VARIABILITY IN PARENTAL AND F_2 POPULATIONS OF WHEAT IN RELATION TO SELECTION FOR YIELD.

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คำอุทิศ

กระผม, คุณพ่อ และพี่ๆทุกคน
ขอมอบคุณค่า และ ความดีเด่น ทั้งปวง
ของปริญญาเอก ให้กับคุณแม่ ที่รักยิ่ง
ของพวกเรา.

DEDICATION

To my mother's hands,
the hands which unaided,
brought me into this world.

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Chapter 5 DISCUSSION

SUMMARY

1. Experiments were conducted on parents and hybrids of wheat to compare the variability within parental populations (P_1 and P_2) and within hybrid (F_2) populations and to examine the effectiveness of selection at the F_2 generation. In 1975, the P_1, P_2 and F_2 of eight crosses were grown at crop density and three of the crosses were also grown at low density. For each of these 24 populations at crop density approximately 450 plants were assessed and for each of the 7 populations at low density 200 plants were assessed.

2. Assessments were made on the characters; head number, total plant weight, total grain weight, main shoot total weight, main shoot grain weight, main shoot grain number, main shoot spikelet number and head length, tiller grain weight, tiller grain number, height. The frequency distribution means, variances, CV's, and skews for each character and population formed the bases of the comparisons.

3. It had been anticipated that as the variances of the F_2 would have genetic and environmental components they would be larger than that of the parents which would have only an environmental component. It was found that the variances for the F_2 were not consistently or significantly larger than the variances of the parents with the exception of height. In several instances the variances of the parents were often significantly different from each other.

4. The range of the F_2 distributions in most circumstances covered the combined ranges of the parental distributions. Transgressive segregation was evident in many characters but its manifestation differed between crop density and low density.

5. Nearly all the distributions were significantly skewed. Those characters which were positively skewed were; head number, total plant

weight, total grain weight, tiller grain weight and tiller grain number, and those that were negatively skewed were; main shoot total weight, main shoot grain weight, main shoot grain number, height, spikelet number and head length. Similar skews were found for the characters at both densities but they were stronger at crop density.

6. Heterosis defined as occurring when the F_2 had a mean value that exceeded the parental means, was evident in many characters at both densities.

7. To study the effect of selection at the F_2, twenty five percent of the F_2 derived lines from three crosses, grown at crop and low density in 1975, were grown as F_4 plots in 1976 (experiment 3) at two locations. Further plot trials were conducted in 1978 but now with fifty percent of the F_2 derived lines from the eight crosses at crop density and the three crosses at low density. F_4 or F_5 plots were grown at two locations. In some trials only one replicate was grown but check plots were given on a grid pattern in the trials.

8. Correlation analyses were used to estimate the relationship between characters measured on the F_2's and their derived line (F_4 or F_5) plot yields.

9. The significant correlations that were found occurred mostly with the characters measured on the main shoot of the F_2's; main shoot total weight, main shoot grain weight and main shoot grain number. A few correlations only were found with total plant weight, total grain weight, tiller grain weight and tiller grain number. Significant correlations occurred mainly in the crosses in which the F_2 showed a larger variance than the parents for that character.

10. Harvest index in the F_2 was not as good as main shoot yield as an indicator of high yield in the subsequent F_4 or F_5 plots. For some crosses in which the main shoot total weight and grain weight had a significant correlation with the F_4 or F_5 yields, the main shoot harvest index also showed a significant correlation.

11. It was concluded that prediction of high yielding genotypes in early generations may become feasible if attention is paid to main shoot yield.

12. The Discussion was concerned with the means and variances of the F_2's, the causes for the positive and negative skews in the populations and the value of various characters in selection procedures.

STATEMENT OF ORIGINALITY

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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INTRODUCTION

The thesis is concerned with selection for yield in segregating generations of crop plants. In the pedigree method of breeding self pollinated crops, crosses are made between two parents in the hope that among the generations of segregating progeny it will be possible to select a homozygous genotype having the desirable features of both parents. The F_2 is the first generation in which segregation is apparent and selection can begin. However, there is a growing body of opinion that selection conducted in this generation is not effective (Bell, 1963; McGinis and Shebeski, 1968; Shebeski and Evan, 1973; Hamblin and Donald, 1973; Phung, 1976).

Various reasons for the ineffectiveness have been suggested including, (1) the effect of heterozygosity - the objective is to produce finally homozygous individuals, (2) environmental heterogeneity in the segregating plot, (3) the occurrence of genotype-environment interactions so that selection undertaken on the F_2 in one site or season is not effective for other sites or seasons, (4) the genotype-density interaction. Selection is conducted often at a low density of planting whereas the selected genotypes are grown finally at a crop (high) density. If the breeder tries to avoid the density interaction, by conducting his selection programme at a crop density, the micro-environment variation may be very large and affect the result. Competition among plants will be severe at crop density. Selection for yield may result in the selection of genotypes with a high competitive ability rather than ones with high yield when grown in a pure stand. Hamblin (1971) concluded that single plant selection for yield was unlikely to be effective unless there was a positive relationship between the yield of genotypes in mixed or segregating population and their yield in pure culture.

Frequency dependent advantage could also affect selection (Phung, 1976). Phung found that a genotype present at a low frequency had a higher yield than if it was present at a high frequency in a mixture or was in pure stand. If frequency dependent advantage operates in a segregating population, an individual plant which is selected for high yield may have this attribute as a result of it's low frequency and not because of it's genetic potential. This type of yield advantage will be lost when the individual is grown as a pure stand.

Phung also found that when yield was measured on single plants grown at a cup density, the F_2 and parental variances were statistically similar in magnitude. However, the variability within the F_2 population should be greater theoretically than in the pure line parents if the parents differ genetically. Variation in the F_2 should be attributable to environmental effects, genetic effects, the interaction between them, and to frequency dependent advantage. If the parental variances were solely environmental, and the F_2 variance was of the same magnitude, it might be assumed that the F_2 variance was environmental and had no genetic basis. Such a conclusion is untenable. If this was true, selection would not result in a genetic change. As Phung obtained only limited results on the matter the subject needs to be investigated further.

It would be of value if selection could be applied in as early a generation as possible. Shebeski (1967) showed that the frequency of desirable genotypes decreased with each generation of selfing. The frequency of plants having all the desirable genes was highest in the F_2 generation. For example, with a cross in which the parents differ by 25 genes affecting yield, about 0.075 per cent of the F_2 or one plant in 1,330 can be expected to contain all the 25 genes whereas the expected percentage is only 0.00005 or one plant in approximately 1.8 million if the selection is delayed until the F_4 generation. Therefore, selection should begin in as early a generation as possible.

In this thesis, further consideration will be given to the occurrence and interpretation of the finding that the F_2 variance may be no greater than the parental variances. Also considered are the problems associated with single plant selection and some procedures will be investigated which may lead to greater success when selecting for yield.

Chapter 1

LITERATURE REVIEW

The literature review consists of two parts. In the first, the problems associated with single plant selection in early generations are discussed. In the second, variability in segregating generations and models of frequency distributions are considered.

(A) Selection in early generation.

1. The various breeding methods. Several methods of breeding have been used with cereals including the pedigree method, bulk populations, composite crosses, and single seed descent. There has been little research to establish which one is the most effective method because strict comparisons are not easy to make and any conclusions would be subject to many conditions. A main difference between the methods is the generation in which selection begins.

In the pedigree method, selection for desirable combinations of characters starts in the F_2 generation. Progenies of the selected plants are grown and further selection is practised in the subsequent generations until F_5 or F_6 by which time homozygosity may be reached (Poehlman, 1959; Allard, 1960). The effectiveness of this method relies on the ability of a breeder to recognize desirable genotypes either by measurement or observation. The high amount of labour and land required is a disadvantage (Harrington, 1952; Elliot, 1958).

In contrast, in the bulk population and the single seed descent methods, selection is delayed until an advanced generation such as F_6 (Hayes, Immer and Smith, 1955; Goulden, 1941). The generation chosen theoretically should depend on the number of genes by which the parents differed but in practise this is not known (Florell, 1929). The idea is to allow the population to become relatively homozygous before selection takes place.

By doing this, in the bulk population method, a large number of undesirable genotypes are carried through unnecessarily. If yield is the main objective of the selection, it is essential that there be a positive correlation between natural selection, fitness and yield for this method to be effective. Otherwise natural selection and competition will result in a loss of the high yielding genotypes.

To achieve homozygosity as quickly as possible, that is to get through several generations rapidly and to avoid the loss of genotypes, the single seed descent method was suggested by Goulden (1941). In this method, one or two progeny from each plant are taken in the successive generations. The generations are advanced rapidly by two or three generations a year and there is no concern about the environment being atypical of crop conditions. By growing seedlings close together, a large number can be grown in a smaller area than with the bulk population method (Grafius, 1965). With this method no natural selection or genetic shift should occur.

Neither the bulk population method nor single seed descent avoid the genetic consequence of delaying selection namely that the frequency of desirable genotypes in the population falls with each generation. For this reason the objective of the present study has been to investigate aspects of pedigree selection.

If selection is practised in an early generation the problems referred to in the Introduction may occur. These problems which are discussed further lead to the reduction of the relationship between yield of single plants and the yield of the derived lines in later generations.

2. Problems involved in selection for yield in early generations.

(a) Heterozygosity.

In many studies of self pollinating species the F_1 has been found to be more vigorous than either parent, a result attributed to heterozygosity, overdominance or heterosis (Immer, 1941; Grafius, 1959; Suneson and Riddle, 1944; Suneson, 1962; Severson and Rassmussan, 1968;

for barley, Hathock and McDaniel, 1973; for oats, Murayama, 1973; Saini *et al.*, 1974; for rice, Briggle *et al.*, 1967 a & b; for wheat) (for review see Briggle, 1963).

In early generations, after crossing two diverse parents, many loci are heterozygous. If overdominance results from this heterozygosity, it will have a large effect on the phenotype and lead to an inefficient evaluation of genotypes as the objective in most breeding programmes is the production of a high yielding homozygous genotype. Overdominance will have the greatest effect on the efficiency of selection, but dominance of any magnitude will lead to inefficiency.

When two varieties are crossed, the F_1 is heterozygous for those loci by which the parents differ. In the F_2, where segregation will take place, ½ of the individuals are homozygous and ½ are heterozygous at a locus. When several genes are involved heterozygous and homozygous plants which contain the same number of desirable alleles may be phenotypically indistinguishable. This makes an evaluation of the effects of heterozygosity difficult to achieve. Furthermore selection may lead to the retention of both homozygous and heterozygous plants. When a further generation is grown, the heterozygous plant will segregate and re-selection will be necessary. Heterozygosity is often suggested as a major factor reducing the efficiency of selection in early generations.

However, in self pollinating crops, there is no direct evidence on the importance of heterozygosity on selection. Theoretically the increased vigour attributed to heterozygosity will fall rapidly as the percentage of heterozygous loci is reduced with each cycle of selfing. The breeder has to decide at which generation the effect of unfixable vigour will be reduced to an unimportant level. Briggle *et al.* (1967 a & b) showed that the yield fell from the F_1 to the F_2 and F_3. A similar result was obtained by Bhatt and Derera (1973a) who found that the yields of F_2 derived lines of four wheat crosses were higher than F_3 derived lines. The yields of F_3 derived lines from three other crosses were higher than that of the corresponding F_4 derived lines.

The apparent yield advantage of heterozygotes affects all methods of selection which have as their objective high yielding homozygotes. In mixed populations of heterozygotes and homozygotes, carried forward under condition of natural selection as in the bulk population method, heterozygotes will persist at a frequency higher than expected from simple genetic theory (Jain and Allard, 1960; Allard and Workman, 1963; Allard and Hansche, 1965; Imam and Allard, 1965; Harding *et al.*, 1966). These studies showed that for populations of lima bean, barley and wild oats, the rate of change in the proportion of heterozygotes within a population was slower than expected with advancing generations. Eventually the percentage of heterozygotes stabilized and reached an equilibrium. In all cases, the heterozygotes had a selective advantage over the homozygotes. If plants are selected for yield, heterozygotes may be picked out in any generation. When single plant selection is delayed to the F_5 or F_6, the high yields of the heterozygotes will still favor their selection and heterozygosity may lead to ineffective selection in any generation.

From the evidence available, no clear cut conclusion can be drawn about the effect of heterozygosity on selection in an early generation. On the other hand, delaying selection until homozygosity had reached a high level may not be desirable. Many useful homozygous genotypes may be lost during the generations required to bring either a whole population forward to homozygosity (the bulk method) or taking one or two progeny per plant through to homozygosity (single seed descent).

In this thesis, no attempt will be made to estimate directly the heterozygosity present instead the expression of variation will be measured in the F_2, selection will be practised in that generation, and the outcome measured in a later generation.

(b) The genotype environment interaction effect.

The yield of a genotype is influenced by differences in climate, soil fertility, season and site. Genotypes and varieties selected in one environment may have a limited value in other environments. Selection experiments or variety trials carried out in one site may be ineffective for other sites and seasons (Horner and Frey, 1951, 1957; Miller *et al.*, 1958; Rassmussan and Lambert, 1961; Allard and Bradshaw, 1964). This type of genotype environment interaction also effects single plant selection as the micro-environment of the plants and the season will influence the outcome (McGinis and Shebeski, 1968; Hamblin and Donald, 1974).

However, the occurrence of this interaction is not a sufficient reason for not undertaking studies of single plant selection. It is necessary to resolve whether the yield or some other character measured on single plants in a mixed population shows a direct association with the yield produced by the corresponding plant when it is grown as a pure stand in the same season and at the same site or in other seasons and sites. If such a relationship could be demonstrated, then the yield or other character of the single plant still could be used as an effective guide to measure the worth of a genotype.

(c) The effect of micro-environment.

In most statistical procedures, the confounding effect of micro-environment on the assessment of material is circumvented by the replication of each entry in the trial. But the replication of each genotype in a cereal F_2 by vegetative propagation is not feasible. Selection within the population must be based on single plants within a block of segregating plants. Variation in the micro-environment in the selection block becomes an important factor affecting the true performance of the plants. If this variation is not taken into account, any selection conducted may be for a plant which is in a superior environment rather than being genetically superior. Because of these difficulties (replication and genetic variability) plant breeders have made many attempts to estimate micro-environmental effects. The methods are not always feasible if many plants are to be grown as they depend on the precise spatial positioning of each plant in the selection block and a record of the position.

One method, the "honeycomb method of selection" was proposed by Fazoulas, (1973). Individual plants are grown in a selection block at the centre and corners of a hexagonal arrangement. A genotype is selected when it produces a yield greater than its six immediate neighbouring plants. However, as the recommended spacing between plants was 50 centimeters, the total area is large and soil heterogeneity is likely to be high. Furthermore, as discussed above, genotypes that perform well at a low density (wide spaced) may not be the highest yielding when grown at crop density and the plant spacing in this technique may be a limiting factor to its success.

A response surface is another technique proposed (Hamblin, 1971; Hamblin, Knight and Atkinson, 1978). A series of polynomial equations is fitted to the yield of individual plants according to their position in the field, in an attempt to calculate a response surface indicating micro-environmental variation. One difficulty is that there is no simple biological basis on which to decide the number of terms to include in the polynomials. However, in the present study neither of these techniques could be applied because of the very large number of single plants and crosses grown. Many thousands of plants were studied; there were too many to record each one's position in the plot during harvest. Although no assessment and correction was undertaken for microenvironmental effects on the single plants corrections that were attempted on the F_4 and F_5 plot yields will be presented.

(d) The effect of competition.

When two or more organisms coexist, they may influence each other by competing for resources that may be in insufficient supply (Birch, 1957). In the plant kingdom, a great deal of work has been done to determine the effect of genotype and environment on competitive ability and yield.

Competition is thought to lead to an inefficiency in the selection of single plants in a segregating population growing at crop density. An inefficiency would occur unless there was a positive correlation between the yield of the individual in the population and its yield in pure stand.

Otherwise selection in the F_2 generation may be for competitive genotypes rather than high yielding genotypes. An early study by Montgomery (1912) showed that genotypes performed differently in pure culture and in mixtures. He found that one variety dominated the mixture very rapidly but it was not necessarily the variety that had the highest yield in pure culture.

Later Harlan and Martini (1938) grew eleven recognisable barley varieties in a mixture, and studied the proportions of these varieties at various locations over a number of years. The results showed, in every location one variety (which differed between locations) quickly became dominant while the others declined to very low proportions. The dominant variety was often the variety grown locally by farmers. At only two locations did the dominant varieties in the mixture differ from the varieties grown by local farmers and in these two cases the preferences of the farmers depended on considerations other than yielding ability. These results suggest that there were differences in competitive ability among varieties a conclusion that was supported by the finding that the frequencies of certain characters controlled by single genes changed rapidly with time in mixed population, some characters survived better in some sites than others (Suneson and Stevens, 1953).

Several studies have shown that the bulk yield of the composite cross populations had steadily increased with time when compared with the control variety "Atlas" suggesting that competition may be leading to the elimination of low yielding genotypes (Suneson, 1956; Jain and Allard, 1960; Allard and Jain, 1962). Jain and Allard took 63 random selections from the F_3, F_6 and F_{13} of composite cross V, and showed that with time both yield and fitness of the population increased in a linear fashion.

However Allard and Adams (1969 a & b) measured the competitive ability of four barley varieties (used by Suneson in 1949), four wheat varieties and eight selections from the F_{18} of composite cross V and noted that in the three sets of comparisons, the lowest yielding lines in pure culture showed the largest increase in yield under competitive conditions. Their method of presentation was however, quite complicated. Nevertheless, it was suggested that the high yielding lines in pure culture were the poorer competitors.

Other results on the relationship between competitive ability and productivity have been available and in some instances the correlation has been positive and in others negative (Sammeta and Levins, 1970). Jennings and co-workers (Jennings and Aquino, 1968; Jennings and Herrera, 1968; Jennings and de Jesus, 1968) working on rice, found a negative association between yield and competitive ability. The high yielding plants in mixture were good competitors and were low yielding when grown in pure stands. They commented that a strong competitive ability was undesirable and appeared to limit the progress through breeding in some tropical breeding programmes.

Johnston (1972) working with a 100 barley varieties and the F_4 and F_6 generations of 48 F_3 derived lines from cross "Proctor * C.I. 3576" grown in mixtures and pure stands respectively, found that there was a highly significant correlation between yields of genotypes in mixtures and yields in pure stands. Although acknowledging that inter-genotypic competition influenced the yield of some genotypes in the mixtures, he concluded that micro-environmental variation was the major factor limiting the efficiency of single plant selection.

Another aspect of yield in mixtures and in pure stands of cereals was the frequency dependent advantage found by Phung and Rathjen (1976 a & b). A genotype at low frequency in a population had a higher yield per plant than when it was present at a high frequency. The conclusion was drawn that if frequency dependent advantage, which is a form of competition operates in a segregating population it may reduce the efficiency of single plant selection. An individual selected for yield may have the attribute as a result of its low frequency and not a genetic potential. This yield advantage will be lost when the individual is grown as a pure stand.

The evidence reviewed appears to indicate that competition may increase or decrease the efficiency of single plant selection when made on plants grown at crop density. No clear cut conclusion can be drawn as to whether competition improves or lowers the efficiency of single plant selection. Furthermore, Johnston (1972) suggested that some findings of a negative relationship between competitive ability and yield in pure stand may have been due to an artifact. He found that selection for high yielding genotypes could be achieved and that there was a positive correlation between yield in mixture and yield in pure stand.

In this thesis plants of the parental and F_2 generations were grown in a competitive situation at crop density and also in a non-competitive low density situation in an attempt to determine if selection in one or the other situation was more efficient.

(e) The relationship between a single plant's performance measured in an early generation and yield of the derived line in a later generation.

Effective selection for yield in an early generation would be of great benefit to plant breeding programmes since it would enable a large number of genotypes to be screened with a minimum of breeding expenditure. McKenzie and Lambert (1961) and Shebeski (1967) suggested that selection for yield should commence in the earliest possible generation. The effectiveness of the selection however, depends on the ability to distinguish differences between genotypes in early generation and on the persistence of these differences in later generations. That is, it depends on a high correlation between the performance of the selected genotypes and the performances of their progenies in later generations.

However, single plant yield and other characters have not been useful as criteria when selecting for high yield in wheat although some characters have been claimed to be better indicators. In the results of the present study, reference will be made to several plant characters which at various time have been suggested as being related to yield. They include primary tiller yield, height, components of yield (spikelet number/head, grain number/head, head number, head length), and harvest index.

1. A single plant's yield. Many authors have obtained relationship between single plant yield in an early generation and the yield of the derived progeny in later generations. Reasonably high correlations have been obtained, McKenzie and Lambert (1961) measured response to selection in F_3 for yield in F_6 in two barley (*Hordeum vulgare* L.) crosses. They reported highly significant intergeneration correlations $r = 0.31$ and $r = 0.54$ for the two crosses. They concluded that selection was effective only in the cross that had a wide range in yield among lines in the replicated F_3 test.

Johnston (1972) obtained a correlation of $r = 0.61$ between single plant yields in F_4 barley and the same lines in F_6 plots. Further he simulated an F_2 by mixing 100 homozygous barley varieties and obtained the correlation of $r = 0.56$ between single plant yield in the mixture and of the varieties in the pure stand. Chowdhry and Sabir (1973) obtained coefficients that ranged between 0.47 to 0.66 for single plant yields in the F_2 and row yields in F_3 and Skorda (1973) obtained correlations up to 0.87. Phung (1976) compared single F_4 plants of wheat with their pure stand, and showed that when a large number of replications (48) were considered the correlation was very high ($r = 0.75$) but when a single replicate was analysed which would be analogous to F_2 selection the correlation varied from $r = 0.29$NS to 0.70***.

2. The components of yield. Plant breeders are always interested to know if any component, or factor, affecting yield can be interpreted genetically more simply than yield itself. Up till now, this has not been a very fruitful line of research possibly because high yield may be achieved by many different pathways and there is little evidence that the components are simply inherited. However the interest remains and several components of yield were investigated in this study.

Several reports on heritability tend to indicate that certain components of grain yield in wheat are more heritable than yield itself. The utilization of the components-of-yield approach would be most effective if the components were: highly heritable, genetically independent, and not associated physiologically.

Johnson *et al.* (1966) suggested that evaluation of the individual yield components might provide a better basis for progeny evaluation than yield itself and McNeal *et al.* (1978) have suggested that kernel weight and kernel number per spike were good characters for indirect selection for yield imporvement. Other authors also have favoured selection for kernel weight as a means of increasing yield (Lebsock and Amaya, 1969; Knott and Talukdar, 1971).

It has been pointed out that yield components develop sequentially and may be genetically independent (Adam, 1967). Thomas, Grafius and Hahn (1971) studied the four sequential characters of yield: heads per plant, spikelets per head, seeds per spikelet and weight per grain. Each character was isolated from its association with the previous character in the sequence by removing the correlation. The characters were then called "transformed characters". They found that the true relative genetic variance of sequential characters examined in this way differed from the apparent genetic variance of the untransformed character. If the characters are strongly correlated there is good evidence that the apparent control over a later character in the sequence is merely a reflection of control by the previous characters. Furthermore, the authors stated that the complex inheritance pattern for yield accounts for a fairly low predictive value of midparent yield in determining progeny yield. The component midparent value in contrast, had a higher predictive value in determining their respective component expression in the progeny. They found that the midparent of the component traits; head per plant and spikelet per head, showed a correlation with progeny yield; these traits were called "influential traits". The hypothesis put forward was that influential traits would not only strongly affect subsequent traits but also would contribute disporportionately to the variance of the complex trait. The conclusion was made that yield prediction is made feasible by ignoring uninfluential and concentrating on one influential component.

In this study, the main shoot yield and tiller yield were considered as the components of the total yield. Also evaluated were the main shoot's spikelet number, head length and grain number and the grain number of the tillers.

3. Yield of the main shoot. An interest in the main shoot lies in the fact that in many regions and seasons in Australia the main shoot may provide most of the yield of the crop. The tillers have only a low, or often no yield (Puckridge and Donald, 1967). In this study results will be presented on the relationship between the main shoot's: total weight, grain weight, grain number, spikelet number, head length and its harvest index for F_2 plants and the yield of the derived lines in later generations (F_4 and F_5).

Few studies have been conducted to investigate the relationship between the main shoot of a single plant in an early generation and yield of the derived lines in a later generation. Alessandroni and Scalfati (1973) suggested that the grain yield per head might give a better prediction of the F_4 plant performances than the yield per plant. They found that the yield per head of F_2 plants was more highly correlated with the F_4 plot yield ($r = 0.18$) than was the yields of the F_2 plants. The authors concluded that early selection for yield per head should be promising for obtaining higher yielding genotypes.

4. Height. Plant height is relevant to wheat breeding for two reasons, one is that tall plants may be more competitive and have higher yields in situations of intergenotypic competition such as occurs when an F_2 population is grown at crop density. The height and competitive ability

may be of no value when grown in pure stand. The second reason is that a short statured plant type (dwarf and semidwarf) is favoured by breeders to reduce lodging and because of the belief held by some physiologists that if fewer resources are expended in straw growth this will leave more for grain yield. But it has been pointed out by Bremner and Davidson (1978) that the greater grain number did not seem to originate in the diversion of assimilate from stem growth to ear growth during pre-anthesis development and also that short straw was not necessary lighter in weight.

With regard to height, competition and yield Hamblin and Donald (1974) obtained a negative correlation between F_3 plant height and F_5 plot yield in barley. They suggested that under some circumstances such as when light intensity becomes a factor of competition limiting plant growth, the breeder can achieve a valuable degree of selection in an early generation by attention to plant height.

In wheat, the introduction of the semidwarf growth habit of Norin 10 into other varieties marked the beginning of new plateaus of yield (Vogel *et al.*, 1956). The improvements were not only for greater yield of grain but also new combinations of plant characters (Vogel *et al.*, 1963).

Gale and Law (1976) reviewed the relation between yield and height in wheat. They showed that plant breeders have pursued the objective of a shorter, stronger stem to prevent lodging. They found there was a positive relation between height and yield within any one height class. This has led them to suggest that breeders should select for "tall dwarfs". Such a suggestion has several advantages, not the least being the more highly heritable nature of the character height compared to that of the yield. Also by not selecting strongly for shortness, the rapid dissipation of much of the variation available for further yield improvement is avoided. One of the conclusions they made was that Gai/Rht 2 has a positive effect on yield via increases in grain number per ear and that maximum yields may be obtained by breeding for "tall dwarfs" within such a height class. This exploits the positive pleiotropic effects of genes controlling height and yield in the presence of the Norin 10 dwarfing genes.

Selection for a short statured rice has been an objective of IRRI. The avoidance of lodging has been equally successful with rice as with wheat. In rice, there is also the contrast between a tall, spreading competitive type that is relatively higher yielding in F_2's grown at high density and a short statured, erect type that is high yielding in pure stand (Jennings and Aquino, 1968).

In the present study, single plant height was measured as the height of the main shoot.

5. Harvest index. One criterion suggested as being associated with yield and being a good indicator when selecting for yield is "harvest index". The term was defined by Donald (1962) as the ratio of grain dry weight to the total above-ground weight at maturity of the crop. He called these components of the ratio "economical yield" and "biological yield" respectively. It was also known as "coefficient of effectiveness" (Nichiporovich, 1960) or "migration coefficient" (Engledow and Wadham, 1923; Tsunoda, 1956). A number of papers have been published suggesting that selection for high harvest index will result in increases in grain yield of cereal crops (Donald, 1968; Chandler, 1969; Singh and Stoskopf, 1971; Syme, 1970, 1972; McEwan, 1973; Nass, 1973; Rosielle and Frey, 1975 a & b; Fischer and Kertesz, 1976; Bhatt, 1976, 1977).

Highly significant positive correlations of grain yield with harvest index have been reported (Singh and Stokopf, 1971; Rosielle and Frey, 1975 a & b; Fischer and Kertesz, 1976). However, since grain yield is a component of the harvest index ratio, correlations between grain yield and harvest index measured on the same plants are likely to be strong correlations for spurious reasons. Supporters of the value of harvest index have referred to the progressive increases in grain yield over time and the associated increases in harvest index of new varieties (Van Dobben, 1962; Sim, 1963), but such progress has resulted from the selection for high yield and not selection for high harvest index itself.

Syme (1972) suggested that there was a great advantage in selecting for harvest index following his study of 16 characters measured on plants grown in a green house of the 49 entries of the International Spring Wheat Nursery (CIMMYT, 1971), he found a remarkably high correlation between single plant harvest index and mean grain yield of the 49 entries obtained from 63 sites widely distributed in the world. Grain weight per plant of the 49 entries in the green house showed no relationship to their mean yield in the world trials. Fischer and Kertesz (1976) also reported a high correlation between the shoot harvest index in space-plant treatments and plot yield in field trials.

In this study, harvest indicies were calculated for the main shoot and for the whole plant.

(B) Variability in parental and F_2 population.

When a quantitative character is measured on a population of plants, the results often conform to a normal distribution. A normal distribution obtained for a population of a pure line cultivar must result from variation in the micro-environment in which the plants are growing or to non genetic differences in the seed. In other populations where genetic differences are present, the variation will have genetical and environmental components. If the plants are growing at high density, the expression of the characters may be strongly influenced by competition. Competition may blur the genetic differences between the plants. In addition, the frequency distribution may show departures from normality.

Koyama and Kira (1956) noted that frequency distributions of individual plant weights in a population are seldom normal, but may exhibit characteristic patterns depending on the stage of growth, environment conditions and the density of plants. For a large number of populations, the frequency distribution changed during growth from a near normal to a positively skewed or L shaped distribution. Their mathematical explanation for this phenomenon was based on the exponential equation of plant growth;

$$w = w_o e^{rt}$$

or as the logarithmic form:

$$\log w = \log w_o + rt$$

$$r = \frac{1}{t} (\log w - \log w_o)$$

where w is a plant weight at the time t, w_o is an initial plant weight, and r is a relative growth rate, e is the exponential value. Four possible models were postulated with either w_o or r or both as a constant or as a normal distributed variable. Since it is unlikely that all plants will have a constant growth rate, the models in which w_o and r or only r are constants were considered as too hypothetical to be ever realized in nature. A constant value of w_o could be achieved by carefully selecting uniform seeds however normally distributed values are more useful. The value of r is generally influenced by variation in the environment. But when the value of r was assumed to be distributed normally and w_o is either constant or normal distribute, then the frequency distribution of log w must be normal. That is the frequency of w is log-normal at any value of t. When not in the logarithmic form, the value of w will conform to a positively skewed distribution.

The authors concluded that the normal distribution in the seeds automatically passes into the asymetric and finally an L-shaped (positively skewed) distribution, even when any individuals were grown without competitic

A negative skew reported by Koyama and Kira (1956) for height or shoot length of touch-me-not (*Impatiens balsamina* L.). A negative skew for shoot elongation was also reported by Hozumi, Koyama and Kira (1955) for yellow dent corn. They found that the correlation between the rate of shoot elongation"r" and the length of the shoot "l" was mostly negative at time "t". This means individuals which were lower in height on a certain day grew more rapidly during the days immediately after it, and vice versa. That is all the plants in the row tend to come up to the level of the highest individual resulting in an equalization in plant height. The authors suggested that the amount of light available for plants in a community is the major factor influencing the rate of shoot elongation.

Phung (1976) showed that the frequency of a genotype present in a population may affect its performance and cause the distribution of plants in the population to be skew. He further compared the variability in an F_2 population with that of the parents and found the differences were not significant. His work was based on only three wheat varieties; Warimek, Wariquam and Halberd and their hybrids. Several points relating to Phung's findings will be considered in this thesis.

(C) Conclusions from the literature review.

The experience gained so far and reviewed in the literature, points to the conclusion that selection in early generations for high yield is seldom effective. This results from the lack of correlation between an individual plant's yield in an early generation and its correspondin progeny yield in a later generation. This may be caused by environmental and other effects.

However, as genetic theory suggests it is advantageous to select in an early generation, it is profitable to continue studies on these generations in an attempt to resolve if account can be taken of the environmental and other effects. For this reason, a series of experiments was set up to consider the following questions.

1. Is it true that segregation in grain yield can not be detected in the F_2 generation in the sense that the F_2 variance is not significantly larger than the parental variances?

2. If the environment has a strong effect on the yield of a single plant, are there any characters which are less affected but which are sufficiently correlated with yield to be useful when selecting?
3. Should selection be based on the yield of all the shoots and tillers on a plant or is the main shoot less affected by the environment?
4. Are the plants with high yield those that tiller most?
5. Can selection be based on the main shoot characters or any other characters at either low or crop density?
6. Should selection be based on harvest index and should it be the harvest index of the main shoot or of the whole plant?
7. Is there any correlation between characters of the F_2 single plants and their corresponding line yields in later generations?

This thesis will describe the experiments examining these questions.

Chapter 2

FREQUENCY DISTRIBUTION IN F_2 AND PARENT POPULATIONS

Introduction

The objective in conducting the experiments was to try to answer the questions reviewed in the previous section. In the first year's experiments the aim was to compare the variability of hybrid (F_2) populations with their parents and to establish the pattern of frequency distributions of characters thought to be related to yield. In a later year, the relation between the yields of the single plants (F_2) and the derived lines, grown in plots, was studied.

There were two experiments in the first year, in which the F_2's and parents were compared. Experiment 1 was concerned with plants grown at crop density and experiment 2 with plants at low density. The results for the two experiments will be presented separately.

Experiment 1. Single plants of F_2's and parents grown at crop density.

(a) Outline of the experiment.

Eight crosses among wheat varieties were studied in 1975 in the field at Roseworthy Agricultural College, South Australia. The area is in the cereal belt, latitude 34°5 South and longitude 138°3 East, and is approximately 60 km. north of Adelaide.

1. The climate and the soil.

The site has a Mediterranean type of climate with cool wet winters and hot dry summers. The mean annual rainfall up to the time of the experiment (for the years 1883-1975) is 440 mm/year (Table 2.0) and the growing season is about 6 to 8 months extending through autumn, winter and spring, from May/June to November/December. The soil is a sandy red brown earth, classified as Dr.2.2.3 in the Australian Factual Key (Northcote, 1965).

2. The material.

The eight crosses were:

cross 1 MM25/4 * MM68/1
cross 2 MKR211/9 * PN28/9
cross 3 MKR211/9 * MM68/1
cross 4 CHAMP/8156/17/52 * PN28/9
cross 5 CHAMP/8156/17/52 * MM68/1
cross 6 CHAMP/8156/17/52 * MMC21/9
cross 7 WW15/RVN/158/14 * PN28/9
cross 8 WW15/RVN/158/14 * MM68/1

These eight crosses were chosen because firstly their parents were among the highest yielding lines in a current wheat breeding programme, and secondly to have representatives of crosses in which parents were similar or dissimilar in origin (A.J. Rathjen personal communication). The pedigrees of the parents were:

MM25/4 (Warimba) ——— MENGAVI * SIETE CERROS

MENGAVI ——— (GABO*MENTANA1/24)*((GABO*EUREKA)*C.I.12632)

SIETE CERROS is a cross between a PENJAMO 62 sib and GABO 55.

MM68/1 is a sister selection to MM25/4

PN28/9 ——— PITIC62 * NAPO63

PITIC62 is from YAKTANA54 with N10B which is a Mexican semidwarf wheat with Columbian ancestry.

NAPO63 is a complex cross with N10B

MKR211/9 ——— ((MEXICO120 * KODA)* RAVEN)

MEXICO120 is from YAKTANA52 with N10B (Yaktana52 and 54 are related but different genotypes)

KODA is from (DUNDEE*KENYA C6042)*(BOBIN2*GAZA)

RAVEN is an Australian variety

MMC21/9 ——— ((MENGAVI*SIETE CERROS)* CRIM)

CRIM is a U.S.A. variety

CHAMP/8156/17/52 ——— ((CHAMPLEIN*8156)*(MENGAVI*8156)*CRIM)

CHAMPLEIN is a French variety.

8156 is a Mexican variety (MEX 22A)

WW15/RVN158/14 ——— (WW15 * RAVEN)

WW15 is from ((LERMA ROJO*N10B)* ANDES)

From these pedigrees, the crosses would be classified

cross 1	MM25/4 * MM68/1	Parents similar origin		
cross 2	MKR211/9 * PN28/9	Parents dissimilar origin		
cross 3	MKR211/9 * MM68/9	"	"	"
cross 4	CHAMP/8156/17/52 * PN28/9	"	"	"

cross 5 CHAMP/8156/17/52 * MM68/9 Parents intermediate origin*

cross 6 CHAMP/8156/17/52 * MMC21/9 " " "

cross 7 WW15/RVN/158/14 * PN28/9 Parents dissimilar origin

cross 8 WW15/RVN/158/14 * MM68/1 " " "

* These were intermediate to some degree in that both parents had some genes from MENGAVI.

The F_1 and F_2 seeds were produced at the Waite Agricultural Research Institute in 1974.

Table 2.0. Long term average rainfall at Roseworthy Agricultural College and rainfall for/1975 in mm.

Month	Average 1883-1975	1975	Month	Average 1883-1975	1975
January	21	14	July	48	64
February	19	2	August	52	31
March	20	67	September	45	69
April	38	10	October	42	90
May	50	71	November	27	17
June	54	8	December	24	6

3. Sowing.

On June 19, 1975 seeds were sown by a machine which sows six row plots. The plots were 5 m. long with 20 cm. between rows. The F_2 and parents were sown in the same plot, as shown in Fig. 2.0. As there were 6 rows, 2 rows were used for borders and one parent row was repeated. There were two replicates. Light rain fell immediately after sowing and emergence was good. The plants were thinned on August 29, 1975 to provide 150 plants per row (equivalent to 180 plants/m^2).

4. Conditions of growth.

Disease incidence was negligible in the 1975 growing season. Some *Septoria* was observed but it did not appear to affect the plants. No lodging occurred nor was there any other damage.

5. Harvesting.

As the objective was to assess individual plants, they were pulled from the soil and taken to the laboratory for measurement and threshing. The two border rows were discarded, only the three inside rows were harvested; these were, the one row of the hybrid (F_2) and two rows of the parents (P_1 and P_2). As the seeds were required for the subsequent generations the air dried seed yields are presented.

6. Characters measured.

After obtaining head number and total plant weight, the main shoot was separated from the tillers. The main shoot could be traced readily from its hypocotyl. Apart from its total weight, grain weight and grain number; height, spikelet number and head length were measured on this main shoot. The characters recorded were:

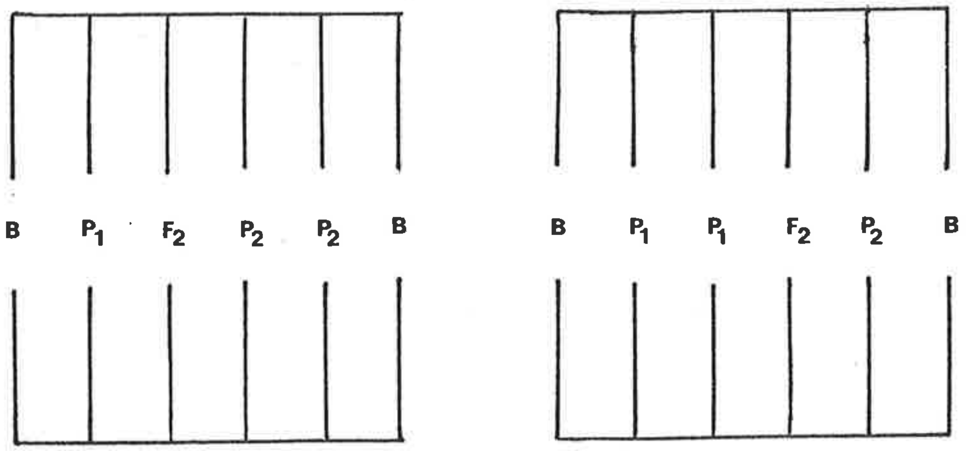
Figure 2.0. Plot layout of experiment 1

B = border row

P_1 = parent 1 row

P_2 = parent 2 row

F_2 = hybrid (F_2) row



1.	Head number	HDNO	
2.	Plant total weight	PLTWT	(g.)
3.	Main shoot total weight	MTWT	(g.)
4.	Height	HT	(cm.)
5.	Spikelet number	SPIKE	
6.	Head length	HDLTH	(cm.)
7.	Main shoot grain weight	MGRWT	(g.)
8.	Main shoot grain number	MGRNO	
9.	Tiller grain weight	TGRWT	(g.)
10.	Tiller grain number	TGRNO	
11.	Total grain weight	TOTGRWT	(g.)

Total grain weight was obtained by summing the main shoot and the tiller grain weights. The derived characters were 1. the harvest index of the whole plant, calculated as the ratio of total grain weight to plant total weight (TOTGRWT/PLTWT), and 2. the harvest index of the main shoot calculated as the ratio of the main shoot grain weight to the main shoot total weight (MGRWT/MTWT).

7. Statistical methods.

The experiments involved a large number of single plants and plots; in 1975 there were 8000 single plants; in 1976 there were 1400 plots and in 1978 7100 plots. In addition, the pedigrees had to be kept for a number of years. The analyses of the data and the production of records was facilitated through the use of a computor. Computor programs in FORTRAN IV enabled the graphing of results, the construction of layouts, the printing of labels for the harvest bags, and the calculation of results. The statistical packages used included Statscript (Lamacraft, 1973), SPSS (Statistical Package for Social Science) (Nei *et al.*, 1975) and Genstat (Alvey *et al.*, 1977). The University of Adelaide CDC 6400 computor was used for all purposes.

(b) Results of experiment 1.

1. Introduction

Before being able to present the combined results for a particular F_2, or parent, in the form of a distribution it was necessary to test whether the replicates were homogeneous. An analysis showed no statistical differences across replicates. Many of the hybrids had parents in common but to ensure precise comparisons, only the results for parents which were adjacent to a particular F_2 are presented with the cross. Somewhat different values were found therefore for any one parent. The mean value, variance, coefficient of variation, and skewness were calculated for each population. These statistics were used in the comparison of the variability between the F_2 and parents of each cross.

The number of plants in the populations were not equal. There were approximately 450 plants in each F_2 population while in the parental populations the number varied from 150 to 450 plants per population. To enable comparisons, the distributions are presented with the percentage number of plants in each class. Bartlett's Chi-square test was used to evaluate homogeneity of population variances and when the test was significant, variances were compared using the one-tail F tests (larger variance/smaller variance).

2. Head number at crop density.

The frequency distributions for head number are shown in Figure 2.2 together with some relevant statistics. Head number per plant was very low as a consequence of the crop density, and the plants on average had about two heads. The distributions were positively skewed (Table 2.2). This form of distribution will be discussed later in relation to the suggestion of Koyama and Kira (1956) that skews are the outcome of one form of plant development. The skews tended to be stronger in the hybrid populations.

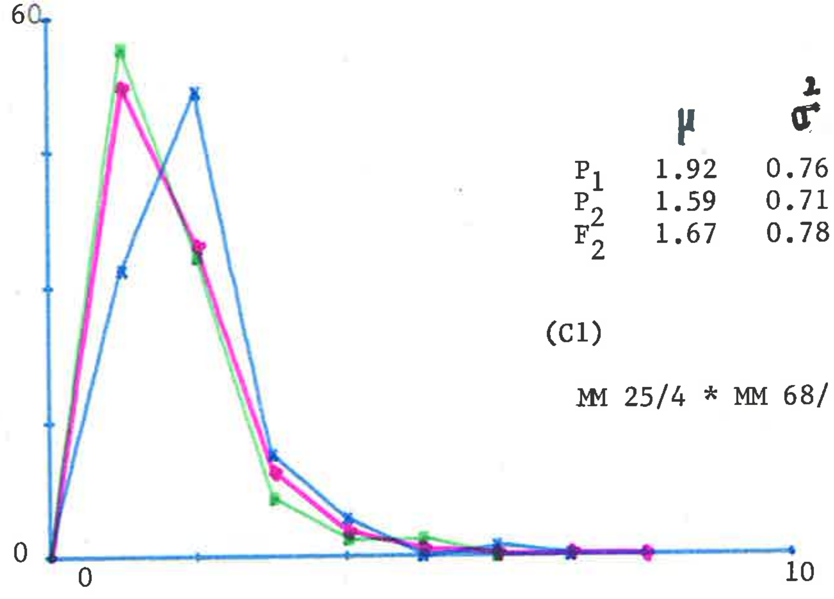
The range of the hybrids was found to often cover the combined ranges of the two parents. Table 2.3 shows that six out of the eight F_2 had maximum values equal or in excess of the values for the parents. Altogether, this indicates genetic segregation in the F_2 populations. The mean values of the hybrids of crosses 1, 3, 5 and 6 were inbetween the two parental means possibly indicating additive gene effects, whereas the F_2 of crosses 2, 4, 7 and 8 had means that exceeded the parental means, indicating possible dominance gene effects.

Population variances, chi-squares of Bartlett's test and variance ratios of parents and F_2's for head number are given in Table 2.1. Heterogeneity of the variances were found in crosses 3, 5, 6, 7, 8. However, in none of the comparisons did the F_2 have a statistically larger variance than both its parents.

Therefore it could not be established statistically for eight different crosses that the F_2 populations had larger variabilities than their parents. This result suggests that there was either a lack of genetic variability or that expression of the character was limited by the environment in the crop density situation.

Figure 2.2. Frequency distributions for head number in eight crosses studied at crop density; the blue and green curves are parent 1 and parent 2 distributions respectively and the red curve is the hybrid F_2 distribution.

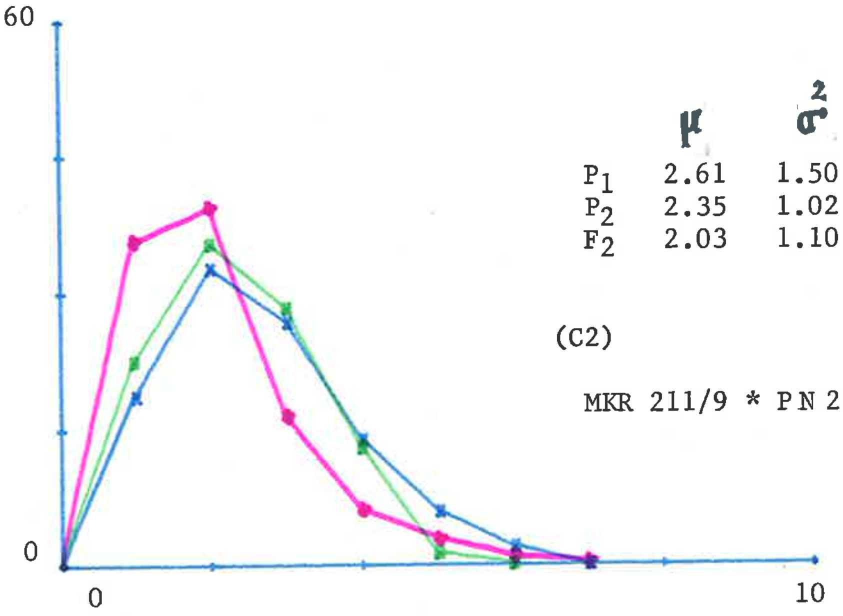
The X axis represents class intervals and the Y the plant frequency in each class as a percentage.



	μ	σ^2	cv
P_1	1.92	0.76	0.46
P_2	1.59	0.71	0.53
F_2	1.67	0.78	0.53

(C1)

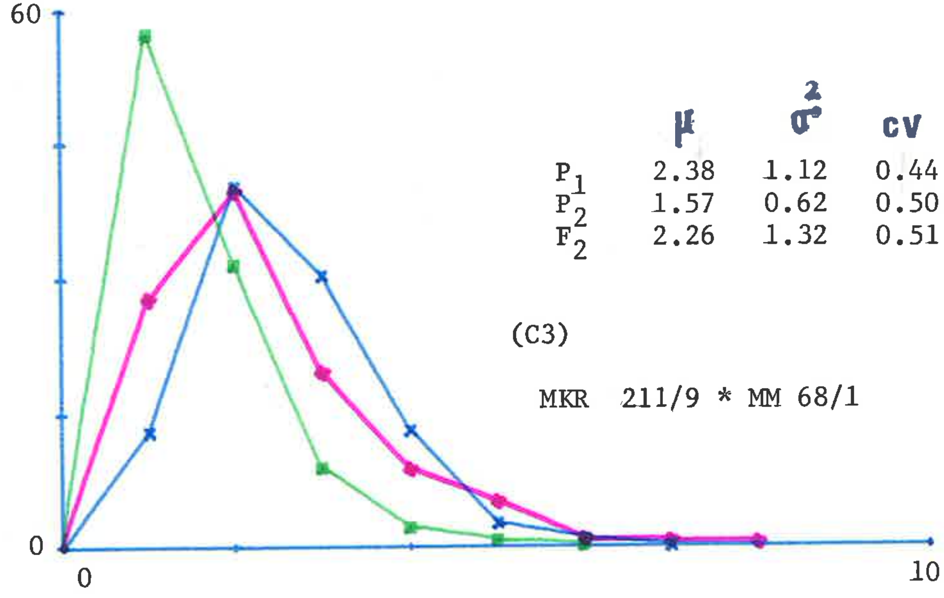
MM 25/4 * MM 68/1



	μ	σ^2	cv
P_1	2.61	1.50	0.47
P_2	2.35	1.02	0.43
F_2	2.03	1.10	0.52

(C2)

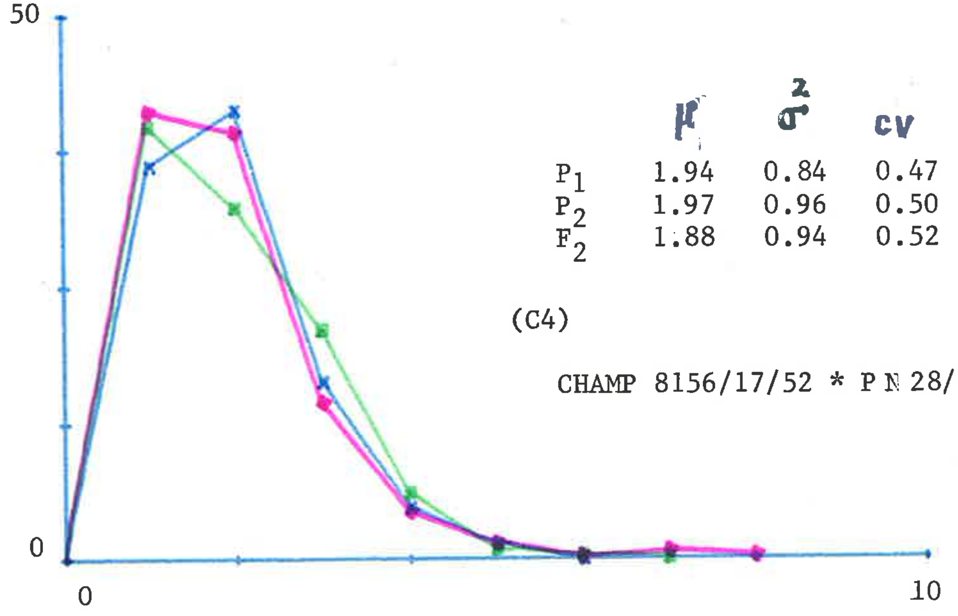
MKR 211/9 * P N 28/9



	μ	σ^2	cv
P_1	2.38	1.12	0.44
P_2	1.57	0.62	0.50
F_2	2.26	1.32	0.51

(C3)

MKR 211/9 * MM 68/1

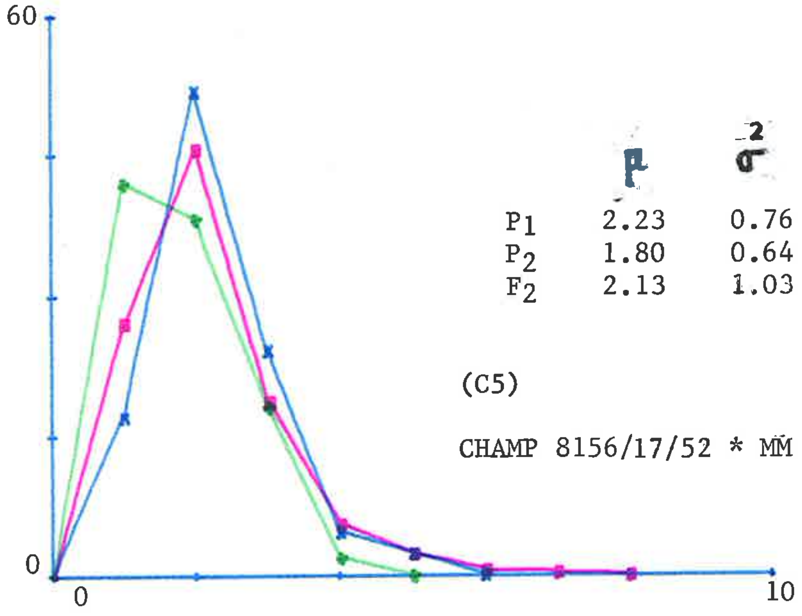


	μ	σ^2	cv
P_1	1.94	0.84	0.47
P_2	1.97	0.96	0.50
F_2	1.88	0.94	0.52

(C4)

CHAMP 8156/17/52 * P N 28/9

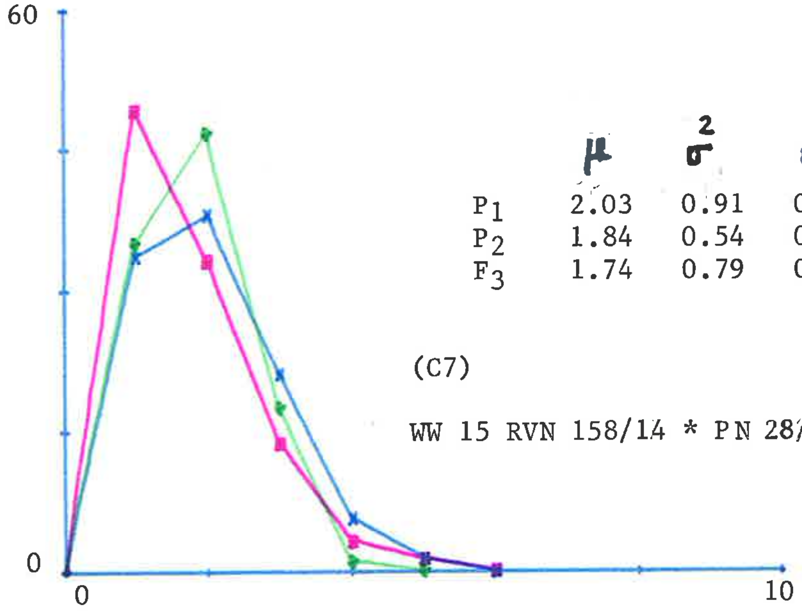
Number of heads per plant - crop density



	μ	σ^2	cv
P_1	2.23	0.76	0.39
P_2	1.80	0.64	0.45
F_2	2.13	1.03	0.48

(C5)

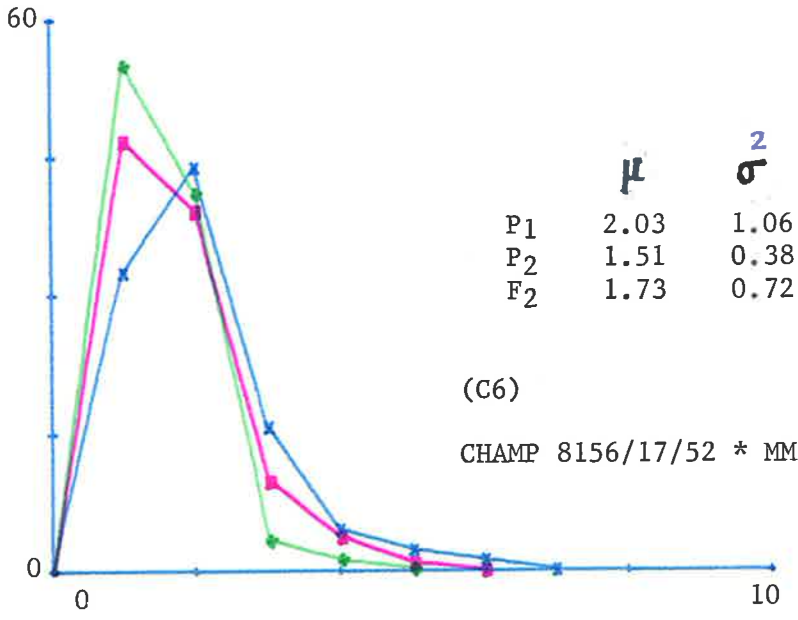
CHAMP 8156/17/52 * MM 68/1



	μ	σ^2	cv
P_1	2.03	0.91	0.47
P_2	1.84	0.54	0.40
F_3	1.74	0.79	0.51

(C7)

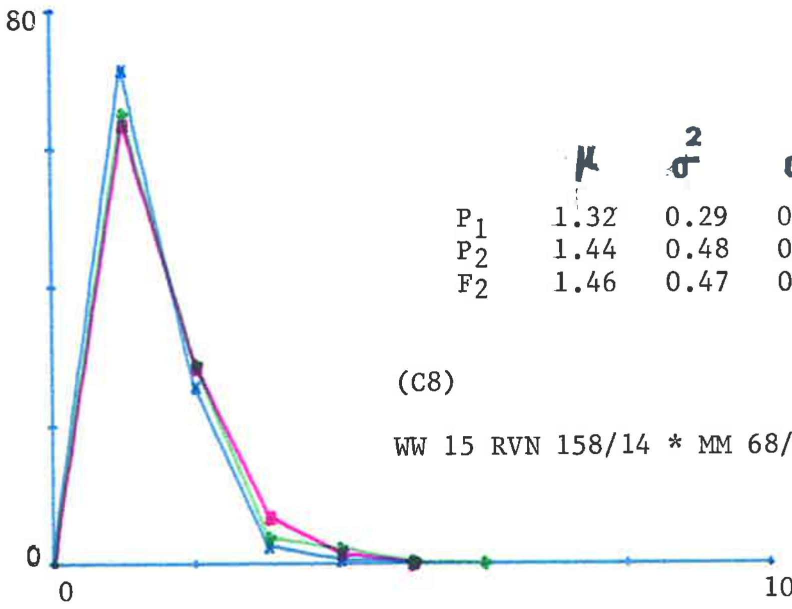
WW 15 RVN 158/14 * PN 28/9



	μ	σ^2	cv
P_1	2.03	1.06	0.51
P_2	1.51	0.38	0.41
F_2	1.73	0.72	0.49

(C6)

CHAMP 8156/17/52 * MMC 21/9



	μ	σ^2	cv
P_1	1.32	0.29	0.41
P_2	1.44	0.48	0.48
F_2	1.46	0.47	0.47

(C8)

WW 15 RVN 158/14 * MM 68/1

Number of heads per plant - crop density

Table 2.1 Variances of parents and F_2's, Chi-squares of Bartlett's test for homogeneity and F test of variance ratios between parents and F_2's for the character; head number per plant

	Variances			Bartlett's Chi-square	Variance ratios[1]		
	P_1	P_2	F_2		$P_1:P_2$	$P_1:F_2$	$P_2:F_2$
cross 1 MM25/4*MM68/1	0.76	0.71	0.78	0.17NS	1.07NS	1.03NS	1.09NS
cross 2 MKR211/9*PN28/9	1.50	1.02	1.10	2.49NS	1.47NS	1.37*	1.07NS
cross 3 MKR211/9*MM68/1	1.12	0.62	1.32	25.04***	1.81***	1.18NS	2.13***
cross 4 CHAMP8156/17/52 *PN28/9	0.84	0.96	0.94	0.92NS	1.14NS	1.12NS	1.02NS
cross 5 CHAMP8156/17/52 *MM68/1	0.76	0.64	1.03	4.93***	1.19NS	1.35NS	1.63***
cross 6 CHAMP8156/17/52 *MMC21/9	1.06	0.38	0.72	11.13***	2.80***	1.47*	1.89***
cross 7 WW15RVN158/14 *PN28/9	0.91	0.54	0.79	3.35*	1.68***	1.15NS	1.46*
cross 8 WW15RVN158/14 *MM68/1	0.29	0.48	0.47	16.52***	1.66***	1.62***	1.02NS

[1] Larger variable divided by smaller variable.

Table 2.2. Coefficient of skewness values for head number per plant of parents and F_2's grown at crop density.

	cross 1	cross 2	cross 3	cross 4	cross 5	cross 6	cross 7	cross 8
parent 1	1.48	0.61	0.60	0.93	0.81	1.32	0.34	1.65
parent 2	1.82	0.30	1.45	0.82	0.60	1.09	0.40	1.85
F_2's	1.82	1.15	0.99	1.50	1.24	1.26	1.20	1.43

Coefficient of skewness for significant difference from zero at the 5% probability level;

= ± 0.389 for sample size of 100 (approximate guide for the parents in crosses 1, 2, 5, 6, 7)

= ± 0.200 for sample size of 400 (approximate guide for all F_2's and parents of crosses 3, 4, 8)

Table 2.3. Minimum and maximum values in the parent and F_2 populations of eight crosses studied at crop density for the character: head number

cross number	minimum			maximum		
	P_1	P_2	F_2	P_1	P_2	F_2
cross 1 MM25/4*MM68/1	1	1	1	6	5	7
cross 2 MKR211/9*PN28/9	1	1	1	6	5	6
cross 3 MKR211/9*MM68/1	1	1	1	6	5	7
cross 4 CHAMP8156/17/52 *PN28/9	1	1	1	5	6	7
cross 5 CHAMP8156/17/52 *MM68/1	1	1	1	5	4	7
cross 6 CHAMP8156/17/52 *MMC21/9	1	1	1	6	4	5
cross 7 WW15RNV158/14 *PN28/9	1	1	1	5	4	5
cross 8 WW15RVN158/14 *MM68/1	1	1	1	4	5	4

3. Total plant weight at crop density.

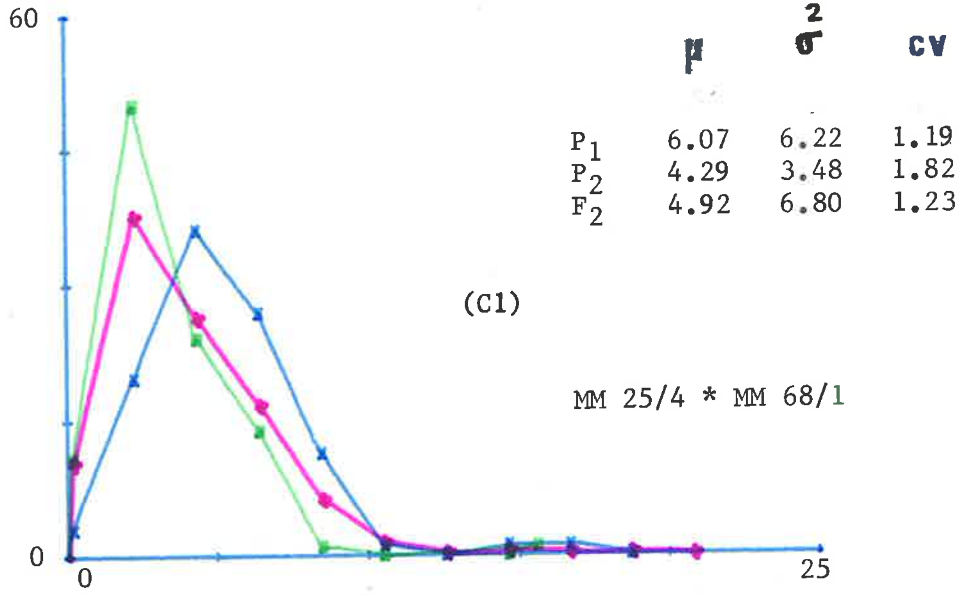
The distributions for total plant weight are shown in Figure 2.3. It was found that the distribution ranges of the F_2's covered the combined ranges of the parents and in general, the mean values were close to the mean of the parents, except in crosses 2 and 8 in which the F_2's had means lower and higher than the parental means respectively, indicating possible dominance gene effects. Table 2.6 shows that for seven out of eight crosses, the F_2's had a lower minimum value and a higher maximum value than the parents.

Table 2.4 contains the variances and other information relating to the testing of the variances of the parents and F_2's. The variances of the three populations in all crosses except cross 8, were heterogeneous however as with head number the F_2 variances were never significantly larger than both parental variances. These results indicate that there were large environmental effects on total plant weight of single plants of the parental populations. Their variation was similar to that of the F_2 population which had both environmental and genetic variation. Again, this may suggest that genetic variation for this character within the F_2 population is poorly expressed relative to the environmental variation.

The strong positive skews were characteristic for total plant weight (Table 2.5).

Figure 2.3. Frequency distributions of plant total weight (PLTWT) for eight crosses studied at crop density; blue and green curves are parent 1 and parent 2 distributions respectively and the red curve is the hybrid F_2 distribution.

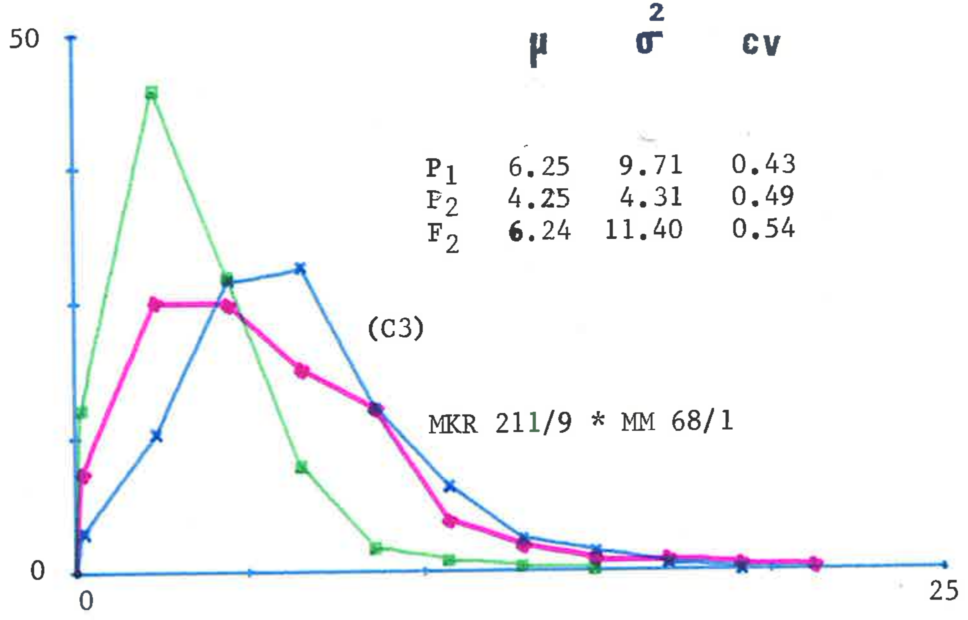
The X axis represents class intervals and the Y plant frequency in each class as a percentage.



	μ	σ^2	cv
P_1	6.07	6.22	1.19
P_2	4.29	3.48	1.82
F_2	4.92	6.80	1.23

(C1)

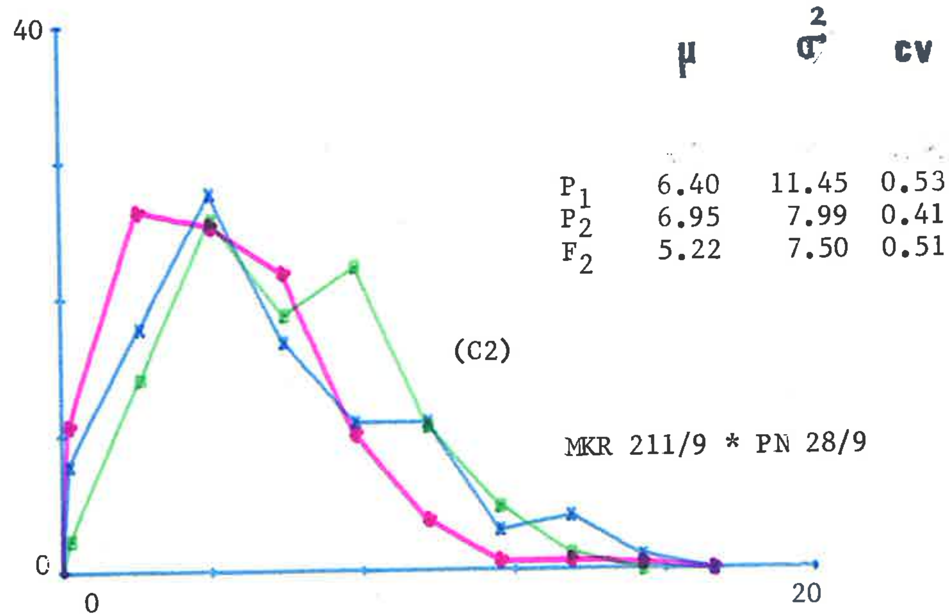
MM 25/4 * MM 68/1



	μ	σ^2	cv
P_1	6.25	9.71	0.43
P_2	4.25	4.31	0.49
F_2	6.24	11.40	0.54

(C3)

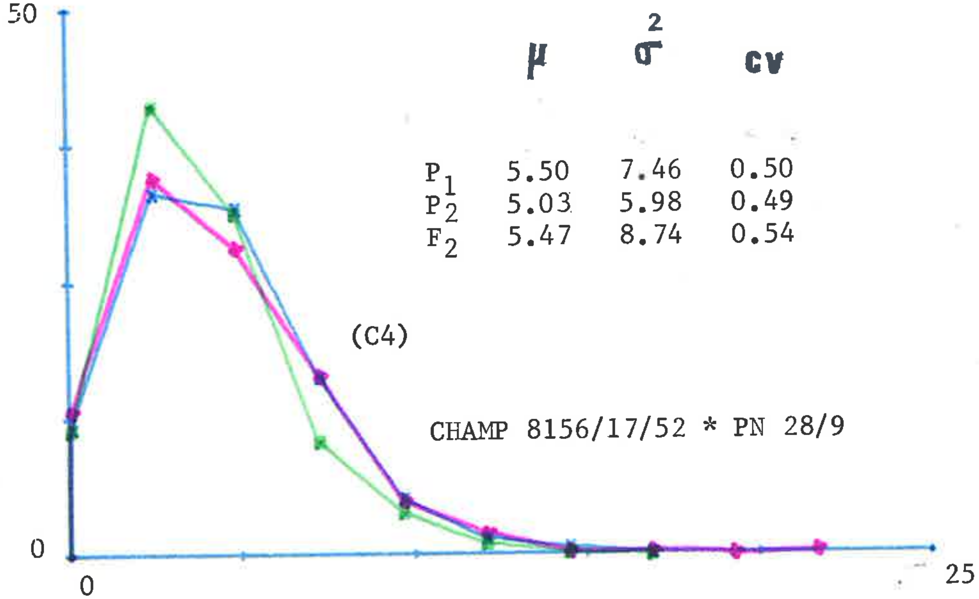
MKR 211/9 * MM 68/1



	μ	σ^2	cv
P_1	6.40	11.45	0.53
P_2	6.95	7.99	0.41
F_2	5.22	7.50	0.51

(C2)

MKR 211/9 * PN 28/9

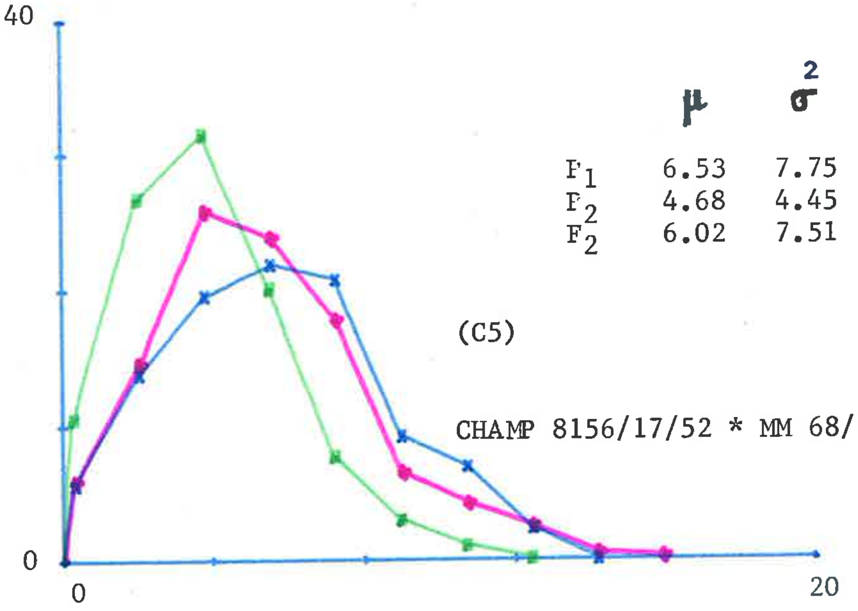


	μ	σ^2	cv
P_1	5.50	7.46	0.50
P_2	5.03	5.98	0.49
F_2	5.47	8.74	0.54

(C4)

CHAMP 8156/17/52 * PN 28/9

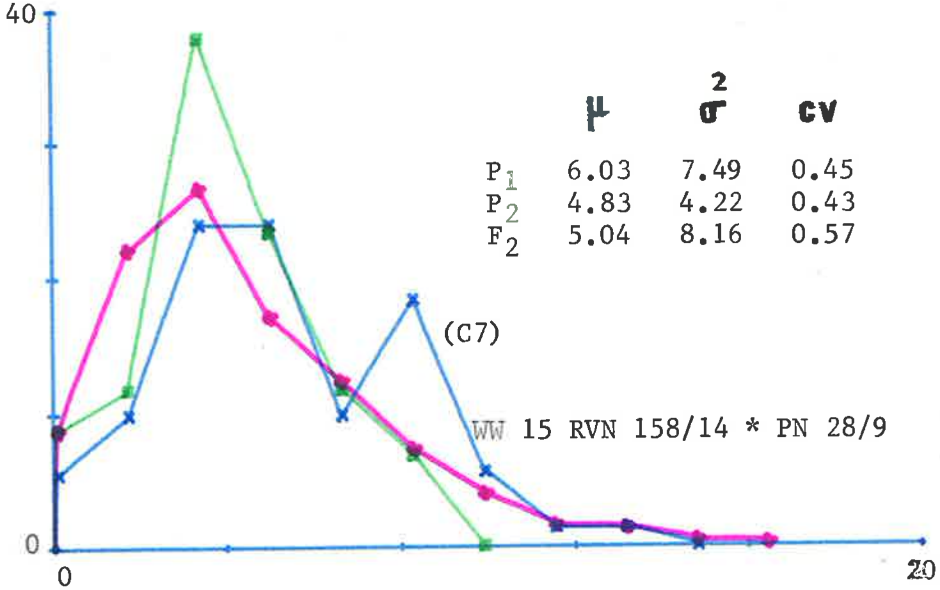
Plant total weight - crop density



	μ	σ^2	cv
P_1	6.53	7.75	0.43
P_2	4.68	4.45	0.45
F_2	6.02	7.51	0.46

(C5)

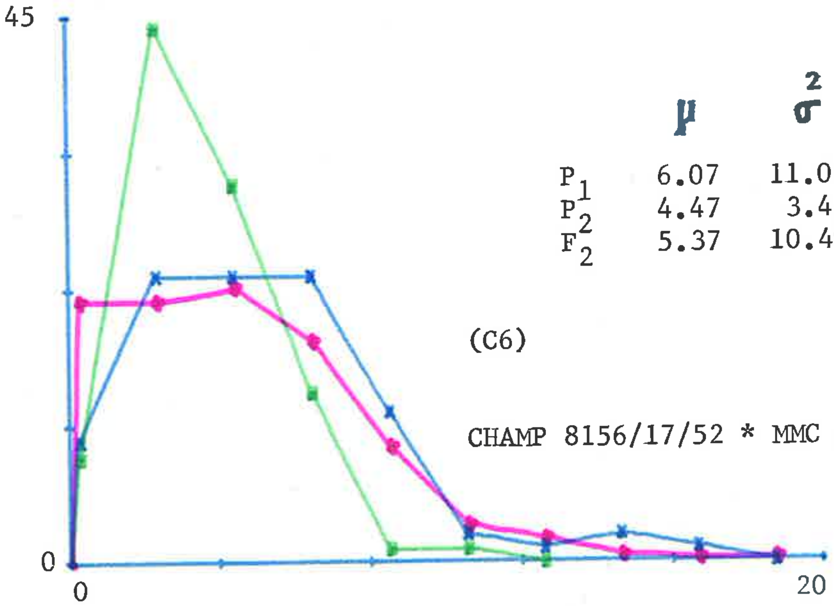
CHAMP 8156/17/52 * MM 68/1



	μ	σ^2	cv
P_1	6.03	7.49	0.45
P_2	4.83	4.22	0.43
F_2	5.04	8.16	0.57

(C7)

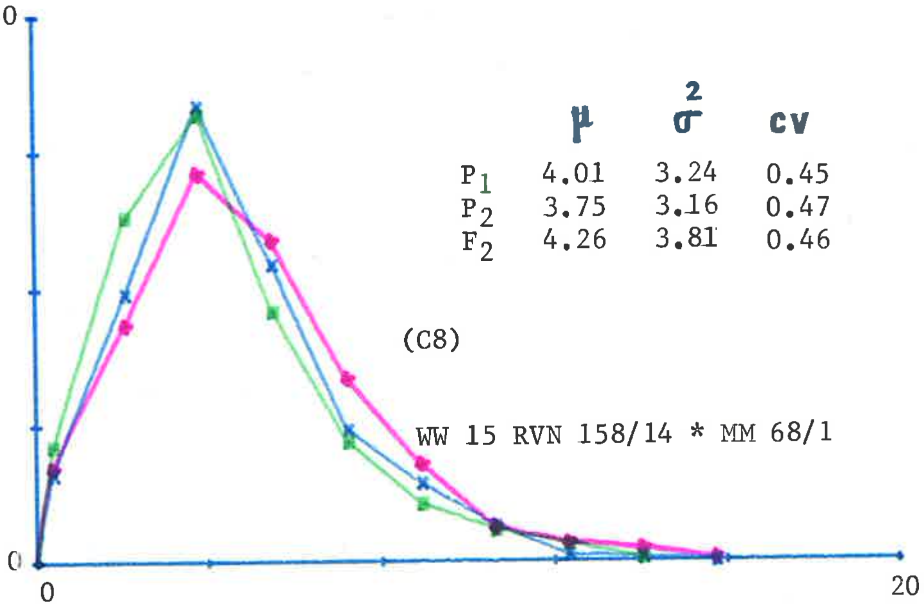
WW 15 RVN 158/14 * PN 28/9



	μ	σ^2	cv
P_1	6.07	11.08	0.55
P_2	4.47	3.47	0.42
F_2	5.37	10.49	0.60

(C6)

CHAMP 8156/17/52 * MMC 21/9



	μ	σ^2	cv
P_1	4.01	3.24	0.45
P_2	3.75	3.16	0.47
F_2	4.26	3.81	0.46

(C8)

WW 15 RVN 158/14 * MM 68/1

Plant total weight - crop density

Table 2.4. Variances of parents and F_2's, Chi-squares of Bartlett's test for homogeneity and F test of variance ratios between parents and F_2's for the character; plant total weight (PLTWT)

	Variances			Bartlett's Chi-square	Variance ratios[1]		
	P_1	P_2	F_2		P_1:P_2	P_1:F_2	P_2:F_2
cross 1 MM25/4*MM68/1	6.22	3.84	6.80	6.08***	1.62*	1.09NS	1.77***
cross 2 MKR211/9*PN28/9	11.45	7.99	7.05	5.31***	1.45NS	1.62***	1.12NS
cross 3 MKR211/9*MM68/1	9.71	4.31	11.04	42.19***	2.25***	1.17NS	2.64***
cross 4 CHAMP8156/17/52*PN28/9	7.46	5.98	8.74	7.05***	1.25*	1.17NS	1.46***
cross 5 CHAMP8156/17/52*MM68/1	7.75	4.45	7.51	5.26***	1.74***	1.03NS	1.68***
cross 6 CHAMP8156/17/52*MMC21/9	11.08	3.47	10.49	18.49***	3.19***	1.06NS	3.02***
cross 7 WW15RVN158/14*PN28/9	7.49	4.22	8.16	7.71***	1.77***	1.09NS	1.93***
cross 8 WW15RVN158/14*MM68/1	3.24	3.16	3.81	2.18NS	1.03NS	1.18NS	1.21NS

[1] Larger variable divided by smaller variable.

Table 2.5. Coefficient of skewness values for plant total weight (PLTWT) of parents and F_2's grown at crop density.

	cross 1	cross 2	cross 3	cross 4	cross 5	cross 6	cross 7	cross 8
parent 1	1.19	0.62	0.59	0.60	0.23	0.90	0.34	0.81
parent 2	1.22	0.20	0.05	0.89	0.42	0.73	0.01	0.39
F_2's	1.23	0.88	0.87	1.06	0.52	0.83	0.86	0.70

Coefficient of skewness for significant difference from zero at the 5% probability level;

= ± 0.389 for sample size of 100 (approximate guide for the parents in crosses 1, 2, 5, 6, 7)

= ± 0.200 for sample size of 400 (approximate guide for all F_2's and parents of crosses 3, 4, 8)

Table 2.6. Minimum and maximum values in the parent and F_2 populations of eight crosses studied at crop density for the character: plant total weight

cross number	minimum			maximum		
	P_1	P_2	F_2	P_1	P_2	F_2
cross 1 MM25/4*MM68/1	0.64	0.87	0.18	17.10	13.03	18.71
cross 2 MKR211/9*PN28/9	0.48	0.61	0.21	15.76	13.57	17.28
cross 3 MKR211/9*MM68/1	0.22	0.40	0.30	18.90	13.17	19.11
cross 4 CHAMP8156/17/52 *PN28/9	0.22	0.62	0.08	16.46	15.02	21.65
cross 5 CHAMP8156/17/52 *MM68/1	1.00	0.60	0.32	13.11	10.98	15.92
cross 6 CHAMP8156/17/52 *MMC21/9	0.29	0.47	0.31	27.36	11.01	18.71
cross 7 WW15RNV158/14 *PN28/9	1.10	0.31	0.10	13.32	9.41	14.87
cross 8 WW15RVN158/14 *MM68/1	0.45	0.32	0.29	11.72	10.28	11.80

4. The main shoot total weight at crop density.

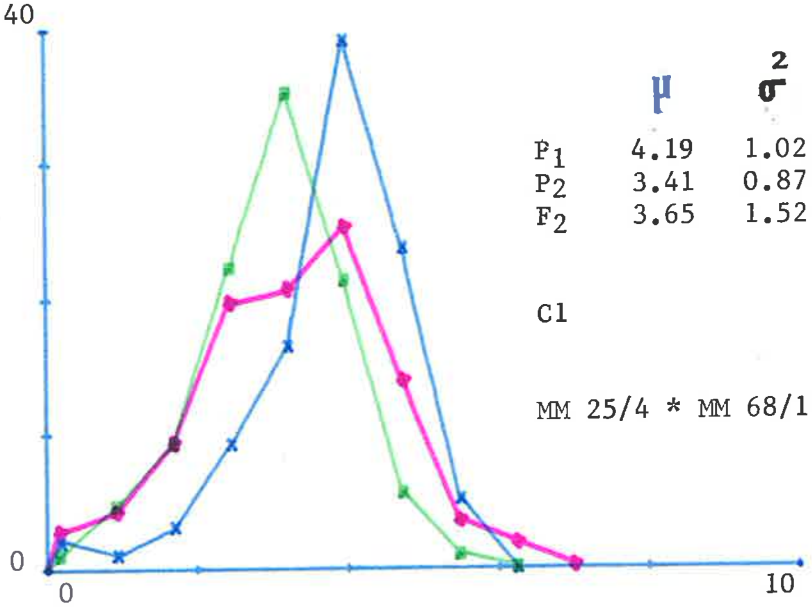
Frequency distributions for the main shoot total weight are presented in Figure 2.4. For most of the F_2's the range of the distribution covered the combined ranges of the parents as was found previously. The hybrid means were close to the mid-parent value except in crosses 1, 4, 5 and 8 in which the F_2 means were higher than the parental means, possibly indicating dominance effects. Furthermore, if heterosis defined as occurring when the F_2 mean is greater than the value of the two parental means then heterosis was evident in these four crosses. Transgressive segregation was found in crosses 1, 3, 4, 5, 6, 7 and 8. This was evident as many extreme individuals, with values exceeding the maximum and minimum values of the parents (Figure 2.4 and Table 2.9). Crosses 1, 3, 6 and 7 showed transgressive segregation without any evidence of heterosis.

Table 2.7 contains the variances which in many crosses, were heterogenous for the three populations (P_1, P_2 and F_2) and the F_2 of crosses 1, 3, 4 and 6 had variances significantly larger than that of both parents. In two other crosses (7 and 8) the F_2 variances were significantly larger than one parent. Therefore for this character; the main shoot total weight, there was clearer evidence of genetic segregation than had been found for head number or total plant weight.

Skewness for the main shoot total weight was different from that for total plant weight, as it was negative (Table 2.8). This suggests that most plants were able to develop main shoots close to their potential and on only a few plants, due to environmental factors, were they limited causing the skew to be negative. It is shown in Table 2.7 that there were no differences between the P_1 and P_2 variances, except for cross 8. This indicates that the micro-environment affected equally, the genotypes' main shoot. For these crosses therefore any differences in the main shoot of the F_2's should have resulted from differences in genetic constitution.

Figure 2.4. Frequency distributions for main shoot total weight (MTWT) for eight crosses grown at crop density; blue and green curves are parents 1 and 2 respectively and the red curve is the F_2 distribution.

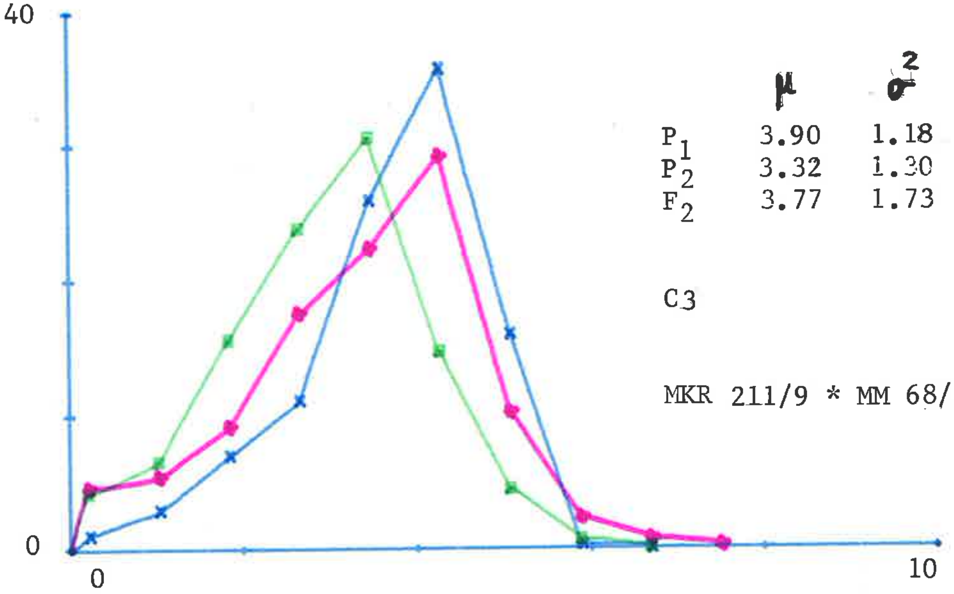
The X axis represents class intervals and the Y plant frequency in each class as a percentage.



	μ	σ^2	cv
P_1	4.19	1.02	0.24
P_2	3.41	0.87	0.27
F_2	3.65	1.52	0.34

C1

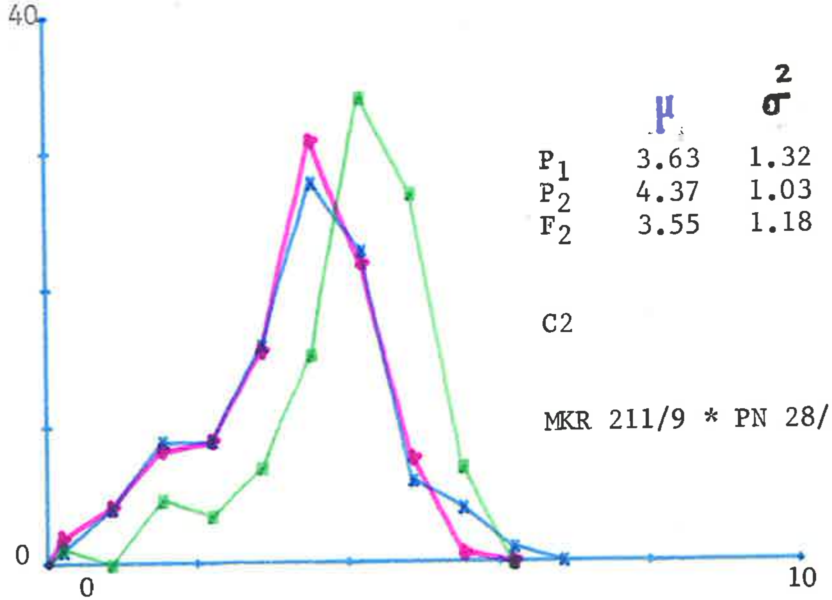
MM 25/4 * MM 68/1



	μ	σ^2	cv
P_1	3.90	1.18	0.28
P_2	3.32	1.30	0.34
F_2	3.77	1.73	0.35

C3

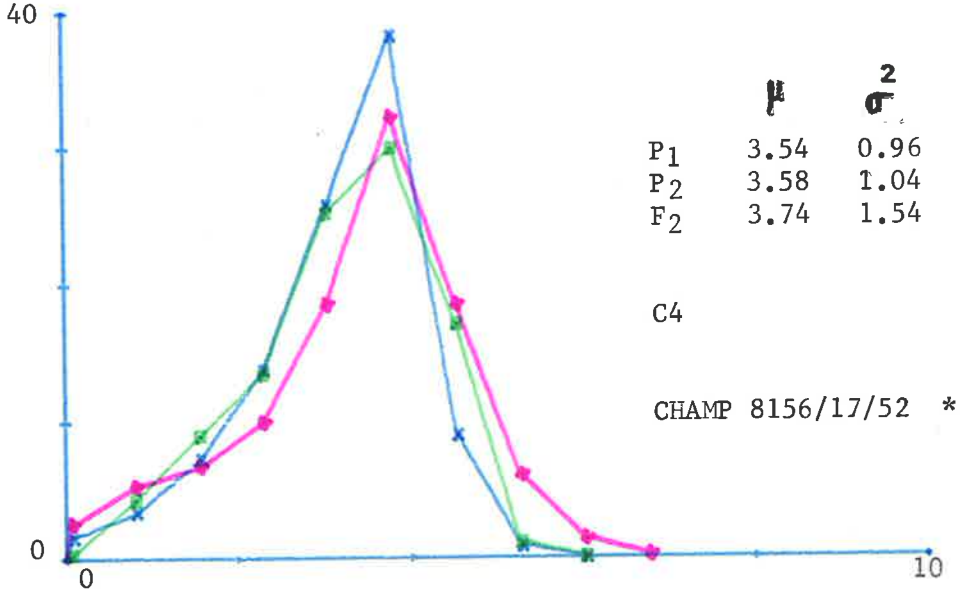
MKR 211/9 * MM 68/1



	μ	σ^2	cv
P_1	3.63	1.32	0.32
P_2	4.37	1.03	0.23
F_2	3.55	1.18	0.31

C2

MKR 211/9 * PN 28/9

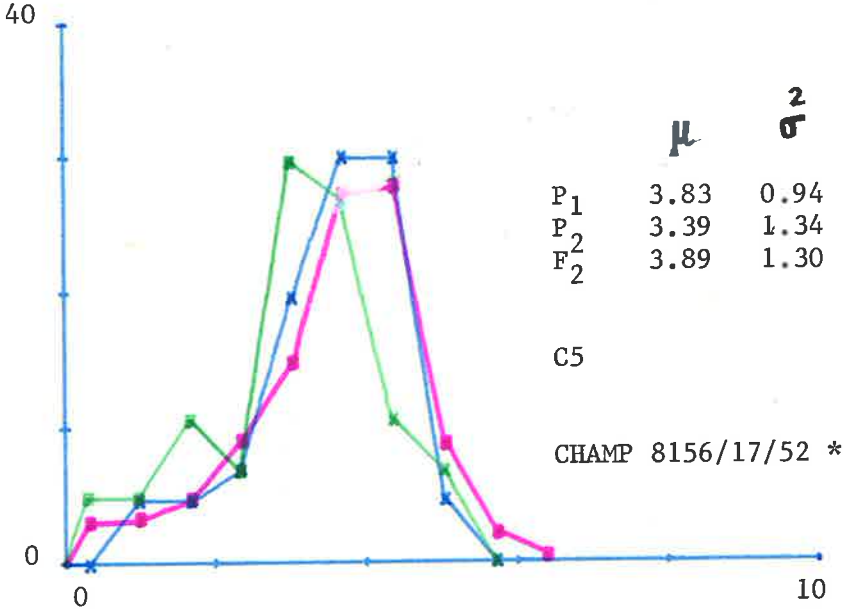


	μ	σ^2	cv
P_1	3.54	0.96	0.28
P_2	3.58	1.04	0.28
F_2	3.74	1.54	0.33

C4

CHAMP 8156/17/52 * PN 28/9

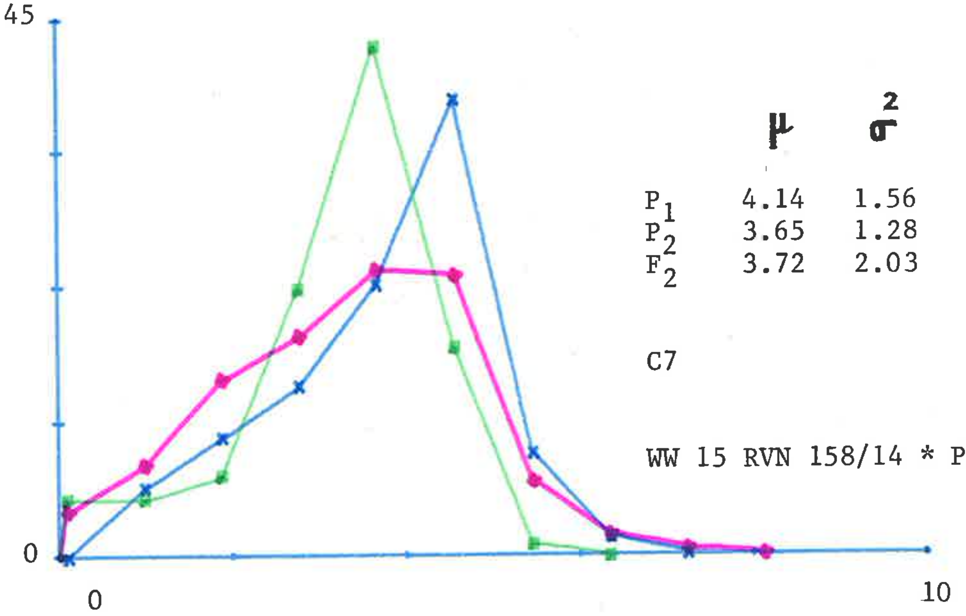
Main shoot total weight - crop density



	μ	σ^2	cv
P_1	3.83	0.94	0.25
P_2	3.39	1.34	0.34
F_2	3.89	1.30	0.29

C5

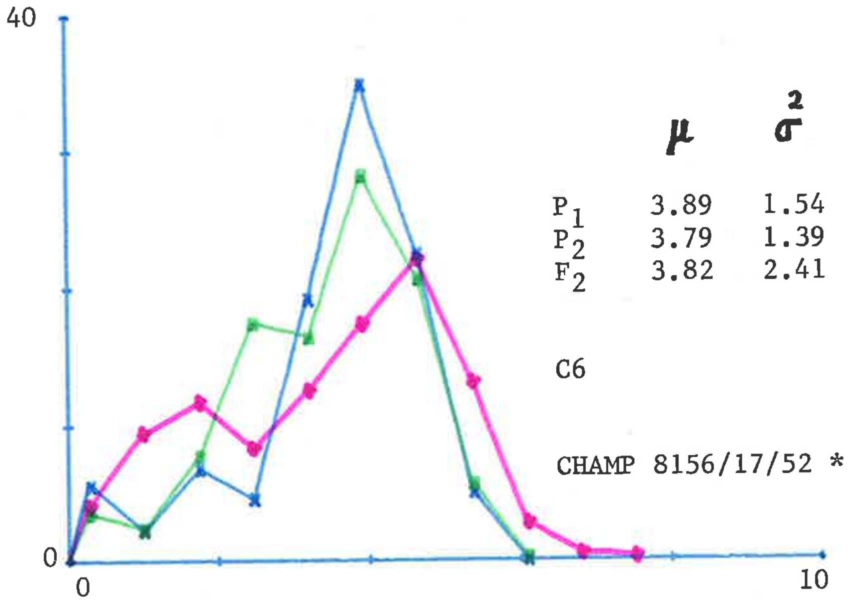
CHAMP 8156/17/52 * MM 68/1



	μ	σ^2	cv
P_1	4.14	1.56	0.30
P_2	3.65	1.28	0.31
F_2	3.72	2.03	0.38

C7

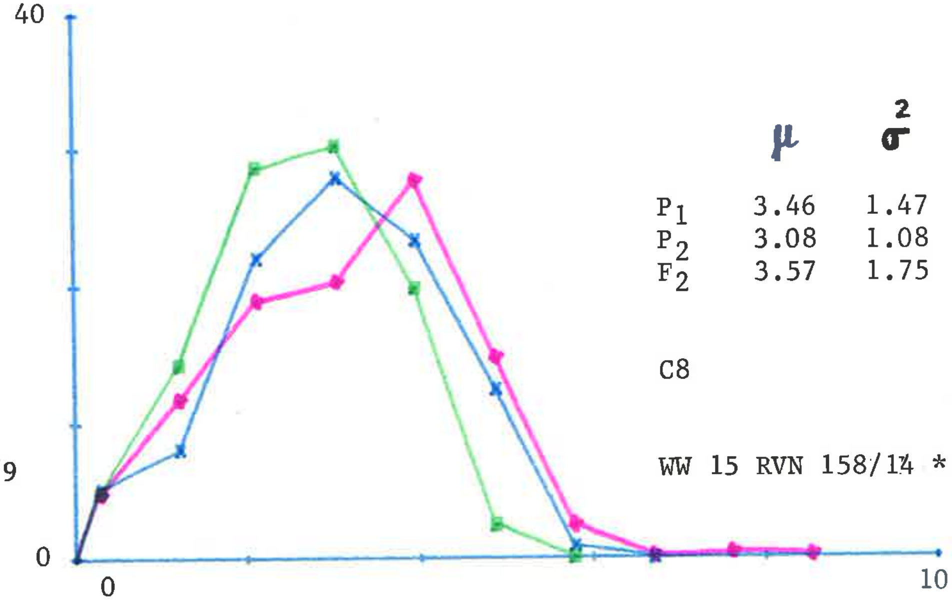
WW 15 RVN 158/14 * PN 28/9



	μ	σ^2	cv
P_1	3.89	1.54	0.32
P_2	3.79	1.39	0.31
F_2	3.82	2.41	0.41

C6

CHAMP 8156/17/52 * MMC 21/9



	μ	σ^2	cv
P_1	3.46	1.47	0.35
P_2	3.08	1.08	0.34
F_2	3.57	1.75	0.37

C8

WW 15 RVN 158/14 * MM 68/1

Main shoot total weight - crop density

Table 2.7. Variances of parents and F_2's, Chi-squares of Bartlett's test for homogeneity and F test of variance ratios between parents and F_2's for the character; the main shoot total weight (MTWT)

	Variances			Bartlett's Chi-square	Variance ratios[1]		
	P_1	P_2	F_2		$P_1:P_2$	$P_1:F_2$	$P_2:F_2$
cross 1 MM25/4*MM68/1	1.02	0.87	1.52	7.72***	1.17NS	1.49*	1.75***
cross 2 MKR211/9*PN28/9	1.32	1.03	1.18	0.69NS	1.28NS	1.12NS	1.14NS
cross 3 MKR211/9*MM68/1	1.18	1.30	1.73	7.80***	1.10NS	1.47***	1.33***
cross 4 CHAMP8156/17/52 *PN28/9	0.96	1.04	1.52	12.19***	1.08NS	1.58***	1.46***
cross 5 CHAMP8156/17/52 *MM68/1	0.94	1.34	1.30	1.90NS	1.43NS	1.38NS	1.03NS
cross 6 CHAMP8156/17/52 *MMC21/9	1.54	1.39	2.41	7.07***	1.11NS	1.56***	1.73***
cross 7 WW15RVN158/14 *PN28/9	1.56	1.28	2.03	4.47***	1.22NS	1.30NS	1.59***
cross 8 WW15RVN158/14 *MM68/1	1.47	1.08	1.75	11.32***	1.36***	1.19NS	1.62***

[1] Larger variable divided by smaller variable.

Table 2.8. Coefficient of skewness values for the main shoot total weight of parents and F_2's grown at crop density.

	cross 1	cross 2	cross 3	cross 4	cross 5	cross 6	cross 7	cross 8
parent 1	-1.13	-0.38	-1.03	-0.97	-1.00	-1.22	-0.69	-0.27
parent 2	-0.39	-1.36	-0.32	-0.63	-0.54	-0.66	-1.15	-0.30
F_2's	-0.34	-0.78	-0.50	-0.69	-0.85	-0.41	-0.28	-0.22

Coefficient of skewness for significant difference from zero at the 5% probability level;

= ± 0.389 for sample size of 100 (approximate guide for the parents in crosses 1, 2, 5, 6, 7)

= ± 0.200 for sample size of 400 (approximate guide for all F_2's and parents of crosses 3, 4, 8)

Table 2.9. Minimum and maximum values in the parent and F_2 populations of eight crosses studied at crop density for the character: the main shoot total weight (MTWT)

cross number	minimum			maximum		
	P_1	P_2	F_2	P_1	P_2	F_2
cross 1 MM25/4*MM68/1	0.64	0.87	0.18	6.00	5.50	7.00
cross 2 MKR211/9*PN28/9	0.48	0.50	0.21	6.18	5.79	5.91
cross 3 MKR211/9*MM68/1	0.22	0.40	0.30	6.10	6.40	7.50
cross 4 CHAMP8156/17/52 *PN28/9	0.22	0.62	0.08	5.44	5.90	6.77
cross 5 CHAMP8156/17/52 *MM68/1	1.00	0.60	0.30	5.30	5.58	6.38
cross 6 CHAMP8156/17/52 *MMC21/9	0.29	0.47	0.31	5.80	6.03	6.83
cross 7 WW15RNV158/14 *PN28/9	1.10	0.31	0.10	6.42	5.48	8.21
cross 8 WW15RVN158/14 *MM68/1	0.45	0.32	0.29	6.15	5.52	8.52

5. The main shoot grain weight at crop density.

The frequency distributions for the main shoot grain weight (Fig. 2.5) had patterns similar to those obtained for the main shoot total weight. The F_2's means for crosses 2, 3, 7 and 8 were between the two parental means while for crosses 4, 5 and 6 the F_2's means exceeded the parental means. This probably indicates that simple additive gene effects operated in crosses 2, 3, 7 and 8, and that an effect of dominance operated in crosses 4, 5 and 6. The F_2 of cross 6 again showed a bimodal distribution similar to that obtained for the main shoot total weight.

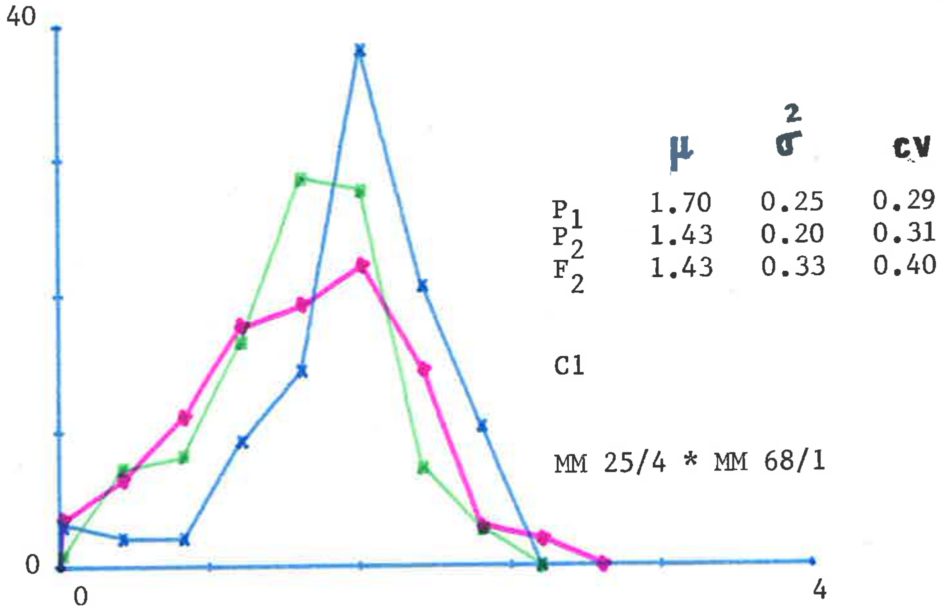
Only in crosses 4 and 6 were the F_2's variances significantly larger than both parents (Table 2.10). In crosses 1, 7 and 8 the F_2's variances were larger than one parent and in the remaining crosses the variances were homogeneous.

Again, here were some individuals with extreme expression in the F_2 populations of crosses 1, 4, 5, 6 and 7 (Figure 2.5 and Table 2.12), as was evident previously in the main shoot total weight.

For many of the crosses, the variances of the two parents were similar, a result that was found previously for the main shoot total weight.

Negative skews occurred again for this character in every population (Table 2.11).

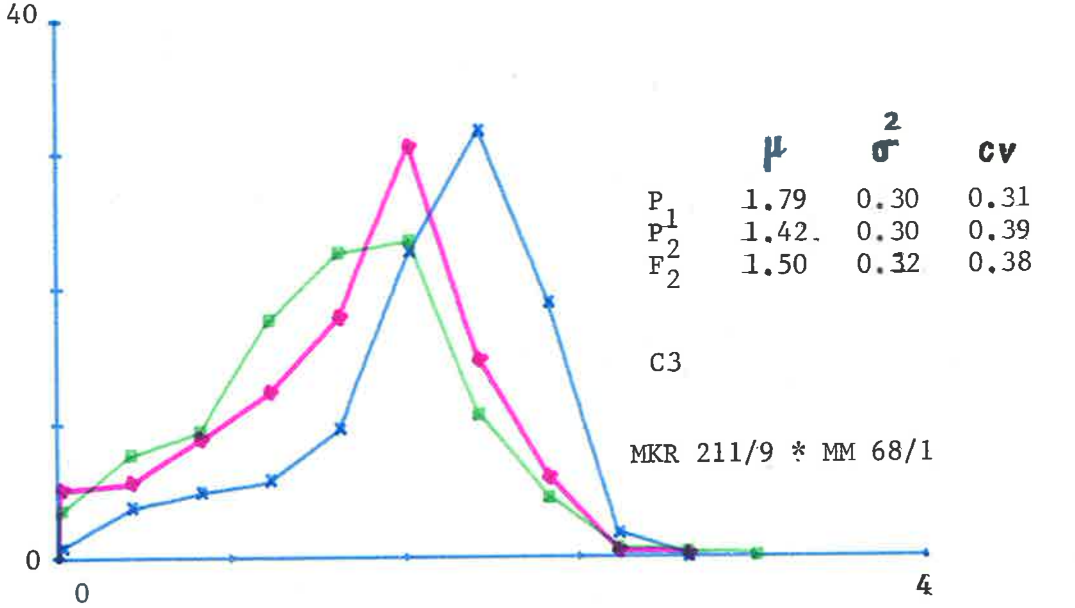
Figure 2.5. Frequency distribution of the main shoot grain weight (MGRWT) from eight crosses grown at crop density; the blue and green curves are parent 1 and parent 2 distributions respectively and the red curve is the hybrid F_2 distribution.
The X axis represents class intervals and the Y the plant frequency in each class as a percentage.



	μ	σ^2	cv
P_1	1.70	0.25	0.29
P_2	1.43	0.20	0.31
F_2	1.43	0.33	0.40

C1

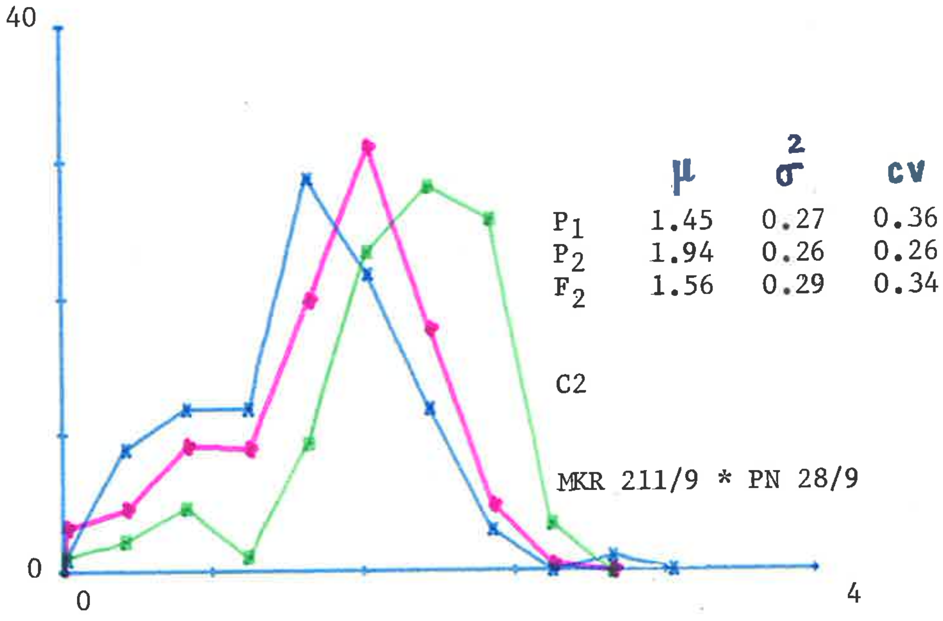
MM 25/4 * MM 68/1



	μ	σ^2	cv
P_1	1.79	0.30	0.31
P_2	1.42	0.30	0.39
F_2	1.50	0.32	0.38

C3

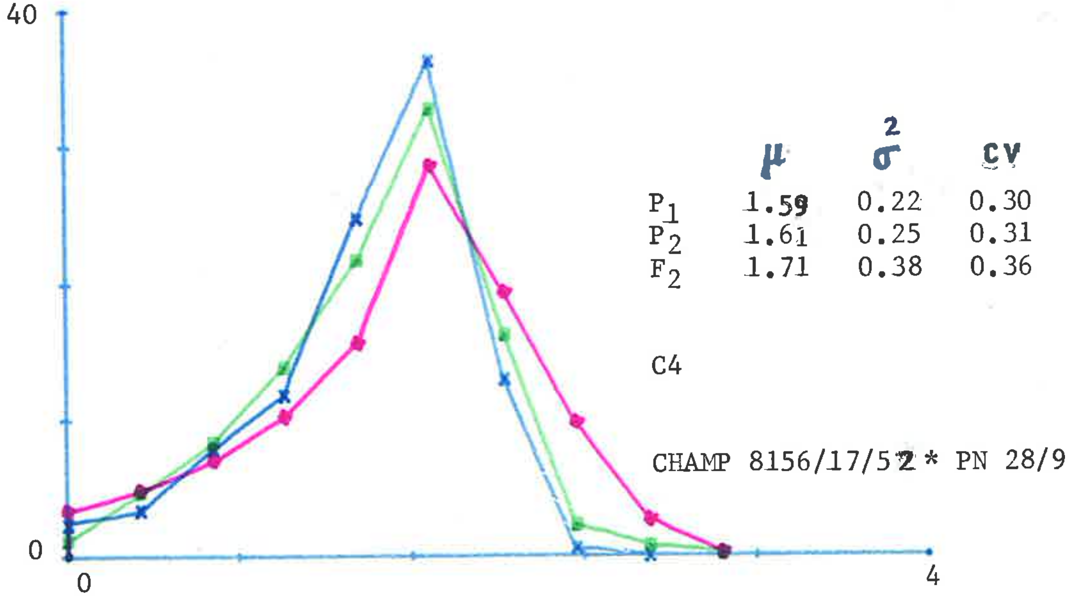
MKR 211/9 * MM 68/1



	μ	σ^2	cv
P_1	1.45	0.27	0.36
P_2	1.94	0.26	0.26
F_2	1.56	0.29	0.34

C2

MKR 211/9 * PN 28/9

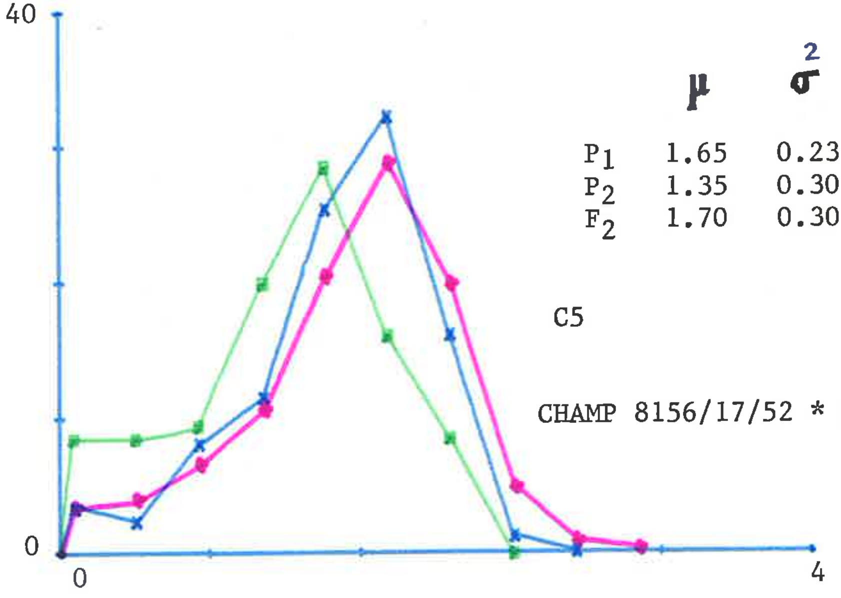


	μ	σ^2	cv
P_1	1.59	0.22	0.30
P_2	1.61	0.25	0.31
F_2	1.71	0.38	0.36

C4

CHAMP 8156/17/52 * PN 28/9

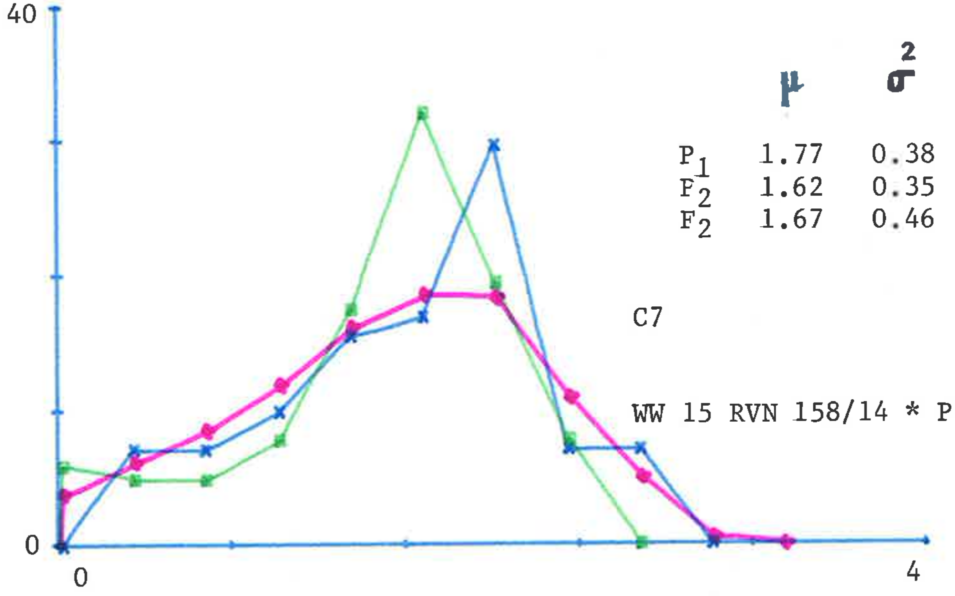
Main shoot grain weight - crop density



	μ	σ^2	cv
P_1	1.65	0.23	0.29
P_2	1.35	0.30	0.41
F_2	1.70	0.30	0.33

C5

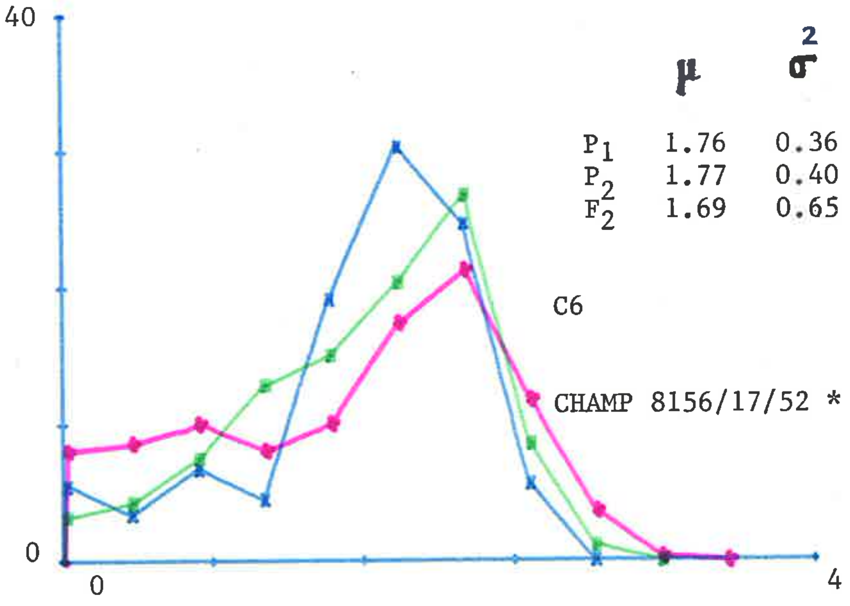
CHAMP 8156/17/52 * MM 68/1



	μ	σ^2	cv
P_1	1.77	0.38	0.35
F_2	1.62	0.35	0.37
F_2	1.67	0.46	0.41

C7

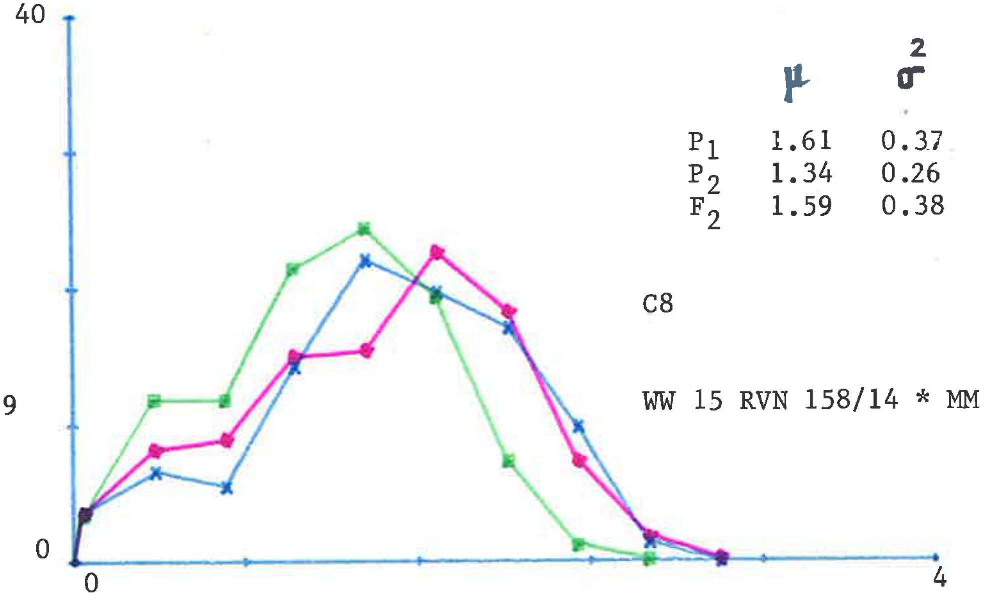
WW 15 RVN 158/14 * PN 28/9



	μ	σ^2	cv
P_1	1.76	0.36	0.34
P_2	1.77	0.40	0.36
F_2	1.69	0.65	0.48

C6

CHAMP 8156/17/52 * MMC 21/9



	μ	σ^2	cv
P_1	1.61	0.37	0.38
P_2	1.34	0.26	0.38
F_2	1.59	0.38	0.39

C8

WW 15 RVN 158/14 * MM 68/1

Main shoot grain weight - crop density

Table 2.10. Variances of parents and F_2's, Chi-squares of Bartlett's test for homogeneity and F test of variance ratios between parents and F_2's for the character; the main shoot grain weight (MGRWT)

	Variances			Bartlett's Chi-square	Variance ratios[1]		
	P_1	P_2	F_2		$P_1:P_2$	$P_1:F_2$	$P_2:F_2$
cross 1 MM25/4*MM68/1	0.25	0.20	0.33	5.52***	1.25NS	1.32NS	1.65***
cross 2 MKR211/9*PN28/9	0.27	0.26	0.29	0.20NS	1.04NS	1.07NS	1.12NS
cross 3 MKR211/9*MM68/1	0.30	0.30	0.32	1.05NS	1.00NS	1.07NS	1.07NS
cross 4 CHAMP8156/17/52 *PN28/9	0.22	0.25	0.38	16.11***	1.14NS	1.73***	1.52***
cross 5 CHAMP8156/17/52 *MM68/1	0.23	0.30	0.30	1.13NS	1.30NS	1.30NS	1.00NS
cross 6 CHAMP8156/17/52 *MMC21/9	0.36	0.40	0.65	10.54***	1.11NS	1.81***	1.63***
cross 7 WW15RVN158/14 *PN28/9	0.38	0.35	0.46	1.78NS	1.09NS	1.21NS	1.31*
cross 8 WW15RVN158/14 *MM68/1	0.37	0.26	0.38	9.58***	1.42***	1.03NS	1.46***

[1] Larger variable divided by smaller variable.

Table 2.11. Coefficient of skewness values for the main shoot grain weight of parents and F_2's grown at crop density.

	cross 1	cross 2	cross 3	cross 4	cross 5	cross 6	cross 7	cross 8
parent 1	-1.06	-0.48	-1.36	-0.89	-1.14	-1.07	-0.64	-0.44
parent 2	-0.41	-1.10	-0.47	-0.75	-0.90	-0.44	-1.23	-0.45
F_2's	-0.38	-0.39	-0.86	-0.85	-0.79	-0.32	-0.54	-0.32

Coefficient of skewness for significant difference from zero at the 5% probability level;

= ± 0.389 for sample size of 100 (approximate guide for the parents in crosses 1, 2, 5, 6, 7)

= ± 0.200 for sample size of 400 (approximate guide for all F_2's and parents of crosses 3, 4, 8)

Table 2.12. Minimum and maximum values in the parent and F_2 populations of eight crosses studied at crop density for the character: the main shoot grain weight (MGRWT)

cross number	minimum			maximum		
	P_1	P_2	F_2	P_1	P_2	F_2
cross 1 MM25/4*MM68/1	0.11	0.32	0.02	2.53	2.41	2.87
cross 2 MKR211/9*PN28/9	0.20	0.19	0.02	2.92	2.75	2.77
cross 3 MKR211/9*MM68/1	0.04	0.10	0.02	2.79	2.90	2.66
cross 4 CHAMP8156/17/52 *PN28/9	0.02	0.20	0.00	2.60	2.84	3.04
cross 5 CHAMP8156/17/52 *MM68/1	0.26	0.12	0.08	2.48	2.36	3.07
cross 6 CHAMP8156/17/52 *MMC21/9	0.10	0.16	0.02	2.77	2.92	3.18
cross 7 WW15RNV158/14 *PN28/9	0.42	0.02	0.02	2.80	2.51	3.01
cross 8 WW15RVN158/14 *MM68/1	0.00	0.08	0.05	3.00	2.52	2.90

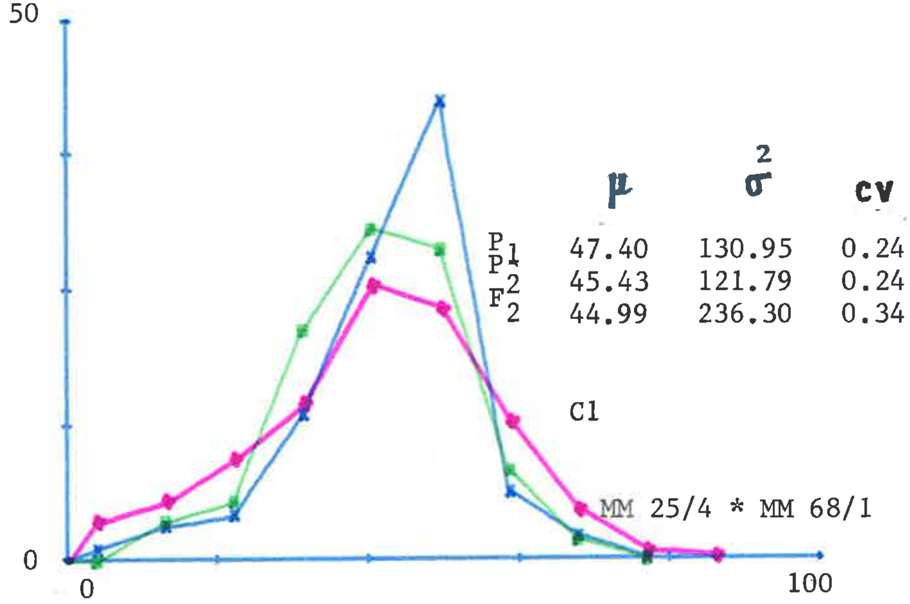
6. The main shoot grain number at crop density.

As the main shoot grain number was closely associated with the main shoot grain weight (their correlation coefficient ranged from 0.820*** to 0.958*** for the different crosses), their frequency distribution patterns were very similar. The distributions for this character are given in Figure 2.6. However, the evidence for a bimodal distribution in cross 6 found for the main shoot total weight and grain weight was now negligible. Heterosis in terms of the mean values was evident in crosses 1, 3, 5 and 8 but the F_2's of crosses 1 and 3 showed a negative heterosis.

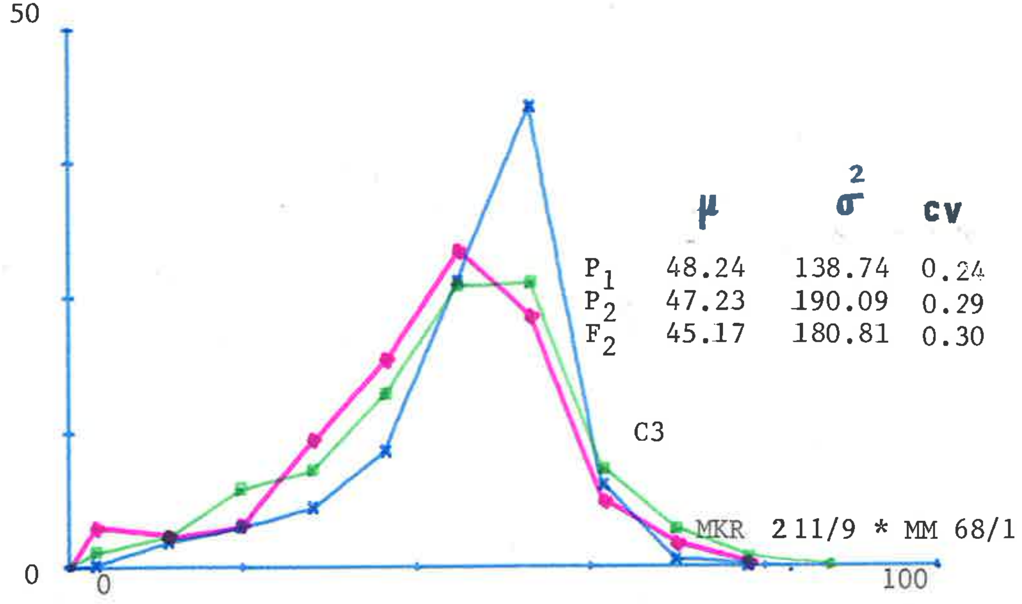
Table 2.15 gives the minimum and maximum values. In most crosses the F_2's had a lower minima than their parents but for the maxima only the F_2 of crosses 1, 5, 6, 7 and 8 had values higher than their parents. The variances are shown in Table 2.13. Although in many crosses the F_2 had larger values than their parents, only in cross 1 was it significantly larger than both parents.

Negative skews were obtained (Table 2.14).

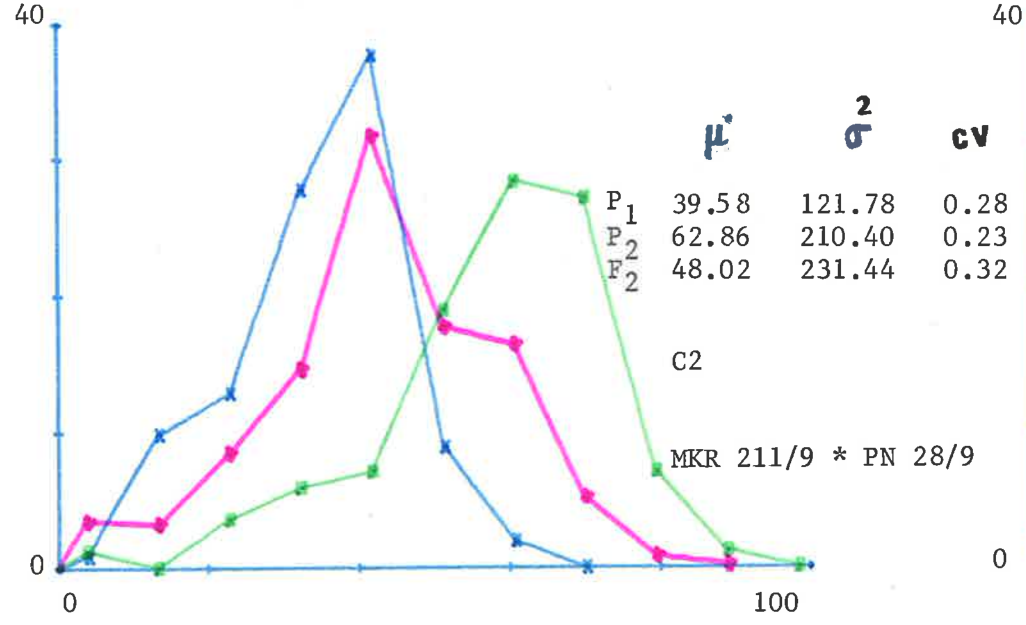
Figure 2.6. Frequency distribution of main shoot grain number (MGRNO) for eight crosses studied at crop density. The blue and green curves are parent 1 and parent 2 distributions respectively and the red is the hybrid F_2 distribution. The X axis represents class intervals and the Y plant frequency in each class as a percentage.



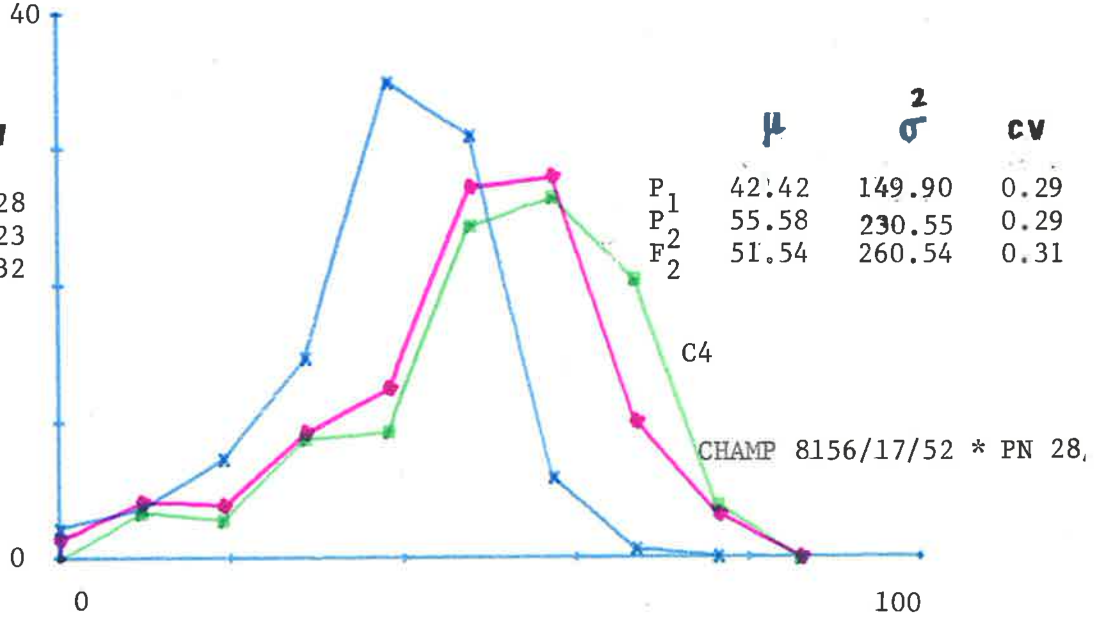
	μ	σ²	cv
P_1	47.40	130.95	0.24
P_2	45.43	121.79	0.24
F_2	44.99	236.30	0.34



	μ	σ²	cv
P_1	48.24	138.74	0.24
P_2	47.23	190.09	0.29
F_2	45.17	180.81	0.30

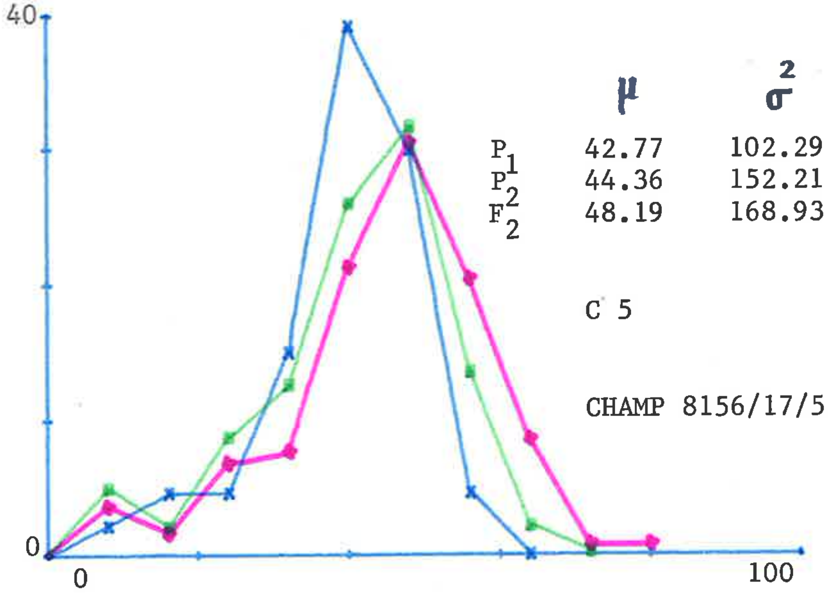


	μ	σ²	cv
P_1	39.58	121.78	0.28
P_2	62.86	210.40	0.23
F_2	48.02	231.44	0.32



	μ	σ²	cv
P_1	42.42	149.90	0.29
P_2	55.58	230.55	0.29
F_2	51.54	260.54	0.31

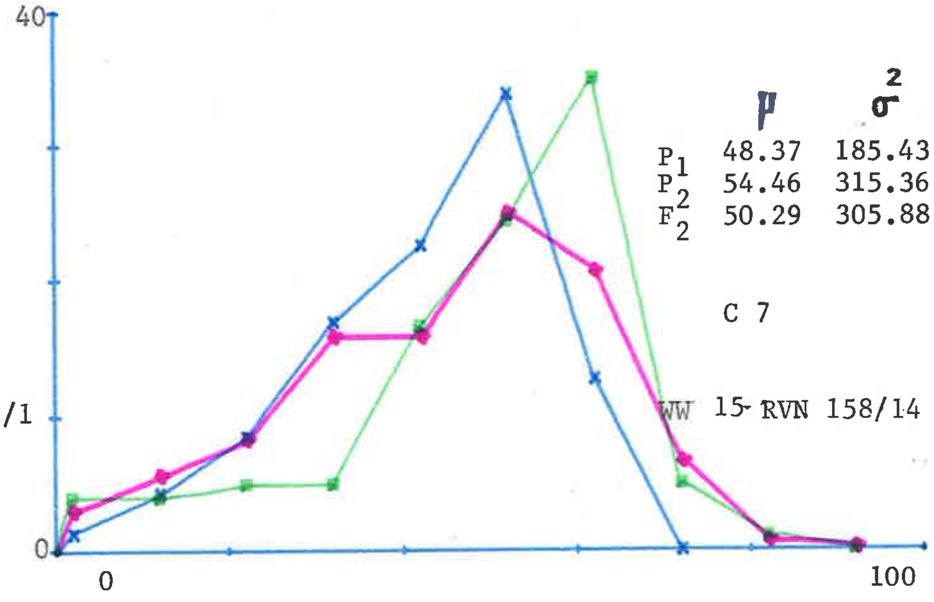
Main shoot grain number - crop density



	μ	σ^2	cv
P_1	42.77	102.29	0.24
P_2	44.36	152.21	0.28
F_2	48.19	168.93	0.27

C 5

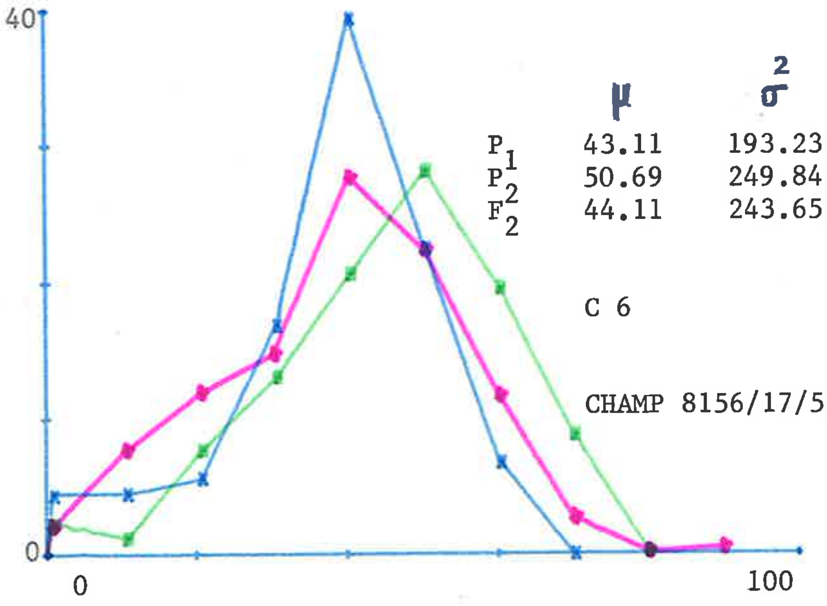
CHAMP 8156/17/52 * MM 68/1



	μ	σ^2	cv
P_1	48.37	185.43	0.28
P_2	54.46	315.36	0.33
F_2	50.29	305.88	0.35

C 7

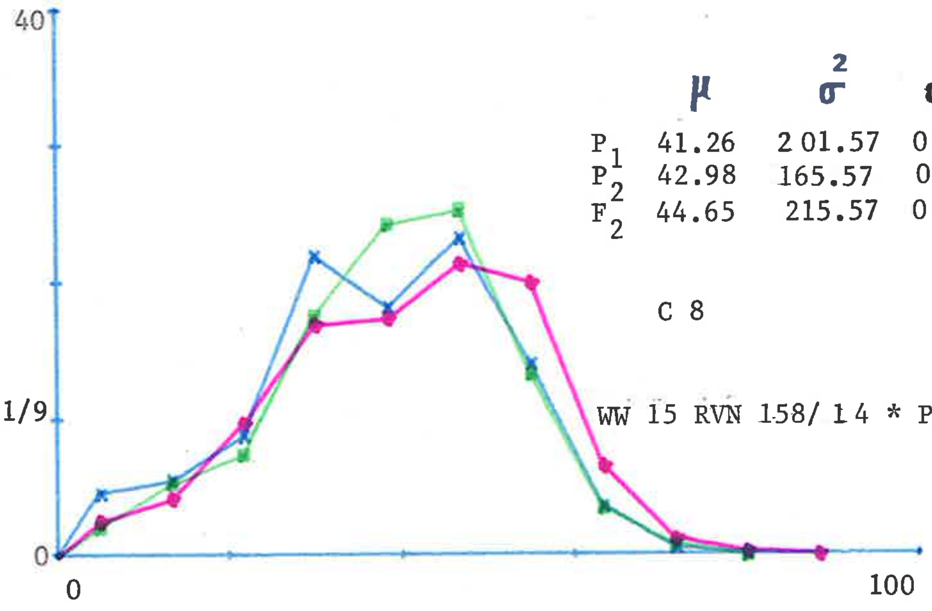
WW 15 RVN 158/14 * PN 28/9



	μ	σ^2	cv
P_1	43.11	193.23	0.32
P_2	50.69	249.84	0.31
F_2	44.11	243.65	0.35

C 6

CHAMP 8156/17/52 * MMC 21/9



	μ	σ^2	cv
P_1	41.26	201.57	0.34
P_2	42.98	165.57	0.30
F_2	44.65	215.57	0.33

C 8

WW 15 RVN 158/14 * PN 68/1

Main shoot grain number - crop density

Table 2.13. Variances of parents and F_2's, Chi-squares of Bartlett's test for homogeneity and F test of variance ratios between parents and F_2's for the character; the main shoot grain number (MGRNO)

	Variances			Bartlett's Chi-square	Variance ratios[1]		
	P_1	P_2	F_2		P_1:P_2	P_1:F_2	P_2:F_2
cross 1 MM25/4*MM68/1	130.95	121.79	236.30	12.33***	1.08NS	1.80***	1.94***
cross 2 MKR211/9*PN28/9	121.78	210.40	231.44	7.32	1.73***	1.90***	1.10NS
cross 3 MKR211/9*MM68/1	138.74	190.09	180.81	8.66***	1.37***	1.30*	1.05NS
cross 4 CHAMP8156/17/52 *PN28/9	149.90	230.55	260.54	14.73***	1.54***	1.74***	1.13NS
cross 5 CHAMP8156/17/52 *MM68/1	102.29	152.21	168.93	3.90*	1.49*	1.65***	1.11NS
cross 6 CHAMP8156/17/52 *MMC21/9	193.23	249.84	243.65	0.98NS	1.29NS	1.26NS	1.03NS
cross 7 WW15RVN158/14 *PN28/9	185.43	315.36	305.88	3.49*	1.70***	1.65***	1.03NS
cross 8 WW15RVN158/14 *MM68/1	201.57	165.51	215.57	3.61*	1.22NS	1.07NS	1.30*

[1] Larger variable divided by smaller variable.

Table 2.14. Coefficient of skewness values for the main shoot grain number of parents and F_2's grown at crop density.

	cross 1	cross 2	cross 3	cross 4	cross 5	cross 6	cross 7	cross 8
parent 1	-1.06	-0.48	-1.36	-0.89	-1.14	-1.07	-0.64	-0.44
parent 2	-0.41	-1.10	-0.47	-0.75	-0.90	-0.44	-1.23	-0.45
F_2's	-0.38	-0.39	-0.86	-0.85	-0.79	-0.32	-0.54	-0.32

Coefficient of skewness for significant difference from zero at the 5% probability level;

= ± 0.389 for sample size of 100 (approximate guide for the parents in crosses 1, 2, 5, 6, 7)

= ± 0.200 for sample size of 400 (approximate guide for all F_2's and parents of crosses 3, 4, 8)

Table 2.15. Minimum and maximum values in the parent and F_2 populations of eight crosses studied at crop density for the character: the main shoot grain number (MGRNO)

cross number	minimum			maximum		
	P_1	P_2	F_2	P_1	P_2	F_2
cross 1 MM25/4*MM68/1	5	15	4	71	72	86
cross 2 MKR211/9*PN28/9	10	10	4	66	89	86
cross 3 MKR211/9*MM68/1	3	9	3	71	78	74
cross 4 CHAMP8156/17/52 *PN28/9	1	12	0	69	86	85
cross 5 CHAMP8156/17/52 *MM68/1	9	9	8	60	65	80
cross 6 CHAMP8156/17/52 *MMC21/9	3	7	1	69	80	90
cross 7 WW15RNV158/14 *PN28/9	12	2	2	72	87	92
cross 8 WW15RVN158/14 *MM68/1	0	5	5	76	72	80

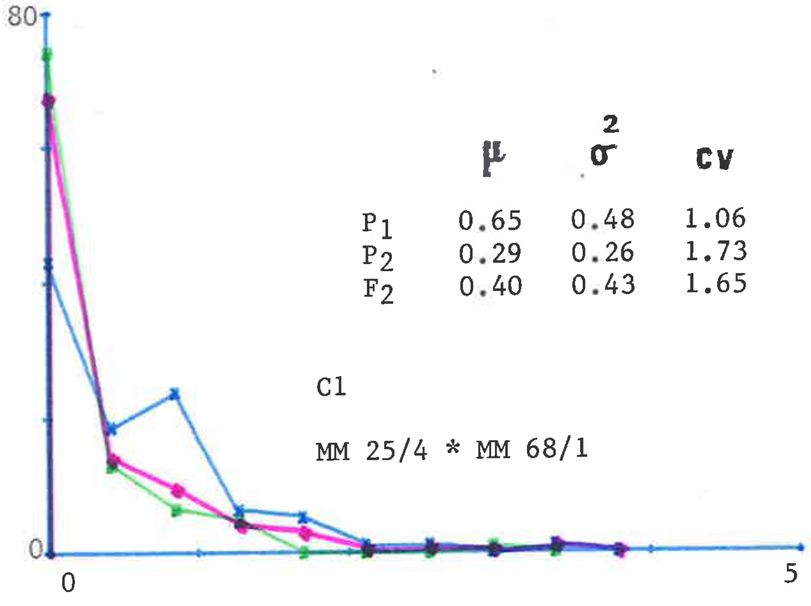
7. Tiller grain weight at crop density.

At crop density many plants produced only a single head. This is shown by the high proportion of plants having a zero value for tiller grain weight (Figure 2.7). The mean value for tiller grain weight was low, ranging from 0.22 to 1.14 g. per plant. The F_2's means fell mostly between the two parental means. Only in crosses 2 and 8 were the F_2's means lower and higher than the parental means, respectively. There was no evidence of heterosis for this character. Although heterosis was not evident transgressive segregation was detected and the F_2's in general had higher maximum values than their parents with the exception of cross 8. All the minimum values were zero (Figure 2.7 and Table 2.18).

The F_2's variances for this character were not larger than for the parents (Table 2.16). This table shows that in seven out of eight crosses, one parent had a significantly higher variance than the other suggesting that there were differences in response among the parents to the microenvironment. The distributions for this character were positively and strongly skewed (Table 2.17). This is a different result from that found for the main shoot grain weight which showed a negative skew. In that both characters are concerned with grain weight, one might have expected them to produce a similar type of frequency distribution (the subject will be further considered in the discussion).

It may have been unjustifiable to calculate coefficients of variation because of the very strong skews. However, as there is no satisfactory procedure to be used in adjusting the result, CV's on the unadjusted data are presented in Figure 2.7.

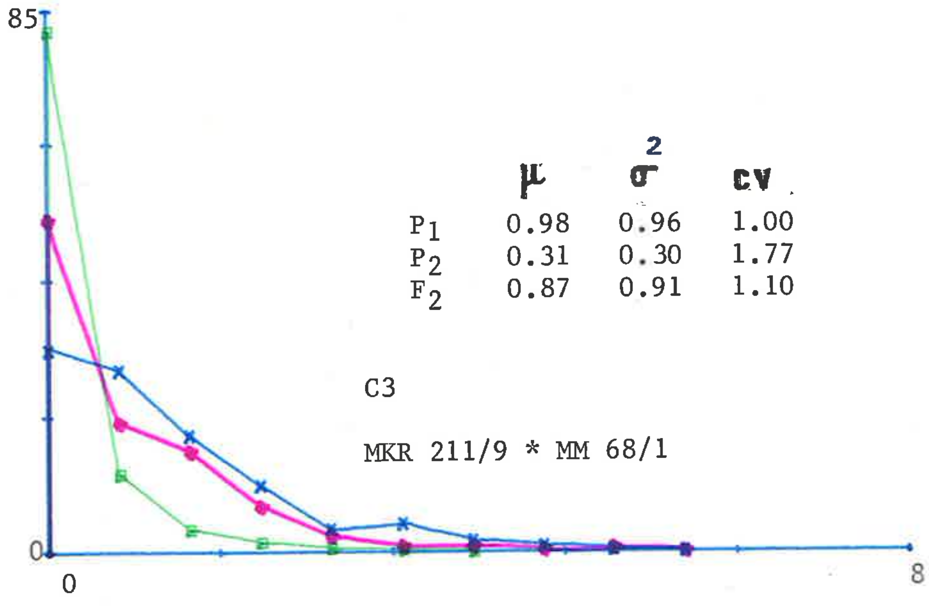
Figure 2.7. Frequency distributions for tiller grain weight for eight crosses grown at crop density. The blue and green curves are the parent 1 and parent 2 distributions respectively and the red is the hybrid F_2 distribution.
The X axis represents class intervals and the Y represents the frequency of plants in each class as a percentage.



	μ	σ^2	cv
P_1	0.65	0.48	1.06
P_2	0.29	0.26	1.73
F_2	0.40	0.43	1.65

C1

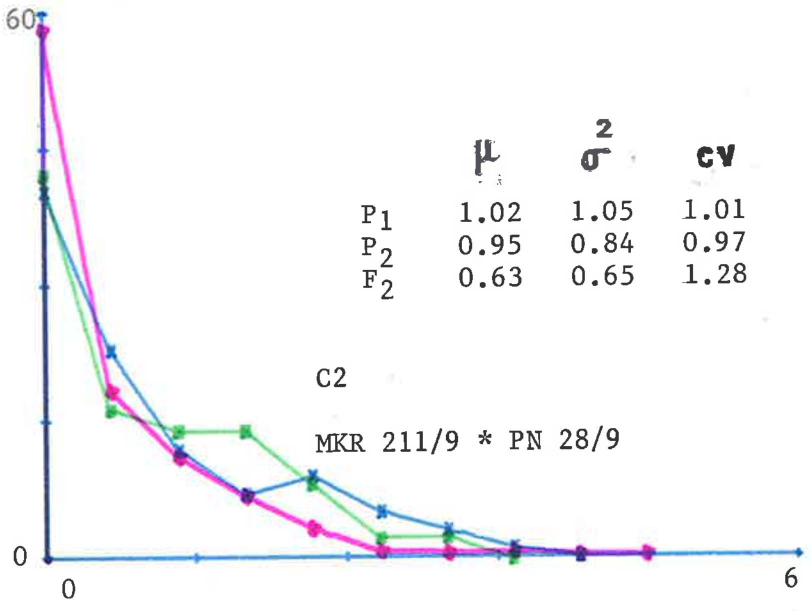
MM 25/4 * MM 68/1



	μ	σ^2	cv
P_1	0.98	0.96	1.00
P_2	0.31	0.30	1.77
F_2	0.87	0.91	1.10

C3

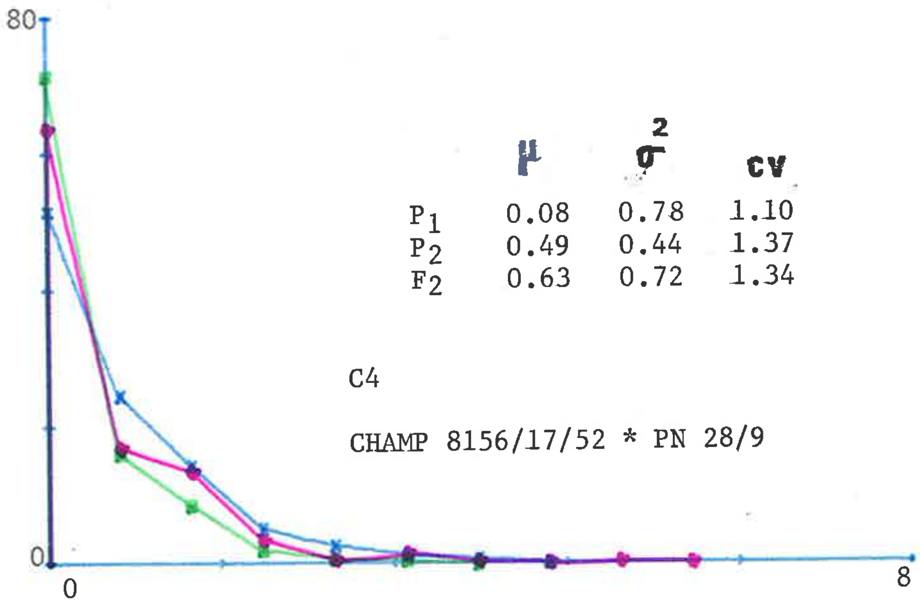
MKR 211/9 * MM 68/1



	μ	σ^2	cv
P_1	1.02	1.05	1.01
P_2	0.95	0.84	0.97
F_2	0.63	0.65	1.28

C2

MKR 211/9 * PN 28/9

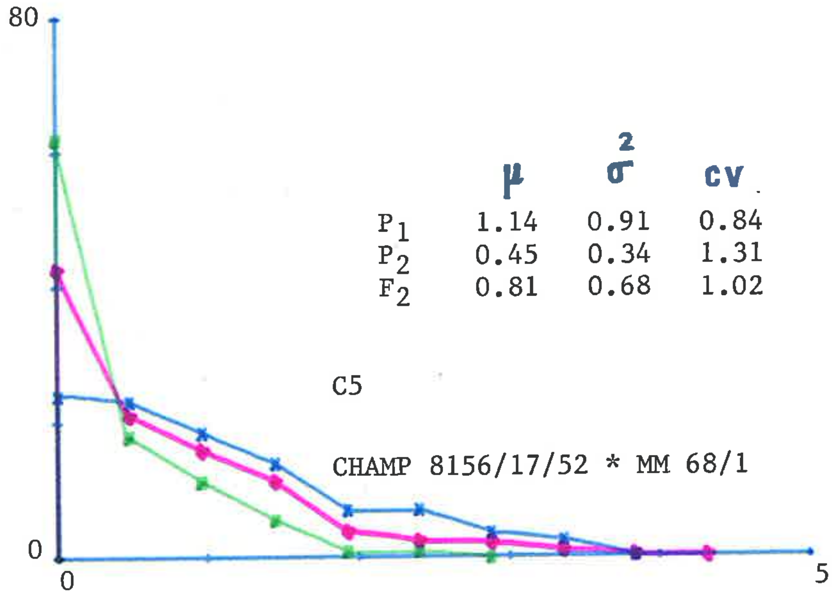


	μ	σ^2	cv
P_1	0.08	0.78	1.10
P_2	0.49	0.44	1.37
F_2	0.63	0.72	1.34

C4

CHAMP 8156/17/52 * PN 28/9

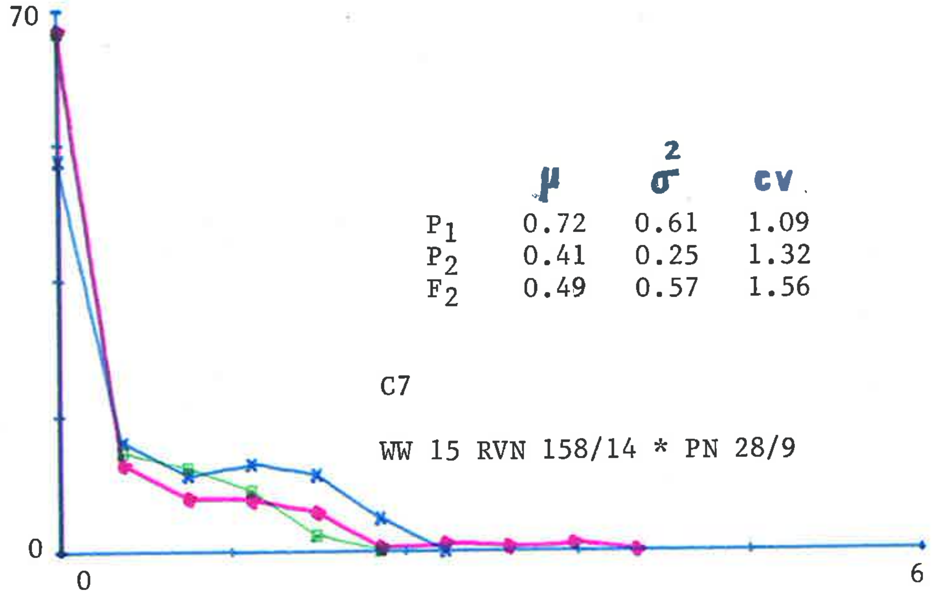
tiller grain weight - crop density



	μ	σ^2	cv
P_1	1.14	0.91	0.84
P_2	0.45	0.34	1.31
F_2	0.81	0.68	1.02

C5

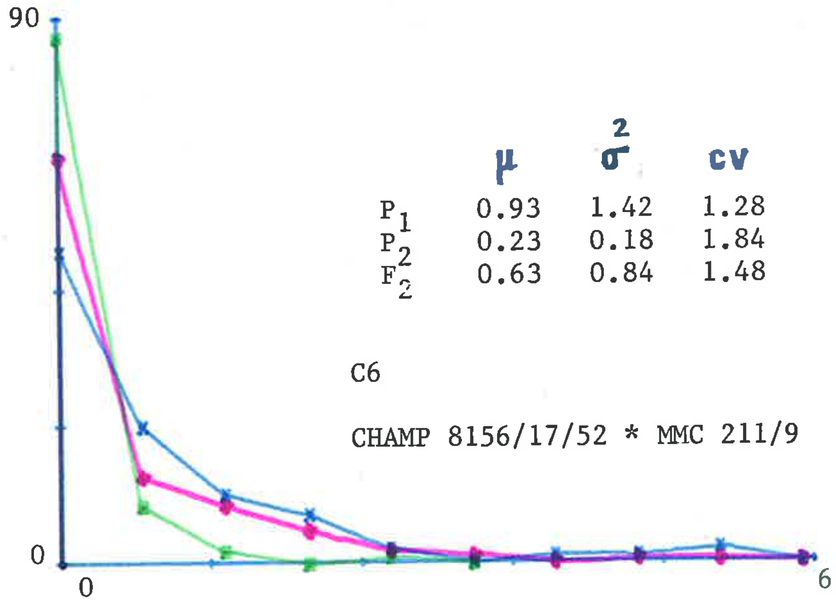
CHAMP 8156/17/52 * MM 68/1



	μ	σ^2	cv
P_1	0.72	0.61	1.09
P_2	0.41	0.25	1.32
F_2	0.49	0.57	1.56

C7

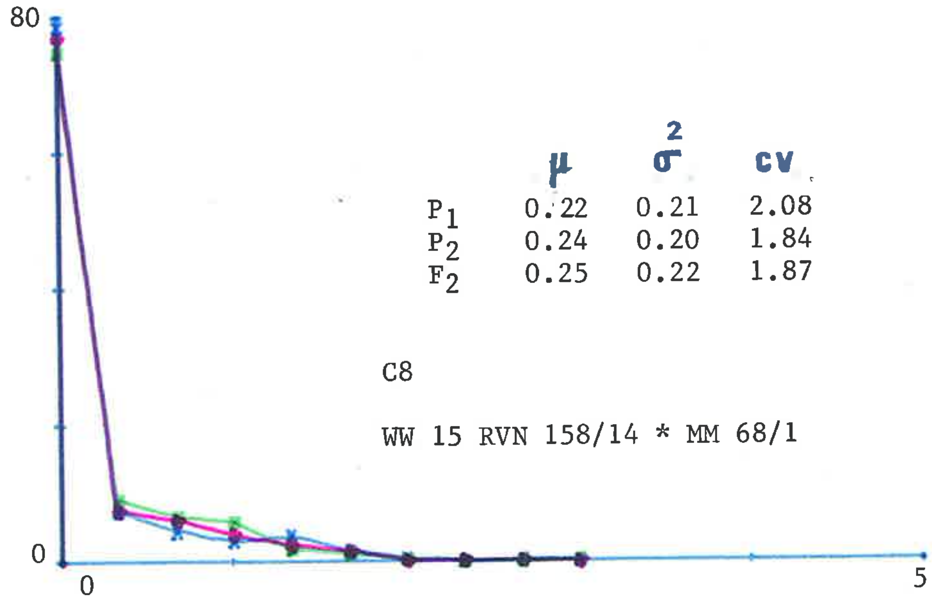
WW 15 RVN 158/14 * PN 28/9



	μ	σ^2	cv
P_1	0.93	1.42	1.28
P_2	0.23	0.18	1.84
F_2	0.63	0.84	1.48

C6

CHAMP 8156/17/52 * MMC 211/9



	μ	σ^2	cv
P_1	0.22	0.21	2.08
P_2	0.24	0.20	1.84
F_2	0.25	0.22	1.87

C8

WW 15 RVN 158/14 * MM 68/1

tiller grain weight - crop density

Table 2.16. Variances of parents and F_2's, Chi-squares of Bartlett's test for homogeneity and F test of variance ratios between parents and F_2's for the character; tiller grain weight (TGRWT)

	Variances			Bartlett's Chi-square	Variance ratios[1]		
	P_1	P_2	F_2		$P_1:P_2$	$P_1:F_2$	$P_2:F_2$
cross 1 MM25/4*MM68/1	0.48	0.26	0.43	5.76***	1.85***	1.12NS	1.65***
cross 2 MKR211/9*PN28/9	1.05	0.84	0.65	5.71***	1.25NS	1.62***	1.29NS
cross 3 MKR211/9*MM68/1	0.96	0.30	0.91	75.19***	3.20***	1.05NS	3.03***
cross 4 CHAMP8156/17/52 *PN28/9	0.78	0.44	0.72	16.27***	1.77***	1.08NS	1.64***
cross 5 CHAMP8156/17/52 *MM68/1	0.91	0.34	0.68	11.78***	2.68***	1.34NS	2.00***
cross 6 CHAMP8156/17/52 *MMC21/9	1.42	0.18	0.84	40.86***	7.89***	1.69***	4.67***
cross 7 WW15RVN158/14 *PN28/9	0.61	0.25	0.57	9.11***	2.44***	1.07NS	2.28***
cross 8 WW15RVN158/14 *MM68/1	0.21	0.20	0.22	0.51NS	1.05NS	1.05NS	1.10NS

[1] Larger variable divided by smaller variable.

Table 2.17. Coefficient of skewness values for tiller grain weight of parents and F_2's grown at crop density.

	cross 1	cross 2	cross 3	cross 4	cross 5	cross 6	cross 7	cross 8
parent 1	1.46	1.00	1.17	1.20	0.62	1.92	0.82	2.38
parent 2	2.29	0.67	2.54	1.78	1.29	3.07	1.30	2.19
F_2's	2.32	1.80	1.63	1.90	1.20	2.06	1.99	2.30

Coefficient of skewness for significant difference from zero at the 5% probability level;

= ± 0.389 for sample size of 100 (approximate guide for the parents in crosses 1, 2, 5, 6, 7)

= ± 0.200 for sample size of 400 (approximate guide for all F_2's and parents of crosses 3, 4, 8)

Table 2.18. Minimum and maximum values in the parent and F_2 populations of eight crosses studied at crop density for the character: tiller grain weight (TGRWT)

cross number	minimum			maximum		
	P_1	P_2	F_2	P_1	P_2	F_2
cross 1 MM25/4*MM68/1	0	0	0	3.67	2.98	3.78
cross 2 MKR211/9*PN28/9	0	0	0	4.21	3.25	4.28
cross 3 MKR211/9*MM68/1	0	0	0	5.70	3.60	5.90
cross 4 CHAMP8156/17/52 *PN28/9	0	0	0	4.62	3.72	5.95
cross 5 CHAMP8156/17/52 *MM68/1	0	0	0	3.67	2.58	4.31
cross 6 CHAMP8156/17/52 *MMC21/9	0	0	0	5.78	2.76	5.90
cross 7 WW15RNV158/14 *PN28/9	0	0	0	2.60	2.20	4.00
cross 8 WW15RVN158/14 *MM68/1	0	0	0	2.74	3.00	2.85

8. Tiller grain number at crop density.

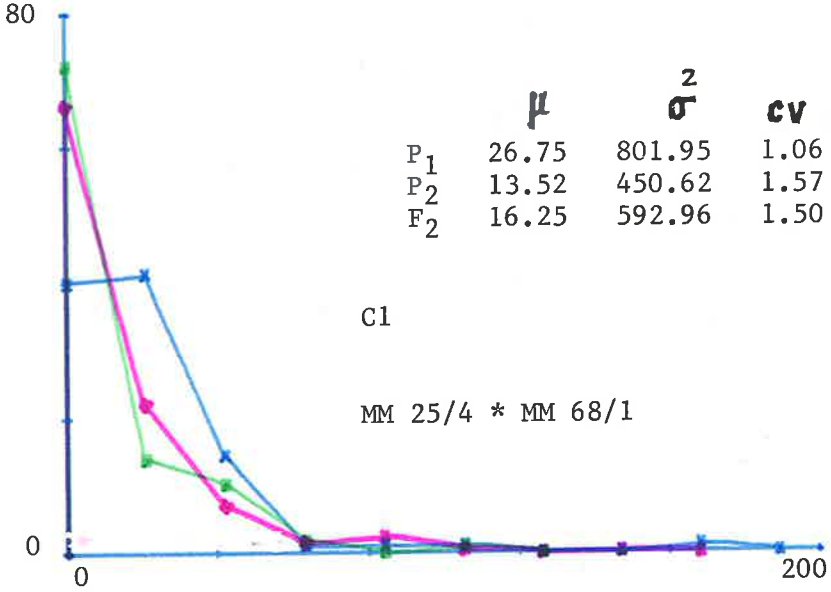
Tiller grain number was closely related to the tiller grain weight. Their correlation coefficient ranged from 0.799*** to 0.975*** in the different crosses and their frequency distributions were similar (Figure 2.8). As many as 75% of the plants in the population did not have any tiller grain when grown at crop density; their yield had been reduced by the large effect of competition in the crop micro-environment. The mean grain number from all the tillers on a plant was in general lower than on the main shoot. This may be seen by comparing Figure 2.8 with Figure 2.6.

The variances in Table 2.19 shows that there were significant differences between the parent 1 and parent 2 variances in most crosses again suggesting that there were differences in response among the parents to the micro-environment and their production of grain on the tillers.

The F_2's variances were not larger than both parental variances. Only in a few crosses were the F_2 variances larger than for one parent. However, most of the F_2 (of crosses 2, 4, 5, 6, 7 and 8) had higher maximum values than their parents (Table 2.21).

Strong positive skews were obtained for this character (Table 2.20).

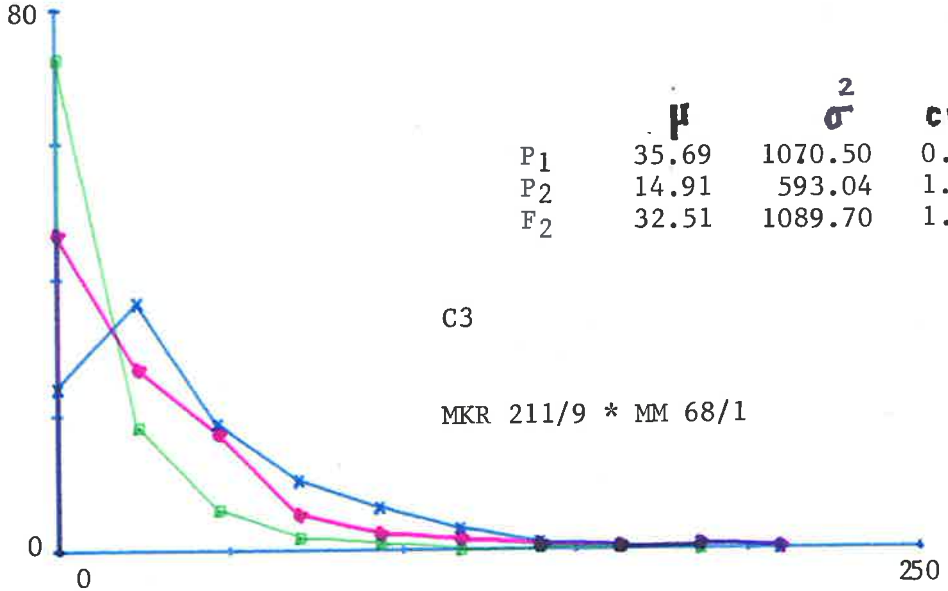
Figure 2.8. Frequency distribution of the tiller grain number from eight crosses studied at crop density. The blue and green curves are the parent 1 and parent 2 distributions respectively and the red is the hybrid F_2 distribution. The X axis represents class intervals and the Y the frequency of plants in each class as a percentage.



	μ	σ^2	cv
P_1	26.75	801.95	1.06
P_2	13.52	450.62	1.57
F_2	16.25	592.96	1.50

C1

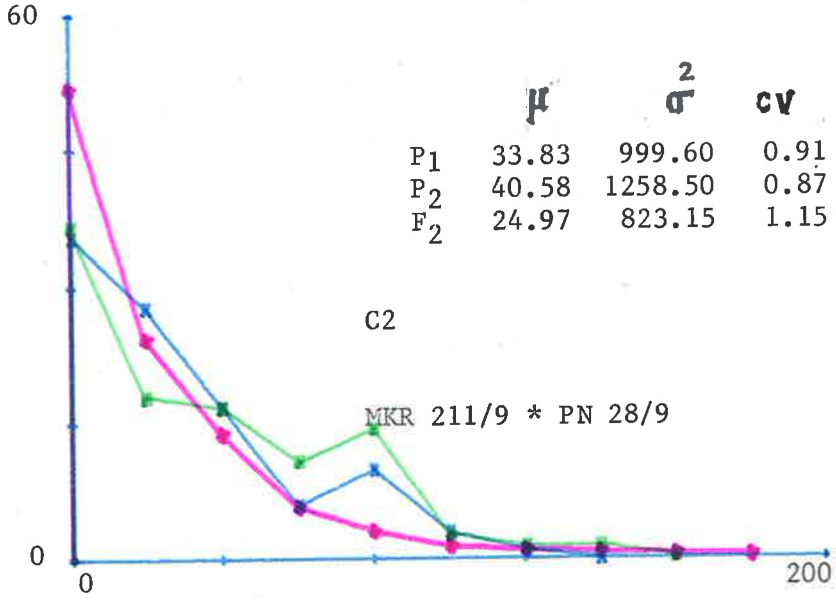
MM 25/4 * MM 68/1



	μ	σ^2	cv
P_1	35.69	1070.50	0.92
P_2	14.91	593.04	1.63
F_2	32.51	1089.70	1.02

C3

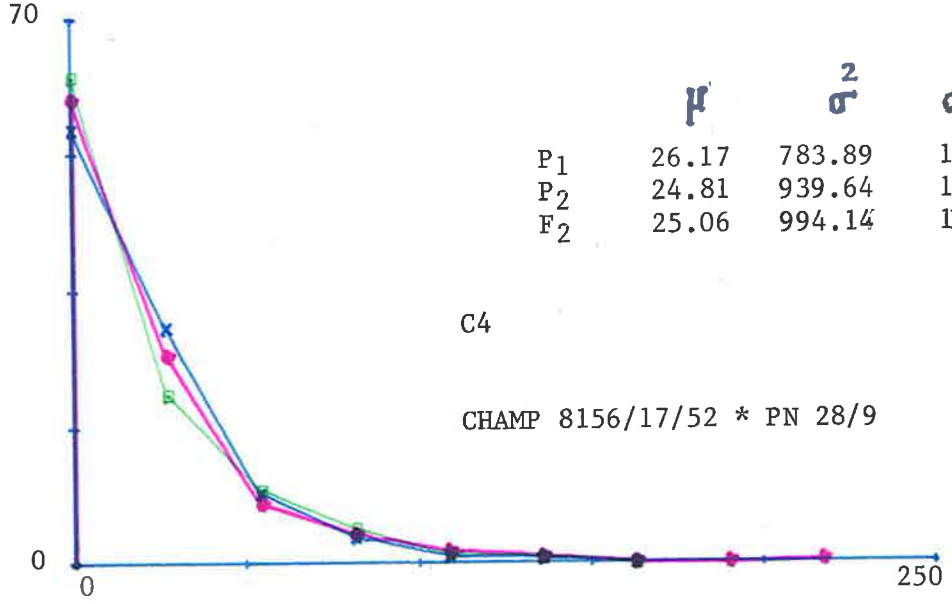
MKR 211/9 * MM 68/1



	μ	σ^2	cv
P_1	33.83	999.60	0.91
P_2	40.58	1258.50	0.87
F_2	24.97	823.15	1.15

C2

MKR 211/9 * PN 28/9

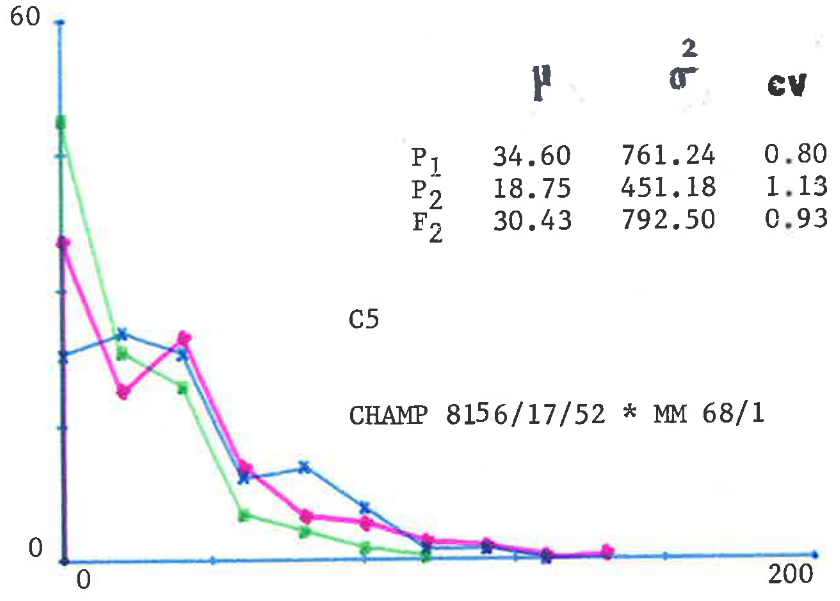


	μ	σ^2	cv
P_1	26.17	783.89	1.07
P_2	24.81	939.64	1.24
F_2	25.06	994.14	1.26

C4

CHAMP 8156/17/52 * PN 28/9

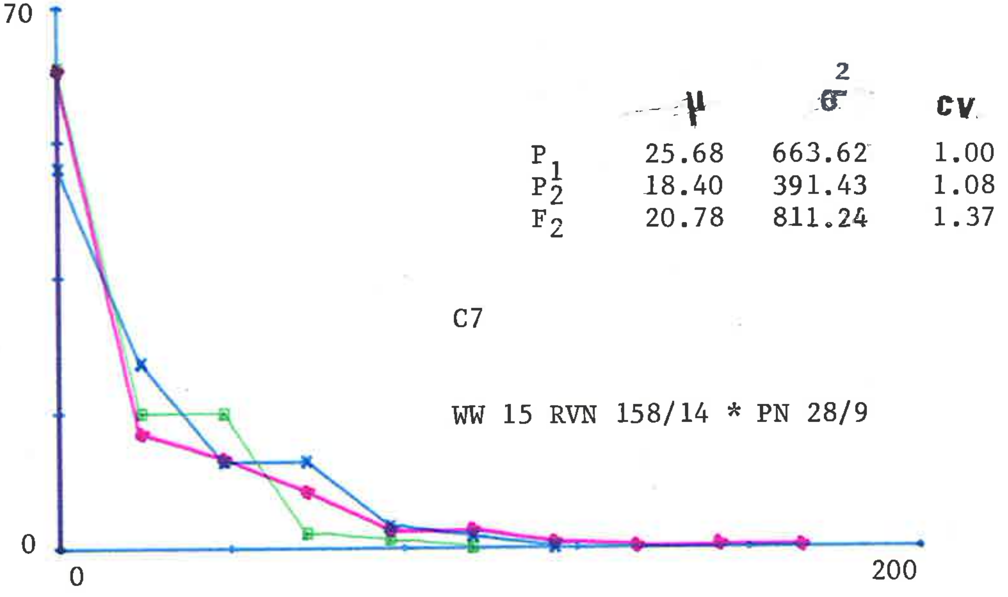
tiller grain number - crop density



	μ	σ^2	cv
P_1	34.60	761.24	0.80
P_2	18.75	451.18	1.13
F_2	30.43	792.50	0.93

C5

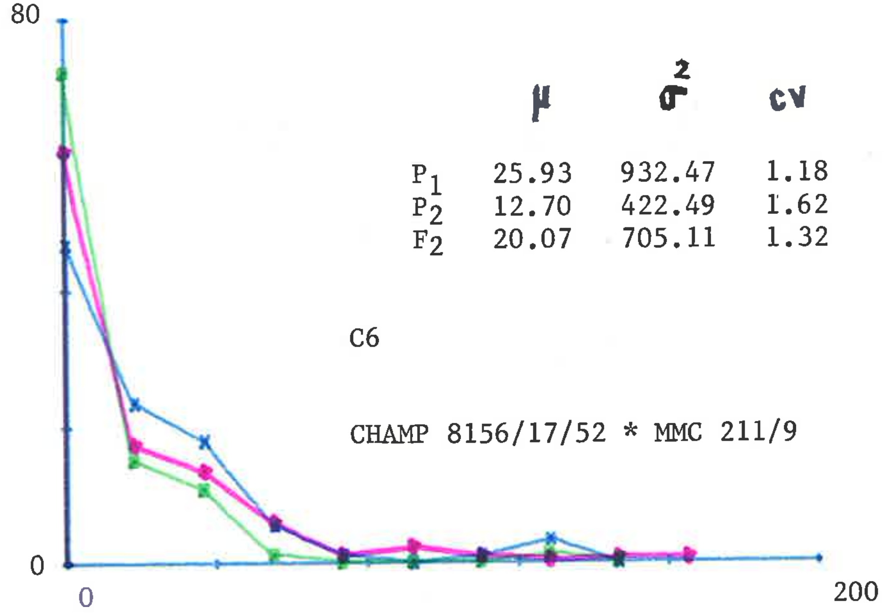
CHAMP 8156/17/52 * MM 68/1



	μ	σ^2	cv
P_1	25.68	663.62	1.00
P_2	18.40	391.43	1.08
F_2	20.78	811.24	1.37

C7

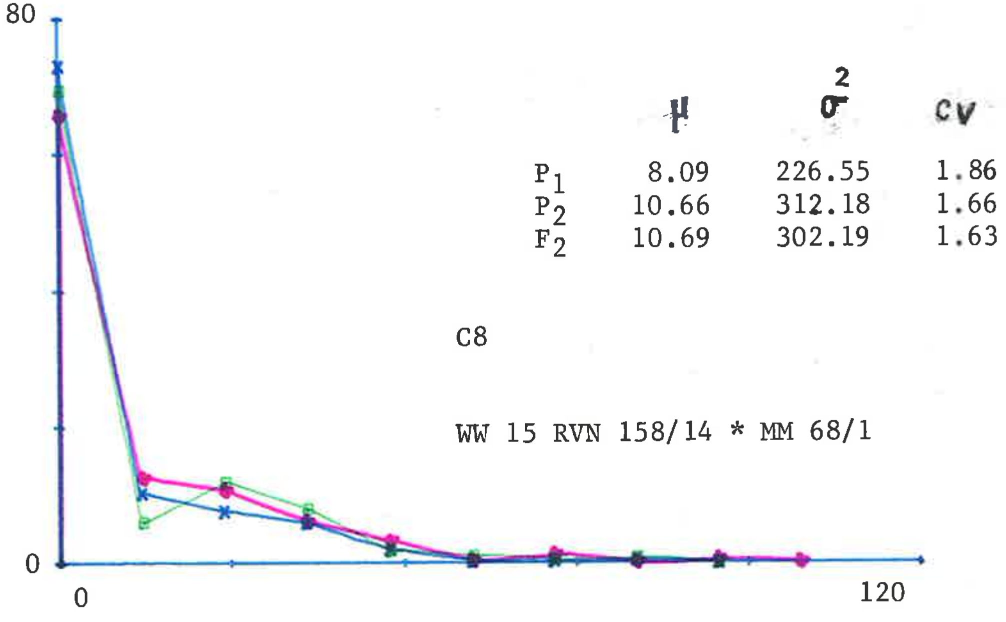
WW 15 RVN 158/14 * PN 28/9



	μ	σ^2	cv
P_1	25.93	932.47	1.18
P_2	12.70	422.49	1.62
F_2	20.07	705.11	1.32

C6

CHAMP 8156/17/52 * MMC 211/9



	μ	σ^2	cv
P_1	8.09	226.55	1.86
P_2	10.66	312.18	1.66
F_2	10.69	302.19	1.63

C8

WW 15 RVN 158/14 * MM 68/1

tiller grain number - crop density

Table 2.19. Variances of parents and F_2's, Chi-squares of Bartlett's test for homogeneity and F test of variance ratios between parents and F_2's for the character; tiller grain number (TGRNO)

	Variances			Bartlett's Chi-square	Variance ratios[1]		
	P_1	P_2	F_2		$P_1:P_2$	$P_1:F_2$	$P_2:F_2$
cross 1 MM25/4*MM68/1	801.95	450.62	592.96	4.23	1.78***	1.35*	1.32NS
cross 2 MKR211/9*PN28/9	999.60	1258.50	823.15	3.79*	1.26NS	1.21NS	1.53***
cross 3 MKR211/9*MM68/1	1070.50	593.04	1089.70	25.78***	1.81***	1.02NS	1.84***
cross 4 CHAMP8156/17/52 *PN28/9	783.89	939.64	994.14	2.80NS	1.20NS	1.27*	1.06NS
cross 5 CHAMP8156/17/52 *MM68/1	761.24	451.18	792.50	5.76***	1.69***	1.04NS	1.76***
cross 6 CHAMP8156/17/52 *MMC21/9	932.47	422.49	705.11	6.95***	2.21***	1.32NS	1.67***
cross 7 WW15RVN158/14 *PN28/9	663.62	391.43	811.24	9.43***	1.70***	1.22NS	2.07***
cross 8 WW15RVN158/14 *MM68/1	226.55	312.18	302.19	6.54***	1.38***	1.33***	1.03NS

1 Larger variable divided by smaller variable.

Table 2.20. Coefficient of skewness values for tiller grain number of parents and F_2's grown at crop density.

	cross 1	cross 2	cross 3	cross 4	cross 5	cross 6	cross 7	cross 8
parent 1	2.38	0.81	1.19	1.28	0.61	1.83	0.87	2.04
parent 2	1.91	0.60	2.25	1.44	0.84	2.94	0.88	1.70
F_2's	1.99	1.57	1.57	1.92	0.99	1.81	1.59	1.90

Coefficient of skewness for significant difference from zero at the 5% probability level;

= ± 0.389 for sample size of 100 (approximate guide for the parents in crosses 1, 2, 5, 6, 7)

= ± 0.200 for sample size of 400 (approximate guide for all F_2's and parents of crosses 3, 4, 8)

Table 2.21. Minimum and maximum values in the parent and F_2 populations of eight crosses studied at crop density for the character: tiller grain number (TGRNO)

cross number	minimum			maximum		
	P_1	P_2	F_2	P_1	P_2	F_2
cross 1 MM25/4*MM68/1	0	0	0	189	116	162
cross 2 MKR211/9*PN28/9	0	0	0	122	143	180
cross 3 MKR211/9*MM68/1	0	0	0	209	163	196
cross 4 CHAMP8156/17/52 *PN28/9	0	0	0	154	156	244
cross 5 CHAMP8156/17/52 *MM68/1	0	0	0	119	93	144
cross 6 CHAMP8156/17/52 *MMC21/9	0	0	0	139	138	165
cross 7 WW15RNV158/14 *PN28/9	0	0	0	101	81	172
cross 8 WW15RVN158/14 *MM68/1	0	0	0	90	87	103

9. Total grain weight per plant at crop density.

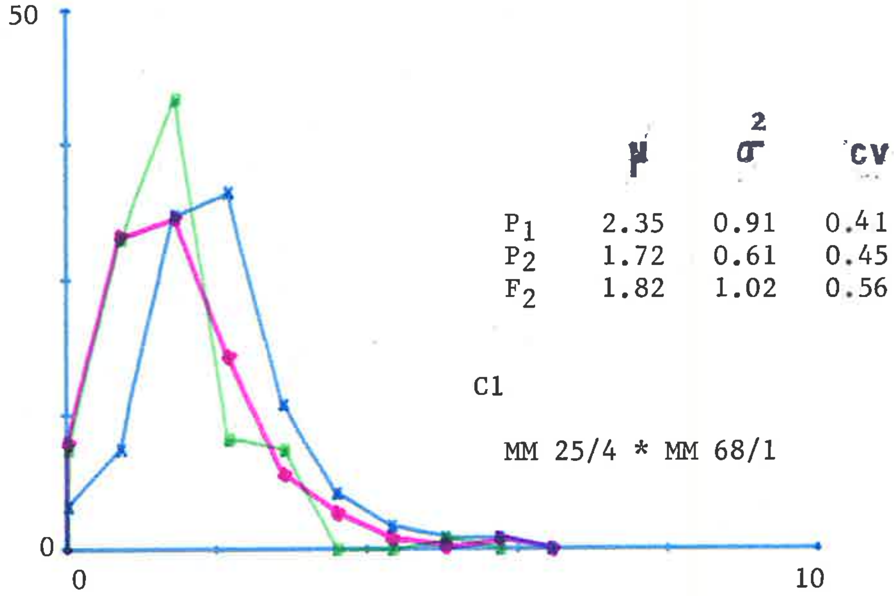
Many of the features of the distributions for total grain weight were similar to those for total plant weight discussed previously. The two characters were highly correlated in this experiment with an average correlation coefficient of 0.955*** (in individual crosses the correlations ranged from 0.627*** to 0.989***). Figure 2.9 shows the distributions of the parents and F_2's for this character. It will be seen again that the F_2's distributions covered the combined ranges of the two parents and their means were intermediate between the parental means. There was little evidence of heterosis as nearly all of the F_2's means were neither greater nor lower than the parental means. There was evidence of transgressive segregation however as in all crosses there were several individuals with values that exceeded values in the parental population (Table 2.24).

The F_2's variances for this character were not significantly greater than both parental variances (Table 2.22). The small differences among the CV's suggest that the P_1, P_2 and F_2 variances within a cross were similar.

Positive skews were obtained (Table 2.23). It will be recalled that the distribution for the main shoot grain weight was negative and the distribution for tiller grain weight was strongly positive. This second component therefore, although much smaller in mean value, has given the positive skew to the distribution of total grain weight.

Figure 2.9. Frequency distribution of the total grain weight from eight crosses studied at crop density. The blue and green curves are the parent 1 and parent 2 distributions respectively, the red curve is the hybrid F_2 distribution.

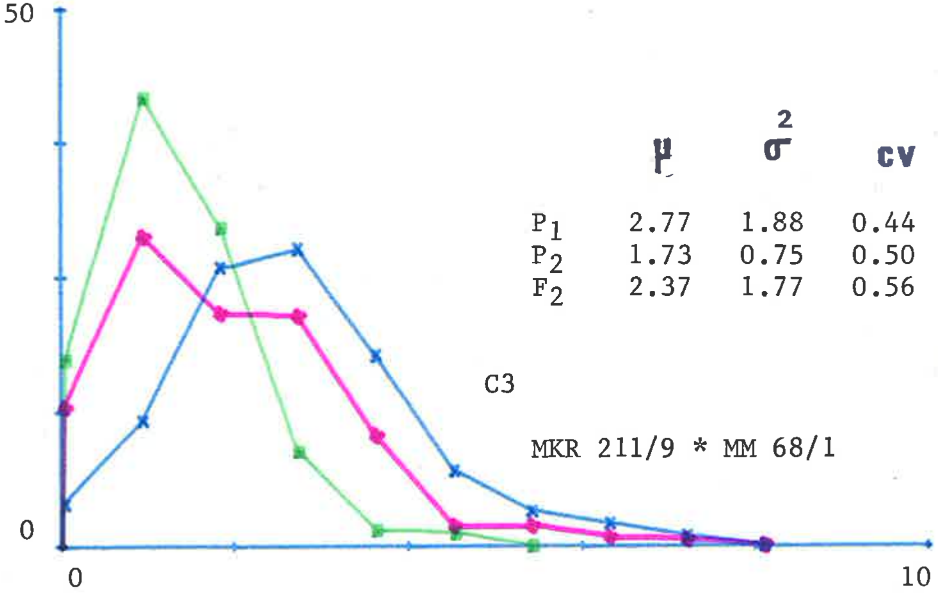
The X axis represents class intervals and the Y the frequency of plants in each class as a percentage.



	μ	σ^2	cv
P_1	2.35	0.91	0.41
P_2	1.72	0.61	0.45
F_2	1.82	1.02	0.56

C1

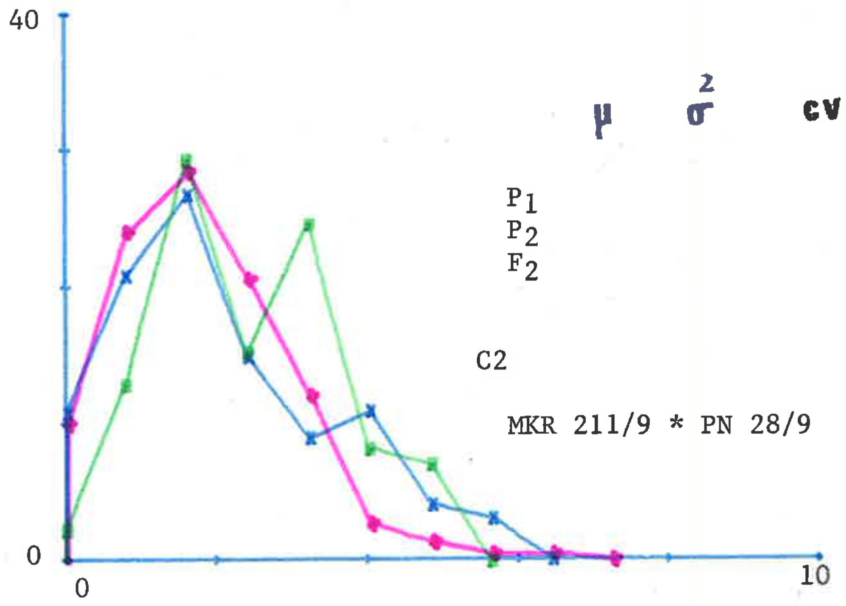
MM 25/4 * MM 68/1



	μ	σ^2	cv
P_1	2.77	1.88	0.44
P_2	1.73	0.75	0.50
F_2	2.37	1.77	0.56

C3

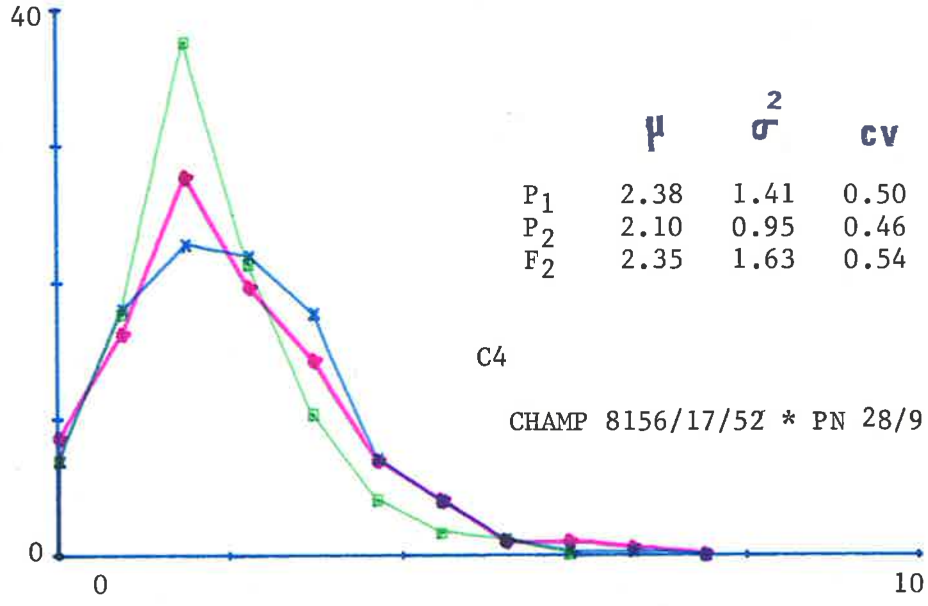
MKR 211/9 * MM 68/1



	μ	σ^2	cv
P_1			
P_2			
F_2			

C2

MKR 211/9 * PN 28/9

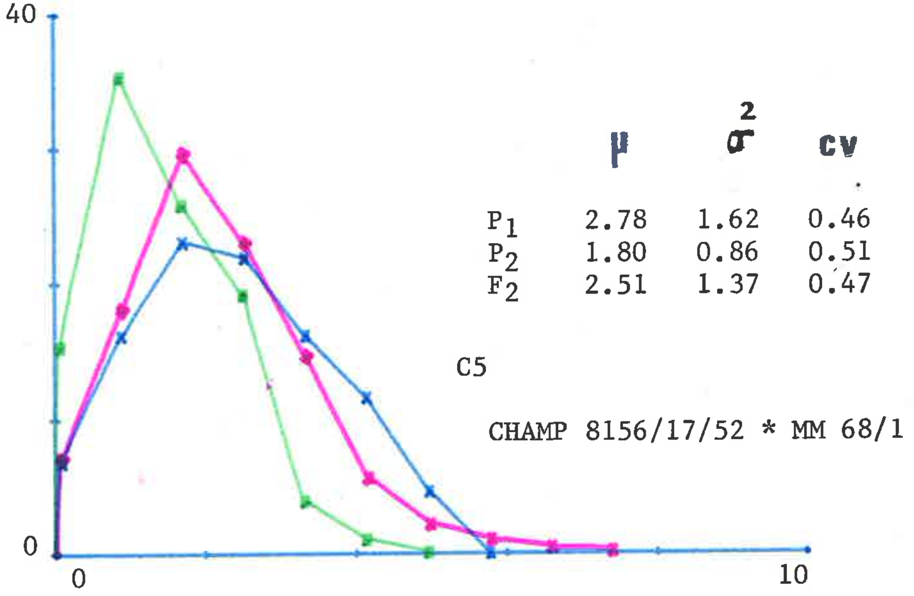


	μ	σ^2	cv
P_1	2.38	1.41	0.50
P_2	2.10	0.95	0.46
F_2	2.35	1.63	0.54

C4

CHAMP 8156/17/52 * PN 28/9

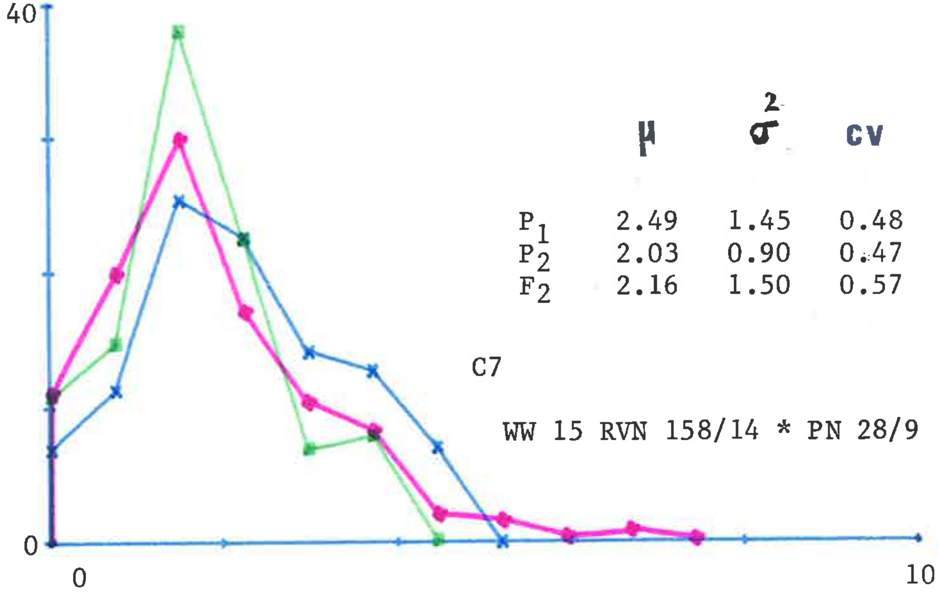
Plant total grain weight - crop density



	μ	σ^2	cv
P_1	2.78	1.62	0.46
P_2	1.80	0.86	0.51
F_2	2.51	1.37	0.47

C5

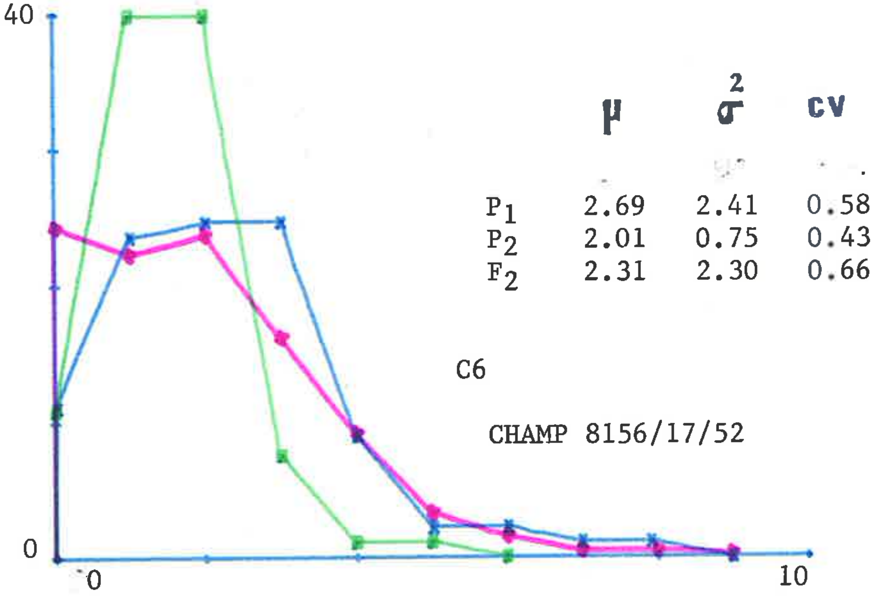
CHAMP 8156/17/52 * MM 68/1



	μ	σ^2	cv
P_1	2.49	1.45	0.48
P_2	2.03	0.90	0.47
F_2	2.16	1.50	0.57

C7

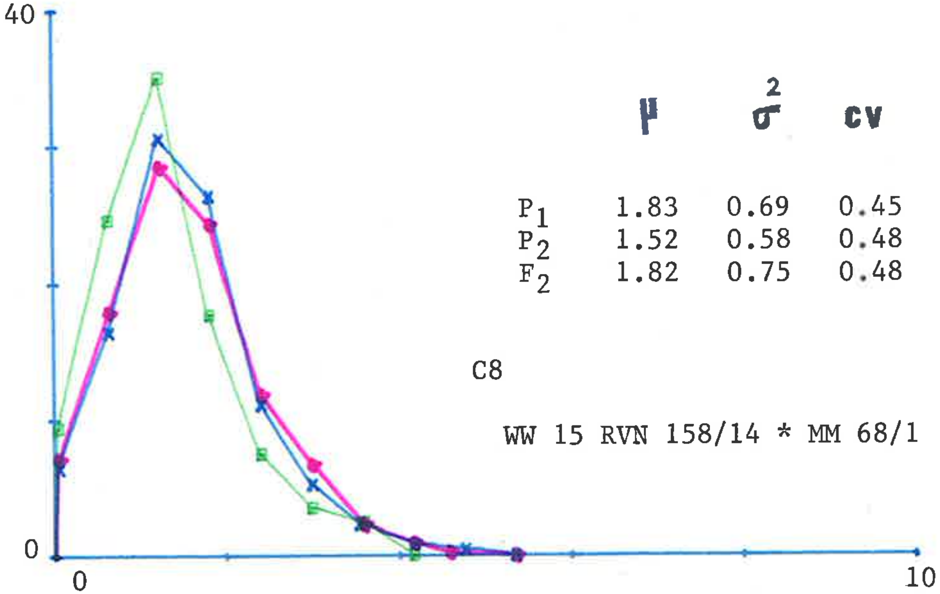
WW 15 RVN 158/14 * PN 28/9



	μ	σ^2	cv
P_1	2.69	2.41	0.58
P_2	2.01	0.75	0.43
F_2	2.31	2.30	0.66

C6

CHAMP 8156/17/52



	μ	σ^2	cv
P_1	1.83	0.69	0.45
P_2	1.52	0.58	0.48
F_2	1.82	0.75	0.48

C8

WW 15 RVN 158/14 * MM 68/1

Plant total grain weight - crop density

Table 2.22. Variances of parents and F_2's, Chi-squares of Bartlett's test for homogeneity and F test of variance ratios between parents and F_2's for the character; total grain weight per plant (TOTGRWT)

	Variances			Bartlett's Chi-square	Variance ratios[1]		
	P_1	P_2	F_2		$P_1:P_2$	$P_1:F_2$	$P_2:F_2$
cross 1 MM25/4*MM68/1	0.92	0.61	1.02	5.18***	1.51*	1.11NS	1.67***
cross 2 MKR211/9*PN28/9	1.92	1.46	1.30	10.83***	1.32NS	1.48***	1.12NS
cross 3 MKR211/9*MM68/1	1.88	0.75	1.77	32.28***	2.51***	1.06NS	2.36***
cross 4 CHAMP8156/17/52 *PN28/9	1.41	0.95	1.63	23.87***	1.48***	1.16NS	1.72***
cross 5 CHAMP8156/17/52 *MM68/1	1.62	0.86	1.37	8.01***	1.88***	1.18NS	1.59***
cross 6 CHAMP8156/17/52 *MMC21/9	2.41	0.75	2.30	1.27NS	3.21***	1.05NS	3.07***
cross 7 WW15RVN158/14 *PN28/9	1.45	0.90	1.50	5.05***	1.61***	1.03NS	1.67***
cross 8 WW15RVN158/14 *MM68/1	0.69	0.58	0.75	5.77***	1.19NS	1.09NS	1.29***

[1] Larger variable divided by smaller variable.

Table 2.23. Coefficient of skewness values for total grain weight per plant of parents and F_2's grown at crop density.

	cross 1	cross 2	cross 3	cross 4	cross 5	cross 6	cross 7	cross 8
parent 1	0.85	0.69	0.57	0.54	0.19	0.96	0.28	0.69
parent 2	1.19	0.21	0.93	0.80	0.41	0.36	0.10	0.75
F_2's	1.17	0.83	0.82	0.87	0.58	0.80	0.91	0.59

Coefficient of skewness for significant difference from zero at the 5% probability level;

= ± 0.389 for sample size of 100 (approximate guide for the parents in crosses 1, 2, 5, 6, 7)

= ± 0.200 for sample size of 400 (approximate guide for all F_2's and parents of crosses 3, 4, 8)

Table 2.24. Minimum and maximum values in the parent and F_2 populations of eight crosses studied at crop density for the character: total grain weight per plant

cross number	minimum			maximum		
	P_1	P_2	F_2	P_1	P_2	F_2
cross 1 MM25/4*MM68/1	0.11	0.32	0.02	6.13	5.39	6.45
cross 2 MKR211/9*PN28/9	0.20	0.19	0.02	6.17	5.55	7.26
cross 3 MKR211/9*MM68/1	0.15	0.10	0.05	8.10	5.28	7.77
cross 4 CHAMP8156/17/52 *PN28/9	0.02	0.20	0.00	6.72	5.92	8.37
cross 5 CHAMP8156/17/52 *MM68/1	0.32	0.12	0.08	5.68	4.35	7.38
cross 6 CHAMP8156/17/52 *MMC21/9	0.10	0.16	0.02	8.01	5.11	8.97
cross 7 WW15RNV158/14 *PN28/9	0.42	0.02	0.02	5.19	4.23	6.84
cross 8 WW15RVN158/14 *MM68/1	0.10	0.08	0.05	5.03	4.05	5.34

10. Height of the main shoot at crop density.

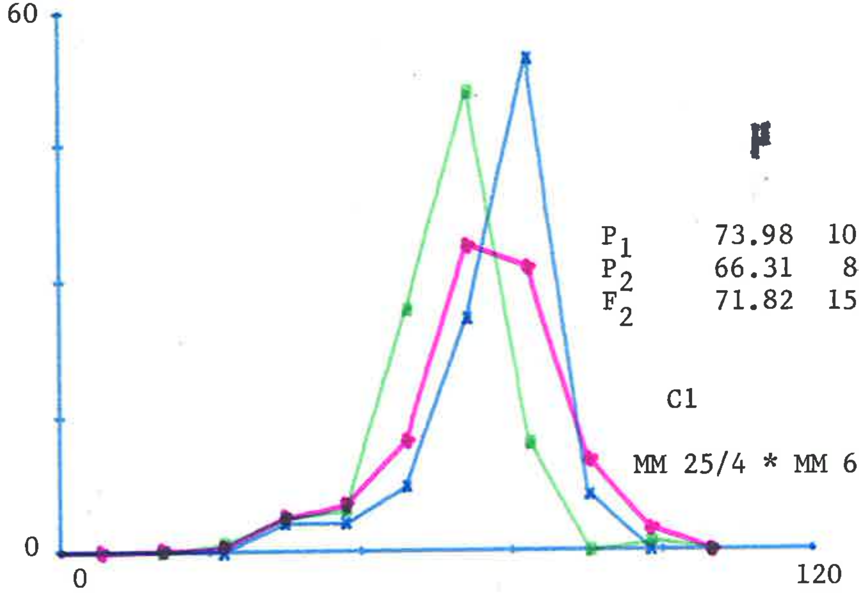
The frequency distributions for this character are shown in Figure 2.10. The F_2's distributions conform to the genetic model expected in that they showed a wide distribution and their ranges covered the combined ranges of the parental distributions. There was no indication that major genes were involved in these distributions. The F_2's means in general were intermediate between the two parental means, except in crosses 2 and 8 in which the F_2's means were lower and higher than the parental means respectively. This indicates negative and positive heterosis in these two crosses. Although heterosis was not evident in the other crosses (crosses 1, 2, 3, 4 and 7), transgressive segregation was apparent (Figure 2.10 and Table 2.27). The coefficients of variation were comparatively small varying between 8 and 22%. In all the previous characters the CV were far greater often being in excess of 50 to 60% which was partly a consequence of their skews.

The variances, chi-square of Bartlett's test and variance ratios are shown in Table 2.25. In contrast to most of the other characters studied, the F_2's variance for height clearly provided evidence of segregation and in five out of the eight crosses the F_2's variances were significantly larger than both parental variances. Some were twice as large (in crosses 3, 4, 6 and 7). In cross 5 the parent 2 (MM68/1) had the largest variance.

Negative skews were obtained for height (Table 2.26). Possible reason for the negative skews for plant height were referred to in the Literature Review and will be considered further in the discussion.

Figure 2.10. Frequency distributions for main shoot height for eight crosses studied at crop density. The blue and green curves are the parent 1 and parent 2 distributions respectively and the red curve is the hybrid F_2 distribution.

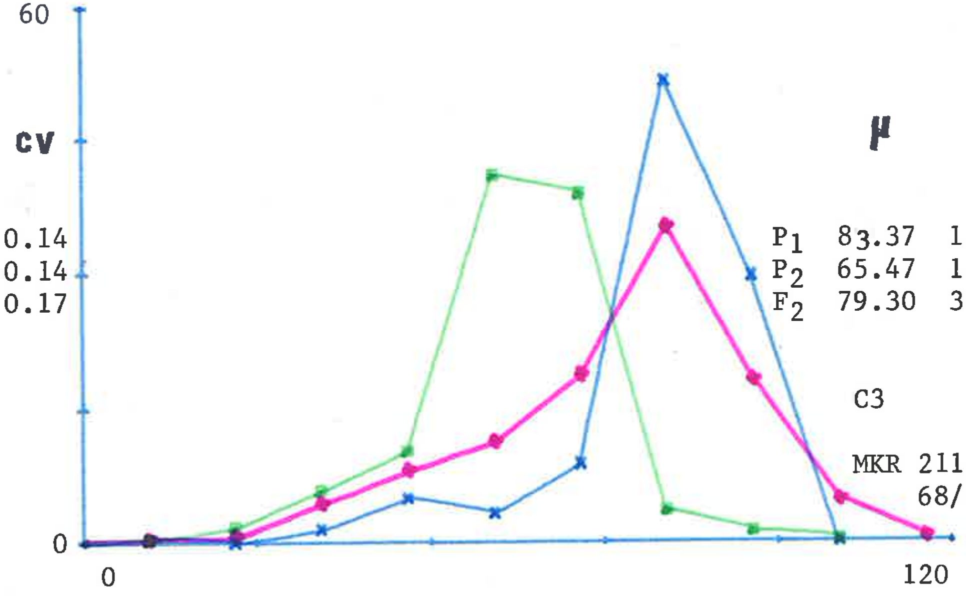
The X axis represents class intervals and the Y plant frequency in each class presented as a percentage.



	μ	σ^2	cv
P_1	73.98	103.97	0.14
P_2	66.31	85.12	0.14
F_2	71.82	156.40	0.17

C1

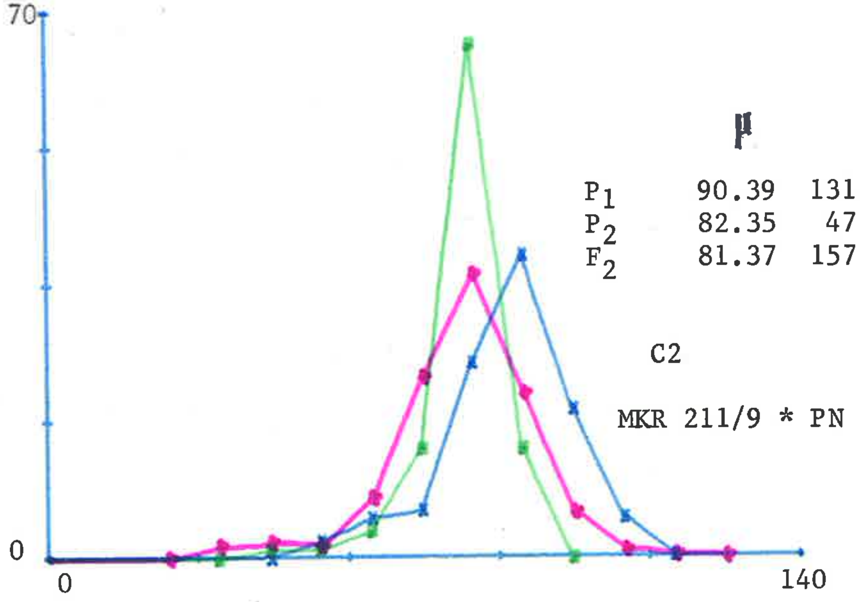
MM 25/4 * MM 68/1



	μ	σ^2	cv
P_1	83.37	175.44	0.1
P_2	65.47	124.59	0.1
F_2	79.30	304.82	0.2

C3

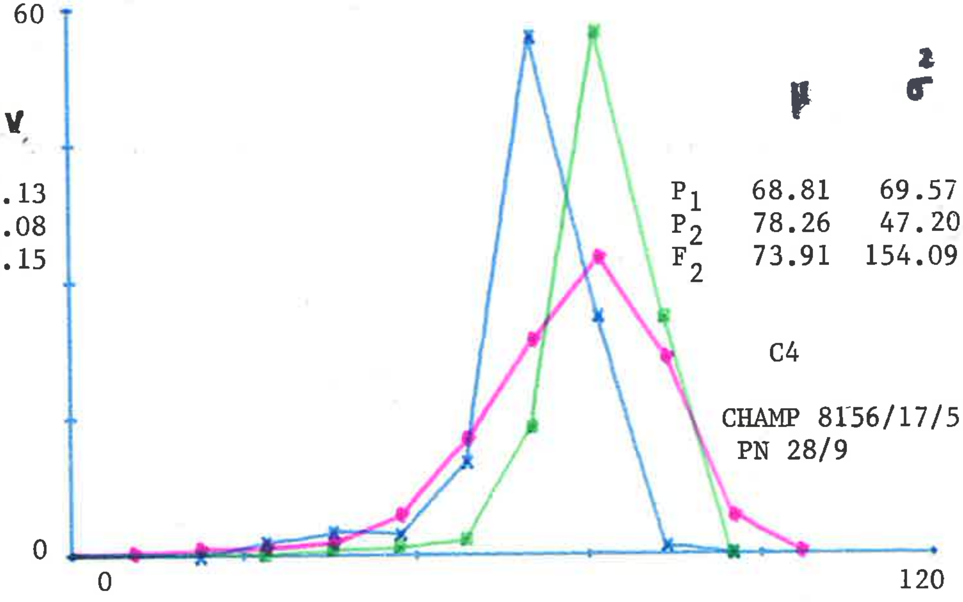
MKR 211/9 * MM 68/1



	μ	σ^2	cv
P_1	90.39	131.93	0.13
P_2	82.35	47.35	0.08
F_2	81.37	157.21	0.15

C2

MKR 211/9 * PN 28/1

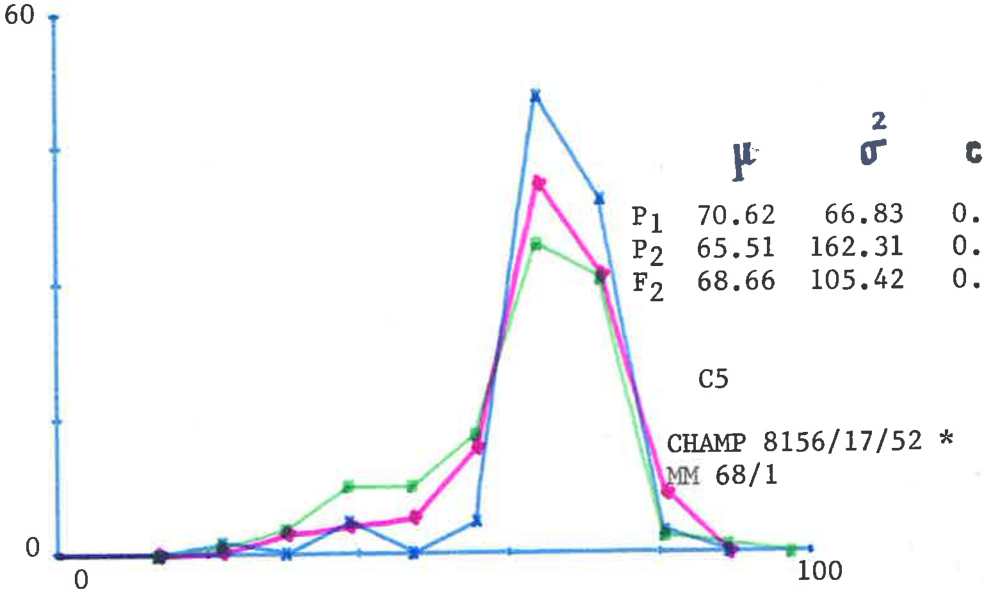


	μ	σ^2	cv
P_1	68.81	69.57	0.12
P_2	78.26	47.20	0.09
F_2	73.91	154.09	0.17

C4

CHAMP 8156/17/52 *
PN 28/9

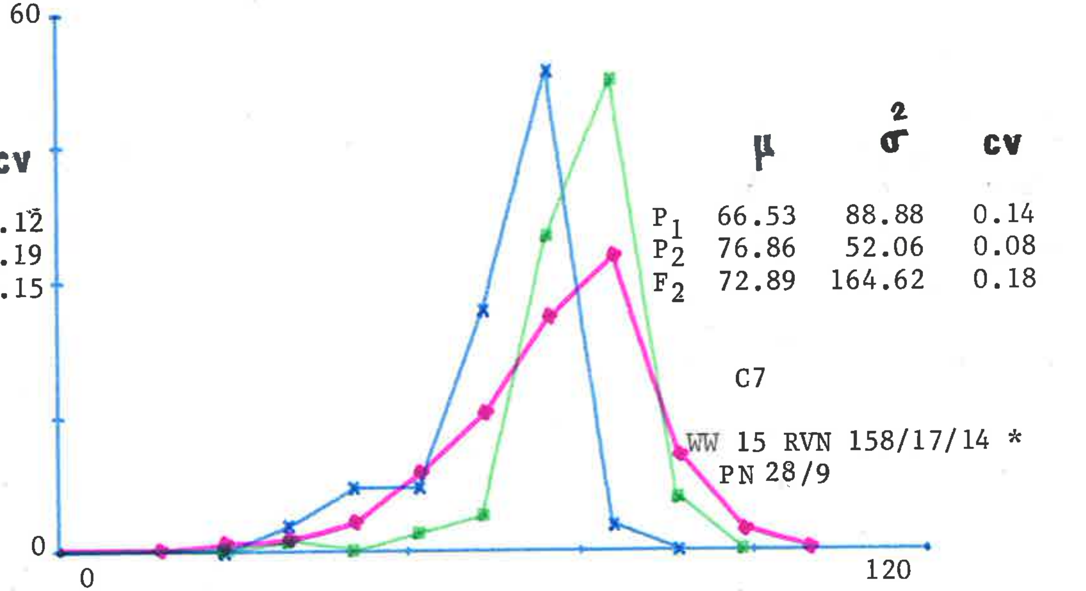
height - crop density



	μ	σ^2	cv
P_1	70.62	66.83	0.12
P_2	65.51	162.31	0.19
F_2	68.66	105.42	0.15

C5

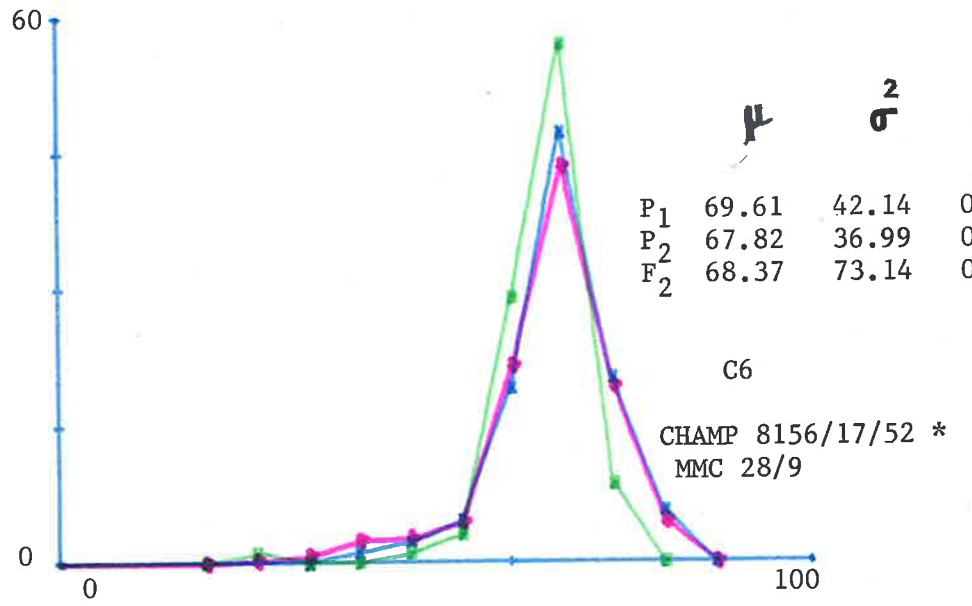
CHAMP 8156/17/52 *
MM 68/1



	μ	σ^2	cv
P_1	66.53	88.88	0.14
P_2	76.86	52.06	0.08
F_2	72.89	164.62	0.18

C7

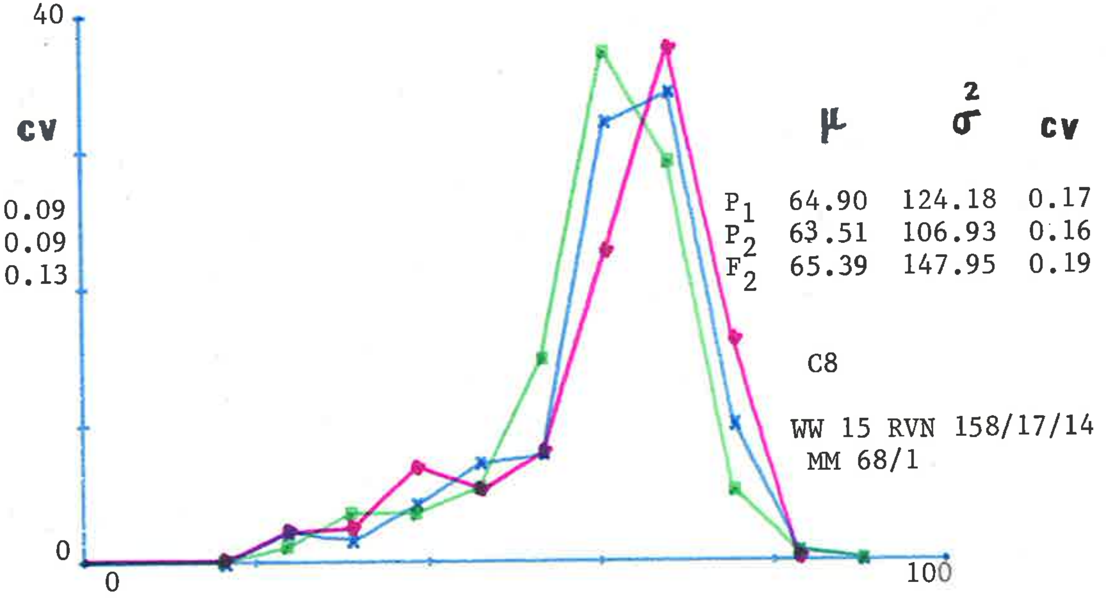
WW 15 RVN 158/17/14 *
PN 28/9



	μ	σ^2	cv
P_1	69.61	42.14	0.09
P_2	67.82	36.99	0.09
F_2	68.37	73.14	0.13

C6

CHAMP 8156/17/52 *
MMC 28/9



	μ	σ^2	cv
P_1	64.90	124.18	0.17
P_2	63.51	106.93	0.16
F_2	65.39	147.95	0.19

C8

WW 15 RVN 158/17/14
MM 68/1

height - crop density

Table 2.25. Variances of parents and F_2's, Chi-squares of Bartlett's test for homogeneity and F test of variance ratios between parents and F_2's for the character; height (HT)

	Variances			Bartlett's Chi-square	Variance ratios[1]		
	P_1	P_2	F_2		$P_1:P_2$	$P_1:F_2$	$P_2:F_2$
cross 1 MM25/4*MM68/1	103.97	85.12	156.40	9.06***	1.22NS	1.50*	1.84***
cross 2 MKR211/9*PN28/9	131.93	47.35	157.21	19.34***	2.79***	1.19NS	3.32***
cross 3 MKR211/9*MM68/1	175.44	124.59	304.82	35.49***	1.41***	1.74***	2.45***
cross 4 CHAMP8156/17/52 *PN28/9	69.57	47.20	154.09	72.92***	1.47***	2.21***	3.26***
cross 5 CHAMP8156/17/52 *MM68/1	66.83	162.31	105.42	9.17***	2.32***	1.58***	1.54***
cross 6 CHAMP8156/17/52 *MMC21/9	42.14	36.99	73.14	10.57***	1.14NS	1.74***	1.98***
cross 7 WW15RVN158/14 *PN28/9	88.88	52.06	164.62	24.24***	1.71***	1.85***	3.16***
cross 8 WW15RVN158/14 *MM68/1	124.18	106.93	147.95	5.30***	1.16NS	1.19NS	1.38***

[1] Larger variable divided by smaller variable.

Table 2.26. Coefficient of skewness values for height of parents and F_2's grown at crop density.

	cross 1	cross 2	cross 3	cross 4	cross 5	cross 6	cross 7	cross 8
parent 1	-1.60	-0.81	-2.32	-2.24	-2.59	-1.01	-1.24	-1.34
parent 2	-1.06	-1.81	-0.92	-1.76	-0.96	-3.07	-2.01	-1.30
F_2's	-0.65	-0.95	-0.77	-0.91	-1.42	-1.37	-0.79	-1.28

Coefficient of skewness for significant difference from zero at the 5% probability level;

= ± 0.389 for sample size of 100 (approximate guide for the parents in crosses 1, 2, 5, 6, 7)

= ± 0.200 for sample size of 400 (approximate guide for all F_2's and parents of crosses 3, 4, 8)

Table 2.27. Minimum and maximum values in the parent and F_2 populations of eight crosses studied at crop density for the character: height

cross number	minimum			maximum		
	P_1	P_2	F_2	P_1	P_2	F_2
cross 1 MM25/4*MM68/1	39.60	29.50	16.31	87.20	96.50	130.70
cross 2 MKR211/9*PN28/9	53.50	50.40	31.80	114.10	96.20	116.60
cross 3 MKR211/9*MM68/1	11.30	23.50	8.9	104.10	99.50	116.20
cross 4 CHAMP8156/17/52 *PN28/9	29.70	38.50	17.80	85.10	90.20	101.30
cross 5 CHAMP8156/17/52 *MM68/1	28.00	22.00	21.80	81.90	97.40	87.00
cross 6 CHAMP8156/17/52 *MMC21/9	42.30	30.00	26.20	82.70	76.60	87.20
cross 7 WW15RNV158/14 *PN28/9	39.00	38.10	22.70	77.30	88.40	103.40
cross 8 WW15RVN158/14 *MM68/1	25.50	23.70	24.50	88.80	90.30	82.80

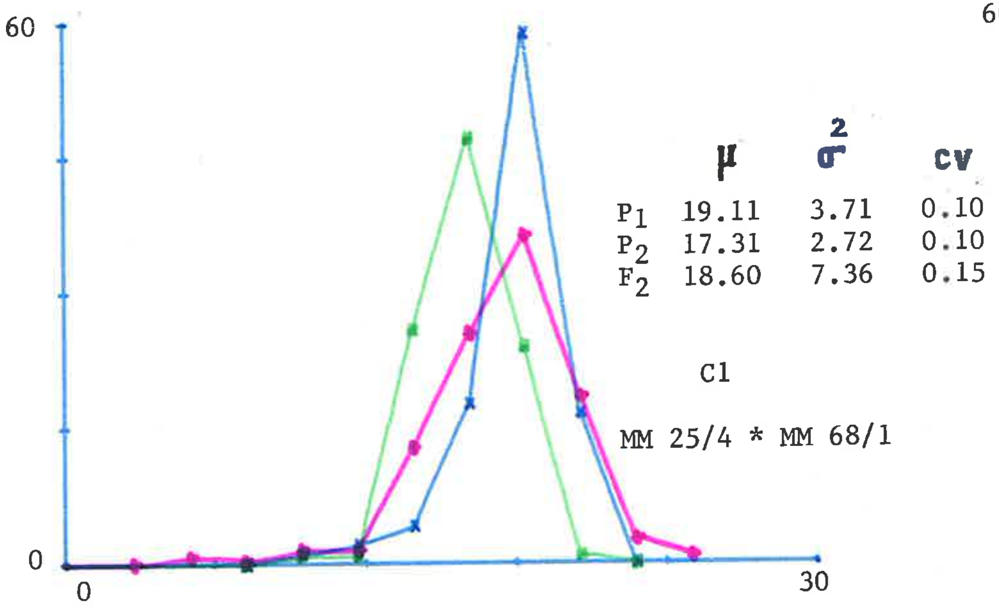
11. Spikelet number of the main shoot at crop density.

The distributions for spikelet number showed some very clear patterns (Figure 2.11) indicating situations where the parents and F_2 were almost identical (cross 6), to where the F_2 was intermediate between two different parents (cross 3) and to a situation that resembled dominance (cross 4). The pattern for cross 3 was almost a perfect example to demonstrate a quantitative genetical model. The F_2's ranges covered the combined ranges of the parental distributions and transgressive segregation was evident in crosses 1, 2, 5, 6, 7 and 8 (Table 2.30).

The variances for this character are presented in Table 2.28. The F_2's variances of crosses 1, 4, 5 and 7 were significantly larger than both their respective parental variances, whereas in crosses 2, 3 and 8 the F_2 was significantly different only from one parent. As with height, the CV for spikelet number were small.

Strongly negative skews were obtained for this character (Table 2.29).

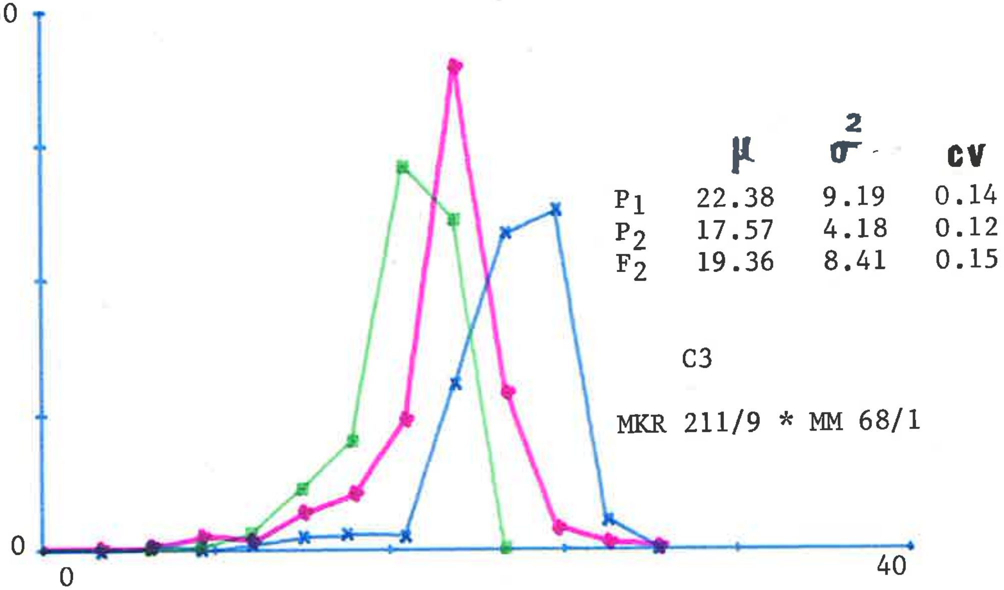
Figure 2.11. Frequency distribution for main shoot spikelet number for eight crosses studied at crop density. The blue and green curves are the parent 1 and parent 2 distributions respectively and the red curve is the hybrid F_2 distribution.
The X axis represents class intervals and the Y plant frequency in each class presented as a percentage.



	μ	σ^2	cv
P_1	19.11	3.71	0.10
P_2	17.31	2.72	0.10
F_2	18.60	7.36	0.15

C1

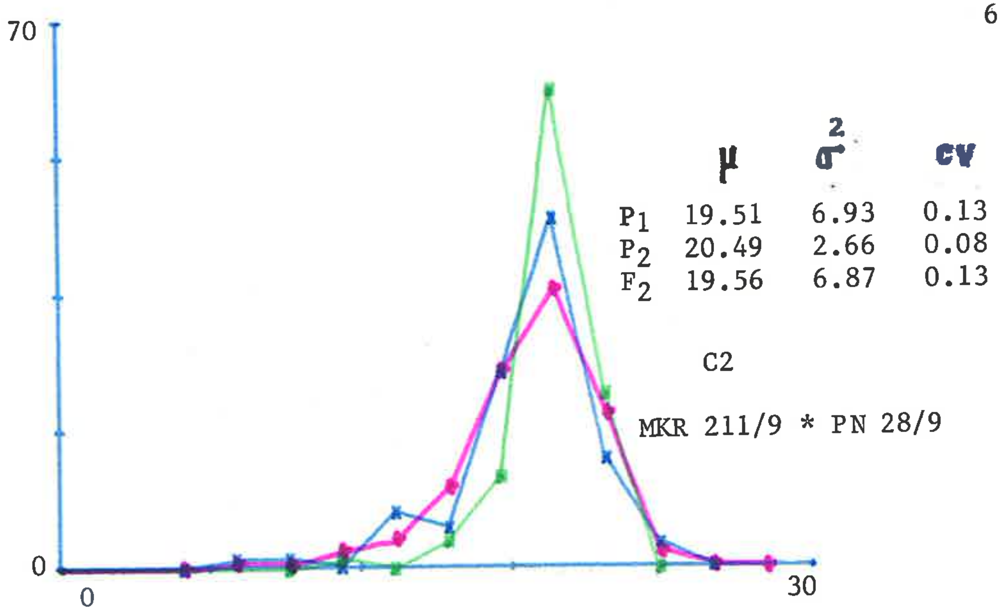
MM 25/4 * MM 68/1



	μ	σ^2	cv
P_1	22.38	9.19	0.14
P_2	17.57	4.18	0.12
F_2	19.36	8.41	0.15

C3

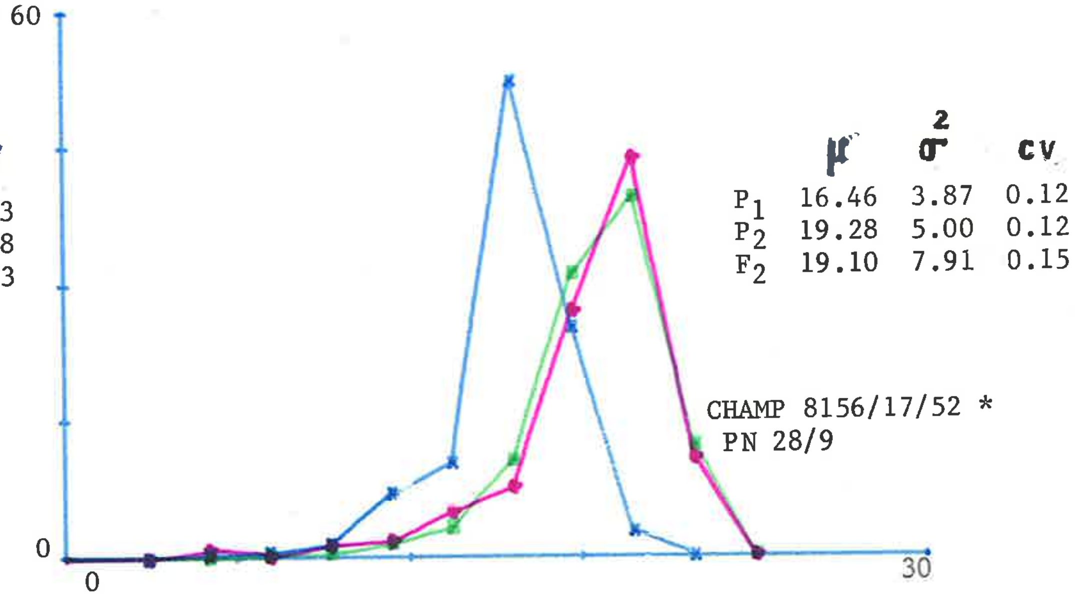
MKR 211/9 * MM 68/1



	μ	σ^2	cv
P_1	19.51	6.93	0.13
P_2	20.49	2.66	0.08
F_2	19.56	6.87	0.13

C2

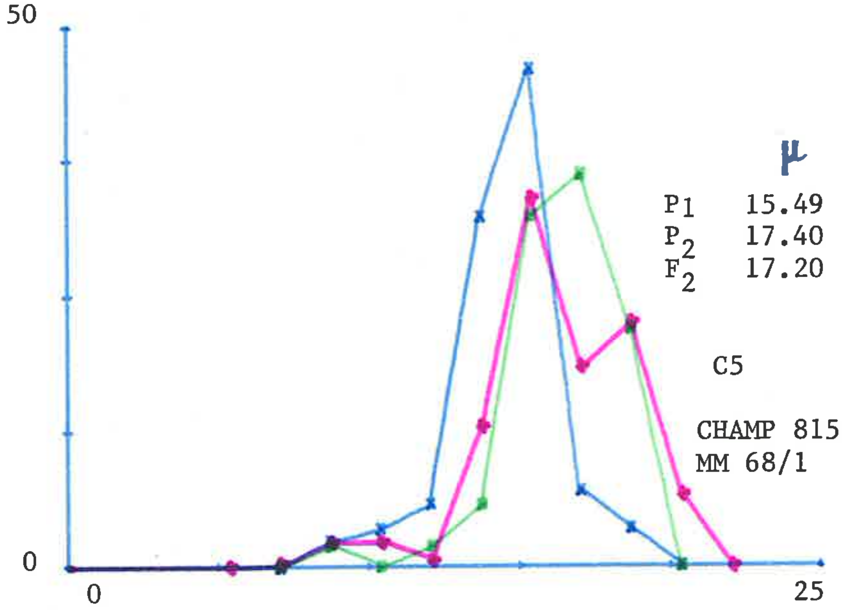
MKR 211/9 * PN 28/9



	μ	σ^2	cv
P_1	16.46	3.87	0.12
P_2	19.28	5.00	0.12
F_2	19.10	7.91	0.15

CHAMP 8156/17/52 *
PN 28/9

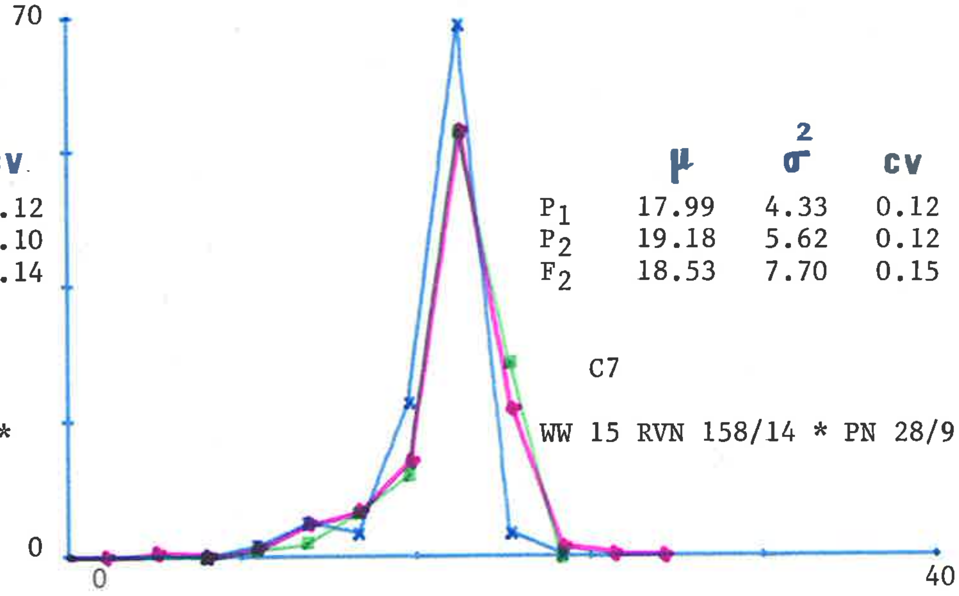
spikelet number - crop density



	μ	σ^2	cv
P_1	15.49	3.58	0.12
P_2	17.40	3.01	0.10
F_2	17.20	6.02	0.14

C5

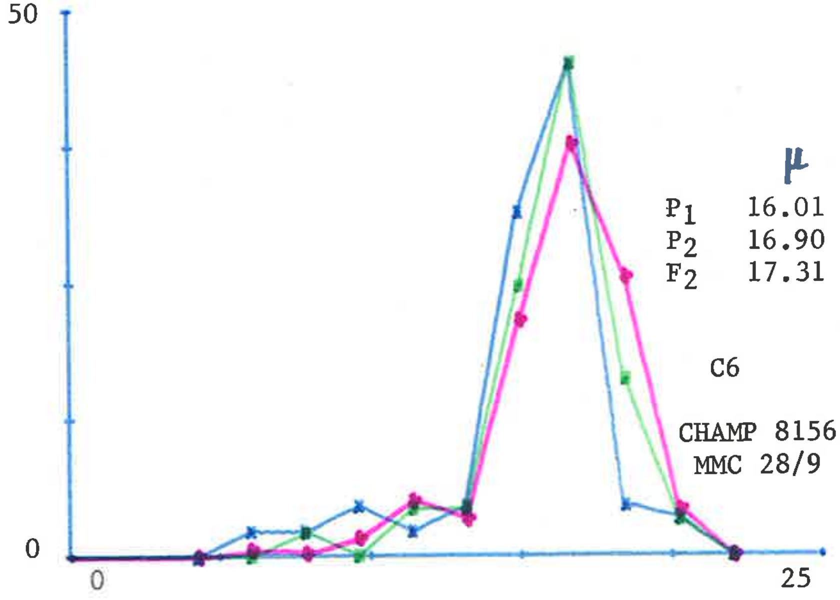
CHAMP 8156/17/52 *
MM 68/1



	μ	σ^2	cv
P_1	17.99	4.33	0.12
P_2	19.18	5.62	0.12
F_2	18.53	7.70	0.15

C7

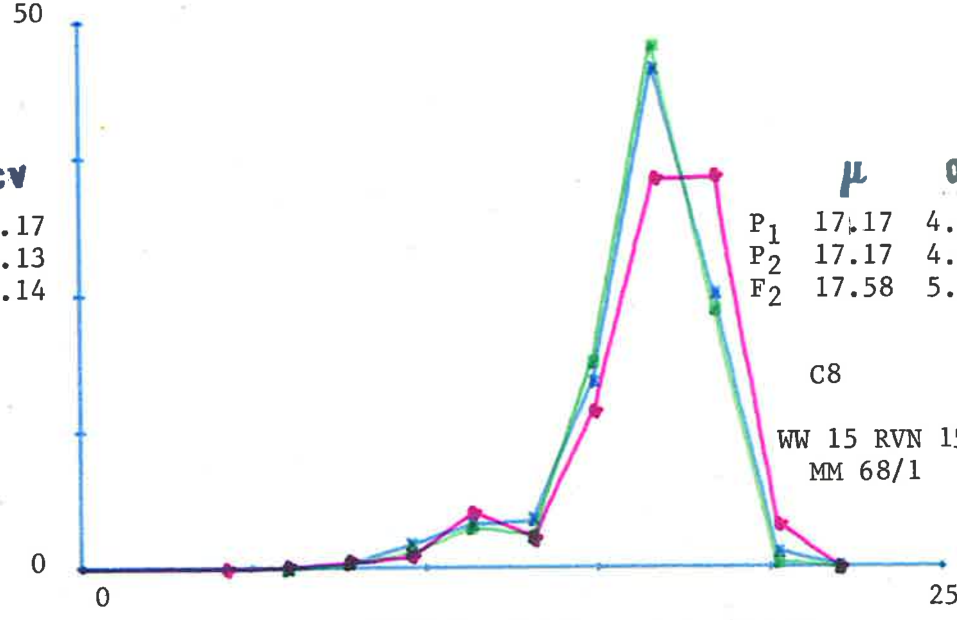
WW 15 RVN 158/14 * PN 28/9



	μ	σ^2	cv
P_1	16.01	7.35	0.17
P_2	16.90	5.18	0.13
F_2	17.31	5.69	0.14

C6

CHAMP 8156/17/52 *
MMC 28/9



	μ	σ^2	cv
P_1	17.17	4.37	0.12
P_2	17.17	4.02	0.12
F_2	17.58	5.31	0.13

C8

WW 15 RVN 158/14 *
MM 68/1

spikelet number - crop density

Table 2.28. Variances of parents and F_2's, Chi-squares of Bartlett's test for homogeneity and F test of variance ratios between parents and F_2's for the character; the main shoot spikelet number (SPIKE)

	Variances			Bartlett's Chi-square	Variance ratios[1]		
	P_1	P_2	F_2		$P_1:P_2$	$P_1:F_2$	$P_2:F_2$
cross 1 MM25/4*MM68/1	3.71	2.72	7.36	22.27***	1.36NS	1.98***	2.71***
cross 2 MKR211/9*PN28/9	6.93	2.66	6.87	13.02***	2.61***	1.01NS	2.58***
cross 3 MKR211/9*MM68/1	9.19	4.18	8.41	21.35***	2.20***	1.09NS	2.01***
cross 4 CHAMP8156/17/52 *PN28/9	3.87	5.00	7.91	25.46***	1.29***	2.04***	1.58***
cross 5 CHAMP8156/17/52 *MM68/1	3.58	3.01	6.02	10.95***	1.19NS	1.68***	2.00***
cross 6 CHAMP8156/17/52 *MMC21/9	7.35	5.18	5.69	1.64NS	1.42NS	1.29NS	1.10NS
cross 7 WW15RVN158/14 *PN28/9	4.33	5.26	7.70	5.56***	1.30*	1.74***	1.37***
cross 8 WW15RVN158/14 *MM68/1	4.37	4.02	5.31	4.61***	1.09NS	1.22NS	1.32***

[1] Larger variable divided by smaller variable.

Table 2.29. Coefficient of skewness values for the main shoot spikelet number of parents and F_2's grown at crop density.

	cross 1	cross 2	cross 3	cross 4	cross 5	cross 6	cross 7	cross 8
parent 1	-1.87	-1.43	-2.34	-1.24	-0.63	-1.47	-1.88	-1.26
parent 2	-0.74	-2.12	-1.46	-1.24	-1.81	-1.28	-1.46	-1.37
F_2's	-1.18	-1.20	-1.38	-1.96	-0.91	01.09	-1.57	-1.27

Coefficient of skewness for significant difference from zero at the 5% probability level;

= ± 0.389 for sample size of 100 (approximate guide for the parents in crosses 1, 2, 5, 6, 7)

= ± 0.200 for sample size of 400 (approximate guide for all F_2's and parents of crosses 3, 4, 8)

Table 2.30. Minimum and maximum values in the parent and F_2 populations of eight crosses studied at crop density for the character: the main shoot spikelet number (SPIKE)

cross number	minimum			maximum		
	P_1	P_2	F_2	P_1	P_2	F_2
cross 1 MM25/4*MM68/1	11	11	5	22	21	25
cross 2 MKR211/9*PN28/9	9	12	7	24	23	26
cross 3 MKR211/9*MM68/1	6	8	5	26	21	26
cross 4 CHAMP8156/17/52 *PN28/9	7	8	5	21	24	24
cross 5 CHAMP8156/17/52 *MM68/1	9	10	7	20	20	22
cross 6 CHAMP8156/17/52 *MMC21/9	6	8	6	21	21	22
cross 7 WW15RNV158/14 *PN28/9	10	10	4	21	22	25
cross 8 WW15RVN158/14 *MM68/1	9	8	6	21	21	22

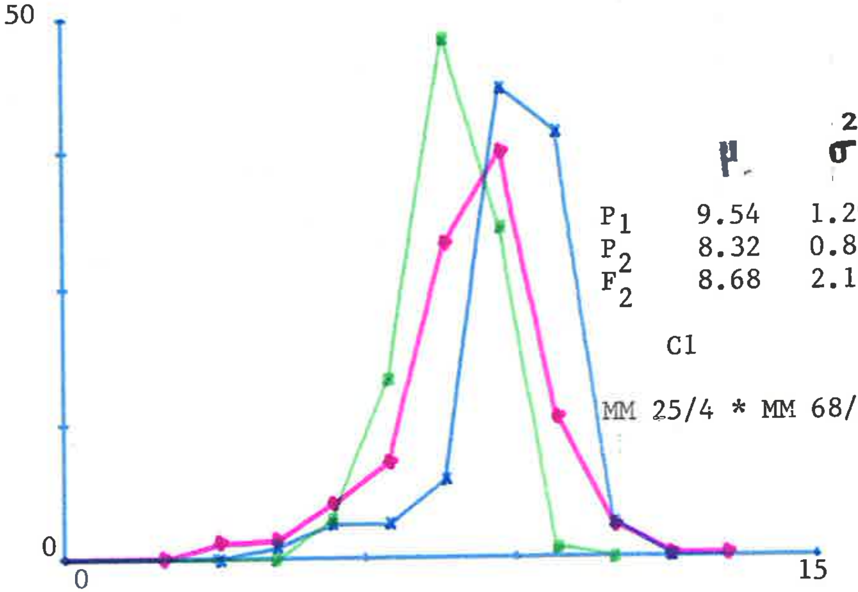
12. Head length of the main shoot at crop density.

The lengths of the heads on the main shoots were measured without the awns. In general, the distributions conformed to what was expected from a segregating population in that the F_2's means, with some exceptions, were intermediate between the parental means while the range covered the combined ranges of the parents (Figure 2.12). This was evident in crosses 1, 3, 4 and 7 indicating possible simple additive gene effects. The F_2 of crosses 2, 5, 6 and 8 show some indication of heterosis but cross 2 shows negative heterosis and the others positive heterosis. Transgressive segregation was evident in crosses 5, 6 and 8 (Figure 2.12 and Table 2.33).

In spite of having many lower minimum values and higher maximum values than their parents (Table 2.33), the F_2's variances with two exceptions were not greater than their parental variances (Table 2.31).

Negative skews were obtained (Table 2.32). A negative skew has been characteristic of the distributions of the characters measured on the main shoot throughout this study while a positive skew has been found for the total plant weight, total grain weight and characters measured on the tillers.

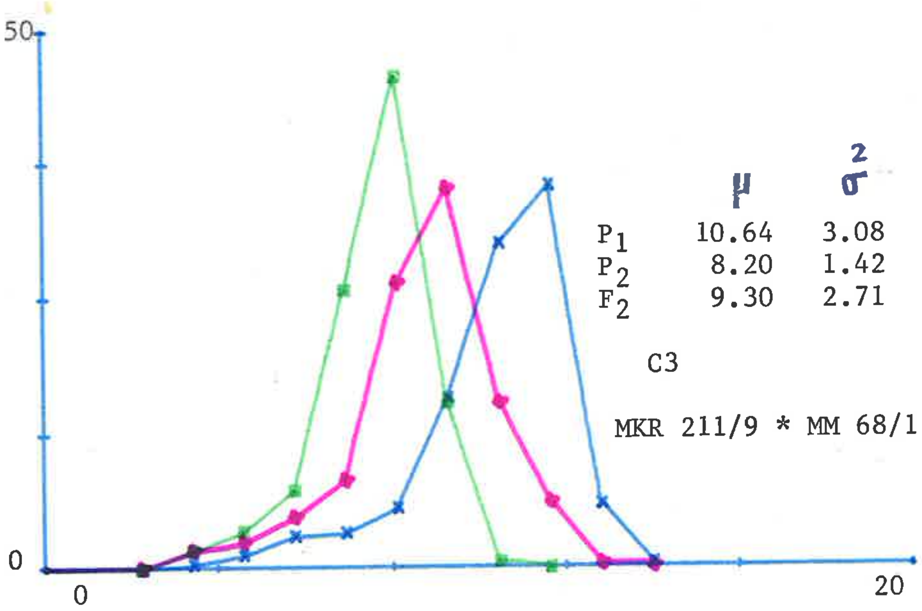
Figure 2.12. Frequency distribution of the head length on the main shoot for eight crosses studied at crop density. The blue and green curves are the parent 1 and parent 2 distributions respectively and the red curve is the hybrid F_2 distribution.
The X axis represents class intervals and the Y plants frequency in each class as a percentage.



	μ	σ^2	cv
P_1	9.54	1.29	0.12
P_2	8.32	0.81	0.11
F_2	8.68	2.12	0.17

C1

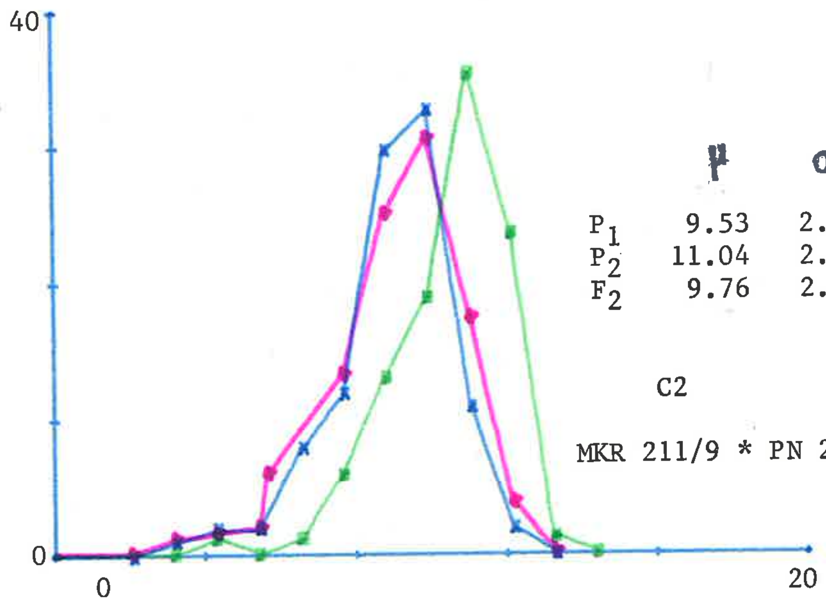
MM 25/4 * MM 68/1



	μ	σ^2	cv
P_1	10.64	3.08	0.16
P_2	8.20	1.42	0.15
F_2	9.30	2.71	0.18

C3

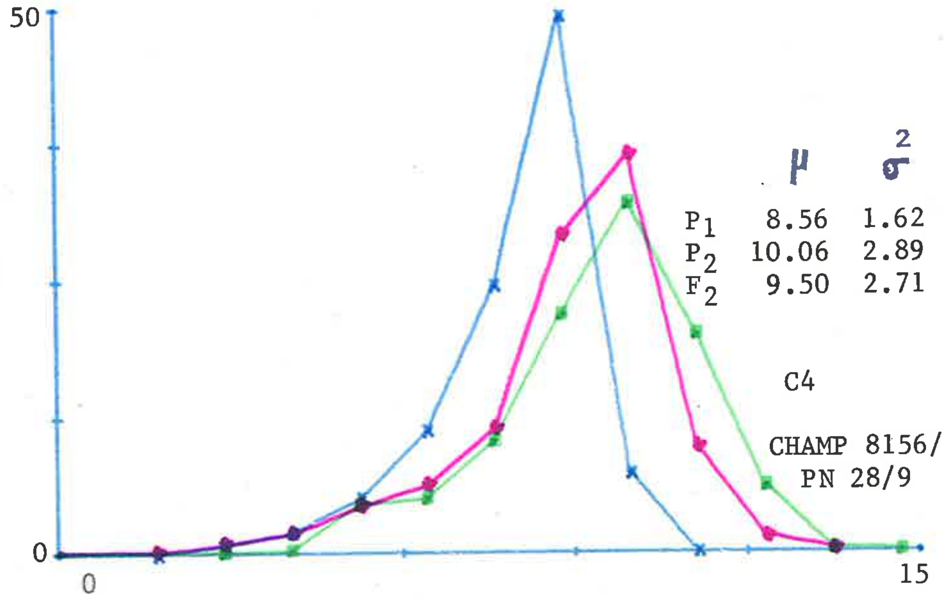
MKR 211/9 * MM 68/1



	μ	σ^2	cv
P_1	9.53	2.58	0.17
P_2	11.04	2.30	0.14
F_2	9.76	2.76	0.17

C2

MKR 211/9 * PN 28/9

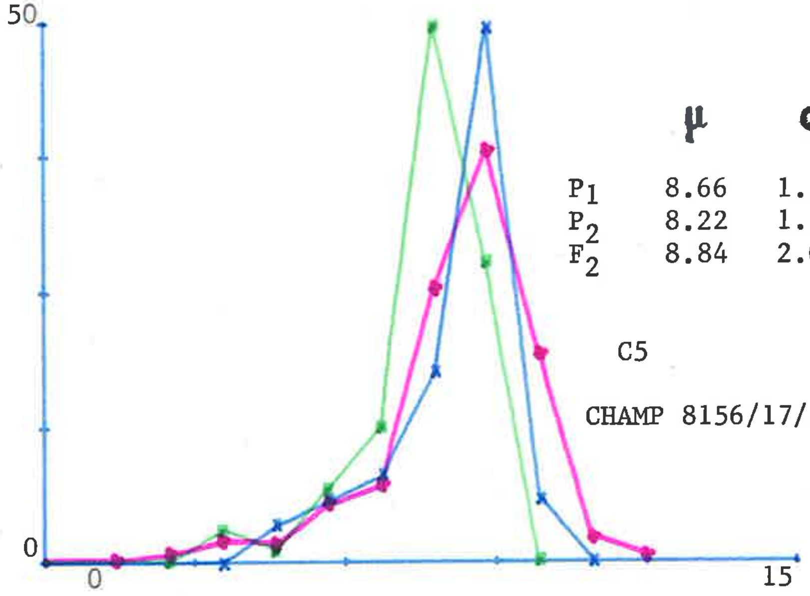


	μ	σ^2	cv
P_1	8.56	1.62	0.15
P_2	10.06	2.89	0.17
F_2	9.50	2.71	0.17

C4

CHAMP 8156/17/52 *
PN 28/9

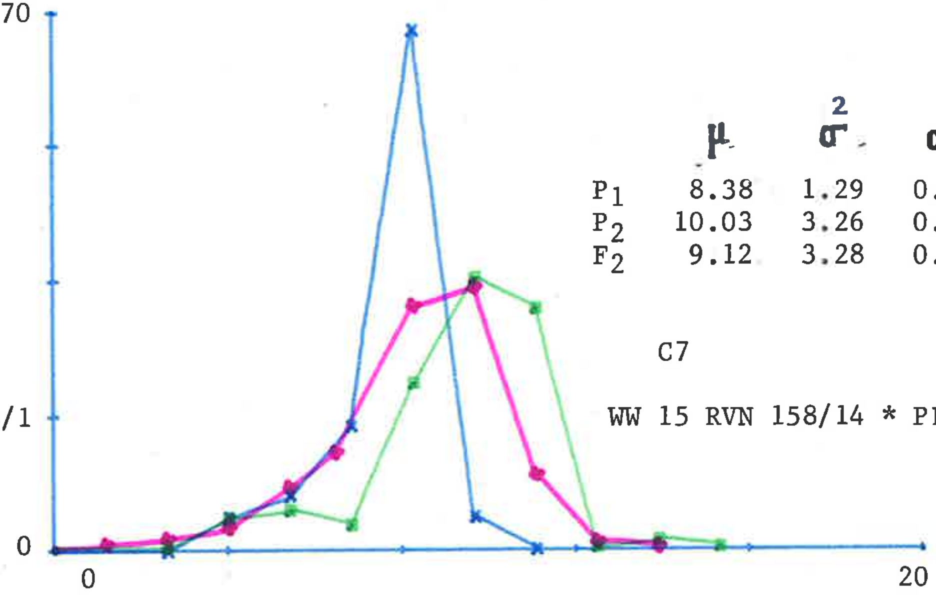
head length - crop density



	μ	σ^2	cv
P_1	8.66	1.35	0.13
P_2	8.22	1.24	0.14
F_2	8.84	2.04	0.16

C5

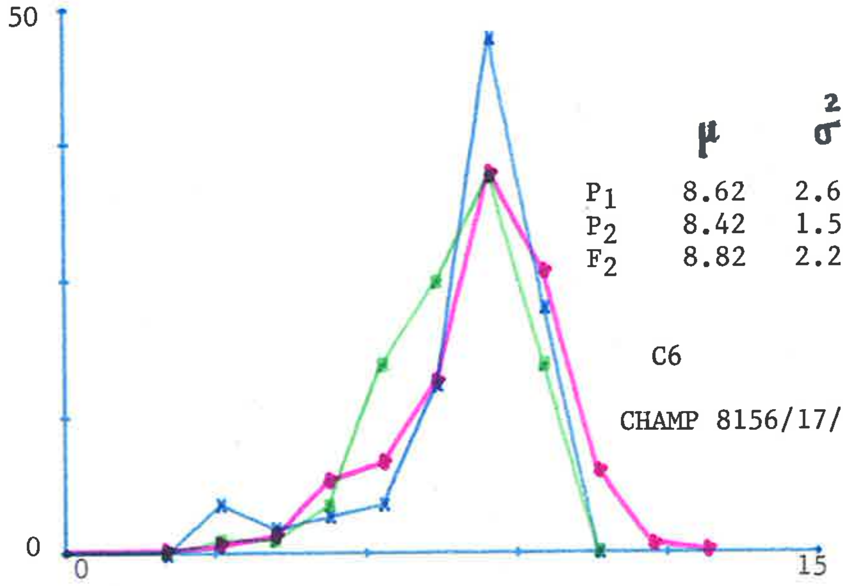
CHAMP 8156/17/52 * MM 68/1



	μ	σ^2	cv
P_1	8.38	1.29	0.14
P_2	10.03	3.26	0.18
F_2	9.12	3.28	0.20

C7

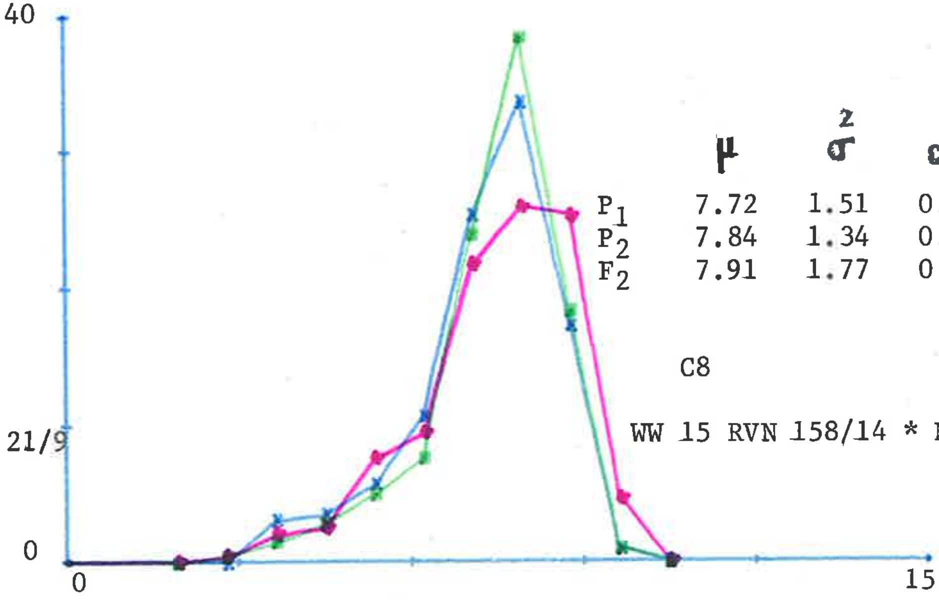
WW 15 RVN 158/14 * PN 28/9



	μ	σ^2	cv
P_1	8.62	2.60	0.19
P_2	8.42	1.57	0.15
F_2	8.82	2.21	0.17

C6

CHAMP 8156/17/52 * MMC 21/9



	μ	σ^2	cv
P_1	7.72	1.51	0.16
P_2	7.84	1.34	0.15
F_2	7.91	1.77	0.17

C8

WW 15 RVN 158/14 * MM 68/1

head length - crop density

Table 2.31. Variances of parents and F_2's, Chi-squares of Bartlett's test for homogeneity and F test of variance ratios between parents and F_2's for the character; head length of the main shoot (HDLTH)

	Variances			Bartlett's Chi-square	Variance ratios^1		
	P_1	P_2	F_2		P_1:P_2	P_1:F_2	P_2:F_2
cross 1 MM25/4*MM68/1	1.29	0.81	2.12	18.16***	1.59*	1.64***	2.62***
cross 2 MKR211/9*PN28/9	2.58	2.30	2.76	0.16NS	1.12NS	1.07NS	1.20NS
cross 3 MKR211/9*MM68/1	3.08	1.42	2.71	23.46***	2.17***	1.14NS	1.91***
cross 4 CHAMP8156/17/52 *PN28/9	1.63	2.89	2.71	16.82***	1.77***	1.66***	1.07NS
cross 5 CHAMP8156/17/52 *MM68/1	1.35	1.24	2.04	6.09***	1.09NS	1.51*	1.65***
cross 6 CHAMP8156/17/52 *MMC21/9	2.60	1.57	2.21	2.95*	1.66*	1.18NS	1.41*
cross 7 WW15RVN158/14 *PN28/9	1.29	3.26	3.28	10.58***	2.53***	2.54***	1.10NS
cross 8 WW15RVN158/14 *MM68/1	1.51	1.34	1.77	3.91*	1.13NS	1.17NS	1.32*

[1] Larger variable divided by smaller variable.

Table 2.32. Coefficient of skewness values for head length of the main shoot of parents and F_2's grown at crop density.

	cross 1	cross 2	cross 3	cross 4	cross 5	cross 6	cross 7	cross 8
parent 1	-1.81	-1.04	-1.48	-1.34	-1.50	-1.90	-1.56	-1.08
parent 2	-0.51	-1.78	-1.13	-0.66	-1.53	-0.99	-1.30	-1.32
F_2's	-0.88	-1.00	-0.77	-1.09	-1.31	-0.85	-1.40	-0.90

Coefficient of skewness for significant difference from zero at the 5% probability level;

= ± 0.389 for sample size of 100 (approximate guide for the parents in crosses 1, 2, 5, 6, 7)

= ± 0.200 for sample size of 400 (approximate guide for all F_2's and parents of crosses 3, 4, 8)

Table 2.33. Minimum and maximum values in the parent and F_2 populations of eight crosses studied at crop density for the character: head length of the main shoot (HDLTH)

cross number	minimum			maximum		
	P_1	P_2	F_2	P_1	P_2	F_2
cross 1 MM25/4*MM68/1	5.1	5.5	3.1	11.4	10.0	13.2
cross 2 MKR211/9*PN28/9	4.1	4.9	3.2	12.5	13.3	13.1
cross 3 MKR211/9*MM68/1	4.0	3.8	3.4	14.0	10.5	13.7
cross 4 CHAMP8156/17/52 *PN28/9	3.2	4.8	2.9	10.9	13.5	13.1
cross 5 CHAMP8156/17/52 *MM68/1	4.7	4.1	2.5	10.2	9.7	12.0
cross 6 CHAMP8156/17/52 *MMC21/9	2.7	3.7	3.1	10.5	10.4	12.7
cross 7 WW15RNV158/14 *PN28/9	4.5	4.2	1.2	10.0	13.9	13.3
cross 8 WW15RVN158/14 *MM68/1	3.8	3.5	2.8	10.0	9.9	10.5

(c) Summary of results from experiment 1.

1. Evidence for the F_2's having larger variances than both parental variances was not consistent. It occurred only with characters measured on the main shoot. For the other characters such as; head number, plant total weight, total grain weight which is plant yield, tiller grain weight and tiller grain number, the F_2's variances were found only to be significantly larger than one parental variance or not to be different.

2. The parental variances were in many instances found to be significantly different from each other although according to theory, differences between plants of a parental population are attributable only to environmental differences and the resulting variances are often anticipated to be homogeneous.

3. Transgressive segregation was again found very often for the characters measured on the main shoot but only infrequently for characters such as; head number, plant total weight, total grain weight, tiller grain weight and tiller grain number.

4. Negative skews occurred for all characters measured on the main shoot: the main shoot total weight, grain weight, grain number, height, head length and spikelet number.

5. Positive skews occurred for the characters; head number, plant total weight, total grain weight, tiller grain weight and tiller grain number.

6. In several instances, genetic segregation conformed to a simple quantitative genetic model in that the distributional range of the F_2 covered the combined ranges of the parents and the F_2 mode was intermediate between the modes of the parents. Understandably the segregation usually was most clear when the parental modes were of very different value.

7. Some crosses showed much greater evidence of genetic segregation and transgressive segregation. They were crosses 4 (CHAMP/8156/17/52 * PN28/9), 6 (CHAMP/8156/17/52 * MMC21/9), and 8 (WW15/RVN/158/14 * MM68/1).

Experiment 2. Single plants of F_2's and parents grown at low density.

The objectives of experiment 2 were similar to those of experiment 1. Its purpose was to measure the variation in F_2 and parent populations when grown at low density and to determine if selection could be conducted more or less efficiently at low density than at crop density.

(a) Outline of the experiment.

Experiment 2 was conducted in the same site, year and season as experiment 1 and the details of climate and soil reviewed for the first experiment are equally relevant.

1. The material.

Only three of the eight crosses of experiment 1 were grown in experiment 2 due to limitations in the number of F_2 seeds available. The crosses were:

cross 3	MKR211/9 * MM68/1
cross 7	WW15RVN158/14 * PN28/9
cross 8	WW15RVN158/14 * MM68/1

2. Sowing.

Seeds were sown by machine on June 19, 1975. Parents and hybrids were sown in separate plots. As some of parents were in common in the different crosses only the four different parents were grown. In this way it was possible to reduce the large labour requirement in measuring the characters on the large plants that developed under low density. The plots contained six rows, 2.5 metre long with 25 cm. between rows.

The plants were thinned on September 1, 1975 to leave 13 plants in a row at a nominal distance apart of 20 cm. (equivalent to 25 plants per m^2). The commercial variety Halberd was grown in the border outer two rows, and there were four replicates.

Other details of the experiment concerning disease, lodging, damage, harvesting and the measurements and statistical methods were the same as for experiment 1.

(b) Results of experiment 2.

1. Introduction. An analysis of variance was undertaken and as the replicate effect was found to be nonsignificant the values from the four replications were combined to give the frequency distributions. Each distribution is based on approximately 200 plants. Mean values, variances, coefficient of variation and skewness values were calculated for each population using the same procedure as in experiment 1. The frequency distributions for the ten characters of the F_2's and parents will be presented and as the number of plants in the populations were unequal, the distributions are presented with percentage values in each class. Comparisons will be drawn between each F_2 and its parents and between the results for these low density plants and the plants at the crop density of experiment 1.

2. Head number per plant at low density.

The very low competition between plants that occurred at the low density enabled the development of a greater number of heads per plant than at crop density. Each plant had approximately four to five times the number of heads (Figure 2.13). An interesting result was present in the variances. Whereas at crop density the F_2's variances for head number were of a similar magnitude to that of the parents (Table 2.1), at low density the F_2's had larger variances than their parents with all but one of them being significant (Table 2.35). The frequency distributions show that the F_2's distributions covered the combined range of the parental distributions and that there was transgressive segregation with F_2 minimum and maximum values exceeding the values of the parents (Table 2.37 and Figure 2.13).

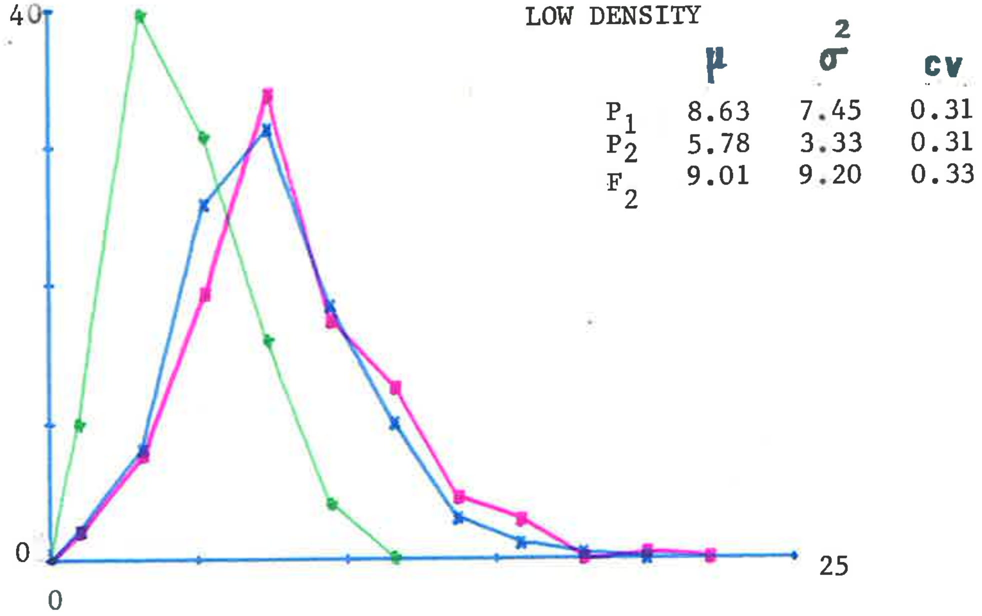
The F_2's means for this character were greater than the mid parent values. This occurred at both densities, further supporting the evidence for an effect of gene dominance. The F_2's of crosses 3 and 8 had means higher than both their respective parents, thus showing heterosis.

The positive skews of the frequency distributions noted above for crop density were found again (Table 2.36).

Figure 2.13. Frequency distribution of the head number from three crosses studied at low density. The blue and green curves are for parent 1 and parent 2 distributions respectively and the red is the hybrid F_2 distribution.

The X axis represents class intervals and the Y represents the number of plants in each class as a percentage.

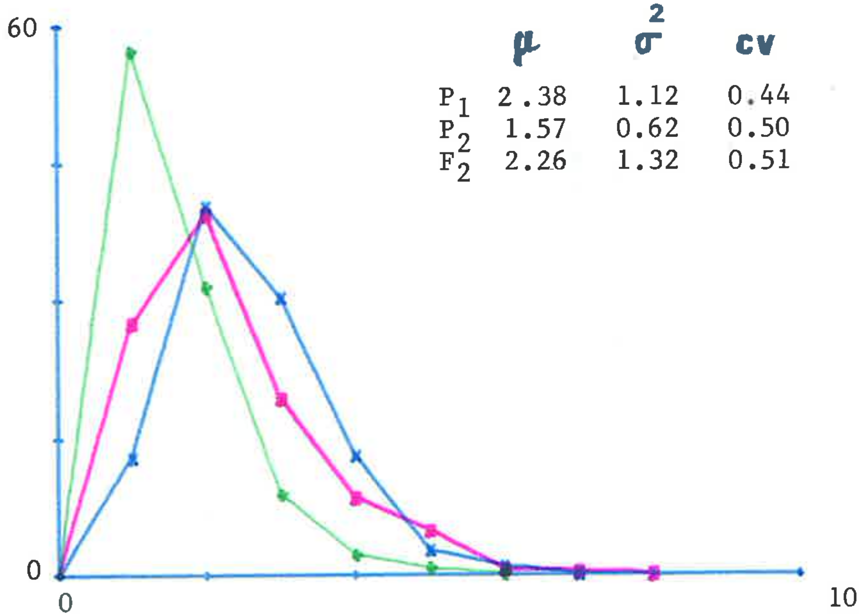
MKR 211/9 * MM 68/1



LOW DENSITY

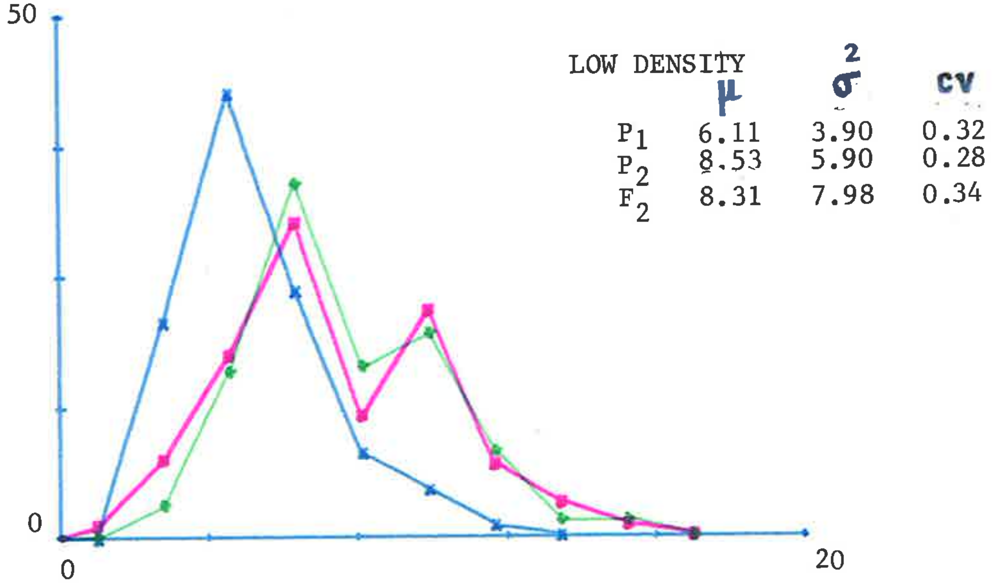
	μ	σ^2	cv
P_1	8.63	7.45	0.31
P_2	5.78	3.33	0.31
F_2	9.01	9.20	0.33

CROP DENSITY



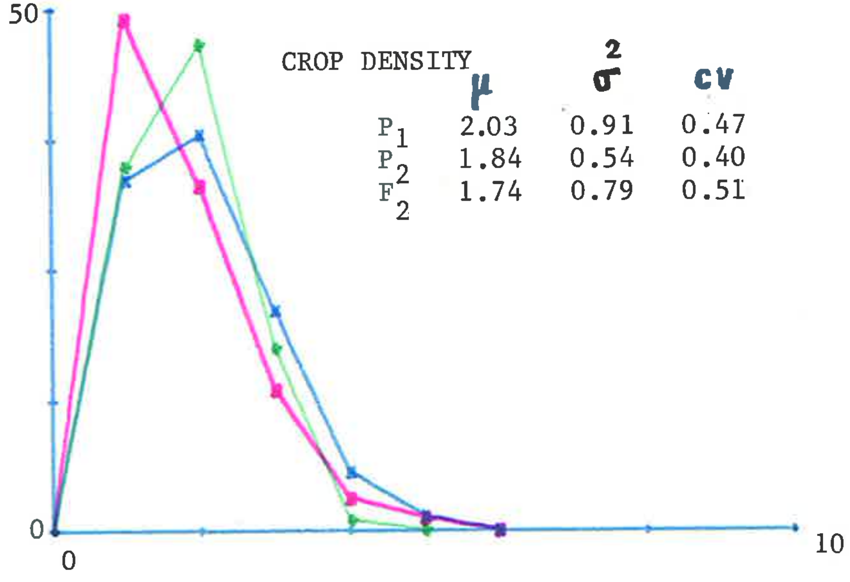
	μ	σ^2	cv
P_1	2.38	1.12	0.44
P_2	1.57	0.62	0.50
F_2	2.26	1.32	0.51

WW-15 RVN 158/14 * PN 28/9



LOW DENSITY

	μ	σ^2	cv
P_1	6.11	3.90	0.32
P_2	8.53	5.90	0.28
F_2	8.31	7.98	0.34

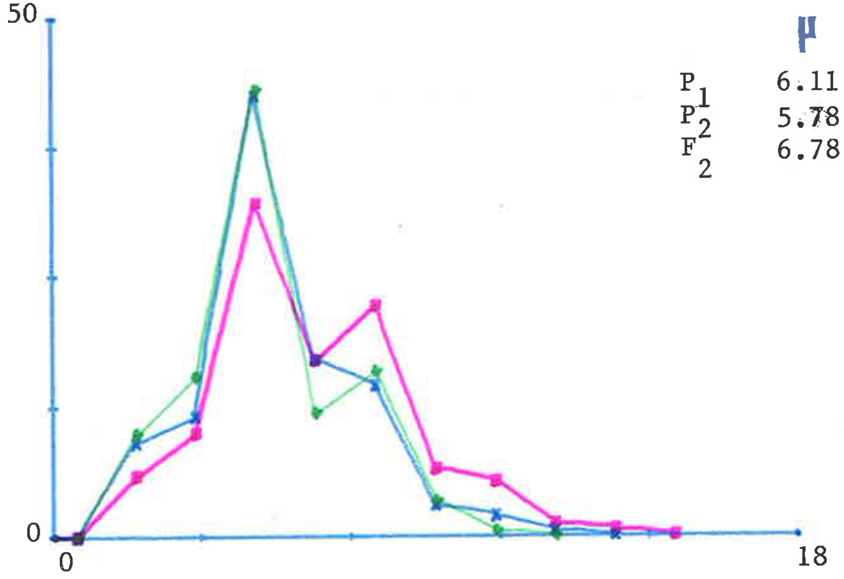


CROP DENSITY

	μ	σ^2	cv
P_1	2.03	0.91	0.47
P_2	1.84	0.54	0.40
F_2	1.74	0.79	0.51

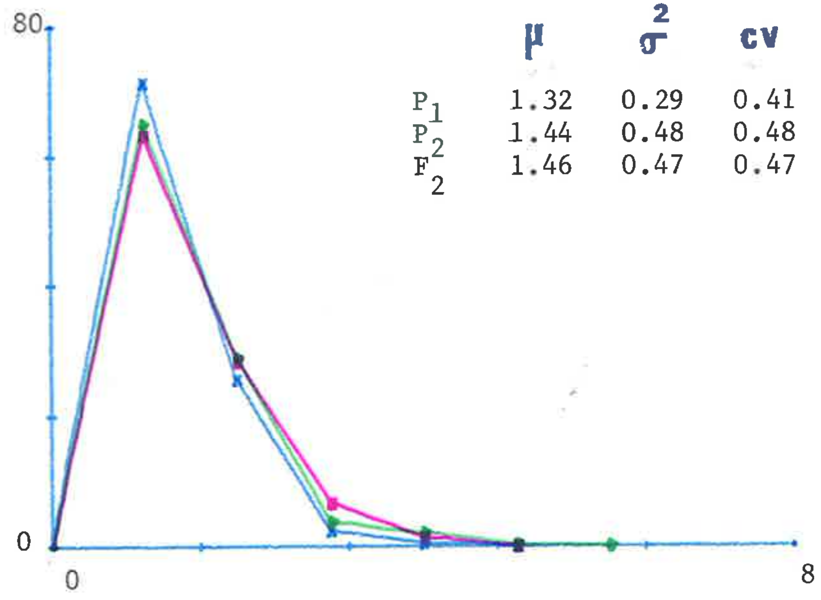
WW-15 RVN 158/14 * MM 68/1

LOW DENSITY



	μ	σ^2	cv
P_1	6.11	3.90	0.32
P_2	5.78	3.33	0.31
F_2	6.78	5.66	0.35

CROP DENSITY



	μ	σ^2	cv
P_1	1.32	0.29	0.41
P_2	1.44	0.48	0.48
F_2	1.46	0.47	0.47

Table 2.35. Variances of parents and F_2's, Chi-square of Bartlett's test for homogeneity and F test of variance ratios between parents and F_2's grown at low density for character; head number (HDNO)

	Variances			Bartlett's Chi-square	Variance ratios[1]		
	P_1	P_2	F_2		$P_1:P_2$	$P_1:F_2$	$P_2:F_2$
cross 3 MKR211/9 * MM68/1	7.45	3.33	9.20	27.29***	2.24***	1.23NS	2.77***
cross 7 WW15 RVN158/14 * PN28/9	3.90	5.90	7.98	12.25***	1.51***	2.05***	1.35*
cross 8 WW15RVN158/14 * MM68/1	3.90	3.33	5.66	7.02***	1.17NS	1.45***	1.70***

[1] Larger variance divided by smaller variance.

Table 2.36. Coefficient of skewness values for head number per plant of parents and F_2's grown at low density.

	Coefficient values
cross 3 - F_2 (MKR211/9 * MM68/1)	0.44
cross 7 - F_2 (WW15RVN158/14 * PN28/9)	0.27
cross 8 - F_2 (WW15RVN158/14 * MM68/1)	0.45
parent - MKR211/9	0.42
parent - PN28/9	0.50
parent - WW15RVN158/14	0.60
parent - MM68/1	0.44

Coefficient of skewness for significant difference from zero at the 5% probability level;

= ± 0.280 for sample size of 200 (approximate guide for parents and F_2's at low density).

Table 2.37. Minimum and Maximum values in the parent and F_2 populations of three crosses studied at low density for the character: head number

cross number (low density)	minimum			maximum		
	P_1	P_2	F_2	P_1	P_2	F_2
cross 3 MKR211/9*MM68/1	2	2	1	18	11	20
cross 7 WW15RVN158/14 * PN28/9	3	3	2	13	16	17
cross 8 WW15RVN158/14 * MM68/1	3	2	2	13	11	15

3. Plant total weight at low density.

The frequency distributions for plant total weight were slightly dissimilar to those obtained at crop density in that differences between the parents and F_2's were more pronounced at low density (Fig. 2.15). The F_2's had ranges that again covered the combined ranges of the parental distributions and in all the three crosses the minimum and maximum values for the F_2 exceeded the values in the parental populations (Table 2.40). At crop density (experiment 1), the F_2's means for this character were in general intermediate between the parental means, but at low density, the F_2's means were higher than both parents. This indicates heterosis and also suggests that under reduced competition, the hybrids performed relatively better than their parents for total plant weight. At low density, the mean values for all populations were again four to five times greater than the corresponding means obtained at crop density.

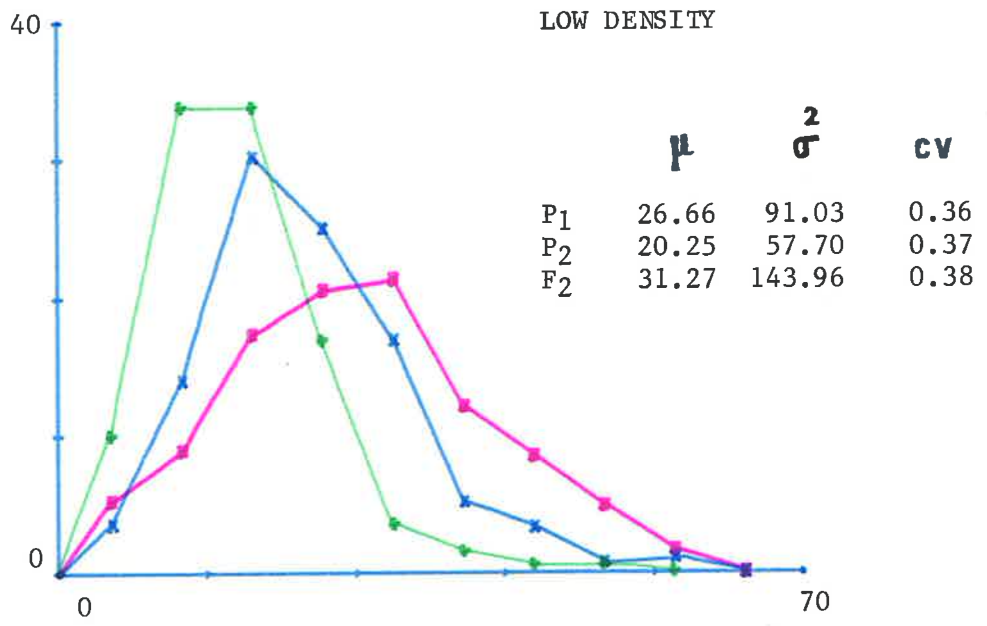
The F_2 variances were significantly greater than those of the parents (Table 2.38). However, to some degree this resulted from the larger values involved in the variances and the CV's were only slightly larger than at low density.

Positive skews were obtained at low density as they had been at crop density for plant total weight (Table 2.39).

Figure 2.14. Frequency distributions of the plant total weight from three crosses studies at low density; blue and green curves represent the parent 1 and parent 2 distributions respectively, the red represents the hybrid F_2 distribution.

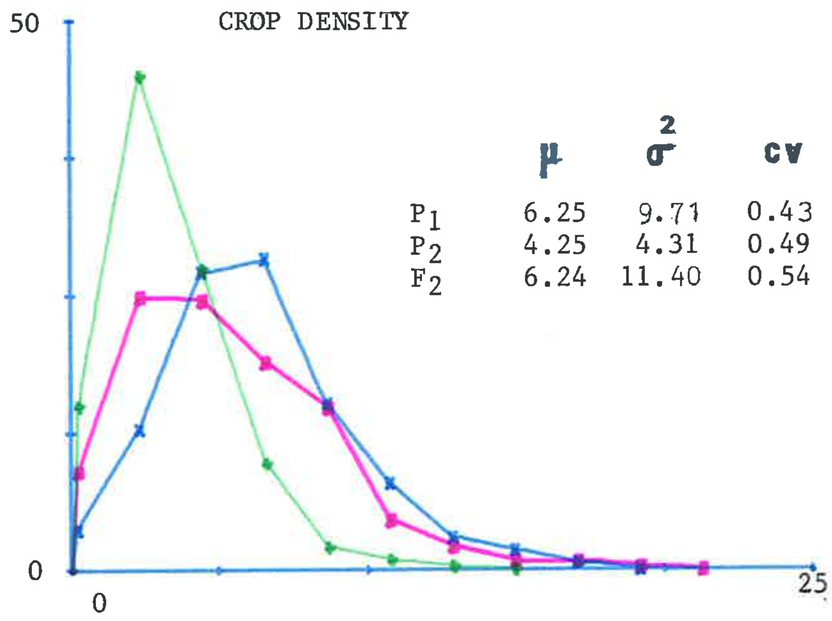
The X axis represents class intervals and the Y represents the number of plants in each class as a percentage.

MKR 211/9 * PN [illegible]/1



LOW DENSITY

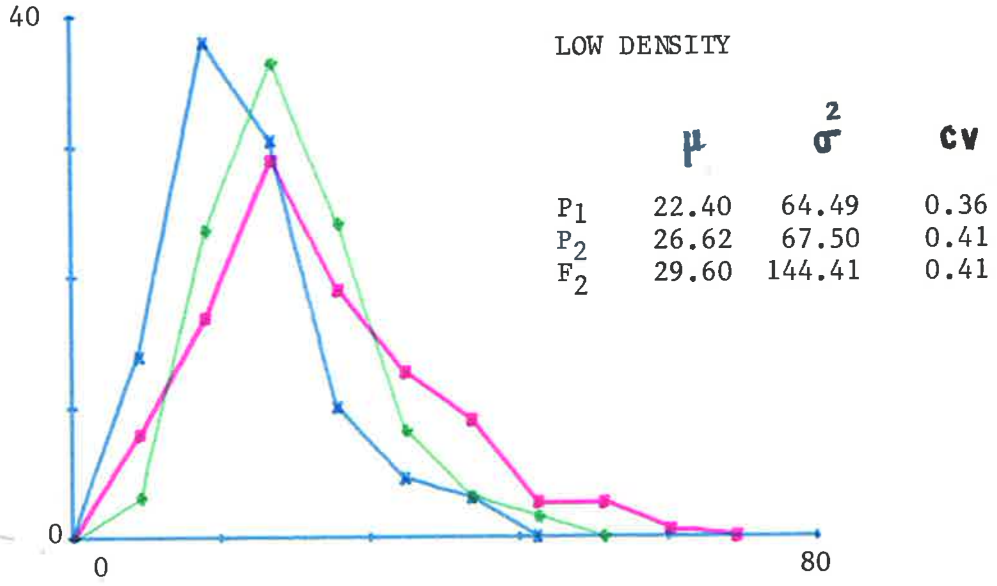
	μ	σ^2	cv
P_1	26.66	91.03	0.36
P_2	20.25	57.70	0.37
F_2	31.27	143.96	0.38



CROP DENSITY

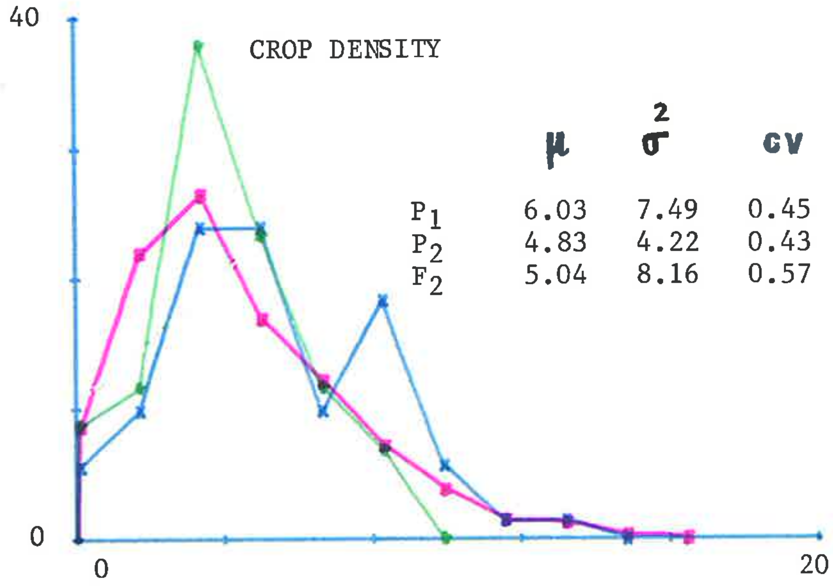
	μ	σ^2	cv
P_1	6.25	9.71	0.43
P_2	4.25	4.31	0.49
F_2	6.24	11.40	0.54

WW-15 RVN 158/14 * PN 28/9



LOW DENSITY

	μ	σ^2	cv
P_1	22.40	64.49	0.36
P_2	26.62	67.50	0.41
F_2	29.60	144.41	0.41

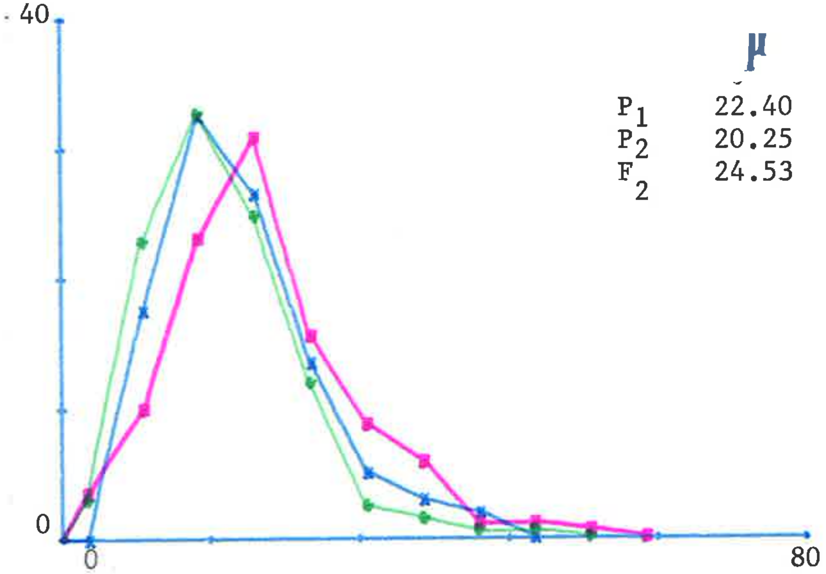


CROP DENSITY

	μ	σ^2	cv
P_1	6.03	7.49	0.45
P_2	4.83	4.22	0.43
F_2	5.04	8.16	0.57

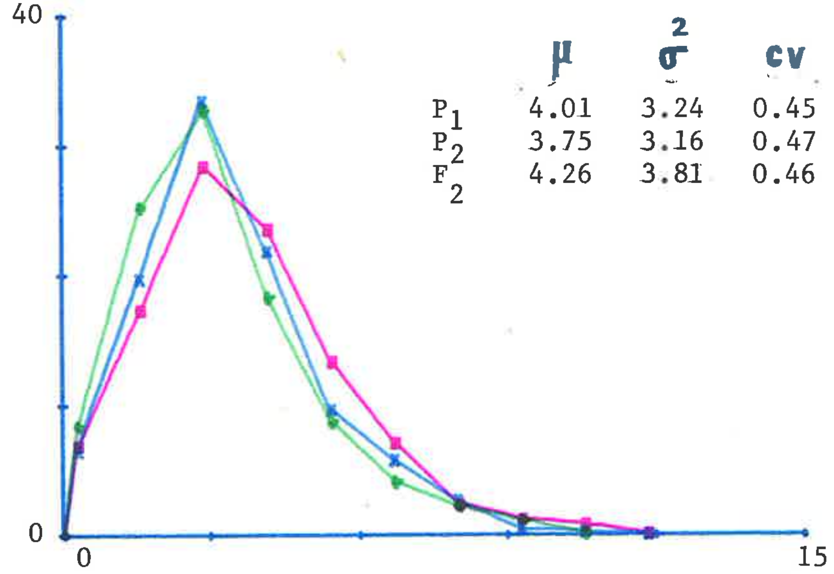
WW-15 RVN 158/14 * MM 68/1

LOW DENSITY



	μ	σ^2	cv
P_1	22.40	64.49	0.36
P_2	20.25	57.70	0.37
F_2	24.53	94.23	0.39

CROP DENSITY



	μ	σ^2	cv
P_1	4.01	3.24	0.45
P_2	3.75	3.16	0.47
F_2	4.26	3.81	0.46

Table 2.38. Variances of parents and F_2's, Chi-square of Bartlett's test for homogeneity and F test of variance ratios between parents and F_2's grown at low density for character; plant total weight (PLTTWT)

	Variances			Bartlett's Chi-square	Variance ratios[1]		
	P_1	P_2	F_2		P_1:P_2	P_1:F_2	P_2:F_2
cross 3 MKR211/9 * MM68/1	91.03	57.70	143.96	22.62***	1.57***	1.58***	2.49***
cross 7 WW15 RVN158/14 * PN28/9	64.49	67.50	144.41	20.98***	1.05NS	2.24***	2.14***
cross 8 WW15RVN158/14 * MM68/1	64.49	57.70	94.23	12.01***	1.11NS	1.46***	1.63***

[1] Larger variance divided by smaller variance.

Table 2.39. Coefficient of skewness values for plant total weight of parents and F_2's grown at low density.

	Coefficient values
cross 3 - F_2 (MKR211/9 * MM68/1)	0.286
cross 7 - F_2 (WW15RVN158/14 * PN28/9)	0.705
cross 8 - F_2 (WW15RVN158/14 * MM68/1)	0.648
parent - MKR211/9	0.801
parent - PN28/9	0.663
parent - WW15RVN158/14	0.589
parent - MM68/1	1.097

Coefficient of skewness for significant difference from zero at the 5% probability level;

= ± 0.280 for sample size of 200 (approximate guide for parents and F_2's at low density).

Table 2.40. Minimum and Maximum values in the parent and F_2 populations of three crosses studied at low density for the character: plant total weight

cross number (low density)	minimum			maximum		
	P_1	P_2	F_2	P_1	P_2	F_2
cross 3 MKR211/9*MM68/1	7.50	5.80	5.07	59.10	56.60	64.52
cross 7 WW15RVN158/14 * PN28/9	9.50	8.42	7.20	49.68	52.88	71.12
cross 8 WW15RVN158/14 * MM68/1	9.50	5.80	2.87	49.68	56.50	56.78

4. Main shoot total weight at low density.

Frequency distributions for this character for parents and hybrids grown at low and crop density are given in Figure 2.15. The F_2's ranges often covered the ranges of the parents. There also was evidence of transgressive segregation and many of the minimum and maximum values in the F_2's were higher and lower respectively than the values in the parental populations (Table 2.43).

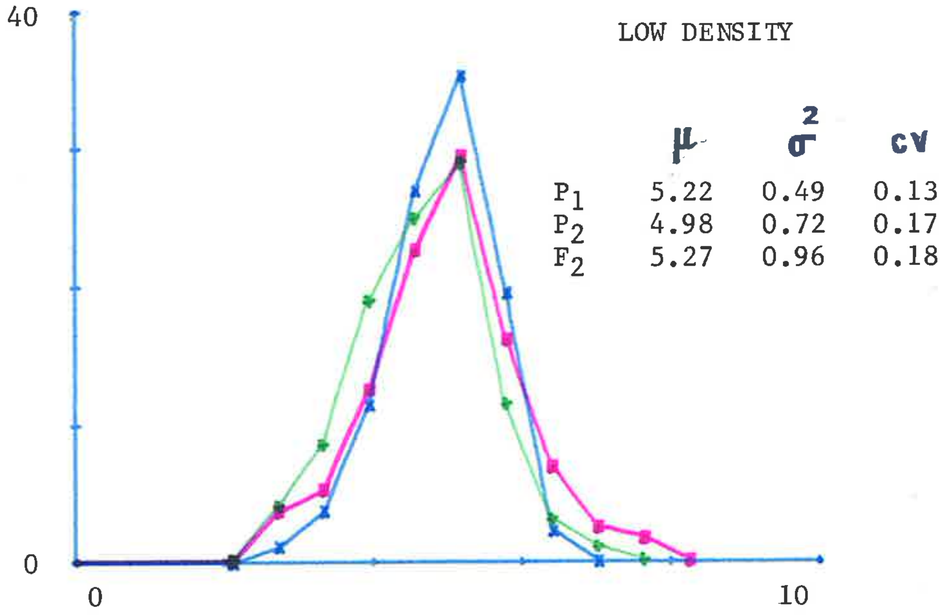
For this character there was a smaller reduction across density than had been found for plant total weight, or head number both of which were strongly affected by competition. It is generally accepted that competition reduces tillering which will in turn reduce head number and plant weight. But with the main shoot, it might have been expected that competition would have had a small, to negligible, effect. It was found in the three crosses that there were reductions from the low to the crop density but these reductions were not of great magnitude when compared with other characters.

The F_2's variances were significantly larger than both the parental variances for all the crosses at low density (Table 2.41). The distributions for this character were either normal or had negative skews (Table 2.42).

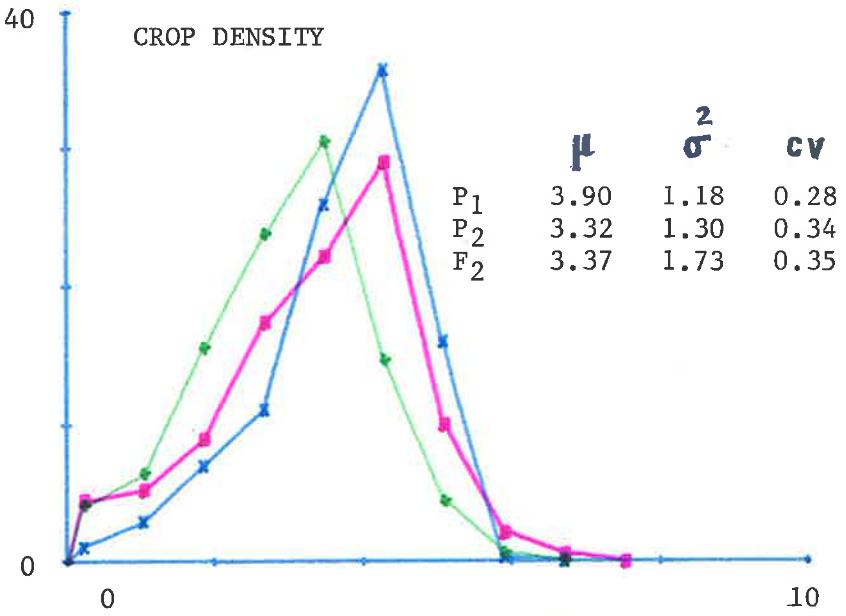
Figure 2.15. Frequency distribution of the main shoot total weight from three crosses studied at low density. The blue and green curves are the parent 1 and parent 2 distributions respectively, and the red curve is the hybrid F_2 distribution.

The X axis represents class intervals and the Y represents the number of plants in each class as a percentage.

MKR 211/9 * MM 68/9

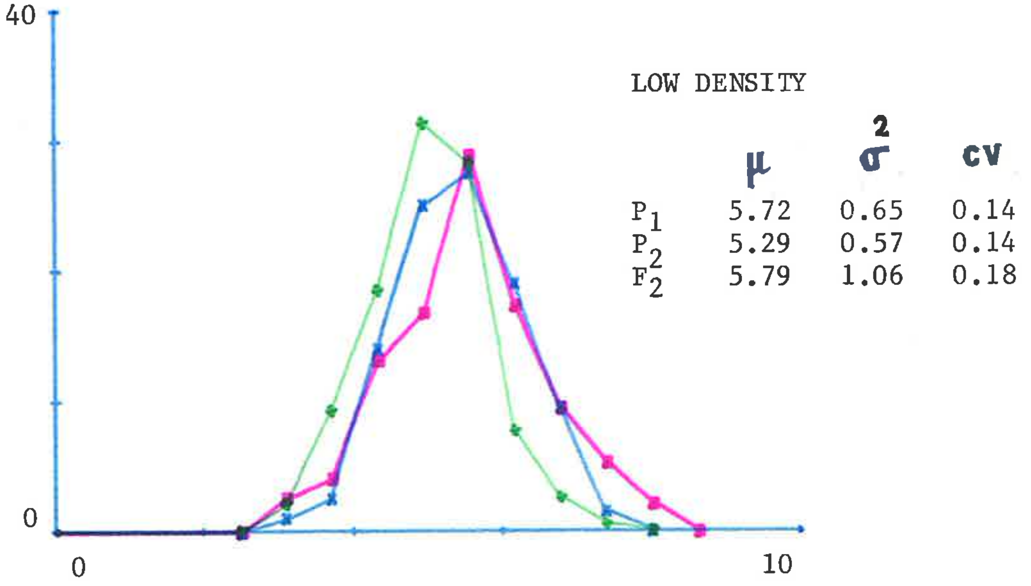

LOW DENSITY

	μ	σ^2	cv
P_1	5.22	0.49	0.13
P_2	4.98	0.72	0.17
F_2	5.27	0.96	0.18

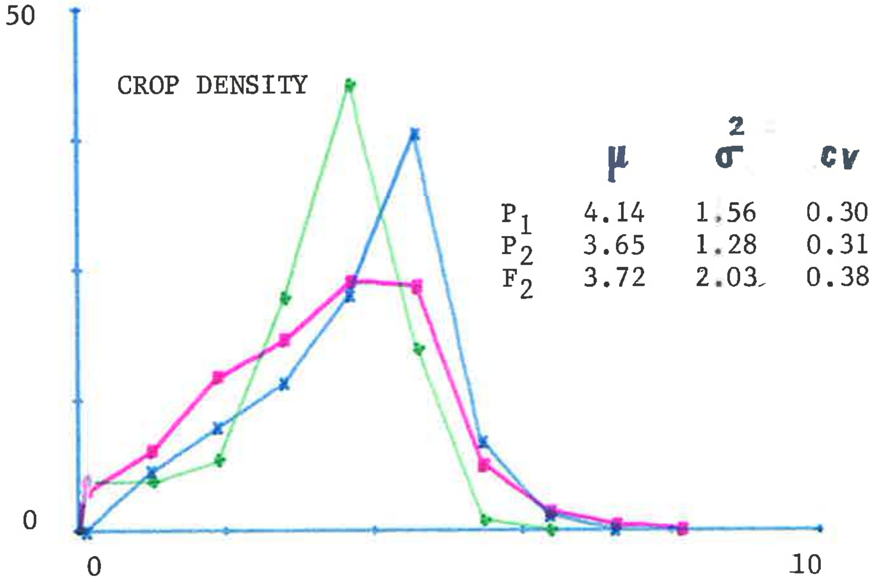

CROP DENSITY

	μ	σ^2	cv
P_1	3.90	1.18	0.28
P_2	3.32	1.30	0.34
F_2	3.37	1.73	0.35

WW-15 RVN 158/14 * PN 28/9


LOW DENSITY

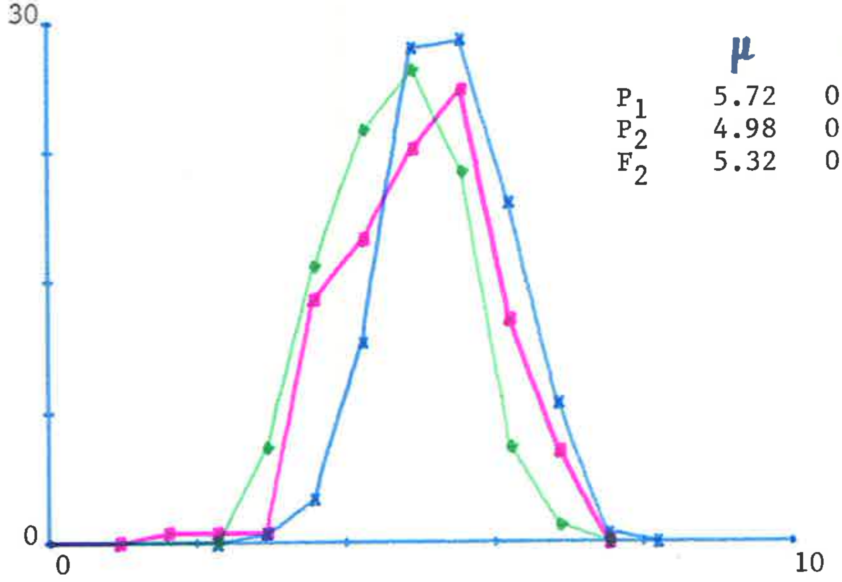
	μ	σ^2	cv
P_1	5.72	0.65	0.14
P_2	5.29	0.57	0.14
F_2	5.79	1.06	0.18


CROP DENSITY

	μ	σ^2	cv
P_1	4.14	1.56	0.30
P_2	3.65	1.28	0.31
F_2	3.72	2.03	0.38

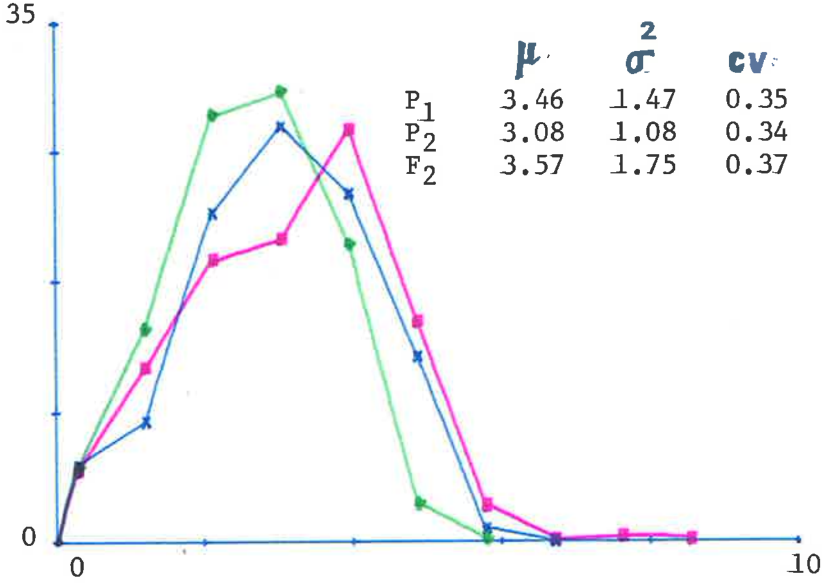
WW-15 RVN 158/14 * MM 68/1

LOW DENSITY



	μ	σ^2	cv
P_1	5.72	0.65	0.14
P_2	4.98	0.72	0.17
F_2	5.32	0.91	0.18

CROP DENSITY



	μ	σ^2	cv
P_1	3.46	1.47	0.35
P_2	3.08	1.08	0.34
F_2	3.57	1.75	0.37

Table 2.41. Variances of parents and F_2's, Chi-square of Bartlett's test for homogeneity and F test of variance ratios between parents and F_2's grown at low density for character; main shoot total weight (MTWT)

	Variances			Bartlett's Chi-square	Variance ratios[1]		
	P_1	P_2	F_2		$P_1:P_2$	$P_1:F_2$	$P_2:F_2$
cross 3 MKR211/9 * MM68/1	0.49	0.72	0.96	14.44***	1.47***	1.96***	1.33***
cross 7 WW15 RVN158/14 * PN28/9	0.65	0.57	1.06	10.97***	1 . 14NS	1.63***	1.86***
cross 8 WW15RVN158/14 * MM68/1	0.65	0.72	0.91	2.96*	1.11NS	1.40***	1.26*

[1] Larger variance divided by smaller variance.

Table 2.42. Coefficient of skewness values for main shoot total weight of parents and F_2's grown at low density.

	Coefficient values
cross 3 - F_2 (MKR211/9 * MM68/1)	0.043
cross 7 - F_2 (WW15RVN158/14 * PN28/9)	0.001
cross 8 - F_2 (WW15RVN158/14 * MM68/1)	-0.395
parent - MKR211/9	-0.498
parent - PN28/9	-0.117
parent - WW15RVN158/14	-0.728
parent - MM68/1	-0.078

Coefficient of skewness for significant difference from zero at the 5% probability level;

= ± 0.280 for sample size of 200 (approximate guide for parents and F_2's at low density).

Table 2.43. Minimum and Maximum values in the parent and F_2 populations of three crosses studied at low density for the character: main shoot total weight

cross number (low density)	minimum			maximum		
	P_1	P_2	F_2	P_1	P_2	F_2
cross 3 MKR211/9*MM68/1	3.05	2.97	2.72	6.86	7.28	8.25
cross 7 WW15RVN158/14 * PN28/9	3.15	3.43	3.08	7.52	7.40	8.61
cross 8 WW15RVN158/14 * MM68/1	3.15	2.97	1.60	7.52	7.28	7.15

5. The main shoot grain weight.

It may be seen from Figure 2.16 that the patterns of the distributions for main shoot grain weight were similar over low and crop density. The F_2's means were intermediate between the parental means except for cross 7, where the differences were small.

The variances present in Table 2.44 showed that only the F_2's variance of cross 7 was larger significantly than both its parental variances. The F_2's variance in cross 3 was significantly different only from parent 1, and in cross 8 the variances were homogeneous. There was also a small difference between the minimum and maximum values in the three populations of the three crosses and only the F_2 of cross 7 had values outside those of its parents (Table 2.46).

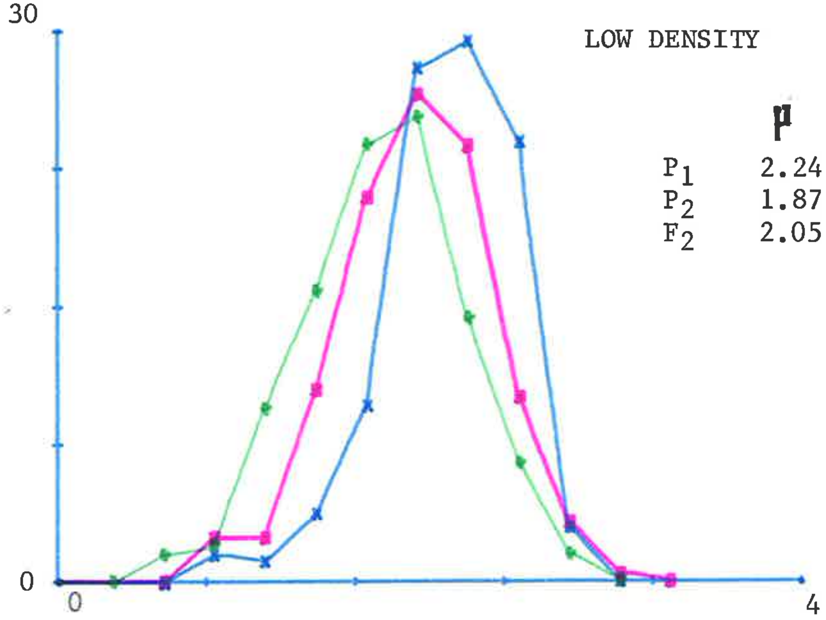
The negative skews obtained for this character at crop density also occurred at low density (Table 2.45).

Figure 2.16. Frequency distribution of the main shoot grain weight for three crosses studied at low density; blue and green curves are parent 1 and parent 2 distributions respectively, the red curve is the hybrid F_2 distribution.

The X axis represents class intervals and the Y represents the number of plants in each class as a percentage.

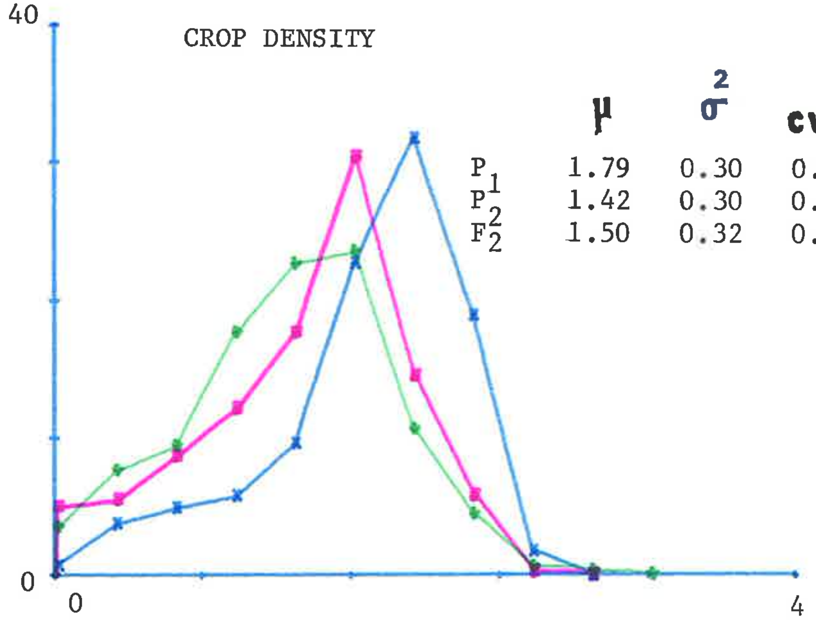
MKR 211/9 * MM 68/1

LOW DENSITY



	μ	σ^2	cv
P_1	2.24	0.12	0.15
P_2	1.87	0.18	0.22
F_2	2.05	0.16	0.19

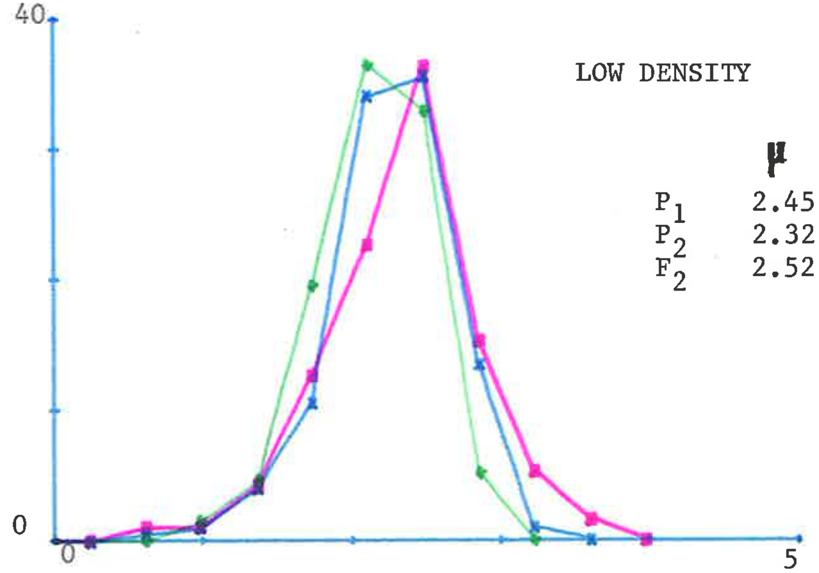
CROP DENSITY



	μ	σ^2	cv
P_1	1.79	0.30	0.31
P_2	1.42	0.30	0.39
F_2	1.50	0.32	0.38

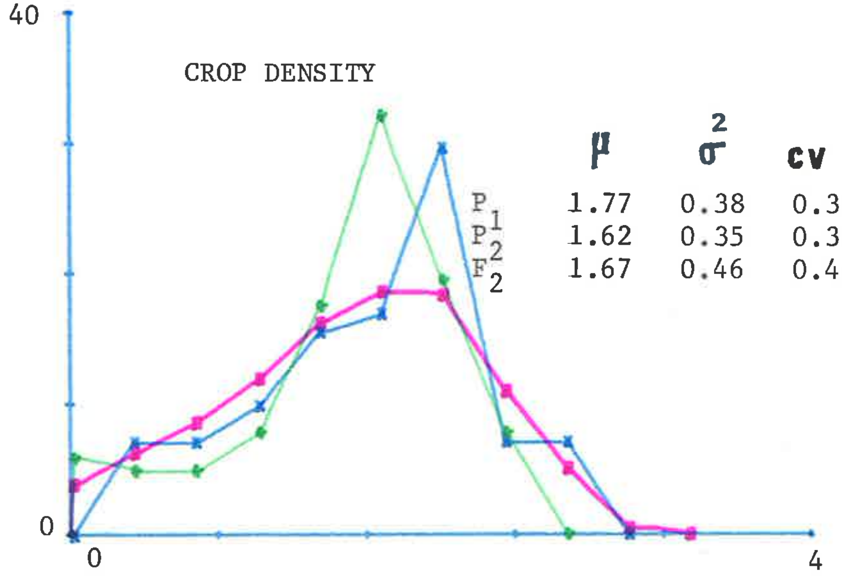
WW-15 RVN 158/14 * PN 28/9

LOW DENSITY



	μ	σ^2	cv
P_1	2.45	0.17	0.17
P_2	2.32	0.12	0.15
F_2	2.52	0.26	0.20

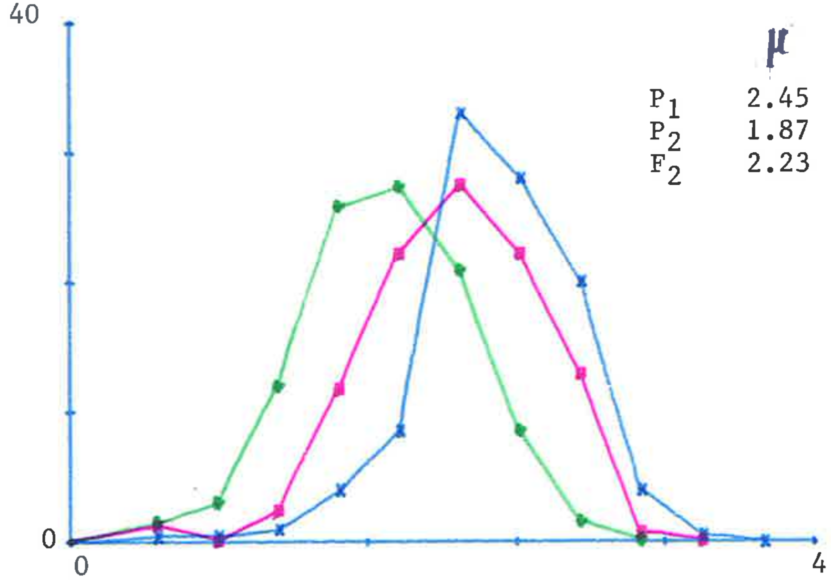
CROP DENSITY



	μ	σ^2	cv
P_1	1.77	0.38	0.35
P_2	1.62	0.35	0.37
F_2	1.67	0.46	0.41

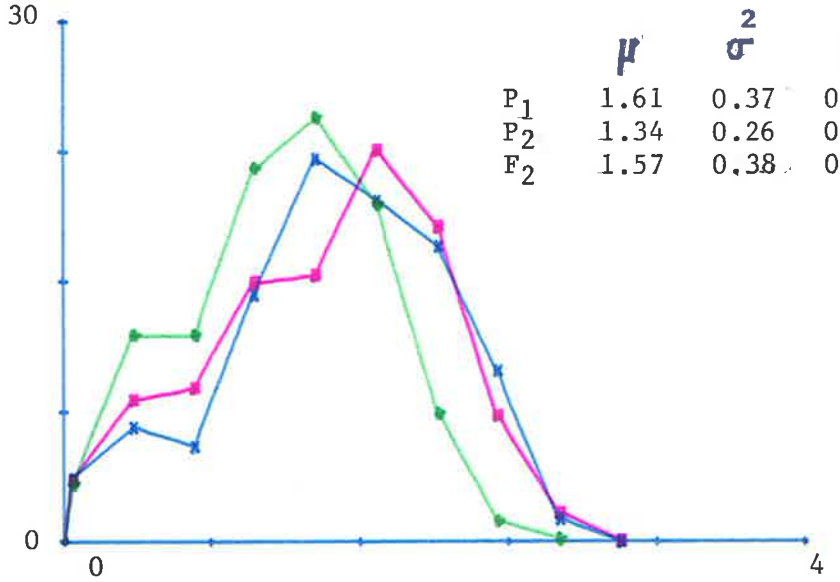
WW-15 RVN 158/14 * MM 68/1

LOW DENSITY



	μ	σ^2	cv
P_1	2.45	0.17	0.17
P_2	1.87	0.18	0.22
F_2	2.23	0.20	0.20

CROP DENSITY



	μ	σ^2	cv
P_1	1.61	0.37	0.38
P_2	1.34	0.26	0.38
F_2	1.57	0.38	0.39

Table 2.44. Variances of parents and F_2's, Chi-square of Bartlett's test for homogeneity and F test of variance ratios between parents and F_2's grown at low density for character; main shoot grain weight (MGRWT)

	Variances			Bartlett's Chi-square	Variance ratios[1]		
	P_1	P_2	F_2		$P_1:P_2$	$P_1:F_2$	$P_2:F_2$
cross 3 MKR211/9 * MM68/1	0.12	0.18	0.16	5.50***	1.50***	1.33*	1.13NS
cross 7 WW15 RVN158/14 * PN28/9	0.17	0.12	0.26	13.57***	1.42*	1.53***	2.17***
cross 8 WW15RVN158/14 * MM68/1	0.17	0.18	0.20	1.05NS	1.06NS	1.18NS	1.11NS

[1] Larger variance divided by smaller variance.

Table 2.45. Coefficient of skewness values for main shoot grain weight of parents and F_2's grown at low density.

	Coefficient values
cross 3 - F_2 (MKR211/9 * MM68/1)	-0.317
cross 7 - F_2 (WW15RVN158/14 * PN28/9)	-0.454
cross 8 - F_2 (WW15RVN158/14 * MM68/1)	-0.667
parent - MKR211/9	-0.831
parent - PN28/9	-0.419
parent - WW15RVN158/14	-0.854
parent - MM68/1	-0.229

Coefficient of skewness for significant difference from zero at the 5% probability level;

= ± 0.280 for sample size of 200 (approximate guide for parents and F_2's at low density).

Table 2.46. Minimum and Maximum values in the parent and F_2 populations of three crosses studied at low density for the character: main shoot grain weight

cross number (low density)	minimum			maximum		
	P_1	P_2	F_2	P_1	P_2	F_2
cross 3 MKR211/9*MM68/1	0.99	0.57	0.92	2.90	2.90	3.02
cross 7 WW15RVN158/14 * PN28/9	0.70	1.23	0.61	3.40	3.17	3.97
cross 8 WW15RVN158/14 * MM68/1	0.70	0.57	0.47	3.40	2.90	3.18

6. Main shoot grain number.

As expected with these characters and the material in this study the patterns obtained for grain number (Fig. 2.17) were similar to those obtained above for the main shoot grain weight (the correlation coefficient between them ranged from 0.613*** to 0.871***). The F_2's variances were not larger than the parental variances (Table 2.47). The F_2 of cross 7 which had a significantly larger variance than its parents for the main shoot grain weight, did not have a larger variance for grain number. The F_2's means were in general intermediate between the parental means, which is suggestive of additive genetic effects.

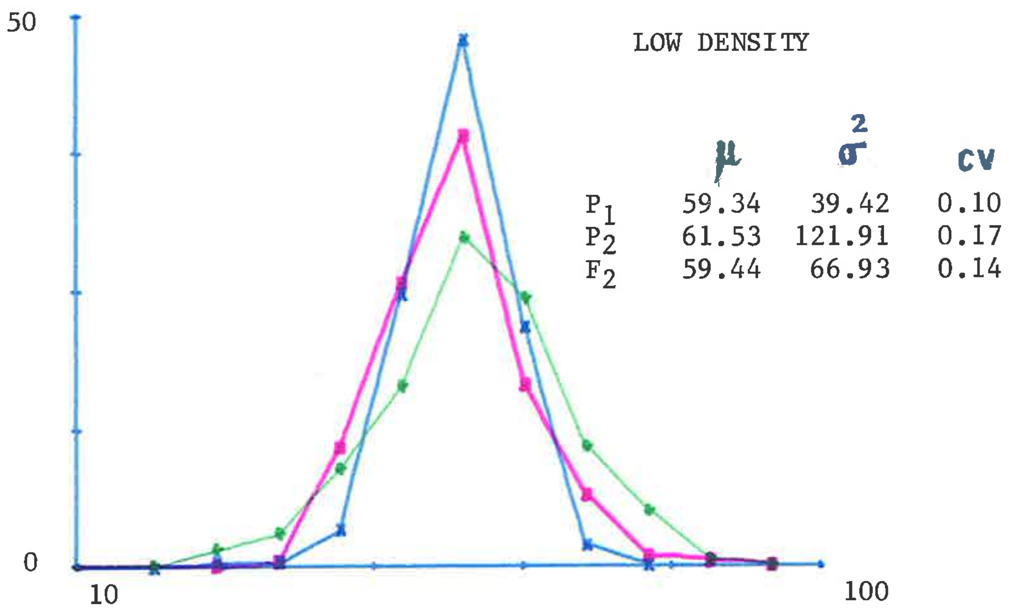
The minimum and maximum values showed that only in the F_2 of cross 8 did values exceed those of the parents (Table 2.49).

Negative skews were obtained for most distributions (Table 2.48) but these were not as pronounced as at crop density.

Figure 2.17. Frequency distribution of the main shoot grain number from three crosses studied at low density; blue and green curves are the parent 1 and parent 2 distributions respectively, the red curve is the hybrid F_2 distribution.

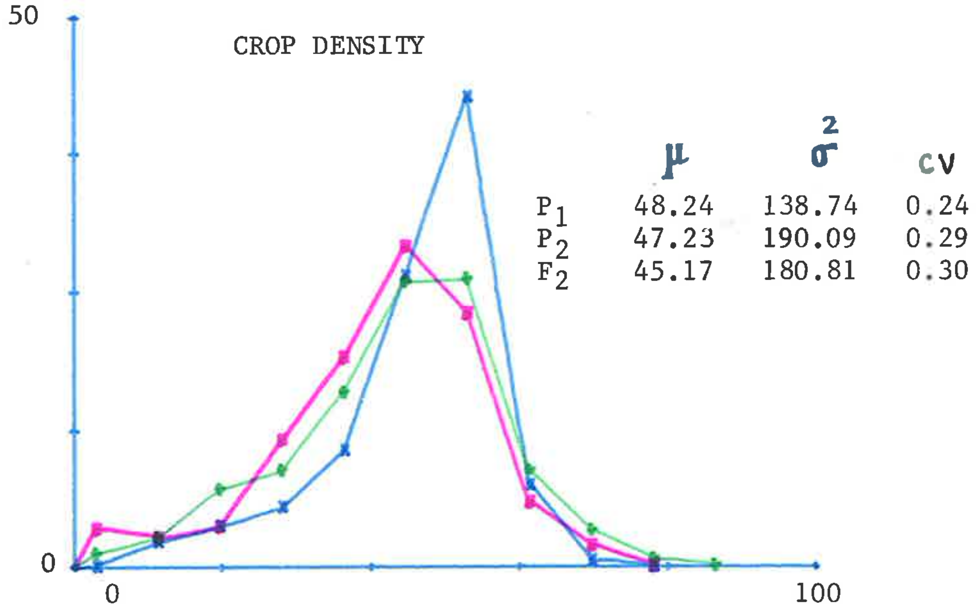
The X axis represents class intervals and the Y represents the number of plants in each class as a percentage.

MKR 211/9 * MM 68/1



LOW DENSITY

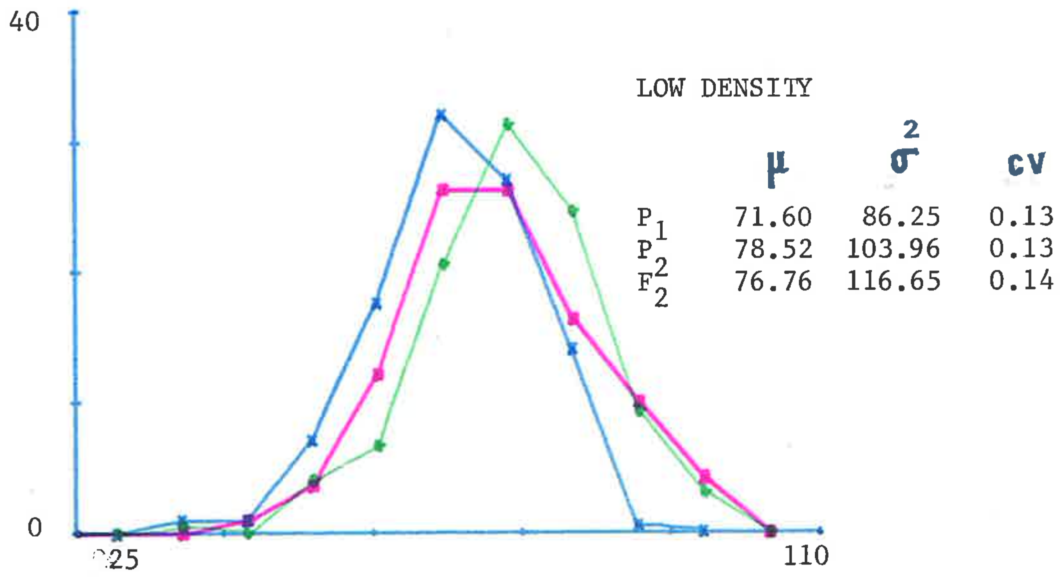
	μ	σ^2	cv
P_1	59.34	39.42	0.10
P_2	61.53	121.91	0.17
F_2	59.44	66.93	0.14



CROP DENSITY

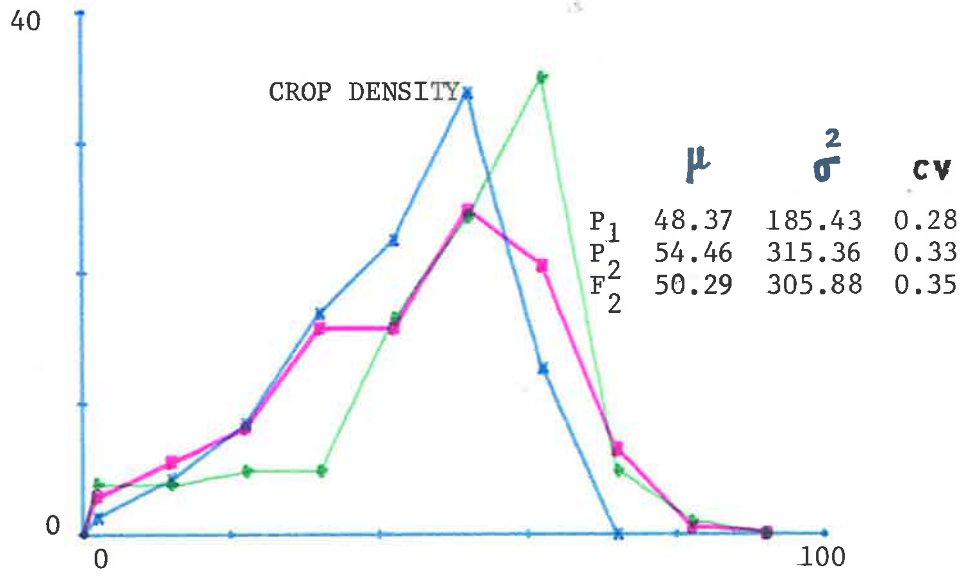
	μ	σ^2	cv
P_1	48.24	138.74	0.24
P_2	47.23	190.09	0.29
F_2	45.17	180.81	0.30

WW-15 RVN 158/14 * PN 28/9



LOW DENSITY

	μ	σ^2	cv
P_1	71.60	86.25	0.13
P_2	78.52	103.96	0.13
F_2	76.76	116.65	0.14

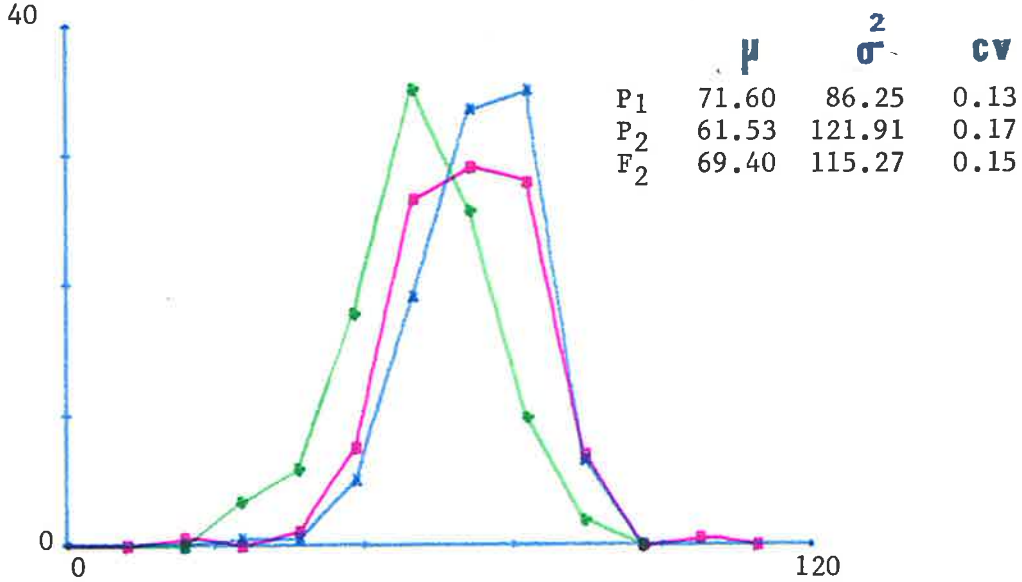


CROP DENSITY

	μ	σ^2	cv
P_1	48.37	185.43	0.28
P_2	54.46	315.36	0.33
F_2	50.29	305.88	0.35

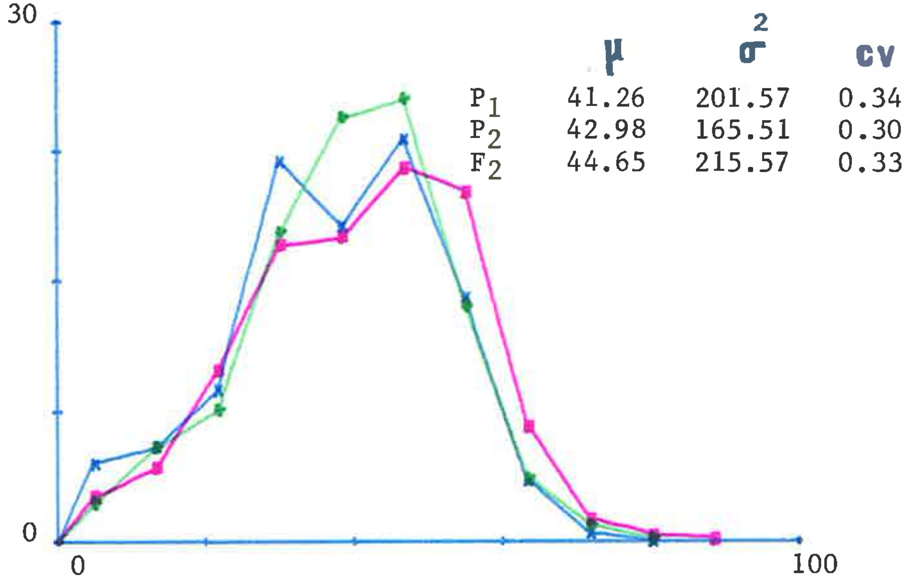
WW-15 RVN 158/14 * MM 68/1

LOW DENSITY



	μ	σ^2	cv
P_1	71.60	86.25	0.13
P_2	61.53	121.91	0.17
F_2	69.40	115.27	0.15

CROP DENSITY



	μ	σ^2	cv
P_1	41.26	201.57	0.34
P_2	42.98	165.51	0.30
F_2	44.65	215.57	0.33

Table 2.47. Variances of parents and F_2's, Chi-square of Bartlett's test for homogeneity and F test of variance ratios between parents and F_2's grown at low density for character; main shoot grain number

	Variances			Bartlett's Chi-square	Variance ratios[1]		
	P_1	P_2	F_2		P_1:P_2	P_1:F_2	P_2:F_2
cross 3 MKR211/9 * MM68/1	39.42	121.91	66.93	37.41***	3.09***	1.70***	1.82***
cross 7 WW15 RVN158/14 * PN28/9	86.25	103.96	116.65	2.23NS	1.21NS	1.35*	1.12NS
cross 8 WW15RVN158/14 * MM68/1	86.25	121.91	115.27	3.30*	1.41*	1.34*	1.05NS

[1] Larger variance divided by smaller variance.

Table 2.48. Coefficient of skewness values for main shoot grain number of parents and F_2's grown at low density.

	Coefficient values
cross 3 - F_2 (MKR211/9 * MM68/1)	0.466
cross 7 - F_2 (WW15RVN158/14 * PN28/9)	0.066
cross 8 - F_2 (WW15RVN158/14 * MM68/1)	-0.612
parent - MKR211/9	-0.759
parent - PN28/9	-0.334
parent - WW15RVN158/14	-0.642
parent - MM68/1	-0.346

Coefficient of skewness for significant difference from zero at the 5% probability level;

= ± 0.280 for sample size of 200 (approximate guide for parents and F_2's at low density).

Table 2.49. Minimum and Maximum values in the parent and F_2 populations of three crosses studied at low density for the character: main shoot grain number

cross number (low density)	minimum			maximum		
	P_1	P_2	F_2	P_1	P_2	F_2
cross 3 MKR211/9*MM68/1	27	29	40	73	88	94
cross 7 WW15RVN158/14 * PN28/9	37	40	45	90	100	104
cross 8 WW15RVN158/14 * MM68/1	37	29	19	90	88	102

7. Tiller grain weight at low density.

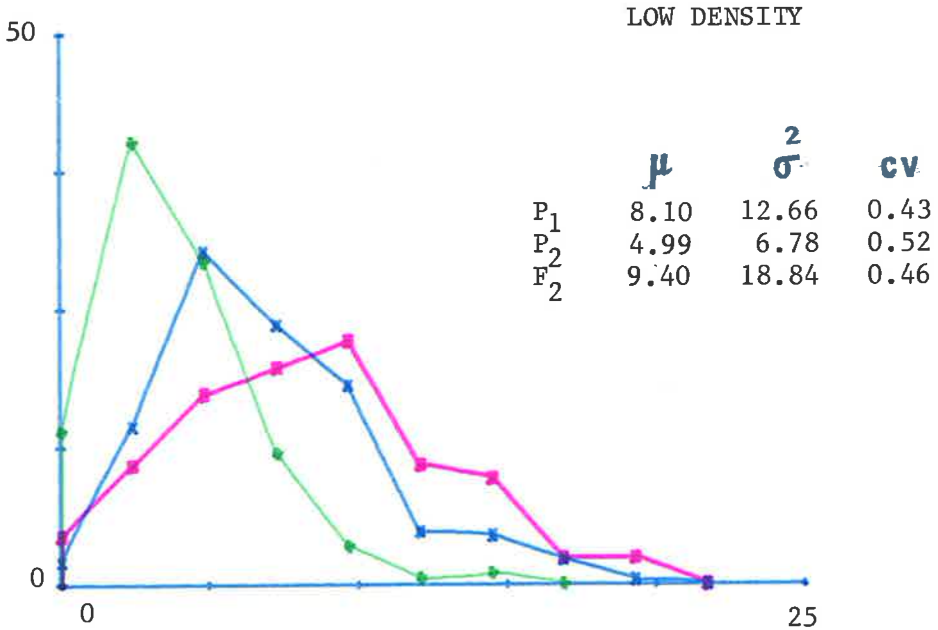
At low density the yields of the plants were determined mainly by the production of the tillers, and in this experiment 80 percent of the total grain weight was borne by the tillers. In contrast, at crop density in experiment 1 only 30 percent of total grain weight came from the tillers. This is one of the reasons for the failure of single plant selection for yield at low density to provide high yielding genotypes at crop density. At low density, genotypes with a high tillering ability will be selected and this ability will not confer high yield at crop density.

Frequency distributions for tiller grain weight are given in Figure 2.18. They show that the F_2's ranges in general covered the combined ranges of the parental distributions. Their means were higher than the respective parental means and this was clear evidence of heterosis. In contrast there was no such clear evidence at crop density. Transgressive segregation also was more evident at low density.

For all the crosses at low density, the F_2's had a larger variance than the variances of the parents (Table 2.50). This was related however to the high values of the F_2 as the CV's were not very different (Figure 2.18). With regard to the minimum and maximum values, the F_2's showed the lowest minimum values and with one exception the maximum values (Table 2.52).

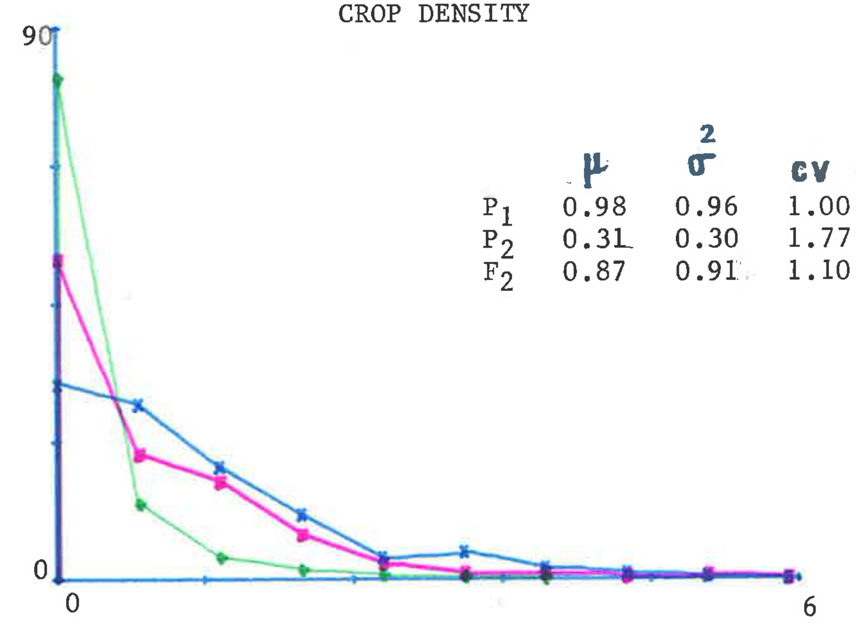
Large positive skews in the distributions were again obtained for this character (Table 2.51). One obvious difference was that at crop density there were many plants with a zero yield from the tillers whereas at low density few plants fell into the zero class.

Figure 2.18. Frequency distribution of the tiller grain weight from three crosses studied at low density; blue and green curves represent the parent 1 and parent 2 distributions respectively, the red represents the hybrid F_2 distribution.
The X axis represents class intervals and the Y represents the number of plants in each class as a percentage.



LOW DENSITY

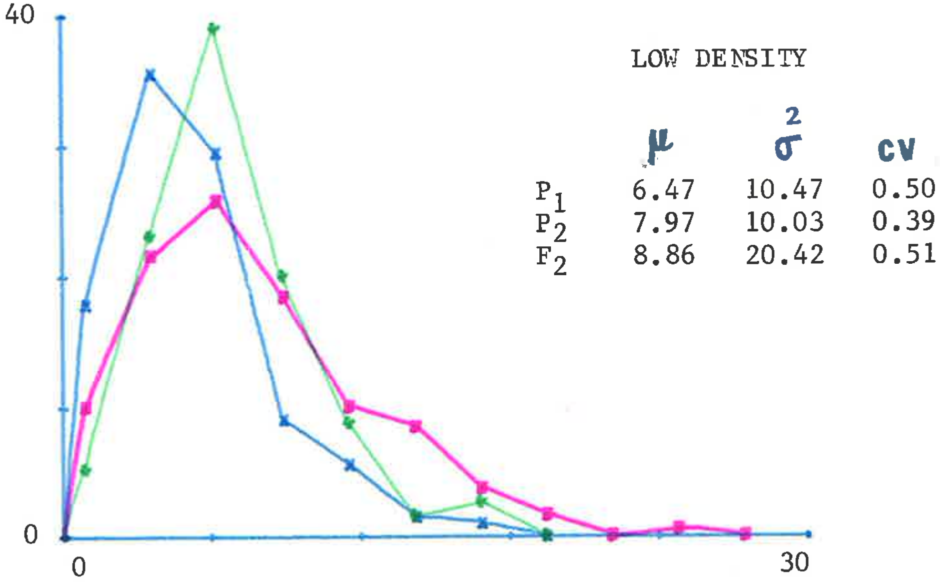
	μ	σ^2	cv
P_1	8.10	12.66	0.43
P_2	4.99	6.78	0.52
F_2	9.40	18.84	0.46



CROP DENSITY

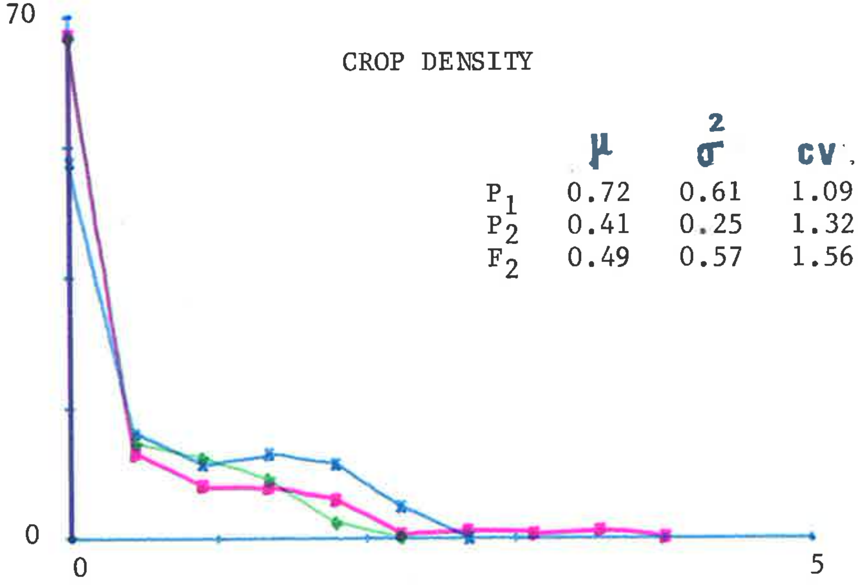
	μ	σ^2	cv
P_1	0.98	0.96	1.00
P_2	0.31	0.30	1.77
F_2	0.87	0.91	1.10

WW-15 RVN 158/14 * PN 28/9



LOW DENSITY

	μ	σ^2	cv
P_1	6.47	10.47	0.50
P_2	7.97	10.03	0.39
F_2	8.86	20.42	0.51

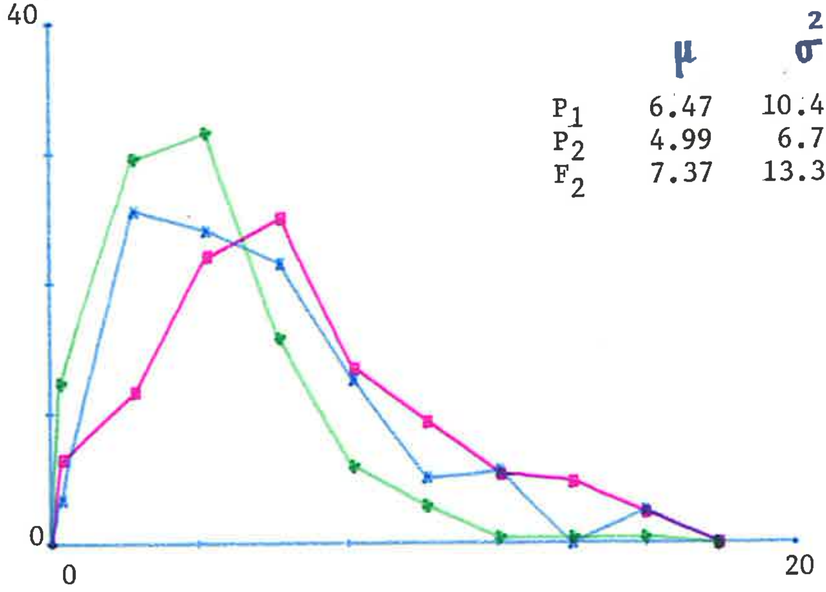


CROP DENSITY

	μ	σ^2	cv
P_1	0.72	0.61	1.09
P_2	0.41	0.25	1.32
F_2	0.49	0.57	1.56

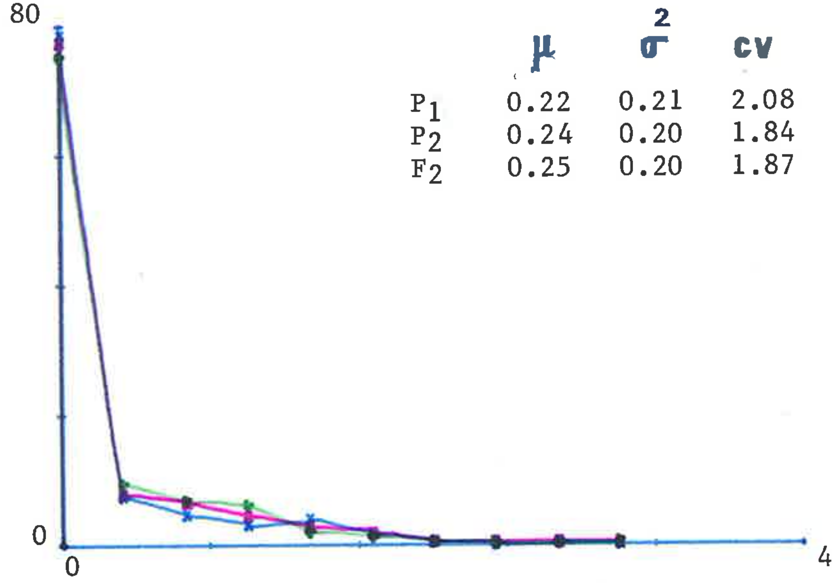
WW-15 RVN 158/14 * MM 68/1

LOW DENSITY



	μ	σ^2	cv
P_1	6.47	10.47	0.50
P_2	4.99	6.78	0.51
F_2	7.37	13.30	0.49

CROP DENSITY



	μ	σ^2	cv
P_1	0.22	0.21	2.08
P_2	0.24	0.20	1.84
F_2	0.25	0.20	1.87

Table 2.50. Variances of parents and F_2's, Chi-square of Bartlett's test for : homogeneity and F test of variance ratios between parents and F_2's grown at low density for character; tiller grain weight

	Variances			Bartlett's Chi-square	Variance ratios[1]		
	P_1	P_2	F_2		$P_1:P_2$	$P_1:F_2$	$P_2:F_2$
cross 3 MKR211/9 * MM68/1	12.66	6.78	18.84	27.02***	1.86***	1.49***	2.77***
cross 7 WW15 RVN158/14 * PN28/9	10.47	10.03	20.42	16.14***	1.04NS	1.95***	2.04***
cross 8 WW15RVN158/14 * MM68/1	10.47	6.78	13.30	10.62***	1.54***	1.27NS	1.96***

[1] Larger variance divided by smaller variance.

Table 2.51. Coefficient of skewness values for tiller grain weight of parents and F_2's grown at low density.

	Coefficient values
cross 3 - F_2 (MKR211/9 * MM68/1)	0.318
cross 7 - F_2 (WW15RVN158/14 * PN28/9)	0.772
cross 8 - F_2 (WW15RVN158/14 * MM68/1)	0.599
parent - MKR211/9	0.837
parent - PN28/9	0.784
parent - WW15RVN158/14	1.074
parent - MM68/1	1.199

Coefficient of skewness for significant difference from zero at the 5% probability level;

= ± 0.280 for sample size of 200 (approximate guide for parents and F_2's at low density).

Table 2.52. Minimum and Maximum values in the parent and F_2 populations of three crosses studied at low density for the character: tiller grain weight

cross number (low density)	minimum			maximum		
	P_1	P_2	F_2	P_1	P_2	F_2
cross 3 MKR211/9*MM68/1	0.88	0.56	0.00	21.68	16.80	21.10
cross 7 WW15RVN158/14 * PN28/9	0.92	1.05	0.93	17.45	19.08	24.74
cross 8 WW15RVN158/14 * MM68/1	0.92	0.56	0.31	17.45	16.80	17.92

8. Tiller grain number at low density.

The results for grain number on the tillers closely reflect those obtained for tiller grain weight. At low density the plants produced 10 to 15 times as much grain from the tillers as at crop density (Figure 2.19). The F_2 means were higher than their parental means and transgressive segregation was evident.

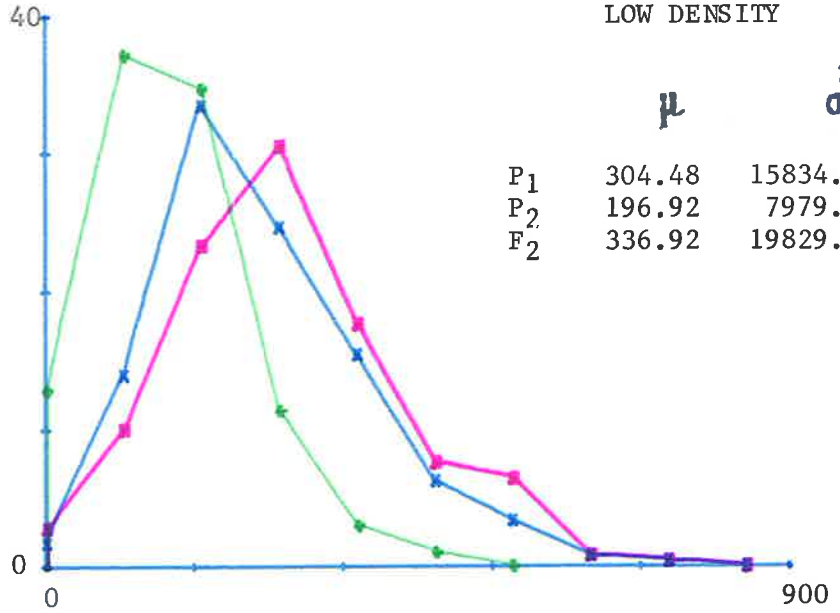
From Table 2.53 it will be seen that the F_2 variances of crosses 7 and 8 were significantly larger than their parental variances. The minimum and maximum values for the F_2 were more extreme than for the parents (Table 2.55).

Positive skews were obtained for this character (Table 2.54) but again there were differences across density and there were fewer values in the zero class at low density.

Figure 2.19. Frequency distribution of the tiller grain number from three crosses studied at low density; blue and green curves are the parent 1 and parent 2 distributions respectively, the red is the hybrid F_2 distribution.

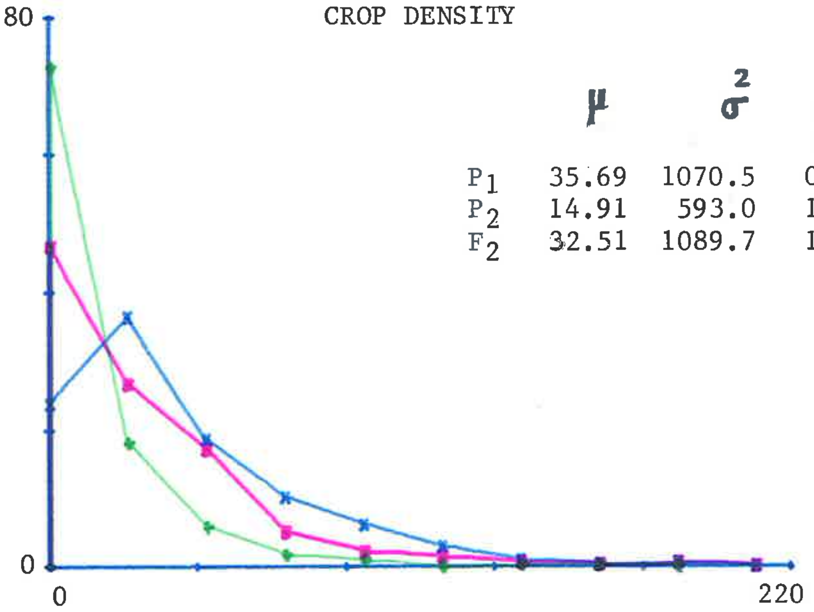
The X axis represents class intervals and the Y represents the number of plants in each class as a percentage.

LOW DENSITY



	μ	σ^2	cv
P_1	304.48	15834.4	0.41
P_2	196.92	7979.9	0.45
F_2	336.92	19829.4	0.42

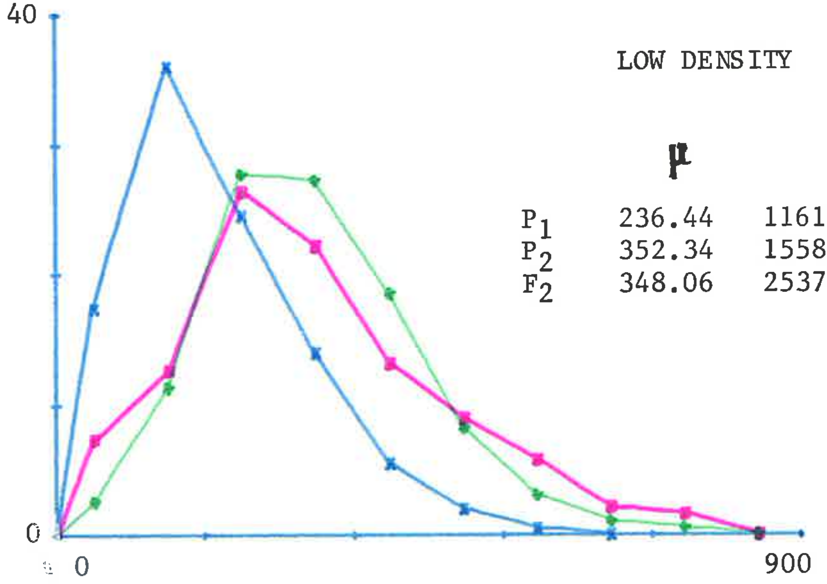
CROP DENSITY



	μ	σ^2	cv
P_1	35.69	1070.5	0.92
P_2	14.91	593.0	1.63
F_2	32.51	1089.7	1.02

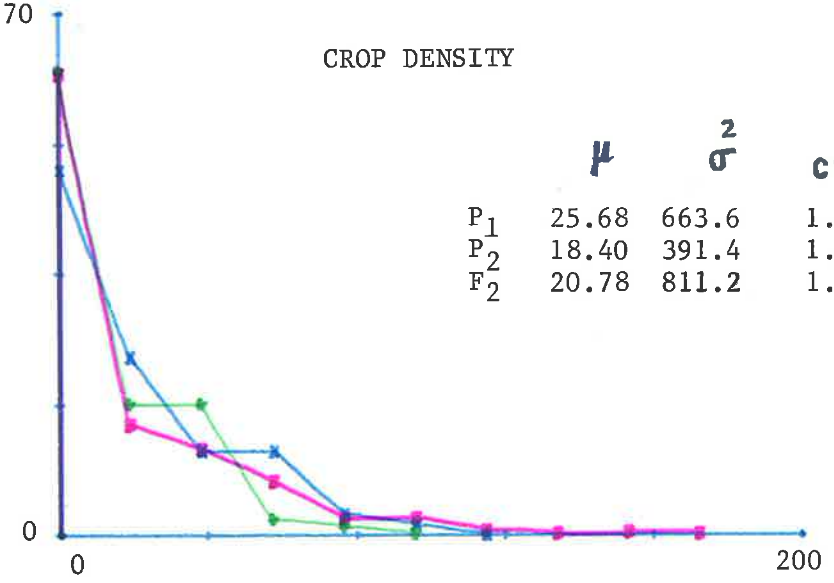
WW-15 RVN 158/14 * PN 28/9

LOW DENSITY



	μ	σ^2	cv
P_1	236.44	11619.1	0.46
P_2	352.34	15588.6	0.35
F_2	348.06	25370.4	0.46

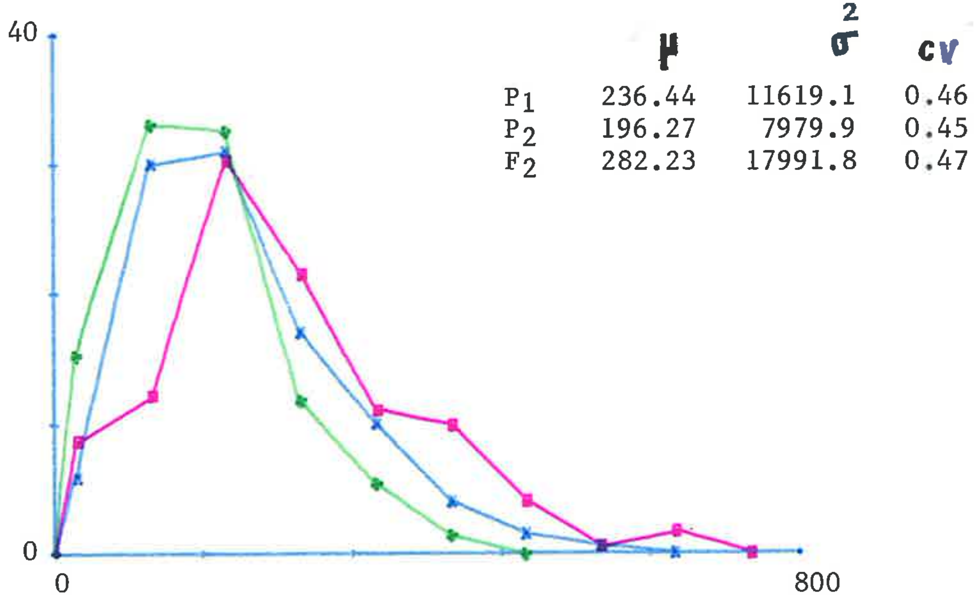
CROP DENSITY



	μ	σ^2	cv
P_1	25.68	663.6	1.00
P_2	18.40	391.4	1.08
F_2	20.78	811.2	1.37

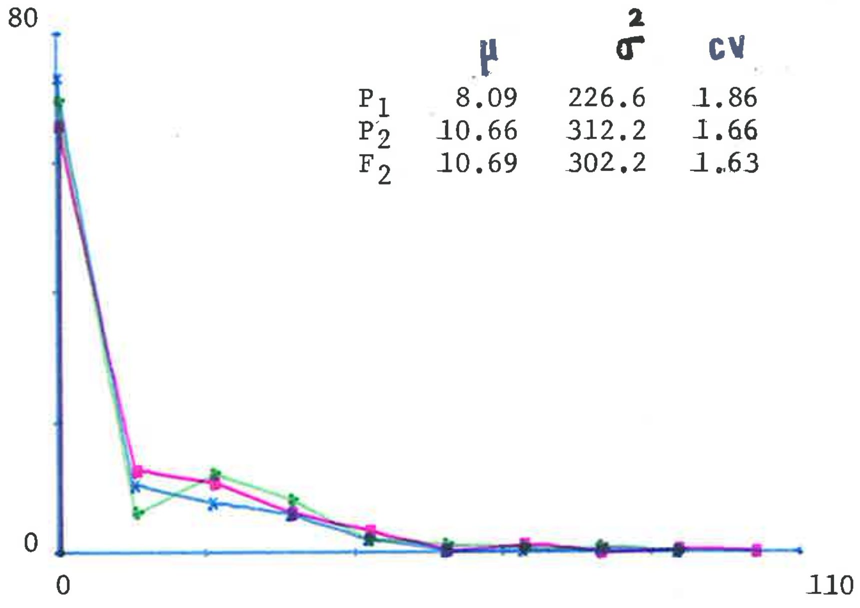
WW-15 RVN 158/14 * MM 68/1

LOW DENSITY



	μ	σ^2	cv
P_1	236.44	11619.1	0.46
P_2	196.27	7979.9	0.45
F_2	282.23	17991.8	0.47

CROP DENSITY



	μ	σ^2	cv
P_1	8.09	226.6	1.86
P_2	10.66	312.2	1.66
F_2	10.69	302.2	1.63

Table 2.53. Variances of parents and F_2's, Chi-square of Bartlett's test for homogeneity and F test of variance ratios between parents and F_2's grown at low density for character; tiller grain number

	Variances			Bartlett's Chi-square	Variance ratios[1]		
	P_1	P_2	F_2		$P_1:P_2$	$P_1:F_2$	$P_2:F_2$
cross 3 MKR211/9 * MM68/1	15834.4	7917.8	19828.4	21.87***	2.00***	1.25NS	2.50***
cross 7 WW15 RVN158/14 * PN28/9	11619.1	15588.6	25370.4	15.30***	1.34*	2.18***	1.63***
cross 8 WW15RVN158/14 * MM68/1	11619.1	7917.8	17991.8	15.35***	1.47***	1.55***	2.27***

[1] Larger variance divided by smaller variance.

Table 2.54. Coefficient of skewness values for tiller grain number of parents and F_2's grown at low density.

	Coefficient values
cross 3 - F_2 (MKR211/9 * MM68/1)	0.381
cross 7 - F_2 (WW15RVN158/14 * PN28/9)	0.612
cross 8 - F_2 (WW15RVN158/14 * MM68/1)	0.744
parent - MKR211/9	0.779
parent - PN28/9	0.561
parent - WW15RVN158/14	0.915
parent - MM68/1	0.614

Coefficient of skewness for significant difference from zero at the 5% probability level;

= ± 0.280 for sample size of 200 (approximate guide for parents and F_2's at low density).

Table 2.55. Minimum and Maximum values in the parent and F_2 populations of three crosses studied at low density for the character: tiller grain number

cross number (low density)	minimum			maximum		
	P_1	P_2	F_2	P_1	P_2	F_2
cross 3 MKR211/9*MM68/1	34	34	00	785	482	846
cross 7 WW15RVN158/14 * PN28/9	62	92	46	616	824	847
cross 8 WW15RVN158/14 * MM68/1	62	34	24	616	482	746

9. Total grain weight per plant at low density.

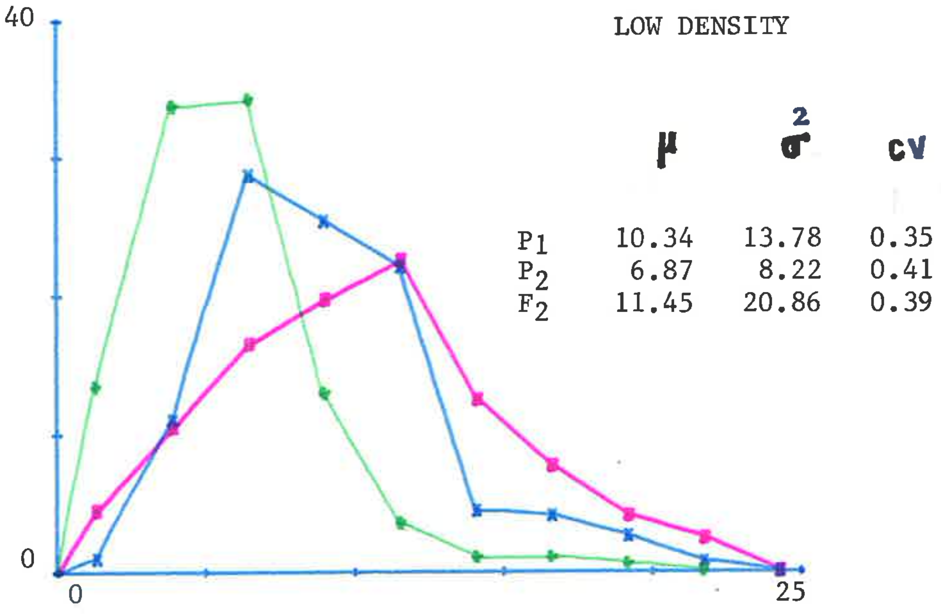
As total grain weight is a summation of main shoot grain weight and tiller grain weight and because tiller grain weight was so much greater at low density it is understandable that large differences in total grain weight were obtained across the two densities (Figure 2.20). Hybrid vigour was obtained at low density whereas at high density the F_2's means never exceeded the top parent. It will be realised that, for low density, of the two components of total plant yield, the main shoot mean yield did not show heterosis over the higher parent whereas the mean yield of the tillers of the F_2 were clearly heterotic. At high density there was no clear evidence of a heterotic effect among the tillers and none was apparent for the total grain weight.

The range of the F_2's distributions covered the combined ranges of the two parents and the F_2's had minimum and maximum values which exceeded the parents (Table 2.58). Table 2.56 contains the variances for this character at low density. The F_2's had variances significantly larger than the parents. However, the high variances in the F_2's were associated with high mean values and the CV's of the three populations showed small differences.

Positive skews were obtained (Table 2.57). These result from the summation of a main shoot distribution that was negative and a tiller distribution that was positive.

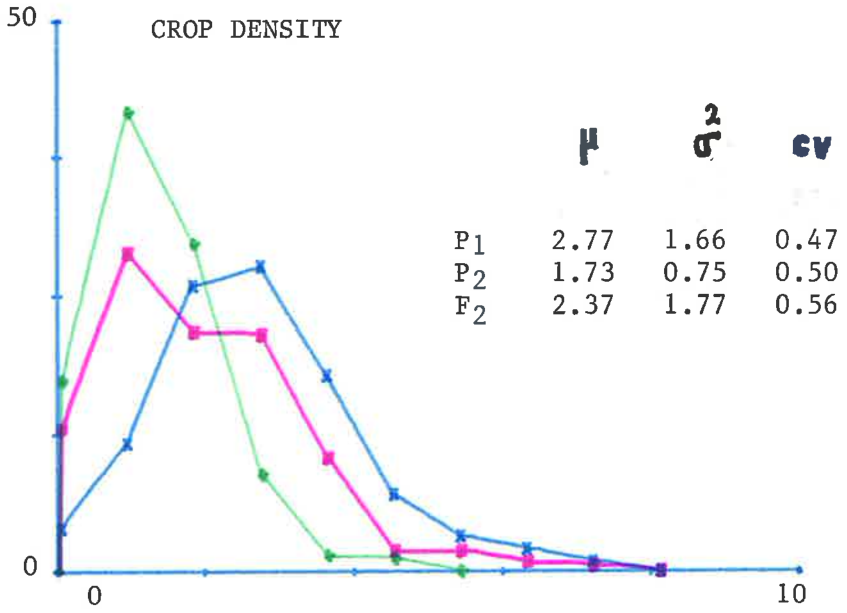
Figure 2.20. Frequency distribution of the total grain weight from three crosses studied at low density; blue and green curves represent the parent 1 and parent 2 distributions respectively, the red represents the hybrid F_2 distribution.
The X axis represents class intervals and the Y represents the number of plants in each class as a percentage.

MKR 211/9 * MM 68/1



LOW DENSITY

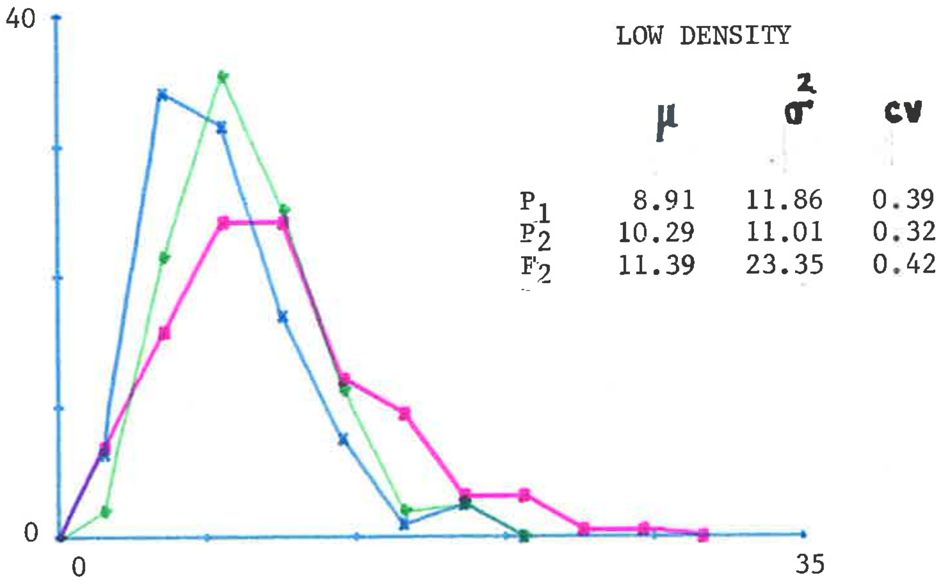
	μ	σ^2	CV
P_1	10.34	13.78	0.35
P_2	6.87	8.22	0.41
F_2	11.45	20.86	0.39



CROP DENSITY

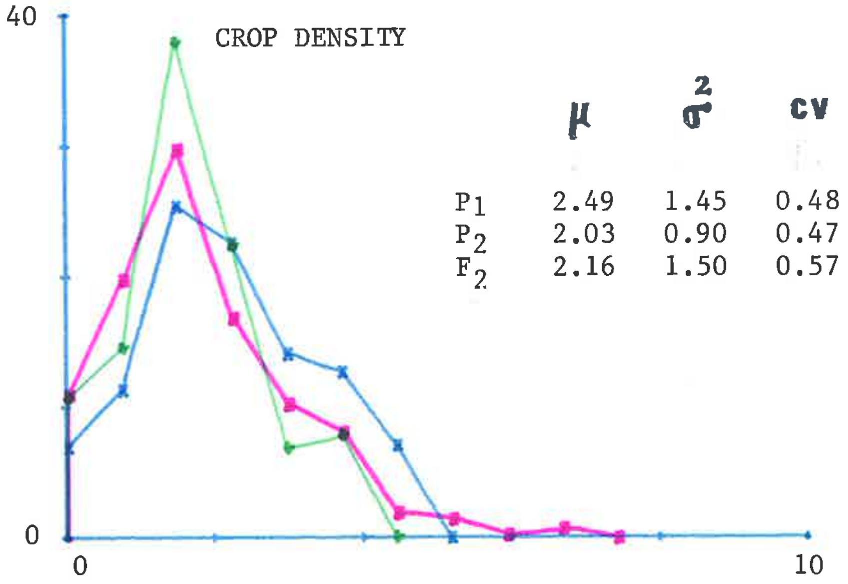
	μ	σ^2	CV
P_1	2.77	1.66	0.47
P_2	1.73	0.75	0.50
F_2	2.37	1.77	0.56

WW-15 RVN 158/14 * PN 28/9



LOW DENSITY

	μ	σ^2	CV
P_1	8.91	11.86	0.39
P_2	10.29	11.01	0.32
F_2	11.39	23.35	0.42

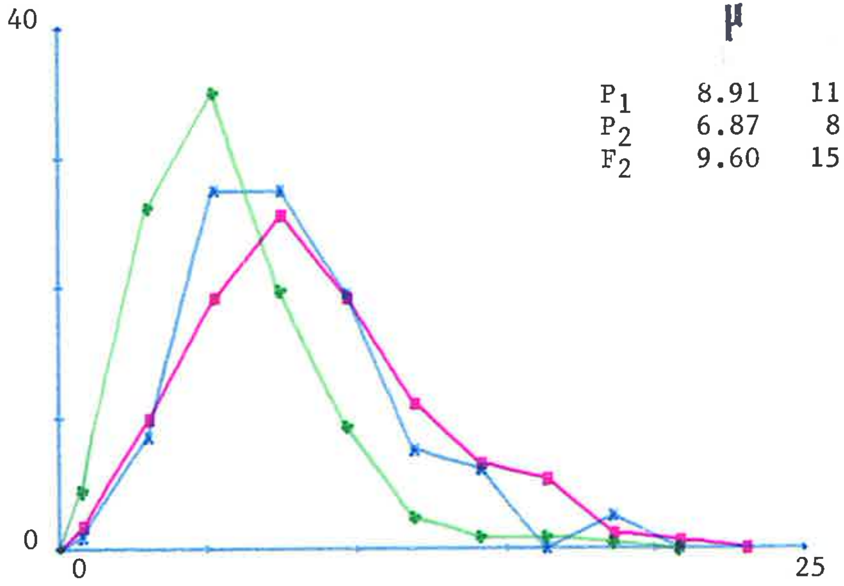


CROP DENSITY

	μ	σ^2	CV
P_1	2.49	1.45	0.48
P_2	2.03	0.90	0.47
F_2	2.16	1.50	0.57

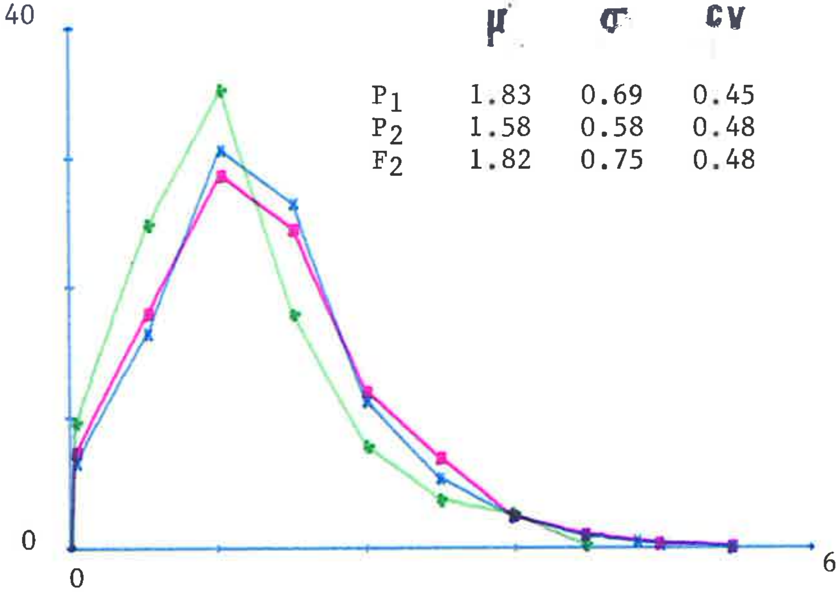
WW-15 RVN 158/14 * MM 68/1

LOW DENSITY



	μ	σ^2	cv
P_1	8.91	11.86	0.39
P_2	6.87	8.22	0.41
F_2	9.60	15.13	0.40

CROP DENSITY



	μ	σ^2	cv
P_1	1.83	0.69	0.45
P_2	1.58	0.58	0.48
F_2	1.82	0.75	0.48

Table 2.56. Variances of parents and F_2's, Chi-square of Bartlett's test for homogeneity and F test of variance ratios between parents and F_2's grown at low density for character; the total grain weight

	Variances			Bartlett's Chi-square	Variance ratios[1]		
	P_1	P_2	F_2		$P_1:P_2$	$P_1:F_2$	$P_2:F_2$
cross 3 MKR211/9 * MM68/1	13.78	8.22	20.86	20.04***	1.67***	1.51***	2.54***
cross 7 WW15 RVN158/14 * PN28/9	11.86	11.01	23.35	17.42***	1.07NS	1.96***	2.12***
cross 8 WW15RVN158/14 * MM68/1	11.86	8.22	15.13	8.65***	1.44***	1.27*	1.84***

[1] Larger variance divided by smaller variance.

Table 2.57. Coefficient of skewness values for the total grain weight of parents and F_2's grown at low density.

	Coefficient values
cross 3 - F_2 (MKR211/9 * MM68/1)	0.262
cross 7 - F_2 (WW15RVN158/14 * PN28/9)	0.667
cross 8 - F_2 (WW15RVN158/14 * MM68/1)	0.497
parent - MKR211/9	0.772
parent - PN28/9	0.728
parent - WW15RVN158/14	0.972
parent - MM68/1	1.078

Coefficient of skewness for significant difference from zero at the 5% probability level;

= ± 0.280 for sample size of 200 (approximate guide for parents and F_2's at low density).

Table 2.58. Minimum and Maximum values in the parent and F_2 populations of three crosses studied at low density for the character: total grain weight

cross number (low density)	minimum			maximum		
	P_1	P_2	F_2	P_1	P_2	F_2
cross 3 MKR211/9*MM68/1	3.40	1.24	1.88	24.23	19.39	23.38
cross 7 WW15RVN158/14 * PN28/9	2.40	2.53	2.13	20.40	21.69	27.39
cross 8 WW15RVN158/14 * MM68/1	2.40	1.24	0.78	20.40	19.39	20.79

10. Height at low density.

At low density although the main shoot is not always taller than the tillers as it is at crop density, measurements were made on the main shoot and the values are compared.

The frequency distributions for height of the three crosses at the two densities were almost identical with the F_2's distributions being intermediate between the parents. For cross 3, the difference between the means of the parents was quite large and it might have been thought that a major gene was involved, however there was no suggestion of bimodality in the F_2's distribution. It may be concluded that the differences were influenced by many genes.

The plants on average were taller at low density and mean and mode values were greater. At crop density there were a greater number of short plants which had been affected by competition. With regard to the minimum and maximum values considerable differences were obtained between populations for the tallest plants. The F_2's of crosses 3 and 7 had plants that were much taller than plants in the parental populations (Table 2.61).

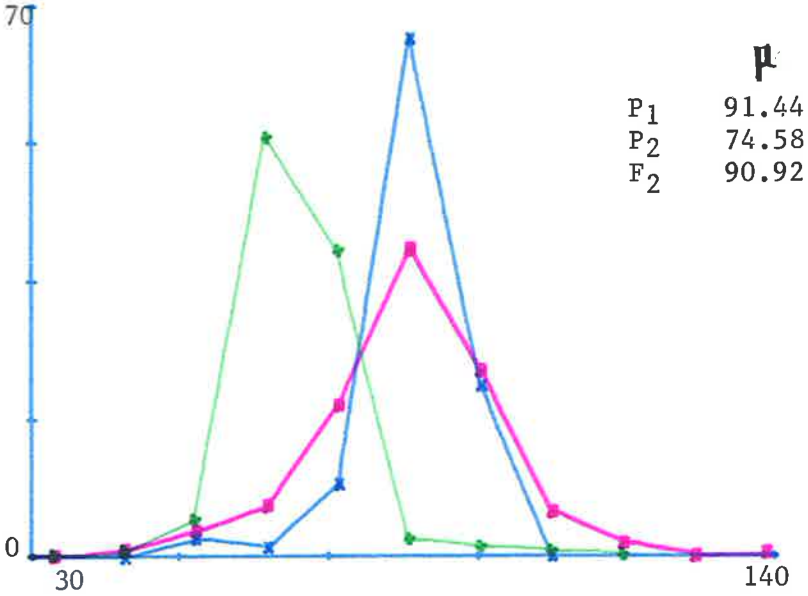
The F_2's variances were significantly larger than that of the parents, showing clearly the effects of segregation (Table 2.59). Figure 2.21 shows that the F_2's ranges covered the combined range of the parents and transgressive segregation was evident especially in crosses 3 and 7.

The CV's for height at crop density were greater than at low density. This was not unexpected however, as competition is a major factor affecting plant height at crop density and etiolation leads to a uniformity of height. The average values of the parents and F_2 of cross 8 demonstrate the effect of competition. At low density both parents were tall and the F_2 was shorter. But when under competition at crop density the F_2 was taller. This may raise the question of whether a hybrid on average is a better competitor than its parents.

The skewness for height at low density was negative and only MM68/1 had a positive skew (Table 2.60).

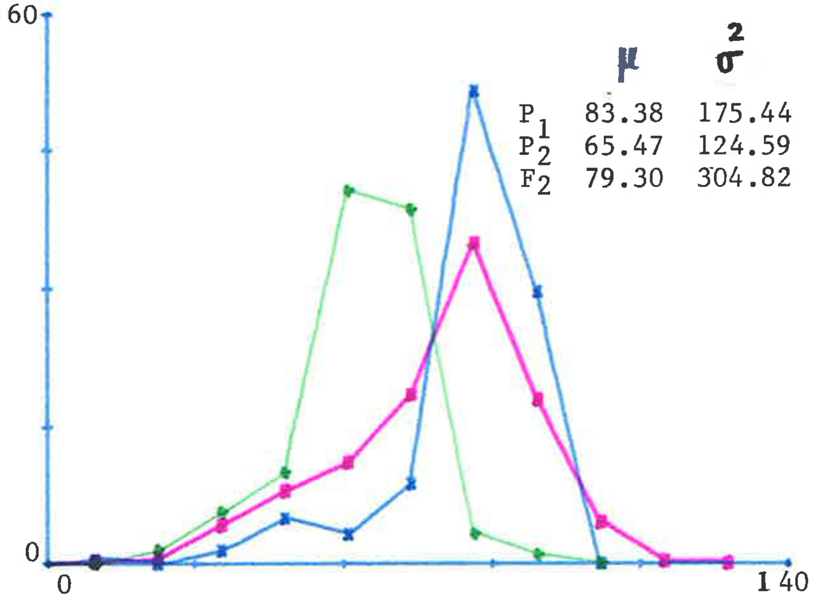
Figure 2.21. Frequency distributions of height of the main shoot for three crosses grown at low density; blue and green curves are parent 1 and parent 2 distributions respectively and the red curve is the hybrid F_2 distribution.
The X axis represents class intervals and the Y represents the number of plants in each class as a percentage.

LOW DENSITY



	μ	σ^2	cv
P_1	91.44	51.12	0.08
P_2	74.58	47.69	0.09
F_2	90.92	168.79	0.14

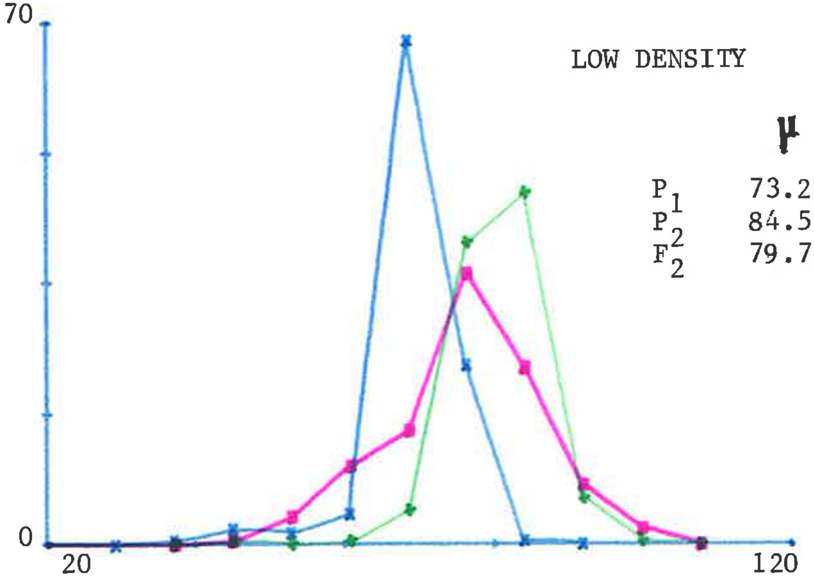
CROP DENSITY



	μ	σ^2	cv
P_1	83.38	175.44	0.16
P_2	65.47	124.59	0.17
F_2	79.30	304.82	0.22

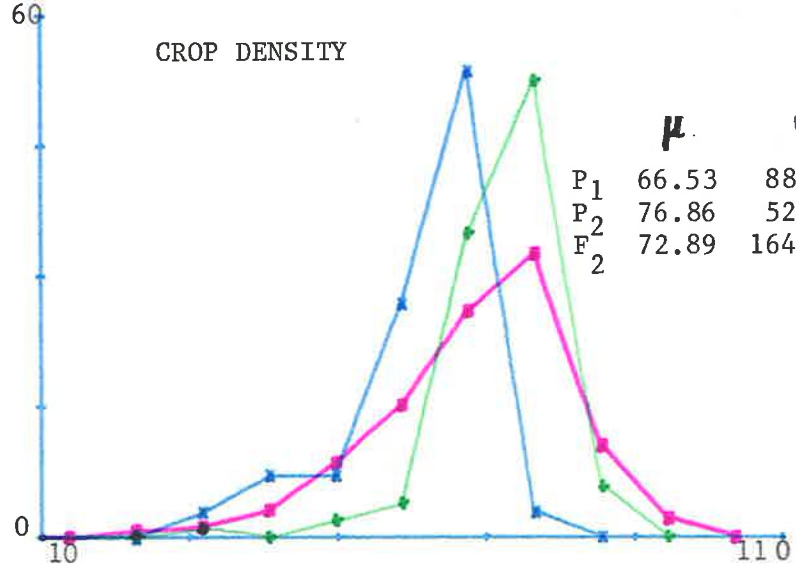
WW-15 RVN 158/14 * PN 28/9

LOW DENSITY



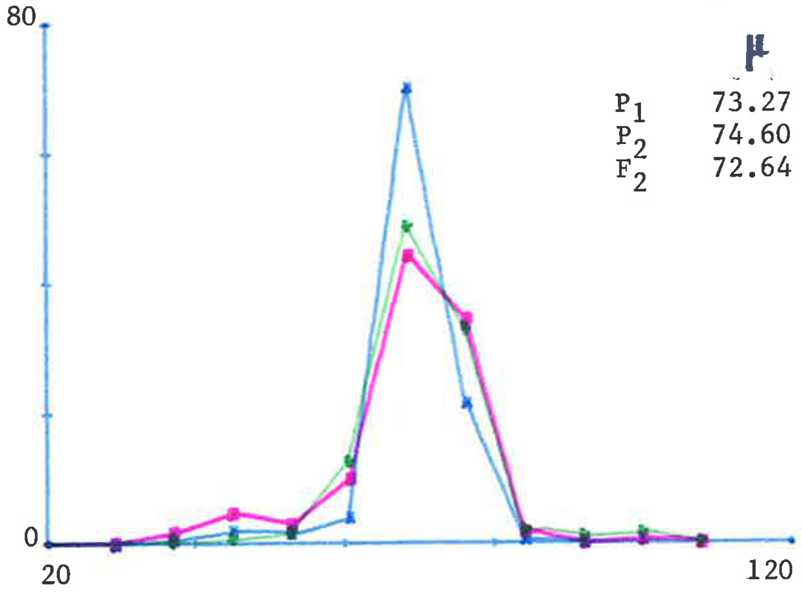
	μ	σ^2	cv
P_1	73.27	35.25	0.08
P_2	84.51	32.13	0.06
F_2	79.73	104.85	0.13

CROP DENSITY

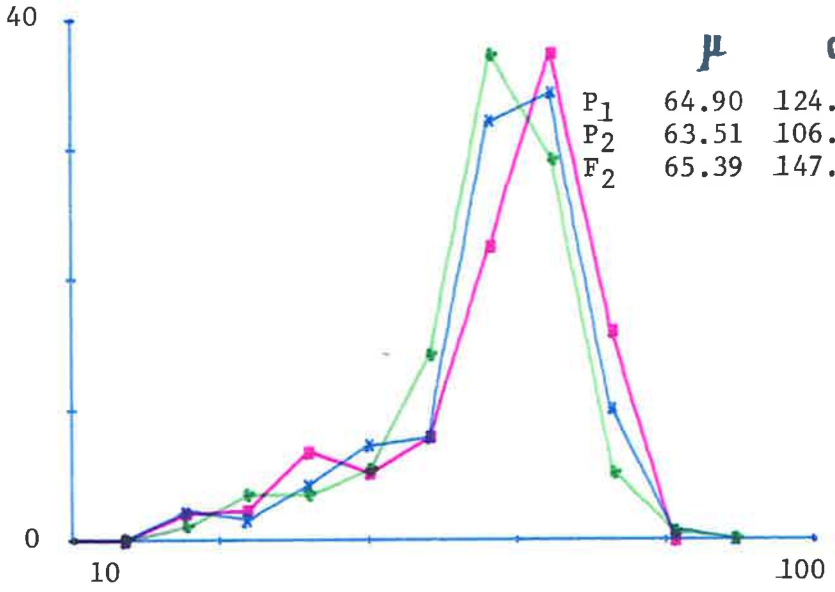


	μ	σ^2	cv
P_1	66.53	88.88	0.14
P_2	76.86	52.06	0.09
F_2	72.89	164.62	0.18

WW-15 RVN 158/14 * MM 68/1


LOW DENSITY

	μ	σ^2	cv
P_1	73.27	35.25	0.08
P_2	74.60	47.69	0.09
F_2	72.64	86.41	0.13


CROP DENSITY

	μ	σ^2	cv
P_1	64.90	124.18	0.17
P_2	63.51	106.93	0.16
F_2	65.39	147.95	0.19

Table 2.59. Variances of parents and F_2's, Chi-square of Bartlett's test for homogeneity and F test of variance ratios between parents and F_2's grown at low density for character; height

	Variances			Bartlett's Chi-square	Variance ratios[1]		
	P_1	P_2	F_2		$P_1:P_2$	$P_1:F_2$	$P_2:F_2$
cross 3 MKR211/9 * MM68/1	51.12	47.69	168.79	65.12***	1.07NS	3.30***	3.54***
cross 7 WW15 RVN158/14 * PN28/9	35.25	32.13	104.85	44.76***	1.10NS	2.97***	3.26***
cross 8 WW15RVN158/14 * MM68/1	35.25	47.69	86.41	19.63***	1.35*	2.45***	1.81***

[1] Larger variance divided by smaller variance.

Table 2.60. Coefficient of skewness values for height of parents and F_2's grown at low density.

	Coefficient values
cross 3 - F_2 (MKR211/9 * MM68/1)	-0.405
cross 7 - F_2 (WW15RVN158/14 * PN28/9)	-0.300
cross 8 - F_2 (WW15RVN158/14 * MM68/1)	-1.267
parent - MKR211/9	-1.723
parent - PN28/9	-0.983
parent - WW15RVN158/14	-2.560
parent - MM68/1	0.903

Coefficient of skewness for significant difference from zero at the 5% probability level;

= ± 0.280 for sample size of 200 (approximate guide for parents and F_2's at low density).

Table 2.61. Minimum and Maximum values in the parent and F_2 populations of three crosses studied at low density for the character: height

cross number (low density)	minimum			maximum		
	P_1	P_2	F_2	P_1	P_2	F_2
cross 3 MKR211/9*MM68/1	60.50	47.70	43.80	106.3	107.8	138.6
cross 7 WW15RVN158/14 * PN28/9	37.00	51.50	52.40	90.2	101.8	107.5
cross 8 WW15RVN158/14 * MM68/1	37.00	47.70	40.50	90.2	107.8	103.2

11. Spikelet number of the main shoot at low density.

There was not much difference in the pattern of the frequency distributions for this character across the two densities. The F_2 of cross 3 again showed a leptokurtic type of distribution having its mode intermediate between the two modes of the parents, and its range covered the combined range of the two parents (Figure 2.22).

The differences in the population means over the densities were small as were the CV's indicating that there was not a strong environmental effect on the expression of the character. The F_2 of cross 3 had its mean close to the mid parent value indicating possibly additive gene effects. In contrast the F_2 of crosses 7 and 8 had means that well exceeded the mid parent values indicating possible dominance effects.

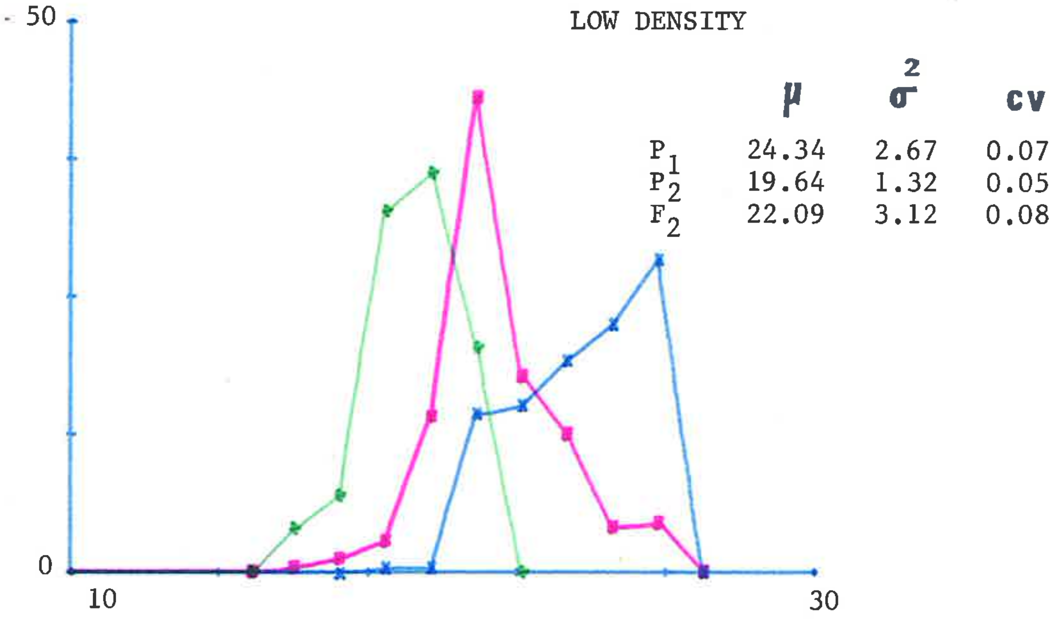
In general the F_2's had larger variances than the parents (Table 2.62). There was not much difference between the minimum values of the parent and F_2 populations however, with regard to the maximum value, in crosses 7 and 8 these were higher in the F_2 than the parents (Table 2.64).

Negative skews were obtained for most distributions of this character at low density (Table 2.63).

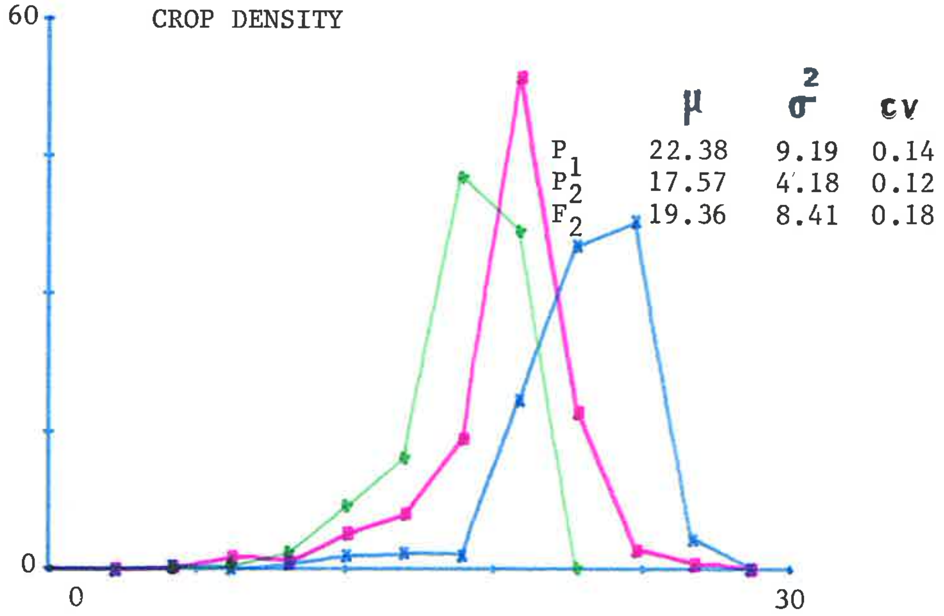
Figure 2.22. Frequency distribution of the main shoot spikelet number from three crosses studied at low density; blue and green curves are parent 1 and parent 2 distributions respectively and the red curve is the hybrid F_2 distribution.

The X axis represents class intervals and the Y represents the number of plants in each class as a percentage.

MKR 211/9 * MM 68/1

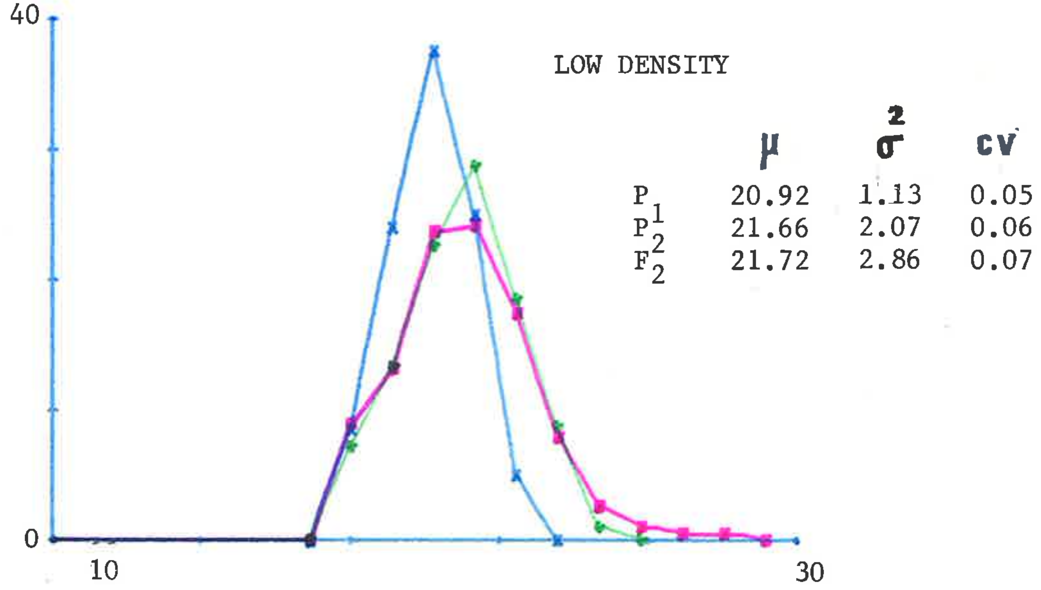


	μ	σ^2	cv
P_1	24.34	2.67	0.07
P_2	19.64	1.32	0.05
F_2	22.09	3.12	0.08

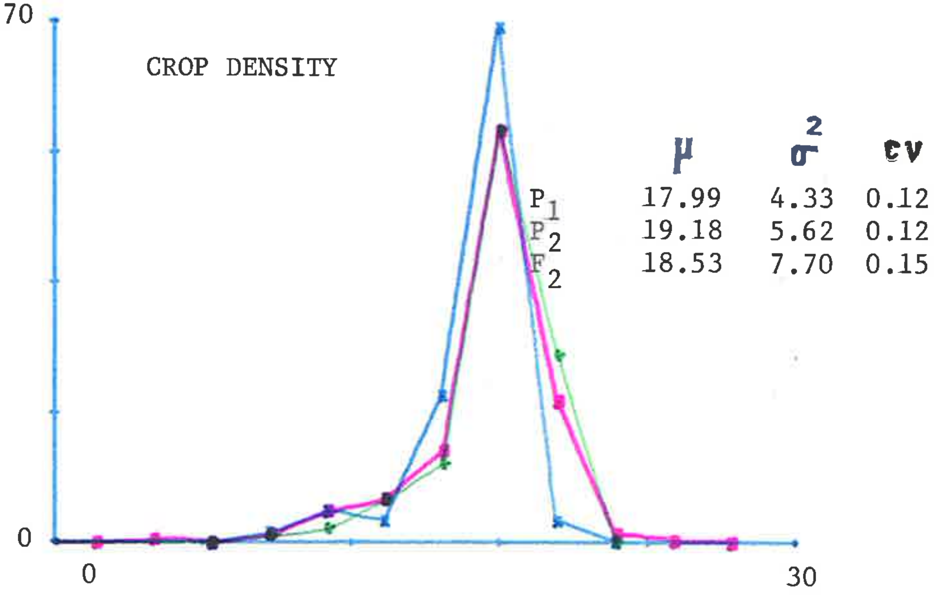


	μ	σ^2	cv
P_1	22.38	9.19	0.14
P_2	17.57	4.18	0.12
F_2	19.36	8.41	0.18

WW-15 RVN 158/14 * PN 28/9



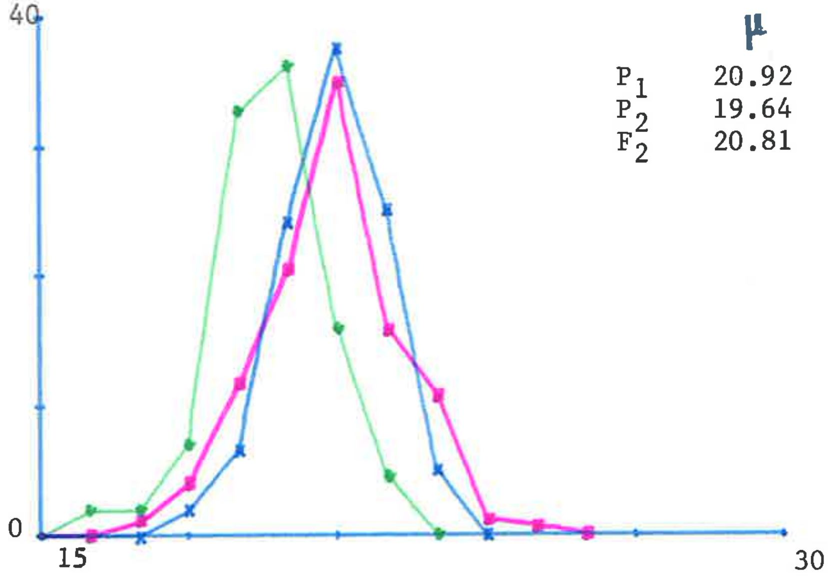
	μ	σ^2	cv
P_1	20.92	1.13	0.05
P_2	21.66	2.07	0.06
F_2	21.72	2.86	0.07



	μ	σ^2	cv
P_1	17.99	4.33	0.12
P_2	19.18	5.62	0.12
F_2	18.53	7.70	0.15

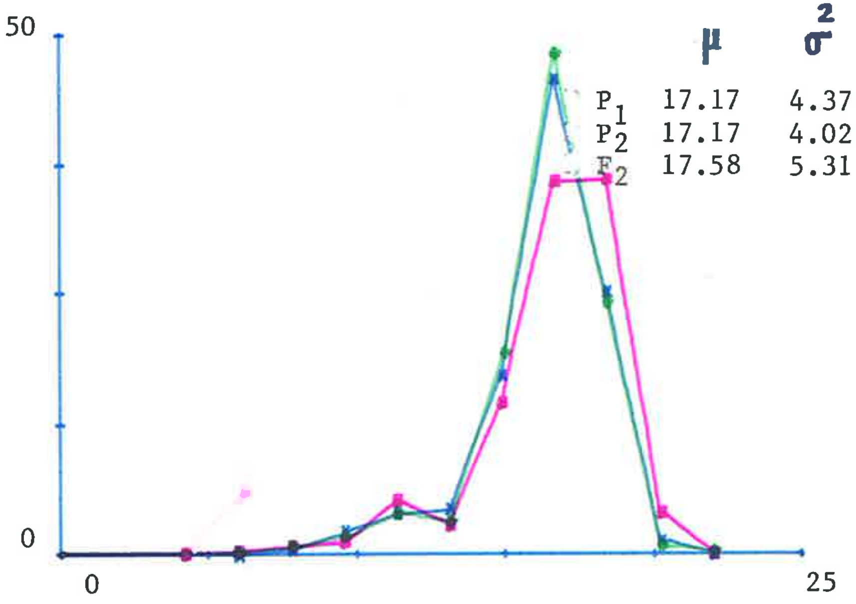
WW-15 RVN 158/14 * MM 68/1

LOW DENSITY



	μ	σ^2	cv
P_1	20.92	1.13	0.05
P_2	19.64	1.32	0.05
F_2	20.81	1.97	0.07

CROP DENSITY



	μ	σ^2	cv
P_1	17.17	4.37	0.12
P_2	17.17	4.02	0.12
F_2	17.58	5.31	0.13

Table 2.62. Variances of parents and F_2's, Chi-square of Bartlett's test for homogeneity and F test of variance ratios between parents and F_2's grown at low density for character; main shoot spikelet number

	Variances			Bartlett's Chi-square	Variance ratios[1]		
	P_1	P_2	F_2		$P_1:P_2$	$P_1:F_2$	$P_2:F_2$
cross 3 MKR211/9 * MM68/1	2.67	1.32	3.12	20.53***	2.02***	1.17NS	2.36***
cross 7 WW15 RVN158/14 * PN28/9	1.13	2.07	2.86	20.48***	1.83***	2.53***	1.38*
cross 8 WW15RVN158/14 * MM68/1	1.13	1.32	1.97	7.82***	1.17NS	1.74***	1.49***

[1] Larger variance divided by smaller variance.

Table 2.63. Coefficient of skewness values for main shoot spikelet number of parents and F_2's grown at low density.

	Coefficient values
cross 3 - F_2 (MKR211/9 * MM68/1)	0.239
cross 7 - F_2 (WW15RVN158/14 * PN28/9)	0.395
cross 8 - F_2 (WW15RVN158/14 * MM68/1)	-0.084
parent - MKR211/9	-0.407
parent - PN28/9	-0.237
parent - WW15RVN158/14	-0.311
parent - MM68/1	-0.495

Coefficient of skewness for significant difference from zero at the 5% probability level;

= ± 0.280 for sample size of 200 (approximate guide for parents and F_2's at low density).

Table 2.64. Minimum and Maximum values in the parent and F_2 populations of three crosses studied at low density for the character: main shoot spikelet number

cross number (low density)	minimum			maximum		
	P_1	P_2	F_2	P_1	P_2	F_2
cross 3 MKR211/9*MM68/1	19	16	17	27	22	27
cross 7 WW15RVN158/14 * PN28/9	18	18	18	23	25	28
cross 8 WW15RVN158/14 * MM68/1	18	16	17	23	22	25

12. Head length of the main shoot at low density.

The frequency distributions for head length were similar over the two densities (Figure 2.23). Crosses 3 and 7 demonstrate a clear genetic model of segregation in which the F_2's had modes intermediate between the two parental modes and ranges that covered the combined range of the parents.

The F_2 of cross 3 had a mean close to the mid parent value indicating possible additive gene effects but in crosses 7 and 8 the F_2s had mean values that exceeded the mid parent values indicating possible dominance gene effects. This result was evident for both low and crop densities and had been found for spikelet number.

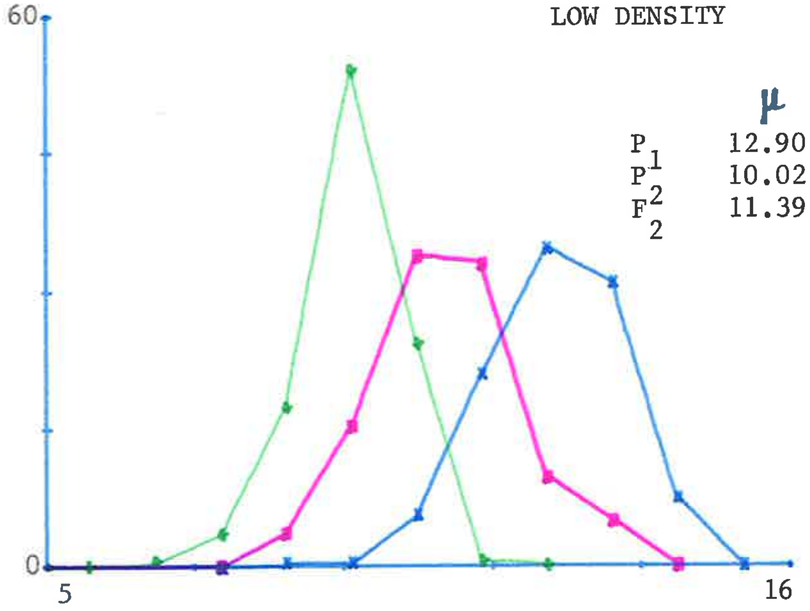
The variances showed that only the F_2 of cross 8 had a significantly larger variance than the parents (Table 2.65) and this was the only cross in which the minimum and maximum values exceeded the parents (Table 2.67).

The distributions were normal or showed negative skews (Table 2.66).

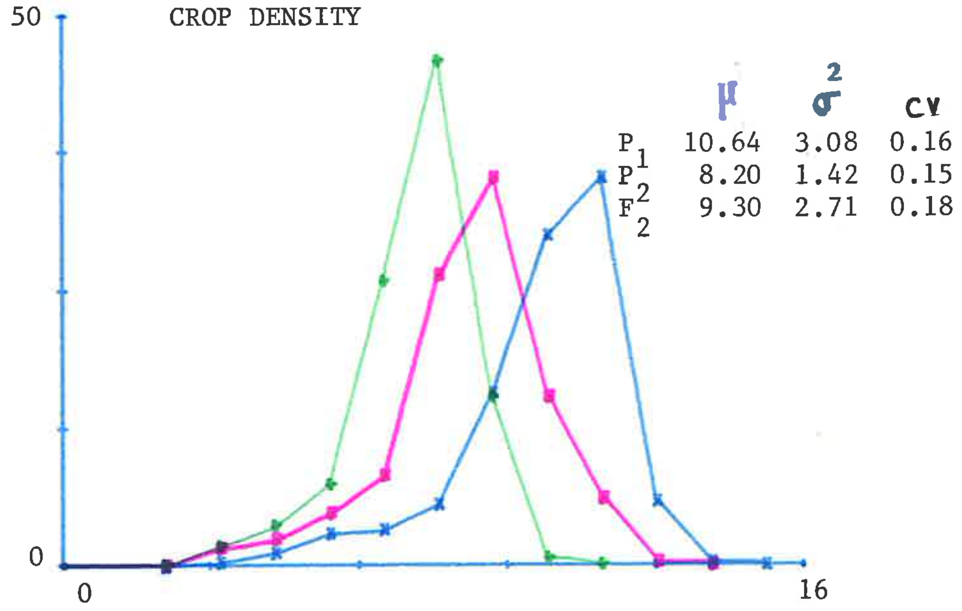
Figure 2.23. Frequency distribution of the main shoot head length for three crosses grown at low density; blue and green curves are the parent 1 and parent 2 distributions respectively, the red curve is the hybrid F_2 distribution.

The X axis represents class intervals and the Y represents the number of plants in each class as a percentage.

MKR 211/9 * MM 68/1

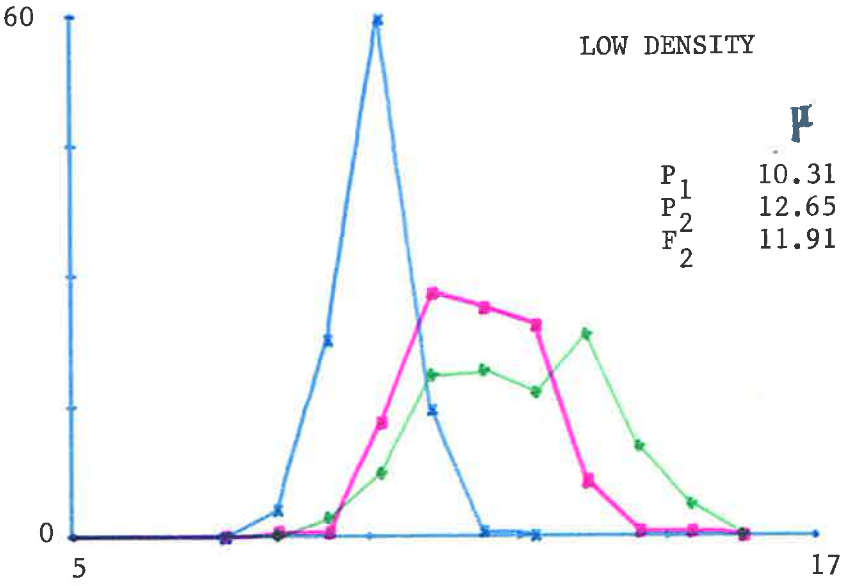

LOW DENSITY

	μ	σ^2	cv
P_1	12.90	0.96	0.07
P_2	10.02	0.45	0.06
F_2	11.39	1.12	0.09

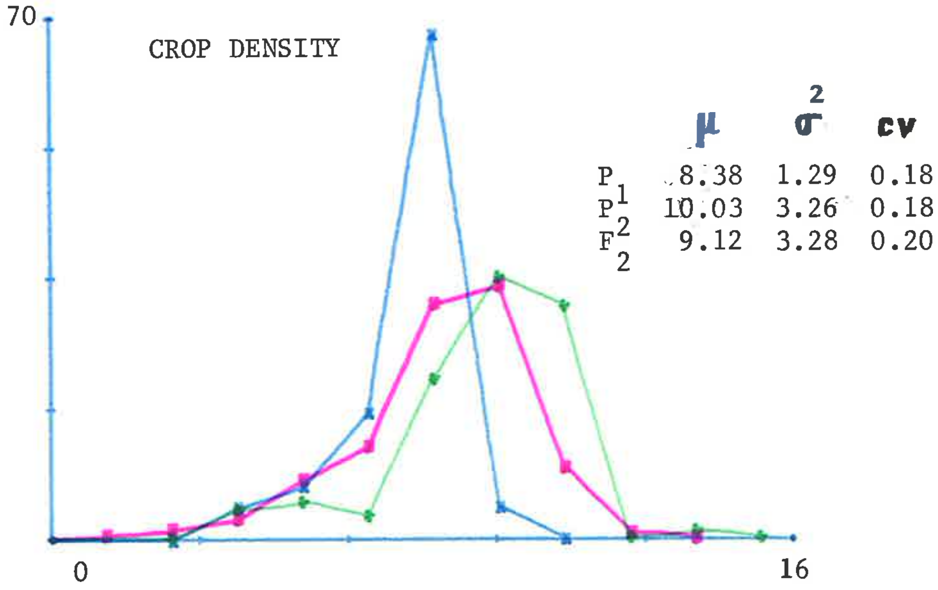

CROP DENSITY

	μ	σ^2	cv
P_1	10.64	3.08	0.16
P_2	8.20	1.42	0.15
F_2	9.30	2.71	0.18

WW-15 RVN 158/14 * PN 28/9


LOW DENSITY

	μ	σ^2	cv
P_1	10.31	0.32	0.05
P_2	12.65	1.87	0.11
F_2	11.91	1.00	0.08

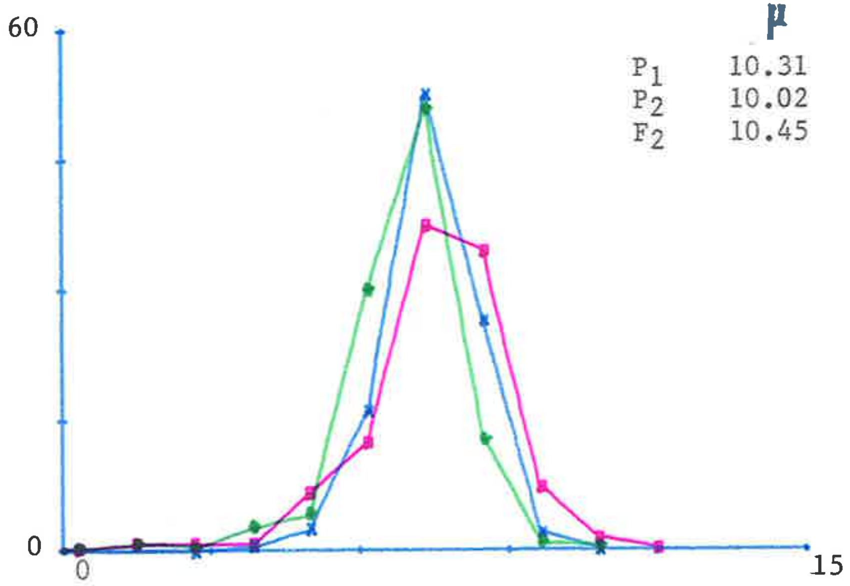

CROP DENSITY

	μ	σ^2	cv
P_1	8.38	1.29	0.18
P_2	10.03	3.26	0.18
F_2	9.12	3.28	0.20

WW-15 RVN 158/14 * MM 68/1

LOW DENSITY

	μ	σ^2	CV
P_1	10.31	0.32	0.05
P_2	10.02	0.45	0.06
F_2	10.45	0.80	0.08



CROP DENSITY

	μ	σ^2	CV
P_1	7.72	1.51	0.16
P_2	7.84	1.34	0.15
F_2	7.91	1.77	0.17

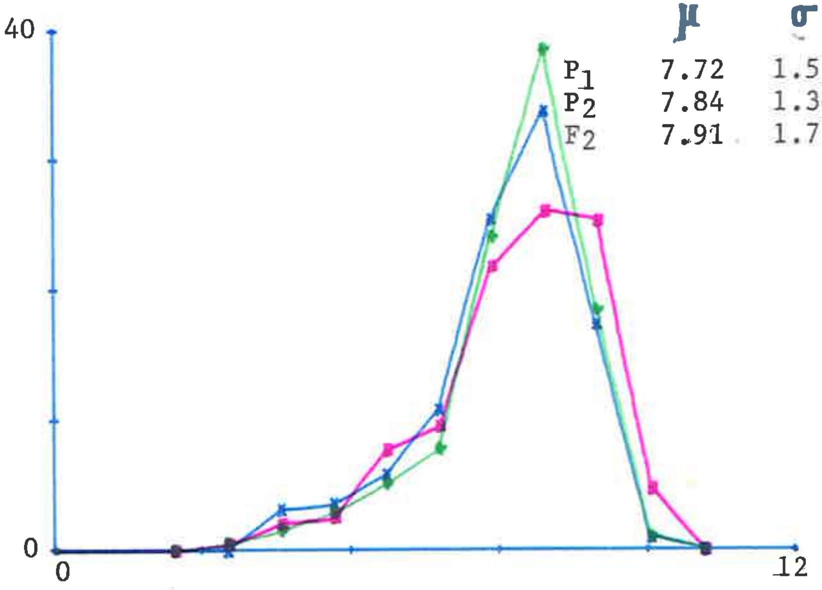


Table 2.65. Variances of parents and F_2's, Chi-square of Bartlett's test for homogeneity and F test of variance ratios between parents and F_2's grown at low density for character; main shoot head length

	Variances			Bartlett's Chi-square	Variance ratios[1]		
	P_1	P_2	F_2		P_1:P_2	P_1:F_2	P_2:F_2
cross 3 MKR211/9 * MM68/1	0.96	0.45	1.12	22.87***	2.13***	1.17NS	2.49***
cross 7 WW15 RVN158/14 * PN28/9	0.32	1.87	1.10	69.20***	5.84***	3.13***	1.87***
cross 8 WW15RVN158/14 * MM68/1	0.32	0.45	0.80	20.63***	1.41*	2.50***	1.78***

[1] Larger variance divided by smaller variance.

Table 2.66. Coefficient of skewness values for main shoot head length of parents and F_2's grown at low density.

	Coefficient values
cross 3 - F_2 (MKR211/9 * MM68/1)	0.275
cross 7 - F_2 (WW15RVN158/14 * PN28/9)	0.221
cross 8 - F_2 (WW15RVN158/14 * MM68/1)	-0.948
parent - MKR211/9	-0.386
parent - PN28/9	-0.060
parent - WW15RVN158/14	-0.339
parent - MM68/1	-1.179

Coefficient of skewness for significant difference from zero at the 5% probability level;

= ± 0.280 for sample size of 200 (approximate guide for parents and F_2's at low density).

Table 2.67. Minimum and Maximum values in the parent and F_2 populations of three crosses studied at low density for the character: main shoot head length

cross number (low density)	minimum			maximum		
	P_1	P_2	F_2	P_1	P_2	F_2
cross 3 MKR211/9*MM68/1	9.5	6.6	8.8	15.3	11.5	14.3
cross 7 WW15RVN158/14 * PN28/9	8.3	9.2	8.7	11.8	15.7	15.8
cross 8 WW15RVN158/14 * MM68/1	8.3	6.6	6.0	11.8	11.5	13.0

(c) Summary of results from experiment 2.

1. Under the condition of low density the plants were little affected by competition and much higher values were obtained for: head number, total plant weight, total grain weight, tiller grain weight and tiller grain number than at crop density. But for characters measured on the main shoot the increase under low density was much less.

2. The significant differences between the parental variances found in experiment 1 (crop density) were also evident in this experiment. This occurred again although it was expected that differences between plants in the parental population caused by micro-environmental conditions would be smaller than at crop density.

3. The F_2's consistently had larger variances than their respective parents. However, CV's of the F_2's were often only slightly larger than the parents.

4. Additive and dominance gene effects were evident for all the characters observed and no simple generalization could be made.

5. Genetic segregation was also evident in all the F_2's studied.

6. Heterosis and transgressive segregation was found in many instances. Characters such as tiller grain weight and tiller grain number in particular showed the phenomena. At crop density the phenomena were not evident for these characters.

7. Frequency distributions that conformed with classical quantitative genetic models were found for the P_1, P_2 and F_2 for the characters: height, spikelet number and head length.

8. Positive skews again were characteristic of head number, plant total weight, total grain weight, tiller grain weight and tiller grain number. These were the characters that showed the largest differences across densities.

9. Negative skews were obtained for all characters measured on the main shoot; total weight, grain weight, height, spikelet number and head length.

Chapter 3

EXPERIMENT 3
Study on relationship between F_2s and their derived lines (F_4)

1. Introduction. This experiment was concerned with the relation between characters measured on the single plants in the F_2 (experiments 1 and 2) and plot yields of the selected material in the F_4. From the results of experiments 1 and 2 it was evident that the main shoot was less affected by the micro-environment than the tillers. Furthermore, at crop density the yield of the main shoot was the major component of the total yield of a plant. The interesting question arose: would selection for the main shoot yield in an early generation be successful as a means of increasing plot yield in a later generation? Experiment 3 considers this question with the specific purpose of studying the relationship between main shoot yield and other characters of the F_2 single plants and their derived lines as plot yields in the F_4.

2. Material and method of experiment 3.

a. Genotypes. Three of the eight hybrid populations from experiments 1 and 2 were studied. They were:

cross 3	MKR211/9 * MM68/1
cross 7	WW15/RVN/158/14 * PN28/9
cross 8	WW15/RVN/158/14 * MM68/1

As these crosses had been grown at both crop and low density (experiments 1 and 2 respectively), it was planned to study separately the selections from them making six populations in experiment 3. For each F_2, the distribution of the main shoot grain weight was divided into ten classes. Twenty five percent of the lines were chosen from each class randomly.

b. Seed multiplication and sowing.

Summer 1975-1976. The F_3 generation was grown to provide sufficient seed of an F_4 for sowing as a plot. The multiplication was done in a bird-proof enclosure at the Waite Agricultural Research Institute. This out-of-season multiplication was affected an an insect, the pasture cockchafer (*Aphodius tasmaniae*) and material of cross 8 from low density was insufficient to include in the F_4 trial. The total number of the F_2 derived lines available following multiplication was:

cross 3 - material from experiment 1 - total 96 lines
cross 7 - material from experiment 1 - total 96 lines
cross 8 - material from experiment 1 - total 96 lines
cross 3 - material from experiment 2 - total 56 lines
cross 7 - material from experiment 2 - total 56 lines

Winter 1976. The F_4 lines were studied in plot trials. To reduce the possibility of loss of an experiment due to environmental conditions, the lines from each cross were grown at two sites (Roseworthy and Mortlock). The five populations of each group were sown separately. The wheat variety "Warimba" and a mixture of hybrid wheat seeds (F_8) were used as checks.

c. Sites and climate.

At each site only one replicate was grown. Having only a single replicate did not affect the purpose of the experiment which was to correlate the F_4 results with the F_2 values. The two sites were; site 1 Roseworthy Agricultural College, South Australia.

It is the same site as used for experiments 1 and 2. Apart from the the rainfall of the 1976 season (Table 3.1) other information is given in the review of experiments 1 and 2. The site was sown on July 6, 1976.

site 2 Mortlock Experiment Station, South Australia.

The site is about 150 km. north of Adelaide. The soil is a shallow brown sandy loam on rock (Mulcahey, 1954). The region also has a mediterranean type of climate but a more assured rainfall. Table 3.2 presents rainfall recorded at the station. The trial was sown on July 15, 1976.

The growing season in 1976 was one of the driest on record in South Australia and in particular the early part of the season was exceptionally dry. Sowing was delayed until late June.

The site at Roseworthy was most affected by the dry conditions. At Mortlock although the rainfall was lower than average, plant growth was satisfactory.

d. Field layout.

The design was a fully randomized layout with the F_4's of the crosses in separate blocks. The blocks were laid out as shown in Figure 3.1. Seeds were sown at the rate of 20 gm. per plot in four rows, 2.5 m. long. The distance between rows was 15 cm. and between plots 30 cm. The checks were one in every three plots of the F_4's.

e. Harvesting.

Harvesting was done at Roseworthy on December 15, 1976 and at Mortlock on December 20, 1976 using a stripper harvester.

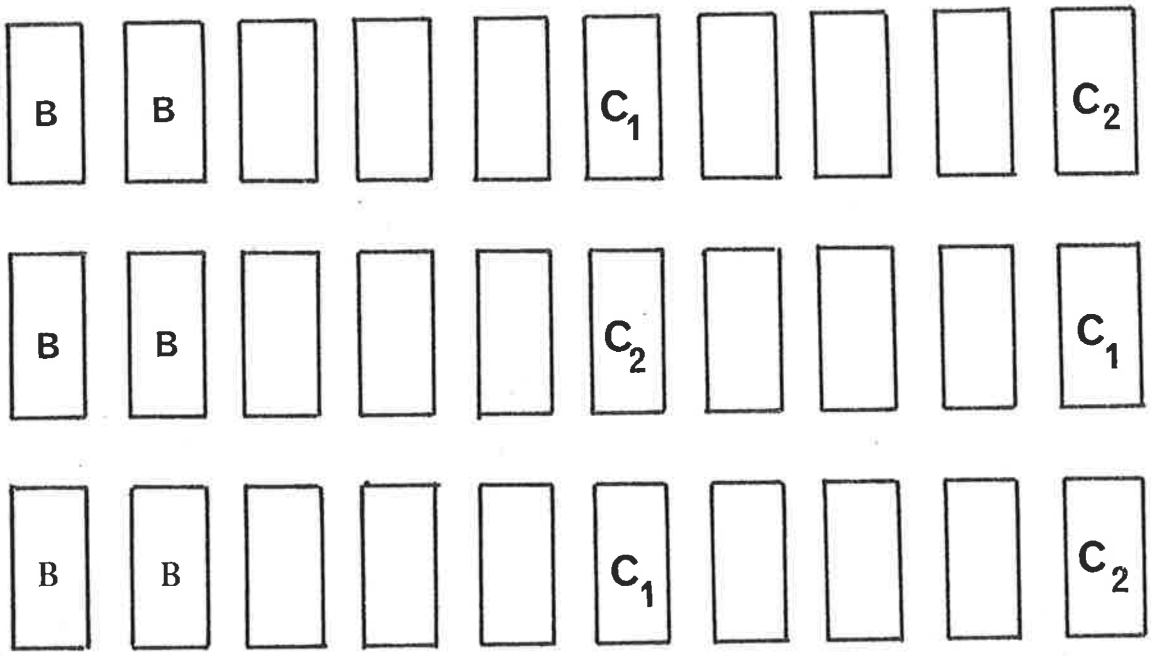
Table 3.1. Monthly rainfall (mm.) at Roseworthy in 1965-1975 and 1976.

Month	1965-1975	1976	1978
January	21	12	14
February	19	21	3
March	20	2	5
April	38	9	36
May	54	12	63
June	48	38	95
July	52	20	107
August	45	33	50
September	42	31	92
October	42	63	18
November	27	35	38
December	24	14	10
Annual total	440	290	531

Table 3.2. Monthly rainfall (mm.) at the Mortlock station in 1965-1975 and 1976.

Month	1965-1975	1976
January	33	2
February	40	21
March	33	9
April	35	13
May	69	19
June	55	41
July	79	18
August	84	51
September	66	54
October	55	103
November	31	57
December	28	12
Annual total	608	400

Figure 3.1. Part of the field plot layout of experiment 3.



B = Border plot

C_1 = Warimba plot

C_2 = Mixture of hybrid seed plot

f. Analysis of results.

The correlations between characters measured in the F_2 single plants and their derived lines (F_4) plot yields were calculated. As the relation between the F_2's yield characteristics (main shoot grain weight, tiller grain weight and total grain weight) and F_4 yields were of particular interest, when the correlation was significant a linear regression was also calculated. This regression would indicate the response to selection in early generations and the F_2 values (MGRWT, TGRWT, TOTGRWT) were considered therefore as the independent variable. The regression was:

$$F_4YLD = a + b(X)$$

where: F_4YLD is an F_4 yield per plot

a is an estimated constant

b is the regression coefficient of (X)

and X is the value of the F_2 yield character (MGRWT, TGRWT, TOTGRWT)

All the calculations were carried out using the computor programme "GENSTAT" (Alvey *et al.*, 1977).

In the text that follows, statistical significance is denoted, * for significance at 5% level, ** at 1% level and *** at 0.1% level.

Correlations were calculated with or without adjustment of the F_4 plot yields for local environmental effects. Adjustments were based on a "moving average" approach. Eight plots, four on one side and four on the other side of the target plot were averaged and the target plot yield expressed as a deviation from this average.

A moving average approach was used in preference to adjustment based on the check plots in view of some current studies that suggest the moving average gives a better evaluation of localised environmental effects (Knight, personal communication).

3. Results

a. Correlation between characters measured on the F_2 single plants and the derived F_4 plot yields.

These correlations are given in Table 3.3 (F_2 at crop density) and Table 3.4 (F_2 at low density). Only in cross 3, grown at Mortlock (with material derived from F_2 at crop density) was there a significant correlation between the F_4 plot yield and the F_2 characters: main shoot total weight, height, spikelet number, head length, main shoot grain weight, main shoot grain number, total grain weight (Table 3.3).

The correlations between characters measured on the F_2 grown at low density and their derived F_4 plot yields were not significant, except for cross 7 grown at Roseworthy in which negative and significant correlations were found between the F_4 plot yield and F_2 characters: height, and head length (Table 3.4). This would imply that the shorter selections of the F_2 gave rise to higher yielding plots at the F_4 than the taller selections.

Correlations between the F_2 characters with the adjusted yield of F_4's are shown also in Table 3.3 and 3.4. Although this adjustment resulted in an increase in some values and a decrease in others, the change was not sufficient to alter the interpretation of the results.

Table 3.3. Correlation between characters measured in F_2 grown at crop density (1975) and yield per plot of the derived F_4 grown at two sites (1976). (All coefficients were non significant unless indicated)

sites	cross no	coefficient of correlation between F_4 plot yield and F_2's character;												
		HDNO	PLTWT	MTWT	HT	SPIKE	HDLTH	MGRWT	MGRNO	TGRWT	TGRNO	TOTGRWT	MHT	TOTHI
Roseworthy	3	0.038	0.021	-0.108	-0.152	0.053	0.006	-0.081	0.024	0.041	0.057	-0.006	-0.004	-0.059
	7	0.034	0.061	0.028	0.103	0.133	0.054	0.039	0.049	0.069	0.073	0.066	0.062	0.053
	8	0.015	0.123	0.141	0.065	0.084	0.165	0.184	0.172	0.072	0.058	0.140	0.125	0.124
Mortlock	3	0.062	0.147	0.285**	0.216*	0.221*	0.254*	0.298**	0.241*	0.168	0.143	0.244*	0.129	0.071
	7	0.189	0.129	0.123	0.144	0.034	0.115	0.161	0.143	0.127	0.181	0.171	0.116	0.103
	8	0.035	0.149	0.141	0.076	0.128	0.118	0.120	0.112	0.102	0.086	0.144	0.024	0.023
		coefficient of correlation between the adjusted F_4 yields and F_2 characters;												
Roseworthy	3	0.048	-0.065	-0.070	-0.083	0.082	0.016	-0.030	0.038	0.062	0.048	0.030	0.071	0.063
	7	0.084	0.119	0.061	0.122	0.115	0.037	0.034	0.049	0.124	0.124	0.100	-0.058	-0.067
	8	0.122	0.191	0.177	0.000	0.117	0.169	0.177	0.206*	0.129	0.148	0.191	0.092	0.078
Mortlock	3	0.111	0.073	0.298**	0.210*	0.283**	0.291**	0.301**	0.240*	0.212*	0.180	0.278**	0.092	0.105
	7	0.215*	0.140	0.105	0.104	0.012	0.097	0.129	0.131	0.151	0.209	0.167	0.051	0.030
	8	0.042	0.079	0.090	0.172	0.154	0.081	0.075	0.059	0.028	0.029	0.070	-0.007	-0.007

Table 3.4. Correlation between characters measured in F_2 grown at low density (1975) and yield per plot of the derived F_4 line grown at two sites (1976). (All coefficients were non significant unless indicated).

sites	cross no.	coefficient of correlation between F_4 plot yield and F_2 characters;												
		HDNO	PLTWT	MTWT	HT	SPIKE	HDLTH	MGRWT	MGRNO	TGRWT	TGRNO	TOTGRWT	MHI	TOTHI
Roseworthy	3	0.101	0.070	0.067	-0.095	0.232	0.214	0.117	0.114	-0.032	0.122	-0.021	0.169	-0.224
	7	0.105	-0.034	0.192	-0.287*	-0.083	-0.459***	-0.183	0.036	-0.018	0.064	-0.037	0.014	-0.022
Mortlock	3	0.059	-0.063	-0.157	-0.168	0.076	0.169	-0.079	0.078	-0.070	0.022	-0.073	0.176	-0.057
	7	-0.111	-0.145	-0.090	0.024	-0.206	-0.105	-0.005	-0.136	-0.098	-0.202	-0.094	0.238	0.236
		coefficient of correlation between the adjusted F_4 yields and F_2 characters												
Roseworthy	3	0.098	0.058	0.170	-0.069	0.259	0.212	0.198	0.089	-0.016	0.067	0.001	0.136	-0.135
	7	0.233	0.126	-0.017	-0.271	0.134	-0.277*	0.003	0.155	0.142	0.198	0.133	0.104	0.056
Mortlock	3	0.209	0.016	-0.110	-0.153	0.153	0.271*	-0.039	0.059	0.007	0.113	0.003	0.162	-0.042
	7	-0.098	-0.154	-0.101	-0.028	-0.242	-0.153	-0.028	-0.153	-0.112	-0.200	-0.110	0.181	0.188

b. Regression analysis of F_4 plot yield on the F_2's: main shoot grain weight, tiller grain weight and total grain weight.

In some instances where the correlation were significant the regressions were calculated and are given with the diagrams in Figure 3.1.

c. Conclusion.

The results obtained in this experiment indicate that with few exceptions the variation in the F_4's yield was not accounted for by variation in the F_2 single plant performances.

Differences in results obtained for cross 3 between the material grown at Roseworthy and at Mortlock were due probably to a limitation in yield imposed by the Roseworthy environment in 1976. This can be judged from the results for the check variety which showed a large difference in yield over the two sites. For check "Warimba", the average yield was 601.8 gm/plot at Mortlock and 293.1 gm/plot at Roseworthy, for the check "mixture of hybrids", the respective yields were 444.3 gm/plot and 225.3 gm/plot.

There was also large environmental variability within a site. At Mortlock, Warimba;s yields ranged from 484.3 to 819.7 gm/plot and the yields of the mixture of hybrid seed from 307.9 to 526.4 gm/plot. At Roseworthy, Warimba;s yield ranged from 127.1 to 374.0 gm/plot and 112.6 to 294.4 gm/plot for yields of the mixture of hybrid seed. The moving average adjustment - for reasons as yet unknown - did little to provide a better assessment of the F_4 yields, despite the environmental variability within the sites.

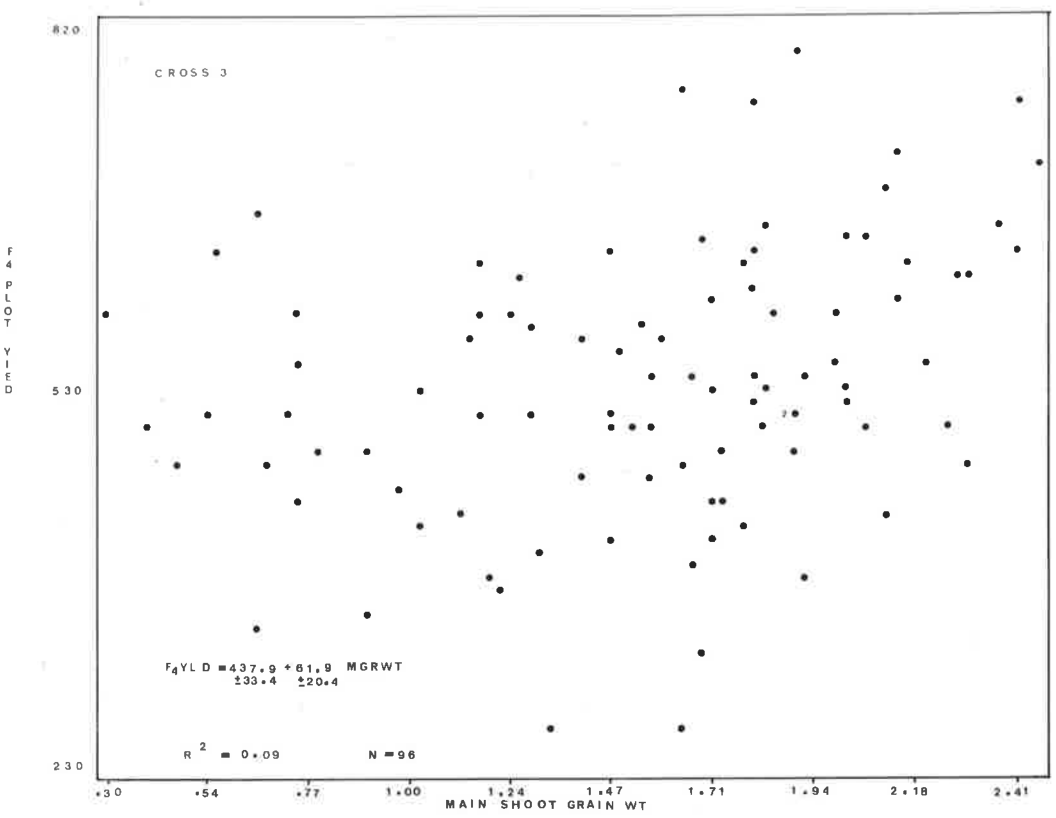
Many questions arose from this experiment. They were:

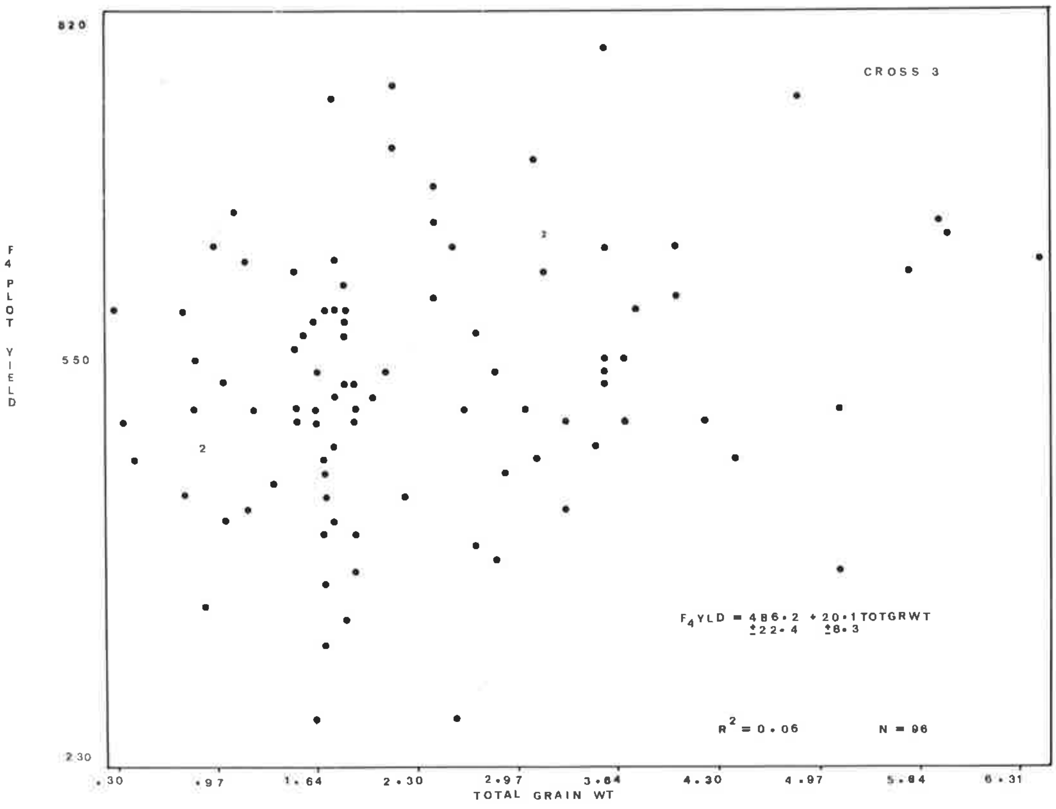
1. Were the highly significant correlations obtained for cross 3 at Mortlock a chance effect or will they occur in other sites and seasons.
2. Was the relationship between generations a result specific to a cross which could not be applied to other crosses?

3. Would the relationship between F_2 and F_4 improve if the F_4 were replicated?
4. Does the relationship improve if the season is more normal?
5. Was the absence of significant results a consequence of the small number of crosses and would they be different if the number of crosses was increased?

These questions will be examined in the next experiment.

Figure 3.1. Regression of F_4 plot yield on the F_2's: main shoot grain weight and total grain weight which showed significant in cross 3.


CROSS 3
F4 PLOT YIELD
820
530
230
F4YLD = 437.9 + 61.9 MGRWT
±33.4 ±20.4
R2 = 0.09
N = 96
.30
.54
.77
1.00
1.24
1.47
1.71
1.94
2.18
2.41
MAIN SHOOT GRAIN WT


CROSS 3
F4 PLOT YIELD
820
550
230
F4YLD = 486.2 + 20.1 TOTGRWT
±22.4 ±8.3
R2 = 0.06
N = 96
.30
.97
1.64
2.30
2.97
3.64
4.30
4.97
5.64
6.31
TOTAL GRAIN WT

Chapter 4

EXPERIMENT 4

Further study on relationship between F_2s and their derived lines (F_4 or F_5)

1. Introduction.

Experiment 4 considered the questions examined in experiment 3 but now all eight crosses were available. There were three replicates of the material, two were at Roseworthy and one at Charlick. The number of the derived F_4 lines for each cross was increased to approximately 200 lines representing about 50% of the total F_2's. For those crosses which were grown at low density in the F_2, the number remained at 56 lines.

2. Material and method.

The eight crosses were those listed in experiment 1. Material from crosses 3, 7 and 8 were at the F_5 generation by 1978, the remaining crosses are F_4's. The process of choosing lines was similar to that used in experiment 3. The exact number of lines in each cross was:

	F_2 at crop density	F_2 at low density
cross 1	187	
cross 2	200	
cross 3	187	56
cross 4	187	
cross 5	187	
cross 6	200	
cross 7	187	56
cross 8	187	

Summer 1977-1978. The seeds of crosses 1, 2, 4, 5, 6 were multiplied to give the F_4 lines. The material of crosses 3, 7 and 8 was available from experiment 3.

Winter 1978. All lines were studied in plot trials with the material from each cross grown in separate blocks, giving 10 blocks.

As the experiment involved 4902 plots it occupied a large area, sufficient to be subject to problems of soil and environmental heterogeneity. To take account of this variation, a check variety was sown in every fourth plot. This increased the number of plots to 6540. There were enough parental seeds of crosses 1, 3 and 8 of the parents to be used as checks. In other instances the check was the variety "Warigal".

b. Site and climate.

Two sites were used:

Roseworthy Agricultural College, South Australia.

Two replications of the ten blocks were grown. The 1978 growing season was reasonably good. The climatic details were presented with experiment 3.

The Charlick Experiment Station, Strathalbyn, South Australia.

The Charlick Experiment Station was newly established in 1978 and soil and climatic information are limited. The station is about 30 km. south of Adelaide and has also a mediterranean type of climate. Rainfall was not recorded at the station in 1978. The nearest station with records was Strathalbyn, 10 km. away (Table 4.1).

Table 4.1. Monthly rainfall (mm.) at Strathalbyn in 1978.

Month	1978	Month	1978
January	13	July	78
February	3	August	87
March	21	September	76
April	42	October	29
May	55	November	39
June	77	December	8
		Total	528

The soil is transitional between a red brown earth and the solonized brown soil. These terms follow the terminology of Stace *et al.* (1968).

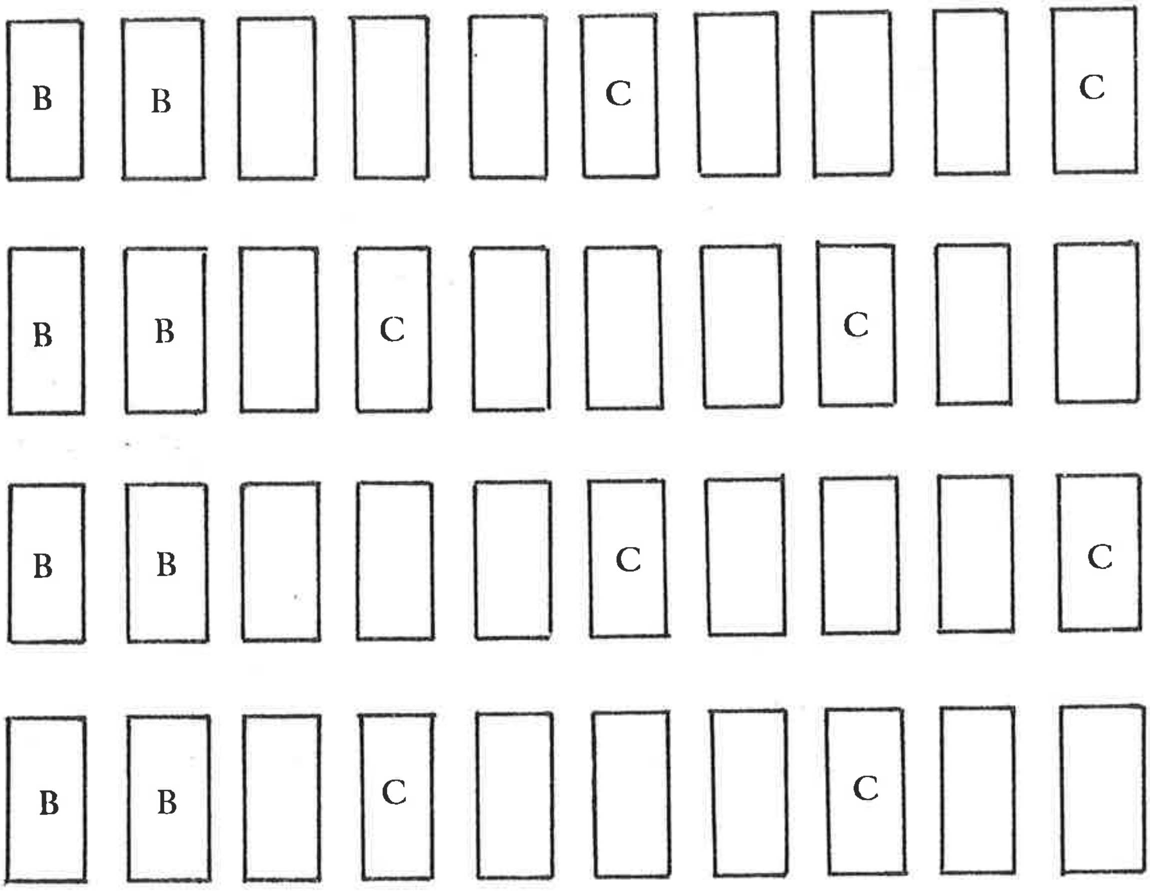
c. Field layout.

The layout and conduct of the experiment was similar to that of experiment 3 except for the arrangement of checks (see Figure 4.1).

d. Sowing and harvesting.

Sowing at Roseworthy was done on June 23, 1978, and harvesting on November 27 to December 8, 1978. The Charlick site was sown on June 30, 1978 and harvested between December 11 to 18, 1978.

Figure 4.1. An example of the plot layout in the 1978 trials.



B = Border plot
C = Check plot

3. Results.

Correlation analysis was again used to evaluate the relationships between the

F_2 and F_4 of crosses 1, 2, 4, 5 and 6

and between F_2 and F_5 of crosses 3, 7 and 8.

When the correlations between the F_2 grain yield (MGRWT, TGRWT and TOTGRWT) and the F_4 or F_5 plot yield were significant, linear regressions were calculated with the F_2's grain yield as the independent variable. Analyses were done using GENSTAT (Alvey *et al.*, 1977). As the replications occupied a large area and as two sites were involved the results are presented separately.

a. Correlation between characters measured on F_2's and their derived F_4 or F_5's plot yields.

The correlations were with few exceptions low and non significant (Table 4.3). Correlations between the F_2 main shoot yield and the derived line yields were obtained in some crosses, the most consistent being cross 6. Total grain weight and total plant weight were also found to have significant correlations with the derived line yields in the crosses in which a significant correlation with the main shoot were found. The components of yield (head length and spikelet number) were seldom correlated with the F_4 or F_5's yields. Also evident but to a lesser degree and constancy were correlations of derived line yields with the tiller grain weight and number and the associated head number. The correlation of the F_4 or F_5's yields with height were not consistent.

Suggestions have been made that harvest index is less influenced than grain yield by environmental differences and therefore is a criterion of value when selecting indirectly for yield (Donald and Hamblin, 1976; Fischer and Kertesz, 1976). Some evidence for this was obtained for the harvest index of the main shoot but the correlations were no better than with main shoot yield itself. The harvest indices of the whole plants of the F_2's were not correlated with the F_4 or F_5's yields.

The correlations between characters of the F_2's grown at low density (crosses 3 and 7) and their derived line yields (F_5) also tended to be non significant. Cross 3 replicate 1 showed a correlation between the F_5 yield and the F_2's main shoot total weight, grain weight, grain number and harvest index (Table 4.5). The correlation in cross 7 of spikelet number with F_5 yield was an isolated result.

It is usually considered that the poor correlation obtained between F_2 attributes and derived line yields is due to the poor assessment of the F_2 but the lack of correlation in this and other studies may be due also to an inprecise assessment of the F_4's or F_5's. In the present study there was large variation in the micro-environment within a replicate or block. This was indicated by values for the checks (Table 4.5). In an attempt to account for the variation moving averages were used to adjust the F_4 or F_5 plot yields. Correlations between the F_2 characters and these adjusted F_4 or F_5 yields are given in Table 4.4 and 4.6. With few exceptions the coefficients did not change markedly. The improvements were tiller grain weight (TGRWT) and grain number (TGRNO) and harvest index of the whole plant (TOTHI) in cross 6 where they became highly significant. If, as a consequence of an adjustment of the F_4 yields, they became more highly correlated with F_2 tiller grain weight then it is probable that an improvement would occur also in the correlation with the F_2 total harvest index. There were also some increases in the correlations involving head number, spikelet number and head length and derived line yield.

Table 4.3. Correlations between characters measured on F_2's (1975) and their derived F_4 or F_5 plot yield (1978). (F_2s were grown at crop density).

cross no.	rep.	HDNO	PLTWT	MTWT	HT	SPIKE	HDLTH	MGRWT	MGRNO	TGRWT	TGRNO	TOTGRWT	MHI	TOTHI
1 F_4	1	.05	.04	.04	-.03	.07	.04	.06	-.02	.03	.04	.05	.06	.03
	2	-.02	-.07	-.08	-.17**	-.10	-.08	-.03	-.06	.00	-.03	-.02	.07	.06
	3	.22***	.24***	.15*	.14*	.25***	.26***	.14*	.14*	.23***	.23***	.23***	.04	-.03
2 F_4	1	-.09	.00	.00	-.12	.01	.10	.03	.08	.01	.01	.03	.10	.09
	2	.03	.10	.05	-.02	.09	.12	.06	.05	.11	.11	.10	.06	.04
	3	.29***	.03	.02	.07	.08	.11	.05	-.12	.32***	.29***	.24***	.11	.08
3 F_5	1	.07	.12	.12	.03	.16**	.14*	.15*	.14*	.12	.10	.15*	.14*	.14*
	2	.02	.00	-.08	-.05	-.07	-.07	-.05	-.02	.03	.06	.00	.03	-.01
	3	.05	.03	.09	.17**	.03	.01	.06	.06	-.02	.00	.01	-.06	-.08
4 F_4	1	-.07	-.04	.02	-.21***	.04	.01	.05	.06	-.06	-.05	-.02	.07	.03
	2	.08	.12	.15*	.14*	.16*	.15*	.13	.14*	.10	.11	.13	.11	.15*
	3	-.04	.05	.12	.06	.02	.10	.11	.08	.00	.00	.06	.04	.08
5 F_4	1	-.04	-.02	.02	.03	-.03	.01	.03	.01	-.04	-.08	-.04	.06	-.02
	2	.06	.09	.02	-.01	-.07	.01	.03	.06	-.02	.12	-.02	.04	-.02
	3	.09	.02	.04	.04	.03	.04	.04	.03	-.03	.05	-.03	.05	-.03
6 F_4	1	.16**	.26***	.34***	.10	.06	.12	.35***	.27***	.10	.18***	.23***	.26***	.02
	2	.06	.15*	.26***	-.02	.03	.07	.29***	.28***	.02	.09	.14*	.28***	.03
	3	.12	.17**	.20***	.10	.05	.10	.23***	.19***	.12	.13	.19***	.24***	.10
7 F_5	1	.00	.03	-.01	-.03	.06	.00	.01	.01	.08	.06	.06	.02	.05
	2	.11	.05	-.06	-.11	-.09	-.07	-.08	-.07	.12	.12	.03	-.13	-.13
	3	-.14*	-.09	-.08	-.11	-.02	-.03	-.05	-.04	-.06	-.05	-.07	.03	.07
8 F_5	1	.05	.06	.05	.05	.01	.05	.03	.08	.06	.05	.05	-.02	.00
	2	-.08	.02	.07	.01	.04	.05	.08	.06	-.03	-.04	.03	-.02	.01
	3	.03	-.05	-.11	-.08	-.05	-.03	-.10	-.08	.02	.02	-.06	-.02	-.06

Table 4.4. Correlation between characters measured on F_2's (1975) grown at crop density and the adjusted yields of the derived F_4 or F_5's (1978).

cross no.	rep.	HDNO	PLTWT	MTWT	HT	SPIKE	HDLTH	MGRWT	MGRNO	TGRWT	TGRNO	TOTGRWT	MHI	TOTHI
1	1	0.23***	0.09	0.05	-0.11	0.08	0.08	0.04	0.01	0.10	0.14	0.09	-0.04	-0.07
	2	-0.01	-0.06	-0.08	-0.13	-0.11	-0.07	-0.03	-0.07	-0.01	-0.03	-0.02	0.09	0.07
	3	0.23***	0.24***	0.13	0.05	0.22***	0.22***	0.12	0.12	0.25***	0.26***	0.23***	0.00	-0.06
2	1	0.01	0.11	0.07	-0.07	0.07	0.13	0.09	0.12	0.11	0.11	0.12	0.09	0.06
	2	0.08	0.12	0.05	0.02	0.14*	0.13	0.06	0.05	0.15*	0.15*	0.13	0.08	0.06
	3	0.19***	0.20***	0.10	0.11	0.13	0.15*	0.10	0.02	0.22***	0.22***	0.20***	0.09	0.06
3	1	0.09	0.12	0.11	0.08	0.14*	0.13	0.13	0.10	0.12	0.11	0.14*	0.10	0.08
	2	0.03	0.07	0.02	0.08	0.04	-0.01	0.02	0.08	0.10	0.10	0.08	-0.01	0.01
	3	0.05	0.04	0.09	0.16**	0.04	0.02	0.05	0.06	-0.01	0.01	0.01	-0.07	-0.10
4	1	-0.07	-0.05	0.03	-0.19***	0.03	0.01	0.07	0.06	-0.08	-0.08	-0.03	0.09	0.04
	2	0.09	0.07	0.06	0.06	0.04	0.01	0.07	0.06	0.08	0.10	0.08	0.08	0.10
	3	-0.04	0.05	0.14*	0.09	0.06	0.17**	0.14*	0.10	0.01	0.00	0.06	0.06	0.09
5	1	-0.16**	-0.11	0.00	0.13	-0.05	-0.03	0.03	-0.02	0.00	-0.16**	0.00	0.13	0.01
	2	0.03	0.01	-0.05	-0.01	-0.09	-0.06	-0.04	0.02	0.00	0.03	0.00	-0.02	0.00
	3	0.01	-0.03	0.00	0.04	0.03	0.02	-0.01	0.00	-0.04	0.01	-0.04	-0.01	-0.02
6	1	0.13	0.26***	0.36***	0.04	0.15**	0.16**	0.38***	0.35***	0.15*	0.17**	0.28***	0.29***	0.28***
	2	0.11	0.23***	0.29***	-0.02	0.05	0.07	0.31***	0.28***	0.15*	0.16**	0.25***	0.26***	0.26***
	3	0.20***	0.23***	0.29***	0.13	0.11	0.15*	0.26***	0.22***	0.17**	0.21***	0.23***	0.18**	0.13
7	1	-0.04	0.04	0.02	0.04	0.08	0.01	0.03	0.03	0.08	0.06	0.06	-0.03	0.00
	2	0.22***	0.14*	0.06	0.00	0.05	0.04	0.01	0.17	0.15*	0.15*	0.10	-0.16**	-0.19***
	3	-0.10	-0.11	-0.10	-0.13	-0.05	-0.05	-0.09	-0.07	-0.08	-0.06	-0.10	-0.02	0.02
8	1	-0.06	-0.02	0.05	0.01	0.03	0.06	0.05	0.03	-0.09	-0.07	-0.02	-0.02	-0.01
	2	0.02	0.04	0.04	0.04	0.00	0.04	0.02	0.06	0.04	0.03	0.03	-0.06	-0.06
	3	0.08	0.03	-0.01	-0.07	0.02	0.05	-0.02	0.02	0.04	0.05	0.01	-0.05	-0.09

Table 4.5. Correlations between characters measured on F_2 grown at low density and their derived F_5 plot yield (1978).
Rep. 1 and 2 were grown at Roseworthy and Rep. 3 at Charlick.

cross no.	rep.	HDNO	PLTWT	MTWT	HT	SPIKE	HDLTH	MGRWT	MGRNO	TGRWT	TGRNO	TOTGRWT	MHI	TOTHI
3 F_5	1	-.04	.03	.29**	.13	.17	.20	.37***	.27*	.05	.01	.08	.29**	.22
	2	-.21	-.02	.12	.10	.04	-.06	.16	.05	.00	-.05	.01	.11	.17
	3	.00	-.09	.06	-.07	.12	.25*	.07	.07	-.07	-.01	-.06	.05	.02
7 F_5	1	-.03	-.08	-.07	-.07	.19	-.09	-.10	-.03	-.09	-.02	-.09	-.13	-.15
	2	.22	.19	.16	-.17	.33***	.23	.14	.23	.14	.24	.14	-.19	-.25*
	3	.05	.01	-.05	-.14	.01	.00	-.13	-.06	.01	.01	.00	-.24	-.05

Table 4.6. Correlations between characters measured on F_2 (1975) grown at low density and the adjusted yields of the derived F_5 (1978)

cross no.	rep.	HDNO	PLTWT	MTWT	HT	SPIKE	HDLTH	MGRWT	MGRNO	TGRWT	TGRNO	TOTGRWT	MHI	TOTHI
3	1	-0.13	0.06	0.30	0.22	0.18	0.09	0.34***	0.20	0.08	0.00	0.11	0.20	0.28**
	2	-0.15	0.02	0.16	0.10	0.08	-0.02	0.19	0.13	0.03	0.00	0.04	0.10	0.14
	3	0.03	-0.10	-0.04	-0.14	0.07	0.19	-0.10	-0.02	-0.09	-0.01	0.09	0.06	-0.05
7	1	-0.23	-0.34***	-0.30**	-0.17	-0.03	-0.10	-0.31**	-0.24	-0.31**	-0.28*	-0.32***	-0.16	-0.05
	2	0.18	0.29**	0.24	0.26*	0.30**	0.31**	0.28*	0.27*	0.30**	0.24	0.31**	0.20	0.22
	3	-0.04	-0.06	0.00	-0.03	-0.05	-0.07	0.06	0.00	-0.05	-0.07	-0.04	0.15	0.07

Table 4.7. Variation in yields of the check plots within the experimental block in 1978.

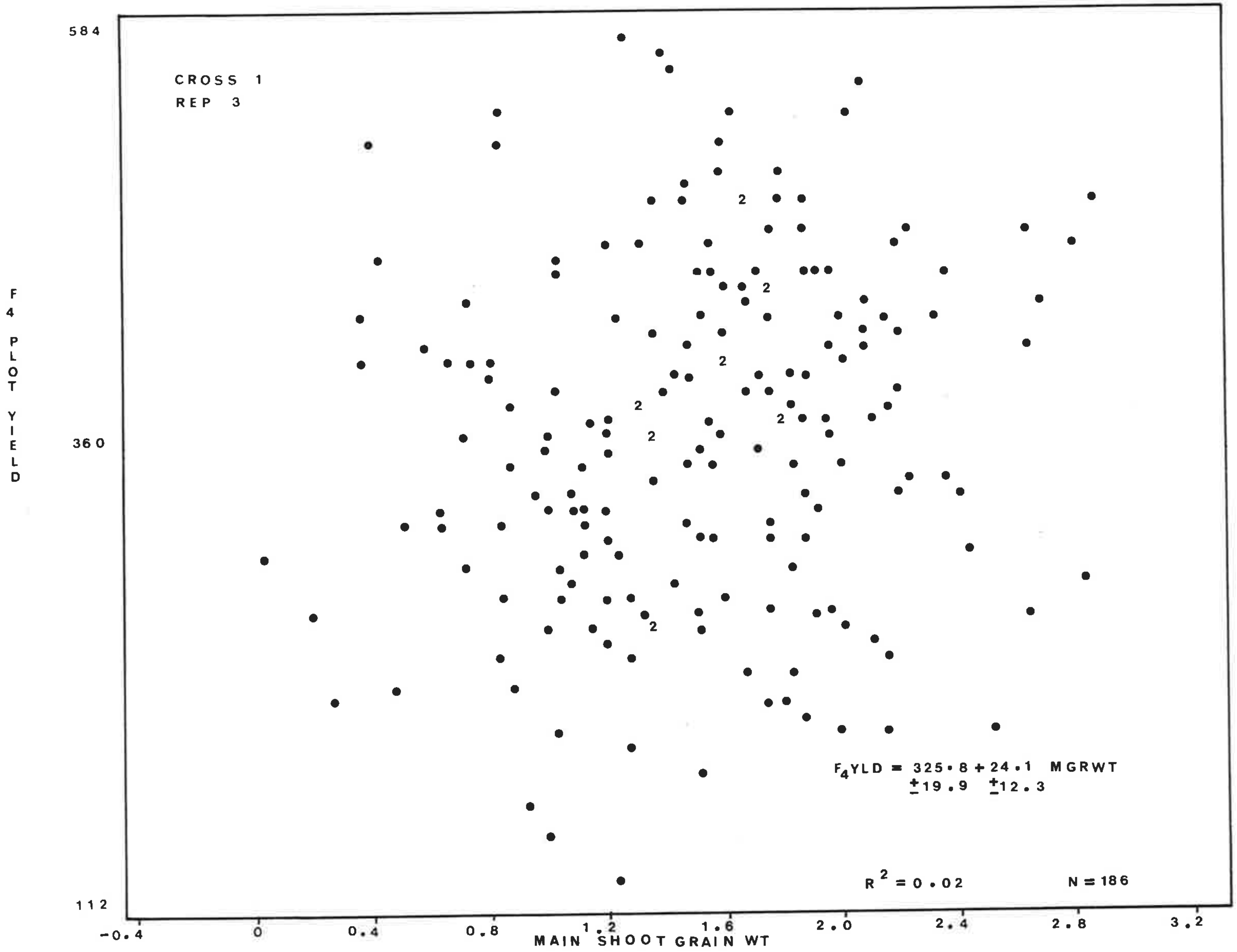
		yield per plot (gm.)					
		Rep 1		Rep 2		Rep 3	
		min.	max.	min.	max.	min.	max.
1	check 1 MM25/4	318	898	441	796	167	453
	check 2 MM68/1	183	739	268	747	175	441
2	check 1 MKR211/9	521	878	579	1010	305	832
	check 2 Warigal	461	904	544	921	82	331
3	check 1 MKR211/9	583	1003	502	1050	229	531
	check 2 MM68/1	441	798	331	891	263	609
4	check 1 Warigal	193	942	378	829	164	730
	check 2 Warigal	163	930	470	854	150	541
5	check 1 Warigal	390	926	376	849	232	505
	check 2 MM68/1	345	925	159	793	189	527
6	check 1 Warigal	401	789	368	833	219	486
	check 2 MMC21/9	500	941	464	936	156	452
7	check 1 WW15/RVN/158/14	558	1061	457	969	163	424
	check 2 Warigal	397	912	319	907	202	457
8	check 1 WW15/RVN/158/14	321	1045	444	945	378	910
	check 2 MM68/1	287	948	434	818	128	448

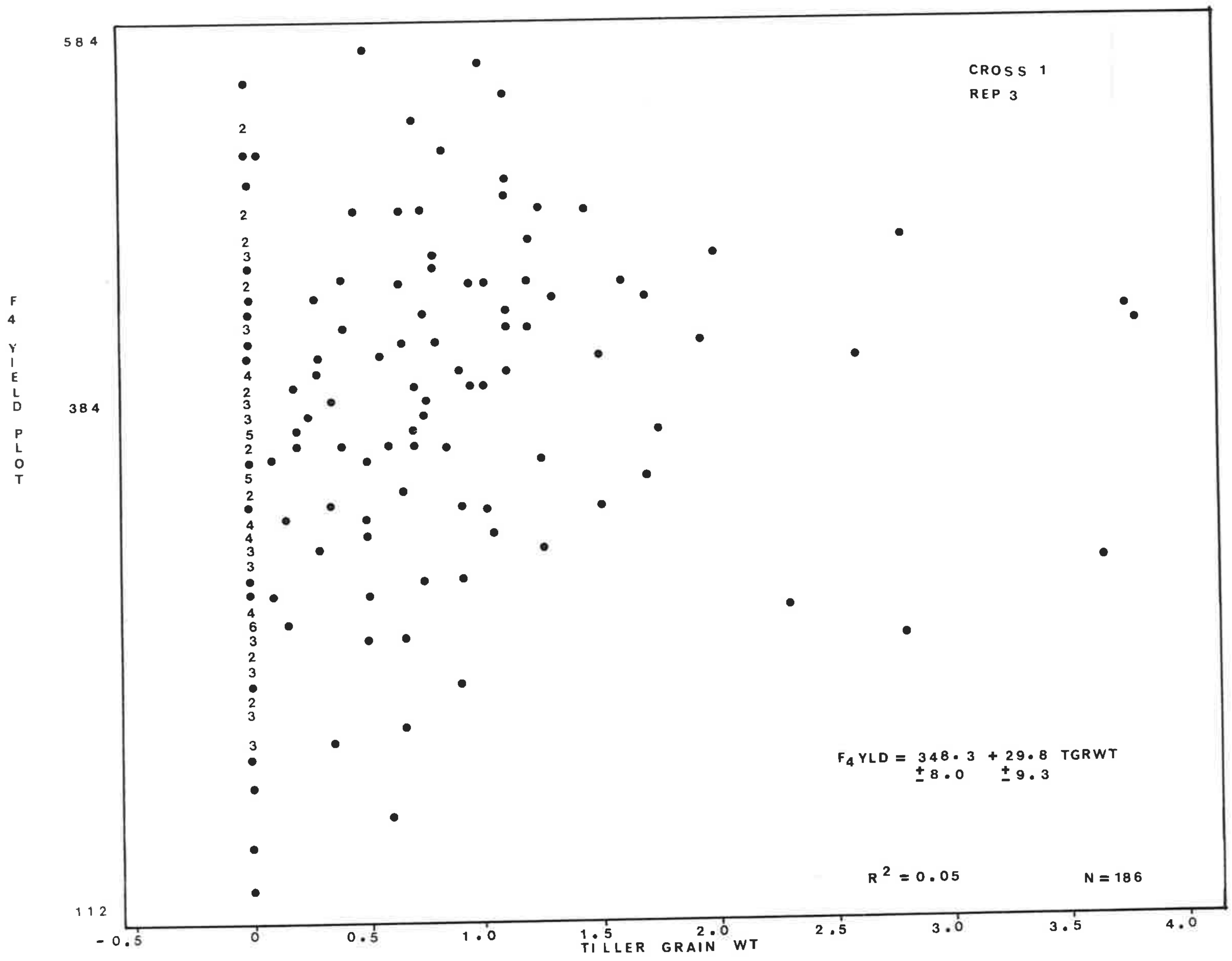
b. The regression of F_4 or F_5 yield on the F_2's main shoot grain weight, tiller grain weight and total grain weight.

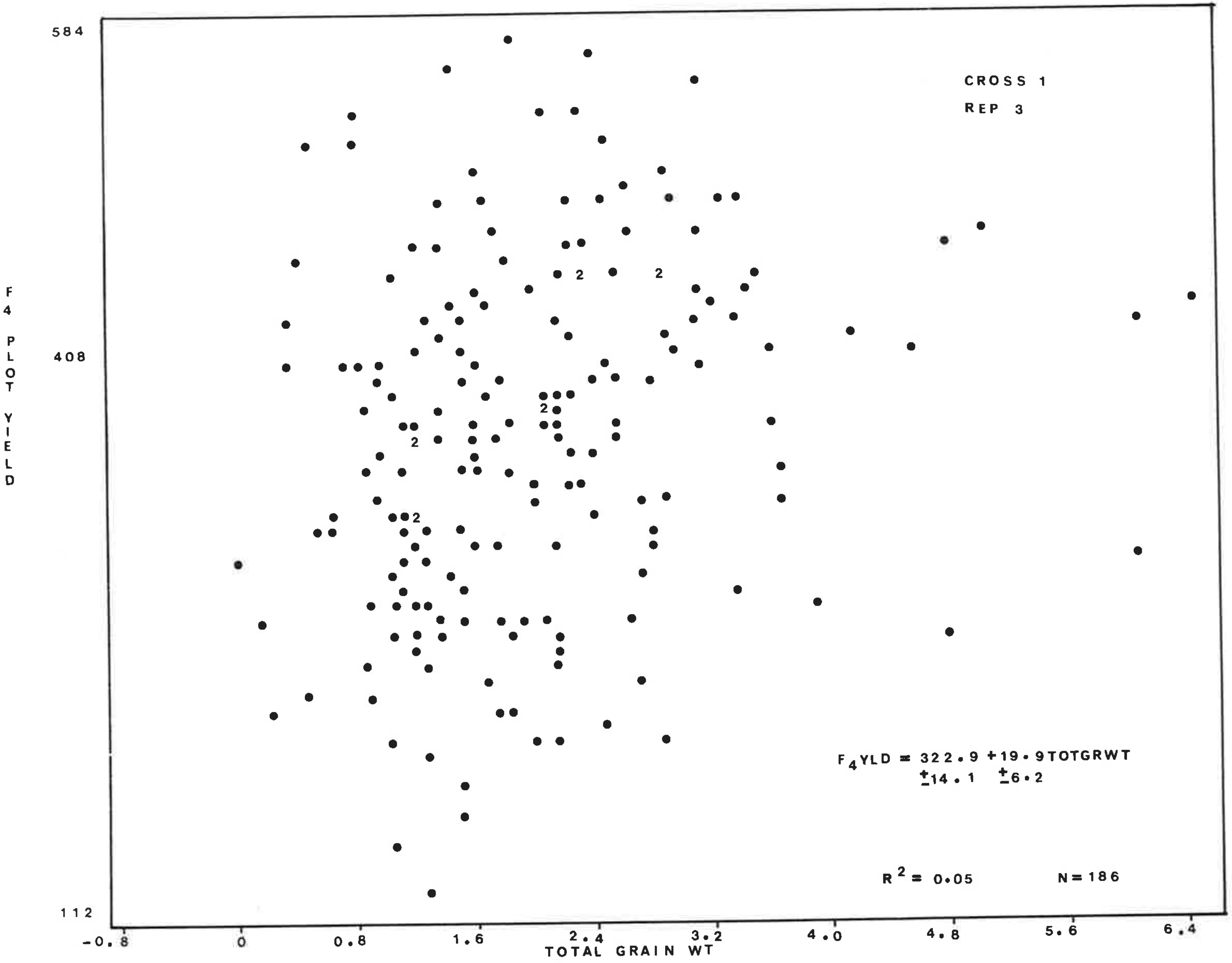
The regression values were calculated but a few examples only are presented in the diagrams.

The graph (Fig. 4.1) relating tiller grain weight to F_4 plot yield illustrates a problem that arose with some of the data. The choice among the F_2's of lines to continue to the F_4 generation was based on subdividing the main shoot grain weight distribution into classes and taking 50% of the lines at random from each class. This procedure would have resulted in an almost random selection of F_2 plants, but as many of the plants had no tillers there are a corresponding number of zero values in the graph. The distribution of the tiller grain weight values is obviously not normal and it may not be strictly justifiable to calculate a correlation or regression.

Figure 4.1. Examples of the regressions of F_4 yields on the F_2's main shoot grain weight, tiller grain weight and total grain weight.


CROSS 1
REP 3
F4 PLOT YIELD
584
360
112
-0.4
0
0.4
0.8
1.2
1.6
2.0
2.4
2.8
3.2
MAIN SHOOT GRAIN WT
2
F4YLD = 325.8 + 24.1 MGRWT
±19.9 ±12.3
R2 = 0.02
N = 186

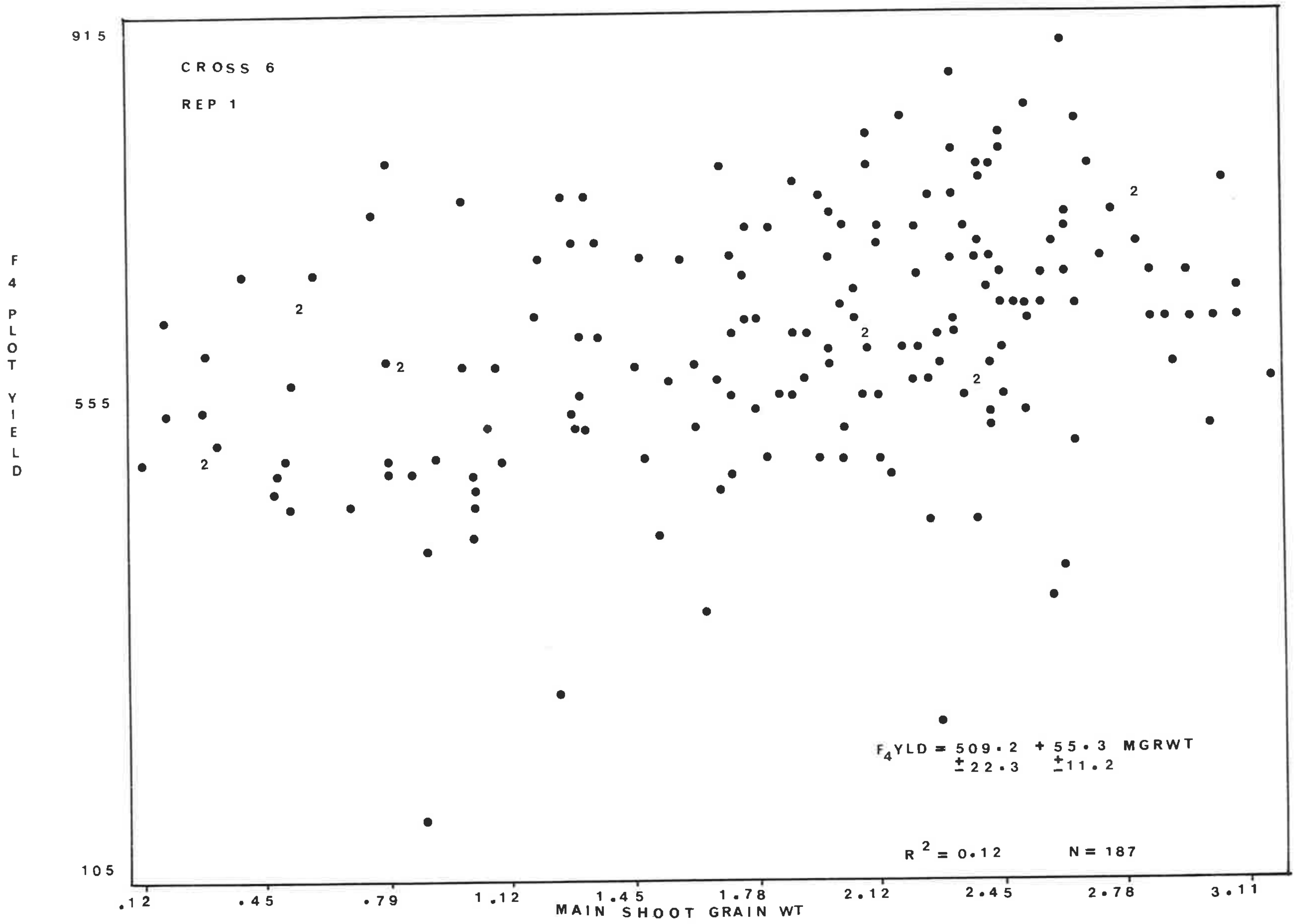

CROSS 1
REP 3
F4 YIELD PLOT
584
384
112
-0.5
0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
4.0
TILLER GRAIN WT
F_4 YLD = 348.3 + 29.8 TGRWT
± 8.0 ± 9.3
R^2 = 0.05
N = 186

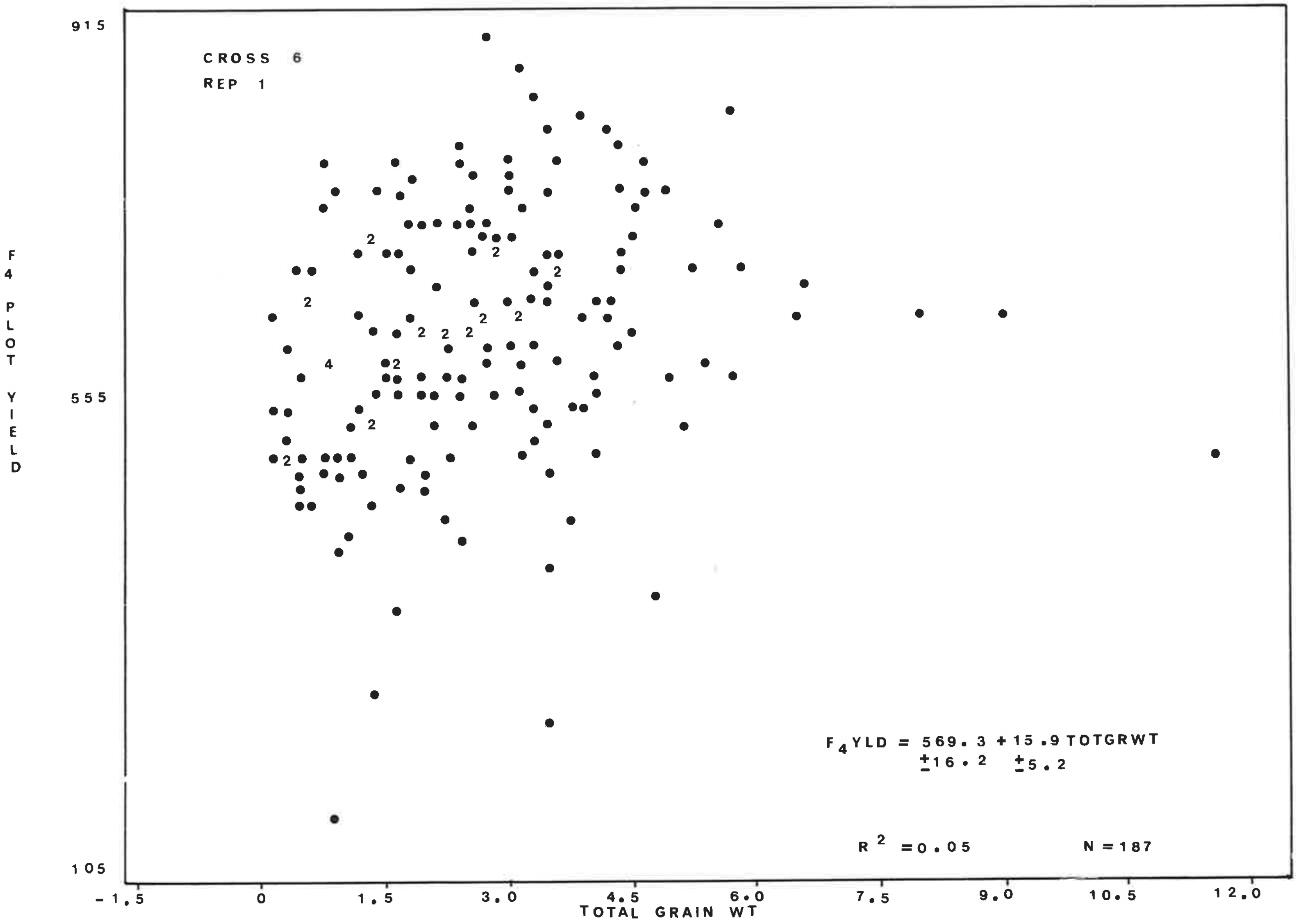


CROSS 1
REP 3

$$F_4YLD = 322.9 + 19.9\,TOTGRWT$$
$$\pm 14.1 \quad \pm 6.2$$

$R^2 = 0.05$ N = 186


CROSS 6
REP 1
F4 PLOT YIELD
915
555
105
.12
.45
.79
1.12
1.45
1.78
2.12
2.45
2.78
3.11
MAIN SHOOT GRAIN WT
F_4YLD = 509.2 + 55.3 MGRWT
± 22.3 ± 11.2
R^2 = 0.12
N = 187


CROSS 6
REP 1
F4 PLOT YIELD
915
555
105
-1.5
0
1.5
3.0
4.5
6.0
7.5
9.0
10.5
12.0
TOTAL GRAIN WT
F4YLD = 569.3 + 15.9 TOTGRWT
±16.2 ±5.2
R2 = 0.05
N = 187

Chapter 5

DISCUSSION

The discussion will be concerned with several aspects of the results in particular the mean values of the populations (P_1, P_2 and F_2), their variances, their skews and the outcome of selection.

1. The mean values of the various generations.

At crop density (experiment 1) in most instances the F_2's means were intermediate between the parental means. In a few instances only did positive heterosis occur with the F_2's means slightly in excess of the parental means and then it was more evident for the characters: main shoot total weight, grain weight, grain number, spikelet number and head length than for plant total weight, tiller grain weight or grain number. There was no evidence of heterosis for total grain weight at crop density (Table 5.1 and Figure 5.1a to 5.1k).

At low density (experiment 2), the evidence for heterosis was different, more marked and more consistent. For the three crosses studied at low density, the F_2's showed positive heterosis for total plant weight, total grain weight, tiller grain weight and grain number (also Table 5.1 and Figure 5.1a to 5.1k). As tiller grain weight and grain number are components of total plant weight and grain weight, it was the heterotic development of the tillers that was the main factor in this result. The suggestion that tiller development is the important factor is supported by the occurrence of transgressive segregation for tiller grain weight and grain number detected at low density and not at crop density.

A difference in the development of tillers is probably the explanation for the failure of selections for high yielding genotypes on single plants grown at low density to provide high yielding genotypes when grown at crop density in later generations. Selection for yield made at low density is selection for genotypes with a high proportion of their yield arising from tillers and this advantage will be lost when the genotypes are grown at crop density, resulting in failure of the selection procedure.

The main shoot's yield on the other hand, may give more reliable information as a guide to high yielding genotypes when a selection is performed on single plants at crop density. The main shoot yield results appeared to be less profoundly influenced by the environment and the main shoot provides the major part of the yield at the crop density.

It is difficult to visualise any general and simple interpretation of the results in quantitative genetic terms. A feature of the means obtained in experiments 1 and 2 was that for any character, the mean of the F_2 could vary from a value close to the midparent $((P_1 + P_2)/2)$ to a heterotic value exceeding either parent negatively or positively (Table 5.1 and Figure 5.1a to 5.1k).

Table 5.1. Number of crosses in which the mean of the F_2 was lower, intermediate or higher than the respective parents. In experiment 1, 8 crosses were grown at crop density. In experiment 2, 3 of these crosses (number 3, 7 and 8) were grown at low density.

character		cross number		
		lower	intermediate	higher
Head number	exp.1	2,4,7	1,3,5,6	8
	exp.2	0	7	3,8
Plant total weight	exp.1	2	1,3,4,5,6,7	8
	exp.2	0	0	3,7,8
Main shoot total weight	exp.1	2	1,3,6,7	4,5,8
	exp.2	0	8	3,7
Height	exp.1	2	1,3,4,5,6,7	8
	exp.2	8	3,7	0
Spikelet number	exp.1	0	1,2,3,4,5,7	6,8
	exp.2	0	3,8	7
Head length	exp.1	0	1,2,3,4,5,7	6,8
	exp.2	0	3,7	8
Main shoot grain weight	exp.1	6	1,2,3,7,8	4,5
	exp.2	0	3,8	7
Main shoot grain number	exp.1	1,3	2,4,6,7	5,8
	exp.2	0	7,8	3
Tiller grain weight	exp.1	2	1,3,4,5,6,7	8
	exp.2	0	0	3,7,8
Tiller grain number	exp.1	2	1,3,4,5,6,7	8
	exp.2	0	7	3,8
Total grain weight	exp.1	2	1,3,4,5,6,7,8	0
	exp.2	0	0	3,7,8

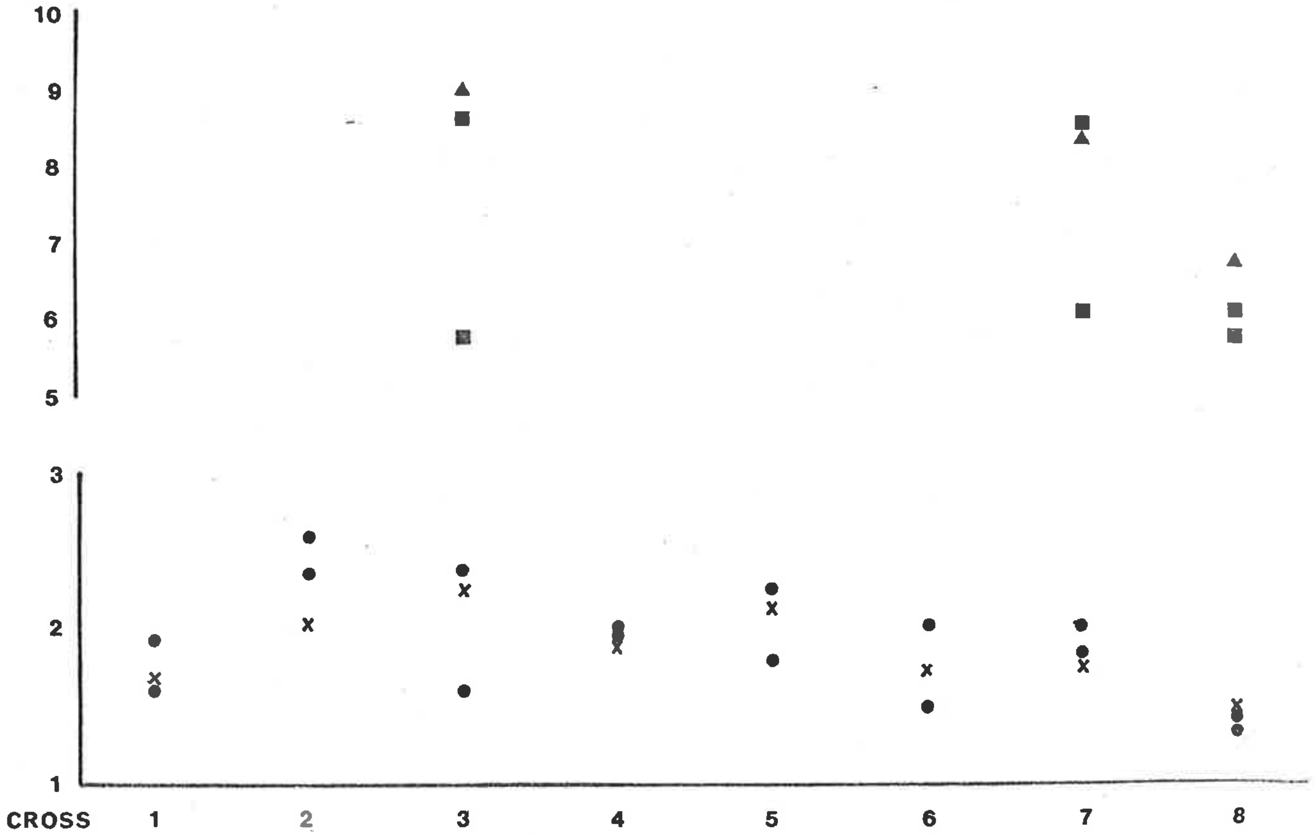
Figure 5.1 (a to k). The F_2 and parental means obtained for eleven characters observed from crosses studied in experiments 1 and 2. Note the break in scale on the y axis.

● is parental mean observed at crop density (exp.1)

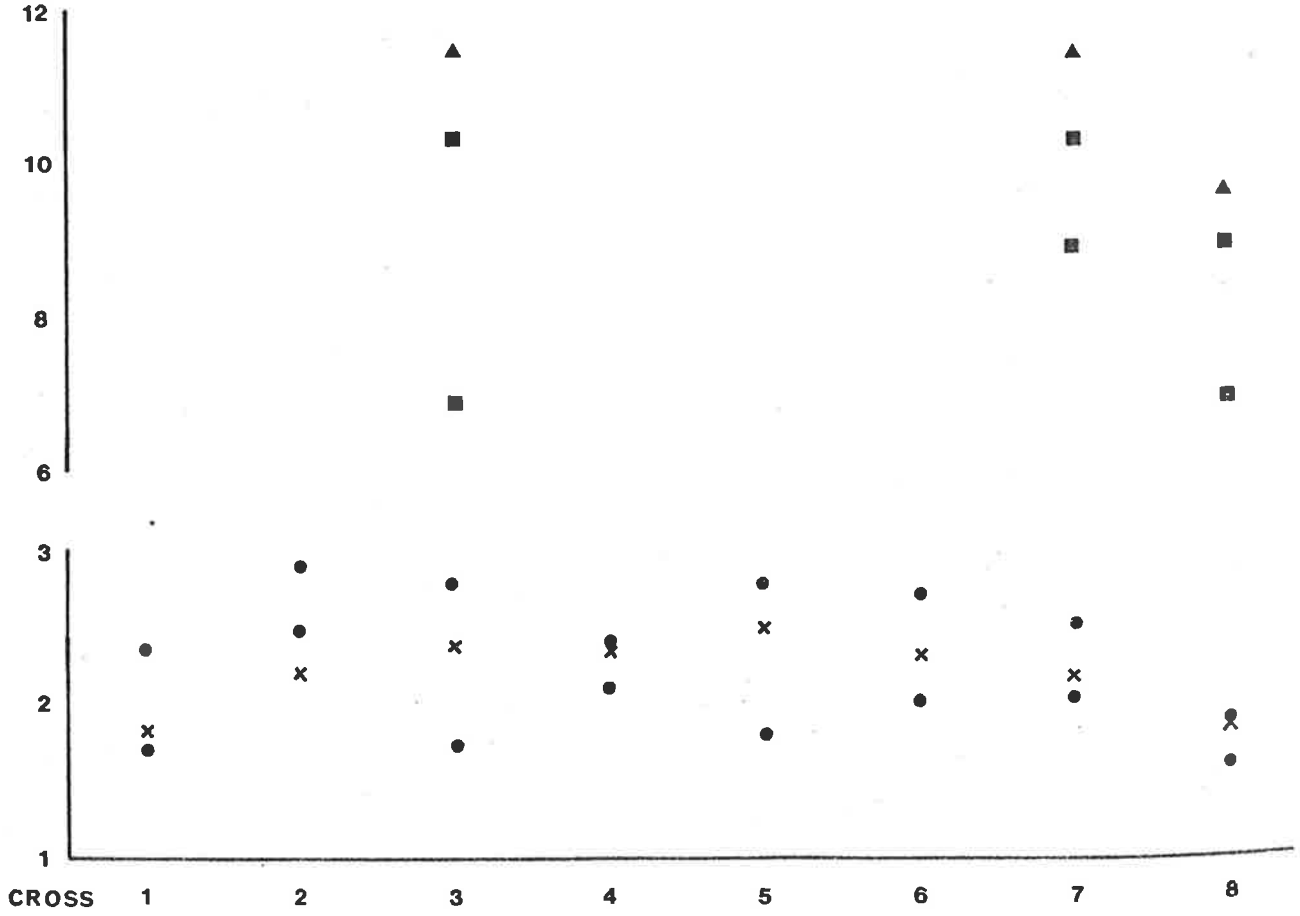
x is F_2's mean observed at crop density (exp.1)

■ is parental mean observed at low density (exp.2)

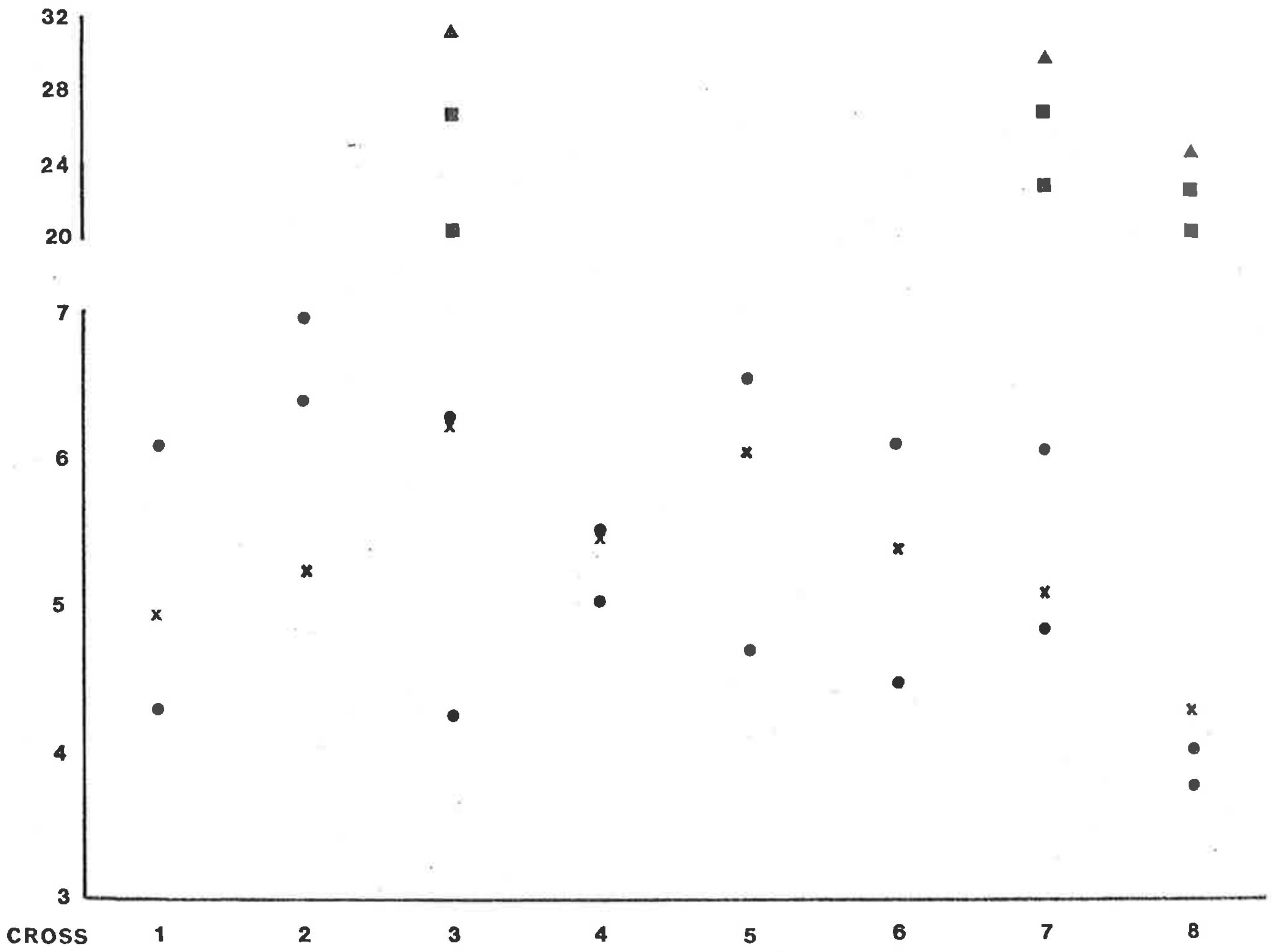
▲ is F_2's mean observed at low density (exp.2) a – HEAD NO



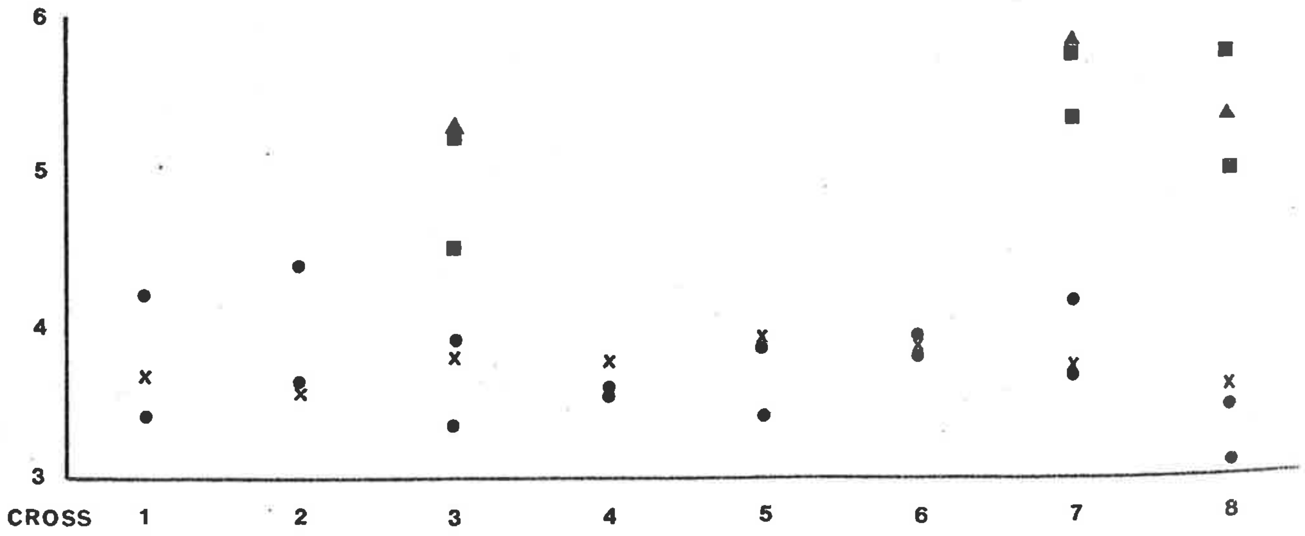
b – TOTAL GRAIN WT



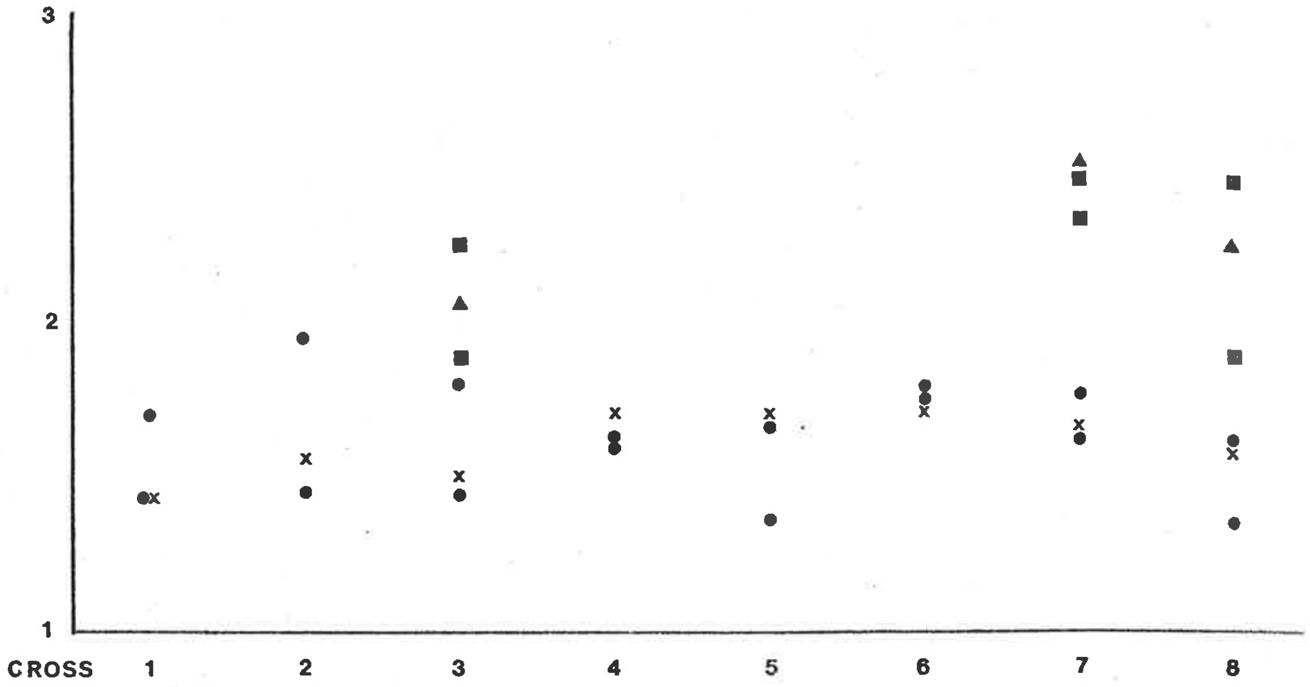
C – TOTAL PLANT WT



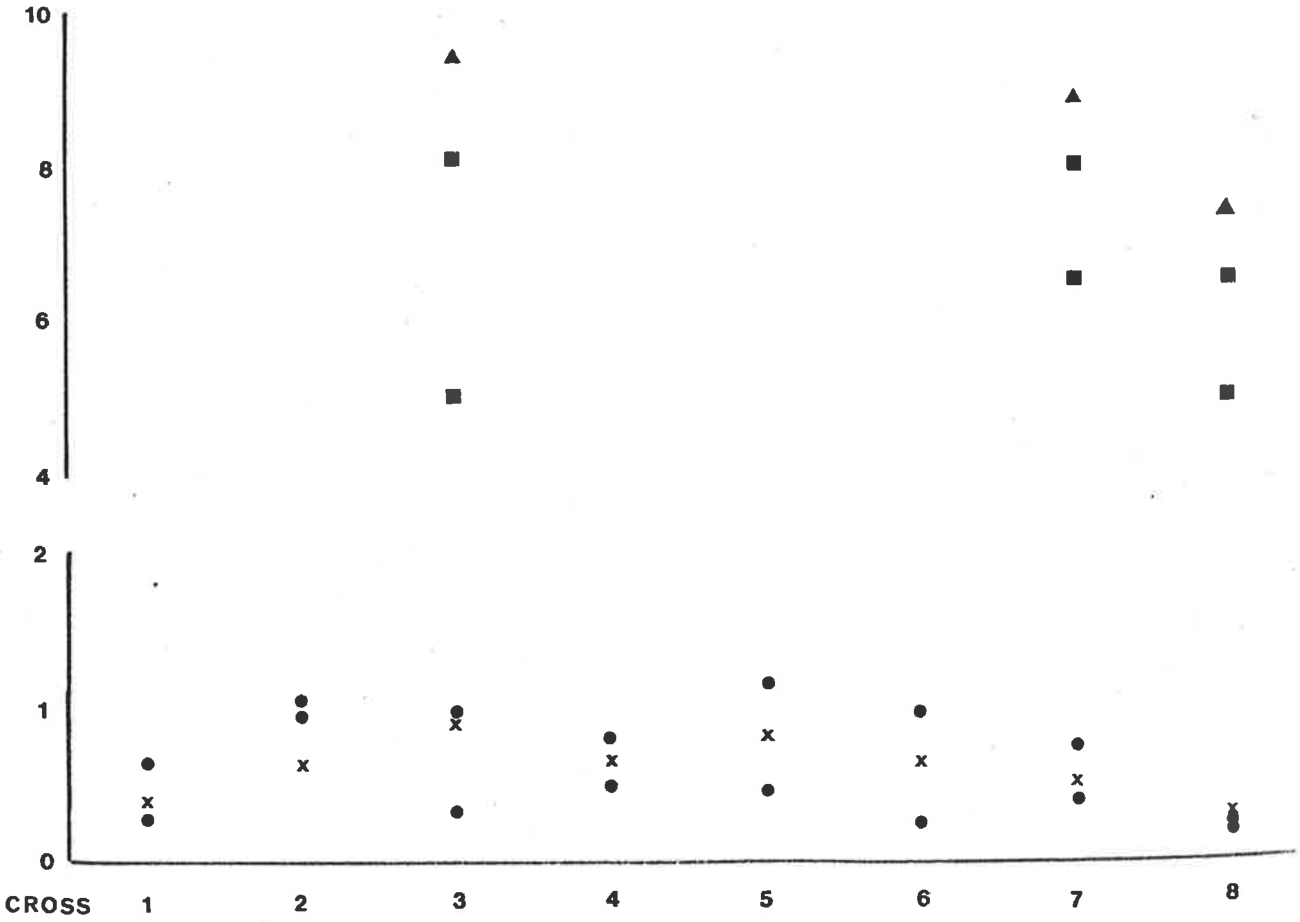
d – MAIN SHOOT TOTAL WT

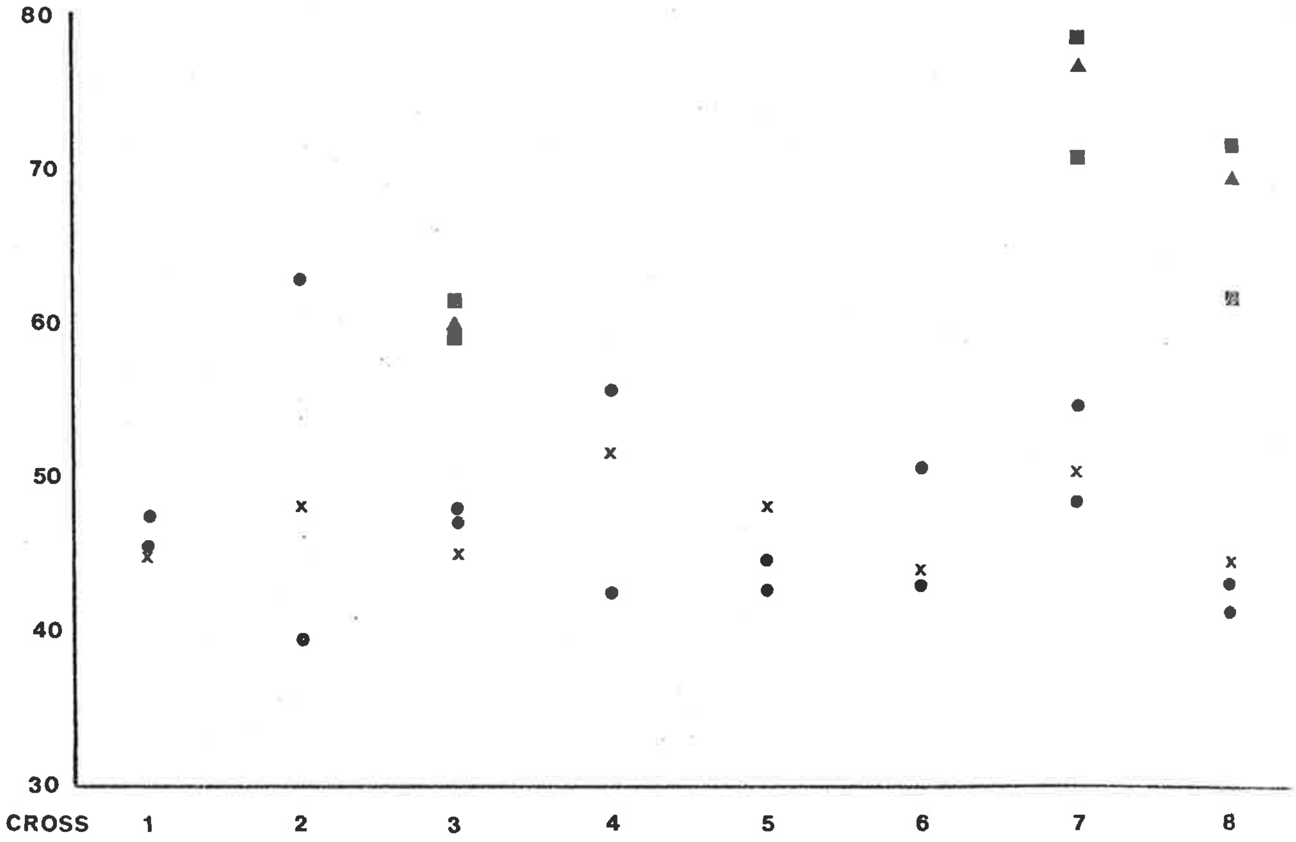


e – MAIN SHOOT GRAIN WT

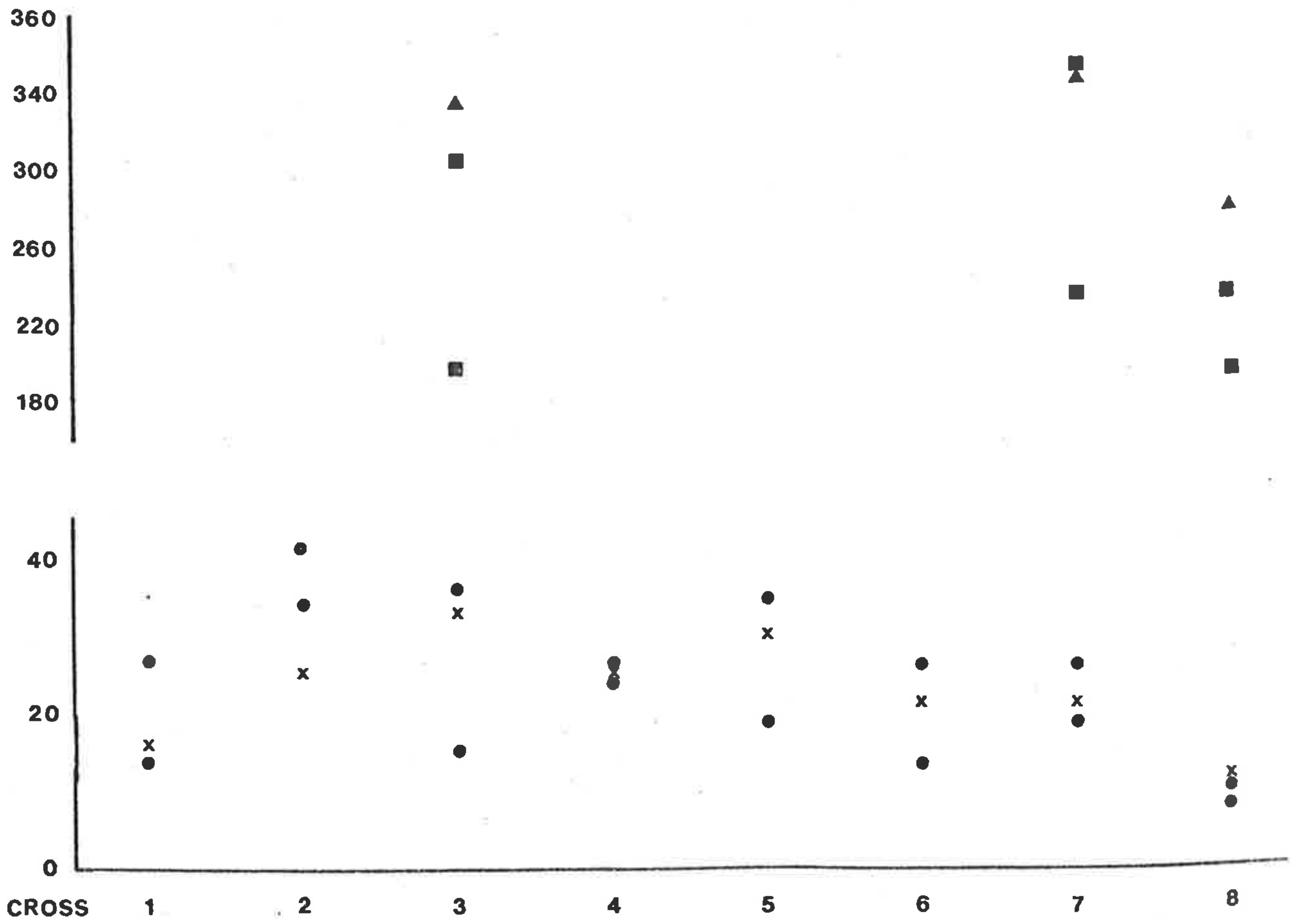


f – TILLER GRAIN WT



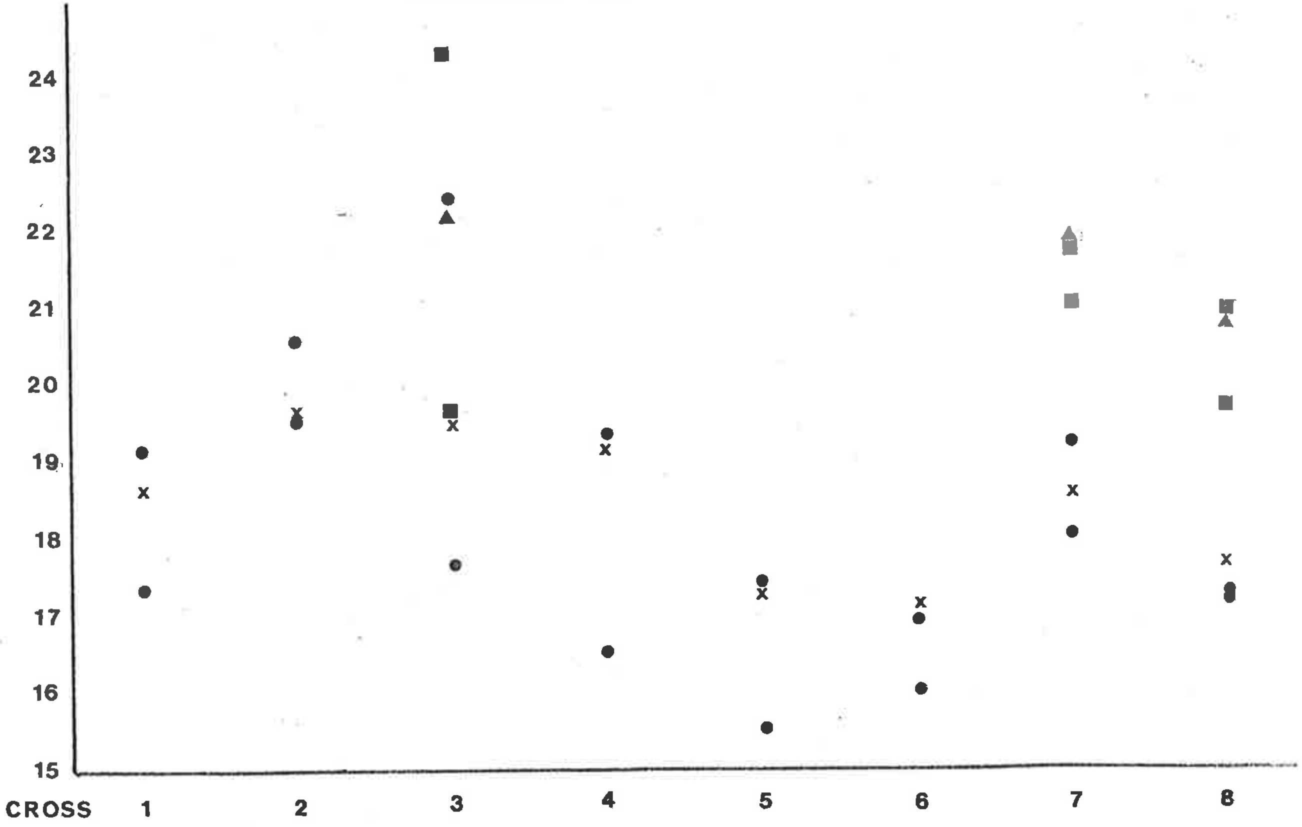


g – MAIN SHOOT GRAIN NO

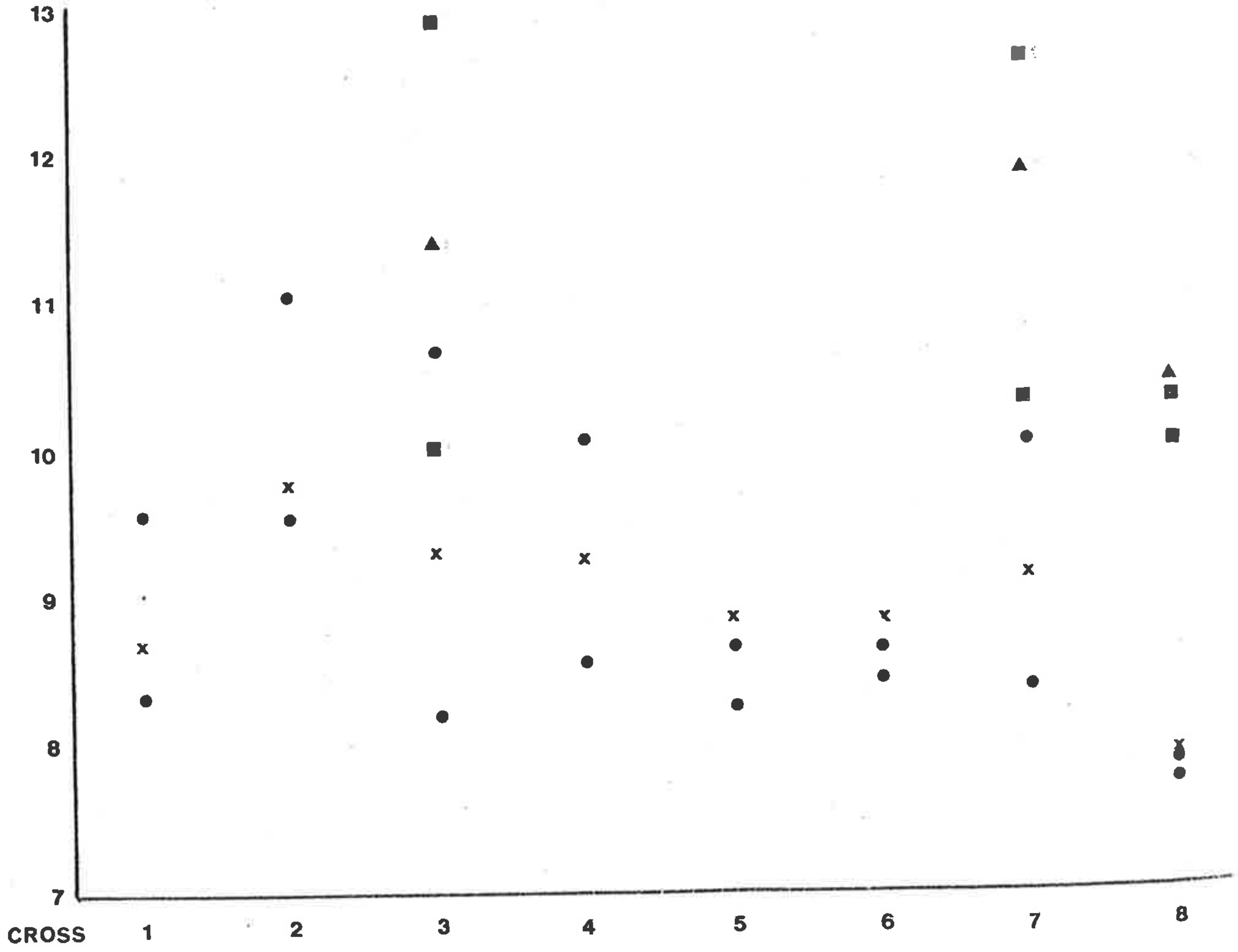


h – TILLER GRAIN NO

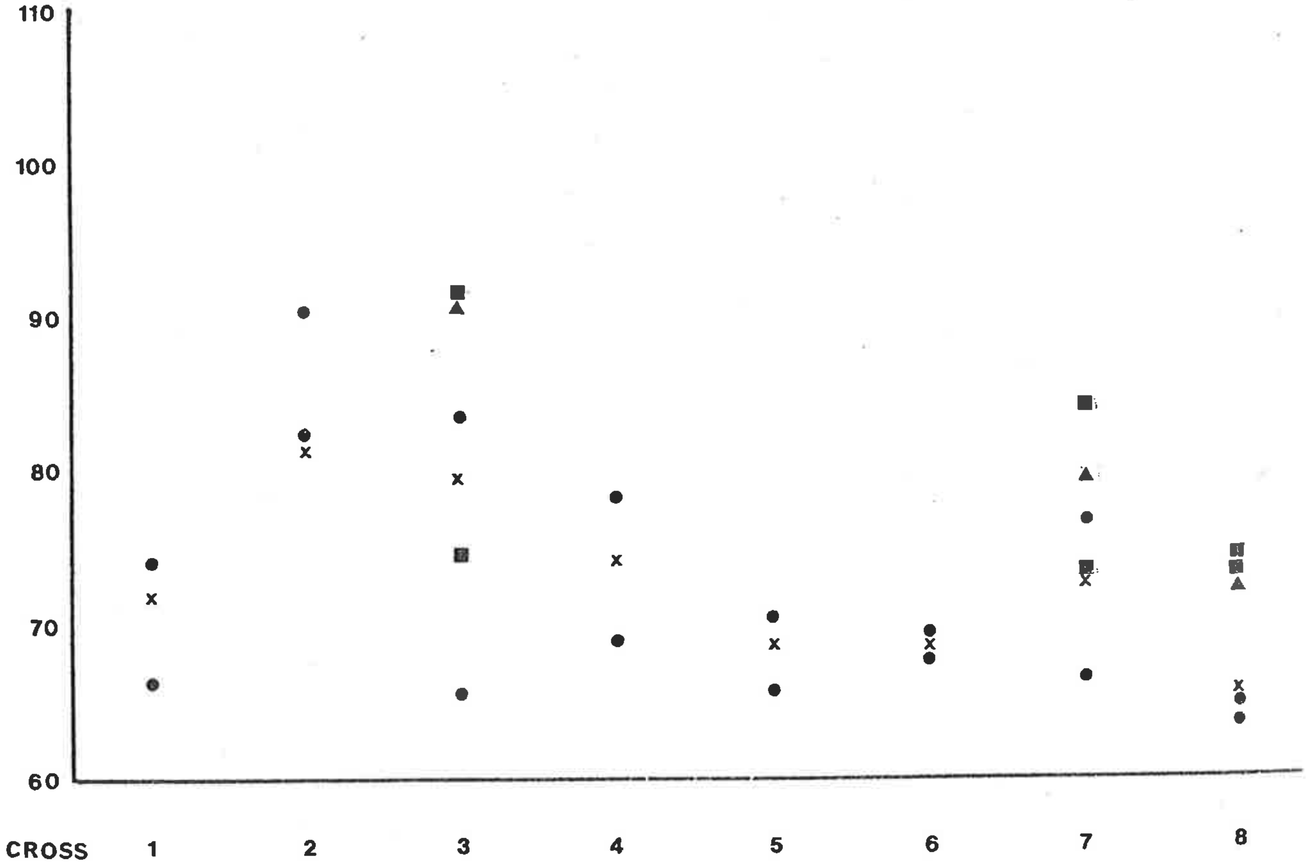
i – SPIKELET NO



j – HEAD LENGTH



k – HEIGHT



2. Variances.

Although there were genetic differences between the parents in each cross and segregation would have occurred, the evidence that the F_2's had a significantly larger variance than the parents was not consistent. At crop density, F_2 variances larger than those of the parents were found more regularly for characters measured on the main shoot; total weight, grain weight, grain number, height, spikelet number and head length, than on the characters; plant total weight, head number, tiller grain weight, tiller grain number and total grain weight. Height was the character, most consistent in showing genetic segregation in the F_2. At low density, most of the F_2's variances were larger than the parental variances and in particular those relating to the tillers - head number, tiller grain weight and tiller grain number (Table 5.2). However these changes were less marked if account is taken of the increases in the mean values. The coefficient of variation of the parents and the F_2 showed only small differences (Table 5.3).

In many quantitative genetic tests it is assumed that the variance attributable to the environment is similar between parents and between parents and the F_2. However it has been suggested on theoretical grounds that variation in parental populations caused by the environment should not be expected to be similar (Knight, 1971). The results obtained in these two experiments support this suggestion, as in many instances the parental variances were significantly different from each other indicating that the genotypes reacted differently to the environment. It is therefore unlikely that parental variances will always give a true measure of the environmental variance present in a segregating population. Falconer (1967) suggested that the environmental variance measured in an inbred line was specific to that genotype and other genotypes may be more or less sensitive to environmental influences. This may therefore affect the estimation of a variance in a mixed genotype population such as an F_2.

He also pointed out that the environmental variance of a mixed genotype population may not be the same as that measured in the genetically uniform population. Furthermore in general, it was found that inbred lines often show more environmental variance; they are less buffered than non inbred or hybrid lines. This may partially explain why the parental variances were not different from the F_2 variances in this study. In fact, the results indicate that the micro-environmental variation of single plants in the parental populations was often approximately equal to the sum of the genetic and micro-environmental variations of the single plants in the F_2 population.

Despite this, there was evidence of genetic segregation in the F_2 populations. The distributional range covered the combined ranges of the parents, the F_2 means were often intermediate between the two parental means, and extreme individuals did occur in the F_2's distributions. It may be interpreted that some F_2 individuals showed an accumulation of favorable dominant genes leading to a higher expression than either parent. Neither the variances nor the mean values of the F_2's provide conclusive information in themselves on the value of an F_2 for selection and it may be necessary to also take account of selection of extreme individuals.

Table 5.2. Variances of P_1, P_2 and F_2 of crosses studied at two densities.

Crop density		HDNO	PLTWT	MTWT	HT	SPIKE	HDLTH	MGRWT	MGRNO	TGRWT	TGRNO	TOTGRWT
cross 1 MM25/4*MM68/1	P_1	0.76	6.22	1.02	103.9	3.71	1.29	0.25	130.9	0.48	801.9	0.92
	P_2	0.71	3.84	0.87	85.1	2.72	0.81	0.20	121.8	0.26	450.6	0.61
	F_2	0.78	6.80	1.52	156.4	7.36	2.12	0.33	236.3	0.43	592.9	1.02
cross 2 MKR211/9*PN28/9	P_1	1.50	11.45	1.32	131.9	6.93	2.58	0.27	121.8	1.05	999.6	1.92
	P_2	1.02	7.99	1.03	47.4	2.66	2.30	0.26	210.4	0.84	1258.5	1.46
	F_2	1.01	7.05	1.18	157.2	6.87	2.76	0.29	231.4	0.65	823.2	1.30
cross 3 MKR211/9*MM68/1	P_1	1.12	8.18	1.18	175.4	9.19	3.08	0.30	138.7	0.96	1070.5	1.66
	P_2	0.62	4.31	1.30	124.6	4.18	1.42	0.30	190.1	0.30	593.0	0.75
	F_2	1.32	11.40	1.73	304.8	8.41	2.71	0.32	180.8	0.91	1089.7	1.77
cross 4 CHAMP/8156/17/52*PN28/9	P_1	0.84	7.46	0.96	69.6	3.87	1.63	0.22	149.9	0.78	783.9	1.41
	P_2	0.96	5.98	1.04	47.2	5.00	2.89	0.25	230.5	0.44	939.6	0.95
	F_2	0.94	8.74	1.52	154.1	7.91	2.71	0.38	260.5	0.72	994.1	1.63
cross 5 CHAMP/8156/17/52*MM68/1	P_1	0.76	7.75	0.94	66.8	3.58	1.35	0.23	102.3	0.91	761.2	1.62
	P_2	0.64	4.45	1.34	162.3	3.01	1.24	0.30	152.2	0.34	451.2	0.86
	F_2	1.03	7.51	1.30	105.4	6.02	2.04	0.30	168.9	0.68	792.5	1.37
cross 6 CHAMP/8156/17/52*MMC21/9	P_1	1.06	11.08	1.54	42.1	7.35	2.60	0.36	193.2	1.42	932.5	2.41
	P_2	0.38	3.47	1.39	37.0	5.18	1.57	0.40	249.8	0.18	422.5	0.75
	F_2	0.72	10.49	2.41	73.1	5.69	2.21	0.65	243.7	0.84	705.1	2.30
cross 7 WW15/RVN/158/14*PN28/9	P_1	0.91	7.49	1.56	88.9	4.33	1.29	0.38	185.4	0.61	663.6	1.45
	P_2	0.54	4.22	1.28	52.1	5.62	3.26	0.35	315.3	0.25	391.4	0.90
	F_2	0.76	8.16	2.03	164.6	7.70	3.28	0.46	305.9	0.57	811.2	1.50
cross 8 WW15/RVN/158/14*MM68/1	P_1	0.29	3.24	1.47	124.2	4.37	1.51	0.37	201.6	0.21	226.6	0.69
	P_2	0.48	3.16	1.08	106.9	4.02	1.34	0.26	165.5	0.20	312.2	0.58
	F_2	0.47	3.81	1.75	147.9	5.31	1.77	0.38	215.6	0.22	302.2	0.75
Low density												
cross 3 MKR211/9*MM68/1	P_1	7.45	91.0	0.49	51.1	2.67	0.96	0.12	39.4	12.7	15834.	13.8
	P_2	3.33	57.7	0.72	47.7	1.32	0.45	0.18	121.9	6.8	7980.	8.2
	F_2	9.20	143.9	0.96	168.8	3.12	1.12	0.16	66.9	18.8	19829.	20.9
cross 7 WW15/RVN/158/14*PN28/9	P_1	3.90	64.5	0.65	35.3	1.13	0.32	0.17	86.3	10.5	11619.	11.9
	P_2	5.90	67.5	0.57	32.1	2.07	1.87	0.12	104.0	10.0	15588.	11.0
	F_2	7.98	144.4	1.06	104.9	2.86	1.00	0.26	116.7	20.4	25370.	23.4
cross 8 WW15/RVN/158/14*MM68/1	P_1	3.90	64.5	0.65	35.3	1.13	0.32	0.17	86.3	10.5	11619.	11.9
	P_2	3.33	57.7	0.72	47.7	1.32	0.45	0.18	121.9	6.8	7980.	8.2
	F_2	5.66	94.2	0.91	86.4	1.97	0.80	0.20	115.3	13.3	17992.	15.1

Table 5.3. CV's of P_1, P_2 and F_2 of crosses studied at two densities.

		HDNO	PLTWT	MTWT	HT	SPIKE	HDLTH	MGRWT	MGRNO	TGRWT	TGRNO	TOTGRWT
Crop density												
cross 1	P_1	0.46	0.41	0.24	0.14	0.10	0.12	0.29	0.24	1.06	1.06	0.41
	P_2	0.53	0.53	0.27	0.14	0.10	0.11	0.31	0.24	1.73	1.57	0.45
	F_2	0.53	0.53	0.34	0.17	0.15	0.17	0.40	0.34	1.65	1.50	0.56
cross 2	P_1	0.47	0.53	0.32	0.13	0.13	0.17	0.36	0.28	1.01	0.91	0.56
	P_2	0.43	0.41	0.23	0.08	0.08	0.14	0.26	0.23	0.97	0.87	0.42
	F_2	0.52	0.51	0.31	0.15	0.13	0.17	0.34	0.32	1.28	1.15	0.52
cross 3	P_1	0.44	0.46	0.28	0.16	0.14	0.16	0.31	0.24	1.00	0.92	0.47
	P_2	0.50	0.49	0.34	0.17	0.12	0.15	0.39	0.29	1.77	1.63	0.50
	F_2	0.51	0.54	0.35	0.22	0.15	0.18	0.38	0.30	1.10	1.02	0.56
cross 4	P_1	0.47	0.50	0.28	0.12	0.12	0.15	0.30	0.29	1.10	1.07	0.50
	P_2	0.50	0.49	0.28	0.09	0.12	0.17	0.31	0.27	1.37	1.24	0.46
	F_2	0.52	0.54	0.33	0.17	0.15	0.17	0.36	0.31	1.34	1.26	0.54
cross 5	P_1	0.39	0.43	0.25	0.12	0.12	0.13	0.29	0.24	0.84	0.80	0.46
	P_2	0.45	0.45	0.34	0.19	0.10	0.14	0.41	0.28	1.31	1.13	0.51
	F_2	0.48	0.46	0.29	0.15	0.14	0.16	0.33	0.27	1.02	0.93	0.47
cross 6	P_1	0.51	0.55	0.32	0.09	0.17	0.19	0.34	0.32	1.28	1.18	0.58
	P_2	0.41	0.42	0.31	0.09	0.13	0.15	0.36	0.31	1.84	1.62	0.43
	F_2	0.49	0.60	0.41	0.13	0.14	0.17	0.48	0.35	1.48	1.32	0.66
cross 7	P_1	0.47	0.45	0.30	0.14	0.12	0.14	0.35	0.28	1.09	1.00	0.48
	P_2	0.40	0.43	0.31	0.09	0.12	0.18	0.37	0.33	1.32	1.08	0.47
	F_2	0.51	0.57	0.38	0.18	0.15	0.20	0.41	0.35	1.56	1.37	0.57
cross 8	P_1	0.41	0.45	0.35	0.17	0.12	0.16	0.38	0.34	2.08	1.86	0.45
	P_2	0.48	0.47	0.34	0.16	0.12	0.15	0.38	0.30	1.84	1.66	0.48
	F_2	0.47	0.46	0.37	0.19	0.13	0.17	0.39	0.33	1.87	1.63	0.48
Low density												
cross 3	P_1	0.31	0.36	0.13	0.08	0.07	0.07	0.15	0.10	0.43	0.41	0.35
	P_2	0.31	0.37	0.17	0.09	0.05	0.06	0.22	0.17	0.52	0.45	0.41
	F_2	0.33	0.38	0.18	0.14	0.08	0.09	0.19	0.14	0.46	0.42	0.39
cross 7	P_1	0.32	0.36	0.14	0.08	0.05	0.05	0.17	0.13	0.50	0.46	0.39
	P_2	0.28	0.31	0.14	0.06	0.06	0.11	0.15	0.13	0.39	0.35	0.32
	F_2	0.34	0.41	0.18	0.13	0.07	0.08	0.20	0.14	0.51	0.46	0.42
cross 8	P_1	0.32	0.36	0.14	0.08	0.05	0.05	0.17	0.13	0.50	0.46	0.39
	P_2	0.31	0.37	0.17	0.09	0.05	0.06	0.22	0.17	0.51	0.45	0.41
	F_2	0.35	0.39	0.18	0.13	0.07	0.08	0.20	0.15	0.49	0.47	0.40

3. Skewness in the distributions as an indication of the micro-environment effect.

Strong and consistent skews were obtained for many of the characters studied some being positive and others negative. As mentioned in the Literature review, skews have been interpreted as being the outcome of known growth processes (Koyama and Kira, 1956).

It was found both at crop density (experiment 1) and low density (experiment 2) that the height distributions were negatively skewed (Table 5.4 and 5.5) with the skews less pronounced at low density where the competition would have been less. Plants could grow as tall as their genetic potential would provide and be near their maximum expression for height. Only a few plants, in which the main shoot was damaged by disease or pests, would there be an inability to reach the maximum height. These plants would therefore form the negative tail of the distribution.

At crop density, height may be influenced by differences in light intensity and competition (Yoda *et al.*, 1957). Reducing the amount of light received by a shoot may promote its elongation by etiolation (Leopold and Kriedemann, 1975; Yoda *et al.*, 1957). The effect will cause shorter shoots to accelerate their stem elongation relatively to the taller shoots so there is less shading from the taller neighbours. This process will tend to produce a population of individuals with similar height. Any plants unable to maintain the approximate height of the population and unable to elongate will become progressively more shaded. They will form the negative tail of the distribution. The effect of competition on height- a tendency to equalise- is the opposite of what is commonly considered for the competition effect on tillering and growth which is; the larger the plant the more it will enlarge.

In addition to the skew for height it was found that all of the characters assessed on the main shoot had negatively skewed distributions (Table 5.4 and 5.5). For these other characters such as head length, the negatively skewed distribution is unlikely to be affected by the micro-environment to the same extent as height. It is suggested that in the developing head (inflorescence) the genetic constitution usually plays a greater role than the environment. Plants have a certain potential to develop their head length, spikelet number etc. which depends mainly on the controlling genes. There is therefore a genetically predetermined length of head or number of spikelets per head, and only a few fall below the levels as a result of damage or disease. Again a negative skew is expected for such characters.

If the reason for the main shoot having a negative skew is that it is more strongly influenced by the genotype of the plant than the micro-environment, then the question arises as to the distribution of the first tiller on a plant and the distribution of the next tiller etc. In theory these will also have predetermined upper limits to their sizes. In addition if a plant with a big main shoot tended to produce a big first tiller, then we would expect a similar type of frequency distribution for both characters; both would be negatively skewed. This expectation proved to be incorrect.

Information on the frequency distribution of the first tiller formed on plants was obtained from the populations in experiment 1 by examining those plants with only one tiller. It was found (Table 5.6 and Figure 5.2) that the distribution for the total weight of the first tiller had a positive skew as did the first tiller grain weight. This picture was obtained by the hybrid (F_2) population and the pure lines. The result suggests either a lack of association between the main shoot and the first tiller or that the association was reduced by the micro-environmental effect.

A complete lack of association seems unlikely as the initial growth of a first tiller is dependent on the main shoot for its carbohydrate and nutrients supply and does not become independent until it has developed about three mature leaves (Evans *et al.*, 1975). Table 2.80 presents the values for the correlation between the two characters. The values although very low confirm the existence of the association.

A greater micro-environmental effect on the first tiller therefore is more likely. It is known that the micro-environment has a marked effect on a related process, tillering and includes factors such as: planting depth (Percival, 1921), temperature (Taylor and McCall, 1936), light intensity (Khalil, 1956; Friend, 1965, 1966), and nutrition (Asana *et al.*, 1966). From Figure 2.24 it can be seen that most of the first tillers were either without a head or a head without grain. As many as 85 per cent (cross 8) of the first tillers had a zero grain weight. Ranking the main shoot and the first tiller grain weight showed that plants which produced a lower grain weight of the main shoot tended to produce also a lower first tiller grain weight. In fact the plants with the lowest main shoot grain weight were also the plants with the lowest first tiller grain weight. This result together with the large number of degree of freedom (around 200) may have lead to the highly significant correlations obtained in Table 5.7.

It is suggested therefore that there is a masked association between the main shoot and the tillers. It is masked due to a stronger influence of the micro-environment on the tillers than on the main shoot. The first tillers have not reached their genetically determined potential because of the strong conditions of competition that occurred at crop density. Theoretically the first tillers should conform to a negative distribution but under conditions of competition and stress their distribution may be positive. It was not feasible to test the hypothesis on the plants at low density as the first tillers on these plants could not be distinguished from the many other tillers.

The explanation for the positive skews obtained for total plant weight and total grain weight may be based on the exponential equation for plant growth considered by Koyama and Kira (1956) which is:

$$w = w_o e^{rt}$$

where: w is the plant weight at the time t

w_o is the initial plant weight

r is relative growth rate

e is the exponential value

In the F_2 populations if w_o and r were normally distributed, the distribution of w (total plant weight, total grain weight, tiller grain weight etc.) would become log normal and therefore positively skewed on an additive scale. In the parental populations, w_o would also be normal as a result of variation in seed size. Although the genetic component of r is expected to be constant for the plants of any one parental population r itself could be normally distributed. This is because the variation in seed size as well as sowing depth could cause the variation in seedling emergence and early development. In the parental populations also w becomes log normal. This will occur even under non or low competitive conditions as was the case in experiment 2. If competition becomes intense the positive skew may become stronger as was the case of experiment 1 (crop density) (Table 5.6 and 5.7).

Types of distribution skewness as a guide for single plant selection.

Selection in early generations based on single plants will be affected by the type of frequency distribution and whether it is positively or negatively skewed. The discussion above suggested that the positive skew distributions of total plant weight and total grain weight were influenced and accentuated by the effect of competition and the relative growth rate. Koyama and Kira (1956) also found a close relation between competition, self-thinning and positive skews of total plant weight. This implies that plants with the smallest values in the distribution were at a disadvantage as a result of their lower competitive ability and plants with high value are ones which have gained some advantage from competitive dominance. Selection for plants of high total plant weight is therefore a selection for a genotype with a high competitive ability and this may be of no advantage when grown in pure stand and furthermore the high values of the plants in the positive tail of the distribution will not reflect their true genetic potential. A small genetic advantage may have been accentuated.

A negatively skewed distribution on the other hand, indicates that there were a large number of plants in the highest class. Differences among these plants although small would be largely determined by their differences in genetic constitution. Selection based on these differences therefore may be relatively more effective.

Table 5.4. Coefficient values of skewness for characters observed from F_2's and parental populations of eight crosses studied at crop density.

	HDNO	PLTWT	MTWT	HT	SPIKE	HDLTH	MGRWT	MGRNO	TGRWT	TGRNO	TOTGRWT
cross 1											
P_1	1.48	1.19	-1.13	-1.60	-1.87	-1.81	-1.06	-1.06	1.46	2.38	0.85
P_2	1.82	1.22	-0.39	-1.06	-0.75	-0.51	-1.06	-0.41	2.29	1.91	1.19
F_2	1.82	1.23	-0.34	-0.65	-1.18	-0.88	-0.24	-0.38	2.32	1.99	1.17
cross 2											
P_1	0.61	0.62	-0.38	-0.80	-1.43	-1.04	-0.17	-0.48	1.00	0.81	0.69
P_2	0.30	0.20	-1.36	-1.18	-2.12	-1.18	-1.24	-1.10	0.67	0.60	0.21
F_2	1.15	0.88	-0.78	-0.95	-1.19	-1.00	-0.74	-0.39	1.80	1.57	0.83
cross 3											
P_1	0.60	0.59	-1.03	-2.32	-2.34	-1.48	-1.10	-1.36	1.17	1.19	0.57
P_2	1.45	0.05	-0.32	-0.92	-1.46	-1.13	-0.27	-0.47	2.54	2.25	0.93
F_2	0.99	0.87	-0.50	-0.77	-1.38	-0.78	-1.04	-0.86	1.63	1.57	0.82
cross 4											
P_1	0.93	0.60	-0.97	-2.24	-1.24	-1.34	-1.01	-0.89	1.20	1.28	0.54
P_2	0.82	0.89	-0.63	-1.76	-1.24	-0.66	-0.65	-0.75	1.78	1.44	0.80
F_2	1.50	1.06	-0.69	-0.91	-1.96	-1.09	-0.63	-0.83	1.90	1.92	0.87
cross 5											
P_1	0.81	0.23	-1.00	-2.59	-0.63	-1.50	-0.93	-1.14	0.62	0.61	0.19
P_2	0.60	0.42	-0.54	-0.96	-1.81	-1.53	-0.48	-0.90	1.29	0.84	0.41
F_2	1.24	0.52	-0.85	-1.42	-0.91	-1.31	-0.72	-0.79	1.20	0.99	0.58
cross 6											
P_1	1.32	0.90	-1.22	-1.07	-1.47	-1.90	-1.12	-1.07	1.92	1.83	0.96
P_2	1.09	0.73	-0.66	-3.07	-1.28	-0.99	-0.61	-0.44	3.07	2.94	0.36
F_2	1.26	0.83	-0.41	-1.37	-1.09	-0.85	-0.43	-0.32	2.06	1.81	0.80
cross 7											
P_1	0.74	0.34	-0.69	-1.24	-1.88	-1.56	-0.53	-0.64	0.82	0.87	0.28
P_2	0.40	0.01	-1.15	-2.01	-1.46	-1.30	-0.96	-1.23	1.30	0.88	0.10
F_2	1.20	0.86	-0.28	-0.70	-1.57	-1.40	-0.42	-0.54	1.99	1.59	0.91
cross 8											
P_1	1.65	0.81	-0.27	-1.34	-1.26	-1.08	-0.41	-0.44	2.38	2.04	0.68
P_2	1.85	0.39	-0.30	-1.30	-1.37	-1.32	-0.25	-0.45	2.19	1.70	0.75
F_2	1.43	0.70	-0.22	-1.28	-1.27	-0.90	-0.37	-0.32	2.30	1.90	0.59

Table 5.5. Coefficient values of skewness for characters observed from F_2's and parental populations of three crosses studied at low density.

	HDNO	PLTWT	MTWT	HT	SPIKE	HDLTH	MGRWT	MGRNO	TGRWT	TGRNO	TOTGRWT
cross 3											
F_2	0.44	0.29	0.04	-0.41	0.24	0.28	-0.32	0.47	0.32	0.38	0.26
cross 7											
F_2	0.27	0.71	0.00	-0.30	0.40	0.22	-0.45	0.07	0.77	0.61	0.67
cross 8											
F_2	0.45	0.65	-0.40	-1.27	-0.08	-0.95	-0.67	-0.61	0.60	0.74	0.50
parents											
MKR211/9	0.42	0.80	-0.50	-1.72	-0.41	-0.39	-0.83	-0.76	0.84	0.78	0.77
PN28/9	0.60	0.66	-0.12	-0.98	-0.24	-0.06	-0.42	-0.33	0.78	0.56	0.73
WW15RVN 158/14	0.60	0.59	-0.73	-2.56	-0.31	-0.34	-0.58	-0.64	1.07	0.92	0.97
MM68/1	0.44	1.10	-0.08	0.90	-0.50	-1.18	-0.23	-0.35	1.20	0.61	1.08

Table 5.6. Coefficient of skewness values calculated from the population of plants having only two culms (the main shoot and one tiller). Negative skews were obtained for the main shoot and a positive skew for the tiller (values obtained for crop density of experiment 1). The character symbols are defined in the footnote.

	Coefficient values of skewness for					
	PLTWT	MTWT	TWT	MGRWT	TGRWT	TOTGRWT
F_2 population of						
cross 1	0.22	-0.13	0.44	-0.28	0.77	0.11
cross 2	0.04	-1.17	0.76	-1.06	0.94	0.05
cross 3	0.18	-0.55	0.49	-0.71	0.55	0.09
cross 4	0.11	-0.92	0.60	-0.83	0.77	0.22
cross 5	-0.04	-0.84	0.43	-0.74	0.61	0.05
cross 6	-0.04	-0.84	0.68	-0.87	0.72	-0.02
cross 7	0.24	-0.78	0.97	-0.83	1.33	0.28
cross 8	0.04	-0.50	0.97	-0.56	1.25	0.02
pure lines						
MM68/1	0.03	-0.63	0.71	-0.60	1.05	-0.01
MKR211/9	-0.14	-0.79	0.03	-0.93	0.16	-0.11

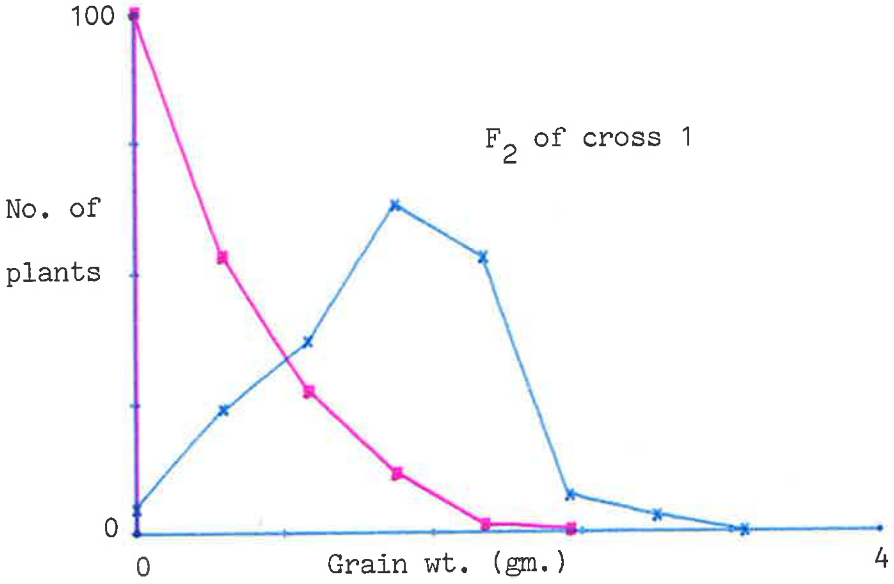
Coefficient of skewness for significant difference from zero at 5% probability level is ± 0.280.

PLTWT	-	plant total weight
MTWT	-	main shoot total weight
TWT	-	tiller total weight
MGRWT	-	main shoot grain weight
TGRWT	-	tiller grain weight
TOTGRWT	-	total grain weight

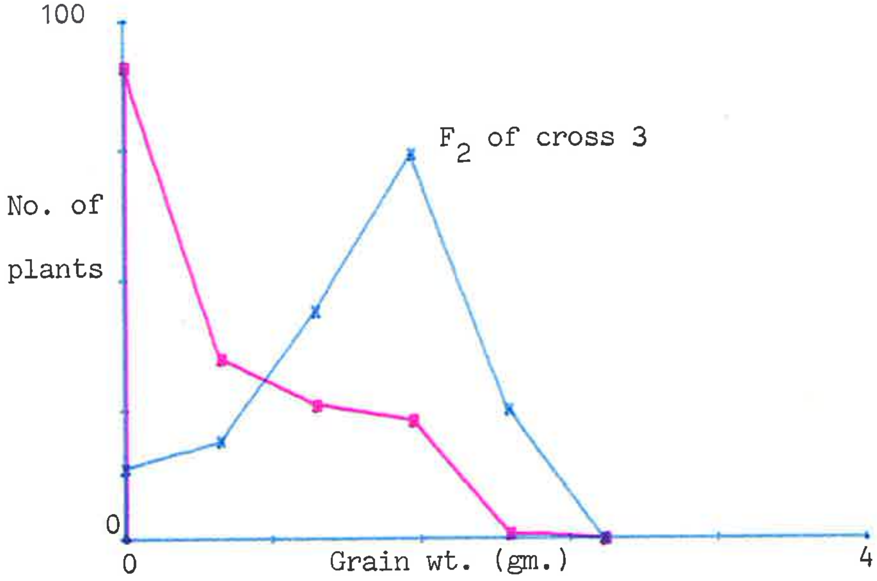
Table 5.7. Correlations between the main shoot total weight (MTWT) and tiller total weight (TWT) and between the main shoot grain weight (MGRWT) and tiller grain weight (TGRWT).

	Coefficient of correlation.	
	MTWT and TWT	MGRWT and TGRWT
F_2 population of		
cross 1	0.165 *	0.191 **
cross 2	0.165 *	0.191 **
cross 3	0.354 ***	0.335 ***
cross 4	0.592 ***	0.644 ***
cross 5	0.405 ***	0.436 ***
cross 6	0.384 ***	0.362 ***
cross 7	0.456 ***	0.498 ***
cross 8	0.186 *	0.214 **
Pure lines		
MM68/1		
MKR211/9		

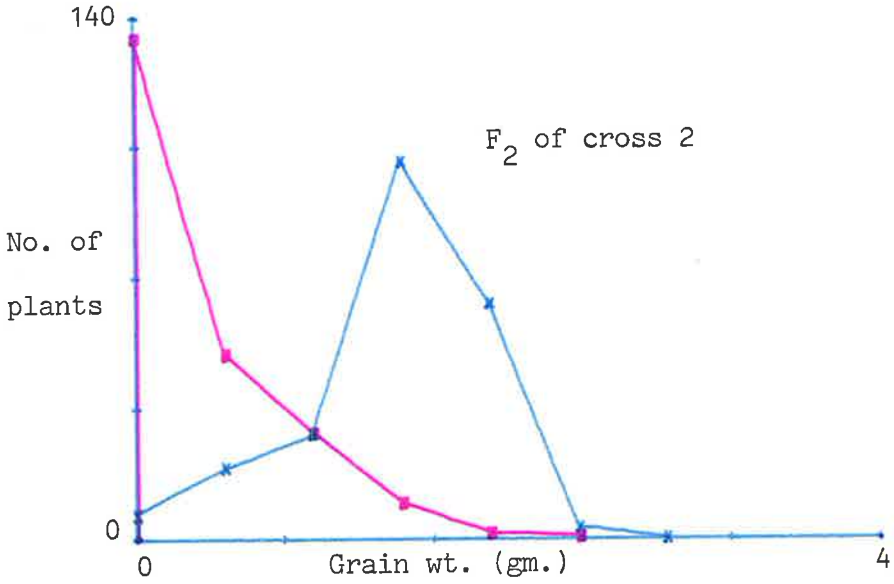
Figure 5.2. Frequency distributions of the main shoot and the first tiller from the hybrid (F_2) populations of eight crosses studied in experiment 1; the blue curve represents the main shoot distribution and the red represents the first tiller distributions.



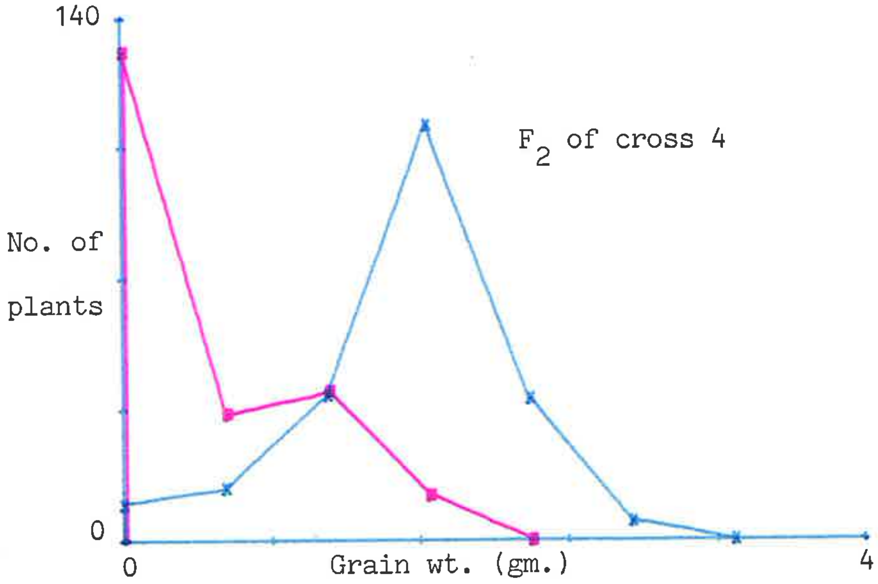
F$_2$ of cross 1



F$_2$ of cross 3

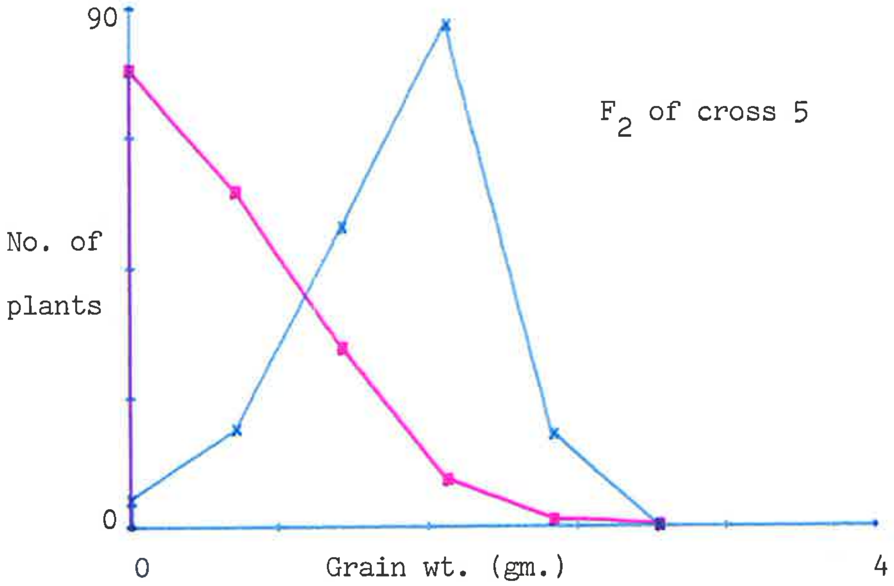


F$_2$ of cross 2

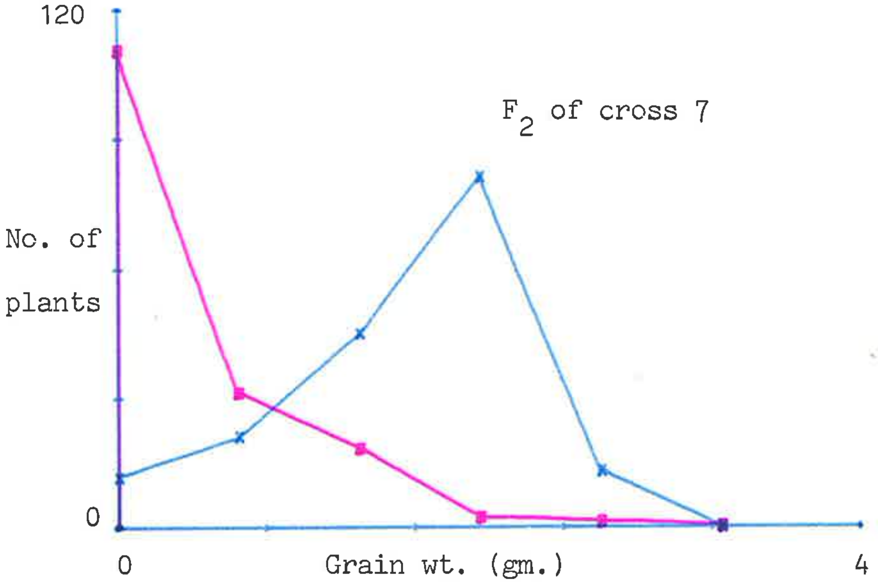


F$_2$ of cross 4

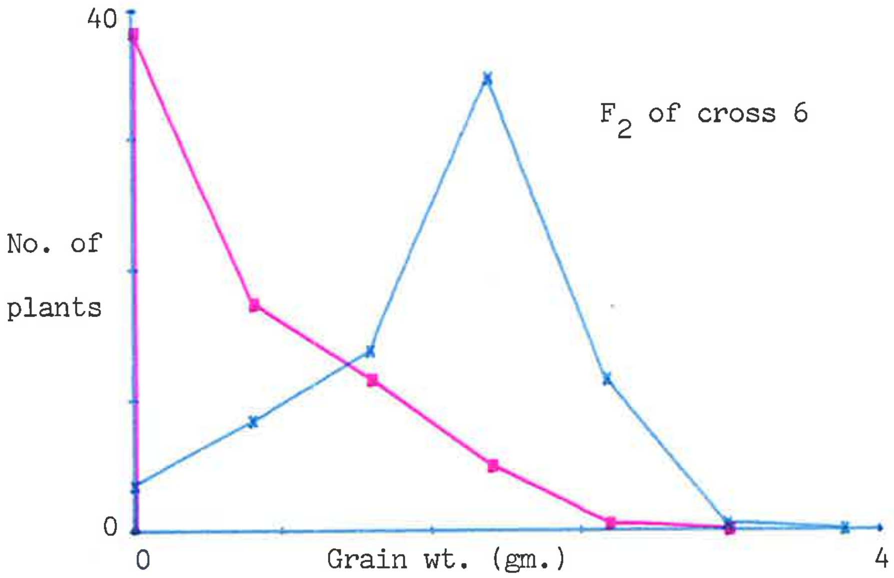
BLUE = Main shoot
RED = Tiller



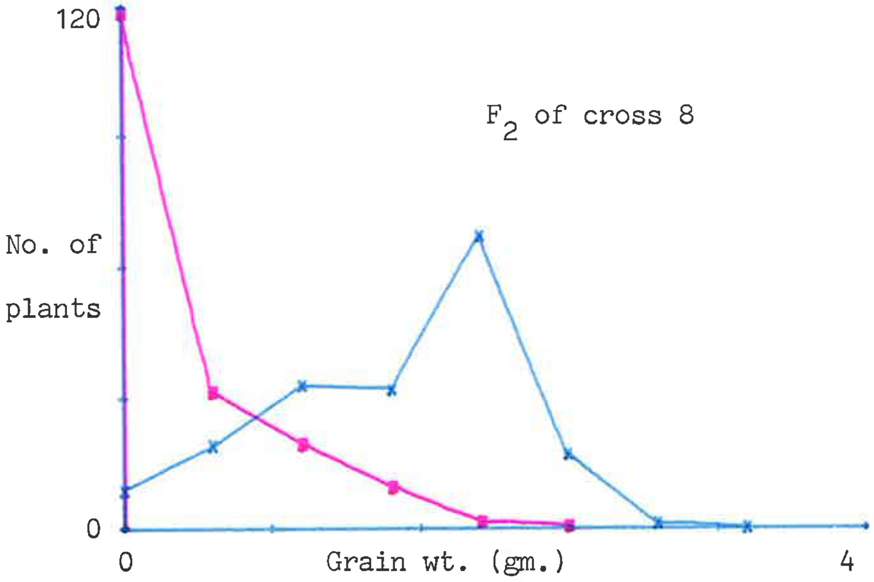
F$_2$ of cross 5



F$_2$ of cross 7



F$_2$ of cross 6



F$_2$ of cross 8

4. The bimodal distributions obtained for main shoot total weight and main shoot grain weight in cross 6.

Bimodal distributions were found for the main shoot total weight and grain weight in the F_2 of cross 6 (CHAMP/8156/17/52 * MMC28/9) (Figure 5.3). If the main shoot weights were divided at 2.49 g. for main shoot total weight and at 1.07 g. for main shoot grain weight, it would give the following number of plants in the two divisions;

	low weight		high weight		
	observed	expected	observed	expected	total
1. MTWT	88	89	268	267	356
2. MGRWT	96	89	260	267	356

Testing these numbers for a 1 : 3 segregation with 1 degree of freedom gave as χ^2

1. for the main shoot total weight: 0.015 which has probability of 0.90
2. for the main shoot grain weight: 0.735 which has probability between 0.30 and 0.50 (Fisher and Yates, 1963). This suggests that the results fit a 1 : 3 ratio, and that a dominant gene is affecting the main shoot yields in this cross. Minor genes would also be involved. The hypothesis that main shoot characters in this cross may be influenced by a major gene needs further testing by repeating the F_2, by growing an F_1, F_3 or by backcrosses.

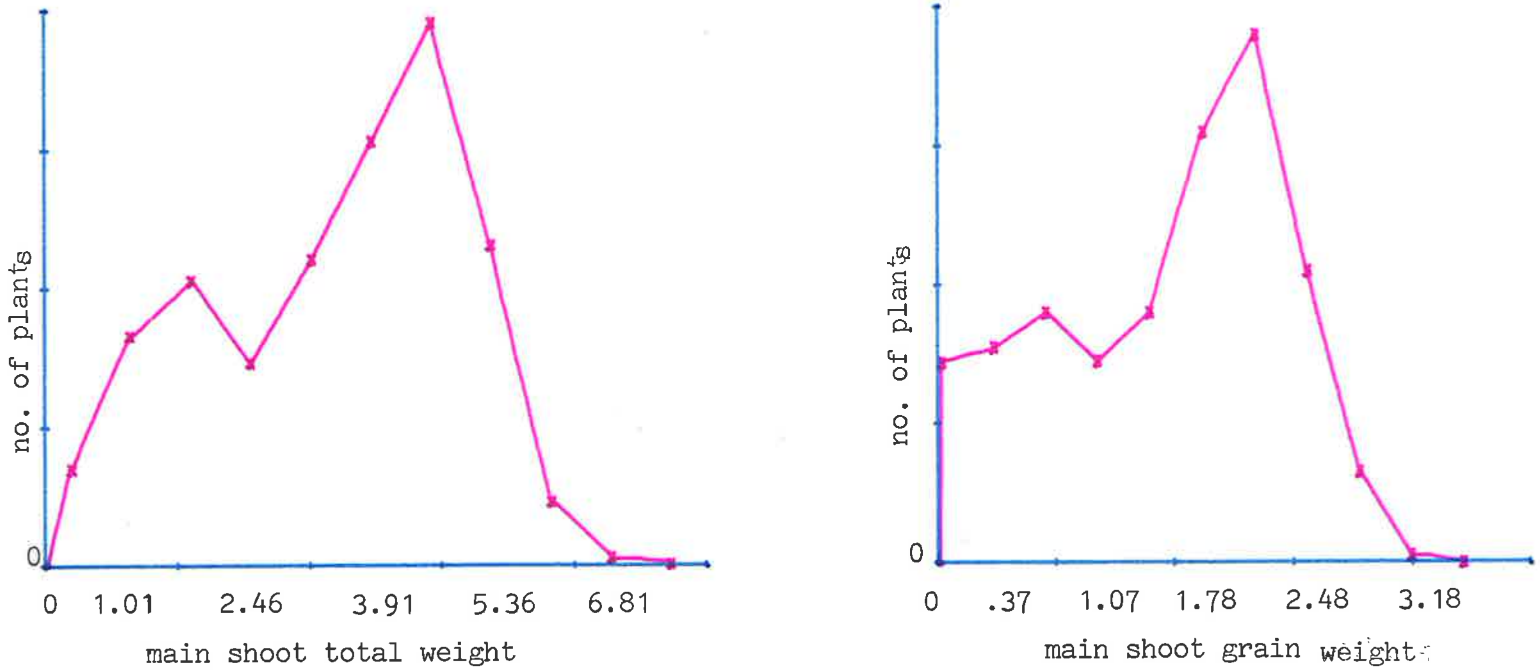


Figure 5.3. Frequency distributions of the F_2 of cross 6 (CHAMP8156/17/52 * MMC28/9) for the main shoot total weight and main shoot grain weight, showing the bimodal distribution.

5. Correlations between F_2 single plant yield and F_4 or F_5 plot yields.

Although results obtained in experiment 3 gave little indication that F_4 yields were accounted for by the regression on the F_2 single plant performances, results obtained in experiment 4 were more satisfactory with several characters showing some association. Variation in the results was expected to some degree as only combinations in which the parents differ will there be significant results and only some crosses will show a relation between F_2 and F_4 or F_5. In fact the relationship obtained in one cross should not be expected to occur in other crosses. The occurrence or non occurrence of significant correlations in a cross was not related to the differences in origin of the parents referred to in the Material and Methods. However, with only eight crosses under study this was probably too small a sample for a general result to be apparent.

The suggestion was made in experiments 1 and 2, that as the main shoot yield was less likely to be affected by the environment, it may be a promising indicator of yield in the derived lines in a later generation. The results of experiment 4 showed that the main shoot total weight, grain weight and grain number were better predictors of F_4 and F_5 yields than total plant weight or tiller grain weight or total grain weight. The very consistent results obtained in cross 6 was not surprising in view of its high values for variance and CV. for the main shoot total weight and grain weight compared to the other twenty three populations studied in experiment 1 (see Table 5.2 and 5.3). This suggests that the site and seasonal effects encountered were overcome by attention to the relation between the main shoot yield and the yield of the derived lines in later generations. It was not found, and would not be expected, that this will occur in all crosses or with all sites and seasons. If for instance a disease was present and there was genetic variation for resistance the present relation may not hold.

In regard to the F_2's grown at low density and their derived F_4 or F_5's, the lack of relationship in cross 7 was not unexpected as none had been found at crop density. For cross 3 a significant correlation was obtained for the F_4 and F_5 yields and the main shoot grain weight but not with the tiller grain weight or total grain weight. These results may confirm the suggestion made in the discussion previously that heterosis obtained for tiller grain weight and total grain weight in the F_2's grown at low density will be lost once the plants were grown under the competitive conditions of crop density where differences in tillering ability are of limited or no significance.

Interpretation of relationships between characters measured on the F_2's and their derived line (F_4 or F_5) yields was in some degree limited by the design of the experiment. The use of more than one genotype as a check, either Warimba and a mixture of hybrid seed in experiment 1 or P_1, P_2 and Warigal in experiment 2, in practice was not a good approach to the matter of assessing environmental variability within the F_4 and F_5 field trials. Having two checks in the same experiment meant a widening of the distance between plots of an identical check, as a result they appeared in every eighth position instead of in every fourth plot. This reduces the efficiency of adjustment and led to the adoption of a "Moving average" for adjustment. This led to some improvement but not such as to change the biological conclusions from the study.

In this study, many results were obtained. It would have been possible to analyse them in several different ways. Only those analyses thought to be most relevent to the objectives of the study were undertaken.

6. The importance of harvest index measured on the F_2's and their derived F_4 or F_5 yields.

There was little evidence to support the suggestion that the harvest index of the whole plant was a good indicator of yield performance

(Van Dobben, 1962; Syme, 1963, 1968, 1972; Cannel, 1968; Chandler, 1969; Bhatt, 1977; Fischer, 1975; Fischer and Kertesz, 1976). The results showed that harvest index and in particular harvest index of the main shoot will have a significant correlation with F_4 or F_5 yield if there is a significant correlation between the main shoot yield and the F_4 or F_5. There were instances where the F_2's main shoot yield and F_4 or F_5 yields were significantly correlated, but the whole plant harvest index was not correlated.

It is therefore concluded that harvest index was not as good as main shoot yield when selecting for high yielding genotypes.

GENERAL CONCLUSION

The conclusion made by other workers and referred to in the literature review, that selection for yield in an F_2 is ineffective when the objective is to produce high yielding lines, was only partially true in the present study. In three out of the eight crosses some association were detected between F_2 yield and the derived lines yield. In the other crosses the yield variation may have been too small for a differential in selection to be effective. This may be a common occurrence in breeding programmes which involve existing high yielding lines.

As it appears to be extremely difficult to identify the genetic differences in yield among F_2 plants, dependence may have to be placed on the main shoot yield which is less affected by the variation in the environment. Yield prediction may become feasible by ignoring the tillers' yield and concentrating on the main shoot's yield.

It is concluded that variances of the F_2 will often be no larger than the parental variances. At crop density, in most instances the F_2 variances for total yield were not significantly larger than the parental variances, but for the main shoot yield F_2 variances were larger. At low density, the F_2 variances for total plant yield and tiller yield were often significantly larger than the parental variances. However, this was partially associated with an increase in the means.

It is also concluded that neither the main shoot harvest index nor harvest index of the whole plant were better indicators when selecting for high yield than main shoot yield itself.

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