii) Lodging resistance:

Vogel et al. (1963), Porter et al. (1964) and Woodward (1966).

(iv) Shade tolerance:

Sakai and Gotoh (1955), Pal et al. (1960), Stinson and Moss (1960), Williams (1968) and Colville (1968) and

(v) Maturity:

Blum (1970).

2.8.2. Nitrogen

The responses of genotypes to nitrogen applications have been studied extensively in wheat. They fall into three general categories:

(i) no genotype x nitrogen interaction:

McNeal and Davis (1954) and McNeal et al. (1971).

(ii) a genotype x nitrogen interaction occurs, but there is no change in ranking:

Lamb and Salter (1936) and Woodward (1966). In the former study no simple transformation would have eliminated the interaction.

(iii) a genotype x nitrogen interaction occurs, with a change in ranking of genotypes:

Worzella (1943), Widdowson (1959), Pendleton and Dungan (1960) and Beech and Norman (1968).

Since nitrogen is an important component of many chemicals involved in plant metabolism, nitrogen deficiency may be expected to have a complex retarding effect on plant growth.

Differences in response to nitrogen have been attributed to differential responses of the yield components (Frey, 1959), differences in the uptake of nitrogen and its translocation to the grain (Woodruff, 1972) as well as to factors allowing formation of a greater number of grains per head (Fisher, 1973; Holmes, 1973).

Excessive levels of nitrogen in the field may lead to a greatly increased leaf area and a consequent greater depletion of soil moisture (Barley and Naidu, 1964). Differences in response to high nitrogen may therefore be attributed to differences in the development of leaf area, leaf display and water use. Alternatively, differences in lodging resistance may be important (Vogel *et al.*, 1963).

However, in a glasshouse situation where water supply is adequate and lodging prevented, nitrogen toxicity is induced by high soil salinity. Differences in salinity tolerance of a series of wheat genotypes to NO_3^- and NaCl has been found (Torres and Bingham, 1973). In their study a later maturing variety was much more tolerant than earlier maturing varieties. Super-optimal salt concentrations were postulated to act by:

(i) diversion of energy for osmotic adjustment rather than growth.

(ii) directly retarding essential metabolism, and

(iii) upsetting turgor pressure relations.

2.8.3. Phosphorus

Differences between genotypes in their responses to levels of phosphorus have been observed and attributed to different requirements, different abilities to obtain phosphorus from the soil or tolerate toxic levels (Asher and Loneragan, 1967; Jessop, 1974; Jones, 1974).

In a study of Australian and introduced wheat varieties, Jessop (1974) noted that varieties of Mexican origin had a greater response to applied phosphorus. These varieties reached a higher yield but at a higher optimum level of applied phosphorus.

Responses to phosphorus have been attributed to many mechanisms. One suggestion was that differences in the branching of the root system varied the ability of the plants to absorb phosphorus (Smith, 1934) or that there were differences in the depth of rooting, but the suggestion was later refuted (Baker et al., 1970; Baker et al., 1971). The accumulation of phosphorus (Gosline et al., 1964) and the efficiency of utilisation have been found to have a genetic basis (Lipsett, 1964).

Phosphorus toxicity has been observed in the field when the roots of young seedlings penetrated a superphosphate band in a light sandy soil (Loneragan et al., 1966). Symptoms of toxicity were expressed as a necrosis extending from the tips of the leaves and occurred when the phosphorus concentration in the leaf reached 4 - 5% of the dry weight (Bhatti and Loneragan, 1970a,b). Phosphate concentrations in the cell sap reached 200 mM with osmotic pressures as high as 10 atmospheres. Such pressures may have upset the water relations of the leaves. Excess phosphorus may interfere with the utilisation of other components of plant metabolism (Rossitter, 1952; Warren and Benzian, 1959; Asher and Loneragan, 1967).

2.8.4. Nitrogen x Phosphorus Interaction

There is abundant evidence to suggest a positive interaction may occur between nitrogen and phosphorus supply to a plant (Shear et al., 1946) so that growth is greatest where an increase in one nutrient is associated with an increase in the other. Further, it has been found that increases in the supply of nitrogen lead to a greater demand for phosphorus (Bennett et al., 1953; Glover, 1953; Bennett et al., 1962) and greater efficiency of phosphorus utilisation (Robertson et al., 1954; Olson and Dreier, 1956).

The complementary action of nitrogen and phosphorus has also been found to act in the alleviation of the toxic effects of one or other nutrient (Rossitter, 1952; Bhatti and Loneragan, 1970a,b). It has been suggested that some dilution effect operates, increasing levels of nitrogen leading to greater top growth and a depression of root growth.

2.9.0. Conclusions to be Drawn from the Literature

A large number of studies have found that the level of heterosis expressed in a particular hybrid changes in different environments. Since heterosis is a measure of the differential performance of related genotypes, namely the two parents and the hybrid, it may be considered in terms of genotype-environment interactions or of the interaction of gene action with environment.

The existing methods used to analyse such interactions have been shown to have limited usefulness and it may be necessary to begin with much simplified situations before an understanding of these interactions is achieved. An analysis of the response to known and controlled environmental variables has been suggested as being a more useful and simplified approach to the study of genotype-environment interactions and the interaction of heterosis with environment (Griffing, 1954; Dowker, 1971; Perkins, 1972).

In many studies it has been found that heterosis was most marked in stress environments such as high temperature and this led Langridge (1962) to suggest a very plausible explanation for heterosis based on enzyme susceptibility to adverse conditions. However, it is evident that heterosis may occur in a more diverse set of environments and even in optimal environments (Spiess, 1967; Li and Redei, 1968; Griffing and Zsiros, 1971). A more general explanation of the interaction of heterosis and environment appears warranted.

Knight (1973) suggested that to obtain a comprehensive picture of the occurrence of heterosis it would be useful to examine the relationships between the responses of parents and their hybrids over a wide range of environments. If, as was suggested, the hybrid had a response intermediate between those of the parents, then the relation of the hybrid to its parents may range from negative to overdominance and heterosis, depending simply on the environment under which it was observed. In such a manner, complex interactions in the genetic relationships of parents and hybrids may be more easily understood.

This approach should not be restricted to yield, but should include the components of yield for which very conflicting results on the occurrence of heterosis have been obtained in the past.

It is commonly believed that heterozygotes are more stable in their response to environment than homozygotes (Parsons, 1959; McWilliam _et al_., 1969). However, much of the literature regarding the superiority of phenotypic stability of heterozygotes over that of homozygotes is conflicting. A number of authors have suggested that much of this conflict arises from the fact that the different results were obtained from different environments (Griffing and Langridge, 1963; Gustafsson and Dormling, 1972). Knight (1973) pointed out that due to the inherent nature of response curves and surfaces variability will increase in sub- and super-optimal environments. Further, for a hybrid which has a response intermediate between that of its parents both the macro- and micro-environmental variability will usually be less than that of one parent and in some environments less than both parents.

An examination of the relationships between response curves and surfaces of parental genotypes and their hybrids will be made in this thesis not only to gain further insight into the interaction of heterosis and environment, but also of the relative phenotypic stability of such genotypes.

Thesis Layout

In this thesis three experiments have been presented in separate sections. Following the presentation of materials, methods and results in each section a discussion is devoted to results relevant to the particular experiment or to make specific comparisons between experiments. Some common aspects of the results of all the experiments are reviewed in the general discussion.

3.0.0. THE EXPERIMENTS

The aim of this study was to examine the relation between genotypic responses to the environment, heterosis and phenotypic stability. Three separate experiments were conducted using wheat as the experimental material. Homozygous parents and F_1 hybrids only were studied to ensure homogeneity and to allow replication across environments.

In Experiment 1 several parents and F_1 hybrids were grown as pure stands at a wide range of densities in the field. Differences in response to density are likely to be the result of differences in response to environmental factors such as light, water and nutrient status and genotypic interactions with these factors.

It became apparent from this experiment that a better understanding of the interaction between heterosis and the environment would be achieved only with a greater degree of control of the environmental factors.

Consequently Experiment 2 was conducted in the glasshouse to examine differences in genotypic response to two controllable factors. Nitrogen (N) and phosphorus (P) fertilisers were applied to the soil at a range of rates designed to produce sub- and super-optimal responses to both nutrients. Because of the many N-P combinations and the need to keep the experiment within manageable proportions only a single F_1 hybrid and its parents were examined. No response to P was achieved in the experiment, either in the sub- or super-optimal ranges. Analysis was restricted therefore to the genotypic response to nitrogen.

This approach was repeated and Experiment 3 successfully examined parental and F_1 hybrid responses to sub-optimal, optimal and super-optimal applications of both N and P fertilisers. This experiment also was grown in the glasshouse using a single F_1 hybrid combination.

3.1.0. Experiment 1

3.1.1. Materials and Methods

(a) Genotypes

Eight hybrids were chosen for study. Four were selected because they had shown differences in the expression of heterosis in tests conducted by the DeKalb Shand Seed Co. (Table 1, Wilson, pers. comm.).

Table 1: Heterosis in DeKalb tested hybrids.

Hybrid	$\frac{(F_1-HP)\%}{HP}$	$\frac{(F_1-MP)\%}{MP}$
Nabawa x Chile 1B	78	81
Heron x Strain 52	54	75
Heron x Gamut	28	40
Festival x Mengavi	-10	-2.5

The remaining four hybrids were produced between locally grown varieties and breeding lines and had not been previously tested.

Halberd x Warimek

Gabo x Wariquam

Halberd x Wariquam

Timgalen x Warimek

The pedigrees of the parents involved in these hybrids are as follows:

Nabawa	Gluyas Early * Bunyip
Chile 1B	Unknown CIMMYT line introduced to Australia by A.T. Pugsley
Heron	((Ranee * Doubbi) * Ranee) * (Insignia) 3 * Insignia 49
Strain 52	(Spica * Koda) * Gabo * Mengavi sib
Gamut	(Gabo * Kenya 324) * Urquiza * Gamenya
Festival	(Kenya C6041 * Baringa) * Pusa III
Mengavi	(Mentana 1124 * (Gabo) 6) * (Eureka * (Gabo) 2) * C.I.12632

Halberd	(Scimitar * Kenya C6042) * Bobin * Insignia 49
Warimek	Mexico 120 * Koda
Wariquam	Mexico 120 * Quadrat
Gabo	Bobin 39 * (Gaza) 2
Timgalen	(Aguilera * Kenya * Marroqui * Supremo) * Gabo * Winglen

(b) Site and climate

Experiment 1 was grown in 1972 at Roseworthy Agricultural College, South Australia. The soil is a sandy red brown earth Dr. 2.2.3. (Northcote, 1971), and is representative of a large area of the wheat belt in South Australia.

This region has a Mediterranean type of climate with hot dry summers and cool wet winters. The normal growing season extends through the autumn, winter and spring (May to November or December) when most of the rain falls and temperatures are mild.

Table 2: Mean monthly maximum and minimum (°C) air temperature at Roseworthy in 1931-1971 and 1972.

Month	1931-1971		1972	
	Min.	Max.	Min.	Max.
January	14.3	28.3	15.0	28.2
February	14.2	28.2	16.3	29.6
March	12.6	26.2	12.1	25.9
April	10.6	21.8	11.9	24.3
May	8.5	19.5	8.8	20.4
June	6.5	15.1	5.4	17.9
July	5.8	14.2	7.6	14.4
August	6.0	15.4	7.5	16.1
September	6.9	18.1	7.8	19.8
October	8.6	25.2	9.2	22.5
November	11.2	24.4	11.0	25.2
December	13.7	26.7	14.0	28.8

Temperature, rainfall and evaporation records at Roseworthy for 1972 are compared with long term averages in Tables 2 and 3. The experiment was sown on 26 and 27 June and harvested at maturity between 7 November and 5 December. Since high density plants matured first, harvesting was done progressively from high to low density.

Table 3: Monthly rainfall (mm) and pan evaporation (mm, Australian tank) at Roseworthy in 1931-1971 and 1972.

Month	1931-1971		1972	
	R	E pan	R	E pan
January	22.5	239	40.0	265
February	19.5	201	45.0	241
March	20.0	165	0.0	215
April	37.5	104	31.0	151
May	50.0	63	23.0	85
June	55.0	40	15.0	76
July	50.0	45	40.0	55
August	54.0	65	78.0	70
September	46.5	95	30.0	145
October	40.5	123	10.0	184
November	26.5	177	12.0	245
December	22.0	235	15.0	315
* Seasonal Total	233.5	590	177.5	817
Annual Total	444.0	1552	339.0	2047

* Seasonal totals were calculated for the period of the experiment between sowing and harvesting.

Rainfall during the growing season in 1972 was restricted mainly to the months of July, August and September. The early part of the season was dry and local seeding operations delayed until reliable rains were recorded late in June. The season ended prematurely in the latter half of September after which low ineffective rains were recorded.

(c) Field layout

All eight hybrids were sown by hand at a range of plant densities (Table 4, p. 35). The seeds were sown on a square-spaced configuration to eliminate the confounding effects of rectangularity and row direction and to ensure ease of access and identification of single plants, particularly at high density.

Table 4: Field plot dimensions.

Density (D)	Plants per M^2	Distance between plants (cm)	Plot width (cm)	Plot length (cm)
1	5.0*	44.7	268.3	223.6
2	17.5	23.9	143.5	119.6
3	61.3	12.7	76.7	63.9
4	214.4	6.8	41.0	34.2
5	750.3	3.6	21.9	18.3

* Geometric progression: ($3.5^{D-1} \times 5.0$)

The experimental design was a split-block type, the five densities being allocated to separate blocks within each of two replications. Each block was laid out, as shown in Figure 1, consisting of 63 contiguous plots sown uniformly at the same configuration and density and surrounded by a border of at least 40 cm width. The hybrid and both parents of each hybrid combination were randomised within three adjacent plots, the eight groups of three plot units also being allocated at random within each block. All remaining plots (R) and borders were sown to the variety Gabo.

Figure 1: Field block layout (Example: Rep 1, Density III).

Border

R	R	R	R	R	R	R	R	R
R	Gabo	WQ	F_1	R	F_1	Her.	S.52	R
R	R	R	Fes.	Men.	F_1	R	R	R
R	WM	F_1	Hal.	R	Chil.	F_1	Nab.	R
R	R	R	Tim.	WM	F_1	R	R	R
R	F_1	WQ	Hal.	R	F_1	Her.	Gam.	R
R	R	R	R	R	R	R	R	R

Nab. - Nabawa, Chil. - Chile 1B, Her. - Heron, S.52 - Strain 52,
Gam. - Gamut, Fes. - Festival, Men. - Mengavi, Hal. - Halberd,
WM - Warimek, WQ - Wariquam, Tim. - Timgalen

(d) Field operations

Densities 1 and 2 were sown using a steel frame, with intersecting strings indicating the seed locations. The remaining higher densities were sown with the assistance of planting boards. For each of these densities a set of two boards comprising a hole board and a peg board were constructed. The holes and pegs were placed at the seed locations. The hole board was placed on the soil surface and the pegs forced through these into the soil. These boards provided a quick and efficient method of sowing seeds at a precise location and depth. One seed only was sown in each location in all plots and missing plants later replaced by a transplanted seedling of the same genotype.

During the season plots were hand-weeded and observations taken on tiller numbers, anthesis dates and flag leaf areas. All test and control plants were individually labelled and harvested.

(e) Characters measured

Twenty plants were randomly selected from each plot after the transplants had been discarded. The following data were recorded for each plant:

(i) Height (primary tiller)
(ii) Head length (" ")
(iii) Head number
(iv) Spikelet number (" ")
(v) Total weight (above ground, air dry)
(vi) Head weight (air dry)
(vii) Grain weight (" ")
(viii) Total grain number
(ix) Grain number per spikelet 1. (5th lowest spikelet, primary tiller)
(x) " " " " 2. (intermediate " , " ")
(xi) " " " " 3. (5th highest " , " ")

Total grain number was counted on an electronic seed counter.

(f) Statistical methods

Statistical analysis of the data in all experiments was performed on the University of Adelaide CDC 6400 computer. Use was made of Fortran programmes and the statistical programme packages Statscript (Lamacraft, 1973) and SPSS (Nie _et_ _al_., 1970, 1975).

(g) Derived characters

Derived characters were calculated as follows:

1) Grain number per head

= Grain number per plant/Head number per plant

2) 1000 Grain weight

= (Grain weight per plant/Grain number per plant) x 1000

3) Harvest index

= (Grain weight per plant/Total weight per plant) x 100%.

(h) Measures of heterosis

Various measures of heterosis were used to describe the relative performance of a hybrid and its parents. They were heterosis relative to the high-parent (HP), the mid-parent (MP), parent one (M1) and parent two (M2) (Table 5).

Table 5: Measures of heterosis, notation and methods of calculation for the hybrid (F_1) between P1 and P2.

Heterosis relative to	Notation	Calculation
High-parent	HP	$\frac{(F_1 - A)}{A} \times 100$
Mid-parent	MP	$\frac{(F_1 - B)}{B} \times 100$
Parent 1 (P1)	M1	$\frac{(F_1 - P1)}{P1} \times 100$
Parent 2 (P2)	M2	$\frac{(F_1 - P2)}{P2} \times 100$

A and B are defined as follows:

A For characters where a comparison with the high-performing parent is biologically meaningful (total weight, grain weight).

If $P1 \geqslant P2$, $A = P1$

$P2 > P1$, $A = P2$

B $= (P1 + P2)/2$.

3.1.2. Results

Experiment 1 was designed to study the response to a wide range of density and inter-plant competition. The highest density was chosen to induce intense inter-plant competition but without causing the death of plants before maturity. However, in some plants growth was retarded to the extent that the head failed to emerge and no grain was produced. This was more commonly observed in the parental plots. Such plants have been included in the analysis of responses and heterosis but excluded from some calculations of C.V.'s (Figs. 11, 12 and 13, pp. 68, 69 and 70).

Although the growing season was not particularly favourable in terms of rainfall, very high yields were achieved at some densities indicating that the experiment did provide a suitable environment for exhibiting a range of differences. Yields of 4.5 - 5.0 tonnes/ha were obtained under the best conditions.

Genotypic responses will be considered in relation to changes in heterosis with plant density. Further consideration will be given to changes in the relationships between grain yield and the components of yield and the stability of performance of hybrids and their parents across environments (macro-environmental variability) and within environments (micro-environmental variability).

(a) Plant Density Response and Heterosis

Set out in Table 6 are the mean values for heterosis over all plant densities. The values ranging up to 59.8% above the high-parent demonstrate clearly the hybrid vigour expressed. It may be noted that the mean levels of heterosis observed in Experiment 1 did show some agreement with those available for the DeKalb Shand test (Table 1, p. 32 Also in the table are the levels of significance for the heterosis x density interactions determined from analyses of variance. These

Table 6: Mean heterosis over density relative to the high-parent (HP) and the mid-parent (MP) and the levels of significance of the deviations for heterosis x density interactions.

Hybrid		Grain weight /sq metre		Total weight /sq metre		Height	
		Het.	Sig.[1]	Het.	Sig.	Het.	Sig.
Nab x	HP	34.0	*	25.0	NS	14.0	*
Chil	MP	49.0	*	37.0	*	22.0	*
Her x	HP	50.2	NS	44.9	NS	9.9	NS
S 52	MP	72.7	NS	62.8	NS	17.6	NS
Her x	HP	59.8	NS	58.9	NS	17.2	NS
Gam	MP	78.0	NS	73.9	NS	23.4	NS
Fes x	HP	-11.5	NS	7.2	NS	-5.3	NS
Men	MP	-5.5	NS	17.3	NS	6.3	NS
Hal x	HP	27.0	NS	23.6	NS	14.1	NS
WM	MP	43.4	*	38.7	NS	18.6	NS
Gabo	HP	35.0	NS	37.0	NS	17.8	**
x WQ	MP	71.6	NS	65.7	NS	22.3	NS
Hal x	HP	29.4	NS	26.8	NS	10.6	*
WQ	MP	41.8	NS	36.8	NS	17.6	*
Tim x	HP	-8.4	NS	5.0	NS	5.7	*
WM	MP	5.2	NS	12.9	NS	7.5	*

[1]

*	indicates significance at 5% level
**	indicates significance at 1% level
***	indicates significance at 0.1% level
NS	Not significant, i.e. the variance ratio had a probability greater than 5%

This notation for statistical significance is used throughout this thesis.

levels of significance indicate whether the expression of heterosis has changed with density.

Three types of responses of hybrids relative to their parents for the character grain weight m^{-2} are evident in Table 6. In the first the hybrid showed a constant superiority across densities, in the second no superiority and in the third a change in superiority with density. The three hybrids Heron x Strain 52, Timgalen x Warimek and Halberd x Warimek have been chosen to exemplify in detail these three respective situations.

It should be noted that while these three hybrids have been chosen on the basis of their different responses in grain weight m^{-2}, change in heterosis with plant density for one character does not necessarily imply change in heterosis for other characters. The relative performances for height of the hybrids Halberd x Warimek and Timgalen x Warimek and their respective parents differ from those expressed for grain weight m^{-2}.

In the response curves presented in Figs. 2 to 13 the values have been joined by freehand curves. Some discrepancies between the values of plant performance and heterosis may be apparent as a consequence of calculating heterosis values for each replicate and then obtaining the mean value for inclusion in the graphs.

1. Heron x Strain 52

This hybrid displayed a high level of heterosis relative to its parents at all densities. However, it was not the highest yielding hybrid in the trial being approximately 75% of Halberd x Warimek. It was considerably higher than the highest yielding parents (Halberd, Warimek and Wariquam). The levels of significance for heterosis (Table 7) indicate that no significant changes in heterosis relative to the high-parent, mid-parent and Strain 52 were detected for any character.

Grain weight m^{-2}

The responses of the hybrid and parents for grain weight m^{-2} are exhibited in Fig. 2A. At low density the slope of the response of the hybrid was greater than the more responsive parent, Heron, while at the high densities the hybrid had a response slope intermediate between those of the parents. As a result the hybrid expressed heterosis relative to the high-parent at all densities but was greater at the intermediate densities. No significant changes were detected over the range of densities sampled.

Total weight m^{-2}

A similar relative response was shown by the hybrid for total weight m^{-2} as for grain weight (Fig. 2C, p. 44).

Harvest index

Harvest index, for all three genotypes declined with increasing density. This was to be expected from a field experiment conducted in a relatively short growing season with hot dry conditions prevailing during anthesis and the grain-filling period. Plants growing at high density would have been under considerably more stress during this period resulting in a relatively lower grain production. It is interesting to note that, of the two parents, Heron had the highest harvest index at the four lower densities, but was the highest yielding parent only at 17.5 and 61.3 plants m^{-2}.

The hybrid response was more similar to that of Strain 52 since the harvest index of Heron was severely decreased at high density (Fig. 2E, p. 44). Consequently, heterosis relative to Heron and the mid-parent increased significantly at the highest density (Fig. 2F, p. 44).

Table 7: Heron x Strain 52. Analyses of variance of heterosis relative to the high-parent (HP), the mid-parent (MP), Heron (M1) and Strain 52 (M2). The values in the table are levels of significance of the heterosis x density interaction.

Char.	HP	MP	M1	M2
Grain weight/m^2	NS	NS	NS	NS
Total weight/m^2	NS	NS	NS	NS
Harvest index	NS	NS	NS	NS
Height	NS	NS	**	NS
Head length	NS	NS	***	NS
1000 Grain weight	NS	NS	NS	NS
Grain number/m^2	NS	NS	*	NS
Grain number/head	NS	NS	*	NS
Head number/m^2	NS	NS	NS	NS

Height

Both Heron and the hybrid displayed an optimum for height at an intermediate density. Lower heights at low density may have been a response to the lack of mutual shelter against wind, an effect intensified in this experiment by square-spacing. Similarly at high density, the square-spacing and short, relatively dry growing season may have combined to overcome etiolation commonly observed at high plant densities.

Heterosis relative to the high-parent, Strain 52, was expressed at

Figure 2

Heron x Strain 52 - Response to density

(A,B)	Grain weight m^{-2}
(C,D)	Total weight m^{-2}
(E,F)	Harvest index
(A,C,E)	Response to density by Heron (■- – – -■), Strain 52 (●– – –●) and Heron x Strain 52 (▲———▲).
(B,D,F)	Heterosis relative to the high-parent (▽———▽), mid-parent (△– – – -△), Heron (□) and Strain 52 (○).

Least significant differences at the 5% level are indicated for heterosis

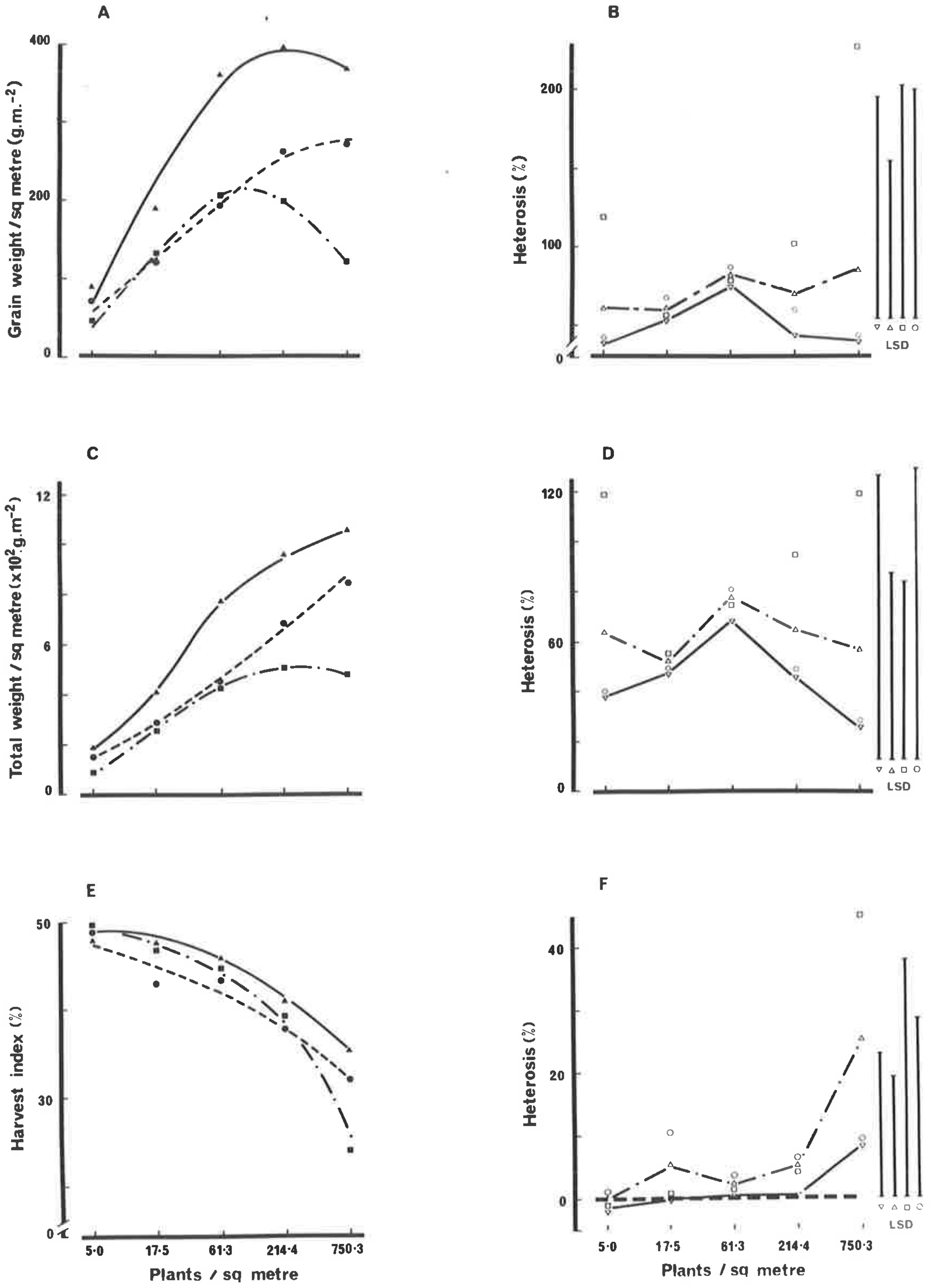

A
Grain weight / sq metre (g.m.$^{-2}$)
400
200
0
B
Heterosis (%)
200
100
0
▽ △ □ ○
LSD
C
Total weight / sq metre (x10^2.g.m^{-2})
12
6
0
D
Heterosis (%)
120
60
0
▽ △ □ ○
LSD
E
Harvest index (%)
50
30
0
5·0
17·5
61·3
214·4
750·3
Plants / sq metre
F
Heterosis (%)
40
20
0
▽ △ □ ○
LSD
5·0
17·5
61·3
214·4
750·3
Plants / sq metre

Figure 3

Heron x Strain 52 - Response to density

(A,B)	Height
(C,D)	Head length
(E,F)	Head number m^{-2}
(A,C,E)	Response to density by Heron (■- — -■), Strain 52 (●- - -●) and Heron x Strain 52 (▲——▲)
(B,D,F)	Heterosis relative to the high-parent (▽——▽), mid-parent (△- — -△), Heron (□) and Strain 52 (○)

Least significant differences at the 5% level are indicated for heterosis

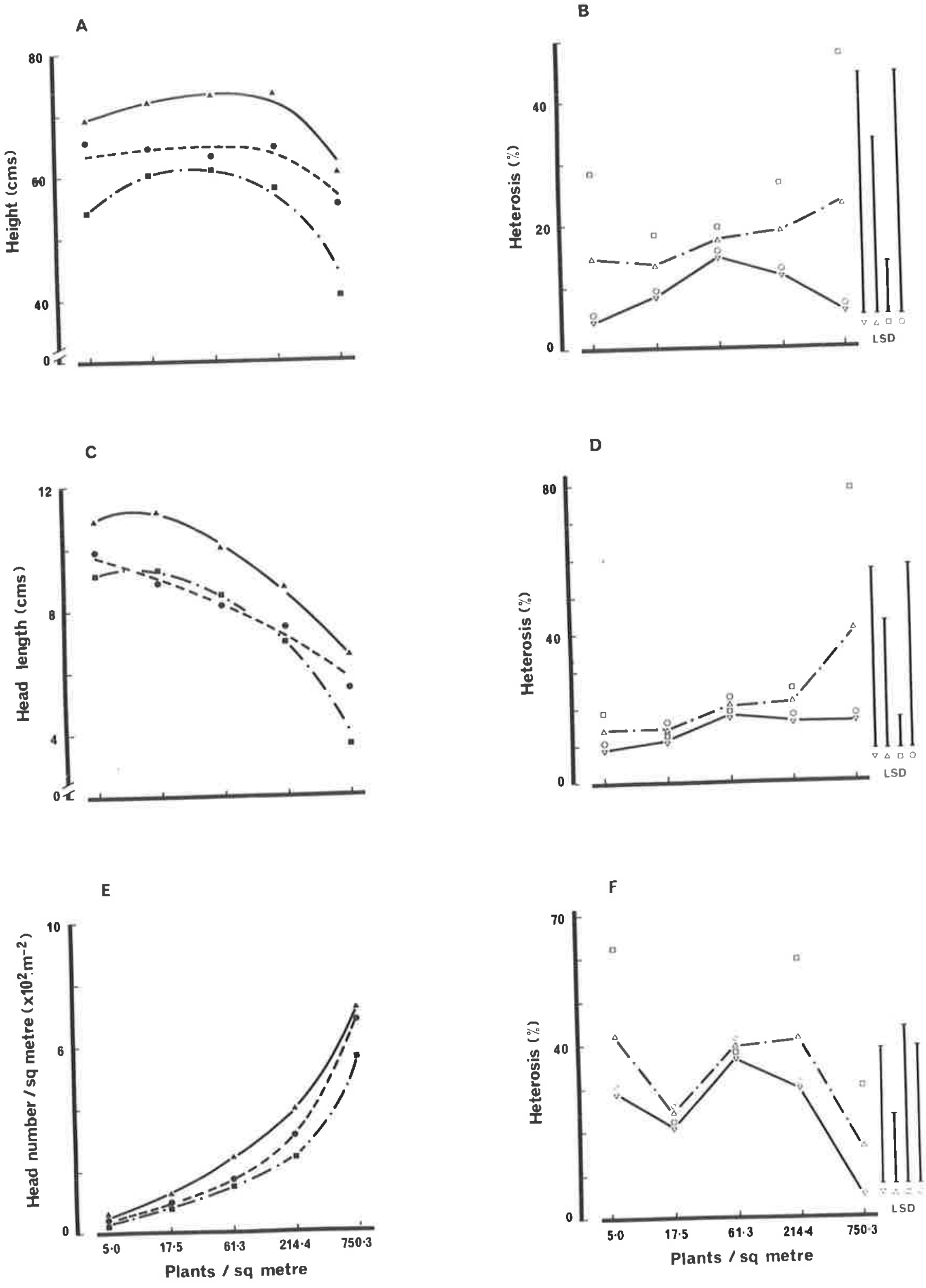
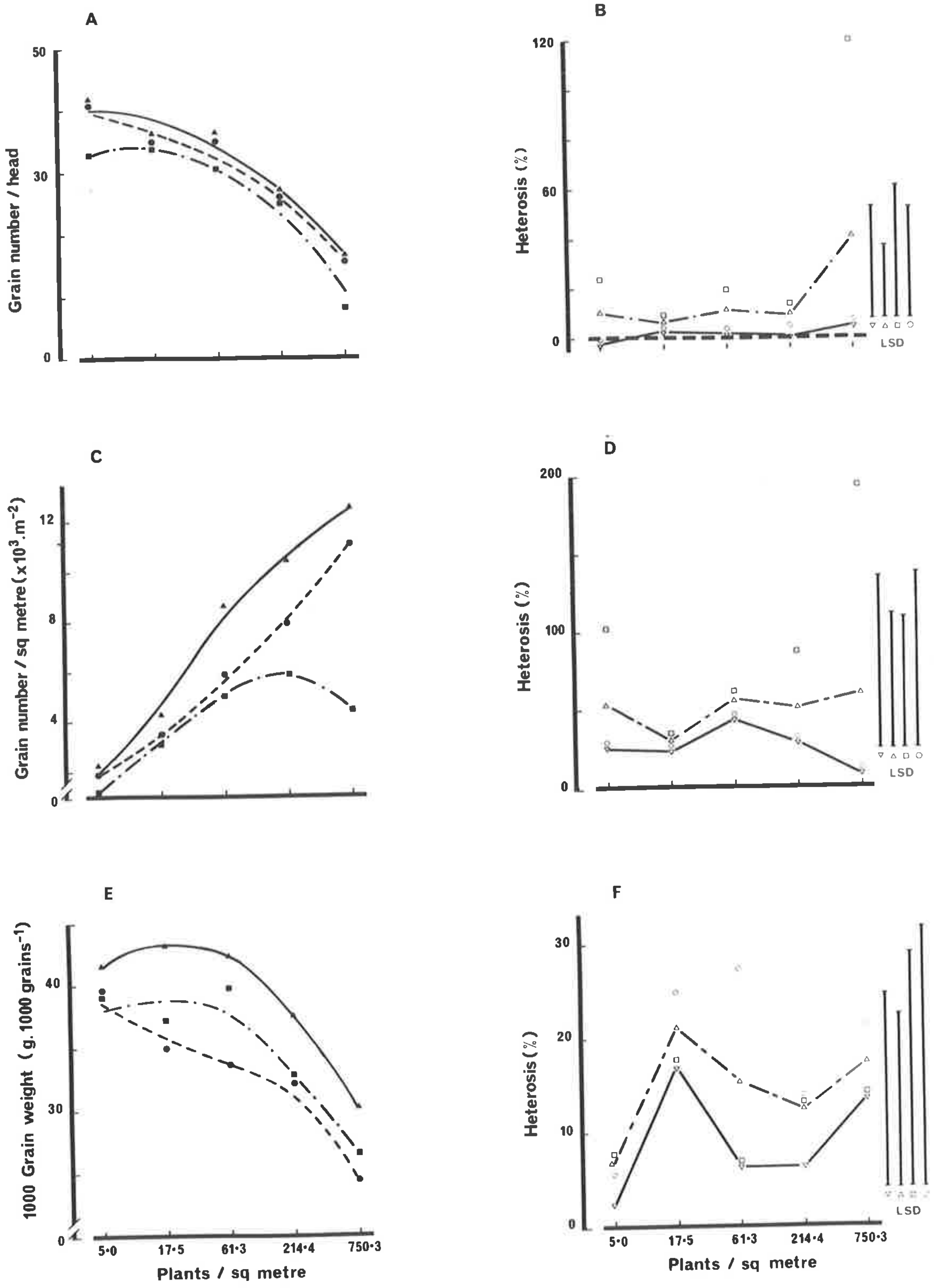

A
Height (cms)
80
60
40
0
B
Heterosis (%)
40
20
0
▽ △ □ ○
LSD
C
Head length (cms)
12
8
4
0
D
Heterosis (%)
80
40
0
▽ △ □ ○
LSD
E
Head number / sq metre (x10^2.m^{-2})
10
6
0
5·0
17·5
61·3
214·4
750·3
Plants / sq metre
F
Heterosis (%)
70
40
0
LSD
5·0
17·5
61·3
214·4
750·3
Plants / sq metre

Figure 4

Heron x Strain 52 - Response to density

(A,B)	Grain number/head
(C,D)	Grain number m^{-2}
(E,F)	1000 Grain weight
(A,C,E)	Response to density by Heron (■----■), Strain 52 (●- - -●) and Heron x Strain 52 (▲——▲)
(B,D,F)	Heterosis relative to the high-parent (▽——▽), mid-parent (△- — -△), Heron (□) and Strain 52 (○)

Least significant differences at the 5% level are indicated for heterosis


A
Grain number / head
50
30
0
B
Heterosis (%)
120
60
0
LSD
C
Grain number / sq metre (x10^3.m^{-2})
12
8
4
0
D
Heterosis (%)
200
100
0
LSD
E
1000 Grain weight (g.1000 grains^{-1})
40
30
0
5·0
17·5
61·3
214·4
750·3
Plants / sq metre
F
Heterosis (%)
30
20
10
0
LSD
5·0
17·5
61·3
214·4
750·3
Plants / sq metre

all plant densities with no significant change in this measure of heterosis being observed (Fig. 3B, p. 45). The hybrid response again was apparently more similar to that of Strain 52.

Head length of the primary tiller

The head length of the hybrid exceeded the lengths of both Heron and Strain 52 at all densities (Fig. 3C, p. 45). The head length of Heron declined markedly at high density resulting in a significant increase in heterosis relative to this parent. However, because of the similarity of head length responses of Strain 52 and the hybrid, no significant changes in heterosis relative to either the high- or mid-parents were observed (Fig. 3D, p. 45).

2. Timgalen x Warimek

Timgalen x Warimek was chosen as an example of those hybrids whose performance relative to their parents for grain weight m^{-2} did not change significantly with density and which failed to display heterosis relative to the high-parent at any density. Levels of significance of analyses of variance of heterosis values are shown in Table 8.

Grain weight m^{-2}

The response of the hybrid for this character was intermediate between those of its parents and is given in Fig. 5A.

Total weight m^{-2}

Although the parental response patterns for this character were similar to those for grain weight m^{-2}, the hybrid response was no longer intermediate but slightly above that of the highest yielding parent Warimek (Fig. 5C, p. 49). A low level of heterosis relative to the high-parent was observed at all densities (Fig. 5D, p. 49).

Table 8: Timgalen x Warimek. Analyses of variance of heterosis relative to the high-parent (HP), the mid-parent (MP), Timgalen (M1) and Warimek (M2). The values in the table are levels of significance of the heterosis x density interaction.

Char.	HP	MP	M1	M2
Grain weight/m^2	NS	NS	NS	NS
Total weight/m^2	NS	NS	NS	NS
Harvest index	*	NS	NS	*
Height	*	*	*	*
Head length	*	NS	NS	*
1000 Grain weight	NS	NS	NS	NS
Grain number /m^2	NS	NS	NS	NS
Grain number/head	NS	NS	NS	NS
Head number/m^2	NS	NS	NS	NS

Harvest index

The highest yielding parent, Warimek, also had the highest harvest index at all densities. The grain producing ability of the hybrid as measured by the harvest index was much lower than this parent at all densities and particularly the higher densities (Fig. 5E, p. 49). This result is very different therefore from the first hybrid considered, Heron x Strain 52, in which the hybrid showed an increasing superiority in harvest index over the highest yielding parent with density.

Figure 5

Timgalen x Warimek - Response to density

(A,B) Grain weight m^{-2}

(C,D) Total weight m^{-2}

(E,F) Harvest index

(A,C,E) Response to density by Timgalen (■- - -■), Warimek (●- — -●) and Timgalen x Warimek (▲——▲)

(B,D,F) Heterosis relative to the high-parent (▽——▽), mid-parent (△- — -△), Timgalen (□) and Warimek (○)

Least significant differences at the 5% level are indicated for heterosis

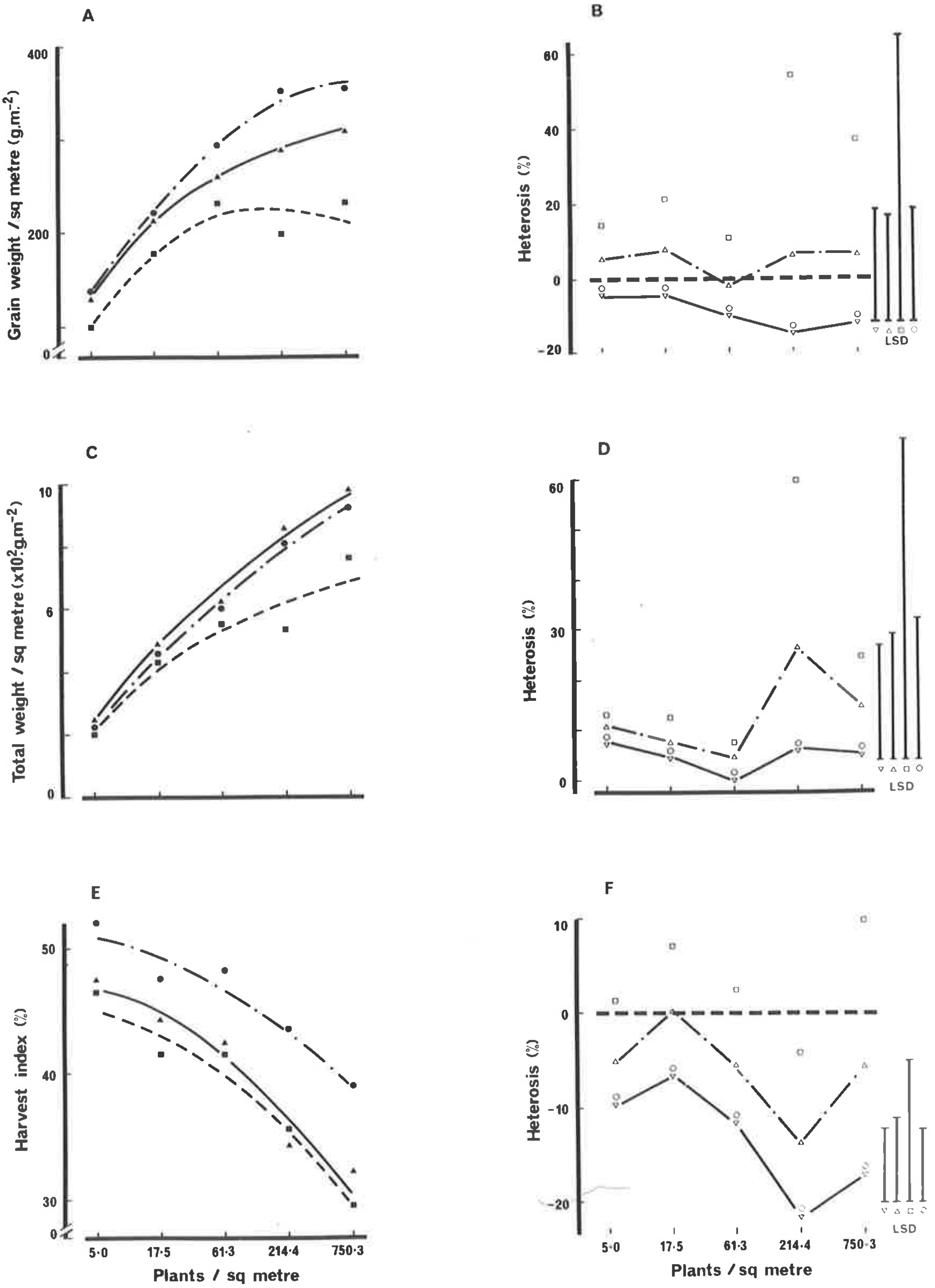

A
Grain weight / sq metre (g.m.$^{-2}$)
400
200
0
B
Heterosis (%)
60
40
20
0
-20
LSD
C
Total weight / sq metre (x10^{2}g.m^{-2})
10
6
0
D
Heterosis (%)
60
30
0
LSD
E
Harvest index (%)
50
40
30
0
5·0
17·5
61·3
214·4
750·3
Plants / sq metre
F
Heterosis (%)
10
0
-10
-20
LSD
5·0
17·5
61·3
214·4
750·3
Plants / sq metre

Figure 6

Timgalen x Warimek - Response to density

(A,B)	Height
(C,D)	Head length
(E,F)	Head number m^{-2}
(A,C,E)	Response to density by Timgalen (■- - -■), Warimek (●------●) and Timgalen x Warimek (▲——▲)
(B,D,F)	Heterosis relative to the high-parent (▽——▽), mid-parent (△- — -△), Timgalen (□) and Warimek (○)

Least significant differences at the 5% level are indicated for heterosis

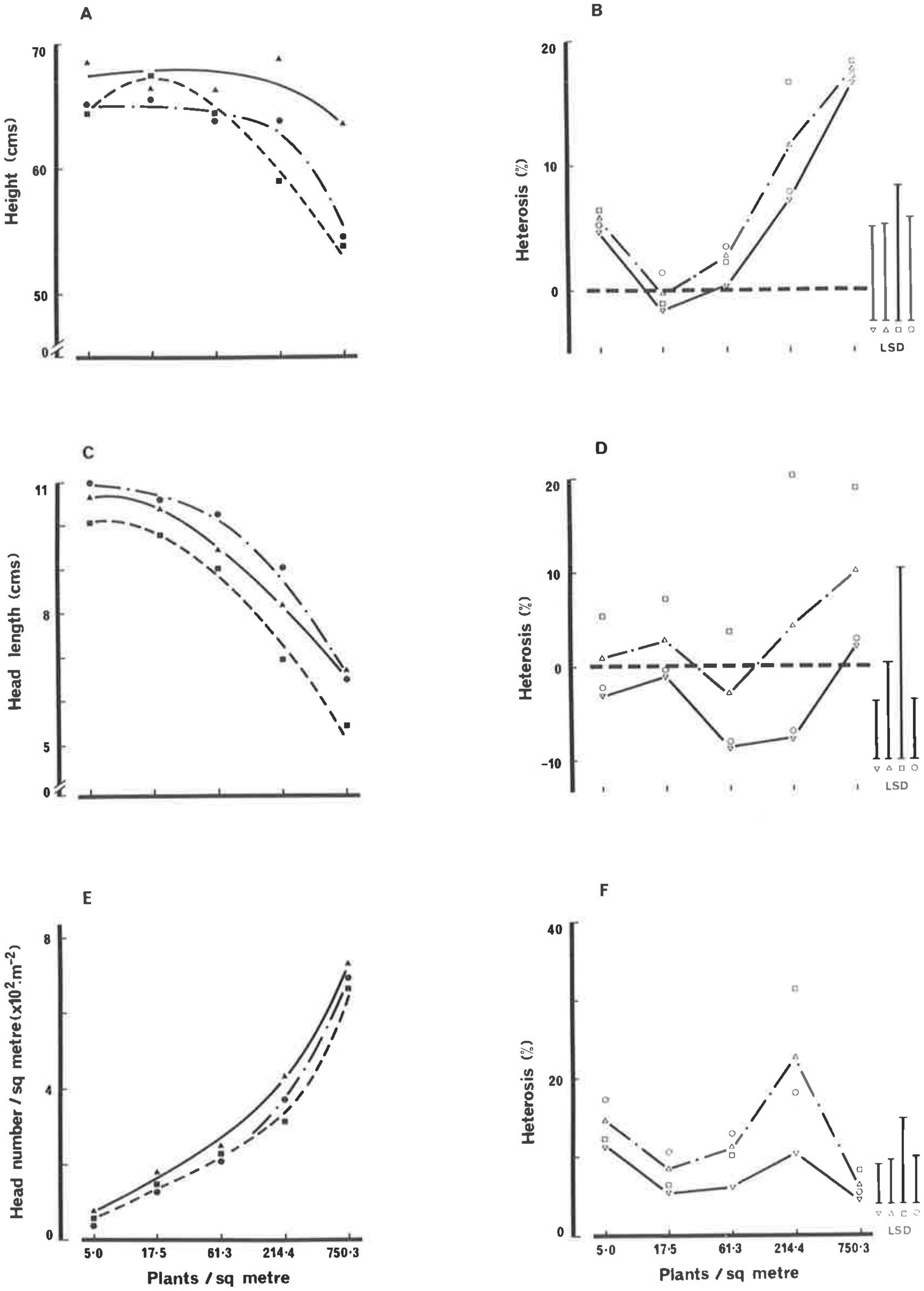
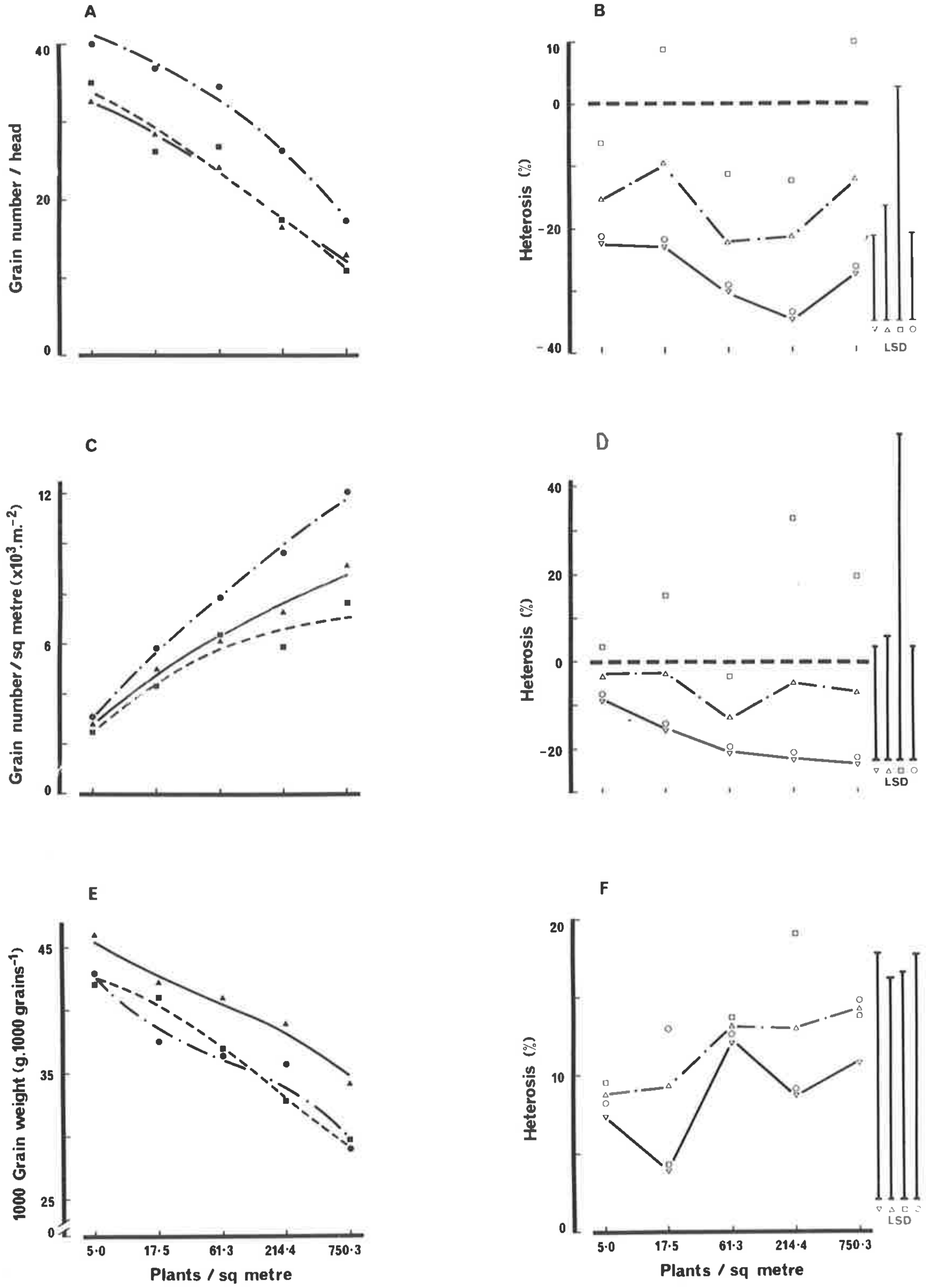

A
Height (cms)
70
60
50
0
B
Heterosis (%)
20
10
0
LSD
C
Head length (cms)
11
8
5
0
D
Heterosis (%)
20
10
0
-10
LSD
E
Head number / sq metre (x10^2.m^{-2})
8
4
0
5·0
17·5
61·3
214·4
750·3
Plants / sq metre
F
Heterosis (%)
40
20
0
LSD
5·0
17·5
61·3
214·4
750·3
Plants / sq metre

Figure 7

Timgalen x Warimek - Response to density

(A,B)	Grain number/head
(C,D)	Grain number m^{-2}
(E,F)	1000 Grain weight
(A,C,E)	Response to density by Timgalen (■– – –■), Warimek (●- — -●) and Timgalen x Warimek (▲———▲)
(B,D,F)	Heterosis relative to the high-parent (▽———▽), mid-parent (△- — -△), Timgalen (□) and Warimek (○)

Least significant differences at the 5% level are indicated for heterosis


A
Grain number / head
0
20
40
B
Heterosis (%)
-40
-20
0
10
LSD
C
Grain number / sq metre (x10³.m.⁻²)
0
6
12
D
Heterosis (%)
-20
0
20
40
LSD
E
1000 Grain weight (g.1000 grains⁻¹)
0
25
35
45
5·0
17·5
61·3
214·4
750·3
Plants / sq metre
F
Heterosis (%)
0
10
20
5·0
17·5
61·3
214·4
750·3
Plants / sq metre
LSD

Height

Heterosis relative to the high-parent was observed at all densities with one possible exception at 17.5 plants m^{-2} (Fig. 6A, p. 50) the density at which Timgalen attained its maximum height. However, as density was increased the height of both parents declined relative to that of the hybrid resulting in a significant increase in the heterosis values. The change in heterosis relative to Warimek was lower than that relative to Timgalen, indicating that, like total weight m^{-2}, Warimek had a more dominant influence on the height response of the hybrid.

Head length of the primary tiller

The hybrid response for head length was intermediate between those of both parents (Fig. 6C, p. 50). Heterosis relative to Timgalen increased with density while the negative heterosis relative to Warimek was significantly lower at 61.3 and 214.4 plants m^{-2} than at other densities.

3. Halberd x Warimek

The parents of this hybrid were two of the highest yielding grown in Experiment 1. They produced a highly vigorous F_1 which expressed a variable heterosis for grain weight m^{-2}; in the range 0 - 50% greater than the higher parent. Levels of significance of analyses of variance of heterosis are shown in Table 9.

Grain weight m^{-2}

The relative grain yield response of Halberd x Warimek displayed similar features to that of Heron x Strain 52. While the grain weight m^{-2} produced by the hybrid exceeded that of both parents at all densities, the hybrid was intermediate in the slope of its response at low densities but more responsive to changes in density in the high density range (Fig. 8A, p. 55). The hybrid response overall, however, was more similar to that of Warimek, since heterosis relative to this parent changed little over the range of densities. On the other hand, heterosis relative to the mid-parent and Halberd was significantly lower at 17.5 plants m^{-2} than at the lowest and highest densities (Fig. 8B, p. 55).

Total weight m^{-2}

The results for total weight were very similar to those for grain weight m^{-2} (Fig. 8C, p. 55).

Heterosis relative to both the mid-parent and Halberd were significantly greater at the lowest and highest densities (Fig. 8D, p. 55). The hybrid response relative to Warimek did not change significantly with density indicating that for this character also, hybrid response was dominated by this parent.

Harvest index

The response of the hybrid for harvest index was unlike that shown by either of the hybrids considered previously, Heron x Strain 52 or Timgalen x Warimek. Halberd x Warimek, while having a lower index than both parents at low density had a significantly higher index at the higher densities (Fig. 8E, p. 55). This occurred despite the fact that the components of harvest index, grain weight m^{-2} and total weight m^{-2}, did not show a significant change in heterosis relative to Warimek.

It should be pointed out that even though the grain yield of the hybrid exceeded the high-parent by more than 20% at five plants m^{-2}, the harvest index of the hybrid was lower than those of both parents at this density. At higher densities, however, a similar ranking of genotypes occurred for grain weight m^{-2} and harvest index.

Table 9: Halberd x Warimek. Analyses of variance of heterosis relative to the high-parent (HP), the mid-parent (MP), Halberd (M1) and Warimek (M2). The values in the table are levels of significance of the heterosis x density interaction.

Char.	HP	MP	M1	M2
Grain weight/m^2	NS	*	*	NS
Total weight/m^2	NS	NS	*	NS
Harvest index	NS	*	*	NS
Height	NS	NS	*	NS
Head length	NS	*	NS	NS
1000 Grain weight	NS	**	*	NS
Grain number/m^2	NS	NS	*	NS
Grain number/head	*	*	**	*
Head number/m^2	NS	NS	*	NS

<u>Height</u>

Again there was evidence for height being greater at the intermediate densities (Fig. 9A, p. 56). Halberd was affected by density to a greater extent than either Warimek or the hybrid. Since the hybrid displayed heterosis relative to the high-parent at all densities, this measure of heterosis as well as heterosis relative to Halberd and the mid-parent changed significantly with density, being greater at the low and high densities (Fig. 9B, p. 56).

The height response of Halberd x Warimek like that of Timgalen x

Figure 8

Halberd x Warimek - Response to density

(A,B)	Grain weight m^{-2}
(C,D)	Total weight m^{-2}
(E,F)	Harvest index
(A,C,E)	Response to density by Halberd (■- - - -■), Warimek (●- - - -●) and Halberd x Warimek (▲——▲)
(B,D,F)	Heterosis relative to the high-parent (▽——▽), mid-parent (△- — -△), Halberd (□) and Warimek (○)

Least significant differences at the 5% level are indicated for heterosis

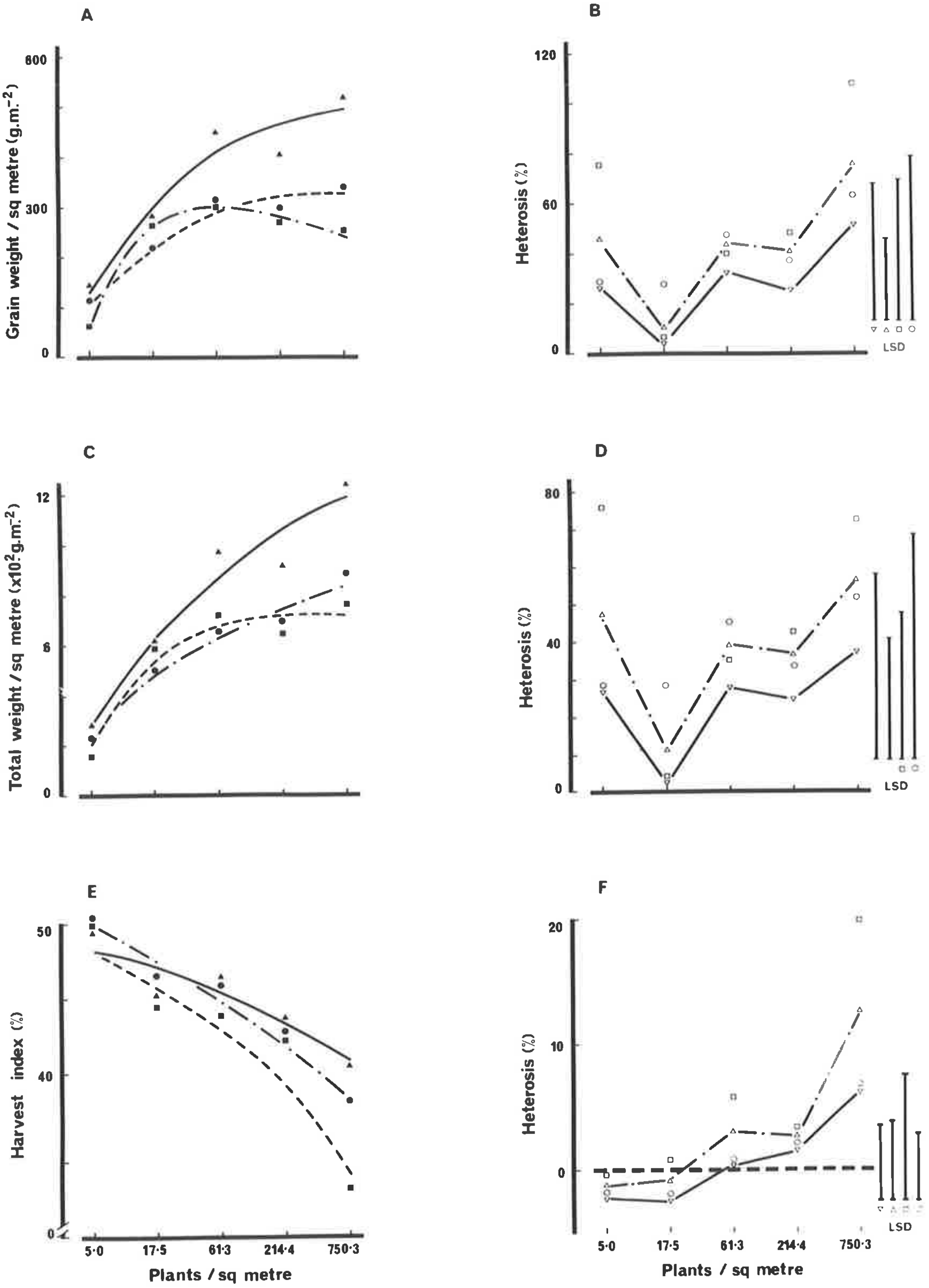

A
Grain weight / sq metre (g.m.$^{-2}$)
600
300
0
B
Heterosis (%)
120
60
0
LSD
C
Total weight / sq metre (x10^{2}g.m.$^{-2}$)
12
6
0
D
Heterosis (%)
80
40
0
LSD
E
Harvest index (%)
50
40
0
F
Heterosis (%)
20
10
0
LSD
5·0
17·5
61·3
214·4
750·3
Plants / sq metre

Figure 9

Halberd x Warimek - Response to density

(A,B)	Height
(C,D)	Head length
(E,F)	Head number m^{-2}
(A,C,E)	Response to density by Halberd (■- - -■), Warimek (●-—-●) and Halberd x Warimek (▲——▲)
(B,D,F)	Heterosis relative to the high-parent (▽——▽), mid-parent (△-—-△), Halberd (□) and Warimek (○)

Least significant differences at the 5% level are indicated for heterosis

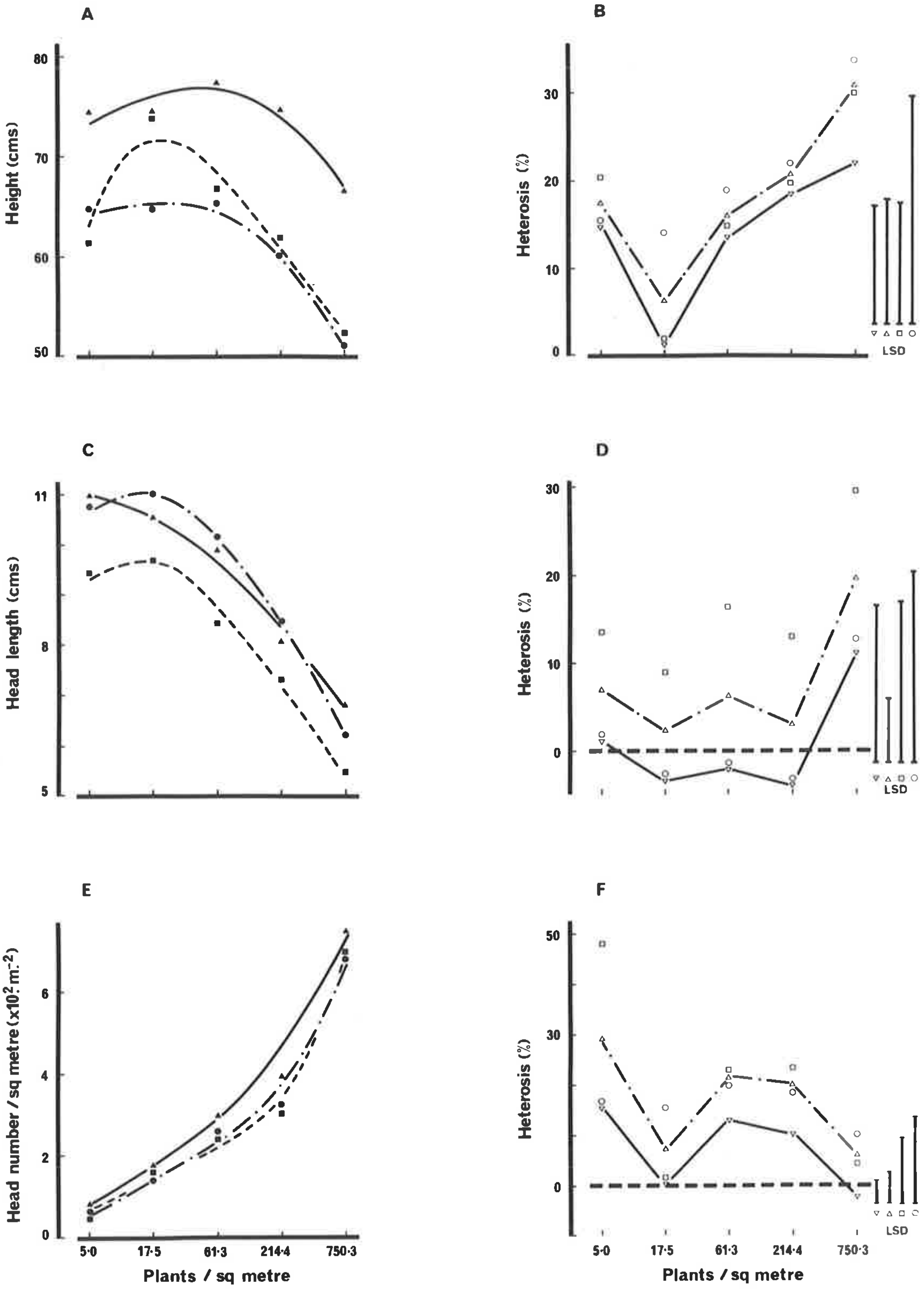
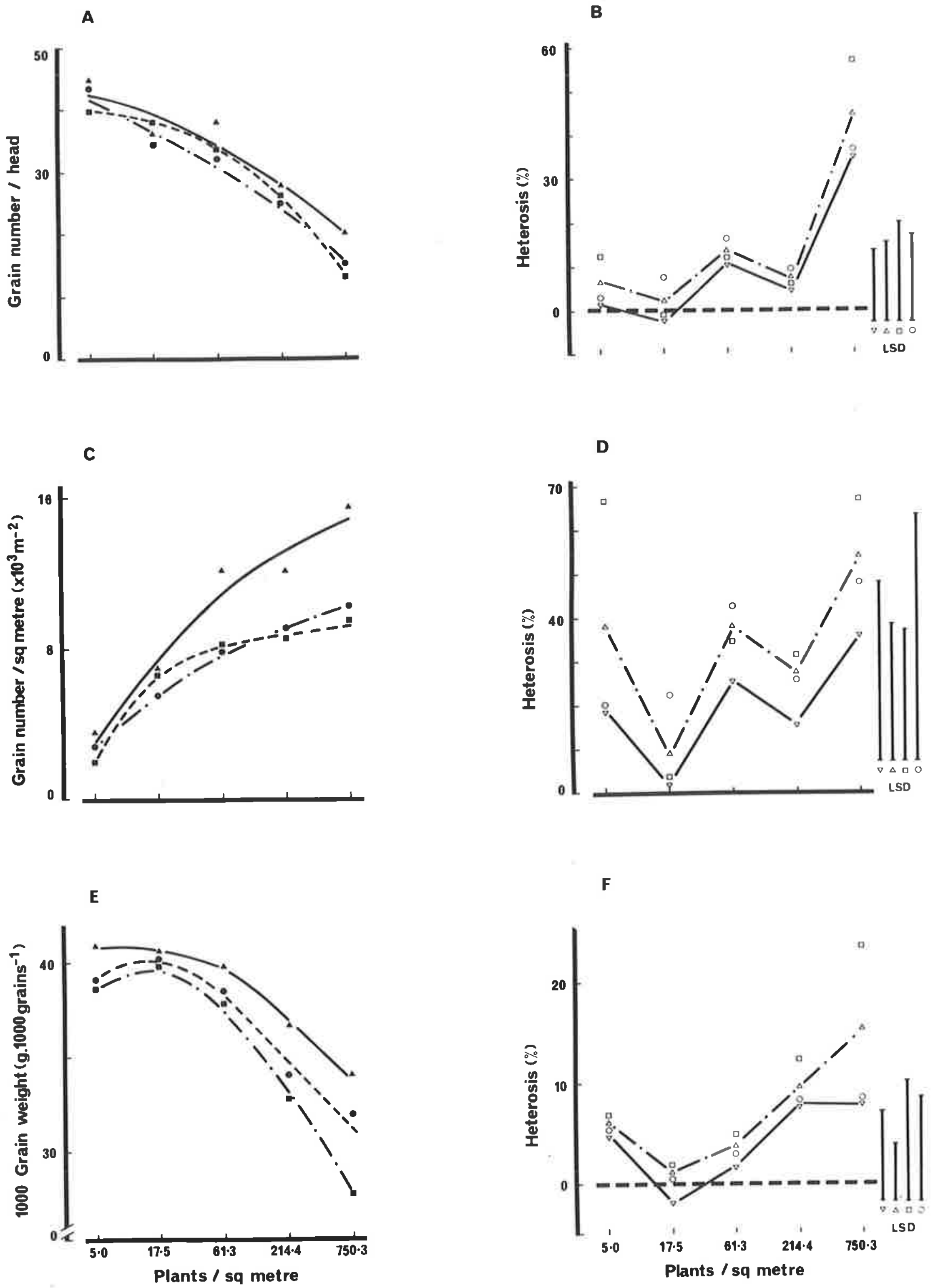

A
Height (cms)
80
70
60
50
B
Heterosis (%)
30
20
10
0
▽ △ □ ○
LSD
C
Head length (cms)
11
8
5
D
Heterosis (%)
30
20
10
0
▽ △ □ ○
LSD
E
Head number / sq metre (x10^2 m^{-2})
6
4
2
0
5·0
17·5
61·3
214·4
750·3
Plants / sq metre
F
Heterosis (%)
50
30
0
▽ △ □ ○
LSD
5·0
17·5
61·3
214·4
750·3
Plants / sq metre

Figure 10

Halberd x Warimek - Response to density

(A,B)	Grain number/head
(C,D)	Grain number m^{-2}
(E,F)	1000 Grain weight
(A,C,E)	Response to density by Halberd (■- - -■), Warimek (●-— -●) and Halberd x Warimek (▲——▲)
(B,D,F)	Heterosis relative to the high-parent (▽——▽), mid-parent (△-—-△), Halberd (□) and Warimek (○)

Least significant differences at the 5% level are indicated for heterosis


A
Grain number / head
50
30
0
B
Heterosis (%)
60
30
0
LSD
C
Grain number / sq metre (x10^{3}m^{-2})
16
8
0
D
Heterosis (%)
70
40
0
LSD
E
1000 Grain weight (g.1000 grains^{-1})
40
30
0
5·0
17·5
61·3
214·4
750·3
Plants / sq metre
F
Heterosis (%)
20
10
0
LSD
5·0
17·5
61·3
214·4
750·3
Plants / sq metre

Warimek was dominantly influenced by Warimek. However, the hybrid was consistently 10 - 15 cms taller than Warimek.

Head length of the primary tiller

The head length response of the hybrid was also similar to Warimek.

On the one hand, heterosis relative to Warimek, the high-parent, did not change significantly with density, while on the other hand, heterosis relative to both Halberd and the mid-parent were found to increase significantly at high density (Fig. 9D, p. 56).

(b) Plant Density Response and Grain Yield Components

The components of yield may be considered as developing in the phases shown below. Tillering by the plant and the development of heads, occurs in the first phase. Secondly, the setting of grain is determined by the result of the first phase and the number of grains set per head. Production of grain weight m^{-2} in the final phase is the result of components involved in the first two phases and the average grain weight (1000 grain weight) developed during the grain-filling period. Such a subdivision of yield components allows an examination of relative plant performance during three periods of crop growth, tillering, anthesis and fertilisation and grain filling.

Phase 1. Head number m^{-2}

x

Phase 2. ↓ Grain number per head
(derived)

Grain number m^{-2}

x

Phase 3. ↓ 1000 grain weight
(derived)

Grain weight m^{-2}

1. Heron x Strain 52

It will be recalled that Heron x Strain 52 was chosen as an example of those hybrids in which heterosis for grain weight occurred but there was no detectable change across density.

The contribution of the components to the grain weight m^{-2} heterosis changed with density (Figs. 3 and 4, pp. 45 and 46, Table 10, p. 59). Heterosis at low density was due mainly to head number. This effect was reduced at higher density where the contribution from grain number per head was more important. Little change was observed in the level of heterosis expressed by 1000 grain weight.

Table 10: Heron x Strain 52. Heterosis relative to the high-parent (HP) and mid-parent (MP) for the grain weight components and grain weight m^{-2}.

HP			Plants m^{-2}		
	5.0	17.5	61.3	214.4	750.3
Head number m^{-2}	27.3	22.1	36.1	30.4	6.3
Grain number /head	-0.4	5.0	4.3	3.8	6.9
1000 Grain weight	2.5	17.2	6.2	5.9	13.9
Grain weight m^{-2}	37.8	53.7	73.6	43.9	42.0
MP					
Head number m^{-2}	42.1	25.3	39.8	41.5	16.7
Grain number /head	10.6	5.6	11.4	8.6	40.7
1000 Grain weight	6.1	21.2	15.5	13.0	17.6
Grain weight m^{-2}	61.9	60.9	81.4	70.3	89.2

2. Timgalen x Warimek

This hybrid did not express heterosis relative to the high-parent for grain weight m^{-2}. It can be seen that this was due to the low expression of grain number per head and the failure of the other components to compensate (Figs. 6 and 7, pp. 50 and 51, Table 11, p. 60).

Table 11: Timgalen x Warimek. Heterosis relative to the high-parent (HP) and mid-parent (MP) for the grain weight components and grain weight m^{-2}.

	Plants m^{-2}				
HP	5.0	17.5	61.3	214.4	750.3
Head number m^{-2}	11.5	7.0	7.3	10.7	5.4
Grain number /head	-22.6	-23.0	-30.5	-34.6	-27.2
1000 Grain weight	7.8	3.9	12.0	8.6	11.1
Grain weight m^{-2}	-2.2	-1.9	-9.9	-16.0	-12.0
MP					
Head number m^{-2}	14.2	8.6	11.8	23.1	6.8
Grain number /head	-15.3	-10.0	-22.1	-21.4	-12.2
1000 Grain weight	8.7	9.4	13.2	13.1	14.5
Grain weight m^{-2}	5.4	8.1	-0.7	6.3	6.9

3. Halberd x Warimek

The expression of grain yield components developed by this hybrid changed with density in a similar manner to those of Heron x Strain 52. Heterosis for head number declined while grain number per head increased at high density. However, heterosis expressed by 1000 grain weight also increased with density (Figs. 9 and 10, pp. 56 and 57, Table 12, p. 61).

Table 12: Halberd x Warimek. Heterosis relative to the high-parent (HP) and mid-parent (MP) for the grain weight components and grain weight m^{-2}.

	Plants m^{-2}				
HP	5.0	17.5	61.3	214.4	750.3
Head number m^{-2}	15.5	0.1	13.2	10.1	-2.4
Grain number /head	2.4	-1.6	11.4	6.8	35.1
1000 Grain weight	5.2	-2.1	2.9	8.0	8.1
Grain weight m^{-2}	24.7	0.6	32.3	26.1	51.5
MP					
Head number m^{-2}	29.7	7.0	21.6	20.3	6.8
Grain number /head	7.2	3.0	13.7	7.5	45.2
1000 Grain weight	5.4	1.1	4.0	9.9	15.2
Grain weight m^{-2}	45.7	10.6	44.0	40.5	76.2

(c) Macro-environmental Variability

Macro-environmental variability has been calculated as the variance of the means at the five plant densities. The variances for Heron x Strain 52, Timgalen x Warimek and Halberd x Warimek are presented in Tables 13 to 15.

Both hybrids which expressed heterosis relative to the high-parent for grain weight m^{-2}, Heron x Strain 52 and Halberd x Warimek displayed no tendency to be more stable than their parents over density. In fact one of the hybrids, Heron x Strain 52 was significantly more variable than its parents (Table 13, p. 63). This result was to be expected considering that Heron x Strain 52 and Halberd x Warimek were more responsive than their parents in the high and low density ranges respectively (Figs.2 and 8, pp. 44 and 55).

The variance expressed by Timgalen x Warimek for height was significantly lower than that obtained for the parents since the height of the hybrid was not as greatly affected by density in either the low or high density ranges (Table 14, p. 64, Fig. 6, p. 50). This situation occurred even though the hybrid was taller than both parents at four of the five densities. The heights of Heron x Strain 52 and Halberd x Warimek also exhibited heterosis relative to their high-parents at all densities and had variances lower than one and both parents respectively (Figs. 3 and 9, pp. 45 and 57).

It may be concluded from these results that there was no evidence from this density experiment that the hybrids were consistently less variable or more stable than their parents across a range of densities.

Table 13: Heron x Strain 52 - Macro-environmental variability measured as variances over density, levels of significance of differences between genotypes and L.S.D.'s at the 5% level of significance.

Char.	Heron	Strain 52	Heron x Strain 52	Sig. (%)	L.S.D. 5%
Grain weight/m^2	5785	8677	20316	*	4714
Total weight/m^2	38839	87749	146795	NS	92289
Harvest index	170.37	68.84	51.52	NS	178.58
Height	77.99	26.58	44.55	NS	161.65
Head length	5.584	2.811	3.260	NS	6.619
Head number/m^2	49379	72375	77470	NS	31460
Grain number/head	113.52	100.39	105.48	NS	158.02
Grain number/m^2	4.23E+6[1]	14.85E+6	19.39E+6	NS	26.87E+6
1000 Grain weight	42.55	31.56	38.42	NS	67.20

[1] E+6 = x 10^6

Table 14: Timgalen x Warimek - Macro-environmental variability measured as variances over density, levels of significance of differences between genotypes and L.S.D.'s at the 5% level of significance.

Char.	Timgalen	Warimek	Timgalen x Warimek	Sig. (%)	L.S.D. 5%
Grain weight/m^2	3089	11603	7214	NS	25910
Total weight/m^2	44438	83026	91929	NS	82770
Harvest index	68.61	40.03	46.78	NS	38.27
Height	31.879	25.018	9.112	*	10.08
Head length	4.128	4.372	3.056	NS	3.736
Head number/m^2	54370	65545	70923	NS	26466
Grain number/head	78.31	92.46	65.41	NS	76.80
Grain number/m^2	4.55E+6[1]	13.68E+6	7.35E+6	NS	10.71E+6
1000 Grain weight	42.10	30.35	25.14	NS	27.79

[1] E+6 = x10^6

Table 15: Halberd x Warimek - Macro-environmental variability measured as variances over density, levels of significance of differences between genotypes and L.S.D.'s at the 5% level of significance.

Char.	Halberd	Warimek	Halberd x Warimek	Sig. (%)	L.S.D. 5%
Grain weight/m^2	9093	8454	23145	NS	23890
Total weight/m^2	61732	61940	145475	NS	155146
Harvest index	57.85	53.22	18.05	NS	112.69
Height	72.99	49.30	19.06	NS	74.34
Head length	3.695	4.272	3.159	NS	5.201
Head number/m^2	62436	63418	66702	NS	93287
Grain number/head	36.09	28.95	30.10	NS	31.44
Grain number/m^2	8.87E+6[1]	8.91E+6	20.88E+6	NS	20.18E+6
1000 Grain weight	32.71	21.84	10.94	NS	20.05

[1] E+6 = x 10^6

(d) Micro-environmental Variability

The form of presentation of results so far has been to plot a character, such as grain weight m^{-2}, on the y-axis and density of plants on the x-axis of a graph. This presentation was adopted as being customary for studies of the effect of density on plant performance.

A different presentation will be adopted when considering micro-environmental variability to enable comment on some recent concepts concerned with this form of variability. Knight (1973) has suggested that plant-to-plant variability will be greater in environmental conditions removed from the optimum and be least at the optimum. When there is a marked change in response to the environment and a steep slope on the response curve, the micro-environmental variability from plant-to-plant will be greater than at the optimum.

Graphical presentation of this concept involves values on the x-axis rising from sub-optimal to optimal to super-optimal conditions if these are feasible. With density being varied this would be analogous to a small area per plant rising to a large area per plant. Values of area per plant to be used in this alternative form of presentation are given in Table 16.

Table 16: Plant densities and corresponding areas per plant studied in Experiment 1.

Plant density (plants m^{-2})	Area per plant (sq cm)
5.0	2000
17.5	571
61.3	163
214.4	47
750.3	13

The magnitude of micro-environmental variation is often estimated as a variance or standard deviation (S.D.). Presented in Figs. 11 to 13 respectively is the relation between area per plant and grain weight per plant, area per plant and height, the mean slopes of the response curves between successive values of area per plant and the corresponding S.D.'s for the three hybrid combinations.

The S.D.'s for grain weight per plant were not smaller in the optimal conditions of large area per plant as a measure of micro-environmental variation was expected to be (Figs. 11A, 12A and 13A). This is due to the fact that tillering is a multiplicative process that affects the number of heads on a plant and also grain weight. The present result was a manifestation of the common finding that the S.D. increases with the mean.

This same feature may be observed when comparing the S.D.'s for the hybrids Heron x Strain 52 and Timgalen x Warimek with their parents. Larger S.D.'s were obtained at four of the five densities for Heron x Strain 52 than for both parents. This hybrid expressed heterosis relative to the high-parent at all densities. Timgalen x Warimek had an intermediate grain weight and intermediate or low S.D.'s. There is no evidence in this data to suggest that a hybrid is less variable than its parents.

On the other hand, examination of the S.D.'s of Halberd x Warimek, a hybrid which also expressed heterosis relative to the high-parent at all densities, reveals that the hybrid had a lower S.D. than both parents at the four lower values of area per plant (Fig. 13A). The hybrid S.D. was in fact relatively lower than parental S.D.'s in the lower areas.

In contrast to grain weight, height is not the result of a multiplicative growth process. The parental S.D.'s for height were large in the sub-optimal environments of small area per plant where the

Figure 11

Heron x Strain 52 - Micro-environmental variability

(A,B,C)	Grain weight/plant
(D,E,F)	Height
(A,D)	Standard deviations
(B,E)	Response to density and mean slope between densities
(C,F)	Coefficients of variation
For:	Heron (■— — —■), (□— — —□)
	Strain 52 (●- — -●), (○- — -○)
	Heron x Strain 52 (▲ —— ▲), (△ —— △)
	Open symbols in (C) represent C.V.'s calculated excluding plants which failed to produce grain

Least significant differences at the 5% level are indicated for C.V.'s

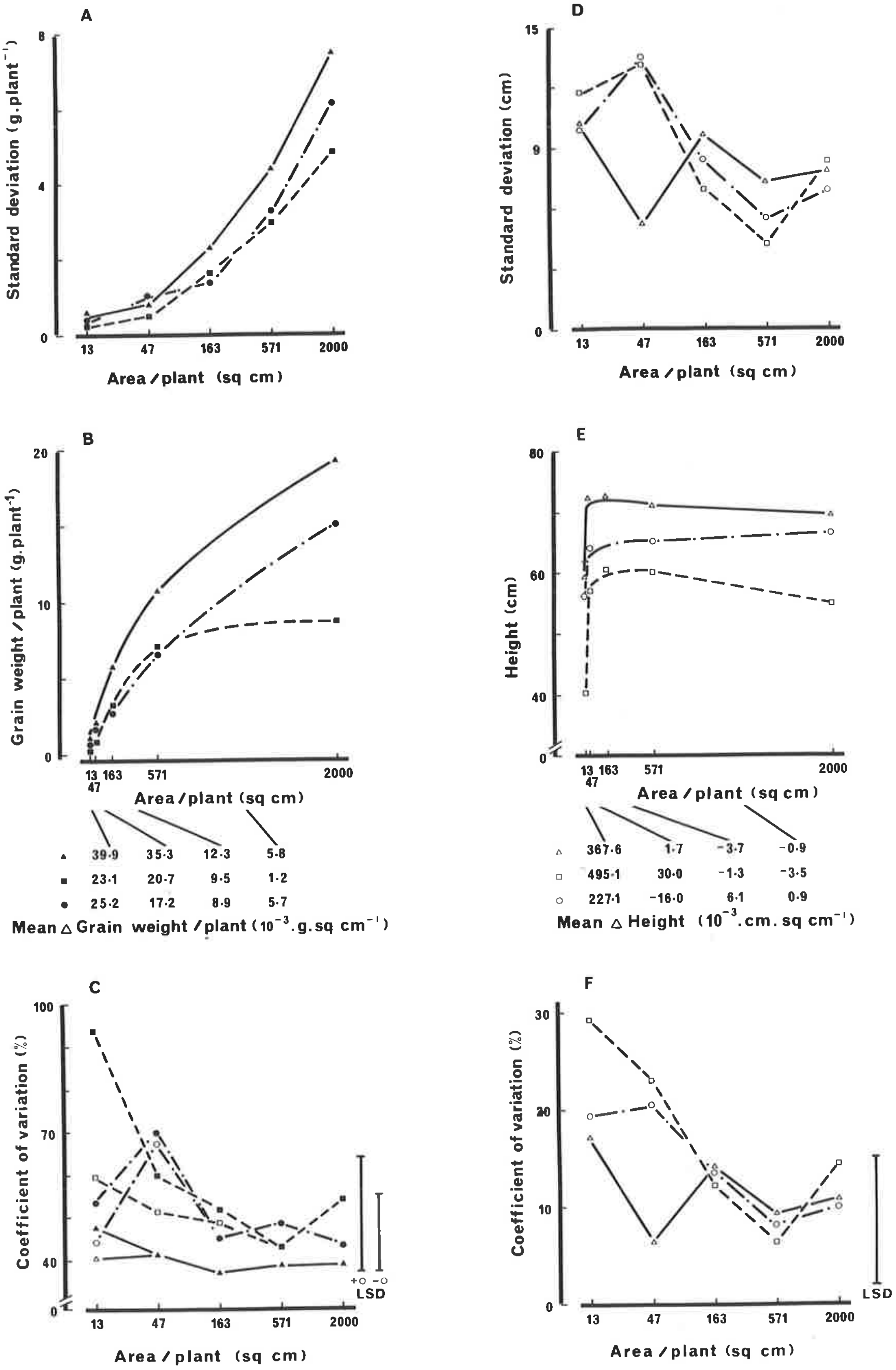

A
Standard deviation (g.plant^{-1})
0
4
8
13
47
163
571
2000
Area / plant (sq cm)
B
Grain weight / plant (g.plant^{-1})
0
10
20
13 163
47
571
2000
Area / plant (sq cm)
▲ 39·9 35·3 12·3 5·8
■ 23·1 20·7 9·5 1·2
● 25·2 17·2 8·9 5·7
Mean △ Grain weight / plant (10^{-3}.g.sq cm^{-1})
C
Coefficient of variation (%)
0
40
70
100
13
47
163
571
2000
+○ −○
LSD
Area / plant (sq cm)
D
Standard deviation (cm)
0
9
15
13
47
163
571
2000
Area / plant (sq cm)
E
Height (cm)
0
40
60
80
13 163
47
571
2000
Area / plant (sq cm)
△ 367·6 1·7 −3·7 −0·9
□ 495·1 30·0 −1·3 −3·5
○ 227·1 −16·0 6·1 0·9
Mean △ Height (10^{-3}.cm. sq cm^{-1})
F
Coefficient of variation (%)
0
10
20
30
13
47
163
571
2000
LSD
Area / plant (sq cm)

Figure 12

Timgalen x Warimek - Micro-environmental variability

(A,B,C)	Grain weight/plant
(D,E,F)	Height
(A,D)	Standard deviations
(B,E)	Response to density and mean slope between densities
(C,F)	Coefficients of variation
For:	Timgalen (■– – – ■), (□– – –□) Warimek (●- — -●), (○- — -○) Timgalen x Warimek (▲ —— ▲), (△ —— △) Open symbols in (C) represent C.V.'s calculated excluding plants which failed to produce grain

Least significant differences at the 5% level are indicated for C.V.'s

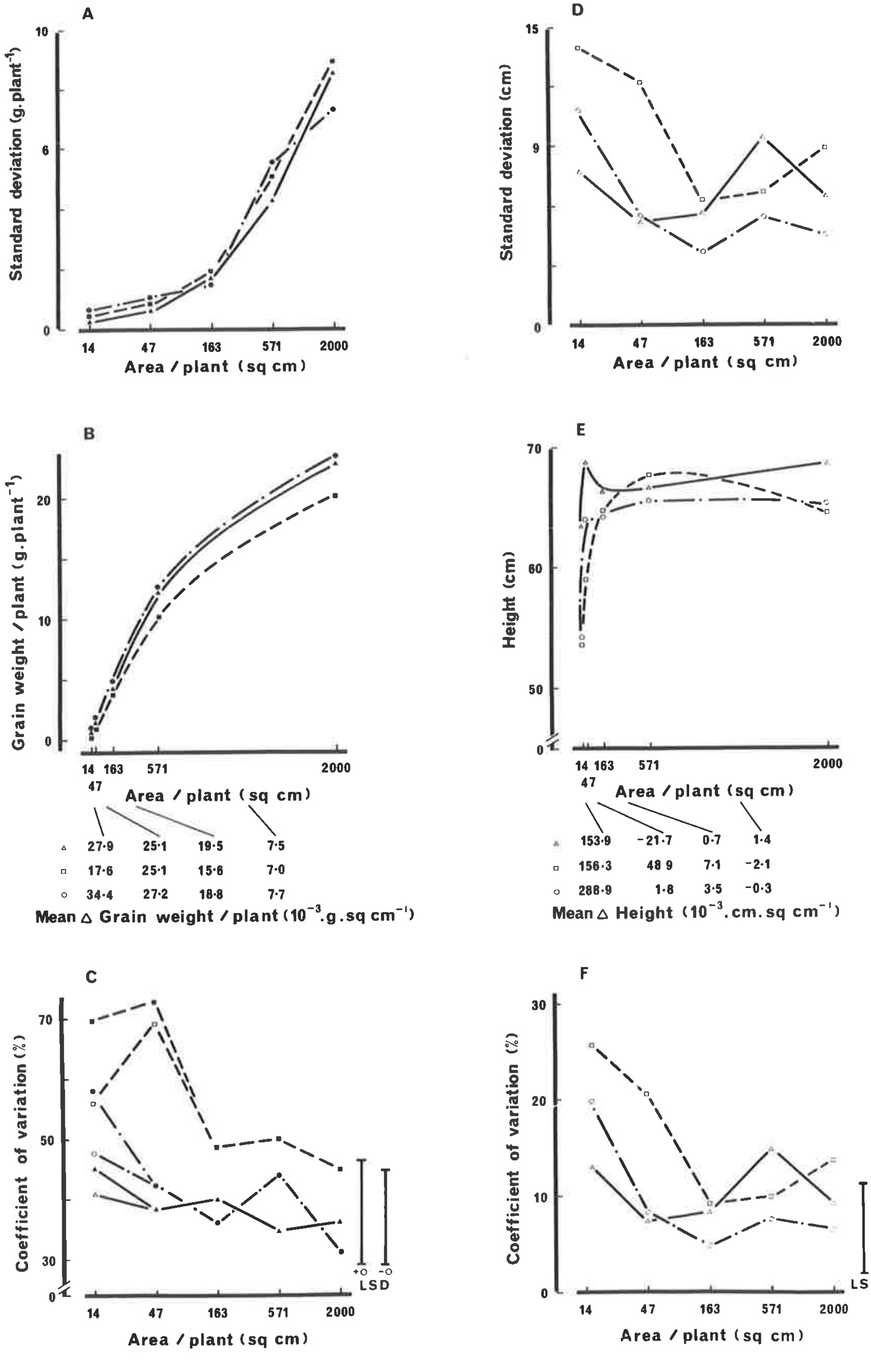
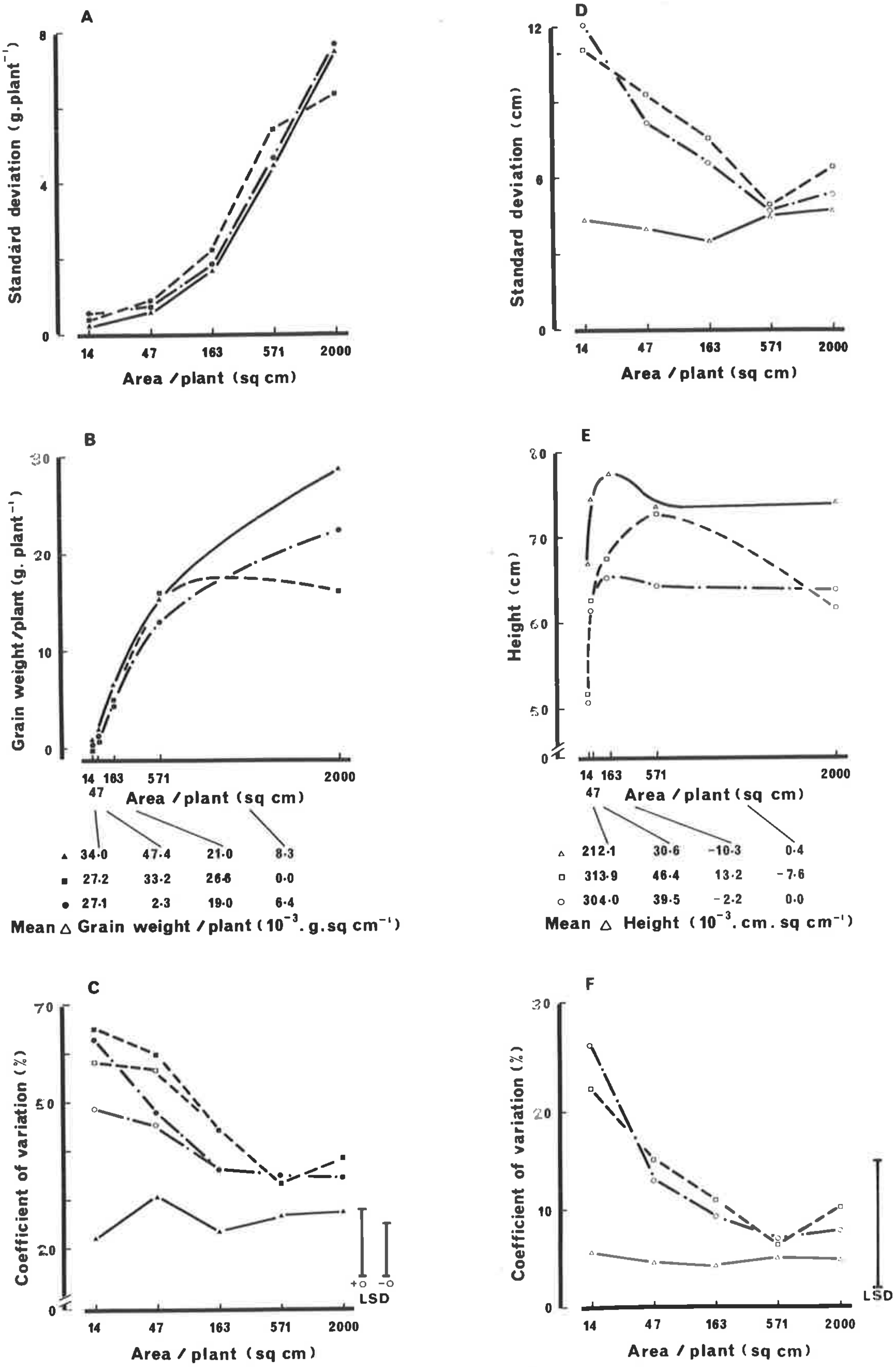

A
Standard deviation (g.plant^{-1})
10
6
0
14
47
163
571
2000
Area / plant (sq cm)
D
Standard deviation (cm)
15
9
0
14
47
163
571
2000
Area / plant (sq cm)
B
Grain weight / plant (g.plant^{-1})
20
10
0
14 163 571 2000
47
Area / plant (sq cm)
△ 27·9 25·1 19·5 7·5
□ 17·6 25·1 15·6 7·0
○ 34·4 27·2 18·8 7·7
Mean △ Grain weight / plant (10^{-3}.g.sq cm^{-1})
E
Height (cm)
70
60
50
0
14 163 571 2000
47
Area / plant (sq cm)
△ 153·9 −21·7 0·7 1·4
□ 156·3 48 9 7·1 −2·1
○ 288·9 1·8 3·5 −0·3
Mean △ Height (10^{-3}.cm.sq cm^{-1})
C
Coefficient of variation (%)
70
50
30
0
14
47
163
571
2000
Area / plant (sq cm)
+O
-O
LSD
F
Coefficient of variation (%)
30
20
10
0
14
47
163
571
2000
Area / plant (sq cm)
LSD

Figure 13

Halberd x Warimek - Micro-environmental variability

(A,B,C)	Grain weight/plant
(D,E,F)	Height
(A,D)	Standard deviations
(B,E)	Response to density and mean slope between densities
(C,F)	Coefficients of variation
For:	Halberd (■– – – –■), (□– – – –□) Warimek (●- —- ●), (○- — -○) Halberd x Warimek (▲ —— ▲), (△ —— △) Open symbols in (C) represent C.V.'s calculated excluding plants which failed to produce grain

Least significant differences at the 5% level are indicated for C.V.'s


A
Standard deviation (g.plant⁻¹)
0
4
8
14
47
163
571
2000
Area / plant (sq cm)
D
Standard deviation (cm)
0
6
12
14
47
163
571
2000
Area / plant (sq cm)
B
Grain weight / plant (g. plant⁻¹)
0
10
20
30
14
47
163
571
2000
Area / plant (sq cm)
▲ 34·0 47·4 21·0 8·3
■ 27·2 33·2 26·6 0·0
● 27·1 2·3 19·0 6·4
Mean △ Grain weight / plant (10⁻³. g.sq cm⁻¹)
E
Height (cm)
0
50
60
70
80
14
47
163
571
2000
Area / plant (sq cm)
△ 212·1 30·6 -10·3 0·4
□ 313·9 46·4 13·2 -7·6
○ 304·0 39·5 -2·2 0·0
Mean △ Height (10⁻³. cm. sq cm⁻¹)
C
Coefficient of variation (%)
0
20
50
70
14
47
163
571
2000
Area / plant (sq cm)
+○
-○
LSD
F
Coefficient of variation (%)
0
10
20
30
14
47
163
571
2000
Area / plant (sq cm)
LSD

slopes of the response curves were greater (Figs. 11 to 13). The S.D.'s expressed by the hybrid genotypes Heron x Strain 52 and Timgalen x Warimek showed a tendency to be lower than their parents at small areas per plant although they were not significantly lower than one or both parents (Figs. 11D and 12D, pp. 68 and 69). On the other hand, Halberd x Warimek was significantly less variable than both parents at small area per plant and also less responsive to changes in area per plant (Figs. 13D and 13E, p. 70).

Because means and S.D.'s for grain weight were positively correlated, it is not possible to make an unconfounded interpretation of micro-environmental variation based on S.D. To take account of the association and to make meaningful comparisons between genotypes and densities, the coefficient of variation (C.V.) has been used (Figs. 11, 12, 13).

In general there was a fall in C.V. with increasing area per plant, the parents showing a greater fall than the hybrids. The fall in two of the hybrids Heron x Strain 52 and Halberd x Warimek was negligible. The lower variability of the hybrids relative to their parents for grain weight at small area per plant was not a consequence of lower response to changes in area per plant. In fact both hybrids were twice as responsive to changes in area per plant in this range.

It is important to note that this lower variability relative to Heron (Fig. 11C, p. 68), Halberd and Warimek (Fig. 13C, p. 70) was accompanied by greater heterosis and therefore larger mean values relative to these parents. The lower variability relative to Halberd and Warimek, however, cannot be attributed to the larger mean of the hybrid since the S.D. of the hybrid was also lower. Similar increases in heterosis at high area per plant were not associated with a reduction in the relative stability of the hybrids. Exclusion from the calculation of C.V.'s of plants which failed to produce any grain did not alter the interpretation of the results.

The hybrid Timgalen x Warimek also showed a tendency to be less variable than its parents but in this instance it was not significantly less variable than Warimek (Fig. 12C, p. 69). Both the S.D. and mean of the hybrid were equivalent to those of Warimek. On the other hand, since the hybrid expressed heterosis relative to Timgalen and had a lower S.D., the C.V. of the hybrid was significantly lower than this parent. This situation occurred despite the hybrid being more responsive than this parent to changes in area per plant.

A similar result occurred for height although no increase in the C.V. of the hybrid was observed at low area per plant.

3.1.3. Discussion

A general conclusion that might be drawn from the experiment was that heterosis for grain yield did not change significantly with density. Only two of the eight hybrids studied displayed significant differences in heterosis across density. Among the remaining hybrids those expressing high (30 - 50%) and no heterosis (-10 - 0%) relative to the high-parent all failed to show significant differences between densities.

This conclusion agrees with the results based on data provided by Briggle et al. (1967a,b) and the conclusions of a number of workers including Fonseca and Patterson (1968) and Zeven (1972).

Differences between hybrid and parental responses were detected in most hybrid combinations although they were not significant. It is believed that they would have been shown to be significant if the response curves could have been delimited more accurately. Experimental errors were large and either more replication or more density levels are required when attempting to establish differences between curves. A similar comment could be made about the studies conducted by Clement (1972) and Zeven (1972).

A number of features of the field environment experienced in this study have important consequences for the interpretation of the results. The wide range of densities from one thirty sixth to four times the commercial density was used to obtain responses in grain weight m^{-2} increasing to an optimum and declining thereafter. However, for most genotypes the grain weight m^{-2} was greatest at the highest density.

The absence of a fall at high density may have been due to the planting configuration and the occurrence of effective rainfall. The square planting may have led to less interplant competition than normally occurs between plants in rows with a rectangular spacing.

Further, the crop was sown relatively late in June and did not develop profusely before hot dry conditions prevailed. During grain-filling plants at high density commonly comprised a single stem and head, the leaves having died before anthesis. Competition created at high density may therefore have been less than occurs in a vigorous crop. However, sufficient photosynthate was produced by the stems and heads to result in high grain weight m^{-2}.

It has been suggested that high levels of heterosis are expressed only by hybrids between low yielding parents (Williams and Gilbert, 1960). The results of this experiment do not support this suggestion as the hybrid Halberd x Warimek expressed high levels of heterosis up to 50% relative to the highest parent in the experiment. These occurred at densities where the yields of the parents were high ($\sim$ 5.0 tonnes/ha) not only in relation to other varieties in Experiment 1 but also to commercial crops in the same area (G.J. Hollamby, pers. comm.).

Total weight m^{-2}, unlike grain weight m^{-2} is expected to show an asymptotic relationship with density (Holliday, 1960a,b; Donald, 1963). However, in the same manner that the grain weight m^{-2} of many genotypes failed to reach an optimum, the total weight m^{-2} of the same genotypes did not reach an asymptote.

The harvest index of all genotypes declined with increasing density and the proportion of resources available to the crop during the grain-filling period must have declined with density. Although Heron x Strain 52 and Halberd x Warimek displayed heterosis for grain and total weight at all densities, the harvest indices of these hybrids exceeded both respective parents only at high density.

Both Timgalen and the hybrid Timgalen x Warimek tended to have a low grain number per head. For this character the hybrid was not intermediate or superior to its parents but similar to the low parent. There was no obvious intrinsic aspect of the experiment to account for this as the hybrid reached anthesis at a similar time to most other genotypes and was therefore not subject to more extreme environmental conditions at this stage. Further, heterosis was observed for both other yield components, head number m^{-2} and 1000 grain weight.

As has been shown, Heron x Strain 52 and Halberd x Warimek expressed heterosis for height at all densities and for head length at the highest density. These may have been important factors contributing to the occurrence of heterosis for grain weight at the higher densities. Under these conditions most leaf tissue had died by anthesis leaving the upper stem and head to provide photosynthate during the grain-filling period.

There was less plant-to-plant variation when the plants were spaced out than when in high density. This was evident for the measure of C.V. A similar result has been previously reported by Stern (1965) for Subterranean clover. At high density a pattern of dominance and suppression is believed to have developed despite the efforts taken to develop uniform plant communities by selecting seeds of uniform size and precision square-planting.

Since Heron x Strain 52 and Halberd x Warimek had higher means than their parents at all densities (areas per plant) it would be expected that more intense competition and consequently stronger patterns of dominance and suppression should develop in plots of these hybrids, particularly at high density. However, the hybrids were less variable than their respective parents in terms of both grain weight and height in the sub-optimal conditions of low area per plant but had similar variabilities in the optimal conditions of high area per plant. This indicates that the hybrids were less susceptible to the development of dominance and suppression relationships under conditions of high interplant competition.

The relationship between hybrid and parental responses was analysed using the multiple regression analysis developed by Knight (1971). However, significant coefficients were not obtained because of the limited number of densities observed.

Study of the responses of parents and their hybrids to plant density has provided a number of useful insights into the occurrence of heterosis. However, variation in density involves non-independent variation from optimal (low density) to sub-optimal (high density) levels of a complex of environmental factors including light, water and nutrients.

A more meaningful analysis of the interaction of heterosis and environment should be achieved by studying responses to individual independent factors of the environment. In this manner wide ranges of each factor varying from sub- to super-optimal levels may be sampled to identify the relationships between hybrid and parental response.

3.2.0. Experiment 2

3.2.1. Materials and Methods

(a) Genotypes

The hybrid Heron x Strain 52 was chosen for this glasshouse experiment as it had exhibited high levels of hybrid vigour for grain yield at all densities in Experiment 1 in the field. Excessive differences in plant height had not occurred thus ensuring that severe competition would not occur between adjacent pots in the glasshouse. The pedigrees of these genotypes are set out in Section 3.1.1a.

(b) Soil

To obtain responses to applied N and P in the sub- and super-optimal ranges, a soil was required which was initially low in available N and P and with a low P sorption capacity.

Virgin and low fertility soils were sampled in the Palmer, Roseworthy and Reeves Plains areas. A sandy red-brown earth was chosen from Mr. K. Schackley's property at Reeves Plains, S.A. N content was analysed at 3 ppm, the amount required for full seasonal growth of a wheat crop being estimated at 25 ppm (A. Alston, pers. comm.). Available P was found to be 3 ppm with a maximum sorption capacity of 30 ppm.

Nitrogen analysis was performed according to the method of McKenzie and Wallace (1964). Phosphorus determination and sorption capacity were carried out using the methods of Crop Nutrition Group (1970) and Ozanne and Shaw (1967).

(c) Fertilisers

Nitrogen fertiliser as ammonium nitrate (NH_4NO_3, laboratory grade) was applied at eight levels (Table 16, p. 78).

Table 16: Nitrogen fertiliser levels

N level	kg N/ha	ppm N	Total application (NH_4NO_3) g/pot
1	20	4.1	0.17
2	40	8.5	0.33
3	80	16.7	0.66
4	160	33.6	1.31
5	320	66.9	2.61
6	640	134.0	5.23
7	1280	267.8	10.45
8	2560	535.4	20.89

Half the N was applied initially as a nutrient solution when the soil was mixed. The remaining N was applied as a nutrient solution to the pots one month after sowing in order to avoid deaths due to toxicity in the emerging seedlings.

Phosphorus fertiliser as calcium tetrahydrogen di-ortho phosphate ($CaH_2(PO_4)_2 \cdot H_2O$, laboratory grade) was also applied at eight levels (Table 17, p. 78). Being in dry talc form it was mixed with the soil before beginning the experiment.

Table 17: Phosphorus Fertiliser Levels

P level	kg P/ha	ppm P	$CaH_2(PO_4)_2 \cdot H_2O$ g/pot
1	10	2.14	0.10
2	20	4.28	0.20
3	40	8.34	0.39
4	80	16.69	0.78
5	160	33.37	1.56
6	320	66.95	3.13
7	640	133.91	6.26
8	1280	267.69	12.51

Potassium sulphate (K_2SO_4, laboratory grade) at a rate of 50 kg K/ha (0.27 g K_2SO_4/pot) and micronutrients at rates indicated in Table 18 were applied to all pots.

Table 18: Basal Rates of Micronutrients

Micronutrient	Rate (g/pot)
$MnSC_4 \cdot H_2O$	0.04515
H_3BO_3	0.01489
$ZnSO_4 \cdot 7H_2O$	0.02978
$CuSO_4 \cdot 5H_2O$	0.00075
$Na_2MoO_4 \cdot 2H_2O$	0.03723

(d) Soil and pot preparation

The soil was screened through a half-inch sieve to remove stones and vegetable matter. The fertilisers were mixed with the soil using a concrete mixer in three-pot batches to allow allocation of a pot to each genotype within a replication from each batch. Nitrogen and potassium were added as solutions and phosphorus as a dry talc. 11.5 kg of dry soil was packed into each pot (17.5 cm dia. x 38.0 cm height) which had been lined with a plastic bag.

Soil samples submitted for pathogen analysis revealed a moderate nematode infestation. The pots were fumigated with Nemagon 90 (R) (active constituents: 1,2 dibromo-3-chlorpropane (DBCP) 85% wt./vol.) at the recommended rate of five kg/ha, the fumigant being released from the soil two days before sowing.

(R) Registered trade name, Shell Chemical (Aust.) Pty. Ltd.

(e) Experimental design and glasshouse layout

The experimental design was a complete factorial with two replications, eight levels of N, eight levels of P and three genotypes, Heron, Strain 52 and their F_1. The 64 N-P fertiliser combinations were randomly allocated within a replication. The three genotypes were distributed randomly to one of the three contiguous pots of each N-P combination. The pots were placed adjacent to one another in three double offset rows. A single pair of guard pots were located at both ends of each double row.

(f) Glasshouse operations

The experiment was sown on 12 and 13 July, 1973, all seeds being pregerminated in petri dishes at 21°C. Five seeds were planted in each pot, one in the centre and four surrounding in a square pattern. If a seed failed to germinate, its position was occupied with a transplant of the same genotype grown in unfertilised soil.

One metre dowels were placed in the pots to carry a clip-on wire loop (17.5 cm dia.) which supported the plants and prevented lodging.

The centre plant in every pot was removed at one month after sowing for determination of N and P content. However, the results of these analyses were not of direct relevance to the major aspects of this study and are not presented in this thesis. At the same time 600 g of washed half inch gravel was applied as a mulch to reduce evaporation and prevent disturbance of the soil surface during watering. A 17 cm sisalation shade was placed around the rim of all pots.

Water content in the soil was monitored by weighing the pots and was maintained in the range 8% (v/v) to 15% (15% is field capacity). Water consumption was initially measured three weeks after sowing and weekly thereafter for the remainder of the experiment. The water applied was filtered rain water. Figure 14 shows the layout of pots within the glasshouse and the method of watering.

Heading and anthesis dates were recorded on every head in the experiment. Harvesting of the pots began on 29 November, 1973.

Figure 14

General view of glasshouse layout and watering method

(g) Characters measured

The following data were recorded on all plants.

(i)	Heading Date	(all heads)
(ii)	Anthesis Date	(" ")
(iii)	Head Length	(" ")
(iv)	Total Spikelet Number	(" ")
(v)	Sterile Spikelet Number	(" ")
(vi)	Maximum Grain Number per Spikelet	(" ")
(vii)	Height *	
(viii)	Total Weight	(per plant)
(ix)	Grain Weight	(all heads)
(x)	Grain Number	(" ")

* Height was measured from ground level to the top of the glumes on one tiller only per plant.

(h) Derived characters

Derived characters were calculated as follows:

1) Spikelet number per head

= Spikelet number per plant/Head number per plant

2) Grain number per spikelet

= Grain number per plant/Spikelet number per plant

3) 1000 Grain weight

= (Grain weight per plant/Grain number per plant) x 1000

4) Harvest index

= (Grain weight per plant/Total weight per plant) x 100%

(i) Measures of heterosis

The measures of heterosis were the same as those employed in Experiment 1. They were heterosis relative to the high-parent (HP), mid-parent (MP), parent one (M1) (Heron) and parent two (M2) (Strain 52) and have been described in Section 3.1.1.

(j) Statistical methods

The relationship between parental and hybrid performance has been examined using a multiple regression analysis.

The regression was

$$y_{12} = a + b_1P_1 + b_2P_2$$

where:

y_{12}	hybrid value
a	constant
b_1	Heron coefficient
P_1	Heron value
b_2	Strain 52 coefficient
P_2	Strain 52 value

The calculations for this procedure were carried out using Statscript (Lamacraft, 1973).

3.2.2. Results

Experiment 2 was designed to study genotypic interactions with N and P. Results of anaylses of individual genotypes are given in Table ✓ 19 in which grain yield and plant size characters are displayed first, followed by the components of yield. No response to P was observed. The few significant P effects, and the N x P interactions, present in Table 19 are attributed to chance. Further analyses utilised the P treatments as replicates.

The absence of P deficiency symptoms in the low P treatments is believed to have been due to the Nemagon 90 (R) fumigation treatment destroying soil micro-organisms and producing a small pool of available N and P. Such an increase in available N was insufficient to alleviate the sub-optimal N response, but the increase in available P was adequate to eliminate P deficiency symptoms.

The failure to obtain P toxicity may have been due to inadequate levels of applied P. From theoretical calculations involving the P sorption capacity of the soil, 30 ppm, and the ability of wheat plants to withstand high levels of available P, the two highest rates of P application were considered sufficient to induce P toxicity symptoms (Table 17, p. 78). This was not the case and in further trails ✓ following this experiment it was found that much higher levels of P were required to induce a toxic response (Table 25, p. 111).

(a) Nitrogen Response and Heterosis

The design of the experiment was successful in obtaining sub-optimal, optimal and super-optimal responses to N. Figure 15 indicates that all three ranges were sampled; an optimum in terms of grain and total weight being achieved at 1280 kg N/ha. N responses at heading for Heron, Heron x Strain 52 and Strain 52 are also shown in Figure 16.

Table 19: Analyses of variance for characters measured on Heron, Strain 52 and their F_1.

Heron			Strain 52			F_1		
N	P	N x P	N	P	N x P	N	P	N x P
Grain weight per plant								
***	NS	NS	***	NS	NS	***	NS	NS
Total weight per plant								
***	*	NS	***	NS	NS	***	NS	NS
Harvest index								
***	NS	NS	***	NS	NS	***	NS	NS
Height								
***	NS	NS	***	NS	NS	***	NS	NS
Head length								
***	NS	NS	***	NS	NS	***	NS	NS
Head number per plant								
***	NS	NS	***	**	NS	***	**	NS
Spikelet Number per head								
***	NS	NS	***	NS	NS	***	NS	NS
Spikelet number per plant								
***	NS	NS	***	NS	NS	***	NS	NS
Grain number per spikelet								
***	NS	NS	***	NS	NS	***	NS	NS
Grain number plant								
***	NS	NS	***	NS	NS	***	NS	NS
1000 Grain weight								
NS	NS	NS	***	*	NS	***	NS	NS

Differences in response to N between the three genotypes have been considered in terms of changes in heterosis. Responses to N are presented as freehand curves in Figs. 15 to 21. Fig. 15A, for example, contains the response of the grain weight of Heron, Strain 52 and their F_1. The fourth curve in the graph is the fitted multiple regression curve for the hybrid. Reference to the fitted curve results will be presented later.

Levels of heterosis relative to the high- and mid-parents are also shown in these Figures. Again as in Experiment 1 it is possible that a slight discrepancy may occur between the observed values in the two graphs because the mean value of heterosis calculated in the two replications was included in the graph.

Grain weight per plant

Heron was the highest yielding parent at all levels of N and was more responsive than Strain 52 to increases in N application. Further, at the super-optimal level of N, Heron was not so severely affected (Fig. 15A, p. 89).

At low levels of N the hybrid did not express heterosis relative to the high-parent but was intermediate between the parents. However, the hybrid was more responsive than both parents to increases in N application and not as greatly depressed by the toxic level of N. As a result, heterosis increased with N (Fig. 15B, p. 89).

Total weight per plant

For this character also, Heron was the high-parent at most levels of N. It was similarly more responsive to N and not as greatly reduced by the high level of N as Strain 52. The hybrid, on the other hand, produced more total weight than both parents at all levels of N (Fig. 15C, p. 89). Heterosis, however, did not increase with N but was significantly higher on either side of the optimum, that is at the

Table 20: Analyses of variance for heterosis relative to the high-parent (HP), mid-parent (MP), Heron (M1) and Strain 52 (M2).

Nitrogen

N

	HP	MP	M1	M2
Grain weight per plant	NS	NS	NS	NS
Total weight per plant	NS	*	NS	*
Harvest index	*	NS	**	NS
Height	***	***	***	***
Head length per head	***	***	*	***
Head number per plant	**	***	***	***
Spikelet number per head	***	***	***	***
Spikelet number per plant	***	***	***	***
Grain number per spikelet	**	**	**	*
Grain number per plant	*	***	NS	***
1000 Grain weight	NS	NS	**	*

intermediate (160 kg N/ha) and toxic levels (2560 kg N/ha) (Table 20 p. 87).

Harvest index

There was an increase in harvest index with N over the entire range of N levels although Strain 52 and the hybrid showed some tendency to decline at the highest level of N. An increase is contrary to the result of most field experiments in which harvest index declines with N (Gardener and Rathjen, 1975) as a consequence of the greater growth and more intense interplant competition for factors such as light, water and nutrients at the higher levels of N. In the present experiment these factors were not likely to be limiting at any level of N.

Since the total N application was added to the soil early in the growth of the plants, N deficiency was first observed in the low N treatments and sequentially in the higher treatments. As a result plants in the lower N levels utilised most available N in the vegetative components produced early in the season while the higher levels had relatively more N available for use in grain production.

The ranking of the parents for harvest index was similar to that for grain and total weight at all levels of N except at 1280 kg N/ha. On the other hand, although the hybrid expressed heterosis for grain and total weight at most levels of N, heterosis for harvest index occurred only at the near-optimal level of N, 640 kg/ha (Fig. 15F, p.89). At other levels of N the hybrid had a harvest index equivalent to that of the lowest yielding parent, Strain 52. Consequently, significant differences were observed for heterosis relative to the high-parent between N levels (Table 20, p. 87).

Height

The height of both parents was constant at lower levels of N and declined at higher levels (Fig. 17A, p. 92). Heron was more responsive

Figure 15

Response to nitrogen

(A,B)	Grain weight/plant
(C,D)	Total weight/plant
(E,F)	Harvest index
(A,C,E)	Response to nitrogen by Heron (■— — —■), Strain 52 (●·——·●), Heron x Strain 52 (▲——▲) and fitted values for the hybrid estimated from the multiple regression analysis (··········)
(B,D,F)	Heterosis relative to the high-parent (▽——▽), mid-parent (△·——·△), Heron (□) and Strain 52 (○)

Least significant differences at the 5% level are indicated for heterosis

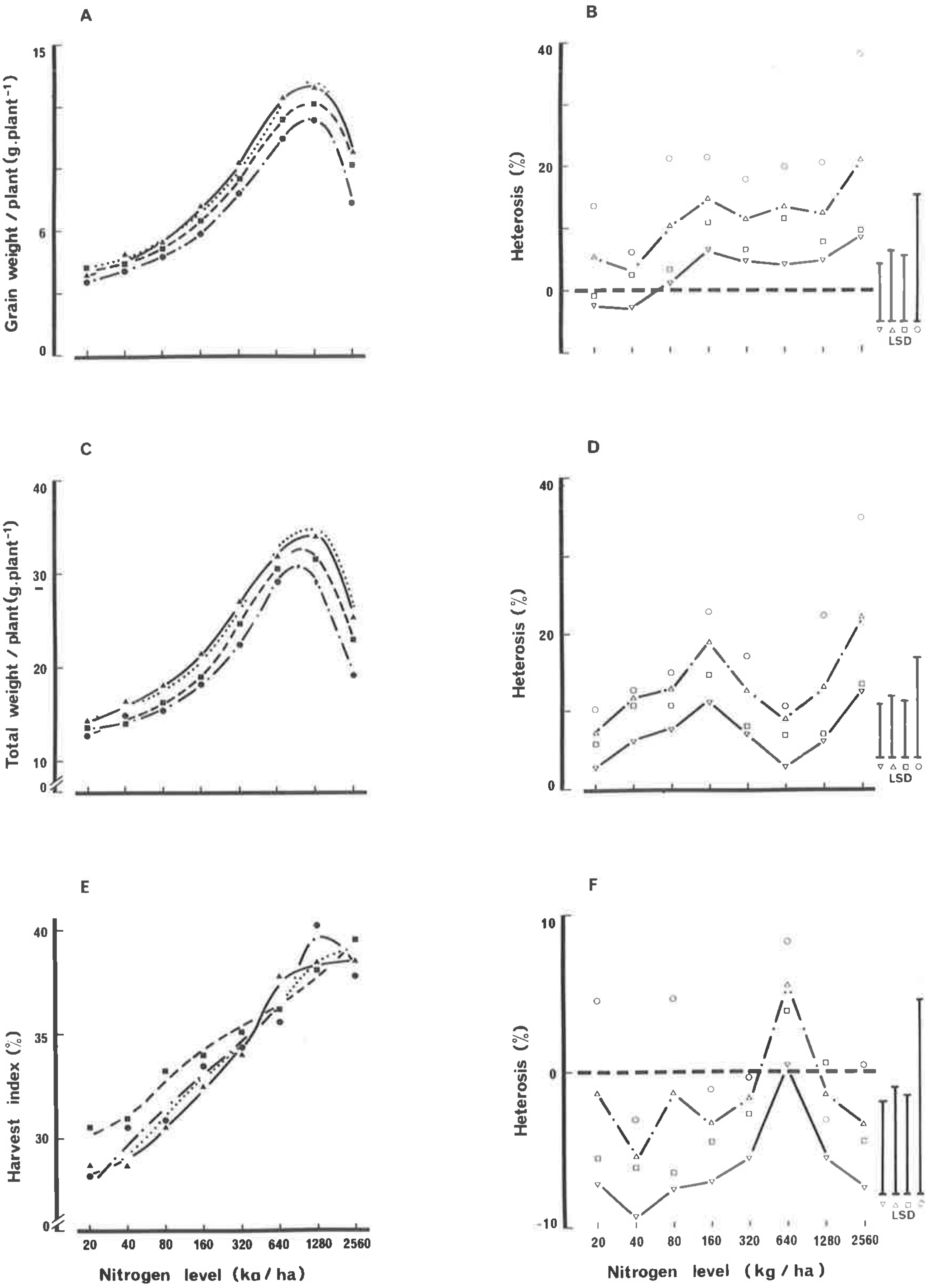

A
Grain weight / plant (g.plant⁻¹)
15
6
0
B
Heterosis (%)
40
20
0
▽ △ □ ○
LSD
C
Total weight / plant (g.plant⁻¹)
40
30
20
10
0
D
Heterosis (%)
40
20
0
▽ △ □ ○
LSD
E
Harvest index (%)
40
35
30
0
20
40
80
160
320
640
1280
2560
Nitrogen level (kg / ha)
F
Heterosis (%)
10
0
-10
▽ △ □ ○
LSD
20
40
80
160
320
640
1280
2560
Nitrogen level (kg / ha)

Figure 16

Nitrogen responses at heading for Heron,

Heron x Strain 52 and Strain 52


14
24
34
44
54
64
74
84
54
64
74
84
14
24
34
44
54
64
74
84

to N, being the tallest parent at low and shortest at high N. The response of the hybrid, however, was unlike that of either parent. This genotype increased in height in the low N range reaching an optimum at 160 kg N/ha and decreased at high N. Since the hybrid was responsive in both the low and high N ranges, heterosis was significantly higher at intermediate levels (Fig. 17B, p. 92).

Head length

While head lengths for the hybrid were equal to or greater than those for the longest parent, Strain 52, the shape of its response curve was similar to Heron being consistently 1 - 1.5 cm longer than this parent (Fig. 17C, p. 92). As a result, heterosis was observed at all levels of N, but was significantly greater at the intermediate levels of N (160 - 640 kg N/ha).

(b) Multiple Regression Analysis

The multiple regression procedure described in Section 3.2.1. has been used to estimate the relationship between hybrid and parental performance. The estimated values for the hybrid calculated from these regressions are presented with the observed values in Figs. 15 to 19.

For the characters grain and total weight, more than 99% of the variation in hybrid response is accounted for by the regression on parental performance (Table 21, p. 93). Further, the values calculated were a good estimate of hybrid performance at all levels of N (Fig. 15A, 15C, p. 89).

These equations showed that variation in hybrid yield could be strongly related to variation in the yield of the high-parent Heron. The regression constants were small relative to yields at most levels of N and the b value for Strain 52 was low and non-significant. Similar results were obtained for harvest index, head length and the yield components, head number per plant, spikelet number per head and

Figure 17

Response to nitrogen

(A,B)	Height
(C,D)	Head length
(A,C)	Response to nitrogen by Heron (■– – –■), Strain 52 (●-— -●), Heron x Strain 52 (▲ ——▲) and fitted values for the hybrid estimated from the multiple regression analysis (·············)
(B,D)	Heterosis relative to the high-parent (▽ —— ▽), mid-parent (△-—-△), Heron (□) and Strain 52 (○)

Least significant differences at the 5% level are indicated for heterosis

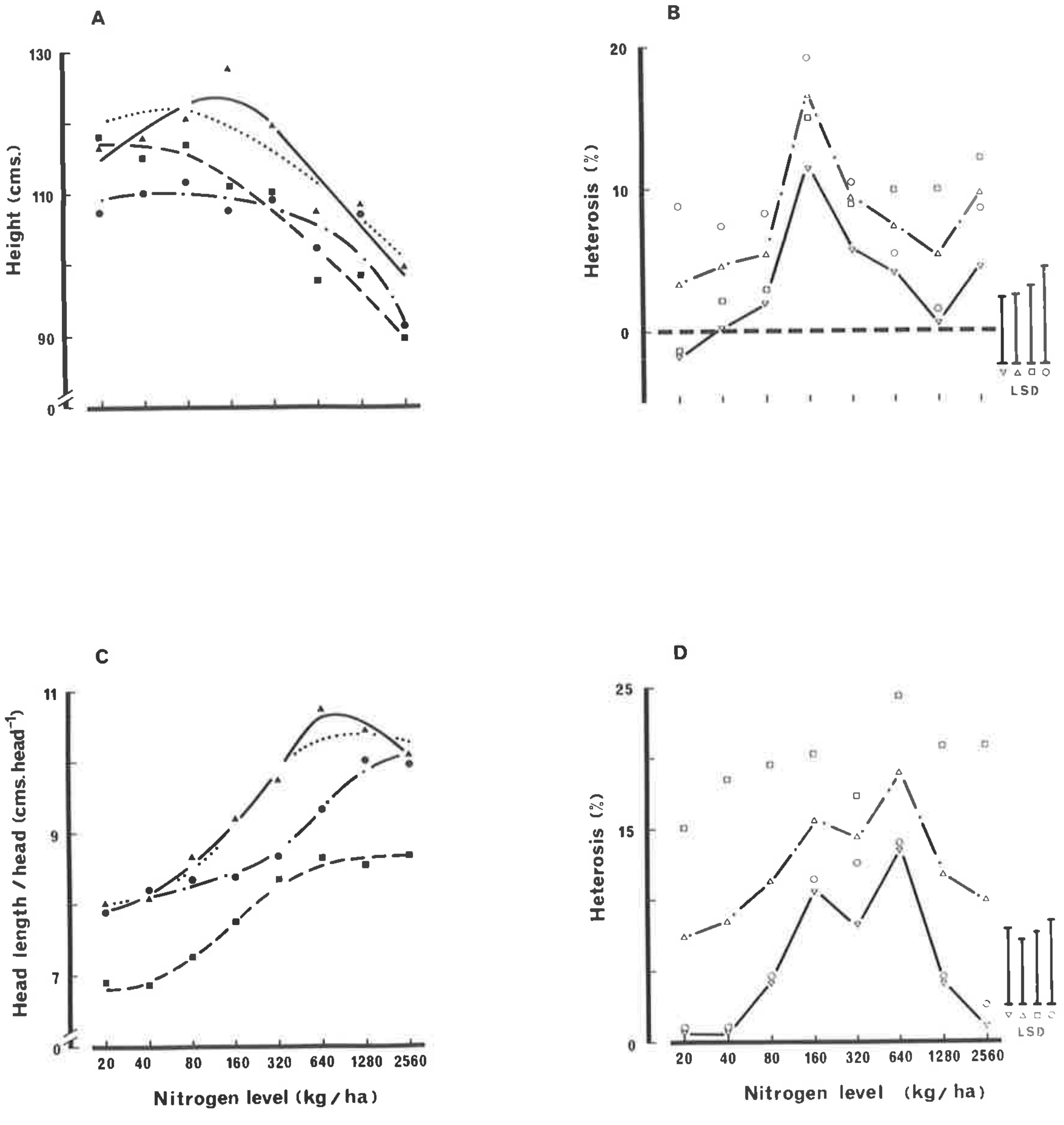

A
Height (cms.)
130
110
90
0
B
Heterosis (%)
20
10
0
▽ △ □ ○
LSD
C
Head length / head (cms.head^{-1})
11
9
7
0
20 40 80 160 320 640 1280 2560
Nitrogen level (kg / ha)
D
Heterosis (%)
25
15
0
▽ △ □ ○
LSD
20 40 80 160 320 640 1280 2560
Nitrogen level (kg / ha)

Table 21: Multiple regression of hybrid on parental values.

Char.	Variable	B	S.E.	R^2	F
Grain weight /plant	Constant	-0.40	1.19		
	Heron	1.25	0.11	1.00	124.6***
	Strain 52	-0.14	0.12	0.00	1.4
Total weight /plant	Constant	1.52	5.21		
	Heron	1.31	0.17	1.00	62.0***
	Strain 52	-0.31	0.19	0.00	2.8
Harvest index	Constant	-9.37	15.55		
	Heron	1.05	0.35	0.95	8.8*
	Strain 52	0.20	0.28	0.00	0.5
Height	Constant	16.52	71.93		
	Heron	0.50	0.35	0.72	2.0
	Strain 52	0.42	0.58	0.03	0.5
Head length	Constant	-1.13	3.02		
	Heron	1.33	0.26	0.96	25.3***
	Strain 52	0.00	0.25	0.00	0.0
Head number /plant	Constant	1.11	0.96		
	Heron	0.61	0.10	0.96	34.4**
	Strain 52	0.06	0.16	0.00	0.1
Spikelet number /head	Constant	4.66	7.36		
	Heron	1.22	0.25	0.90	23.5**
	Strain 52	-0.25	0.22	0.02	1.3
Spikelet number /plant	Constant	19.65	30.76		
	Heron	0.69	0.18	0.92	15.1*
	Strain 52	0.13	0.21	0.01	0.4
Grain number /spikelet	Constant	-0.35	0.32		
	Heron	1.19	0.19	0.87	40.6***
Grain number /plant	Constant	-3.76	58.38		
	Heron	0.84	0.20	0.99	18.5**
	Strain 52	0.18	0.26	0.00	0.5
1000 Grain weight	Constant	0.16	14.40		
	Heron	0.65	0.35	0.13	3.5
	Strain 52	0.42	0.11	0.67	15.9*

grain number per spikelet (Table 21, p. 93).

However, a different result was obtained for height. As has already been shown, the height response of the hybrid was unlike that of either parent. As a result the b values of the parents were non-significant (Table 21, p. 93).

(c) Nitrogen Response and Grain Yield Components

The components of yield measured in Experiment 2 could be considered as developing in succession in three phases:

Phase 1. Head no. plant x Spikelet no. head
↓
Phase 2. Spikelet no. plant x Grain no. spikelet
↓
Phase 3. Grain no. plant x 1000 Grain weight
↓
Grain weight plant

The relative performance of the parents for the grain yield components commonly changed between successive components and exhibited compensation (Figs. 18 and 19, pp. 95 and 96). For example, over the whole range of N levels Heron produced a greater number of heads per plant but Strain 52 developed a greater number of spikelets per head. Further, this compensation also occurred where parental ranking changed with N level, as shown by grain number per plant and 1000 grain weight.

The hybrid was generally not intermediate between the parents for any of the components. Head number produced by the hybrid was either less than both or intermediate between the parents, while spikelet number per head, the other component combining to produce spikelet number per plant, was intermediate at low N levels and equivalent to the high-parent, Strain 52, at higher levels of N.

It has already been shown that hybrid performance for all

Figure 18

Response to nitrogen

(A,B)	Head number/plant
(C,D)	Spikelet number/head
(E,F)	Spikelet number/plant
(A,C,E)	Response to nitrogen by Heron (■— — —■), Strain 52 (●-—— -●), Heron x Strain 52 (▲ —— ▲) and fitted values for the hybrid estimated from the multiple regression analysis (·········)
(B,D,F)	Heterosis relative to the high-parent (▽ —— ▽), mid-parent (△-—— -△), Heron (□) and Strain 52 (○)

Least significant differences at the 5% level are indicated for heterosis

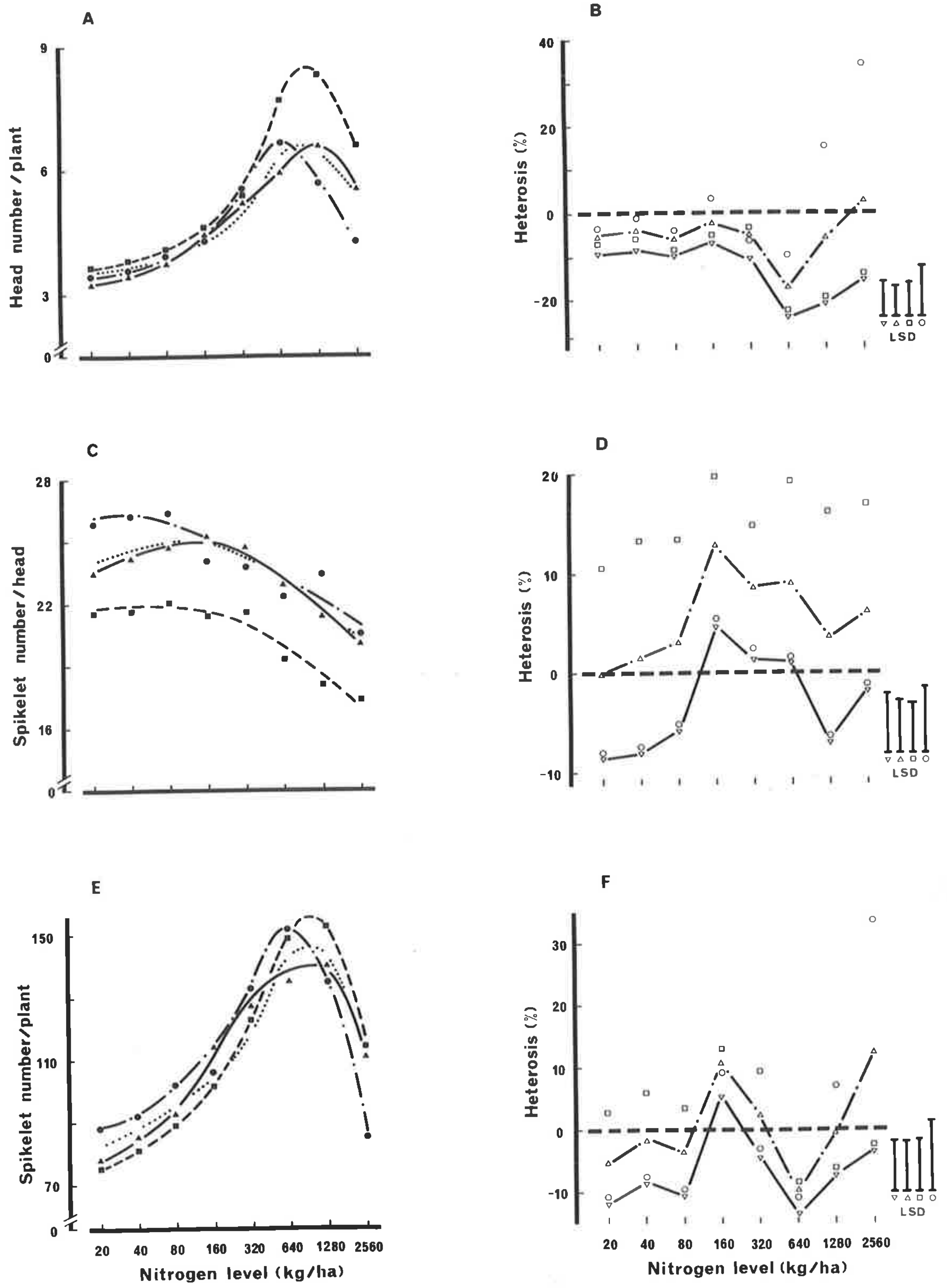
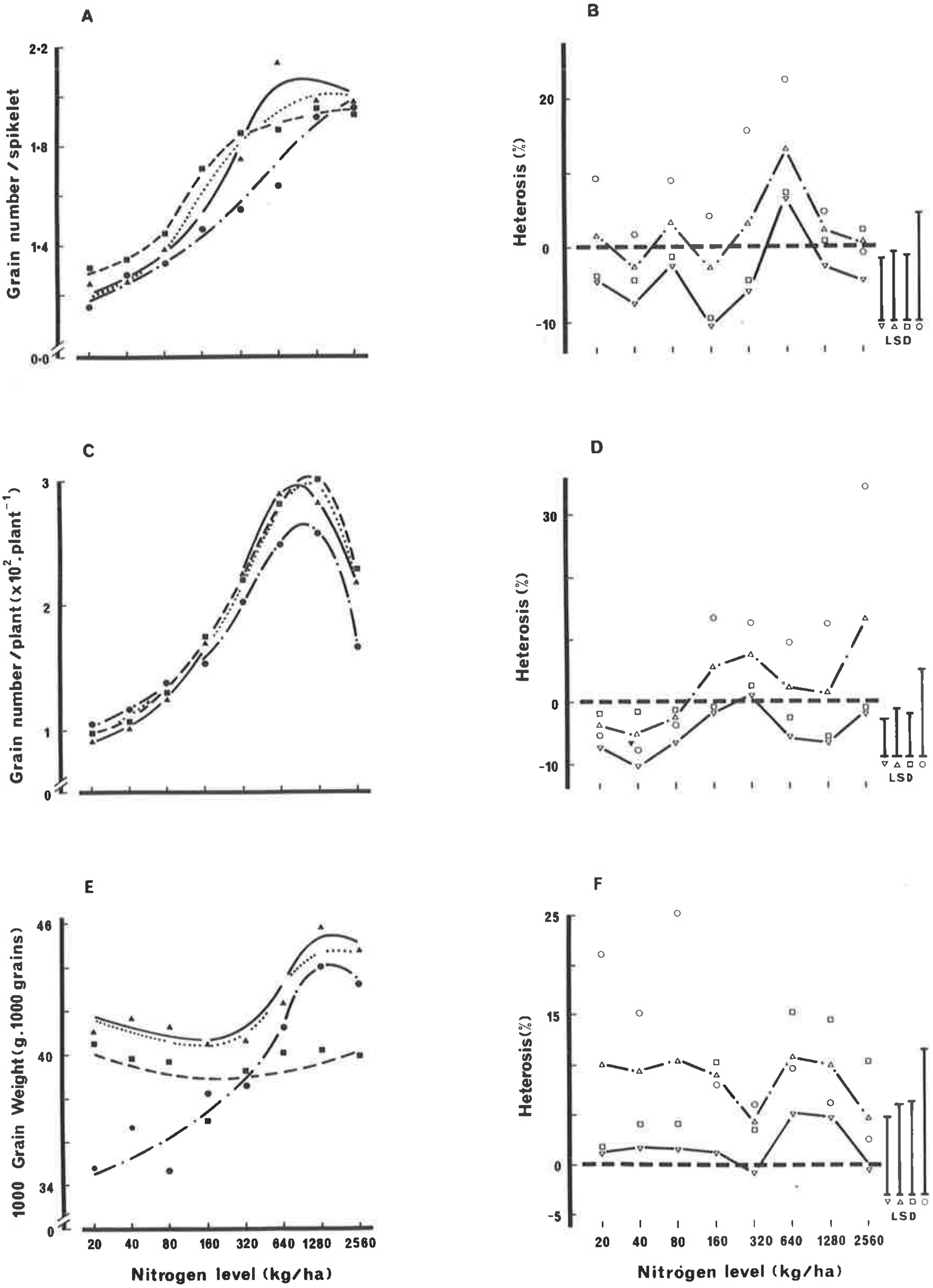

A
Head number / plant
0
3
6
9
B
Heterosis (%)
-20
0
20
40
LSD
▽ △ □ ○
C
Spikelet number / head
0
16
22
28
D
Heterosis (%)
-10
0
10
20
LSD
▽ △ □ ○
E
Spikelet number/plant
0
70
110
150
20 40 80 160 320 640 1280 2560
Nitrogen level (kg/ha)
F
Heterosis (%)
-10
0
10
20
30
LSD
▽ △ □ ○
20 40 80 160 320 640 1280 2560
Nitrogen level (kg/ha)

Figure 19

Response to nitrogen

(A,B)	Grain number/spikelet
(C,D)	Grain number/plant
(E,F)	1000 Grain weight
(A,C,E)	Response to nitrogen by Heron (■— — —■), Strain 52 (●-—— -●), Heron x Strain 52 (▲ —— ▲) and fitted values for the hybrid estimated from the multiple regression analysis (·········)
(B,D,F)	Heterosis relative to the high-parent (▽ —— ▽), mid-parent (△-—— -△), Heron (□) and Strain 52 (○)

Least significant differences at the 5% level are indicated for heterosis


A
B
C
D
E
F
Grain number / spikelet
2·2
1·8
1·4
0·0
Heterosis (%)
20
0
-10
LSD
Grain number / plant (x10^2. plant^{-1})
3
2
1
0
30
0
-10
1000 Grain Weight (g. 1000 grains)
46
40
34
0
25
15
0
-5
20
40
80
160
320
640
1280
2560
Nitrogen level (kg/ha)

components except 1000 grain weight was closely associated with the expression of Heron (Table 21, p. 93). Expression of components by the hybrid is therefore not likely to be intermediate in all environments, but change with the expression of Heron.

Complex interactions were found to occur between successive components, with varying levels of compensation being observed between different components and N levels. Heterosis relative to the high- and mid-parents for each of the components is displayed in Table 22. The performance of the hybrid relative to the high-parent for head number per plant declined with increase in N. On the other hand, the relative expression of hybrid spikelet number per head was greater at intermediate and high levels of N. As a result, the relative expression of spikelet number per plant by the hybrid was greater in these same ranges of N (Fig. 18F, p. 95).

Hybrid grain number per spikelet displayed some tendency to increase with N relative to the parents. However, a high level of compensation occurred between this component and spikelet number per plant. The relative expression of the hybrid grain number per plant, therefore, did not fluctuate as widely as its components and increased with N level.

Since heterosis for 1000 grain weight was relatively constant across N levels, heterosis for grain weight per plant increased with N. Compensation was also shown by the relative expression of hybrid grain number per plant and 1000 grain weight (Fig. 19, p. 96). As a result the relative contribution to heterosis for yield of each of the components in the three phases varied with N level.

In summary, at low levels of N, heterosis relative to the high-parent was not observed for grain yield since the performance of the hybrid was lower than the high-parent for all components except 1000 grain weight. On the other hand, heterosis for grain weight per plant

Table 22: Heterosis relative to the high-parent (HP) and mid-parent (MP) for grain weight per plant and its components.

HP	Nitrogen level (kg/ha)							
	20	40	80	160	320	640	1280	2560
Head no. /plant	-9.4	-7.8	-9.9	-6.6	-10.4	-23.3	-20.3	-15.8
Spikelet no. /head	-8.8	-7.2	-5.7	4.8	1.9	1.3	-7.5	-1.8
Grain no. /spikelet	-4.7	-7.6	-2.7	-10.5	-5.9	6.5	-2.8	-4.3
1000 Grain weight	1.2	2.7	2.5	1.7	-0.1	5.3	4.5	-0.8
Grain wt. /plant	-2.6	-2.8	1.2	6.4	4.9	4.0	4.9	9.3
MP								
Head no. /plant	-5.2	-3.6	-6.4	-1.2	-5.3	-17.2	-5.8	2.5
Spikelet no. /head	0.0	1.8	2.7	12.5	8.5	9.5	3.2	6.9
Grain no. /spikelet	1.8	-2.5	3.9	-3.8	3.3	14.0	2.1	0.3
1000 Grain weight	9.8	9.0	12.9	8.4	4.1	11.7	10.4	4.8
Grain wt. /plant	5.2	3.5	10.2	14.8	11.5	13.4	12.5	20.8

at optimal and higher levels of N was due not only to 1000 grain weight but also to spikelet number per head and grain number per spikelet. High expression of these components overcame the poor expression of head number in the hybrid.

(d) Macro-environmental Variability

Macro-environmental variability was assessed to determine if this study provided evidence of whether the hybrid was more or less stable across environments than its parents and to identify those features of the hybrid response causing differences. Variabilities were measured as variances calculated over N treatments (Table 23, p. 100).

The macro-environmental variabilities of the parents and hybrid varied according to the characters being studied. On the one hand, for characters involving the accumulation of mass by the plant namely grain and total weight per plant, which displayed heterosis relative to the high-parent in most environments, the hybrid was significantly less stable over N treatments than one or both parents. This was due to the greater responsiveness of the hybrid to increases in N application (Fig. 15, p. 89). On the other hand, greater stability was shown by the hybrid for both head number and spikelet number per plant since its response was not as greatly influenced by change in N level in either the sub- or super-optimal ranges (Fig. 18, p. 95). For example, spikelet number per plant expressed by the hybrid was intermediate at low and high levels of N, but lower than both parents at optimum N. Heterosis was not shown by either of these latter two characters except spikelet number per plant at one level of N.

(e) Micro-environmental Variability

The standard deviation (S.D.) has again been used in this experiment as a measure of micro-environmental variability. For the characters grain and total weight and head number per plant, S.D.'s

Table 23: Macro-environmental variability measured over N treatments, levels of significance of differences between genotypes and L.S.D. at the 5% level of significance

Char.	Heron	Strain 52	F_1	Sig. (%)	L.S.D. 5%
Grain weight per plant	10.77	9.76	13.29	**	1.78
Total weight per plant	57.56	47.24	61.30	***	5.99
Harvest index (%)	14.9	24.6	24.0	**	5.5
Height	144.1	92.8	113.7	**	28.9
Head length	0.66	0.88	1.25	**	0.24
Head number per plant	3.8	1.8	1.8	***	0.7
Spikelet number per head	4.06	6.40	4.14	**	1.59
Spikelet number per plant	1000.1	750.9	684.9	**	183.7
Grain number per spikelet	0.093	0.108	0.133	NS	0.036
Grain number per plant	6390.5	4279.8	5505.8	***	813.7
1000 Grain weight	11.4	27.0	17.7	*	12.2

were found to increase significantly with N level and mean plant performance (Figs. 20A, 20D and 21D respectively, pp. 102 and 103). The S.D.'s for height did not change significantly with N level (Fig. 21A, p. 103).

The hybrid did not appear to show less micro-environmental variation than its parents. Only at intermediate levels of N, 160 and 640 kg N/ha was the hybrid less variable for grain weight per plant. At these levels, heterosis was observed. However, at higher levels where heterosis also occurred, the hybrid was not less variable than its parents. For total weight per plant, a character which expressed heterosis in all environments, the hybrid was more variable than both parents in the majority of environments. Similarly, even though the hybrid displayed heterosis for height at most levels of N, it was generally intermediate in variability (Fig. 21A, p. 103).

For head number per plant a similar ranking of the three genotypes was observed for mean expression and S.D. at most levels of N. The hybrid was more stable than both parents at intermediate N levels since it produced fewer heads than the parents in this range (Fig. 21D, p. 103).

In considering micro-environmental variability in relation to environmental response curves and surfaces, Knight (1973) suggested that the variation would decrease as one approached the optimum as minor differences in the availability of environmental factors would have less effect near the optimum than in sub- and super-optimal environments. He added, however, that this was only one effect among many that could change errors and standard deviations. Because variability increases with the mean, due to the multiplicative nature of plant growth, it may not be possible to observe such a change based solely on S.D. As in Experiment 1 the coefficient of variation (C.V.) was used to overcome this problem. The C.V.'s for several characters

Figure 20

Micro-environmental variability

(A,B,C)	Grain weight/plant
(D,E,F)	Total weight/plant
(A,D)	Standard deviations
(B,E)	Response to nitrogen and mean slope between nitrogen levels
(C,F)	Coefficients of variation
For:	Heron (■– – –■), (□– – –□)
	Strain 52 (●- —— -●), (○- —— -○)
	Heron x Strain 52 (▲ —— ▲), (△ —— △)

Least significant differences at the 5% level are indicated for S.D.'s and C.V.'s

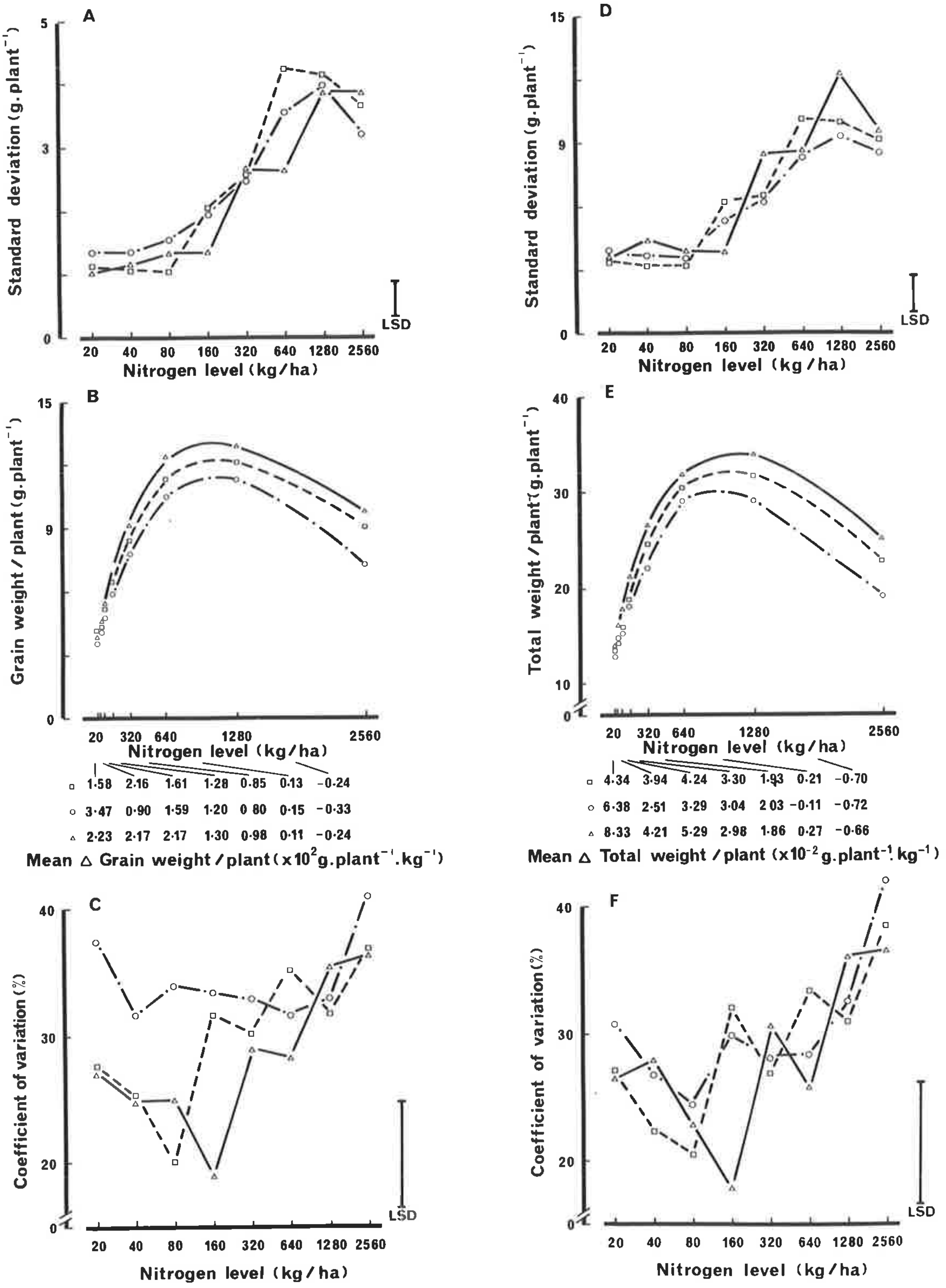
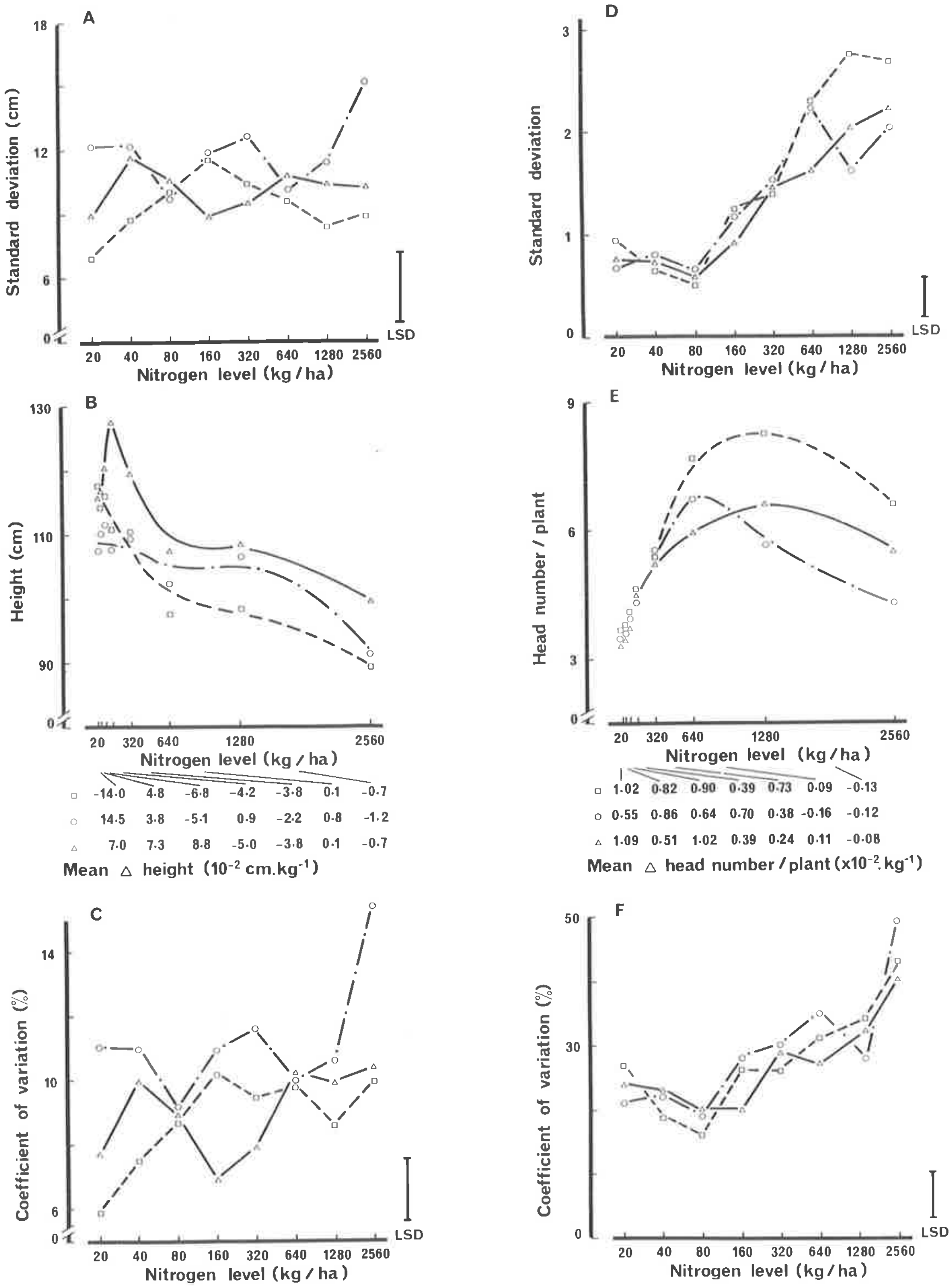

A
Standard deviation (g.plant^{-1})
5
3
0
LSD
20 40 80 160 320 640 1280 2560
Nitrogen level (kg/ha)
D
Standard deviation (g.plant^{-1})
15
9
0
LSD
20 40 80 160 320 640 1280 2560
Nitrogen level (kg/ha)
B
Grain weight / plant (g.plant^{-1})
15
9
0
20 320 640 1280 2560
Nitrogen level (kg/ha)
□ 1·58 2·16 1·61 1·28 0·85 0·13 −0·24
○ 3·47 0·90 1·59 1·20 0 80 0·15 −0·33
△ 2·23 2·17 2·17 1·30 0·98 0·11 −0·24
Mean △ Grain weight / plant (x10^{2}g.plant^{-1}.kg^{-1})
E
Total weight / plant (g.plant^{-1})
40
30
20
10
0
20 320 640 1280 2560
Nitrogen level (kg/ha)
□ 4·34 3·94 4·24 3·30 1·93 0·21 −0·70
○ 6·38 2·51 3·29 3·04 2 03 −0·11 −0·72
△ 8·33 4·21 5·29 2·98 1·86 0·27 −0·66
Mean △ Total weight / plant (x10^{-2}g.plant^{-1}.kg^{-1})
C
Coefficient of variation (%)
40
30
20
0
LSD
20 40 80 160 320 640 1280 2560
Nitrogen level (kg/ha)
F
Coefficient of variation (%)
40
30
20
0
LSD
20 40 80 160 320 640 1280 2560
Nitrogen level (kg/ha)

Figure 21

Micro-environmental variability

(A,B,C)	Height
(D,E,F)	Head number/plant
(A,D)	Standard deviations
(B,E)	Response to nitrogen and mean slope between nitrogen levels
(C,F)	Coefficients of variation
For:	Heron (■———■), (□———□)
	Strain 52 (●-—-●), (○-—-○)
	Heron x Strain 52 (▲ —— ▲), (△ —— △)

Least significant differences at the 5% level are indicated for S.D.'s and C.V.'s


A
Standard deviation (cm)
18
12
6
0
LSD
20 40 80 160 320 640 1280 2560
Nitrogen level (kg / ha)
D
Standard deviation
3
2
1
0
LSD
20 40 80 160 320 640 1280 2560
Nitrogen level (kg / ha)
B
Height (cm)
130
110
90
0
20 320 640 1280 2560
Nitrogen level (kg / ha)
□ -14·0 4·8 -6·8 -4·2 -3·8 0·1 -0·7
○ 14·5 3·8 -5·1 0·9 -2·2 0·8 -1·2
△ 7·0 7·3 8·8 -5·0 -3·8 0·1 -0·7
Mean △ height (10^{-2} cm.kg^{-1})
E
Head number / plant
9
6
3
0
20 320 640 1280 2560
Nitrogen level (kg / ha)
□ 1·02 0·82 0·90 0·39 0·73 0·09 -0·13
○ 0·55 0·86 0·64 0·70 0·38 -0·16 -0·12
△ 1·09 0·51 1·02 0·39 0·24 0·11 -0·08
Mean △ head number / plant (x10^{-2}. kg^{-1})
C
Coefficient of variation (%)
14
10
6
0
LSD
20 40 80 160 320 640 1280 2560
Nitrogen level (kg / ha)
F
Coefficient of variation (%)
50
30
0
LSD
20 40 80 160 320 640 1280 2560
Nitrogen level (kg / ha)

as well as the untransformed responses to N and mean slopes between N levels are presented in Figs. 20 and 21.

The C.V.'s tended to show a J or U shaped response curve but the lowest part of the curve did not correspond to the optimum level of N. The increase in mean values at the optimum was not so great as to lead to a fall in the C.V. in this region. Consequently, the C.V.'s were lowest not at the optimal level of N but at some lower level (Figs. 20C, 20F, 21F, pp. 102 and 103).

This effect was observed for grain weight, total weight (Fig. 20, p. 102) and head number per plant (Fig. 21, p. 103). The C.V.'s for grain weight and total weight per plant of Heron and the hybrid increased with N applications above 160 kg N/ha, although optimum grain and total weights were obtained at 1280 kg N/ha. For Strain 52, the genotype which produced the lowest grain and total weights, the C.V.'s were relatively high at most N levels. No tendency for the C.V. to increase with plant size was observed in this parent.

A similar relationship existed between the variabilities of the hybrid and parents measured by C.V. as existed for the S.D.'s. The hybrid was less variable than both parents for grain weight and total weight per plant at intermediate levels of N but this could not be attributed to the slope of the response curves, since the hybrid was more responsive to N than both parents in this range (Fig. 15, p. 89). The hybrid appeared to be inherently less variable in these environments.

Similarly for height, the C.V. of the hybrid was relatively lower than both parents at 160 and 320 kg N/ha. At these levels of N heterosis was observed and the slope of the hybrid response was greater than both parents (Figs. 21B, 21C, p. 103).

It is also important to note that while the mean values of genotypes may be similar in two different environments, the variabilities expressed by those genotypes may be significantly different.

The mean values of all three genotypes for grain weight per plant at 320 kg N/ha were similar to those at 2560 kg N/ha, however, the S.D.'s were significantly different (Fig. 20B, p. 102). Similar comments could be made about total weight expressed by Heron and Strain 52 and head number per plant shown by Strain 52 and the hybrid (Figs. 20E and 21E, pp. 102 and 103).

3.2.3. Discussion

By varying nitrogen availability, this experiment was successful in creating environments in which the hybrid's performance relative to the high-parent changed significantly.

Some comparisons can be made between the results of this experiment and those of Experiment 1. The differences between these experiments are attributable to the fact that this was a glasshouse experiment and the environments generated were much unlike those sampled in the field.

In Experiment 2 it could be assumed that many factors were supplied at an optimal level. These may have included light, water and nutrients other than N. Plant growth reached an optimum at a level of N much higher than any observed in the field (Gardener and Rathjen, 1975) because the increase in plant size probably did not result in significant increases in competition for other environmental factors. Lodging was prevented.

The response to super-optimal levels was also different from that usually found in the field situation. In this instance plant growth was depressed by the high level of N salts in the soil and not due to the effects of competition or lodging. These features have important consequences for interpreting differences between the parents and hybrid.

The highest levels of heterosis (i.e. 10%) expressed for grain and total weight in the glasshouse were much lower than those observed for the same hybrid at all plant densities in the field where it averaged 50%. There is no readily apparent reason for this difference. Some authors have suggested that heterosis is greater in sub-optimal or stress environments (Langridge, 1962, 1968; Parodi and Patterson, 1973). Since many factors in the field and few factors in the glasshouse may have been sub-optimal, this result might have been considered as support for the hypothesis. However, it must be noted that in the glasshouse heterosis for grain and total weight was greatest around the optimal level of N. This finding is similar to some others involving variation in nutritional status (Burkholder and McVeigh, 1930; Griffing and Zsiros, 1971; Pederson, 1968). The hybrid was more efficient than its parents in the utilisation of N where this was supplied at optimal rates.

The increase in harvest index with N has been explained (Section 3.2.2.) in terms of increased availability of N during grain filling and the lack of competition for other environmental factors, particularly water, at all levels of N. Although the hybrid had the highest grain weight in nearly all environments, its harvest index was generally lower than one or both parents. This result is not attributable to the production of vegetative non-heading tillers since these were only rarely observed at the highest level of N. The greater height of the hybrid and consequent heavier stems may be associated with the lower harvest indices since the hybrid was relatively taller at those N levels where the hybrid harvest index was lower than both parents.

N response for height in the hybrid was unlike both parents. The increase in height of the hybrid with N at low levels of N indicated that it was capable of growth taller than both parents but was restricted in this by the inadequate supply of N. These results again emphasise the difficulty of drawing conclusions about the inheritance or genetic determination of a character if it has been measured in only one or a few restricted environments.

The multiple regression equations that relate the hybrid to the parental responses showed that the hybrid response was closely related to Heron. This was concluded for most characters, irrespective of whether Heron or Strain 52 was the high-parent. In consequence, the performance of the hybrid relative to the high-parent was unlikely to be similar at all levels of N, particularly for characters in which Strain 52 was the high-parent.

Complex interactions were found to occur between successive components. Furthermore, the relative contribution of the components to heterosis for grain yield changed with the environment.

The components that made the major contributions to heterosis for grain yield in this experiment were different from those identified in Experiment 1. In that experiment, heterosis was due to head number at the four lower densities and grain number per head at the highest density. In Experiment 2 it was expected that head number would have made the greatest contribution to grain yield heterosis as light, water, and nutrients other than N, were freely available as they may have been at lower densities in the field. However, head number was the only component not to make a contribution at any level of N.

In both experiments the macro-environmental variability of the hybrid was greater than that of the parents for characters which displayed heterosis. They included grain weight, total weight and head length per head. As suggested previously, this result must take account of the fact that many factors of the environment other than N were probably supplied at optimal levels. A different ranking of the genotypes, in terms of their macro-environmental variabilities to N response, may exist in the field where other factors may be supplied at sub-optimal, optimal or super-optimal levels. This suggestion will be examined further in Experiment 3.

In the analysis of micro-environmental variability a strong association was found between the S.D. and mean in the intermediate and high N range. Because of this association it is not possible to make valid comparisons between variabilities measured in sub-optimal, optimal and super-optimal environments.

The C.V. was used in an attempt to reduce this association by determining variability relative to the mean. However, since the lowest C.V.'s did not occur at the optimal level of N, but at a lower level, the increase in variability with the mean was more than proportional to the mean. Therefore, to eliminate the association between variability and mean, the S.D. should not be estimated relative to the mean, but relative to some power of the mean greater than one to take account of the multiplicative nature of plant growth.

The hybrid was found to be relatively more stable within environments than both parents at intermediate levels of N for characters such as grain weight and height. Greater stability was not observed in either the sub- or super-optimal levels of N. This result is in contrast to that obtained in Experiment 1. In that experiment hybrids were relatively more stable than their parents in the high densities where many factors of the environment would have been available to individual plants at sub-optimal levels.

The difference between these results may be attributed to interplant competition. In both experiments hybrid variability was relatively lower than the parents in those environments in which competition between plants was greatest. As was suggested in Experiment 1 (Section 3.1.3.) the hybrids are apparently less susceptible to the development of dominance-suppression relationships which occur when plants are competing strongly for limited resources.

In Experiment 2 one factor only, N, was successfully varied in the range from sub- to super-optimal levels and it was not possible to study interactions with phosphorus. Another attempt was made in Experiment 3 to ensure a phosphorus response and to study the response of genotypes to two factors.

3.3.0. Experiment 3

3.3.1. Materials and Methods

(a) Genotypes

For this experiment the hybrid Halberd x Warimek was selected. The pedigrees of the parents are set out in Section 3.1.1.

(b) Soil

From previous analysis, a virgin soil from a bushland site at Palmer, S.A. was found to be low in nitrogen and phosphorus content and suitable in texture for pot experimentation. The soil was obtained from a roadside on the western boundary of the property of Mr.A. Krause by permission of the Mannum District Council.

The total nitrogen content of the soil was approximately 3 ppm and the available phosphorus 1-2 ppm with a maximum sorption capacity of 25 ppm.

(c) Fertilizers

Nitrogen fertiliser as ammonium nitrate (NH_4NO_3, laboratory grade) was applied at the eight levels set out in Table 24. Half the N was applied in dry form at soil mixing, while the remainder was added as a nutrient solution one month after sowing.

Table 24: Nitrogen Fertiliser Levels

N level	kg N/ha	ppm N	Total application (NH_4NO_3) g/pot
1	0.0	0.00	0.00
2	91.4	20.39	0.75
3	274.3	60.90	2.24
4	548.6	121.80	4.48
5	914.3	202.83	7.46
6	1371.4	304.24	11.19
7	1920.0	426.04	15.67
8	2560.0	567.97	20.89

Following a series of pilot trials, phosphorus fertiliser was applied at the rates set out in Table 25. "Aerophos-X" (Albright and Wilson (Aust) Ltd.) was used as the phosphorus source. This product consists of 84% mono-calcium phosphate ($CaH_4(PO_4)_2 \cdot H_2O$) and 16% as a combination of unidentified di- and tri-calcium phosphates. The latter 16% is relatively unavailable to the plant (Alston, A; pers. comm.).

Table 25: Phosphorus Fertiliser Levels

P level	kg P/ha	ppm P	$CaH_4(PO_4)_2 \cdot H_2O$ g/pot
1	0	0.00	0.00
2	10	2.29	0.12
3	40	8.96	0.47
4	100	22.12	1.16
5	1000	221.93	11.64
6	5000	1109.44	58.19
7	10000	2218.88	116.38
8	15000	3328.31	174.57

The total phosphorus application was added in the dry form at soil mixing.

Basal rates of potassium sulphate and micronutrients were applied in solution at the same levels as in Experiment 2.

(d) Soil and pot preparation

The soil was handled in the same manner as in Experiment 2 except that it was air-dried to facilitate mixing of the fertiliser and reduce contamination in the mixing process. 10.84 kg dry soil was packed into a plastic-bag lined pot.

The soil was not fumigated as this was believed to have affected phosphorus availability in Experiment 2. There was no evidence subsequently that the plants were affected by any soil pathogen.

(e) Experimental design and glasshouse layout

The same design as in Experiment 2 was used. Greater glasshouse space was available and the pots were spaced 10 cm apart in the row.

(f) Glasshouse operations

All seeds were germinated in petri dishes at 21°C on 20 July, 1974 and transferred to the pots on 22 and 23 July. Four seeds were planted in each pot in a square configuration. Due to the successful induction of poor growth caused by sub- and super-optimal treatments sisalation shades were not applied. Otherwise the operations were the same as in Experiment 2.

(g) Characters measured

The following data were recorded on all plants, excluding transplants.

(i) Heading Date (all heads)
(ii) Anthesis Date (" ")
(iii) Head Length (" ")
(iv) Spikelet Number (" ")
(v) Grain Weight (" ")
(vi) Grain Number (" ")
(vii) Height *
(viii) Total Weight (above ground, per plant)

* Height was measured as in Experiment 2.

(h) Derived characters

Derived characters were calculated as follows:

1) Harvest index

= (Grain weight per plant/Total weight per plant) x 100%.

2) Spikelet number per head

= Spikelet number per plant/head number per plant

3) Grain number per spikelet

= Grain number per plant/Spikelet number per plant

4) 1000 Grain weight

= (Grain weight per plant/Grain number per plant) x 1000

(i) Measures of heterosis

In addition to those measures of heterosis described in section 3.1.1. a further measure of the performance of a hybrid relative to its parents was made in Experiment 3. This was used for the characters time to heading and time to anthesis, where the hybrid was compared to the early parent as follows.

$$\text{EP} = \text{Heterosis relative to the early parent}$$

$$= \frac{(\text{Early parent} - \text{Hybrid})}{\text{Early parent}} * 100\%$$

(j) Statistical methods

Relationships between hybrid and parental performance were again analysed using the multiple regression procedure employed in Experiment 2 and described in Section 3.2.1.

3.3.2. Results

For most characters very highly significant differences between N and P treatments and significant N x P interactions were obtained from the analyses of variance (Table 26, p. 115). Sub- and super-optimal ranges were achieved for both nutrients in terms of grain and total weight (Figs. 28 and 30, pp. 123 and 126). N and P responses at sub-optimal, optimal and super-optimal P and N levels respectively for Halberd, Halberd x Warimek and Warimek are shown in Figures 22 to 27.

N-P response surfaces have been presented as contour maps. Maps for the three genotypes are shown in Figs. 28, 30, 32 and 34, parts A, B and C, while maps of heterosis relative to the high-parent (HP) and mid-parent (MP) are D and F respectively. Sections through the response surfaces at sub-optimal, optimal and super-optimal levels of P and N respectively are shown in Figs. 29, 31, 33 and 35.

Analyses presented for this experiment represent only three of the aspects of the interaction of heterosis and environment investigated in the previous two experiments. These include the relation between N-P response and heterosis, the multiple regression analysis of hybrid on parental performance and a study of macro-environmental variability.

Results of the analyses of yield components are not presented. Because of the larger number of environments sampled in this experiment, the relationships between components in the different environments were found to be extremely complex and did not provide any greater insight into the relationship between yield component interaction and heterosis for grain yield than was found in Experiment 2.

Neither is micro-environmental variability presented since it was not possible to obtain consistent estimates of this variability with four plants grown in each pot for each replicate and environment. The analysis was attempted but no trends were evident in the results to

Table 26: Analyses of variance for characters measured on Halberd, Warimek and their F1.

	Halberd			Warimek			Halberd x Warimek		
	N	P	N x P	N	P	N x P	N	P	N x P
Grain weight per plant	***	***	***	***	***	***	***	***	***
Total weight per plant	***	***	***	***	***	***	***	***	***
Harvest index	***	**	NS	***	***	*	***	***	NS
Height	***	***	**	***	***	NS	***	***	*
Time to heading	***	***	***	NS	***	NS	*	***	***
Time to anthesis	***	***	***	NS	***	*	*	***	***
Head number per plant	***	***	***	***	***	***	***	***	***
Spikelet number per head	***	***	NS	***	***	**	***	***	***
Spikelet number per plant	***	***	***	***	***	***	***	***	***
Grain number per spikelet	***	***	***	***	***	NS	***	***	*
Grain number per plant	***	***	***	***	***	***	***	***	***
1000 Grain weight	***	***	NS	***	***	***	***	***	**

Figure 22

Nitrogen response at 0 kg P/ha

for Halberd, Halberd x Warimek and Warimek

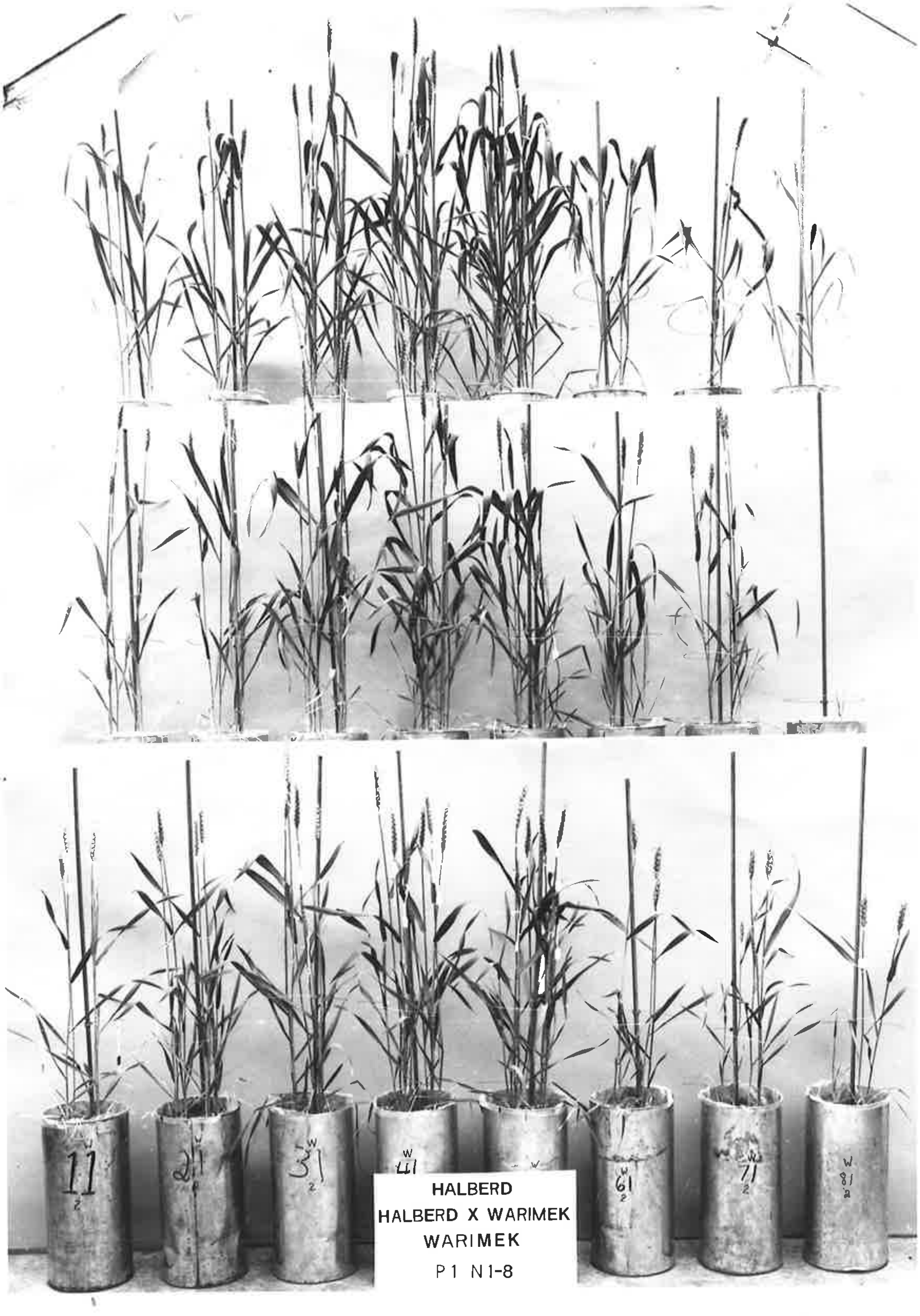

HALBERD
HALBERD X WARIMEK
WARIMEK
P1 N1-8
11
21
31
41
61
71
81

Figure 23

Nitrogen response at 100 kg P/ha for Halberd, Halberd x Warimek and Warimek

This level of P was not that at which maximum grain weight and total weight/plant occurred and therefore differs from that sampled in Figs. 29B, 31B, 33B and 35B. The optimum P level was unknown at the time of photographing.

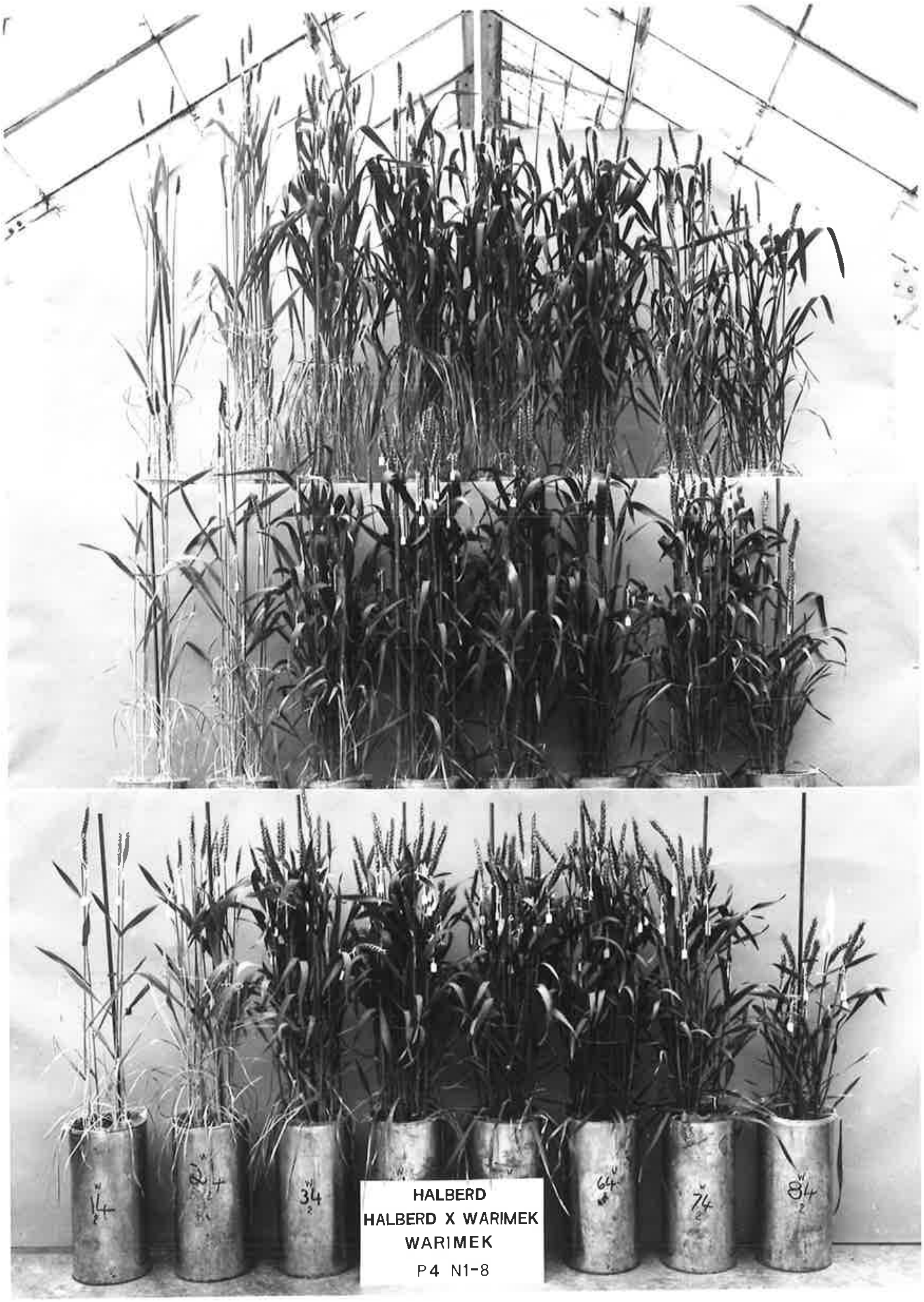

HALBERD
HALBERD X WARIMEK
WARIMEK
P4 N1-8
14
24
34
64
74
84

Figure 24

Nitrogen response at 15000 kg P/ha
for Halberd, Halberd x Warimek and Warimek

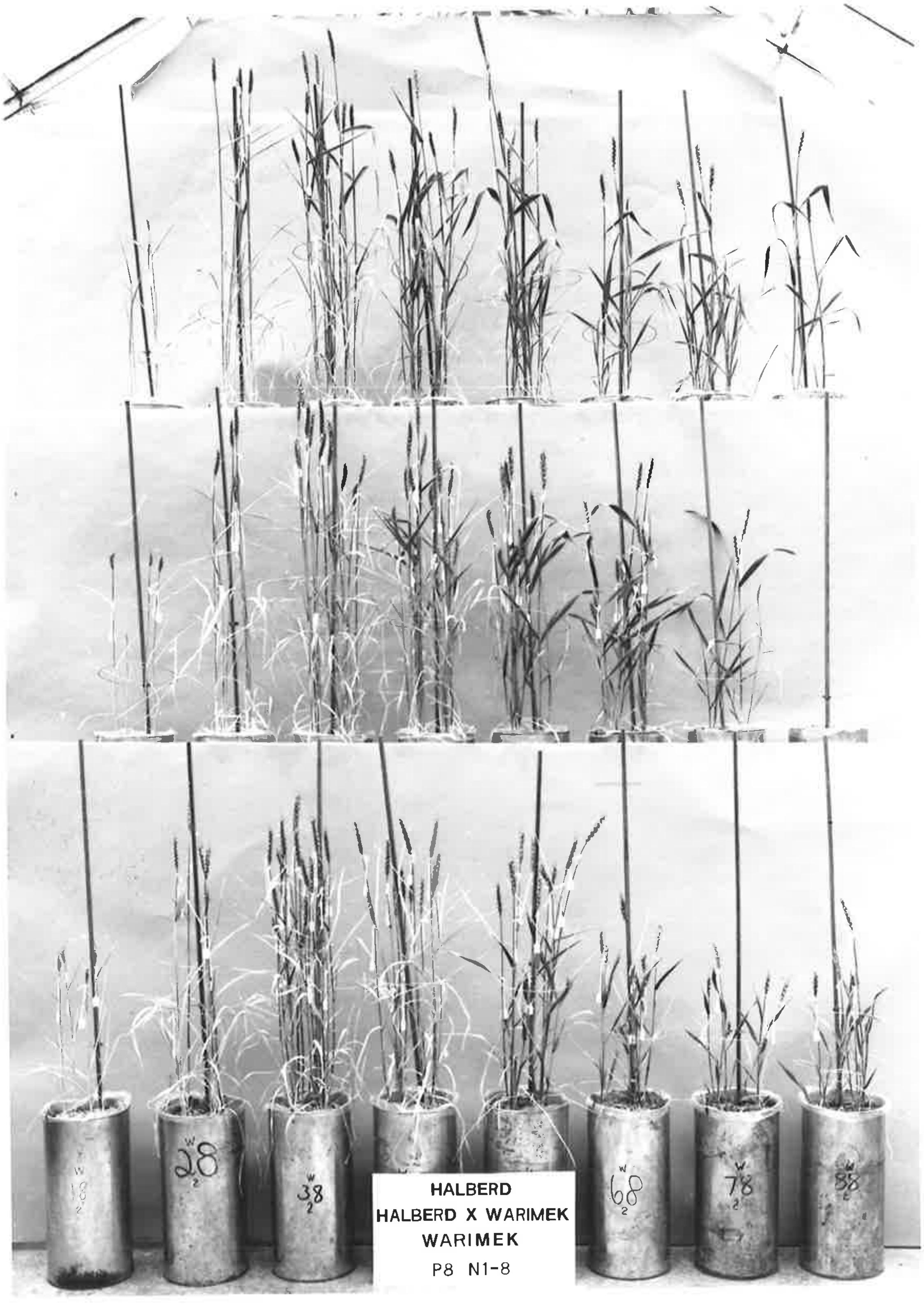

HALBERD
HALBERD X WARIMEK
WARIMEK
P8 N1-8
W 18 2
W 28 2
W 38 2
W 68 2
W 78 2
W 88 2

Figure 25

Phosphorus response at 0 kg N/ha

for Halberd, Halberd x Warimek and Warimek


11
12
13
14
15
16
17
18
HALBERD
HALBERD X WARIMEK
WARIMEK
N1 P1-8

Figure 26

Phosphorus response at 549 kg N/ha for Halberd, Halberd x Warimek and Warimek

This level of N was not that at which maximum grain weight and total weight/plant occurred and therefore differs from that sampled in Figs. 29E, 31E, 33E and 35E. The optimum N level was unknown at the time of photographing.

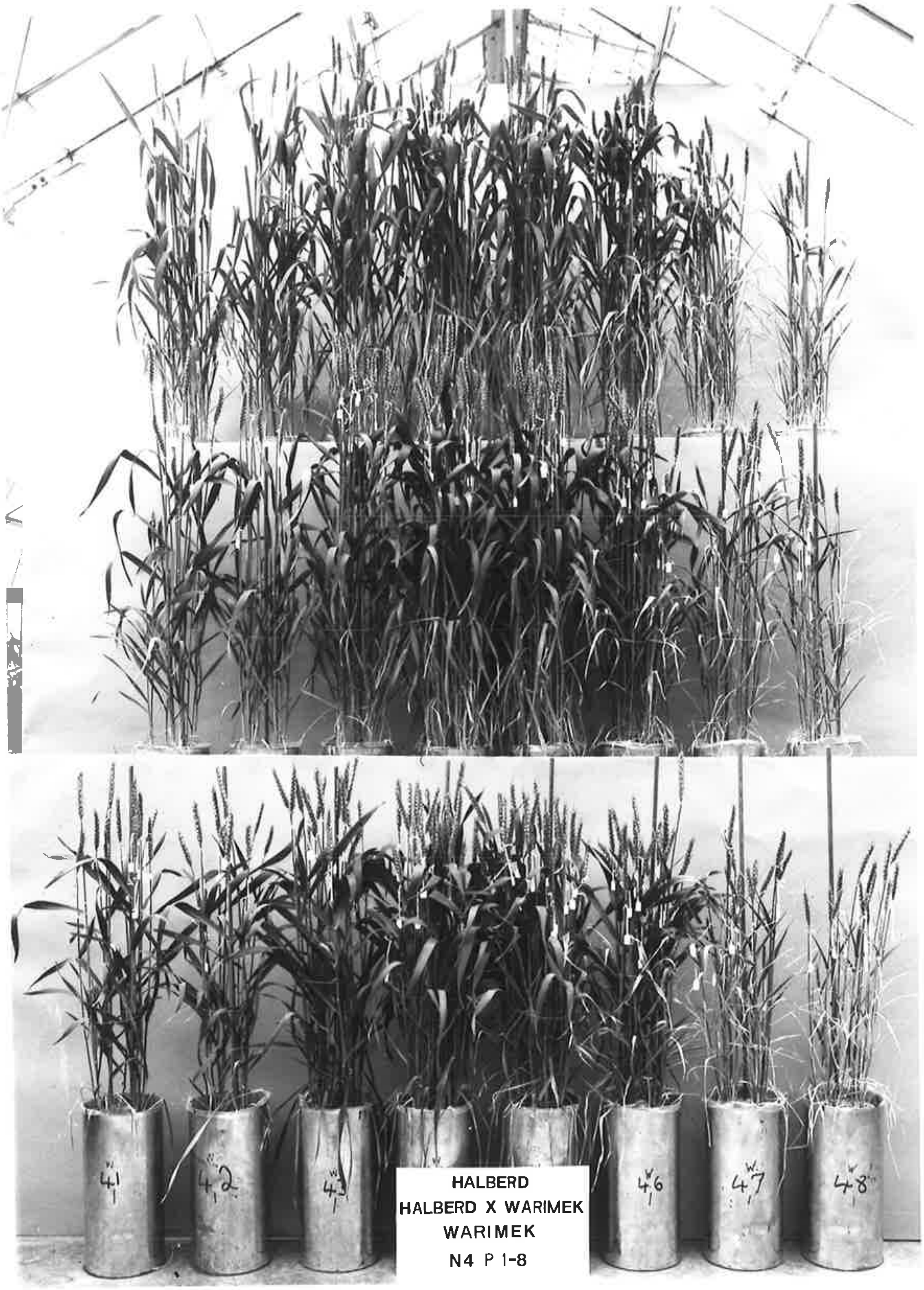

HALBERD
HALBERD X WARIMEK
WARIMEK
N4 P 1-8
W 41 1
W 42 1
W 43 1
W 46 1
W 47 1
W 48 1

Figure 27

Phosphorus response at 2560 kg N/ha
for Halberd, Halberd x Warimek and Warimek


W
81
2
W
82
1
W
83
1
HALBERD
HALBERD X WARIMEK
WARIMEK
N8 P 1-8
W
86
1
87
1
W
88
1

assist in the explanation of differences between genotypes. In Experiment 2 calculation of more accurate S.D.'s and C.V.'s was possible by pooling the plants of the eight P levels.

(a) Nitrogen - Phosphorus Response and Heterosis

Grain weight per plant

Examination of the response surfaces of all three genotypes revealed a number of features of nutrient element balance previously described (Shear *et al.*, 1946). Firstly, response to one nutrient was greater at optimal levels of the other nutrient. Secondly, maximum grain weight was produced at a higher level of a nutrient when the alternative nutrient was supplied at an optimal level than at both sub- and super-optimal levels. For example, optimal grain weight at 0 and 2560 kg N/ha occurred at 100 kg P/ha, but at 1000 kg P/ha at the optimal level of N (914 kg/ha) (Fig. 29, p. 124).

The parental response surfaces showed some differences. The optimal fertiliser levels for Halberd were 1371 kg N/ha and 1000 kg P/ha while for Warimek it was at a similar level of P but at a lower level of N (549-914 kg/ha) (Fig. 28A, 28C, p. 123). Although Halberd produced more grain than Warimek at its optimum, it produced less than Warimek in the lower levels of N at intermediate levels of P (Fig. 29B, p.124).

The response of the hybrid displayed the influence of both parents having a maximum grain weight equivalent to that produced by Halberd, at a level of N intermediate between the levels at which parental optima were observed (Fig. 29B, p.124). The level for P was the same as both parents. As a result, the grain yield of the hybrid exceeded both parents in many of the environments involving the lower N levels at intermediate P levels (Fig. 28D, p.123).

Figure 28

Nitrogen - Phosphorus response

Contour diagrams of grain weight/plant (g. plant^{-1})

(A) Halberd

(B) Halberd x Warimek

(C) Warimek

(D) Heterosis relative to the high-parent

(E) Fitted values for the hybrid estimated from the multiple regression analysis

(F) Heterosis relative to the mid-parent

Parts of the diagrams have been cross-hatched to emphasise the contrasts in the responses

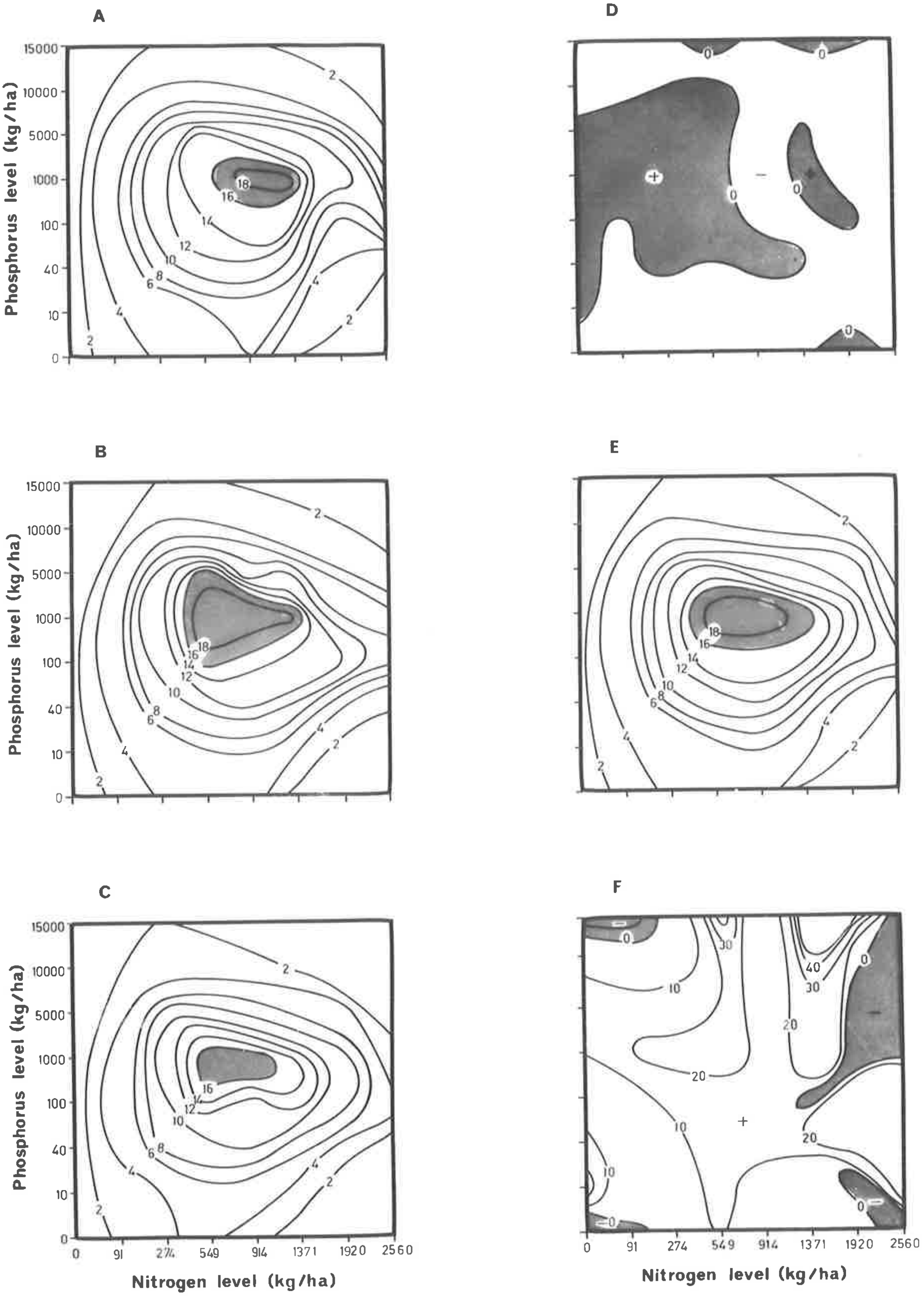

A
Phosphorus level (kg/ha)
15000
10000
5000
1000
100
40
10
0
2
4
6
8
10
12
14
16
18
D
0
+
−
B
Phosphorus level (kg/ha)
2
4
6
8
10
12
14
16
18
E
2
4
6
8
10
12
14
16
18
C
Phosphorus level (kg/ha)
2
4
6
8
10
12
14
16
0
91
274
549
914
1371
1920
2560
Nitrogen level (kg/ha)
F
0
10
20
30
40
+
−
Nitrogen level (kg/ha)

Figure 29

Nitrogen - Phosphorus response

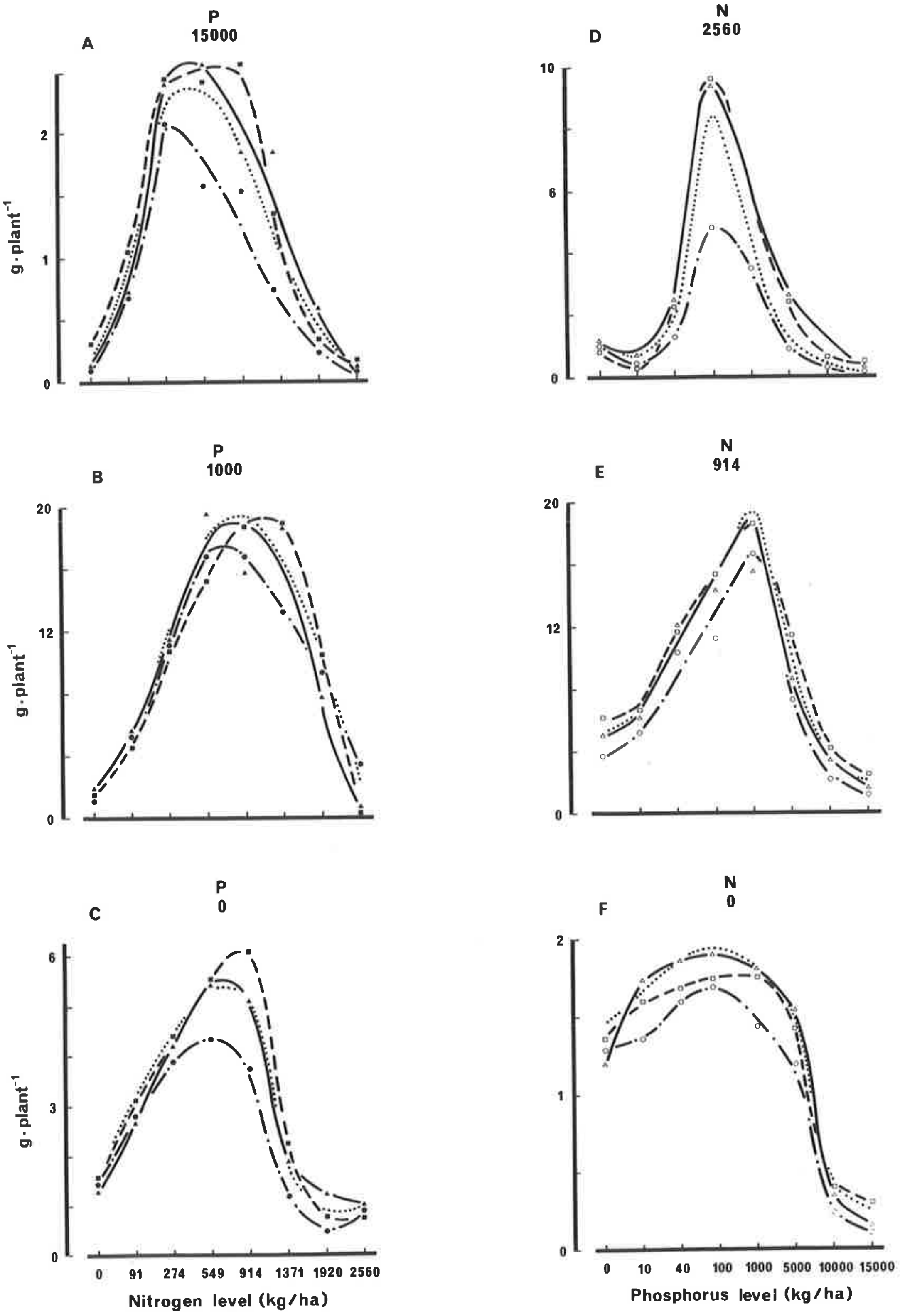
Sections through response surfaces for grain weight/plant

1. Nitrogen response at:
   - (A) 15000 kg P/ha
   - (B) 1000 kg P/ha
   - (C) 0 kg P/ha

   For: Halberd (■— — —■), Warimek (●-——-●), Halberd x Warimek (▲ —— ▲) and fitted values for the hybrid estimated from the multiple regression analysis (·········)

2. Phosphorus response at:
   - (D) 2560 kg N/ha
   - (E) 914 kg N/ha
   - (F) 0 kg N/ha

   For: Halberd (□— — —□), Warimek (○-——-○), Halberd x Warimek (△ ——△) and fitted values for the hybrid estimated from the multiple regression analysis (·--------)


A
P
15000
2
1
0
g·plant⁻¹
D
N
2560
10
6
0
B
P
1000
20
12
0
g·plant⁻¹
E
N
914
20
12
0
C
P
0
6
3
0
g·plant⁻¹
0
91
274
549
914
1371
1920
2560
Nitrogen level (kg/ha)
F
N
0
2
1
0
0
10
40
100
1000
5000
10000
15000
Phosphorus level (kg/ha)

Total weight per plant

Differences between the parental responses for this character were smaller than for grain weight and optima for N and P occurred at the same treatment, 914 kg N/ha and 1000 kg P/ha (Fig. 31B, p.127). Halberd was the high-parent with the greater total weight in all treatments.

The response of the hybrid was intermediate between the parents in most environments and its optimum was at the same level of N and P as the parents. As a result of this similarity no change in the relative performance of the hybrid or heterosis was detected near the optimum. However, heterosis occurred in some marginal environments, low N, intermediate P and high N, intermediate and high P. The occurrence of this heterosis resulted in significant differences being detected for heterosis relative to the high-parent (HP) between N levels (Table 27, p. 128).

Harvest index

At low levels of N and P a harvest index of 40% was observed increasing to 50% at optimal levels of N and P. At super-optimal levels harvest index fell again to values of less than 10% indicating the relatively more severe effect of toxicity on reproductive development than on vegetative growth. The changes in harvest index with N and P were very highly significant (Table 26, p. 115).

The optimum condition for harvest index in Halberd (48%) did not occur in the same environment as grain or total weight optima but at a higher level of N (1920 kg N/ha). The grain weight optimum occurred at 1371 kg N/ha and total weight optimum at 914 kg N/ha.

Harvest index for Warimek exceeded 50% in the range 549-1920 kg N/ha. Consequently, the harvest index of Warimek was greater than Halberd at the lower levels of N and P.

The hybrid expressed an optimum equivalent to Warimek (50%) at

Figure 30

Nitrogen - Phosphorus response

Contour diagrams of total weight/plant (g. plant^{-1})

(A) Halberd

(B) Halberd x Warimek

(C) Warimek

(D) Heterosis relative to the high-parent

(E) Fitted values for the hybrid estimated from the multiple regression analysis

(F) Heterosis relative to the mid-parent

Parts of the diagrams have been cross-hatched to emphasise the contrasts in the responses

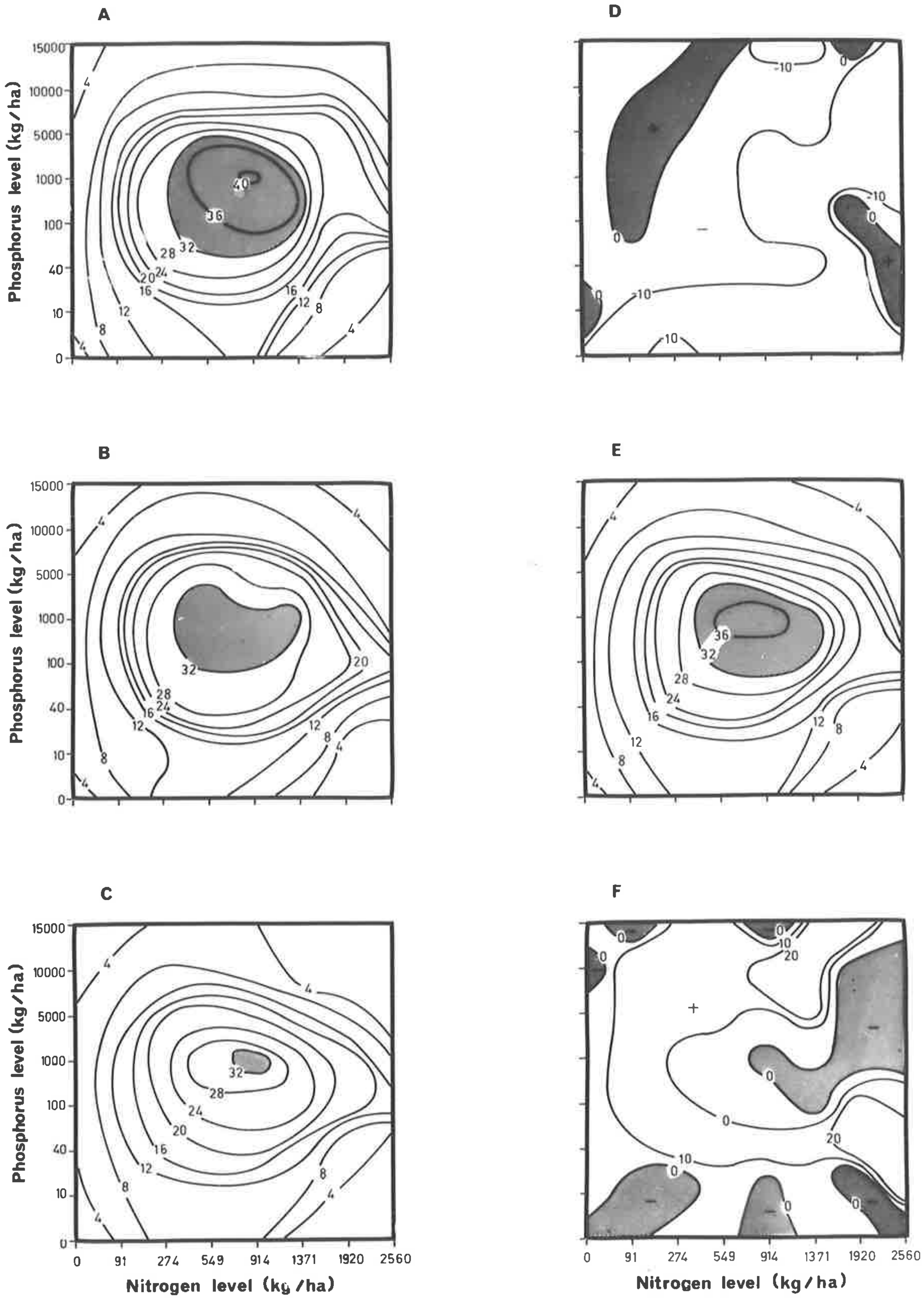

A
B
C
D
E
F
Phosphorus level (kg/ha)
15000
10000
5000
1000
100
40
10
0
Nitrogen level (kg/ha)
0
91
274
549
914
1371
1920
2560
4
8
12
16
20
24
28
32
36
40
0
10
20
-10
+
−

Figure 31

Nitrogen - Phosphorus response

Sections through response surfaces for total weight/plant

1. Nitrogen responses at:

   (A) 15000 kg P/ha

   (B) 1000 kg P/ha

   (C) 0 kg P/ha

   For: Halberd (■— — —■), Warimek (●-—-●), Halberd x Warimek (▲———▲) and fitted values for the hybrid estimated from the multiple regression analysis (········)

2. Phosphorus responses at:

   (D) 2560 kg N/ha

   (E) 914 kg N/ha

   (F) 0 kg N/ha

   For: Halberd (□— — —□), Warimek (○-—-○), Halberd x Warimek (△—— △) and fitted values for the hybrid estimated from the multiple regression analysis (········)

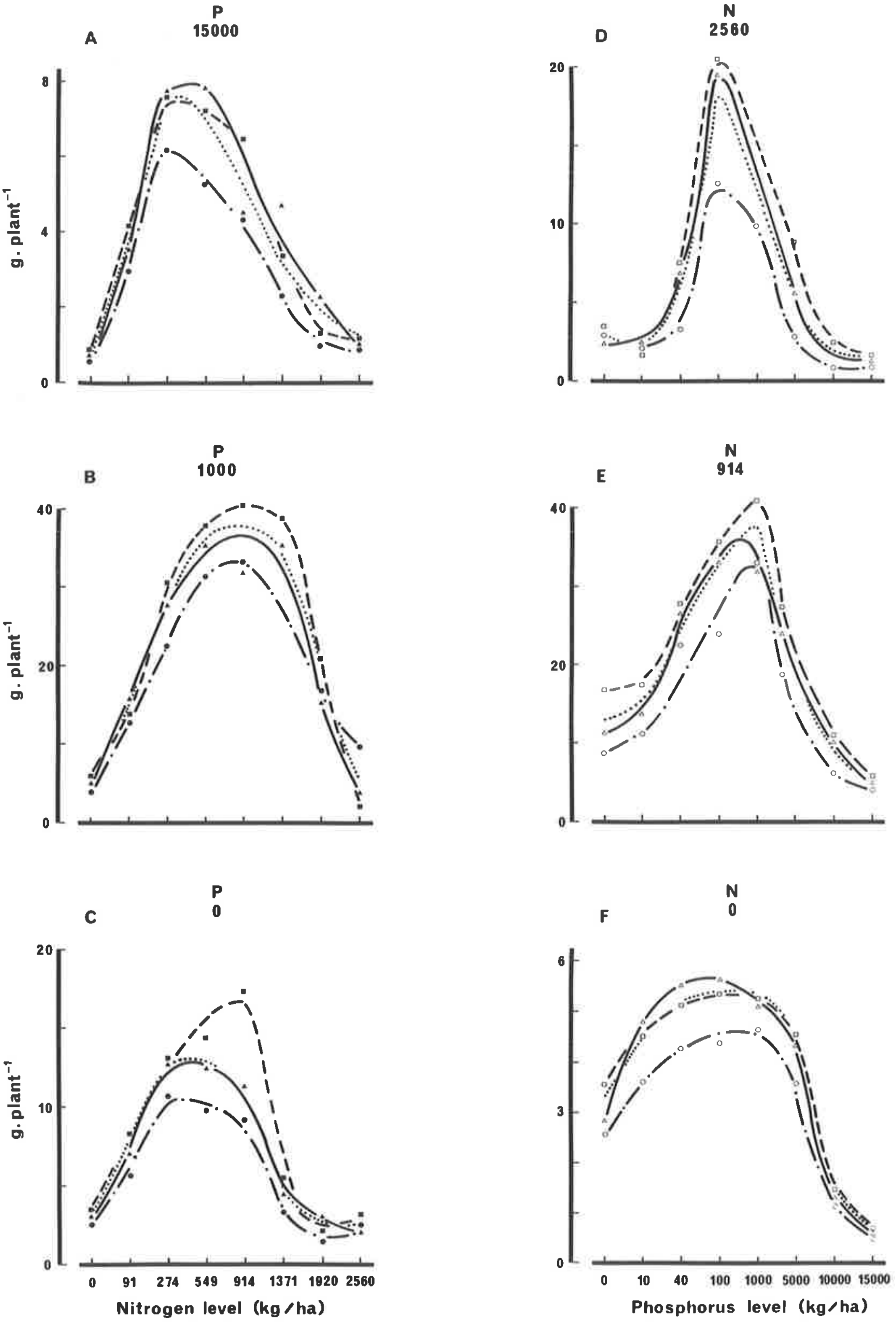

A
P
15000
8
4
0
g. plant^{-1}
D
N
2560
20
10
0
B
P
1000
40
20
0
g. plant^{-1}
E
N
914
40
20
0
C
P
0
20
10
0
g. plant^{-1}
0
91
274
549
914
1371
1920
2560
Nitrogen level (kg/ha)
F
N
0
6
3
0
0
10
40
100
1000
5000
10000
15000
Phosphorus level (kg/ha)

Table 27: Analyses of variance for heterosis relative to the high-parent (HP) and mid-parent (MP).

	HP			MP		
	N	P	N x P	N	P	N x P
Grain weight per plant	NS	NS	NS	NS	NS	NS
Total weight per plant	*	NS	NS	NS	NS	NS
Harvest index	**	NS	NS	*	NS	NS
Height	NS	NS	NS	NS	NS	NS
Head number per plant	***	NS	NS	NS	NS	NS
Spikelet number per head	NS	**	NS	NS	*	NS
Spikelet number per plant	***	NS	NS	NS	NS	NS
Grain number per spikelet	NS	NS	NS	***	NS	*
Grain number per plant	***	NS	*	NS	NS	NS
1000 Grain weight	NS	NS	NS	*	NS	NS

Figure 32

Nitrogen - Phosphorus response

Contour diagrams of harvest index (%)

(A) Halberd

(B) Halberd x Warimek

(C) Warimek

(D) Heterosis relative to the high-parent

(E) Fitted values for the hybrid estimated from the multiple regression analysis

(F) Heterosis relative to the mid-parent

Parts of the diagrams have been cross-hatched to emphasise the contrasts in the responses

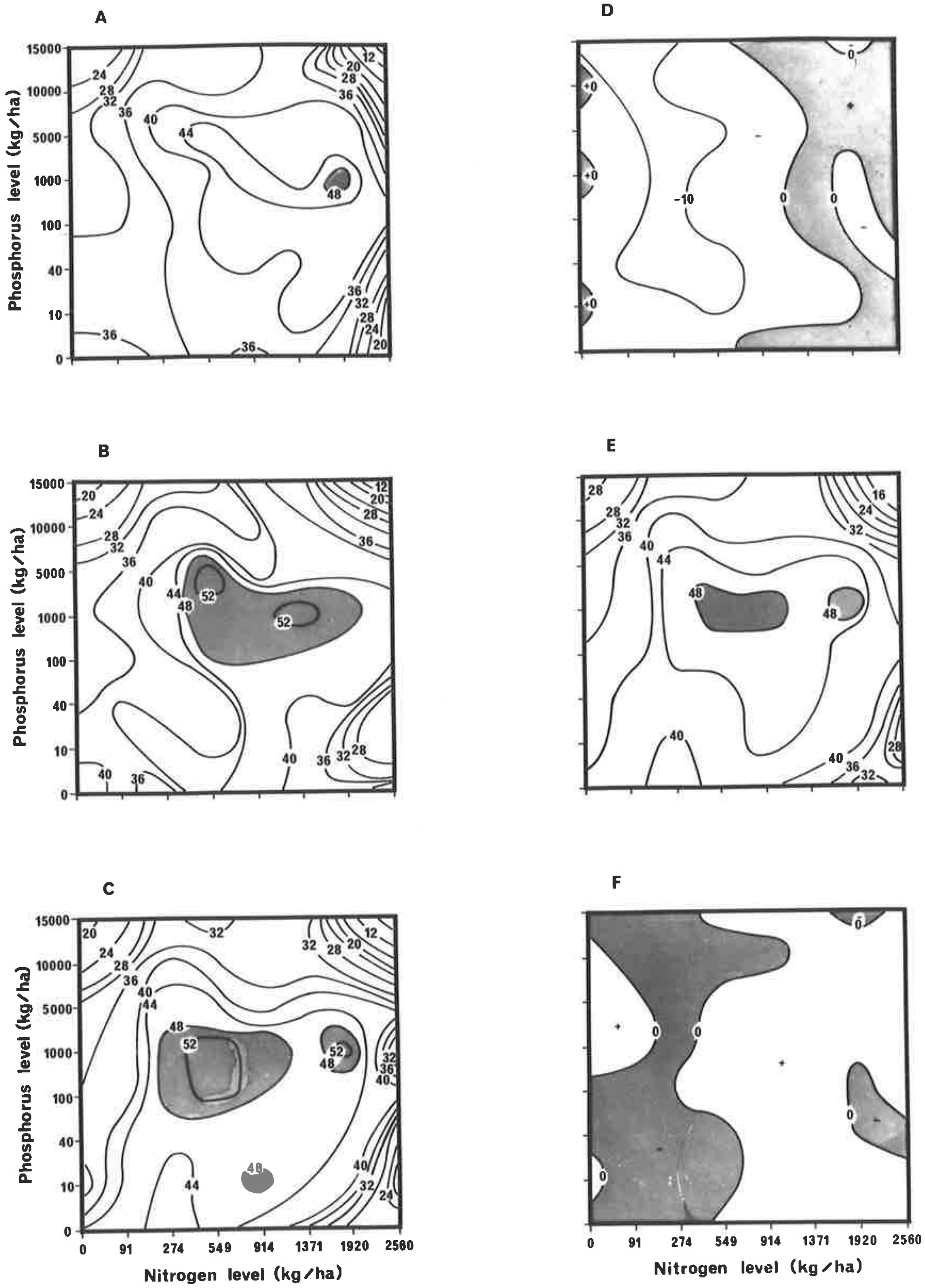

A
B
C
D
E
F
Phosphorus level (kg/ha)
15000
10000
5000
1000
100
40
10
0
Nitrogen level (kg/ha)
0
91
274
549
914
1371
1920
2560
12
20
24
28
32
36
40
44
48
52
16
-10
+0
0

Figure 33

Nitrogen - Phosphorus response

Sections through response surfaces for harvest index

1. Nitrogen response at:

   (A) 15000 kg P/ha

   (B) 1000 kg P/ha

   (C) 0 kg P/ha

   For: Halberd (■- - - -■), Warimek (●- - - - -●)

   and Halberd x Warimek (▲———▲)

2. Phosphorus responses at:

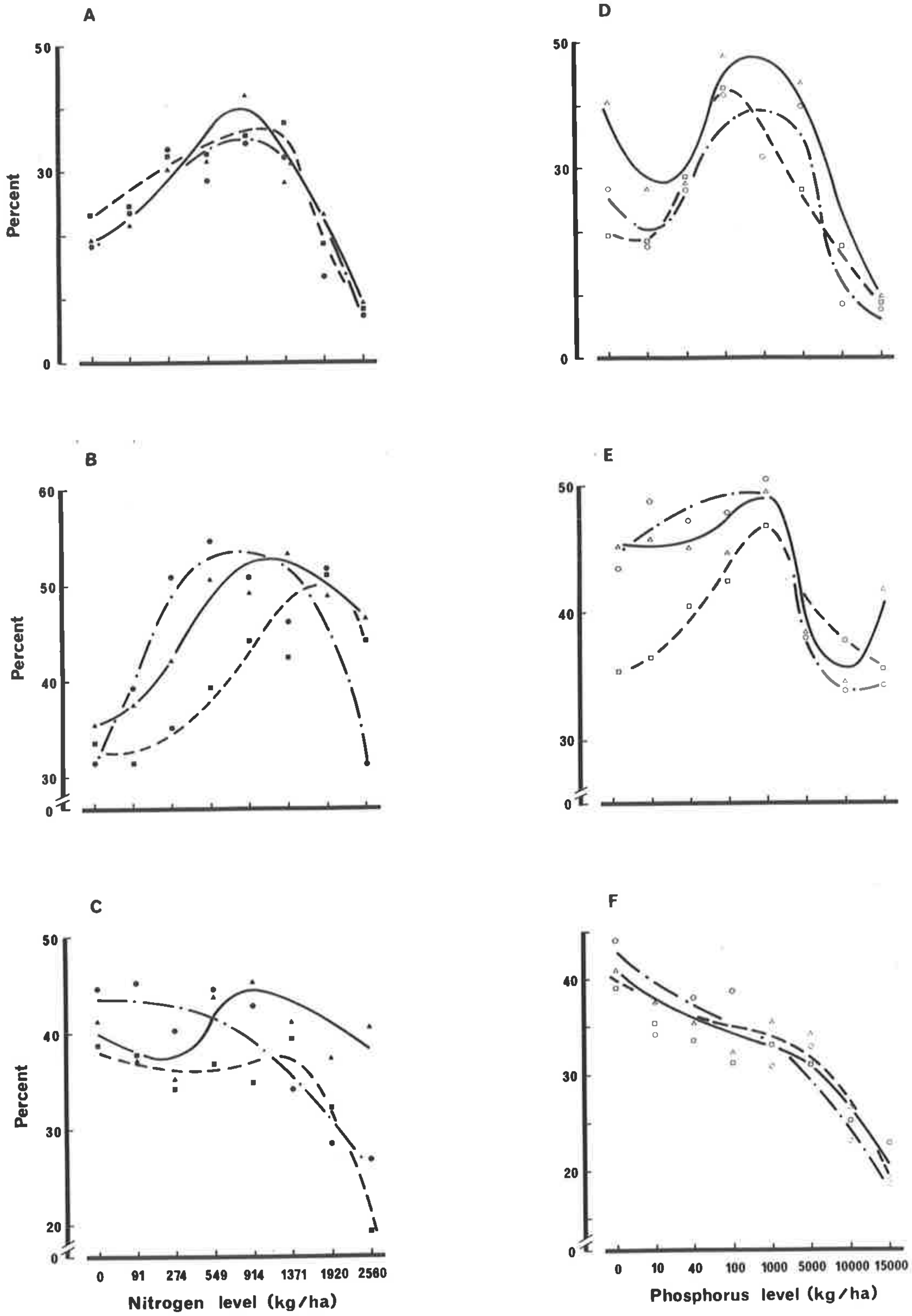
   (D) 2560 kg N/ha

   (E) 914 kg N/ha

   (F) 0 kg N/ha

   For: Halberd (□- - - □), Warimek (○- - - -○)

   and Halberd x Warimek (△ ——— △)


A
D
B
E
C
F
Percent
Percent
Percent
50
30
0
50
30
0
60
50
40
30
0
50
40
30
0
50
40
30
20
0
40
30
20
0
0
91
274
549
914
1371
1920
2560
Nitrogen level (kg/ha)
0
10
40
100
1000
5000
10000
15000
Phosphorus level (kg/ha)

1371 kg N/ha and at the same level of P as both parents (1000 kg/ha). Since grain weight produced by the hybrid was not as greatly depressed by super-optimal levels of N as were parental grain weights, heterosis for harvest index was observed in this range at all levels of P. As a result significant differences were detected between N levels for heterosis relative to both the high- and mid-parents (Table 27, p 128).

Time to heading and anthesis

The number of days from germination of the seed to heading was recorded for each tiller. The criterion for heading was emergence of the lowest spikelet node from the flag leaf sheath. Anthesis was measured as extrusion of the first anthers from any floret. A longer mean time to heading and anthesis would occur for plants grown in treatments which allow more tillers to develop and as this may have no relation to the inherent maturity of the plant, values for the first tiller only on each plant were analysed.

Time to heading changed little across environments and most plants headed within a five day period (Fig. 34, p. 132). The major effects were delayed heading at high and low levels of N and P.

Differences in response were observed between the parents. For Halberd heading was delayed by low and high levels of both N and P. Further, a positive interaction was shown between N and P reducing time to heading. As a result the earliest heading treatments occurred at intermediate to high levels of N and P (Fig. 34A, p. 132).

Although Warimek was the early-parent in all environments, it was delayed only under conditions of low N high P and high N low P, that is in environments in which the greatest imbalance occurred between N and P (Fig. 34C, p. 132). As a result no significant differences were found between N treatments for this parent (Table 26, p. 115).

Heterosis for time to heading and anthesis was considered to occur

Figure 34

Nitrogen - Phosphorus response

Contour diagrams of time to heading (days)

(A) Halberd

(B) Halberd x Warimek

(C) Warimek

(D) Heterosis relative to the high-parent

(E) Fitted values for the hybrid estimated from the multiple regression analysis

(F) Heterosis relative to the mid-parent

Parts of the diagrams have been cross-hatched to emphasise the contrasts in the responses

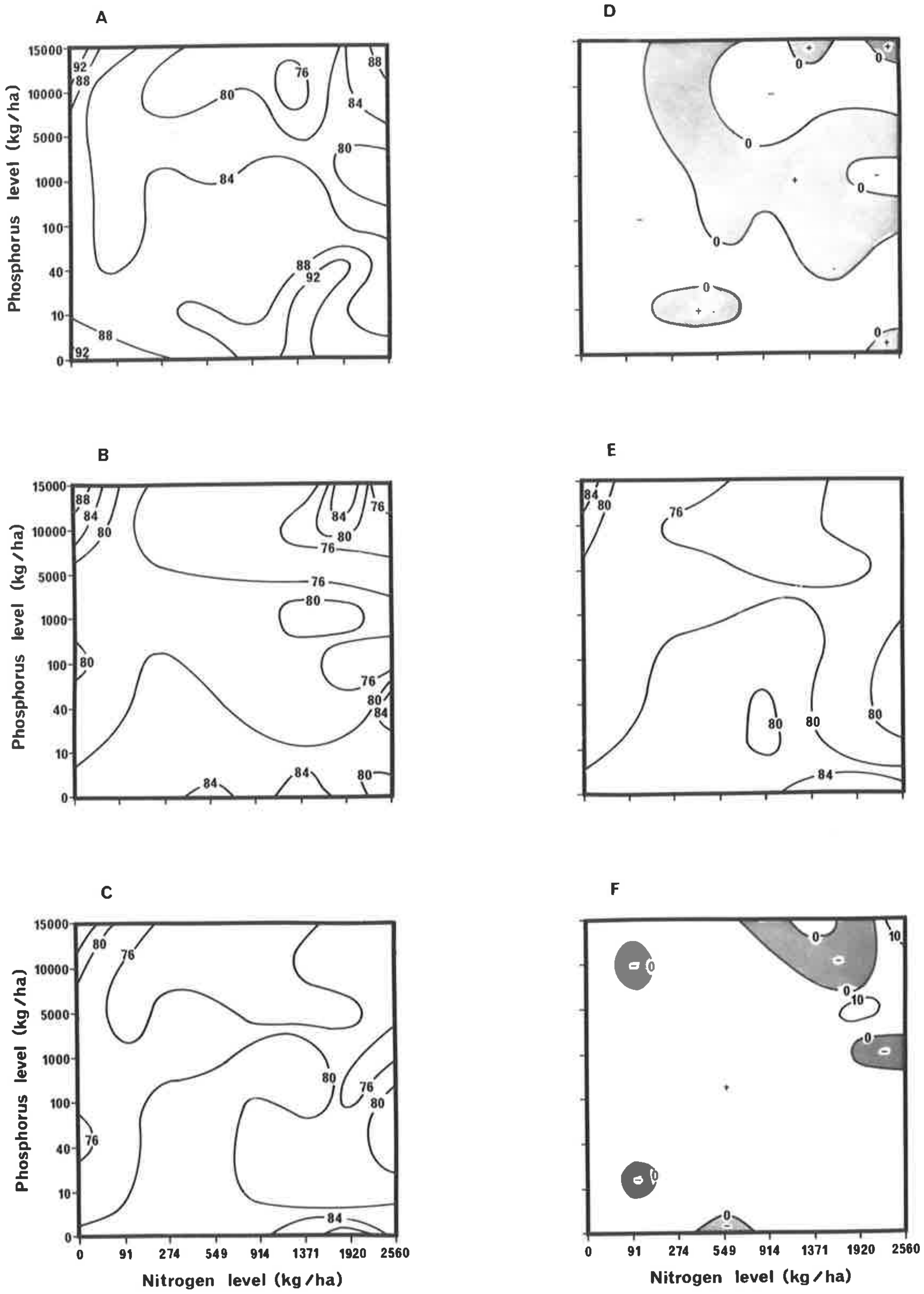

A
D
B
E
C
F
Phosphorus level (kg/ha)
15000
10000
5000
1000
100
40
10
0
Nitrogen level (kg/ha)
0
91
274
549
914
1371
1920
2560
92
88
80
76
84
0
+
-
10

Figure 35

Nitrogen - Phosphorus response

Sections through response surfaces for time to heading

1. Nitrogen responses at:

    (A) 15000 kg P/ha

    (B) 1000 kg P/ha

    (C) 0 kg P/ha

    For: Halberd (■- - - ■), Warimek (●-—-●)

    and Halberd x Warimek (▲——▲)

2. Phosphorus responses at:

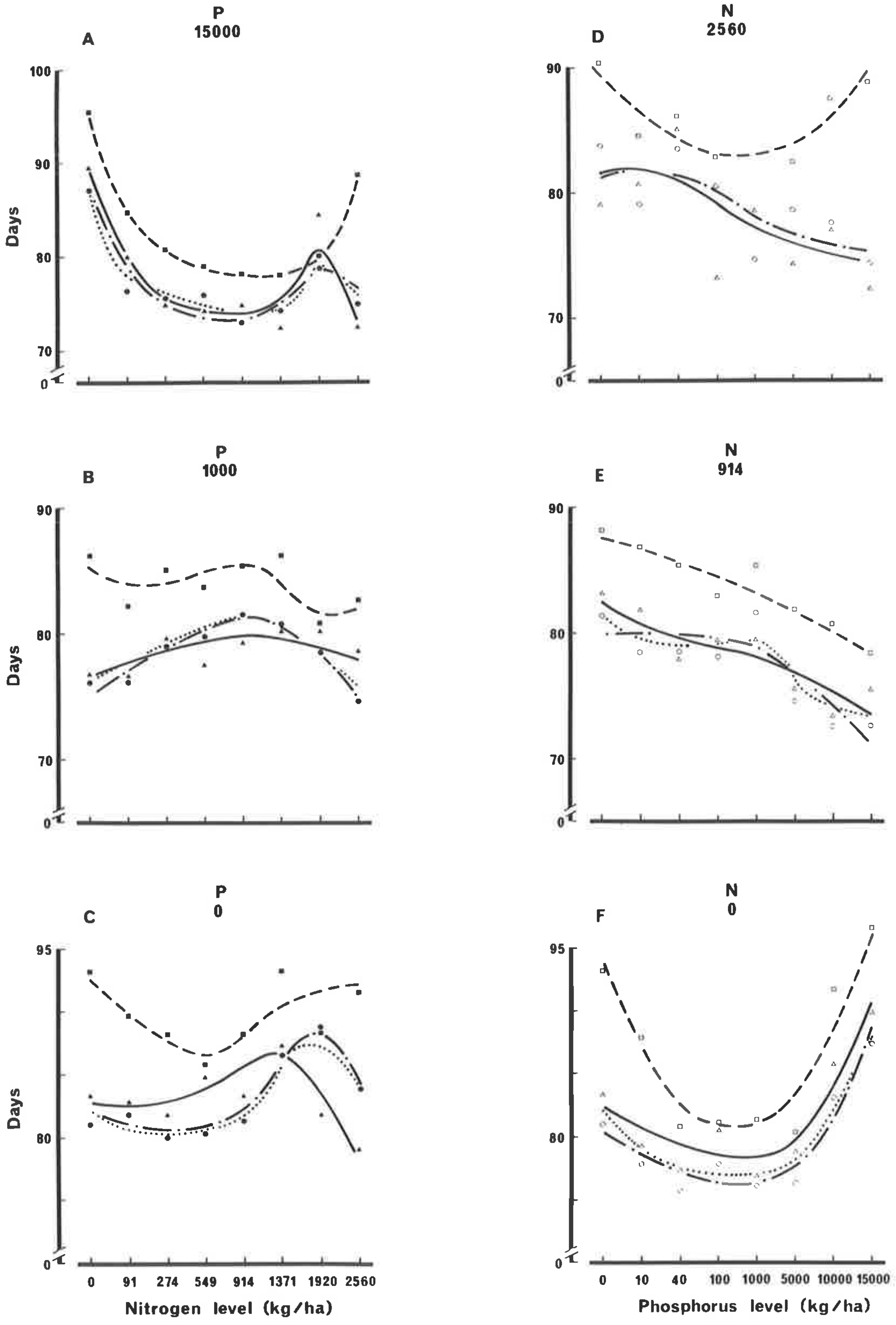
    (D) 2560 kg N/ha

    (E) 914 kg N/ha

    (F) 0 kg N/ha

    For: Halberd (□- - -□), Warimek (○----○)

    and Halberd x Warimek (△——△)


A
P
15000
100
90
80
70
0
Days
D
N
2560
90
80
70
0
B
P
1000
90
80
70
0
Days
E
N
914
90
80
70
0
C
P
0
95
80
0
Days
0
91
274
549
914
1371
1920
2560
Nitrogen level (kg/ha)
F
N
0
95
80
0
0
10
40
100
1000
5000
10000
15000
Phosphorus level (kg/ha)

when the hybrid reached these stages before both parents. Although the mean heading date of the hybrid (79 days) was more similar to the early-parent Warimek (78 days), the performance of the hybrid relative to the early parent changed over N and P. Heterosis was expressed at intermediate and high levels of both nutrients (Fig. 34D, p. 132).

The relative responses of the three genotypes for time to anthesis were similar to those for heading time.

Table 28: Analyses of variance for heterosis relative to the early-parent (EP) and mid-parent (MP)

	EP			MP	
N	P	N x P	N	P	N x P
Time to heading					
NS	NS	NS	*	NS	*
Time to anthesis					
NS	NS	NS	*	NS	NS

(b) Multiple Regression Analysis

The relationships between hybrid and parental performance for the four characters described above have been analysed using the multiple regression procedure described in Section 3.2.1. Hybrid response estimated from the regressions on parental yields are displayed as contour maps in part E of Figs. 28, 30, 32 and 34 and in cross-section in Figs. 29 and 31.

The regression of hybrid grain weight on parental grain weights performed over all 64 N-P treatments revealed that more than 90% of the hybrid variation was accounted for by variation in parental response (Table 29, p. 135). A good estimate of hybrid performance was obtained at all levels of N and P (Fig. 28E, p. 123).

The b values of 0.44 for Halberd and 0.66 for Warimek indicate that hybrid response was more closely associated with Warimek. Since the constant, 0.054g, was small relative to the yields obtained in most environments the estimated equation of the hybrid may be reduced to

$$y = b_1P_1 + b_2P_2$$

or more specifically

$$y = 0.44P_1 + 0.66P_2$$

The hybrid yield could be considered as the weighted resultant of parental yields. Similar results were obtained for total weight per plant, harvest index and time to heading (Table 29).

Table 29: Multiple regression of hybrid value on parental values

Char.	Variable	B	S.E.	R	F
Grain weight	Constant	0.05	0.92		
	Halberd	0.44	0.12	0.02	14.3***
	Warimek	0.66	0.13	0.90	24.9***
Total weight	Constant	0.05	2.23		
	Halberd	0.45	0.11	0.02	17.5***
	Warimek	0.62	0.15	0.90	18.2***
Harvest index	Constant	5.74	4.77		
	Halberd	0.34	0.10	0.05	11.2**
	Warimek	0.54	0.08	0.71	47.0***
Time to heading	Constant	5.30	12.41		
	Halberd	0.15	0.10	0.02	2.4
	Warimek	0.78	0.12	0.61	42.3***

(c) Macro-environmental Variability

When a response surface is obtained the variance of points on the surface can be considered as a measure of macro-environmental variability. An alternative macro-environmental variability may be estimated as the variance of points on the response curves that make up the surface.

Estimates for many of these curves could be obtained. Those that will be considered include the variances of grain and total weight for all three genotypes calculated over N and P response curves at sub-optimal, optimal and super-optimal P and N respectively. These variances as well as the variances over all treatments comprising the N-P response surfaces are presented in Table 30. The response curves from which these latter variances were calculated are displayed in Figs 29 and 31.

As in Experiment 2 the hybrid was more variable than its parents for grain weight per plant. Even though the hybrid had a response with an optimum at a level of N intermediate between those of its parents, the hybrid had a higher mean expression at the optimum.

The response of the hybrid across N at sub- and super-optimal P was generally intermediate between the parents. As a result the variability of the hybrid was intermediate at these P levels (Fig. 29A, 29C, p. 124). However, because of the greater response of the hybrid at the optimal P level, the hybrid was more variable than both parents in this range (Fig. 29B, p. 124).

The expression of heterosis at most levels of P in sub-optimal levels of N resulted in the hybrid being more variable than the parents across P levels. Similarly, at optimal and the highest level of N where hybrid performance was equivalent to the high-parent the hybrid was more variable.

Heterosis for total weight, on the other hand, was expressed only in few environments sub- or super-optimal for one or both nutrients. The relative performance of the hybrid was generally intermediate between the parents (Fig. 31, p. 127). Consequently, the variability of the hybrid was also intermediate (Table 30, p. 137). Only at low N where heterosis occurred, was the hybrid more variable than both parents.

Table 30: Macro-environmental variability measured as variances over all N-P treatments and over N and P at sub-optimal, optimal and super-optimal P and N respectively.

	Overall	Over N			Over P		
		P 0	P 1000	P 15000	N 0	N 914	N 2560
Grain weight per plant							
Halberd	26.5	4.1	36.0	2.2	2.7	28.8	20.9
Warimek	19.4	2.8	26.5	1.3	2.8	28.1	10.3
Halberd x Warimek	28.8	3.5	37.4	2.1	3.3	35.2	23.0
Total weight per plant							
Halberd	141.6	35.6	167.9	16.5	26.4	132.5	96.8
Warimek	74.2	14.0	80.3	7.5	17.8	93.5	41.4
Halberd x Warimek	123.2	20.9	125.2	12.2	27.2	125.9	93.5

3.3.3. Discussion

The range of N levels employed in this experiment was greater than in Experiment 2 because the lowest level was merely virgin soil while the highest level was the same in both experiments. This difference is supported by the fact that at optimum P less grain weight was produced at low N than at comparable levels in Experiment 2 even though Halberd and Warimek were more responsive to N than Heron and Strain 52.

It is probable that the reduction in plant growth at super-optimal levels of N and P was a result of the high levels of salts of these nutrients present in the soil. It could not have been due to lodging or interplant competition for light or water, nor could it have been due to any known imbalance in nutrients other than N and P. The toxic effects of N and P differed. For high N there was a reduction in growth of the whole plant from the time of the second application. This was to be expected since N was supplied in a highly soluble form (NH_3NO_4). The toxicity symptoms for P were observed as a necrosis extending from the tips of the leaves approximately two weeks after the emergence of each leaf. The heads were also affected, spikelets dying from the top of the head at about 14 days. In comparison to N, the P source was relatively insoluble and would be expected to take some time to accumulate to a level where necrosis occurred. These symptoms were similar to those observed by Bhatti and Loneragan (1970a,b).

It has been pointed out that the level of N at which maximum grain weight was produced was higher when the other factor P was supplied at an optimal level than at sub- and super-optimal levels. A similar result was observed for response to P. A generalisation may be drawn that an optimum for a factor will be at a higher level when other factors are nearer to their optima. All factors are thereby interdependent in their effects on character expression. It is understandable therefore that optima for N and P in the glasshouse for spaced plants may be much higher than in the field for plants at commercial densities (Gardener and Rathjen, 1975; Jessop, 1974) where water and light would be supplied at sub-optimal levels. Such differences in environments between the glasshouse and field are likely to cause changes in the relative performance of hybrids and parents.

Grain and Total weight As was found in Experiment 2 heterosis for grain and total weight was less pronounced in the glasshouse than in the field. This result was common to both experiments although two different sets of curves were involved. In many of the environments achieved in the glasshouse Halberd x Warimek did not express heterosis and its maximum was only 15% higher than the high-parent. Whereas in Experiment 1 values ranged up to 50% greater than the high-parent. Apparently the response to environmental factors other than N and P were responsible for the occurrence of high levels of heterosis in the field.

Heterosis for grain weight in this hybrid was observed at both low and optimum N but not at super-optimal levels. In this it is different from Heron x Strain 52 where heterosis did not occur at low N levels but was found to increase with N. It is evident from these results for the N response that heterosis does not only occur in nutritionally optimal environments, as was found for response to P and in other studies (Griffing and Zsiros, 1971), but may be found in a more general range of environments.

Harvest index The ranking of the parents for harvest index changed with N level. At low and intermediate N levels Warimek had the highest harvest index since it produced more grain, it was the shorter parent and had a lower total weight. In fact it was shorter in all environments probably as a result of its Norin 10 ancestry. On the other hand, because Halberd was tall, and therefore likely to have had heavier stems, the greater grain weight produced by this parent at high

N resulted in it having a higher harvest index in this range.

Even though the hybrid displayed heterosis for grain weight in the low and intermediate N levels, heterosis for harvest index was expressed only at the lowest and high N levels. As in Experiment 2, this response could not be attributed to the production of non-heading tillers but to the greater height responsiveness of the hybrid. Although Halberd x Warimek was intermediate in height in all environments, it was closer to the tall parent, Halberd, at intermediate N levels. As a result, at low N, the greater grain weight produced by the hybrid relative to Warimek was not associated with a comparable greater height and therefore total weight, while at high N the reduction in hybrid grain weight relative to Halberd was not as great as the reduction in height and total weight. As a result the genotype producing the greatest amount of grain at most N levels did not have the highest harvest index.

Heading dates The effect of N and P on heading date may be modified by the effect of these fertilisers on other plant processes. Kirby (1967) has suggested that suppression of tillering may speed development. This relationship may explain the delay in heading dates of Warimek and the hybrid at intermediate N levels when comparisons are made at intermediate P. However, at optimum N, earlier maturity was obtained with increasing levels of P, quite unrelated to the production of heads which reached an optimum at 1000 kg P/ha. Similarly, delays in heading at low and high levels of N and P suggest that other processes within the plant were important in controlling maturity.

Multiple regression analysis The relationship between Halberd x Warimek and its parents determined by multiple regression analysis exhibited some differences from that for Heron x Strain 52. Now, the regression coefficients of both parents were significant although the one for Warimek was larger and accounted for a greater proportion of variation in hybrid response. Hybrid performance was more closely associated with that of Warimek. This feature is evident for the grain weight responses where the parents have different N optima. The optimum grain weight for the hybrid occurred at an N level intermediate between the parents, but closer to that of Warimek. Further consideration will be given to this topic in the general discussion.

Macro-environmental variability In this, as in the previous two experiments, the occurrence of heterosis resulted in the macro-environmental variability of the hybrid being greater than the parents. Because heterosis for grain weight occurred at low and intermediate N levels at optimum P, the hybrid was more variable over N at optimum P, but not at sub- or super-optimal P levels. On the other hand, variability higher than both parents was expressed by the hybrid over P levels at all levels of N. This indicates that the hybrid was not necessarily more variable at optimal levels of a nutrient, but could display greater variability at any level of one factor depending on the relative performance of the hybrid and its parents in those environments.

Heterosis for total weight occurred as a general phenomenon only at low N. Consequently, hybrid variability was greater than the parents in this range but not at intermediate and high levels of N.

4.0.0. GENERAL DISCUSSION

(a) Differential Genotypic Response and Heterosis

With some exceptions a general result obtained for grain weight within the three experiments was that the heterosis percentage for a hybrid did not change significantly across environments. However, it is believed in view of some of the other results presented in this thesis that it is very unlikely that grain weight heterosis does not interact with environment. The absence of a significant effect may have been due to:

(i) experiments insufficiently large to accurately identify differences between genotypes
(ii) genotypes too similar in their responses
(iii) environmental factors that did not differentiate adequately between the genotypes, or
(iv) the sampling of a sufficiently wide range of such factors.

(v) pot expt restricted [illegible]

The first of these reasons is believed to have been mainly responsible. Prior to the conduct of Experiments 2 and 3 there were no results available on optimal levels of N or P with regard to the particular soil or genotypes that were tested and it was considered essential to cover a wide range of these fertilisers to ensure obtaining sub-optimal and super-optimal responses. In consequence, it was not possible to accurately define differences at the optima; such a definition could come only from having had many values of N and P close to the optima. Similar comments could be made about the field study conducted in Experiment 1.

Differences were observed in the interaction of parents and hybrids with environment for grain weight although these were not significant. This happened with Heron x Strain 52; despite the fact that heterosis relative to the high-parent varied from 40 to 70% within the field densities and from -2 to 10% within the glasshouse environments. It is believed that these differences are real and would have been significant if more extensive data could have been obtained. Other workers may not have detected differences in heterosis between densities for the same reasons (Briggle et al., 1967a,b; Fonseca and Patterson, 1968; Knott and Sindagi, 1969 and Bitzer et al., 1971).

The figures of 40 to 70% in the field and -2 to 10% in the glasshouse are strongly indicative of a change in heterosis between field and glasshouse experiments although the difference cannot be tested for significance as the results are derived from different experimental designs. The difference was observed for both hybrids grown in the field and glasshouse, Heron x Strain 52 and Halberd x Warimek.

The conclusion by Zeven (1972) that high levels of heterosis observed at low density may also occur at high density cannot be accepted as a general result for all environments. Where differences between environments are more complex than would be expected between a range of densities, such as between different sites and seasons, significant changes in heterosis should occur.

With regard to the diversity of environments within an experiment, this was as great as could be achieved and was not considered responsible for the failure to detect the significant differences in heterosis. This diversity is evident from the plant responses. Grain weight per plant varied from 2 to 30g, 4 to 13g and 1 to 20g in Experiments 1, 2 and 3 respectively. In the latter experiment the response was so great that grain yields of about 1g were achieved at the extremes of sub- and super-optimal environments.

Despite the fact referred to above that there were insufficient levels of N and P to precisely define the optima it is clear that different N optima were observed for the hybrid and parents in Experiment 3. Halberd had an optimum at a higher level of N than Warimek, while the hybrid optimum was intermediate between the parents. Unfortunately, it is difficult to accurately locate the hybrid optimum because of the failure of the critical treatment, 914 kg N/ha and 1000 kg P/ha. The weight of evidence from the surrounding treatments is that the hybrid N optimum did occur between the parents.

The lack of N and P levels in the optimal region and the variability of the data precluded an intense analysis of this region. It it had been possible it is believed that significant interactions between the hybrid and both parents would have been detected and that the increase in heterosis in this region (Fig. 29, p. 124) was due to the fact that the hybrid had a response intermediate between the parents. This result is in agreement with the suggestions of Knight (1973) regarding the relationships between hybrid and parental responses. No other studies are known to have investigated this relationship although results similar to the above are believed to have been observed (Claussen _et_ _al_., 1955; Hiesey, 1963).

It is interesting to note that the ranking of the parental optima with respect to N was not expected from the breeding of the parents. Warimek was selected with short stature for use in the higher fertility areas of the wheat belt of South Australia and was expected to have had a higher N optimum than Halberd which was selected in the drier lower fertility areas.

Unlike grain weight, different genotypic optima were not observed for total weight per plant. Neither was heterosis observed in the optimal region for this character, since the three responses were superimposed centred at a common environment.

Knight's suggestion that heterosis was due to the hybrid having a response intermediate between the parents may not be invalidated by the occurrence of heterosis for grain weight at all densities in the field and at many levels of N in the glasshouse in Experiments 1 and 2.

Factors other than those which were varied across the range of densities and N levels would have been involved in the environments sampled in Experiments 1 and 2. The levels at which these unknown factors were supplied may have been those in which heterosis occurred. For example, it is possible that in a single hybrid combination one parent may have been supplied with some unknown factor at a sub-optimal level while the same level was super-optimal for the other parent. The hybrid therefore may have been growing in conditions close to its optimum and consequently displayed heterosis.

(b) The Relationship between Hybrid and Parental Response

The relationship between hybrid and parental performance has been described by a multiple regression procedure which depicts the hybrid as a weighted mean of the two parents (Knight, 1971). This analysis, although a simplification of the real situation, has proved of value in explaining interactions between hybrid and parental responses. It accounted for a large proportion of the variation in hybrid response and accurately estimated hybrid performance in environments in which heterosis did and did not occur.

The multiple regression analysis differs from analyses developed in quantitative genetics by Bucio Alanis and Hill (1966) and Perkins and Jinks (1968) in that specific regression values are calculated for each parent. A measure of the contribution of each parent to the hybrid value is estimated. Further, the parental yields are not considered as providing a measure of the environment.

A number of features of the hybrid and parental responses may be identified using this analysis. It has been pointed out previously that the parents grown in Experiment 3 had different N optima for grain weight and that the hybrid had an intermediate response with an optimum between the parents. The coefficients of both parents were significant

(Table 29, p. 135) indicating that the hybrid response was associated with the response of both parents. The calculation of positive coefficients for both parents confirms the observation that the hybrid optimum occurred between the parents. However, since the Warimek coefficient was larger than Halberd and accounted for a greater proportion of the variation in hybrid response, the response of the hybrid was more closely associated with Warimek and the hybrid optimum would have been closer to Warimek than Halberd.

Because of the limited number of density environments sampled in Experiment 1 it was not possible to estimate the multiple regression relationship between parental and hybrid responses. From an examination of the responses of grain weight m^{-2} (Fig. 8A, p. 55) and grain weight per plant (Fig. 13B, p. 70) for Halberd, Warimek and the hybrid it is apparent that the hybrid response was more closely associated with Warimek. This parent, therefore appears to have a dominant influence on hybrid performance in a diverse set of situations including field and glasshouse environments.

A different relationship was found to exist between Heron, Strain 52 and their hybrid in Experiment 2 (Table 21, p. 93). In this case only the coefficient for Heron was significant indicating that the hybrid response was almost exclusively associated with this parent and that the hybrid had an optimum at a similar N level as Heron. Similar results were observed for all the components of grain yield except 1000 grain weight. The significance of these results is discussed in a following section.

As was suggested by Knight (1971) the dominance value (h) of the hybrid may be calculated from the equation

$$h = (b_1 - \tfrac{1}{2})\ P_1 + (b_2 - \tfrac{1}{2})\ P_2$$

It is apparent that the h of a hybrid will vary between environments reflecting variation in the parental values.

A new concept of dominance is suggested by the multiple regression analysis where the regression coefficient of a parent may be considered as the dominance contribution by that parent to the hybrid performance. Previous concepts of dominance for a quantitative character assume that the parent with the highest expression made the greatest contribution to expression in the hybrid. However, the multiple regression analysis suggests that this may not necessarily be the case, and in fact the parent with the lower expression, as Warimek was at high N in Experiment 3, may make a greater contribution to hybrid expression. It may be speculated that such a parent possesses a larger proportion of genes conducive to high grain yield but that the expression of these is restricted in certain environments by other characters having an indirect influence on yield. For example, height may affect grain yield by having some control of the size and spatial arrangement of photosynthesising organs or by influencing resistance in the flow of photosynthate to the head through variation in the distance between the flag leaf and head.

When the parental genotypes are combined in the hybrid, different relationships will exist between the genes controlling processes leading to the development of grain yield. In this new situation a larger proportion of favourable genes may be contributed by the low yielding parent through the alleviation of restrictions imposed by a character such as height.

Also implicit in the multiple regression analysis is the fact that the b value of a parent will change depending on the other parent with which it is crossed. The proportion of favourable genes contributed by a particular parent may vary depending on the genetic constitution of the alternate parent. It was not possible to study this aspect in this study since no parent was common to the hybrids grown in the experiments where the multiple regression analysis was feasible.

(c) Macro-environmental Variability

A consistent feature was that the hybrids were more variable than their parents across environments. This was observed for grain weight m^{-2} expressed by a number of hybrids across densities in the field and for grain weight per plant produced by individual hybrids at a range of N levels and N-P combinations respectively in the glasshouse.

It is a result which is contrary to a generally accepted belief that hybrids are relatively more stable over a range of environments due to their superiority in stress (sub- and super-optimal) environments (Finlay, 1963; Frey and Maldonado, 1967; McWilliam *et al*., 1969).

However, it is in agreement with the results of Pederson (1968) who found greater hybrid variability in a range of environments from sub-optimal to optimal nutrient status. Similarly, if macro-environmental variability had been calculated in a number of other studies involving variation in nutritional status, hybrid variability would also have exceeded parental variability since heterosis was greatest in optimal environments (Burkholder and McVeigh, 1930; Griffing and Zsiros, 1971).

Despite the apparent conflict, some consistency does exist. Most studies which have shown hybrids to be more stable over controlled environments have utilised temperature as a variable, while greater hybrid variability has been shown in studies involving variation in nutritional status.

As has been shown the parents grown in Experiment 3 produced maximum grain weight at different levels of N, while the optimum N level of the hybrid occurred between the parents. All three N optima occurred at intermediate levels of N in the range sampled. Since the hybrid had an intermediate response it would be expected to have had a lower variability across N at these intermediate levels.

It is considered more reasonable to study differences in the variability of response at the more intermediate N and P levels, closer to the optima, since the extreme levels of the ranges sampled were much lower and higher than those expected in the field. Further, data obtained in sub- and super-optimal environments did not contribute much information to the nature of responses because of the greater variability of performance in such environments.

It is important to note that while grain weight was consistently more variable across environments, other characters, for example height, did not follow the same pattern. In fact the relative macro-environmental variability of this character changed between experiments, lower and higher variability relative to the parents being expressed across density and N respectively. It is therefore necessary to specify the environmental conditions sampled and the character being studied before general conclusions can be drawn as to the relative variability of hybrids and parents across environments.

(d) Micro-environmental Variability

The general conclusion from the literature was that micro-environmental variability was greater in more sub- and super-optimal environments (Went, 1953; Gustafsson and Dormling, 1972; Knight, 1973). The results of this study agree with this finding. Variability increased with density in the field and with displacement from an intermediate N level in the glasshouse.

It has been suggested that such variability is partly due to minor fluctuations in the availability of environmental factors and in consequence will be greatest on the steep slopes of the response curves, or in other words, variability increases with the slope.

In Experiment 1 the C.V.'s for grain weight/plant and height were greatest on the steep slopes and declined as the slope became smaller. Grain weight per plant is a character which is affected by the multiplicative nature of plant growth and is therefore expected to have a variability which increases with the mean value. In this instance the C.V. accounted for this association between the standard deviation and the mean value and C.V.'s increased with the slope. However, at the higher densities where the slope was greater the variability may not be exclusively attributed to minor fluctuations in the availability of environmental factors but also to the development of dominance-suppression relationships.

In Experiment 2, while there was a tendency for the C.V. to be greater in sub- and super-optimal environments, it was not directly associated with the slope of the response. The lowest C.V.'s were obtained in a slightly sub-optimal rather than in the optimal environment where it was expected. This may have been due to the fact that the multiplicative nature of growth and the dominance-suppression phenomenon would both be expected to contribute to variability in optimal environments. Alternatively, in the favourable conditions of the glasshouse, plants grew in an exponential manner for a longer period leading to a greater variability relative to the mean than was observed in the field. As was suggested in the results, variability measured by the S.D. could be estimated relative to some power of the mean to take full account of the multiplicative nature of plant growth and the development of dominance-suppression relationships.

Ideally the plants should have been grown individually to eliminate dominance-suppression relationships instead of in groups of four per pot as in Experiment 2. However, this was not feasible while keeping the experiment within manageable proportions.

If it is accepted that variability increases with the slope of the response, then genotypes which are most responsive to an environmental factor will be expected to display greater variability. This expectation was not fulfilled when comparisons were made between hybrids and their parents for grain weight per plant. In Experiments 1 and 2, hybrids which expressed heterosis were more responsive than their parents to supply of environmental factors but had lower variabilities. This result was observed at all densities but particularly at high density in the field and at intermediate N in the glasshouse.

Because of these results it cannot be concluded that hybrids are relatively less variable only in sub-optimal environments as was suggested by McWilliam _et al_. (1969).

The lower variability of the hybrids may have been due to a number of factors. The common expectation for similar results is that heterozygotes have a greater internal physiological buffering. Alternatively, the hybrids may have been less responsive to uncontrolled factors of the environment such as light, water and temperature. It has already been pointed out that light will be restricted at both high density and at intermediate N due to the larger total weight per unit area produced in these environments. The hybrids may be less susceptible to the development of dominance-suppression relationships which develop in such situations. Similarly, the hybrids may be less responsive to variation in temperature. A number of recent studies have shown that hybrids are more stable than their parents over a range of temperatures and less sensitive to fluctuations in temperature (Griffing and Langridge, 1963; McWilliam and Griffing, 1965; McWilliam _et al_., 1969).

The results of Experiment 3 cannot be invoked to bear on the question of whether differences in variability between hybrids and parents across levels of one environmental factor could be explained in terms of responsiveness to some other factor. Consistent estimates of

C.V. were not obtained in this experiment because of the limited number of plants available in each environment. Further studies are necessary to resolve whether hybrids are intrinsically less variable than their parents in certain conditions or whether this may be related to lower responsiveness to other factors of the environment.

(e) Transformations

To enable a simple genetic interpretation of results on hybrids many geneticists have attempted to find transformations that would eliminate interactions between genotypes and environments. Comment on the validity of this practice may be made from Experiments 2 and 3 but Experiment 3 will be referred to as the results were more comprehensive. In Experiment 3 the genotypes displayed curvilinear responses to N and P. Further, they had overlapping response curves, that is they changed rank, and they had optima at different levels of N. No simple transformation could eliminate such interactions.

Similarly, no transformation could be expected to induce homogeneity in the error variation (micro-environmental variation). Such homogeneity is necessary for genetic analyses dependent upon least squares procedures for tests of significance.

The micro-environmental variation was found to change between environments, being greater in sub- and super-optimal environments as was found by a number of workers including Went (1953) and Gustafsson and Dormling (1972). However, more specifically in Experiment 2, micro-environmental variation was found to be significantly greater in super-optimal than in sub-optimal environments where the mean expression in both environments was similar.

Any attempt to induce homogeneity by a transformation therefore is unlikely to be successful and may conceal important features of the genotypic responses leading to erroneous conclusions.

(f) Yield Component Interactions and Heterosis

There was no evidence to support the contention that heterosis for a character such as grain weight was due to the multiplicative action of additively inherited components where the parents displayed a reciprocal high expression of the components. This is evident from two points.

Firstly, heterosis for grain yield was expressed by many of the hybrids in Experiment 1 despite the fact that the parents did not display a reciprocally high expression of the components. Commonly the hybrid expressed heterosis for many of the components and consequently for grain yield.

Secondly, in many environments in which the parents displayed a reciprocal high expression for the components, the components were not inherited in an additive manner and there was no heterosis. This was a common result in Experiment 2.

The multiple regression analysis employed in this experiment highlighted the fact that the components were not additively inherited. For all components except 1000 grain weight variation in the hybrid component was closely associated with variation in Heron and not associated with Strain 52 (Table 21, p. 93). As a result expression of a component in the hybrid relative to the mid-parent was unlikely to be similar at all levels of N, particularly for characters in which Strain 52 was the high-parent.

A number of other features regarding the relationships between grain yield and its components are evident from this study.

Different contributions by the components to grain yield heterosis were observed between environments within an experiment and between experiments. In Experiment 1, for many of the hybrids, head number made the greatest contribution at all densities but the highest when grain number per head became more important. Such a change was not unexpected. At lower densities the hybrids tillered more profusely than the parents before interplant competition restricted this activity. However, at the highest density the intense interplant competition which would have developed early in the season restricted most plants to the production of a single tiller. Even though the contributions of the components changed with density a relatively constant level of heterosis for grain yield was observed. The superior growth capability of the hybrids was apparently channelled into the production of larger heads and more grains at high density.

The contributions by the components also changed between N levels in the glasshouse in Experiment 2. At low N, 1000 grain weight was the only component which expressed heterosis, while at intermediate and high N levels this component as well as spikelet number per head and grain number per spikelet displayed heterosis. It may be noted that while heterosis for grain weight per plant did not change significantly with N, significant differences were detected in heterosis for all components except 1000 grain weight (Table 20, p. 87). These results agree with the suggestion by Leng (1963) that the components do not determine the level of grain yield but that they control the distribution of grain yield within the plant. It is more reasonable to assume that grain yield is determined by the interaction of many physiological and morphological characteristics and the components as well as grain yield are just the manifestation of these.

The changes in components in Experiment 2 were more difficult to interpret than in Experiment 1. It would be expected that heterosis at low N should be expressed by the earlier formed components, head number and spikelet number per head, when adequate N is available for greater expression of these. However, this was not the case. At higher levels of N the later formed components, grain number per spikelet and 1000 grain weight may be expected to display greater levels of heterosis than at low N. This expectation was not completely fulfilled since heterosis for 1000 grain weight did not increase with N although grain number per spikelet did show some tendency to increase with N.

Despite the occurrence of heterosis for head number at most densities in the field, this character did not express heterosis at any level of N in the glasshouse in Experiment 2. In fact the relative performance of the hybrid for head number tended to decline as heterosis for grain weight increased with N. This was an unexpected result considering that the range of head numbers per plant developed in the glasshouse (3 - 7) fell mainly within the range observed in the field where head number made an important contribution to heterosis for grain yield. It is not known why heterosis for head number did not occur in the glasshouse. It could not be explained in terms of the occurrence of some stress or the development of interplant competition during the tillering period early in the season. Neither could it be attributed to a later sowing time reducing the time from sowing to elongation and subsequently restricting tillering, since both experiments were sown at a similar time. However, the warmer conditions of the glasshouse may have acted to reduce this time.

Although heterosis for head number occurred at the four lower densities in the field and made the greatest contribution of the components to heterosis for grain yield in these environments, selection for grain yield based on selection for head number is not advocated on two grounds. Firstly, the square-spacing of the field experiment may have allowed heterosis for head number to develop at a higher density than if the experiment had been conducted at a more rectangular spacing as used in commercial practice. Secondly, the absence of heterosis for head number at all levels of N in the glasshouse indicates that environments other than high density may cause a failure of heterosis for this character but not for grain yield.

(g) Selection for Harvest Index

Recently there has been some strong advocacy of harvest index as a character on which to base selection for yield (Donald, 1968; Syme, 1972). Results from the hybrids and parents in this study would not support an approach to selection based on harvest index. In many of the environments sampled high grain weight was not associated with high harvest index. More specifically heterosis for grain weight was not accompanied by heterosis for harvest index. Other workers have also concluded that selection of harvest index is not an efficient means of improving grain yield (Rosielle and Frey, 1975).

For many of the hybrids grown in Experiment 1 heterosis for grain weight at low density was not associated with heterosis for harvest index. However, at high density, high grain weight and high harvest index were more consistently related. In Experiment 2 the lack of association between grain weight and harvest index was due to the greater height and consequent heavier stems of the hybrid. A more complex relationship existed between grain weight and total weight in Experiment 3. Heterosis for grain weight was expressed at low and intermediate N levels, while heterosis for harvest index occurred mainly at the high levels of N.

5.0.0. CONCLUSIONS

The following conclusions are presented to highlight the important findings of the study:

1. Although significant differences in the heterosis percentage for grain weight were not generally observed between environments, it is believed in view of other results presented in this thesis that heterosis does interact with the environment.
2. Where the parents were found to have distinctly different responses and optima, the hybrid had a response intermediate between the parents. Because of this relationship the performance of the hybrid will vary with the environment, heterosis being expected in some environments.
3. Heterosis occurs in a wide range of environments, not only in stress (sub- and super-optimal) environments. This is concluded from two results. Firstly, a constant level of heterosis was commonly observed across density in the field where many factors of the environment would have varied from optimal to sub-optimal levels. Secondly, although heterosis was lower in the glasshouse than in the field, it was greater at optimal levels of N than at sub-optimal levels.
4. The multiple regression analysis employed in this study proved to be a useful procedure in describing the relationship between parental and hybrid response. It accounted for a large proportion of the variation in hybrid response and accurately described hybrid performance in environments in which the hybrid varied from a situation intermediate between the parents to hybrid vigour exceeding both parents.
5. Further study should be made of this procedure, particularly in sets of environments where large interactions occur between hybrids and parents, before it can be accepted as a useful analysis for

quantitative genetics.

6. A new concept of dominance is provided by the multiple regression analysis whereby the regression coefficient of a parent may be considered as the dominance contribution by that parent to the performance of the hybrid.

7. No evidence was found in any of the experiments to suggest that the hybrids were less variable across environments for grain and total weight than their parents. This may not be considered as a general conclusion, as sets of environments can be envisaged where the hybrid is expected to have a lower variability across environments and because other characters, such as height, were found to show less variation across environments in the hybrid.

8. Micro-environmental variability was lower in optimal than in sub- and super-optimal environments. This was believed to be associated with the slope of the response in these environments.

9. The hybrids displayed lower micro-environmental variability than the parents in certain environments. This could not be related to the slopes of their responses since they were more responsive to the environment in these situations. It was not possible to determine whether this discrepancy was due to the hybrids being less responsive to other unknown factors of the environment or having a lower susceptibility to the development of dominance-suppression relationships.

10. It is not considered feasible to employ transformations to eliminate interactions between genotypes, particularly where those genotypes have overlapping responses with different optima. Neither will it be possible to induce homogeneity of error variation (micro-environmental variability) if such variability differs between genotypes and environments. The use of transformations will conceal important features of the responses.

11. The contention that heterosis for grain yield was due to the multiplicative action of additively inherited components where the parents show a reciprocal high expression of the components cannot be accepted as a general explanation of heterosis.

12. Analysis of the grain yield components is not likely to lead to a greater understanding of the plant characters and processes determining grain yield. The grain yield components are not believed to determine yield but are themselves controlled by other more complex physiological and morphological characteristics which determine yield. As was suggested by Leng (1963) the components may only be associated with the distribution of grain yield on the plant.

13. Future analysis of the interaction of heterosis and environment in terms of comparisons of hybrid and parental response should involve the following steps:

    (i) the predetermination of parental responses

    (ii) the selection of parents which display distinctly different responses and optima, i.e. which interact across levels of the chosen environmental factors.

    (iii) the rigorous analysis of hybrid and parental responses in the regions around the parental optima by the sampling of many environments with abundant replication.

    (iv) unless an attempt is being made to study response to different levels of interplant competition, plants should be grown individually to eliminate the effects of interplant competition and the development of dominance-suppression relationships between plants.

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