SINGLE PLANT YIELD AS A SELECTION CRITERION IN BARLEY

R.P. JOHNSTON B.Ag.Sc. (Queensland)

Thesis submitted for the degree of Doctor of Philosophy in the Faculty of Agricultural Science

Dept. of Agronomy

University of Adelaide

1972

Statement

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

TABLE OF CONTENTS

Page

SUMMARY

Two experiments were conducted to investigate the relationship between the yields of genotypes in heterogeneous populations of barley and the yields of the same genotypes when grown in pure stand. It was believed that in some circumstances this relationship could be influenced by the following effects:

i) genotype x plant density interactions

ii) intergenotypic competition

iii) heterozygosity resulting in hybrid vigour

iv) genotype x environment interactions across sites and years

v) micro-environmental variation.

In the first experiment, 100 homozygous varieties of barley were grown in a complex mixture and in pure stand. Attempts were made to improve the accuracy with which genotypes were assessed. Micro-environmental variation was estimated in the mixture by growing a large number of replicates, and in pure stand by the use of a grid of control plots. A constant plant density was used and both mixtures and pure stands were grown at one site in the same season. Hence, intergenotypic competition was believed to be the only effect influencing the above relationship. The second experiment consisted of F4 and F6 generations of 48 F3-derived lines from the cross Proctor x C.I. 3576, grown in mixtures and pure stands respectively.

In both experiments there were very highly significant correlations between yield in mixture and yield in pure stand and, although intergenotypic competition influenced the yield of some genotypes in the mixture, this effect was not large. There was no evidence that the response to competition was correlated with yield, and it was suggested that the negative correlations between competitive ability and yield in pure stand, previously reported, may have been artifacts brought about by unsuitable definitions of competitive ability.

Simulated truncation selection for yield in pure stand indicated that effective selection within the mixtures was possible when based on single plants. It was still more effective when based on the mean yield of each genotype over all replicates of the mixture. It was concluded that micro-environmental variation was the main effect limiting the value of single plant yield as a selection criterion. Methods of estimating micro-environmental variation in situations where replication is not possible, did not improve the efficiency of selection in these experiments, but it is believed that they warrant further study.

Stepwise regression analyses indicated that a combination of several characters measured in mixture accounted for a greater proportion of the variation in pure stand yields than did yield in mixture alone. Nevertheless, yield in mixture was the most significant character entered in the regression equations and it accounted for a greater proportion of the variation in pure stand yields than any other single character measured in the mixture.

The results of these experiments support the contention that survival in mixed populations is usefully associated with yield in pure stand. In addition they suggest that it should be possible to select for yield on a single plant basis, provided that micro-environmental variation can be reduced or estimated.

I. INTRODUCTION

The ultimate objective of most breeding programmes with self-pollinating crops is the selection of superior homozygous genotypes. Following the initial hybridization, the desired level of homozygosity is achieved by a number of generations of self-pollination. Several different methods, such as the pedigree method and the mass or bulk hybrid method, are used to advance material from its highly heterozygous condition in the F2 generation to relative homozygosity in later generations (Harrington, 1952).

During this phase selection is usually based upon characters of high heritability such as single gene resistance to disease, or maturity. Very little emphasis is placed upon selection for yield improvement within crosses, but attempts are made to select between crosses on the basis of bulked early generation yield tests. While these tests may give some indication of the mean yield of the segregates of a cross they cannot give any estimate of the genetic variance within a cross. Consequently the mean yield of a bulked progeny may not be a reliable guide to the genetic worth of individual genotypes which could be isolated from the cross.

It is widely accepted that selection for yielding ability cannot commence until adequate seed is available for yield tests in replicated trials and this is seldom attempted before the F4 generation. The limitations of this procedure include the relatively small sample of segregates which can be handled efficiently in replicated trials and the necessity to maintain some lines of little value for at least several generations before they can be evaluated. It is clear that the efficiency of plant breeding programmes would be improved if some selection pressure for yield improvement could be applied in the early generations.

One approach to this problem has been to allow natural selection to operate within bulked hybrid material for a number of generations in the belief that inferior genotypes will be eliminated because of their low seed yields. However, the success of this method depends upon the relationship which exists between survival in a heterogeneous population and yield in pure stand, and it has been suggested that the genotypes which survive in a mixture are not necessarily high yielding when grown in pure stand.

Both the possibility of selecting for yield in early generations and the value of the bulked hybrid method of breeding depend to a large extent on the relationship between the yields of single plants in heterogeneous populations and the yields of the same genotypes in pure stand. This thesis reports a study which was designed to establish this relationship in barley.

II. REVIEW OF LITERATURE

A. Introduction

One of the aims of most plant breeding programmes is an improvement in yielding ability. Frankel (1947) has suggested that one approach to such improvement would be the accumulation of desirable "yield productivity genes". He contrasts this approach to that of overcoming yield limiting factors such as disease, which in many cases involves selection for simply inherited characters.

This review is concerned mainly with the former approach and deals with yield as a quantitively inherited character. Selection for yield is then an attempt to maximise the probability of selecting genotypes with the desired alleles.

Shebeski (1967) showed that the frequency of plants containing the desired alleles in either the heterozygous or homozygous condition decreased with each generation after the initial hybridization. For example in a cross where only 10 genes are segregating, the frequency of plants with all the desired alleles in either the heterozygous or homozygous state is 5.6% in the F2 generation, 0.9% in the F3 and 0.3% in the F4. When all loci are eventually homozygous only 0.1% of the population will have all the desired alleles.

On a basis of these calculations Shebeski suggested that ideally selection should commence in the F2 generation. He did not consider the effect of heterozygote superiority or of selective advantage of high yielding genotypes, both of which could lead to a higher than calculated frequency of desired genotypes in later generations. However the general conclusion that selection in the F2 would permit a more rapid increase in the frequency of desired genotypes than selection in later generations, remains valid.

Unless adequate methods of clonal propagation are available, selection in the F2 must be based on the performance of single plants. It is commonly believed that, in these circumstances non-genetic variability is so large that genetic differences are concealed. Allard (1960), Bell (1963), Elliott (1958), Harland (1949), Harrington (1932), Hinson and Hanson (1962) and Shebeski (1967) have all stated that selection for yield on the basis of single plant performance in early generations is ineffective. Johnson and Bernard (1963) summarised this belief when they wrote that "experience quickly teaches the futility of selecting for yield among F2 plants".

Experimental evidence on the subject is limited (McGinnis and Shebeski, 1968; Hinson and Hanson, 1962; Voigt and Weber, 1960; Hamblin, 1971). In all available papers the authors contend that selection for yield on a single plant basis is no better than random selection, but both McGinnes and Shebeski (1968) and Hamblin (1971) suggested that inadequate experimental designs could have lead to erroneous conclusions. However neither of their own experiments overcame all the experimental difficulties particularly those relating to genotype x environment interactions.

McGinnis and Shebeski (1968) selected high yielding single plants in an F2 population of barley sown at a density of approximately 3.2 plants per square metre (almost a non-competitive community). In the following year they tested these selections as F3's at approximately 147 plants per square metre (almost a commercial density). The selected population was no better than a control population of random selections.

Hamblin (1971) selected in the F3 generation of a barley cross in 1967 and tested these selections as F5's in 1969 at two levels of nitrogen and at two plant densities. He found no correlation between F3 yield and F5 yield but indicated that his results were possibly confounded. The seasons in the years 1967 and 1969 were climatically very different; in a separate study even homozygous varieties failed to show a correlation for yield between the two years.

However Gardner (1961), using mass selection in maize was successful in obtaining an average progress per generation of 3.93%, which agreed closely with that predicted on the basis of estimates of genetic variance. His technique was to subdivide the selection area into small areas of 40 plants and to select within each area. In this way the effects of micro-environmental variation were reduced and he concluded that he had been able to make genetic progress for yield based essentially on single plant selection.

Although Gardner was successful when he restricted the effect of environmental variation, it would appear that the yield of a single plant grown in one generation of a segregating population was in general an unreliable indication of subsequent pure stand yields of its later-generation derivatives, a result attributed by most authors to large non-genetic plant-to-plant variation which obscures genetic differences. Reasons for the large non-genetic variation have been proposed in the literature but have not been studied closely.

Hinson and Hanson (1962) working with four soybean varieties grown in mixture and in pure stand found no relationship between single plant yield in mixture and crop yield in pure stand and concluded that the performance of single plants in heterogeneous populations may be seriously misleading, mainly because of the differences between genotypes in their reaction to competition and to differences in spacing.

Johnson and Bernard (1963) discussed these problems of competition and spacing in soybeans. If plants of heterogeneous populations were spaced too closely, variability was increased by competition; if spaced too far apart variability was increased by the differential ability of genotypes to utilise space.

Allard (1960) stated that the effect of environment on single plant yields is so large that selection for yield is futile. The effects of heterozygosity are also mentioned by Allard. The vigour of many F2 plants may result from heterozygosity and consequently selection may simply favour the most heterozygous individuals.

Grafius (1952) stated that selection within an F2 is not feasible partly because of environmental variance and partly because of the presence of a large non-heritable component of variance.

The effects which tend to limit the value of single plant yields as a selection criterion are reviewed in the following sections:

1. <u>Interactions due to Plant Density</u>

Single plants are often grown at a wide spacing to eliminate inter-plant competition and to facilitate inspection. If genotype x density interactions occur, selection at wide spacing might favour genotypes with the ability to perform well at that spacing rather than those with the ability to yield well at normal commercial densities.

Many authors have investigated the response of different genotypes to changes in plant density. These experiments have given conflicting results but may be separated into three groups.

a) Large genotype x density interactions have been demonstrated. {Sakai (1965), Kirby (1967), Severson and Rasmusson (1968), Blum (1970) and Gardner (1972) with barley; Probst (1945), Lehmann and Lambert (1960), Hinson and Hanson (1962) and Schuster and Spennemann (1964) with soybeans; Engledow (1925) with wheat; Termunde (1963) with maize; Lazenby and Rogers (1964) with Lolium perenne and Johnston (1971) with kale}.

In this group of results rankings of genotypes for yield changed with density and the performance of a genotype at one density was a poor indication of its performance at another density. This suggests that selection at low density would be of little value when the crop is to be grown at a commercial density.

b) Siemans (1963) and Pendleton and Dungan (1960) working with wheat, Shehata and Comstock (1971) with flax and Giesbrecht (1969) with maize, showed that statistically significant genotype x density interactions occurred but the interactions were not large enough to bring about marked changes in ranking for yield.

c) In other experiments no interaction has been evident and different genotypes have each responded consistently at varying plant density (Rennie, 1957; Guitard et al, 1961; Demirlicakmak et al, 1963; Stickler et al, 1964).

Results such as those in groups b and c suggest that genotypes which perform well at low plant density tend also to be the high yielding genotypes at high plant densities. If this were the case selection could be carried out with confidence at low plant density in the absence of interplant competition. The converse applies to consideration of results in group a.

Knight (1960) discussed the relationship between the performance of genotypes at different densities and suggested that the occurrence or non-occurrence of large interactions would depend on the major environmental factor limiting growth in the experiment and on there being differences between genotypes in their response to the limiting factor. If the limiting factor was of equal importance to close and widely spaced plants, as temperature might be under some circumstances, a good relationship might be expected. If however the major limiting factor was light, nutrients or moisture which differed in their availability to plants at different densities then interactions might occur.

The many examples which do exist, of large interactions between genotypes and plant densities show clearly that the performance of a genotype at low plant density is an unreliable indicator of its performance at high density. Consequently it seems desirable to carry out selection at densities that approximate those of commercial crops.

2. The Confounding Effects of Competition

Plants which are grown at a commercial density are subject to strong interplant competition. In a segregating population the more competitive genotypes may be the ones to have a high yield but this high yield need not necessarily be maintained when grown in pure stand. Consequently the relationship between yielding ability in pure stand and yielding ability when in competition with other genotypes must be established if selection is to be practised with confidence.

Attempts to establish a general relationship between yielding ability in pure stand and in mixed populations have provided conflicting and unsatisfactory results. Some authors have concluded that selection of high yielding genotypes in a competitive situation was effective while others believe that selection should be for low yielding genotypes in competitive situations.

Allard (1960) and Allard and Hansche (1963) concluded that there was "considerable evidence that survival in population is usefully correlated with agricultural value, at least in small grains and lima beans". This conclusion was based partly on work with composite crosses with barley (Suneson, 1956; Allard and Workman, 1963) and lima beans (Allard and Jain, 1962). Results from these studies showed that the mean yield of the populations tended to increase for at least the first 10 to 20 generations. During this period low yielding, poorly adapted genotypes were eliminated or reduced to very low frequencies in the population.

When advanced generations of these crosses were sampled and the selected genotypes tested in pure stand, it was found that many high yielding genotypes were present in the population. The fact that the frequency of genotypes with high pure stand yields, tended to increase in advanced generations (Suneson, 1956; Lohani, 1970) indicated that natural selection in mixed competing populations favoured genotypes of high agricultural value.

Further evidence used by Allard was that of Harlin and Martini (1938) who showed that when a mixture of 11 barley varieties was grown for several years at 10 sites, one variety quickly dominated the mixture. At most sites the dominant variety was the local commercial variety which was probably the highest yielding variety at that site. At the few sites where the dominant variety was not the local commercial variety, there was other evidence to suggest that the dominant variety was high yielding at that site but was unsuitable for commercial production for reasons other than yielding ability.

In contrast to Allard's conclusions, Jennings and his co-workers (Jennings and de Jesus, 1968; Jennings and Herrera, 1968; Jennings and Aquino, 1968) suggested that, in rice, highly competitive but low-yielding genotypes tend to dominate weakly competitive, high yielding genotypes in mixture. Survival in mixed populations was therefore negatively associated with agricultural value and Jennings and Aquino stated that to rice breeders, "competition is undesirable and mitigates against realisation of the major objectives of tropical breeding programmes: lodging resistance, nitrogen responsiveness and high yield potential".

Although they stated this viewpoint, they were able to overcome the undesirable effects of competition by hand rogueing of F2 populations to eliminate tall leafy plant types. When these morphologically distinct types had been removed, competition within the remaining population did not appear to favour low yielding genotypes, as many lines with yields greater than the high yielding parent were present in a random sample of 36 lines from the F6 generation. These data suggest that the negative relationship between yield in mixture and yield in pure stand, existed only when gross morphological differences in plant type were present, and does not indicate any general relationship.

Wiebe et al (1963) also showed a negative relationship. Working with isogenic lines of barley differing only near the Vv locus, they showed that VV (6 row) lines were high yielding in mixture with vv (2 row) lines but low yielding in pure stand. They concluded that "the poorest plants should be saved from an advanced hybrid population rather than the good ones when yield is the criterion for selection".

Jennings and Aquino (1968), Akihama (1967) and Donald (1968) have reported a negative relationship between competitive ability on the one hand and yield in pure stand on the other; information on this relationship is thought to be vital to plant breeding programmes (Sammeta and Levins, 1970). However, competitive ability is normally estimated as a ratio between yield in mixture and yield in pure stand or as the difference between these values. It is therefore a derived character, and the relationship between such estimates of competitive ability and yield in pure stand is a different relationship from that existing between yield in mixture and yield in pure stand. Unless this is recognised, misleading interpretations are possible.

The existence of a negative correlation between competitive ability and yield in pure stand does not necessarily mean that genotypes with high pure stand yields will perform poorly in mixed populations. Nor does it mean that highly competitive genotypes will eventually dominate if a mixture is grown for a number of generations. The following model will illustrate this point.

Competitive ability is often measured as the difference between yield in mixture and yield in pure stand (Akihama, 1967; Sakai and Iyama, 1966; Schutz et al, 1968; McGilchrist, 1965) or the ratio of yield in mixture to yield in pure stand (de Wit, 1961; Thomas, 1970; Hamblin, 1971).

If x_i is the yield of the i^{th} genotype in mixture and y_i is the yield of the same genotype in pure stand, then competitive ability of the i^{th} genotype is by some definitions

$$(c_i) = x_i - y_i.$$

The correlation, r_{CY}, between competitive ability and yield in pure stand would be

$$r_{CY} = \frac{\sum c_i y_i - \frac{\sum c_i \sum y_i}{n}}{\sqrt{\left(\sum c_i^2 - \frac{(\sum c_i)^2}{n}\right) \cdot \left(\sum y_i^2 - \frac{(\sum y_i)^2}{n}\right)}}$$

$$= \frac{\sum (x_i - y_i) \cdot y_i - \frac{\sum (x_i - y_i) \sum y_i}{n}}{\sqrt{\left(\sum (x_i - y_i)^2 - \frac{(\sum (x_i - y_i))^2}{n}\right) \cdot \left(\sum y_i^2 - \frac{(\sum y_i)^2}{n}\right)}}$$

which reduces to

$$r_{CY} = \frac{\left(\sum x_i y_i - \frac{\sum x_i \sum y_i}{n}\right) - \left(\sum y_i^2 - \frac{(\sum y_i)^2}{n}\right)}{\sqrt{\left(\left(\sum x_i^2 - \frac{(\sum x_i)^2}{n}\right) + \left(\sum y_i^2 - \frac{(\sum y_i)^2}{n}\right) - 2\left(\sum x_i y_i - \frac{\sum x_i \sum y_i}{n}\right)\right) \cdot \left(\sum y_i^2 - \frac{(\sum y_i)^2}{n}\right)}}$$

$$= \frac{Cov_{XY} - Var_Y}{\sqrt{\left(Var_X + Var_Y - 2Cov_{XY}\right) \cdot Var_Y}}.$$

In this relationship the sign of the correlation is determined by the numerator $Cov_{XY} - Var_Y$ since the denominator is always positive. Though Cov_{XY} may be positive, the correlation r_{CY} will be negative whenever Var_Y is larger than Cov_{XY}. In such cases however, the positive value for Cov_{XY} alone gives a positive correlation between X and Y, suggesting that the high yielding genotypes in pure stand are also high yielding in mixtures. That is to say, in such a circumstance:

> the correlation between competitive ability and yield in pure stand, r_{CY}, is negative;
> the correlation between yield in mixture and yield in pure stand, r_{XY}, is positive.

When selection is practised in a heterogeneous population it is the correlation r_{XY} and not the correlation r_{CY} that determines the progress. If there is a positive correlation, r_{XY}, between yield in mixture and yield in pure stand, selection for yield in mixed populations will also result in selection and progress for yields in pure stand. This will be valid even if there is a negative correlation between competitive ability (as defined above) and yield in pure stand.

The definition $c_i = x_i - y_i$ is used by Akihama (1967) and, although McGilchrist (1965) and Schutz et al (1968) introduce other terms to the equation, the term $(x_i - y_i)$ is still present. It is clearly hazardous to use or extrapolate from correlations between yield in pure stand and any estimate of competitive ability which includes yield in pure stand as one of its parameters.

Similar problems apply to the use of definitions which calculate competitive ability as a function of the ratio of yield in mixture to yield in pure stand.

Therefore it is doubtful whether the relationship between competitive ability and yield in pure stand per se, is of any value to plant breeding. It certainly does not infer any general relationship between performance in mixture and agricultural value, and it is preferable to study the relationship between yield in mixture and yield in pure stand.

Another difficulty when considering the role of competition in segregating populations is that most evidence on the subject of competition is based on studies carried out with mixtures of small numbers of homozygous varieties.

Allard and Adams (1969) showed that competitive relationships within composite cross populations may be quite different from those operating in mixtures of homozygous genotypes which have been selected for performance in the absence of competition.

The effect, at normal densities, of competition from many different genotypes on the yield of a single plant and thus on single plant selection for yield is poorly understood and clearly warrants further study.

3. The Confounding Effect of Heterozygosity

In the early generations following the cross of two parents, most plants will have some heterozygous loci and in crops where heterosis is common the highest yielding plants could simply be the most heterozygous. Selection of these plants would tend to maintain high levels of heterozygosity but provide little scope for eventual selection of high yielding homozygous varieties.

Whether heterozygosity will be a major effect confounding selection in early generations of self-pollinated crops depends firstly on the level of heterosis evinced by the cross, secondly on the genetic causes of the heterosis, and finally on the extent to which the effects of heterosis are lost with the approach to homozygosity.

Many authors have studied F1 hybrids of wheat (Granhall, 1946; Briggle, 1963; Briggle et al, 1967; Gyawali et al, 1968; Walton, 1971) and barley (Upadhyaya and Rasmussen, 1967; Severson and Rasmussen, 1968; Carleton and Foote, 1968; Clay and Allard, 1969). In most cases the yield of the F1 was higher than the mid-parent and several F1's were superior to the high yielding parent.

Because hand emasculation and pollination of wheat and barley are time consuming, most of these studies were conducted with small numbers of plants, necessitating low plant densities or very small plots. Severson and Rasmussen (1968) and Rosenquist (1931) provided evidence that the yield advantage of F1 hybrids decreased with increasing plant density and was not significant at normal commercial density. Although this finding was not supported by Briggle et al (1967), (they showed that the F1 hybrid was higher yielding than either parent at a wide range of plant densities) the evidence for heterozygous advantage at commercial densities in wheat and barley may be questioned.

In spite of this reservation it does appear that heterosis is displayed by some F1 hybrids in wheat and barley, and hybrid barley is grown commercially.

The genetic processes leading to heterosis are relevant to the present discussion as they affect the approach to selection. Two widely accepted hypotheses have their origin in the early years of this century. Davenport (1908) and Bruce (1910) proposed the "dominance hypothesis" in which hybridization was believed to allow deleterious recessive alleles from one parent to be concealed by dominant alleles from the other parent. In 1908 both Shull and East put forward the "over-dominance hypothesis" based on the belief that there was some physiological advantage in the heterozygous condition per se. An alternative hypothesis is that heterosis for yield is due to multiplicative interaction between the components of yield none of which need show either dominance or over-dominance (Williams, 1959).

If heterosis in a particular cross is due to either dominance or multiplicative interaction of components, it should be possible to select homozygous genotypes equal to the F1 hybrid.

Consequently selection of high yielding genotypes in a segregating population exhibiting this type of heterosis should result in selection of at least a proportion of genotypes with more desirable alleles than either parent.

However, if overdominance is the cause of heterosis the highest yielding genotypes need not include all the desired alleles, and selection of these genotypes need not result in superior homozygotes in subsequent generations.

The effect of self-pollination of the F1 and subsequent generations is to bring about a decrease in the frequency of heterozygous loci. Because heterozygous loci may have a selective advantage over their respective homozygotes, the rate of decrease in heterozygosity may not be a simple halving with each generation, but it will nevertheless be quite rapid in the early generations (Allard and Hansche, 1964).

4. The Micro-Environmental Effect on Single Plants

Since plants of segregating populations of barley cannot be clonally propagated efficiently, or replicated in any other way, differentiation between genotypes must be based on single plants which can be influenced by the micro-environment in which each grows. Unless micro-environmental variation can be controlled or measured, the high yielding selections may be those growing in the most favourable locations.

Methods of overcoming this problem have been suggested.

Hamblin (1971) assumed that genotypes were allocated at random to the locations within the selection area and therefore the yield of a localised group of plants could be used as a measure of the micro-environment within that part of the selection area. Using a regression technique, he fitted a series of polynomial equations to the yield of individual plants. This represented a response surface for the entire area in which the population was grown. The yields of individual plants were then expressed as deviations from the response surface.

He indicated that the surface had limited usefulness in its application to results from the edges of the selection area. In addition the number of terms required in the polynomial equation to represent environmental variation was arbitrary and no objective test of the optimum number of terms to use was available. If enough terms were included, the surface could ultimately follow the actual yields whereas with only terms up to the cubic, the calculated surface was more gently curving than expected. Micro-environmental variation in his experiment was believed to be extreme and could not be represented accurately by polynomial equations.

Hamblin decided that a more useful approach was to express individual plant yields as deviations from the mean of a number of surrounding plants. For each plant in the selection area he calculated the mean yield of a number of neighbouring plants and expressed the yield of the central plant as a deviation from this mean.

Thus Hamblin expressed the yields of individual plants as deviations from either a response surface or the so-called moving mean. The mean is referred to as a moving mean as it is calculated successively for every plant location in the selection area.

Each of these approaches offers some prospect of increasing the efficiency of selection at the single plant level. Unfortunately the year in which Hamblin grew his selection block (1967) was climatically different from the year (1969) in which he tested the offspring of his selected genotypes and he was unable to show whether either technique was successful.

The method used by Gardner (1961), referred to earlier, is similar to Hamblin's moving mean since plants were selected on the relationship of their individual yields to that of the surrounding plants. Gardner selected the highest yielding four plants from each separate group of 40 plants. This is a simpler approach than calculating a moving mean, but has the disadvantage that some plants are selected from each group although some groups may not include high yielding genotypes. Furthermore, plants at one edge of the group of 40 plants are compared with plants at the other edge and the micro-environmental effect may have been different.

In spite of the weaknesses in each of these procedures, selection of individual plants on the basis of their yield, relative to some estimate of the average yield of a local environment, seems more likely to succeed than selection based directly on individual yield. However, before such methods can be soundly evaluated it must be established that neither competition nor heterozygosity are major factors differentiating between yields of single plants in early generations.

If attempts are being made to relate single plant yields in mixture to yield in pure stand, an accurate assessment must be made of both the pure stand yields and the single plant yields. The environmental effect on the pure stand plots must be estimated as accurately as possible. LeClerg (1966) discussed several methods for experiments with large numbers of entries and concluded that the lattice designs were generally more efficient than the randomised block design because estimates of variation within replicates were obtained.

Methods other than the lattice designs have been used in breeding programmes. In one proposed by McGinnis and Shebeski (1968) every third plot was sown to a control variety and the yield of each experimental plot was expressed as a percentage of an adjacent control plot. Similar methods using a regular arrangement of control plots were used by cereal breeders in the early years of this century (McClelland, 1926). In these, the yield of an experimental plot was usually expressed relative to the mean of a number of nearby control plots. Hayes (1925) showed that a similar technique successfully reduced experimental error but he questioned whether this increase in accuracy was "worth the trouble of making the calculations".

Following the development of Fisherian statistics, yield correction based on the inclusion of regular control plots was thought to be unnecessary. However, the first experiment in the present study suggested that the triple lattice design did not provide adequate estimation of variability arising from irregular soil heterogeneity. Lamacraft (pers. comm.) suggested that a method similar to that used by McClelland and discussed by LeClerg (1966) could be more efficient in estimating this type of variation, particularly as the calculations could be handled easily by a computer.

5. Genotype x Environment Interactions over Sites and Seasons

The yield of a single plant is influenced not only by micro-environmental effects but by general effects such as climate and soil fertility which are relatively uniform over the whole selection area during a particular season. These factors will not be similar in different seasons or sites, so that genotypes selected at one site in one season may not prove to be superior genotypes at other sites or in other seasons.

Genotype x environment interactions are of major importance in breeding programmes and have been reported by many authors (Finlay and Wilkinson, 1963; Fowler and Heyne, 1955; Leffel and Hanson, 1961; Salmon, 1951; Horner and Frey, 1957; Rasmussen and Lambert, 1961). The implications of such interactions in plant breeding have been discussed by Allard and Bradshaw (1964) and attempts to overcome the problem were made by Plaisted and

Peterson (1959), Finlay and Wilkinson (1963) and Eberhart and Russell (1966).

The existence of genotype x environment interactions over sites and seasons should not be considered as invalidating the use of single plant yields as a selection criterion. The real question to be answered is whether the yield of a single plant grown in a heterogeneous population of competing genotypes is directly and usefully associated with the yield to be obtained when a pure stand of that same genotype is grown at the same site in the same season. If such a relationship can be demonstrated, the yield of a single plant can be used effectively as one of the measures of the worth of a genotype, just as in evaluations based on plots, yield at one site is used as one of the useful estimates of the value of a genotype.

The question posed here is somewhat different to that posed by McGinnis and Shebeski (1963) and by Hamblin (1971). These investigators showed no relationship between single plant yields in one year and plot yields in another year and they deduced that single plant yields were poor indicators of plot yields.

In both experiments however, large genotype x environment interactions were possible. McGinnis and Shebeski selected at a density where interplant competition was unlikely to be of any significance and tested their selections at a much higher density in another season, while Hamblin conducted his experiments in two entirely different seasons. As they did not show that selection on any basis other than single plant yields was successful under these circumstances, it does not seem reasonable to conclude that single plant selection for yield is of no value in plant breeding.

6. The Selection of Other Plant Characters

It has been suggested that improvements in yield may be achieved if selection is based on certain plant characters or combinations of characters (Donald, 1968; Grafius, 1965). Characters such as the components of yield, plant height, flowering date and measurements of leaf distribution may be less complex characters than yield itself. Consequently they may be less affected by environmental variation and their measurement may provide an accurate measure of the genotype.

One approach to selection for yield based on other characters is the use of a selection index. In studies undertaken on selection for several characters simultaneously, each of which had some economic value, it was concluded that the selection index method was more efficient than other methods of selection provided that realistic estimates of economic worth were available and that accurate measurements were made of 1) genotypic and phenotypic variances and 2) genotypic and phenotypic correlations between each pair of characters (Hazel, 1943; Hazel and Lush, 1942; Young, 1961).

Although the selection index was intended primarily for situations where improvement was desired in several characters, it has also been used where selection was for yield improvement alone. Robinson (1951) showed that the expected genetic advance in maize yield was 30% greater when selection was based on an index including plant height, ears per plant and yield than when based on yield alone. In soybeans Caldwell et al (1966) showed that the maximum gain in yield was obtained when selection was based on an index including yield, height, maturity, lodging, seed size, protein content and oil content. The deletion from the index of any one character, other than yield, did not affect the genetic advance greatly, but the deletion of yield from the index brought about a large reduction in the expected gain in yield. In both these examples of the use of a selection index, it should be noted that yield itself was a major component of the index.

A critical question is then the relation between the characters in an index and yield itself. Brim et al (1959) concluded that in the use of an index more data were needed than it was feasible to collect. However, because of the greater precision with which the genotypic value of such characters can be measured, further attempts should be made to detect useful relationships between various characters and yield.

The characters measured in this study because of their potential influence on yield were:

1) Plant height

If there is any possibility of lodging short plants have an advantage in pure stand because they are less prone to lodging. A secondary advantage of short stature might be a more favourable leaf arrangement (Donald, 1968 and van Dobben, 1965).

On the other hand tall plants might be expected to suppress shorter plants in a competitive situation (Donald, 1963) as was found by Pendleton and Seif (1961) when they grew a brachytic maize genotype in alternate rows with a normal genotype 85 cm taller. The brachytic maize yielded less than when grown in rows as a pure stand.

2) Height to the flag leaf

Thorne (1966) and Cannell (1968) concluded that the flag leaf made significant contributions to the carbohydrate accumulated in the grain. Hence the height of the flag leaf could be important in determining grain yield when in competition with other genotypes. Flag leaves at a low level in the canopy would suffer from shading.

3) Components of yield

Yield of cereals is often analysed in terms of the components of yield which are: plants per unit area, heads per plant, number of seeds per head and seed weight (Grafius, 1965; Whitehouse et al, 1958). Environmental factors early in a growing season affect the number of heads and the number of seeds while seed size is determined by factors operating later in the season, especially after anthesis. Therefore it is possible that the components of yield show differential responses to competition and the relative value of the various components as selection criteria may differ.

4) Heading date

In the mediterranean climate of South Australia, heading date is of importance in determining grain yield of winter cereals. Early varieties have a low yield because of the inadequate size and number of their heads, while late varieties often suffer from moisture stress in the grain filling period. Therefore, it is possible that a curvilinear relationship exists between heading date and yield with an optimum heading date in September for most seasons.

5) Total dry weight

Cannell (1968) stated that "there is no clear indication that the total dry matter yields by modern cereal varieties are higher than those of older varieties". He concluded that breeding had brought about a shift in the distribution of dry matter between the grain and the straw. Donald (1968) expressed similar views and advocated the measurement of total dry matter yield in all breeding programmes in order to calculate the ratio of grain to total dry matter. This ratio was referred to as the Harvest Index by Donald and as the Grain Efficiency Index by Cannell.

Nevertheless it is possible that grain yield could be improved by increasing dry matter yields while maintaining the relative distribution of dry matter to the grain and therefore dry matter yield has some potential as a selection criterion in its own right. Clearly genotypes which are capable of only low dry matter yields are of little value regardless of the relative distribution of dry matter to the grain.

7. Conclusions to be Drawn from the Literature

Knowledge of the relationship between the yield of single plants in heterogeneous populations and yield in pure stand is essential if single plant selection for yield is to be practised and also if composite crosses and other bulked hybrid methods of plant breeding are to be evaluated.

The difficulties in establishing this relationship have been discussed and several factors which influence the yields of single plants in heterogeneous populations have been indicated. It is clear that the effects of heterozygosity and competition are not well understood in populations of many genotypes. Furthermore, variability arising from soil heterogeneity has made it difficult to assess genotypes accurately in both pure stand and mixture. Micro-environmental variation has influenced single plant yields but several methods have been suggested to estimate this effect. In view of the possibilities offered by these methods it seems pertinent to re-examine the relationship of single plant yields in heterogeneous populations and yield in pure stand.

III. THE EXPERIMENTS

A. Introduction

The objective of this study was to establish the relationship between the yield of single plants grown in heterogeneous populations and the yield of the same genotypes in pure stand. Two separate experiments were conducted, each using barley as the test species.

In the first, an attempt was made to eliminate those effects discussed in the literature review that reduce the value of single plant yield as a selection criterion. Thus the study was undertaken on plants grown only at one density; the density used in commercial production.

A large number of homozygous varieties were grown in a mixture and compared with the same varieties grown in pure stand. By using homozygous varieties, heterozygosity was eliminated as a confounding factor. Furthermore single plants of a homozygous variety are genetically identical, replication is possible, and micro-environmental effects can be estimated. In addition to replication attempts were made to estimate micro-environmental variation by using the response surface or moving means suggested by Hamblin (1971) and discussed in the literature review. It was believed that replication, either alone or in association with other techniques should allow accurate assessment of yield in mixture.

Attention was also directed to ensure that pure stand yields were accurately measured. Initially, a triple lattice design was used in the belief that this was the most efficient method of minimizing yield differences due to soil heterogeneity. It was apparent from the results of the first experiment that this design did not allow complete estimation of the soil variation. An alternative design employing regular check plots of a control variety, as suggested by Lamacraft (pers. comm.), was used in the following years.

Genotype x environment interactions involving sites and seasons were avoided by growing plots of both the mixture and pure stands at the same site in a single season.

In this first experiment the only major factor believed to be influencing the relationship between the yield of a single plant in mixture and its yield in pure stand was the difference in the competition they experienced. In the mixture each plant was competing against a large number of different varieties, while in the pure stand plots each plant was competing against plants of its own variety.

It could be argued that the genetic diversity present between the 100 varieties used in the first experiment was larger than would occur within a segregating population. Consequently the second experiment was conducted to examine yields in mixture and in pure stand for segregates of a simple cross.

In this second experiment a mixture was made up of one F4 plant from each of 48 randomly selected F3 plants. In addition seed from each of the F3 plants was advanced to the F6 generation and this was used as the 'pure stand' plots. Thus a comparison was made between the yield in mixture of F4 plants from 48 F3 plants and the yield in pure stand of F6 plots derived from the same F3 plants.

As in the first experiment the possibility of genotype x environment interactions was avoided by growing both F4 and F6 plots at one site in a single season. However, in this experiment some heterozygosity would have been present. In the F4 generation 12.5% of the loci for which the parents differed are expected to be heterozygous while by the F6 generation this level has fallen to 3.125%. It is possible therefore that effects of heterozygosity could have reduced any relationship in this experiment. In addition, 30 separate mixtures of F4 plants from the 48 F3 plants were grown. The 30 mixtures were looked upon as replicates although it was true that the 30 F4 plants from a single F3 were not in fact identical because of segregation. However, micro-environmental effects were assumed to be random and the mean yield of the 30 plants from a single F3 should provide a true estimate of the F4 yield.

The results from the first experiment indicated that the yield of some varieties when grown in a mixture of genotypes were quite different from their yields in pure stand. This might have been caused by differences between genotypes in their response to competition from other genotypes. Other explanations are possible such as experimental error or an interaction between varieties to the separate experimental areas in which the mixture and pure stand plots were grown. Consequently a supplementary experiment was conducted to study in further detail the competitive relationships of some varieties and whether this factor had influenced their yield in mixture.

1. Material Used in the Experiments

Experiment 1: 100 varieties of barley were chosen at random from the barley collection maintained at the Waite Agricultural Research Institute. Details of these varieties and the treatment numbers allocated to them are given in Table 1. These varieties had been grown in 1966 and abundant viable seed was available.

Experiment 1a: On a basis of the results from Experiment 1, three varieties were chosen which had given similar yields in pure stand but very different yields in mixture (Table 2).

If competition was important in determining the yields of these varieties in mixture, it was believed that Cape, Weider and Featherston could be classified as good, average and poor competitors respectively. They therefore were chosen as the material for Experiment 1a.

Experiment 2: A population of 48 F3 plants was selected at random from the cross Proctor x C.I. 3576. This cross was made in 1959 and

TABLE 1 - TREATMENT NUMBERS AND DETAILS OF 100 VARIETIES USED IN EXPERIMENT I.

Treatment Number	W.I. Number	Variety Name	C.I.No.	Country of Origin	Head Type
1	1195	Prior A		Australia	2
2	372	Maraini		Italy	6
3	395	Princess		Sweden	2
4	278	Excelsior	1248	Central Asia	6
5	951	Bankuti Korai		Hungary	2
6	838	Goldfoil	928	U.S.A.	2
7	726	Multan			6
8	579	Californian Mariout	1455	Egypt	6
9	564	Kivan	1016		6
10	636	Quinn	1024	U.S.A.	6
11	781		4334		6
12	787		4387		6
13	560	Bolivia	1257		6
14	586	Newal	6088	Canada	6
15	646	Chilian D	1433		6
16	650	Research		Australia	2
17	814	Black Barbless			6
18	878	Drake		Sweden	2
19	818	Mars	7015	U.S.A.	6
20	886	Rigel		Denmark	2
21	598	Coast 2		U.S.A.	6
22	576	Atlas Vaughn Seln. 13		U.S.A.	6
23	574	Big Boy		U.S.A.	6
24	609	Heitman's Surprise			2
25	563	017			6
26	614	Bolsheviki			6
27	846	Abyssinian intermedium			6
28	695	Arivat	7534	U.S.A.	6
29	867	Dorst		Denmark	2
30	858	Orge Martin 839	11213	Algeria	6
31	819	Peruvian selection			6
32	642	Featherston	1120		6
33	649	Lyallpur		India	6
34	559	Hanna	8106	Austria	2
35	815	Conway			6
36	723	L.O.G.	6168	U.S.A.	2
37	610	Cape		U.S.A.	6
38	624	Austral	6483	Australia	2
39	626	Lechtaler	6488	Austria	2
40	865	Kenia		Denmark	2
41	721	Kozan		Turkey	6
42	648	Gopal	1091		2
43	651	Flynn	1311	U.S.A.	6
44	728	Olympia	6107	Germany	6
45	701	Californian Coast	6115	North Africa	6
46	592	Vaughn	1367	U.S.A.	6
47	827	Velvon II	7088	U.S.A.	6
48	773		4149		6
49	857	Orge Saida	11212	Algeria	6
50	820	Prospect	6339	Canada	6

Treatment Number	W.I. Number	Variety Name	C.I.No.	Country of Origin	Head Type
51	589	Success			6
52	811	Georgia			2
53	577	Arequipa	1256		6
54	734	Telli 194			6
55	776		4228		6
56	775		4226	Egypt	2
57	707	Coast	690	U.S.A.	6
58	731	Rojo	5401	U.S.A.	6
59	866	Carlsberg II		Denmark	2
60	817	Glacier	6976	U.S.A.	6
61	754		1311		6
62	733	Sacramento			6
63	732	Stewart	6112	U.S.A.	6
64	864	Bonus	8093	Sweden	2
65	705	DD		U.S.A.	6
66	870	Piroline	9559	Germany	2
67	588	Zulu	1022		6
68	565	Weider	1021		6
69	862	Ymer		Sweden	2
70	627	Schladener	6490		6
71	768		3576	Egypt	2
72	632	L. Lechtaler			2
73	633	Samaria			2
74	683	BR1239		Canada	6
75	706	Club Mariout	261	Egypt	6
76	590	Trebi	936	Turkey	6
77	575	Compana	5438	U.S.A.	2
78	635	Aegyptische			6
79	772		4147-2		6
80	652	Maltworthy	11390	Australia	2
81	804		6306		6
82	715	India		India	6
83	788		4389		6
84	861	Freja	7130	Sweden	2
85	803		5647		6
86	656	Pannier	1330		6
87	763		2624		6
88	720	Kankyo	5869	U.S.S.R.	2
89	813	Beecher	6566	U.S.A.	6
90	869	Maythorpe	11143	England	2
91	638	Oderbrucker	4666	Germany	6
92	784		4359		6
93	868	Proctor	11143	England	2
94	805		6316		6
95	561	Bel	2071		6
96	709	Gem	7243	U.S.A.	6
97	801		5644		6
98	860	Orge 3270	11215	Algeria	6
99	716	India	4855	India	6
100	630	H. vulgare sp.			6

Table 2

Yield (g.m.$^{-2}$) in Experiment 1 of varieties used in Experiment la

Treatment Number	Variety Name	1969 Pure Stand	1969 Mixture	1970 Pure Stand	1970 Mixture
37	Cape	207	892	241	486
68	Weider	204	726	245	297
32	Featherston	191	310	225	84
Population mean		169	481	216	273

F2 rows were grown in 1962. Random selections from the F2 were made and 100 of these selections were used by Hamblin (1971). The 48 F3-derived lines used in this study were in turn, selected at random from the 100 F3 plants used in his 'low density' experiment. The term 'F3-derived line' refers to material derived from the same F3 plant. F4 and F6 seed of each of these lines was obtained from Hamblin (1971) and the derivation of these seed supplies for a single line is represented in Figure 1. The parents of this cross, Proctor and C.I. 3576, were included in the experiment to give a total of 50 treatments.

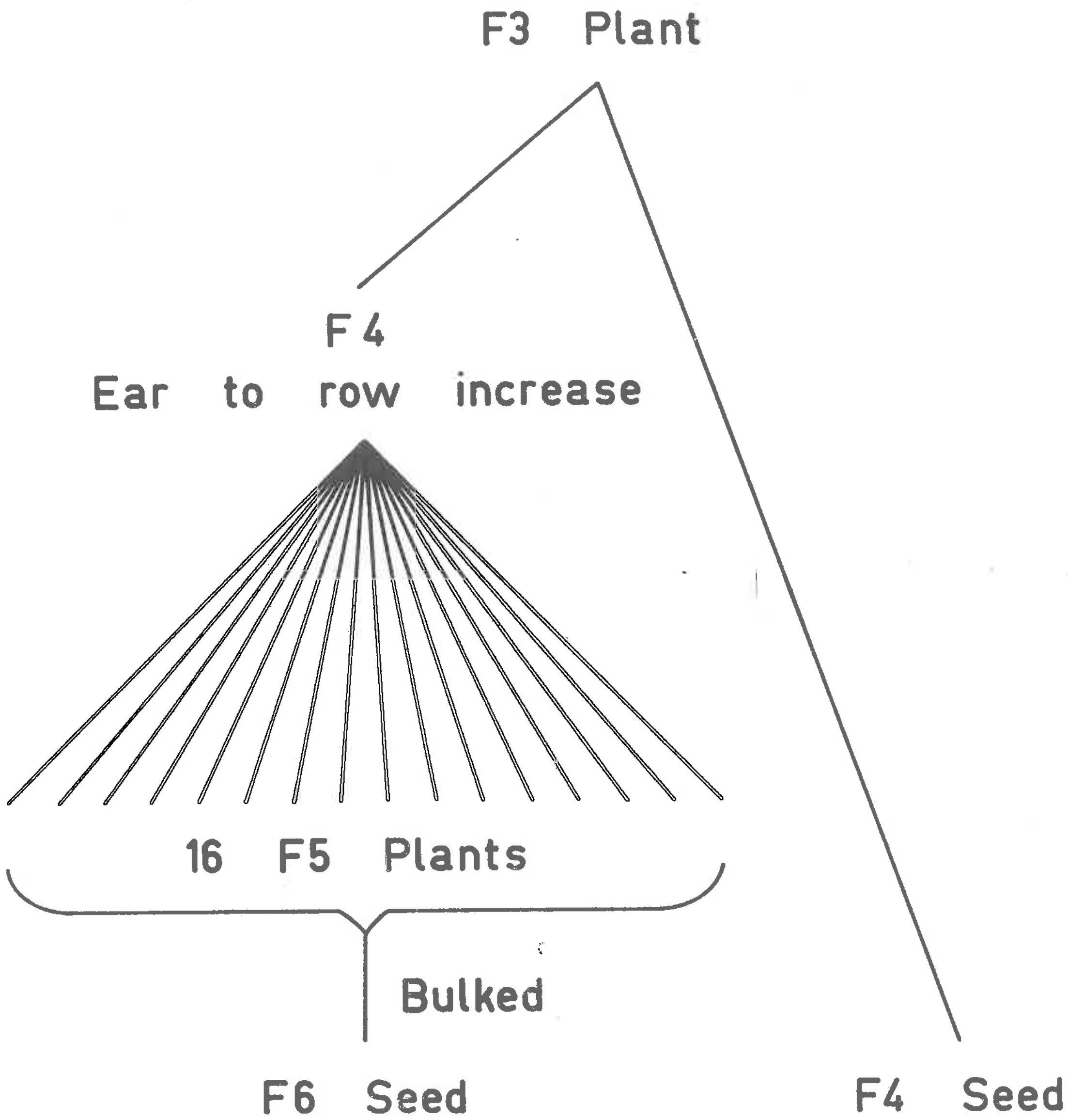
2. Experimental Details

a. Site and climate

Experiment 1 was grown in 1969 at the Waite Agricultural

Figure 1

Schematic representation of the derivation of F4 and F6 generations of one of the 48 F3-derived lines studied in Experiment 2 (Hamblin, 1971).


F3 Plant
F4
Ear to row increase
16 F5 Plants
Bulked
F6 Seed
F4 Seed

Research Institute, Adelaide, South Australia, and again in 1970 at Aldinga, a site in the barley growing area of South Australia approximately 45 kilometres south of Adelaide. Experiment 1a and Experiment 2 were grown at Aldinga in 1971.

The soil at the Waite Institute is a red brown earth of the Urrbrae series (Litchfield, 1951) and that at Aldinga, a greyish brown sandy loam of the Northfield series (Ward, 1966).

The climate in the Adelaide region is of the mediterranean type, the normal growing season is during the winter when rainfall is at a maximum and temperatures are mild. Frosts are uncommon and the growing period extends from May to November or December.

Rainfall records for 1969 at the Waite Institute and for 1970 and 1971 at Aldinga are compared with the long term averages for these sites in Table 3. The rainfall in all seasons was normal although October rainfall was below average in all seasons and especially so in 1969. This resulted in some moisture stress after flowering and late maturing varieties were at a disadvantage.

The experiments were sown on the following dates:

Experiment 1 , 1969	-	June 11
Experiment 1 , 1970	-	June 18
Experiment 1a, 1971	-	June 30
Experiment 2 , 1971	-	June 30

Table 3

Monthly rainfall (mm) for the Waite Institute and Aldinga compared with the long-term averages for these sites

	Waite Institute		Aldinga		
	1969	1925-1969 Mean	1970	1971	1893-1970 Mean
January	10.7	22.1	27.2	6.6	15.7
February	107.3	28.2	3.0	0.0	19.3
March	19.8	20.6	6.6	35.6	21.3
April	54.4	53.1	48.3	98.8	38.6
May	92.8	82.4	65.3	118.1	63.0
June	42.7	75.0	63.0	59.2	76.2
July	99.6	83.6	46.5	45.7	68.3
August	55.9	72.2	72.6	99.1	59.7
September	64.6	59.2	44.4	53.1	52.6
October	2.3	52.6	10.4	27.4	42.7
November	24.7	39.1	24.4	42.7	26.4
December	47.8	30.2	31.0	41.9	20.6
Total	622.6	618.3	442.7	628.2	504.4

b. Description of plots and design

Experiment 1

The plants in mixture: A mixture plot contained one plant of each of the 100 varieties. The plants were arranged in five rows with 20 plants per row. Spacing between plants within the row was 3.5 cm and between rose 17.5 cm. This is a normal density and arrangement for commercial crops in southern Australia.

The equipment used to sow these plots is shown in Plates 1 and 2. A sheet of masonite with holes drilled at 3.5 cm x 17.5 cm spacing was covered on one side with strips of paper towelling. Two seeds of the appropriate variety were placed in each hole and the second side of the masonite sheet was then covered with paper towelling. Boards to sow all the mixture plots were prepared in the laboratory prior to sowing.

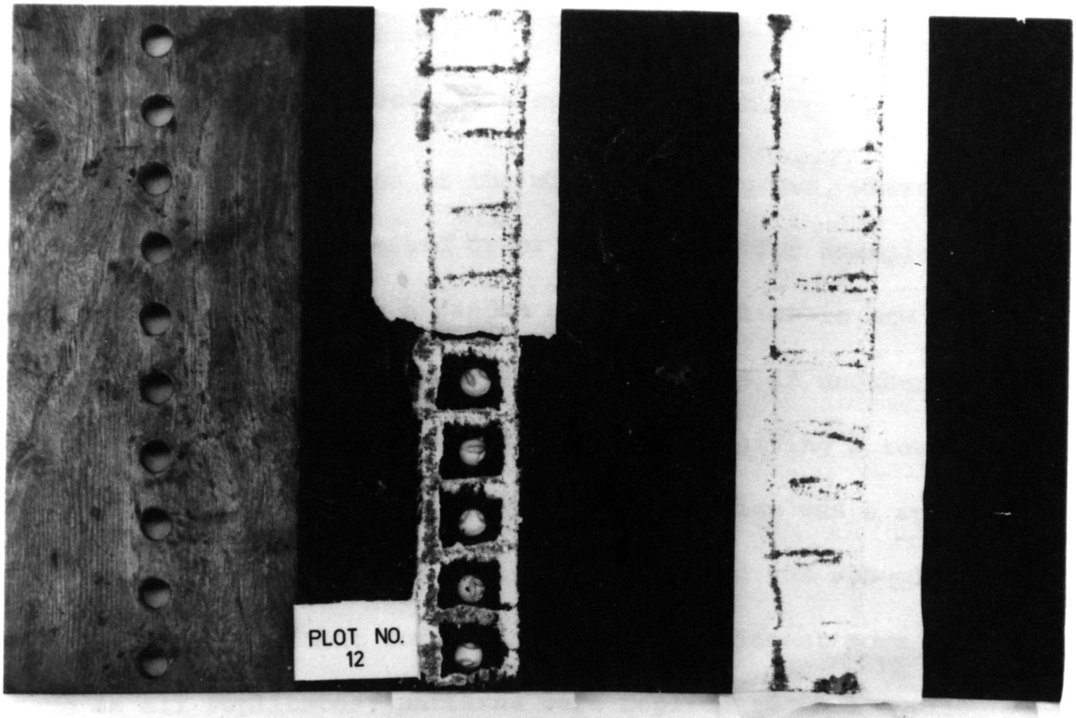
At sowing a plain base board with holes drilled at 3.5 cm x 17.5 cm spacing was placed on the ground and a dibber board with pegs at the same spacing was placed on top of the base board. This was forced into the ground, and then removed, leaving holes of constant depth in the soil. The prepared masonite board holding the seeds was placed on top of the base board and the upper strips of paper towelling removed (Plate 1). The seeds were forced through the lower layer of paper towelling into the soil. The holes were then covered with soil. Plots were later thinned to give one plant per hole. This method was quick and efficient and ensured

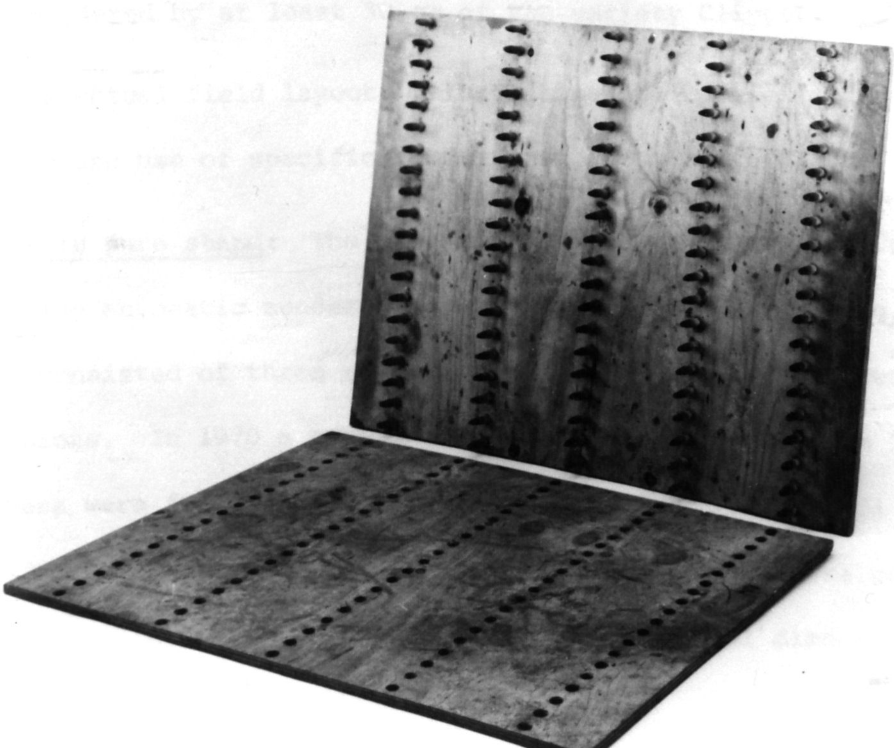
Plate 1

The dark masonite board, with seeds contained in holes between two strips of paper towelling. The paper towelling is partly removed to show the seeds and holes. The masonite board is placed on top of the plain base board but displaced horizontally by one row for illustrative purposes.

Plate 2

The plain base board and the dibber board used to sow the mixture plots for both Experiments 1 and 2.


PLOT NO.
12



placement of the correct seeds at a constant depth.

Four random patterns of the mixture were grown, where a pattern was simply a randomised order of sowing. For example, variety A was surrounded by a random set of varieties in one pattern and by a different random set of varieties in another pattern. Each pattern was replicated four times giving a total of 16 plots of the mixture. The experimental design was a split plot design with the main plots being patterns and the sub-plots, varieties. To ensure that competition between adjacent rows was the same in all replicates, patterns were replicated in a cyclic fashion. Where a pattern was at the end of a replicate a border row of the appropriate varieties was grown. The whole experimental area was bordered by at least 30 cm of the variety Clipper.

The actual field layout, illustrating the cyclic randomisation and the use of specific border rows is shown in Figure 2.

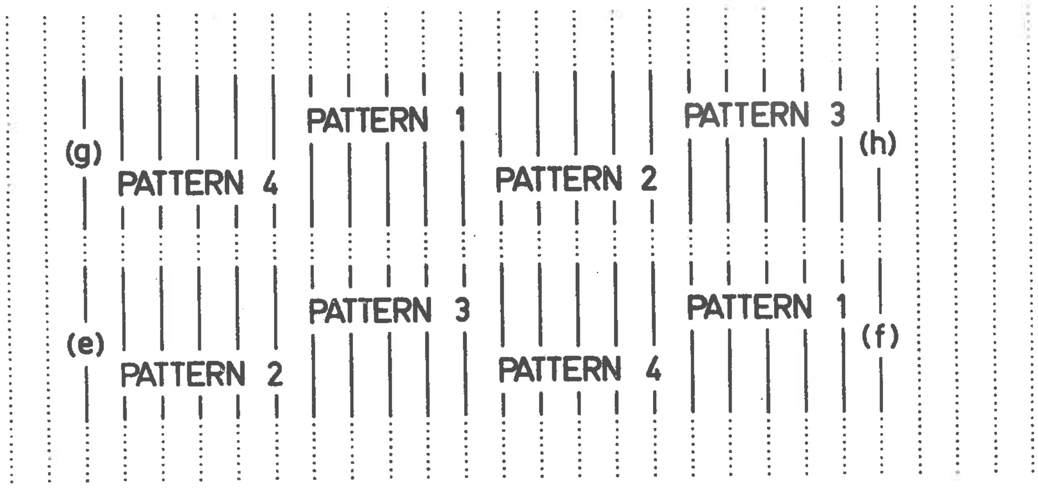
<u>The plants in pure stand</u>: The pure stand plots were sown in 1969 with a Finlay automatic seeder (Finlay, 1963) in plots 3 m long. Each plot consisted of three rows 17.5 cm apart with 36 cm between adjacent plots. In 1970 a cone seeder was used and plots were 5 m long. These were four-row plots with 15 cm between rows and 31 cm between adjacent plots. In both years the ends of plots were cut prior to harvesting to avoid end effects, and the final dimensions of the harvested plots were:

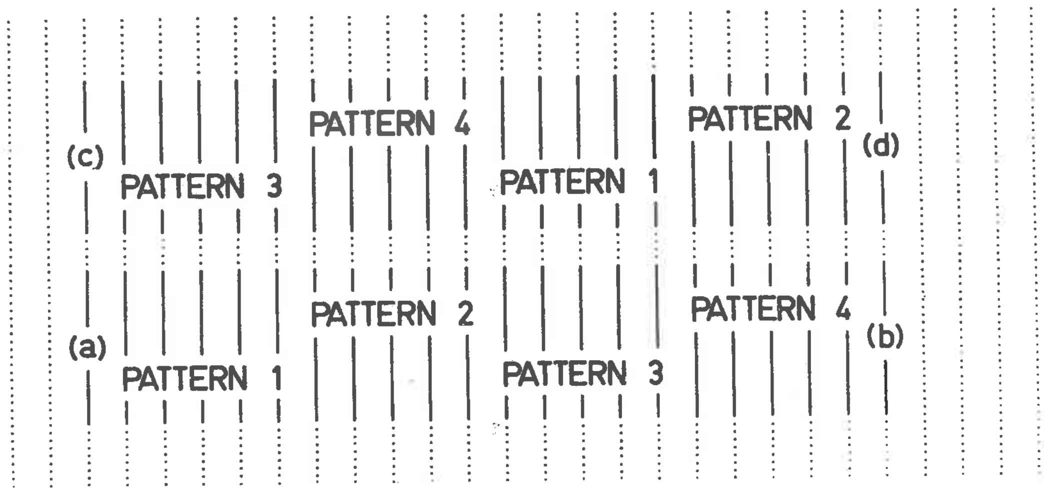
Figure 2

Field layout of mixture plots in 1969 and 1970. Each pattern was a different order of sowing of the 100 varieties. Patterns were randomised in a cyclic fashion and specific border rows, illustrated as rows (a) and (b), were sown to ensure the same competition for the outside rows of patterns in each replicate.

FIELD LAYOUT OF MIXTURES OF 100 VARIETIES,

1969 and 1970





⋮ Border plants —— CLIPPER

(a) = row 5, pattern 4
(c) = row 5, pattern 2
(e) = row 5, pattern 1
(g) = row 5, pattern 3

(b) = row 1, pattern 1
(d) = row 1, pattern 3
(f) = row 1, pattern 2
(h) = row 1, pattern 4

1969 - 2.45 m x 0.71 m

1970 - 3.18 m x 0.76 m.

Seeding rates in both mixture and pure stand were designed to give approximately 165 plants per square metre, the normal seeding rate (about 65 kg per ha) for commercial crops in southern Australia.

In 1969 a 10 x 10 lattice square design with three replicates was used (Cochran and Cox, 1962). Varieties were allocated treatment numbers at random and these numbers have been used throughout the experiment (Table 1).

In 1970 a randomised block design with four replicates was used, but within replicate environmental variation also was estimated by sowing in every fourth plot the commercial variety, Clipper to serve as a control or grid variety. It was intended that yields of the 100 varieties should be adjusted by expressing them as yields above or below the weighted means of adjacent grid plots. This experimental technique was proposed by Lamacraft (pers. comm.) and is now widely used at the Waite Institute.

Experiment 1a

The objective of this experiment was to determine if the assessments of the competitive ability of genotypes were similar when the competitive environment consisted of a specific genotype or a mixture of genotypes.

To investigate this question each of the three varieties was grown in four different competitive situations; one measured the pure stand performance, two measured the effects of competition from the other two varieties (one at a time), and the fourth measured the effect of competition from a mixture of all 100 varieties used in Experiment 1 (Table 4).

Table 4

Description of treatments used in Experiment 1a

Central plant	Surrounding plants in a plot			
Cape	Cape	Weider	Featherston	Mixture of 100 varieties
Weider	Cape	Weider	Featherston	Mixture of 100 varieties
Featherston	Cape	Weider	Featherston	Mixture of 100 varieties

The basic unit in this experiment was a five-row plot with 20 plants per row. The spacing between plants was again 3.5 cm x 17.5 cm. The experiment was sown at Aldinga in 1971 using the same technique and planting boards as in Experiment 1, in a randomised block design with 20 replicates. Measurements were taken on only the central plant of the plot which was similar or dissimilar from the remainder of the plot depending on the treatment.

Experiment 2

A plot of the mixture included one F4 plant of each

F3-derived line and six plants of each parent giving a total of 60 plants per plot. These were sown in three-row plots with 20 plants per row using the same methods and equipment as in Experiment 1. In every alternate row of the experiment plants 3 and 13 were the variety Proctor and plants 8 and 18 were C.I. 3576. In the intervening rows, plants 3 and 13 were C.I. 3576 and plants 8 and 18 were Proctor. As in Experiment 1 plant stands of approximately 165 plants per square metre were obtained for both pure stand and mixture plots. The experimental design was a randomised block with 30 replicates which were separated into three groups each of 10 replicates and these groups were grown at intervals alongside the pure stand experiment.

The treatments used and referred to as 'pure stand' plots were the two parents, Proctor and C.I. 3576, and the bulked F6 seed of each of the 48 F3-derived lines. The cone seeder was used to sow four-row plots 5 m long and the ends were cut before harvest to give a final plot 3.33 m x 0.76 m.

A randomised block design with four replicates was used. As in Experiment 1 in 1970, the variety Clipper was grown as a grid variety in every fourth plot throughout the experiment. The field layout was 12 blocks each containing 23 plots giving a total of 276 plots (200 experimental plots and 76 grid plots).

3. Characters Measured

Experiment 1

Individual plants in the mixtures were labelled and harvested separately. In 1969 measurements were taken on grain yield, total air-dry weight of the plant above ground, number of heads and number of seeds. In addition to these characters in 1970 measurements were made of the number of tillers, height to the top of the head and height to the flag leaf. Two measurements of height were made in view of the possibility of both characters having separate effects on yield in competitive situations (see page 25).

In 1969 the data recorded from the pure stand plots were grain yield, plant height and heading date. A plot was recorded as heading when an estimated 50% of the main tillers showed awns emerging approximately 3 cm. The plots were harvested using a 'Waite Gravelly Harvester' and seed samples were recleaned in the laboratory before weighing.

Samples 37 cm long were taken at random from all four rows of the pure stand plots in 1970. These samples were used to provide measurements of the same characters assessed in the mixtures. Data from the hand harvested samples permitted comparisons to be made between yield components and morphological characters in mixture and in pure stand. It was also possible to study whether any of these characters in mixture were related to yield in pure stand in such a way that they could be used as selection criteria in preference or in addition to yield in mixture.

After the samples were taken the remainder of the plot was harvested with the 'Waite Gravelly Harvester' and grain yield obtained.

Experiment 1a

The central plant of each plot was harvested at maturity and measurements were made of grain yield, total air-dry weight, height, height to the flag leaf, number of heads and number of seeds.

Experiment 2

Both mixture and pure stand plots were handled in exactly the same way as in Experiment 1 in 1970. The same data, except for tiller number, were recorded from single plants of the mixture, from hand harvested samples of the pure stand plots and from machine harvests of the remaining plot. Tiller number was not recorded in this experiment as all elongated tillers had produced heads and no heads had been lost. Consequently the number of heads and tillers was the same.

All appropriate data from these experiments are expressed on a per square metre basis in this thesis. The original data from all experiments are stored on magnetic tape at the Waite

Agricultural Research Institute.

4. Statistical Methods

Extensive use was made of the University of Adelaide CDC6400 computer for all statistical analysis and for recording original data. Programmes were written by the author in Fortran and Statscript (Lamacraft, 1969); BMD Biomedical Computer Programs (Dixon, 1968) were also used for stepwise regression.

Adjustment of yield

Pure stand plot yields in 1970 and 1971 were adjusted using the grid plots described earlier. The adjusted yields were calculated in three steps.

i) As the yield of each grid plot was influenced, not only by its location, but also by experimental error, an attempt was made to reduce experimental error by calculating the weighted mean of several adjacent grid plots. The arrangement of grid plots and the weights given to them in this 'smoothing' process are shown in Figure 3.

Each central grid plot was given a weighting of 4, the grid plots on either side in the same block were given a weighting of 2, and the nearest grid plots in adjacent blocks had a weighting of 1.

If y_i is the yield of the i^{th} grid plot then the 'smoothed' or calculated yield (x_i) for grid plot 4 in Figure 3 is:

$$x_4 = (4y_4 + 2y_3 + 2y_5 + y_1 + y_2 + y_6 + y_7)/12.$$

These weightings were chosen as being proportional to the distances between the centres of grid plots. It was believed that this method would give a good estimate of the true yield expected of Clipper at each location of a grid plot.

ii) The yields expected if Clipper had been grown in the locations of the experimental plots was calculated by linear interpolation between smoothed values of adjacent grid plots in the same block. For experimental plots at the edges of the experiment extrapolation from the nearest grid plot was used.

iii) The deviations of the experimental plots from the expected Clipper yields were then calculated and the adjusted yields of these plots were obtained by adding the deviation to the mean yield of all Clipper grid plots.

Thus the adjusted yields (A') of a plot is expressed by the following equations:

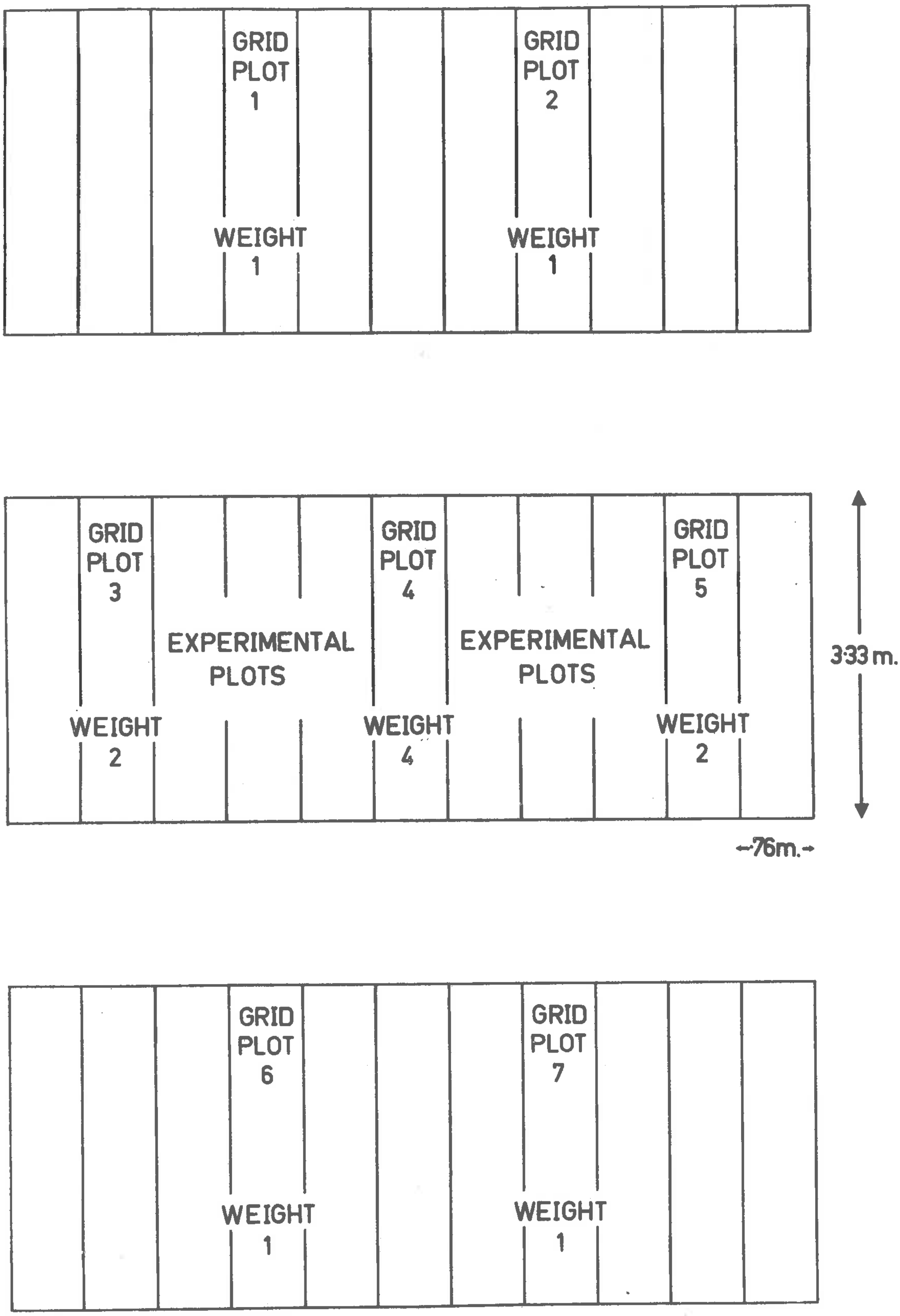
$$A' = A - 0.5(x_i + x_j) + C$$

for experimental plots midway between two grid plots

or $$A' = A - (0.75x_i + 0.25x_j) + C$$

Figure 3

Example of distribution of grid plots and experimental plots. The weights indicated in the diagram are the factors by which the yield of the grid plots were multiplied when calculating a 'smoothed' value for grid plot 4.


GRID PLOT 1
WEIGHT 1
GRID PLOT 2
WEIGHT 1
GRID PLOT 3
WEIGHT 2
EXPERIMENTAL PLOTS
GRID PLOT 4
WEIGHT 4
EXPERIMENTAL PLOTS
GRID PLOT 5
WEIGHT 2
3·33 m.
76m.
GRID PLOT 6
WEIGHT 1
GRID PLOT 7
WEIGHT 1

for experimental plots adjacent to the i^{th} grid plot.

In these equations

A = the actual yield of the experimental plot

C = the mean yield of all Clipper grid plots

x_i and x_j are the smoothed yields of successive grid plots.

This method of yield adjustment is similar to that used by McClelland (1926) and discussed by LeClerg (1966).

Computer programs to make these extensive claculations were written by Rathjen and Lamacraft and allow rapid comparisons of actual and adjusted data to be made.

Stepwise regression: Since a number of characters other than yield were measured on the plants in the mixtures it was possible to determine which of these characters provided the best estimate of yield in pure stand. This was achieved using a stepwise regression analysis (Efroymson, 1962) for which the calculations were carried out using a BMD computer program (Dixon, 1968).

Stepwise regression is essentially a multiple regression analysis in which the least squares method is used to estimate the relationship between a dependent variable and a number of independent variables.

The equation is of the form

$$y = b_0 + b_1x_1 + b_2x_2 + \text{------} + b_nx_n$$

where y is the dependent variable

$x_1, x_2,$ ---- x_n are the independent variables

$b_0, b_1, b_2,$ ---- b_n are the coefficients to be calculated.

In the stepwise regression a number of intermediate regression equations are calculated commencing with the simple linear regression equation

$$y = b_0 + b_1x_1$$

where x_1 is the independent variable having the highest correlation with y. The next equation calculated is

$$y = b_0 + b_1x_1 + b_2x_2$$

where x_2 is the independent variable having the highest partial correlation with y when x_1 is held constant. At each subsequent step the independent variable added to the equation is that which has the highest partial correlation with y, with those independent variables already in the equation being held constant. Any independent variables which do not have significant partial correlations with y are not included in the equation.

IV. RESULTS

A. Experiment 1

An analysis of the results from the mixture plots will be presented first. This will be followed by results from the pure stand plots and finally comparisons will be made of data from both mixture and pure stand.

1. Analysis of Data from Mixture Plots

All data from the mixture plots were analysed as a split plot design with patterns as the main effects and varieties as the sub-plots. The analyses of variance are given in Tables 5 and 6. The total degrees of freedom differ for the two years as there were 106 missing values in 1969 and 57 in 1970. These missing values were for plants damaged or dead prior to harvest.

Tables 5 and 6 indicate that in both years there were very highly significant differences between varieties for yield and all the other characters. Replicate effects were not significant except for grain yield and number of seeds in 1970. Patterns were also not significant for any character in either year.

Of interest is the absence of a significant pattern x variety interaction for yield, indicating that the yield of a variety was not altered by changing the varieties with which it was competing. Such a result is perhaps surprising but in the

Table 5

Analysis of variance for a mixture of 100 varieties, Waite, 1969

(Mean Squares x 10^{-4})

		Dry Wt. g.m.$^{-2}$		Heads m^{-2}	
	D.F.	M.S.	F	M.S.	F
Reps	3	112.1	0.75	5.64	0.82
Patterns (P)	3	193.5		8.14	
Error A	9	150.3		6.85	
Varieties (V)	99	490.0	5.43***	30.73	6.23*** (a)
P x V	297	90.7	1.00	4.74	0.96
Error B	1082	90.2		4.94	

		Seeds m^{-2}		Yield g.m.$^{-2}$	
	D.F.	M.S.	F	M.S.	F
Reps	3	9531	0.64	33.26	1.98
Patterns (P)	3	16720		20.71	
Error A	9	14793		16.82	
Varieties (V)	99	40644	4.79***	68.35	5.33***
P x V	297	9072	1.07	12.57	0.98
Error B	1082	8490		12.81	

(a) * indicates significance at 5% level
** indicates significance at 1% level
*** indicates significance at 0.1% level

This notation for statistical significance is used throughout this thesis.

Table 6

Analysis of variance for a mixture of 100 varieties, Aldinga, 1970

(Mean Squares x 10^{-4})

		Dry Wt. $g.m.^{-2}$		Heads m^{-2}		Tillers m^{-2}	
	D.F.	M.S.	F	M.S.	F	M.S.	F
Reps	3	193.8		7.91	2.13	7.84	3.10
Patterns (P)	3	59.0		5.33		3.58	
Error A	9	73.7		3.72		2.53	
Varieties (V)	99	149.1	4.99***	14.63	3.43***	17.07	5.13***
P x V	297	32.2	1.08	3.46	1.06	3.69	1.11
Error B	1131	29.9		3.26		3.33	

		Height cm		Flag ht cm	
Reps	3	0.1711	1.44	0.2306	3.23
Patterns (P)	3	0.0907		0.0550	
Error A	9	0.1192		0.0715	
Varieties (V)	99	0.1109	7.15***	0.0799	6.89***
P x V	297	0.0187	1.20*	0.0124	1.07
Error B	1131	0.0155		0.0116	

		Seeds m^{-2}		Yield $g.m.^{-2}$	
Reps	3	28741	4.52*	85.85	5.46*
Patterns (P)	3	6001		12.40	
Error A	9	6357		15.73	
Varieties (V)	99	8832	3.43***	24.24	4.53***
P x V	297	2715	1.05	5.88	1.10
Error B	1131	2576		5.35	

Discussion it will be suggested that the mean competitive effect of a randomly chosen group of many neighbours may be relatively uniform.

Attempts were made to adjust the yield of individual plants using the 'moving mean' method suggested by Hamblin (1971). At each location in the experiment the mean yield of the neighbouring plants was calculated and the yield of the central plant expressed as a deviation from this mean. Neighbouring groups of the following sizes were used in these calculations:

i) 3 plants on either side of the central plant in the same row and 3 plants in adjacent rows immediately opposite the central plant;

ii) 3 plants on either side in the same row and 7 plants immediately opposite in the adjacent rows;

iii) 5 plants on either side in the same row and 7 plants immediately opposite in the adjacent rows;

iv) 5 plants on either side in the same row and 11 plants immediately opposite in the adjacent rows.

None of these methods of calculating 'moving means' provided useful adjustment of individual plant yields. When an analysis of variance was calculated for adjusted yields the variance ratio for variety effects was not increased. The major result was to eliminate almost entirely the effects due to replicates and to patterns, particularly when the larger groups were used to calculate the moving means. Expressing the yield of a plant as a deviation from these estimates of moving means was similar to expressing it as a deviation from the mean yield of the plot. This became more noticeable as the size of the neighbouring group was increased.

It may be concluded that the use of a moving mean was of little value when such a small number of plants occurred within each plot.

2. Analysis of Data from Pure Stand Plots

The mean yield of the 100 varieties in 1969 was 168.6g.m.$^{-2}$ which was slightly higher than the mean yield of commercial crops in South Australia in 1969 (110g.m.$^{-2}$). The yields of varieties ranged from 45.0g.m.$^{-2}$ to 279.0g.m.$^{-2}$. The analysis of variance for this data is presented in Table 7.

Table 7

Analysis of variance of grain yield in pure stand, 1969

	D.F.	Mean Square	F
Replicates	2	154495	
Varieties (unadjusted)	99	6352	4.01***
Blocks (adjusted)	27	5561	3.51***
Intra-block error	171	1583	
Total	299		

The use of the triple lattice design which allows the yields of the varieties to be adjusted on the basis of the initial analysis was slightly more efficient that the randomised block design. Following Cochran and Cox (1962)

$$E \text{ (efficiency)} = \frac{\text{Error mean square from randomised block}}{\text{Effective error mean square}}$$

$$\text{Effective error mean square} = E_e \left(1 + \frac{rkw}{k+1}\right)$$

where E_e = intra block error

r = number of replicates

k = units in blocks

w = weighting factor used to adjust block totals.

In this experiment E = 122%, indicating a gain in efficiency from the use of this design. Consequently adjusted variety yields were used as the best estimate of yield in pure stand.

The variance ratio for adjusted variety effects was 4.19 which is significant at the 0.1% level.

Although the triple lattice was more efficient than a randomised block design, there were still serious limitations. It was believed that soil variation in the experimental area was so irregular that the lattice design did not estimate the variation effectively. Small areas of high and low yield were observed within some blocks and it was felt that a method which estimated more localised variation could be more efficient than the triple lattice design.

In an attempt to estimate localised variation a grid of control plots was grown as described on page 47. The grid of control plots was used in conjunction with four replicates in 1970 and the analyses of variance for both actual and adjusted yields are given in Table 8.

Table 8

Analysis of variance of grain yield ($g.m.^{-2}$), 1970

		Actual Yield		Adjusted Yield	
	D.F.	M.S.	F	M.S.	F
Reps	3	7347	3.97***	22592	16.90***
Varieties	99	11917	6.43***	11415	8.54***
Error	297	1852		1337	

The adjustment using the grid plot technique was successful in reducing the error mean square by 28%, while the variance ratios for varieties and replicates were increased. The increase in effects due to replicates was large; its cause is revealed by data presented in Table 9. It should be realised that in this table the variance for the 100 varieties within a replicate has both a variety and an environmental component whereas the variance for the grid plots within a replicate is purely environmental.

Table 9

Mean yields and variances within replicates, 1970

	Actual yields (g.m.$^{-2}$)				Adjusted yields (g.m.$^{-2}$)
	100 Varieties		Clipper grid plots		100 Varieties
	Mean	Variance	Mean	Variance	Mean
Rep 1	224	4132	236	650	197
Rep 2	206	4882	205	2124	210
Rep 3	222	4362	205	1234	226
Rep 4	214	4095	191	805	232

The yields of the grid plots decreased from Replicate 1 to Replicate 4 while no such pattern existed for the mean of the 100 varieties. Thus the mean yield of the 100 varieties increased from a level 12g lower than the mean of the Clipper grid plots in Replicate 1, to 1g greater in Replicate 2, 17g greater in Replicate 3 and 23g greater in Replicate 4. Since the adjusted yields were calculated by adding the individual deviations to the mean yield of all Clipper grid plots (209g.m.$^{-2}$), the means of the adjusted yields of the 100 varieties increased from Replicate 1 to

Replicate 4 as shown in Table 9. When the yields of the 100 varieties were expressed relative to the yield of Clipper a noticeable replicate effect was introduced.

In 1970 samples were harvested by hand from all plots to allow measurements to be made of characters such as numbers of heads and numbers of seeds. The analyses of variance for these characters are given in Table 10. For all characters there were very highly significant differences between varieties.

A comparison was made of the estimates of yield from the hand harvested samples with those from the remainder of the plot harvested by machine. The samples could not be adjusted using the grid plot technique since this requires equal spacing of experimental units and the samples were taken at random from the plots. The sample yields are therefore compared with actual yields in Table 11.

The yields obtained from machine harvesting were approximately 25% lower than yields from hand harvesting. The lower yields must be attributed to general inefficiency of the machine harvesting and to an inability to harvest the grain from late, short tillers which were below the harvesting level. The occurrence of late tillers was stimulated by rain in September and this may not be so pronounced in normal seasons.

An attempt was made to estimate the amount of grain

Table 10

Analyses of variance for characters measured on hand harvested samples from pure stand plots, Aldinga, 1970

(Mean squares x 10^{-4})

		Dry Wt. g.m.$^{-2}$		Tillers m^{-2}		Heads m^{-2}	
	D.F.	M.S.	F	M.S.	F	M.S.	F
Rep	3	138.2	55.44***	8.092	23.00***	7.739	34.12***
Varieties	99	12.9	5.18***	3.402	9.67***	2.187	9.64***
Error	297	2.5		0.352		0.227	
		Height cm		Flag Ht cm			
Rep	3	0.0305	4.32	0.0550	28.1***		
Varieties	99	0.0419	5.94***	0.0332	16.96***		
Error	297	0.0070		0.0019			
		1000 S.W. g		Yield g.m.$^{-2}$			
Rep	3	8.192	38.05***	14.86	40.33***		
Varieties	99	1.914	8.89***	2.57	6.98***		
Error	297	0.215		0.37			

Table 11

Comparison of the hand harvested sample and the machine harvested remainder of the plot, (1970)

		100 Varieties	Clipper Grid Plots
Mean Yield $(g.m.^{-2})$	Hand harvested sample	298	268
	Machine harvested plot	216	209
Coefficient of Variation	Hand harvested sample	20.4	21.6
	Machine harvested plot	19.8	18.4
Correlation between sample yields and plot yields			
1) For all plots		0.66***	0.42***
2) For variety means		0.88***	

which was produced on these tillers. Hand harvested samples from 21 plots of the Clipper grid were studied to determine the height distribution of the grain. Data from these plots are presented in Table 12, and suggest that if the machines were unable to harvest below 50 cm then perhaps as much as 10% of the potential yield was below the harvesting level.. Hence it is believed that approximately 15% of the grain was lost in the harvesting process.

Coefficients of variation were similar for hand harvested samples and machine harvested plots, indicating that there was no greater error in the use of samples. The correlation (0.66)

Table 12

Height distribution of grain yield from 21 plots of the Clipper grid

Height class	Grain yield (g)	Percentage of total yield
0 - 30 cm	11.8	0.8
31 - 40	44.5	3.1
41 - 50	83.5	5.8
51 - 60	227.3	15.7
61 - 70	560.4	38.7
71 - 80	461.6	31.9
81 - 90	58.5	4.0
Total	1447.6	100.0

between a sample yield and the plot yield was very highly significant. A higher correlation (0.88) existed between the variety yields based on the mean of four samples and those based on the mean of four machine harvested plots. In addition there was no significant interaction between variety and method of harvest and it was concluded that samples provided satisfactory estimates of yield and therefore of the other characters.

3. Relationship between Yield in Mixture and Yield in Pure Stand

It was believed, on the basis of data presented in the previous section, that the best estimate of yield in pure stand of the varieties was the adjusted yield calculated from the triple lattice design in 1969 and from the grid plot technique in 1970. Mean yields of varieties in mixture were therefore plotted against adjusted mean yields in pure stand for both 1969 (Fig. 4) and 1970 (Fig. 5).

In both years a greater range in yields was obtained for the mixture than for the pure stand, suggesting that competition brought about increased differentiation between varieties. In addition the mean yields were greater in mixture but this difference cannot be considered as evidence for their superiority as growth was retarded, due to poor drainage in part of the pure stand experiment in 1969, while in both years pure stand yields were lowered by the inefficiency of machine harvesting. The data from hand harvested samples in 1970 indicated that pure stand yields were very similar to yields in mixture (Table 15, pg. 73).

Inspection of the graphs reveals that 6-row varieties were higher yielding than 2-row varieties in both mixture and pure stand. However there was no evidence that one type was more affected by competition than the other.

The correlations between yield in mixture and yield in pure stand illustrated in the graphs are:

Figure 4

Relationship between yield in mixture and yield in pure stand of 100 varieties. Least significant differences at the 5% level are indicated in the diagram. Experiment 1, 1969.

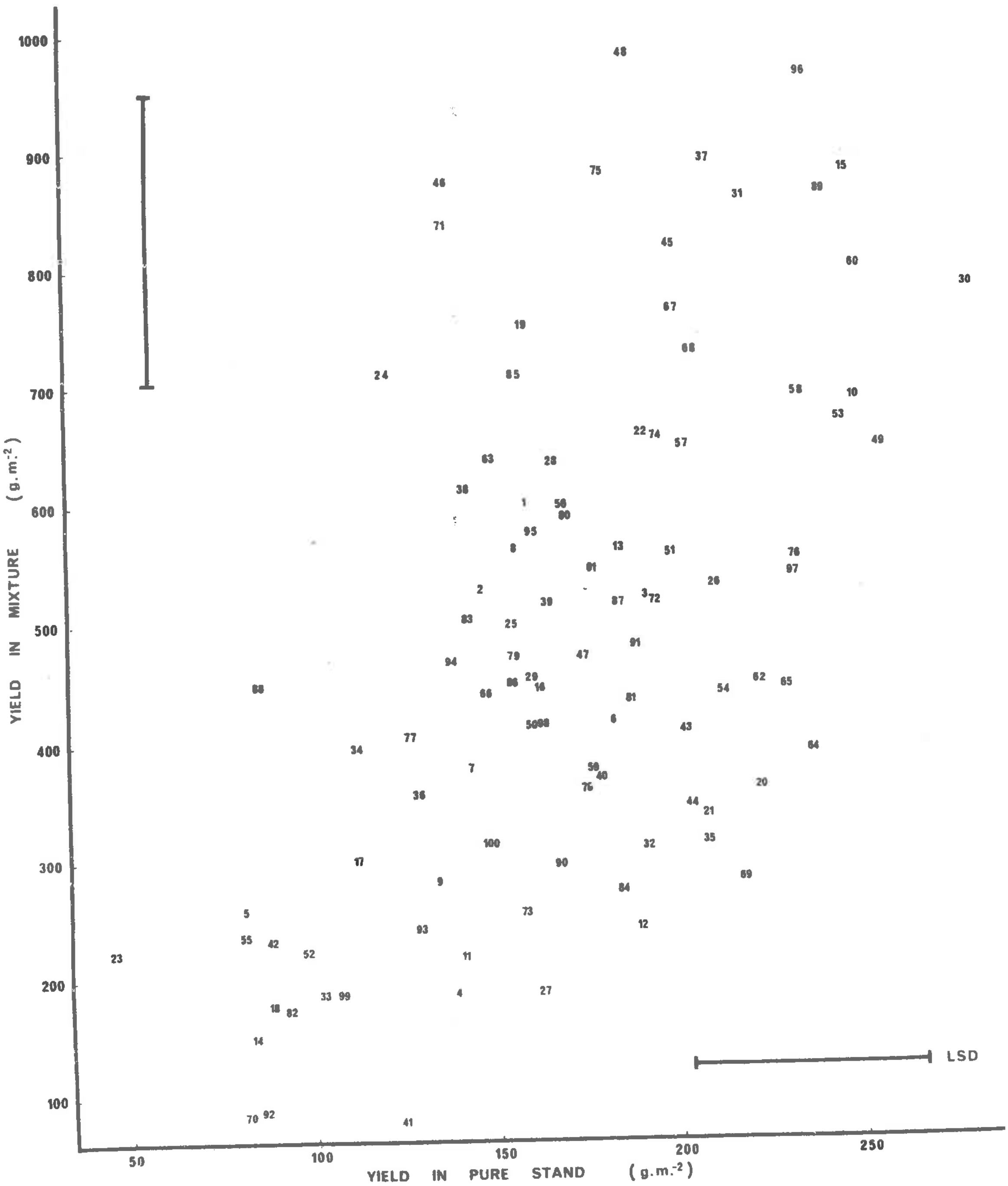
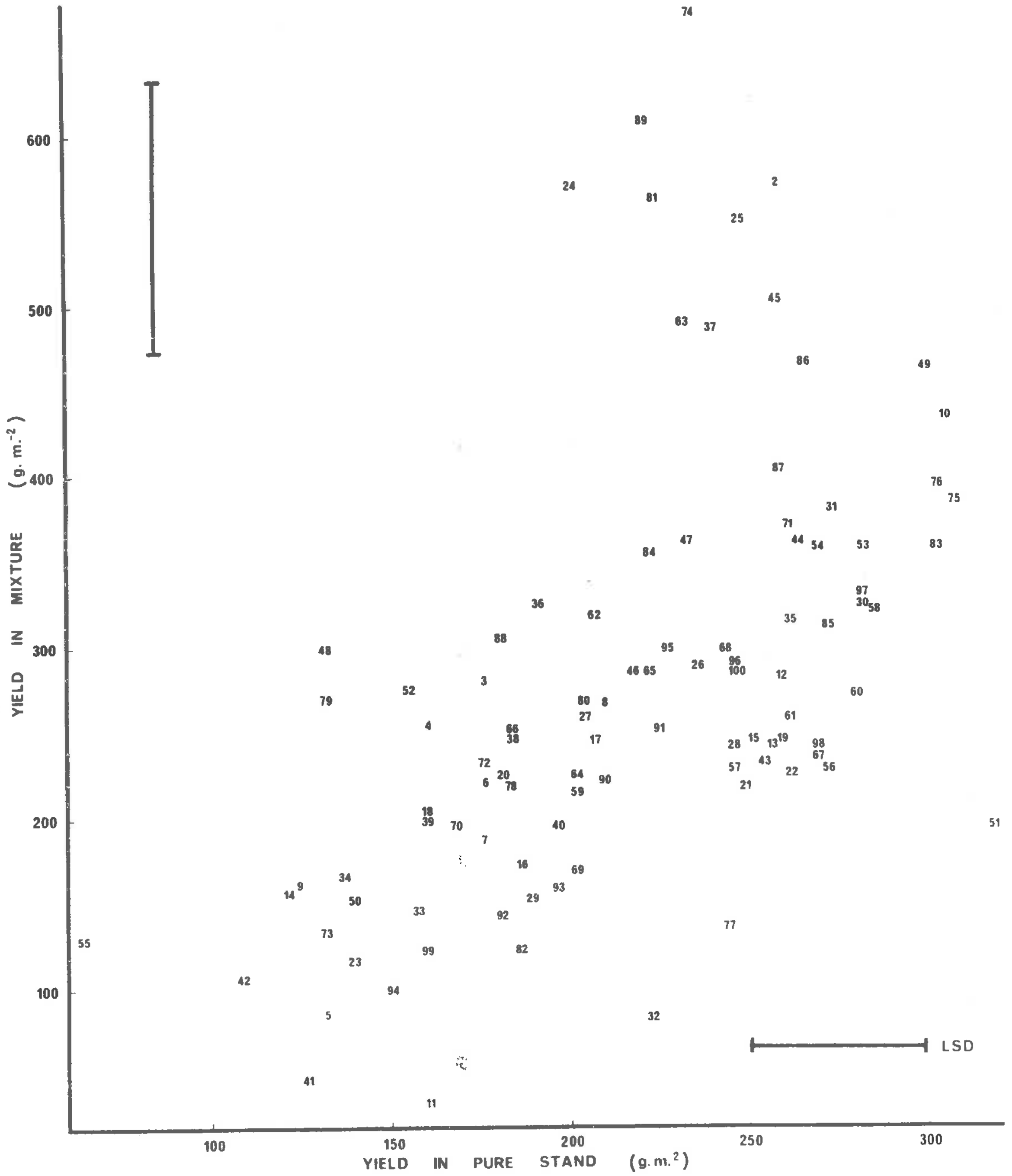

YIELD IN MIXTURE (g.m.$^{-2}$)
1000
900
800
700
600
500
400
300
200
100
YIELD IN PURE STAND (g.m.$^{-2}$)
50
100
150
200
250
LSD

Figure 5

Relationship between yield in mixture and yield in pure stand of 100 varieties. Least significant differences at the 5% level are indicated in the diagram. Experiment 1, 1970.


YIELD IN MIXTURE (g. m.$^{-2}$)
YIELD IN PURE STAND (g. m.$^{-2}$)
LSD
100
200
300
400
500
600
100
150
200
250
300

1969 - 0.56***

1970 - 0.54***.

The value for each variety in the mixture used in these correlations was the mean of 16 plants (i.e. 4 replicates of 4 patterns). The effects of micro-environmental variation within the experimental area have therefore been reduced in these calculations. As this study is concerned with the possibility of selecting on a single plant basis, it is more pertinent to examine the correlation between the yield of single plants in mixture and yield in pure stand. Since each variety was in 16 plots of the mixture it was possible to obtain 16 separate estimates of the correlation in each year. These correlations are given in Table 13. In general they are much lower than those calculated from mean yields and this suggests that micro-environmental variation is a major factor influencing yield in mixture. In most cases, however there is still a significant, positive correlation.

A positive correlation between yield in mixture and yield in pure stand indicates that it should have been possible to select on a single plant basis. To simulate a truncation selection procedure, the highest yielding 20 varieties in each plot of the mixture were identified. The mean yield in pure stand of these 20 varieties was then compared with the mean yield of the whole population of 100 varieties in pure stand.

Table 13

Correlations between single plant yields in mixture and yields in pure stand

Plot	1969	1970
1	0.261**	0.261**
2	0.196*	0.072
3	0.254*	0.116
4	0.158	0.345***
5	0.288**	0.276**
6	0.325***	0.127
7	0.339***	0.133
8	0.323***	0.300**
9	0.272***	0.336***
10	0.440***	0.343***
11	0.370***	0.214*
12	0.300**	0.370***
13	0.350***	0.438***
14	0.340***	0.235*
15	0.324***	0.290**
16	0.202*	0.200*
Over all 16 plots	0.564***	0.538***
Mean of two years	0.657***	

The results of these comparisons are presented in Table 14 for both 1969 and 1970.

In all cases the mean yield of the selected 20 varieties was greater than the mean yield of the whole population and when yield in mixture was based on the mean of all 16 plots of the mixture, the selected population was approximately 20% higher in both years.

To determine whether different selection intensities would have affected the conclusion, truncation selection was also simulated by selecting the highest yielding 10%, 15%, 20% and 25% of varieties on the basis of their mean yields in mixture. The frequency distributions of these selections, together with the distribution of the whole population, are shown in Figures 6 and 7 for 1969 and 1970 respectively. At all selection intensities the selected popolation had a higher mean yield than the original population and selection appeared to be effective.

4. Yield Components and Morphological Characters

In 1970 measurements of yield and several other characters were made on plants from both the mixture and pure stand plots. In addition, from these measurements it was possible to derive the yield components, seeds per head and 1000 seed weight and also the straw weight which was derived as the difference between total dry weight and grain yield. The means of these characters

Table 14

Mean yield in pure stand of the highest yielding 20 varieties from each plot of the mixture compared with (at the bottom of the table)

I. Mean yield in pure stand of 20 varieties with the highest mean yield in mixture

II. Mean yield in pure stand of all 100 varieties

	1969			1970		
Plot	Mean Yield ($g.m.^{-2}$)	%	Standard Deviation	Mean Yield ($g.m.^{-2}$)	%	Standard Deviation
1	187	111	31.9	232	107	38.7
2	195	116	43.5	226	105	42.1
3	182	108	43.3	237	110	40.1
4	185	109	44.4	237	110	51.6
5	192	114	39.3	226	105	48.1
6	186	110	35.1	243	113	37.9
7	193	115	38.3	235	109	56.9
8	199	118	40.1	226	105	39.5
9	183	108	38.1	248	115	36.7
10	194	115	49.7	245	113	37.4
11	201	119	35.5	232	107	45.0
12	194	115	42.4	253	117	38.7
13	188	112	40.5	242	112	43.8
14	197	117	31.9	244	113	45.7
15	197	117	43.7	252	117	41.9
16	185	110	40.1	234	108	42.6
I.	204	121	42.8	261	121	30.4
II.	169	100	47.6	216	100	53.4

Figure 6

Simulated truncation selection at four intensities in a population of 100 homozygous varieties. The distributions indicated are of yield in pure stand for:

i) all 100 varieties

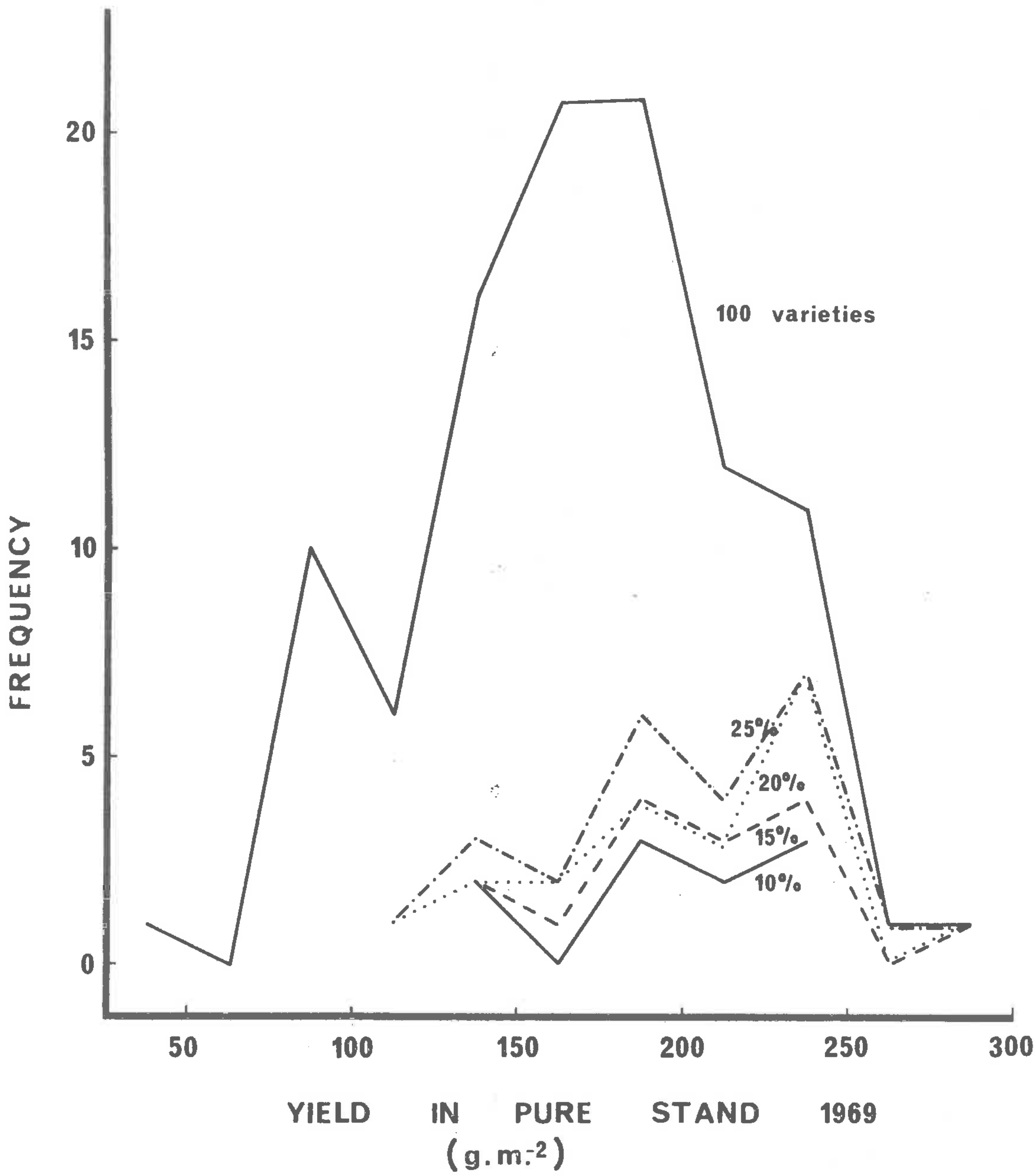
ii) highest yielding 10% of varieties in mixture

iii) highest yielding 15% of varieties in mixture

iv) highest yielding 20% of varieties in mixture

v) highest yielding 25% of varieties in mixture

Experiment 1, 1969.


FREQUENCY
20
15
10
5
0
100 varieties
25%
20%
15%
10%
50
100
150
200
250
300
YIELD IN PURE STAND 1969
(g.m.-2)

<u>Figure 7</u>

Simulated truncation selection at four intensities in a population of 100 homozygous varieties. The distributions indicated are of yield in pure stand for:

i) all 100 varieties

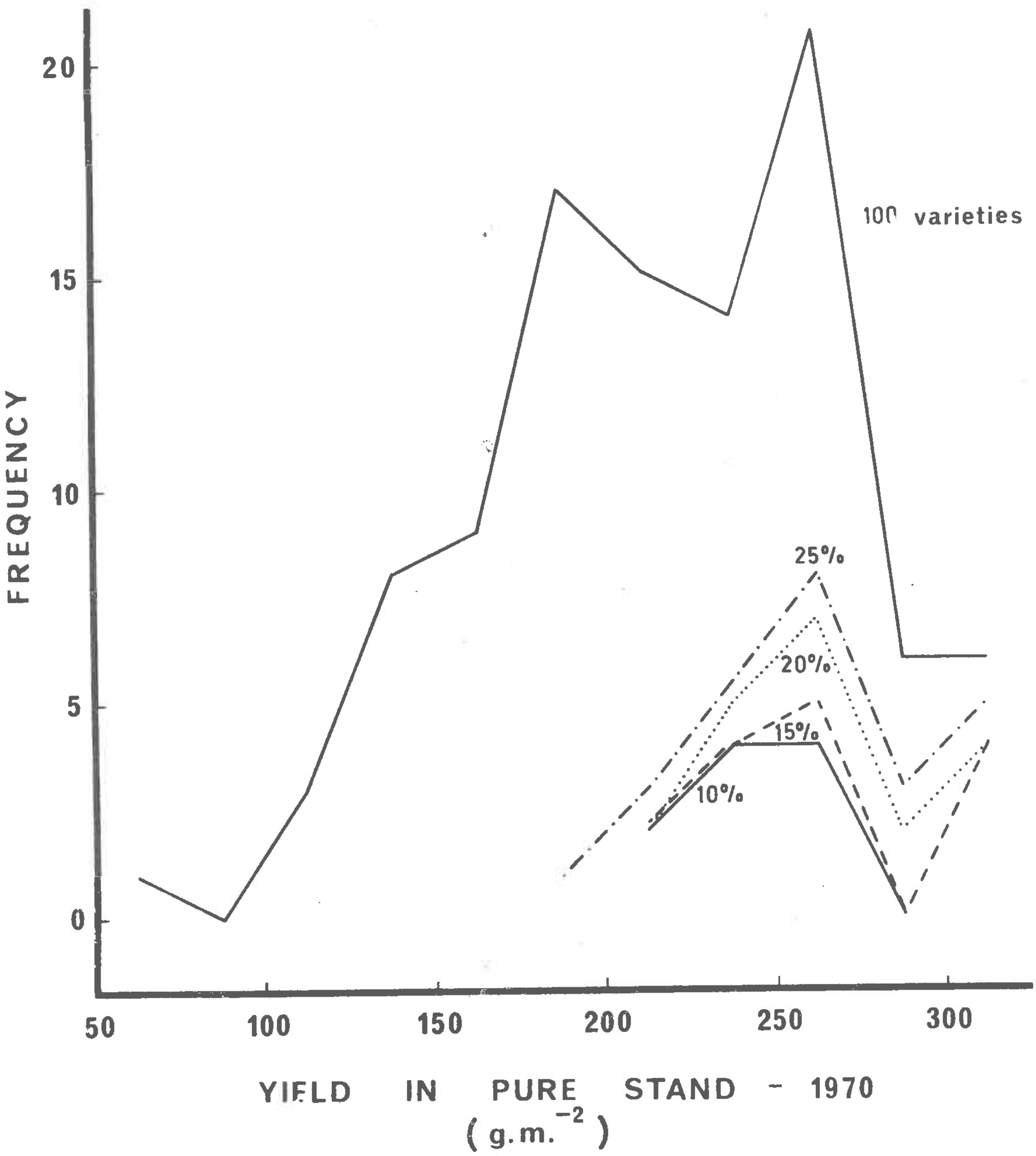
ii) highest yielding 10% of varieties in mixture

iii) highest yielding 15% of varieties in mixture

iv) highest yielding 20% of varieties in mixture

v) highest yielding 25% of varieties in mixture

Experiment 1, 1970.


20
15
10
5
0
FREQUENCY
100 varieties
25%
20%
15%
10%
50
100
150
200
250
300
YIELD IN PURE STAND - 1970
(g.m.$^{-2}$)

are given in Table 15 for both mixture and pure stand.

Table 15

Means and coefficients of variation of characters measured in mixture and in pure stand

	Mixture		Pure Stand	
	Mean	C.V.	Mean	C.V.
Yield (g.m.$^{-2}$)	273	45.7	298	26.8
Straw Weight (g.m.$^{-2}$)	531	36.7	624	18.2
Height (cm)	65	13.2	98	10.5
Flag Height (cm)	57	12.7	84	10.9
No. Tillers (m^{-2})	335	31.3	330	27.9
No. Heads (m^{-2})	292	33.2	263	28.1
Seeds per Head	25	32.4	28	30.7
1000 Seed Weight (g)	38	18.2	42	11.7

The mixture plots and pure stand plots were not intermingled in a randomised layout and a fully rigorous comparison cannot be made but two points are of interest.

Firstly, although there is a tendency for values from mixtures to be lower than from pure stands, this is not the case for the number of tillers and the number of heads per square metre.

Secondly the coefficient of variation in this table is the standard deviation of the variety means expressed as a percentage of the overall mean, and is therefore a measure of the relative genotypic variation. For all characters, the coefficient of variation was higher when measured in mixture than when measured in pure stand.

The data presented in Table 15 indicate that competition increased the differences between varieties for all characters measured. It also had a distinctive effect on the number of tillers and on the number of heads.

These data also provided information on the correlations between characters within a mixture and within pure stand plots and whether the different competitive situations affected the association of characters (Table 16 and 17).

The correlations between characters are similar for the mixture and pure stand data with the exception of correlations with tiller number or head number, again suggesting that tillering most clearly demonstrated the difference between inter-genotypic and intra-genotypic competition. In spite of this there was still a highly significant correlation between tiller number in pure stand and tiller number in mixture (Table 18). A variety that had a high tiller number in the mixture also had a high tiller number in pure stand, although overall the conditions in a mixture apparently favoured tillering and head formation.

Heading date was only correlated with straw weight and the

Table 16

Correlations between characters in pure stand, Experiment 1

	Straw Wt	Height	Flag Ht	Tillers	Heads	Seed Wt	Seeds/Head	Days to Heading
Yield	0.57***	0.35***	0.42***	- 0.12NS	0.10NS	0.52***	0.50***	0.16NS
Straw Wt		0.55***	0.74***	- 0.01NS	0.10NS	0.47***	0.19NS	0.46***
Height			0.86***	- 0.44***	- 0.35***	0.15NS	0.43***	- 0.01NS
Flag Ht				- 0.42***	- 0.35***	0.21*	0.48***	0.37***
Tillers					0.93***	0.04NS	- 0.78***	- 0.11NS
Heads						0.14NS	- 0.71***	- 0.11NS
Seed Wt							- 0.09NS	- 0.02NS
Seeds/Head								0.25*

Table 17

Correlations between characters in mixture

	Straw Wt	Height	Flat Ht	Tillers	Heads	Seed Wt	Seeds/Head	Days to Heading
Yield	0.87***	0.71***	0.71***	0.23*	0.37***	0.70***	0.62***	0.08NS
Straw Wt		0.65***	0.72***	0.42***	0.49***	0.65***	0.37***	0.21*
Height			0.88***	0.02NS	0.15NS	0.55***	0.54***	- 0.09NS
Flag Ht				0.07NS	0.17NS	0.59***	0.50***	0.19NS
Tillers					0.94***	0.16NS	- 0.49***	- 0.10NS
Heads						0.29**	- 0.37***	- 0.20*
Seed Wt							0.29***	0.09NS
Seeds/Head								0.21*

Table 18

Correlations between characters measured in mixture and in pure sand

	Correlation coefficient
Grain yield	0.54***
Straw weight	0.52***
Number of tillers	0.73***
Number of heads	0.67***
Height	0.68***
Flat height	0.72***
1000 seed weight	0.78***
Seeds per head	0.78***

number of seeds per head in both mixture and pure stand, and with flag height in pure stand. The absence of association with other characters is surprising in view of the wide range in heading dates (45 days and 101 days for Bankuti Korai and Schladener respectively).

5. Relationship between Characters in Mixture and Yield in Pure Stand

A stepwise regression analysis was used to establish the best relationship between the dependent variable, yield in pure stand, and the independent variables from the mixture plots. If the stepwise regression was significant for an independent character other than yield, it would indicate that this character could be used to increase the efficiency of selection for yield. The independent variables were yield in mixture, number of tillers, height, and flag height; and the derived characters, seeds per head, seed weight and straw weight. Days to heading and the squared transformation of days to heading were also included as independent variables. The squared transformation was used because it was believed that this transformation would induce linearity into the suspected curvilinear relationship between yield and heading date.

The results of this analysis are presented in Table 19.

Table 19

Stepwise regression of characters in mixture on yield in pure stand

Variable entered in equation	Multiple R	R^2	Increase in R^2	F to enter equation
Yield in mixture	0.539	0.290	0.290	40.1
Straw weight	0.592	0.351	0.060	9.0
Flag height	0.637	0.405	0.055	8.8
Height	0.692	0.478	0.073	13.3

The inclusion of further characters in the equation did not bring about a significant reduction in the residual mean squares. Thus only 47.8% of the variation in pure stand yields could be explained by variation in characters measured in mixture. It is of particular interest that yield in mixture was the character most closely associated with yield in pure stand.

There were several effects which may explain why the regression equation accounted for less than half the variation in pure stand yields.

i) Inter-genotypic competition within the mixture may have affected plant growth to such an extent that a poor relationship existed between plant growth in mixture and yield in pure stand.

ii) Micro-environmental variation within the experimental area may have resulted in inaccurate estimates of yield in both mixture and pure stand.

iii) Interaction between varieties and the two separate experimental areas may have occurred.

iv) The data included in the analysis may have been inadequate because the number of variables was insufficient to account for grain yield, or because the actual measurement of the characters introduced experimental errors.

Referring first to the question of inadequate data, stepwise regression analyses of characters in mixture on yield in mixture, and of characters in pure stand on yield in pure stand, showed that almost all the variation in yield could be explained by variation in characters measured under the same experimental conditions (Tables 20 and 21). In both cases over 90% of the

Table 20

Stepwise regression of characters in mixture on yield in mixture

Variable added	Multiple R	Multiple R^2	Increase in R^2	F to enter equation
1. Straw wt.	0.95	0.90	0.90	908.1
2. No. seeds	0.97	0.95	0.05	101.8
3. No. tillers	0.98	0.96	0.01	14.0

Table 21

Stepwise regression of characters in pure stand on yield in pure stand

Variable added	Multiple R	Multiple R^2	Increase in R^2	F to enter equation
1. Straw wt.	0.89	0.80	0.80	382.0
2. Days to heading	0.91	0.82	0.02	15.3
3. Flat height	0.92	0.84	0.02	9.9
4. No. tillers	0.93	0.86	0.02	15.2
5. No. heads	0.94	0.98	0.03	22.4
6. Days to heading	0.95	0.90	0.01	12.7

variation in yield was explained by the regression equation. Furthermore components of yield were not major factors in the equations while straw weight alone accounted for 80% and 90% of the variation in grain yield in pure stand and mixture respectively. Regression equations which account for such large proportions of the variation in the dependent variable would not be expected if inappropriate variables were used or if the individual characters had been measured inaccurately.

The extent of interaction between varieties and the separate experimental areas could not be evaluated satisfactorily but it is unlikely to have been great in 1970 when the mean yield in mixture (273 $g.m.^{-2}$) was very similar to the mean yield of hand harvested samples from the pure stand plots (298 $g.m.^{-2}$). Since the correlations between yield in mixture and yield in pure stand were similar in the two years it is also probable that interaction was not a major effect in 1969.

Consequently it is believed that the large proportion of unexplained variation in pure stand yields was due mainly to:

1) the effects of inter-genotypic competition in the mixture;

ii) micro-environmental variation which was not estimated completely by replication and adjustment in pure stand or by replication in mixture. It is clear from the relatively large 'least significant differences' indicated in Figures 4 and 5 (pgs. 65 and 66) that the yields of the varieties were not measured with great accuracy in either pure stand or mixture.

6. Comparison of Results in 1969 and 1970

Experiment 1 was grown at the Waite Institute in 1969 and at Aldinga in 1970. Consequently it was possible to compare the results for the two environments to examine the role of genotype x environment interaction and the effectiveness of selection in one year for performance in the other (Table 22).

Table 22

Correlations between yields in mixture and in pure stand for two environments

1969	1970	
	Pure stand	Mixture
Pure stand	0.624***	0.405***
Mixture	0.583***	0.548***

All correlations were very high significant and indicate that the varieties responded similarly to changes in the environment in both mixture and pure stand. In addition the correlations between yield in mixture and yield in pure stand in different environments were similar to those within the same environments (0.56*** in 1969 and 0.54*** in 1970, Table 13). It may be concluded that genotype x environment interaction was not a major effect in this experiment.

B. Results from Experiment 1a

This experiment which was designed to investigate competition between varieties, known from Experiment 1 to differ in their response to competition, was inconclusive because of excessive soil heterogeneity that became evident only late in the season it was grown. Evidence for the yield variability will be presented but the results will not be considered in detail and no conclusions will be drawn from them.

The mean yields of all treatments are given in Table 23.

Table 23

Grain yields of central plant in Experiment 1a ($g.m.^{-2}$)

	Surrounding plants			
	Cape	Wieder	Featherston	Mixture
Cape	384	152	201	152
Weider	294	171	426	327
Featherston	230	234	260	212

L.S.D (5%) = 167 $g.m.^{-2}$

Coefficient of variation = 104%

Significant differences existed between treatments but no pattern of the effects of competition was apparent. Although the three varieties had given similar yields in pure stand in the previous two years (cf. Table 2, pg. 34), Cape had a significantly higher yield than Weider in this experiment. Furthermore the yield of Cape in pure stand was significantly higher than its yield in competition with the other varieties. These results are in contrast to the results of Experiment 1 where Cape yielded more in mixture than in pure stand.

Weider yielded less in pure stand than in mixture while Featherston gave similar yields in all four competitive situations. In Experiment 1 in 1970 Weider had the same yield in mixture as in pure stand and Featherston had a lower yield in mixture than in pure stand. Clearly these results bear little resemblance to those recorded in the previous two years and it is believed that they provide invalid comparisons of the varieties because of the extreme variation within the experiment. This variation was so irregular that replication was of little value as indicated by the coefficient of variation of 104%.

The extent of variation may be further illustrated by studying the yields of Cape when grown in pure stand. The mean yield per plant was 2.37g with a range from 0.13g to 16.14g. The total yield from 20 plants of Cape in pure stand was 47.40g of which 16.14g or 34% was contributed by one plant.

Further evidence for soil heterogeneity at Aldinga in 1971 will be given in the results for Experiment 2. The effect of heterogeneity was more noticeable in Experiment 1a than in the mixtures in Experiment 2 because the area of each replicate was much greater and consequently within-replicate variation was larger.

C. <u>Results for Experiment 2</u>

1. <u>Analysis of Data from F4 Mixture Plots</u>

The analyses of variance for all characters measured on single F4 plants are given in Table 24. For all characters there were very highly significant differences between lines and between replicates. The mean yield of all F3-derived lines was 207.3 $g.m.^{-2}$ with a range from 106 $g.m.^{-2}$ to 411 $g.m.^{-2}$ while the yields of the two parents in the mixture were 402 $g.m.^{-2}$ and 254 $g.m.^{-2}$ for C.I. 3576 and Proctor respectively. Thus both parents yielded well above the mean in mixture.

The parents of the cross have been excluded from the analyses of variance as they served as controls and were represented by six plants of each in a plot, while each F3-derived line was represented by only one F4 plant. The means and standard errors for all characters of the parents are presented in Table 25. C.I. 3576 was the higher yielding variety and exceeded Proctor in all characters except height to the flag leaf. Proctor was the more variable variety having

Table 24

Analysis of Variance for data from single F4 plants, Aldinga 1971.

(mean square x 10^{-4})

		Dry Weight $g.m.^{-2}$		Number of Heads m^{-2}		Grain Yield $g.m.^{-2}$	
	D.F.	Mean Sq.	F	Mean Sq.	F	Mean Sq.	F
Reps	29	64.02	4.66***	9.85	3.08***	12.23	4.52***
Lines	47	41.37	3.01***	14.54	4.55***	10.15	3.75***
Error	1278	13.73		3.19		2.70	
Total	1354						

		Number of Seeds m^{-2}		Height cm		Height to Flag Leaf cm	
	D.F.	Mean Sq.	F	Mean Sq.	F	Mean Sq.	F
Reps	29	5554	4.87***	0.1440	14.64***	0.1212	24.72***
Lines	47	4645	4.08***	0.0672	6.86***	0.0257	5.25***
Error	1278	1139		0.0098		0.0049	
Total	1354						

Table 25

Means and Standard Errors for Proctor and C.I. 3576 in

F4 mixture plots, Experiment 2

Character	Parent	Mean	S.E. (Mean)
Grain yield	C.I. 3576	401.8	18.9
($g.m.^{-2}$)	Proctor	253.9	15.2
Straw weight	C.I. 3576	496.0	21.7
($g.m.^{-2}$)	Proctor	403.4	22.5
Height	C.I. 3576	54.3	0.60
(cm)	Proctor	47.3	0.69
Flag height	C.I. 3576	45.4	0.50
(cm)	Proctor	49.2	0.57
No. heads	C.I. 3576	476.9	17.5
(m^{-2})	Proctor	428.3	15.8
Seeds per head	C.I. 3576	16.0	0.43
	Proctor	16.6	0.46
1000 Seed weight	C.I. 3576	52.6	1.89
(g)	Proctor	35.8	1.25

Footnote: Heads of Proctor did not emerge fully because of moisture stress and height to the top of the head was less than height to the flag leaf.

larger coefficients of variation for all characters.

The data presented in Table 25 are based on a total of 178 plants of each parent as there were 30 replicates and six plants per replicate but for each parent there were two missing plants.

2. Analysis of Data from F6 Pure Stand Plots

The mean yield of the 48 F3-derived lines and the two parents Proctor and C.I. 3576, was 112 g.m.$^{-2}$ which was much lower than the mean yield in Experiment 1. Severe waterlogging occurred in the early stages of growth in areas where massive kunkar deposits were present approximately 25 cm below the soil surface. These calcareous deposits were irregularly distributed and plant growth was very poor in these areas. The presence of these deposits was known prior to the experiment (Ward, 1966) but they had not resulted in extreme variation in previous experiments in the area. The above average rainfall in August resulted in an extended period of waterlogging in irregular areas, and with the increase in error the differences between lines were barely significant when a first analysis was undertaken on the actual yield data. However the grid plot technique was highly successful in accounting for the localised within-replicate variation. Analyses for actual and adjusted data are given in Table 26.

Table 26

Analysis of variance of machine harvested yields from F6 plots, Aldinga, 1971

		Actual Yield		Adjusted Yield	
	D.F.	Mean Sq.	F	Mean Sq.	F
Reps	3	17639	11.2***	1337	2.06
Lines	49	2335	1.48*	1285	1.98***
Error	147	1575		649	

Adjustment of plot yields reduced the error mean square by 59% and increased effects due to lines so that highly significant differences existed between lines. In contrast to Experiment 1 in 1970, replicate effects were reduced and were not significant. In this experiment the variety Clipper responded to environmental variation in a similar way to the lines.

Hand harvested samples were taken at random from all plots and the analyses of variance for characters measured from these samples are presented in Table 27. For all characters there were highly significant replicate effects and significant differences existed between lines for all characters except straw weight and number of seeds. In general variance ratios

Table 27

Analysis of Variance for data from hand harvested samples from F6 plots, Aldinga 1971

(Mean squares 10^{-4})

		Dry Weight ($g.m.^{-2}$)		Number of Tillers m^{-2}		Height cm	
	D.F.	Mean Sq.	F	Mean Sq.	F	Mean Sq.	F
Reps	3	23.30	10.19***	3.514	7.41***	0.0510	7.82***
Lines	49	3.20	1.40	0.869	1.83**	0.0223	3.42***
Error	147	2.29		0.474		0.0065	
Total	199						

		Height to Flag Leaf cm		Number of Heads m^{-2}	
	D.F.	Mean Sq.	F	Mean Sq.	F
Reps	3	0.0361	8.67***	4.105	8.94***
Lines	49	0.0086	2.06***	0.745	1.62*
Error	147	0.0042		0.459	
Total	199				

		Grain Yield $g.m.^{-2}$		Number of Seeds m^{-2}	
	D.F.	Mean Sq.	F	Mean Sq.	F
Reps	3	4.340	10.87***	1833	9.89***
Lines	49	0.600	1.50*	244	1.32
Error	147	0.399		185	
Total	199				

for lines were much smaller than in Experiment 1 in 1970 and this may reflect both a smaller genetic diversity in the population and larger environmental variation than in Experiment 1.

Evidence of large environmental variation is also apparent in the comparison of yield data from hand harvested samples and machine harvested remainders of the plots (Table 28). The coefficients of variation are larger than in Experiment 1.

Table 28

Comparison of hand harvested samples and machine harvested remainder of plot, 1971

		50 Lines	Clipper Grid
Mean yield	Hand harvested samples	161	140
($g.m.^{-2}$)	Machine harvested plots	112	96
C.V.	Hand harvested samples	0.39	0.36
	Machine harvested plots	0.35	0.43
Correlations between sample yield and plot yield			
(1)	For all plots	0.69***	0.76***
(2)	For line means	0.72***	

In addition the correlation between sample yields and plot yields for the Clipper grid plots is larger. Since differences between

Clipper grid plots are due only to environmental variation, this correlation is an environmental correlation. The fact that it is larger in this experiment than in Experiment 1, indicates that environmental variation was larger.

The yields from machine harvesting were approximately 30% lower than yields from hand harvesting, a similar difference to that recorded in Experiment 1. It is clear that the harvesting machines were relatively inefficient but there was no evidence of a line x harvesting method interaction. The correlation between hand harvested yields and machine harvested yields was very highly significant and the coefficients of variation were similar for hand harvested samples and machine harvested plots.

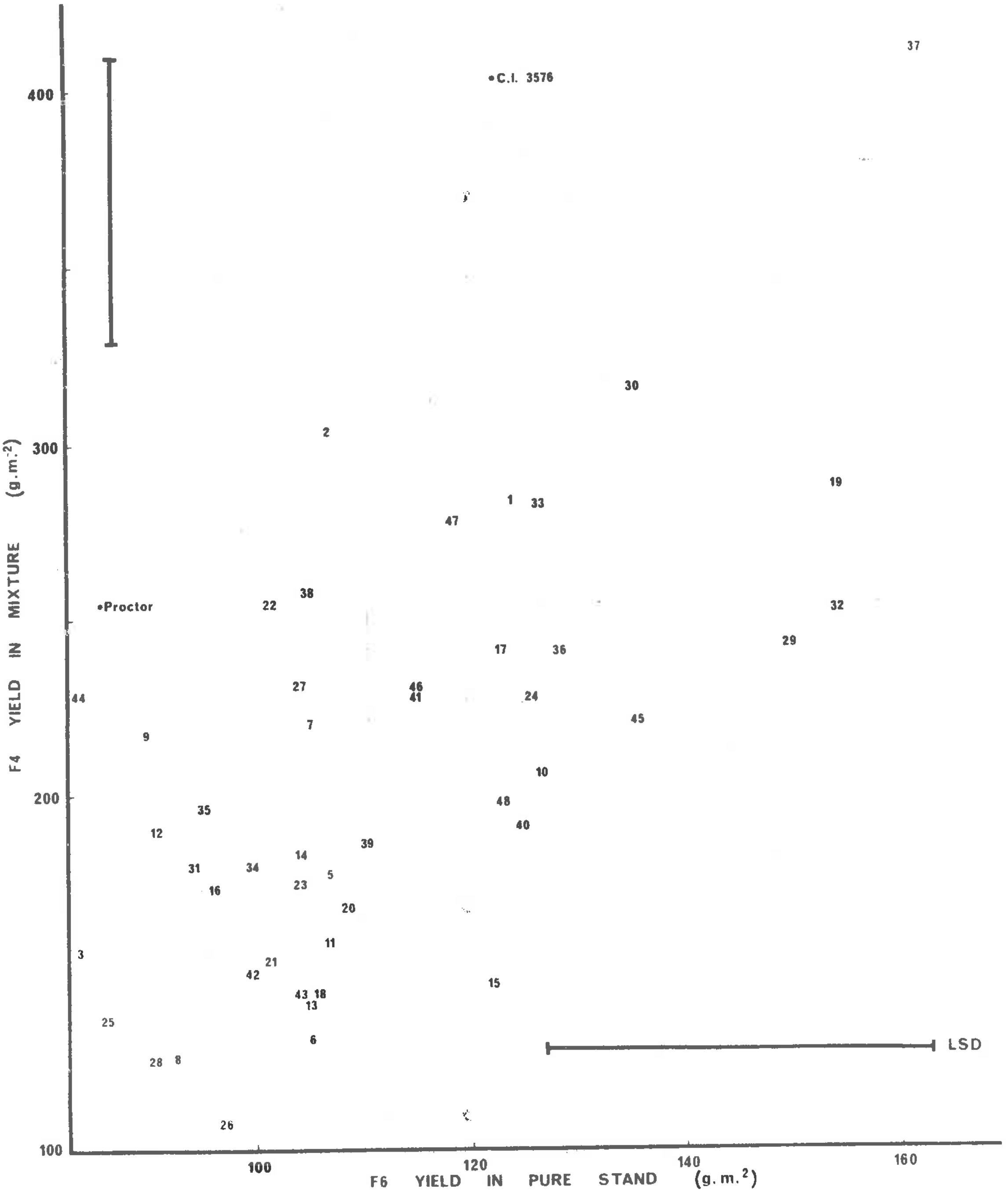
3. Relationship between Yield in Mixture (F4) and Yield in Pure Stand (F6)

In this experiment the relationship was studied between the yield of 48 F3-derived lines in an F4 mixture and in F6 pure stand plots. The mean yields in the F4 have been plotted against adjusted F6 yields in Fig. 8. The correlation coefficient was 0.61*** and was slightly higher than the comparable correlation in Experiment 1.

Thus the mean yield in a heterogeneous population of a number of F4 plants derived from a single F3 plant was positively correlated with the yield of F6 plots derived from the same F3 plant. It should have been possible to select for yield on the

Figure 8

Relationship between yield in mixture and yield in pure stand of 48 F3-derived lines. Least significant differences at the 5% level are indicated in the diagram. Experiment 2, 1971.


37
•C.I. 3576
400
30
2
300
(g.m.-2)
19
1
33
47
F4 YIELD IN MIXTURE
38
•Proctor
22
32
29
17
36
27
46
41
24
44
7
45
9
10
200
48
35
40
12
39
14
31
34
5
23
16
20
11
3
21
42
15
43 18
13
25
6
LSD
28 8
26
100
100
120
140
160
F6 YIELD IN PURE STAND (g.m.-2)

basis of single F4 plants.

The success of such selection was evaluated by simulating truncation selection in the same manner as in Experiment 1. The ten highest yielding F4 plants (approximately 21% of the population) were identified in each of the 30 plots of the mixture. The yield in the F6 of these high yielding lines was compared with the mean yield of the whole F6 population (112 g.m.$^{-2}$). The results of these comparisons are presented in Table 29.

In all but two of the 30 comparisons the mean yield of the selected population was greater than the mean yield of the whole F6 population. When yield in the F4 was based on the mean of all 30 F4 plots, the mean yield of the selected lines in the F6 was 127 g.m.$^{-2}$, approximately 14% higher than the mean yield of the whole F6 population (112 g.m.$^{-2}$).

To test the effectiveness of different selection intensities, the highest yielding 10%, 20%, and 30% of lines were identified on the basis of their mean yields in the F4. The distribution of these lines was compared with the yield distribution of all lines in the F6. These comparisons are illustrated in Fig. 9. It is clear that although some high yielding lines were not identified in the F4, the selected populations had higher mean yields than the original population, and the majority of low yielding lines were successfully eliminated.

Table 29

Yield in the F6 of the highest yielding 10 lines from each F4 plot compared with at the bottom of the table

I. Yield in F6 of 10 lines with the highest mean yield in the F4

II. Yield in the F6 of all 48 lines

Plot	Mean Yield ($g.m.^{-2}$)	%	Standard Deviation	Plot	Mean Yield ($g.m.^{-2}$)	%	Standard Deviation
1	115	103	20.7	16	110	98	24.7
2	117	104	25.2	17	116	104	17.5
3	125	112	19.5	18	117	104	16.9
4	114	102	23.3	19	119	106	13.3
5	121	108	22.7	20	119	106	23.3
6	121	108	18.4	21	122	109	20.1
7	125	112	22.4	22	124	111	17.7
8	113	101	15.5	23	115	103	15.6
9	118	105	22.4	24	120	107	21.1
10	114	102	11.8	25	118	105	23.6
11	122	109	17.4	26	121	108	20.5
12	111	99	18.1	27	123	110	21.3
13	121	108	20.4	28	114	102	23.8
14	125	112	23.8	29	118	105	16.6
15	114	102	20.9	30	123	110	22.3

I. 10 lines with highest mean yield in the F4	127	113	20.4
II. All 48 lines in the F6	112	100	17.9

Figure 9

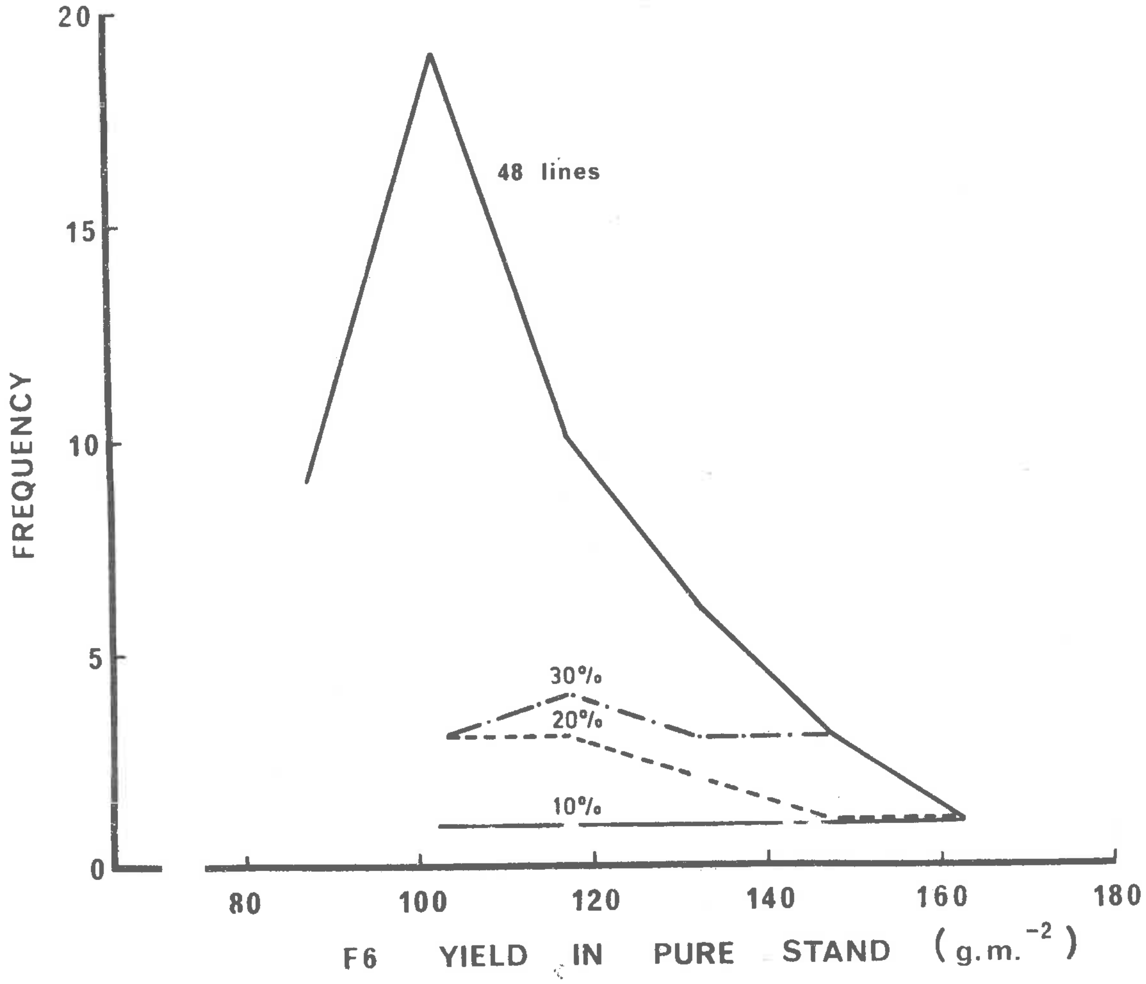
Simulated truncation selection at three intensities in a population of 48 F3-derived lines. The distributions indicated are of yields in pure stand for:

i) all 48 lines

ii) highest yielding 10% of lines in mixture

iii) highest yielding 20% of lines in mixture

iv) highest yielding 30% of lines in mixture.


20
15
10
5
0
FREQUENCY
48 lines
30%
20%
10%
80
100
120
140
160
180
F6 YIELD IN PURE STAND (g.m.$^{-2}$)

4. Yield Components and Morphological Characters

The components of yield, numbers of seeds and seed size were derived from data measured on single F4 plants and on hand harvested samples from the F6 pure stand plots. Straw weight was also derived as the difference between total air-dry weight and grain yield. The means and coefficients of variation of the measured and derived characters are given in Table 30.

Table 30

Means and coefficients of variation of characters measured in mixture and in pure stand

	F4 Mixture		F6 Pure Stand	
	Mean	C.V.	Mean	C.V.
Yield ($g.m.^{-2}$)	211	31.0	162	24.0
Straw wt. ($g.m.^{-2}$)	283	25.9	288	29.3
Height (cm)	52	9.5	65	11.4
Flag ht. (cm)	47	6.5	56	8.3
No. heads (m^{-2})	314	24.3	275	15.6
Seeds per head	15	10.7	13	12.0
1000 seed wt.	45	8.3	32	19.7

The coefficient of variation for each character in this table is the standard deviation of the means of all 48 lines expressed as a percentage of the overall mean and is therefore a measure of the relative genotypic variation in the two environments.

No direct statistical comparison can be made of the data from F4 mixtures and F6 pure stand as these were not grown within the same experiment. Nevertheless, the means for yield and yield components were higher in mixture than in pure stand. It should also be noted that the yield and components of yield of the parents were well above the mean of all lines in the mixture.

The coefficient of variation for yield was much greater in mixture than in pure stand but of the yield components only the number of heads was more variable in mixture than in pure stand. This suggests that, as in Experiment 1, yield differences between lines were increased in mixture and the number of heads was the yield component which most clearly demonstrated this effect.

The correlations between characters measured in mixture and in pure stand are presented in Table 31. All of these correlations were highly significant except those for straw and seed weight which were not significant. In addition, the correlation for seeds per head, although highly significant, explains only 10% of the total variation.

The analysis of variance for characters measured on hand harvested samples from F6 pure stand plots showed no sngnificant differences between lines for straw weight (Table 27, pg. 90).

Table 31

Correlations between characters measured in F4 mixtures and in F6 pure stands, Experiment 2

Character	Correlation Coefficient
Yield (g.m.$^{-2}$)	0.608***
Straw weight	0.106NS
Height	0.588***
Flag height	0.477***
No. heads	0.377***
1000 seed weight	0.122NS
Seeds per head	0.324**

Therefore it is not surprising that there was no correlation between straw weight in mixture and in pure stand. Similarly, high correlations would not be expected for seed weight and for number of seeds per head as both these characters were derived from the measured character, number of seeds, and this character did not differ between lines in pure stand.

Extreme variation in the F6 pure stand plots has also influenced the correlations between characters in pure stand (Table 32). Yield was very highly correlated with straw weight in mixture (Table 33) but no significant correlation existed between these characters in pure stand and this must be

Table 32

Correlation between characters in pure stand, Experiment 2

	Straw Wt.	Height	Flag	Heads	S.W.	Seeds/Head	Days to Heading
Yield	0.163NS	- 0.226NS	- 0.168NS	0.512***	0.208NS	0.343*	- 0.170NS
Straw Wt.		0.415**	0.544***	0.673***	- 0.817***	0.701***	0.094NS
Height			0.946***	- 0.135NS	- 0.326*	0.320*	0.056NS
Flag				0.006NS	- 0.484***	0.490***	0.186NS
Heads					- 0.545***	0.320*	- 0.197NS
S.W.						- 0.598***	- 0.206NS
Seeds/Head							0.355*

Table 33

Correlation between characters in mixture, Experiment 2

	Straw Wt.	Height	Flag	Heads	S.W.	Seeds/Head	Days to Heading
Yield	0.906***	- 0.032NS	0.033NS	0.871***	0.278NS	0.640***	0.045NS
Straw Wt.		0.170NS	0.319*	0.770***	0.158NS	0.695***	0.241NS
Height			0.861***	- 0.279*	0.358*	0.253NS	- 0.016NS
Flag				- 0.144NS	0.043NS	0.444**	0.359*
Heads					- 0.050NS	0.357*	- 0.052NS
S.W.						0.009NS	- 0.316NS
Seeds/Head							0.450***

attributed to the lack of significant differences between lines for straw weight in pure stand. In addition seed weight was negatively correlated with straw weight, height, height to the flag leaf, number of heads and seeds per head in pure stand, while in mixture these correlations were either positive or non-significant. Seed weight in pure stand was derived from the number of seeds and since there were no significant differences between lines for this character, the biological significance of these correlations must be doubted.

The correlation between yield and height is of interest as this correlation was positive and highly significant in Experiment 1 but was not significant in Experiment 2. This difference did not arise as a result of logding as no logding occurred in either Experiment 1 or 2. The changes are believed to reflect differences in the populations studied in these experiments. In Experiment 1 the varieties ranged in height from 71 cm to 117 cm in pure stand while in Experiment 2 the range was only from 45 cm to 76 cm. It was also apparent that the tall, vigorous six-row varieties in Experiment 1 tended to be high yielding.

5. Relationship between Characters in F4 Mixtures and Yield in F6 Pure Stand

This relationship was studied using a stepwise regression analysis with yield in F6 pure stand as the dependent variable and characters from F4 mixtures as the independent variables. The results of this analysis are presented in Table 34.

Table 34

Stepwise regression of characters in F4 mixture on yield in F6 pure stand

Variable entered in equation	Multiple R	R^2	Increase in R^2	F to enter equation
Yield in F4	0.608	0.370	0.370	28.2
Straw wt. in F4	0.778	0.605	0.235	28.0

None of the other independent variables had a significant partial correlation with yield in F6 pure stand and therefore none were included in the equation. Thus 60.5% of the variation in the F6 yield was accounted for by variation in yield and straw weight in the F4 mixture. In experiment 1 yield in mixture and straw weight were also the most important variables in the regression equation but the inclusion of these characters accounted for only 35.1% of the variation in pure stand yield.

V. DISCUSSION

Before discussing the main object of this study, the relationship between single plant yields in heterogeneous populations and yield in pure stand, some matters relevant to this relationship and its experimental verification will be mentioned.

A. Variety x Pattern Interaction

In both 1969 and 1970 there was no indication of a variety x pattern interaction in Experiment 1. It is concluded that the yield of a variety was not affected by changing the neighbours with which it was in direct competition.

Such a result was not expected on the basis of studies with two-component mixtures. Allard and Adams (1969) showed that the yield of a barley variety was greatly influenced by the specific variety with which it was competing. The variety Vaughn suffered a yield reduction of 4% when surrounded by Atlas but increased in yield by 1% when surrounded by Hero. Similar results were obtained by Sandfaer (1970) with European two-row barley varieties.

In the present study, the mixture was made up of 100 different varieties and at the spacing used (3.5 cm x 17.5 cm) it may be assumed that each variety was competing with several neighbouring plants.

If this assumption is valid the net competitive effect of neighbours which compete with a central variety would tend to be constant, as the neighbours are a random sample of the population and as such their mean competitive effect should approximate to the mean competitive effect of the whole population. It is difficult to estimate how many neighbours compete with a plant for nutrients, moisture or light, but several studies suggest that the competitive environment may be extensive.

Harding et al (1966) showed with Phaseolus lunatus that the selective advantage of a genotype was related to its frequency in the population and that the genotype studied remained in the population at a relatively constant frequency of 7% in spite of being at a selective disadvantage at higher frequencies. If its frequency in the population was experimentally reduced from 7% to 3%, its selective advantage increased markedly. This result suggests that the genotype was sensitive to competition from a considerable number of surrounding plants as it responded to a change in the micro-environment brought about by changing only 4% of the surrounding plants.

Sakai (1957) showed that the central plant in a hexagonal planting arrangement was competing against all six neighbours as he found that the central plant responded to competition even when only one of the surrounding plants was of a different genotype.

Allard and Adams (1969) concluded that the yield of a barley variety was similar, when surrounded by a complex mixture, to its mean yield when surrounded in turn by several single varieties.

These experiments suggest that competition may arise from a number of neighbours and not simply from the two closest. It is therefore accepted that the net competitive effect of a complex group of neighbours remained constant in Experiment 1, and that variation in the particular genotypes that surrounded an individual had no effect. When considering the relation between single plant yield in mixture and yield in pure stand it was justified to assume there were no specific effects of neighbours on an individual plant's performance in the mixture.

B. Pure Stand Plot Yields

When trying to establish a relationship it is essential that both dependent and independent variables be assessed as accurately as possible. In both Experiments 1 and 2 yield in pure stand was treated as the dependent variable to be estimated from data on yield and other characters measured in mixture. Yield in pure stand was the adjusted yield of machine harvested plots as it was believed that these were the best estimates of pure stand yield that could be obtained. Two aspects should be mentioned.

a) The method of adjustment

The method of adjustment used in Experiment 1 in 1969 was based on the triple lattice design which is used widely when testing many varieties (LeClerg, 1966). It did reduce the error mean squares and allow greater differentiation between varieties; however, because of the large within block variation (p. 57) it was not used in the following two years.

The grid plot technique was used in Experiment 1 in 1970, and in Experiment 2 and yields were adjusted accordingly. This method is similar to the check plot method used by cereal breeders in the first quarter of this century but which was not continued following the development of Fisherian statistics and the emphasis on replication. McClelland (1926) summarised the assumptions upon which the method was then based.

One was that the yields of both check and test plots were the correct yields for the given plots. It is now accepted that this is not correct as there is experimental error associated with each estimate of yield. In the present study the experimental error associated with the grid plots was reduced by a smoothing process which utilised yield data from several grid plots. Error associated with experimental or test plots was reduced by replication. In these circumstances failure to satisfy McClelland's first requirement does not appear important.

The second assumption mentioned by McClelland was that the yield change from check plot to check plot should be linear. Modern computing facilities allow rapid calculation of non-linear gradients between check plots and this restriction need not apply.

Several different methods were attempted to improve the adjustment of the experimental plots. They were:

i) Smoothed values for the check plots were calculated using weightings which were not directly proportional to the distances between check plots. Thus the relative contributions from nearby check plots to the smoothed value were varied.

ii) The number of check plots which were included in the calculation of a single smoothed value was also altered. Finally for all methods of estimating smoothed check plot values, both fitted curves and linear gradients were used to calculate the expected yield if Clipper had been grown in the location of the experimental plots.

The success of these yield adjustments was evaluated by studying the variance ratio for varieties in the analysis of variance. While several methods of adjustment brought about an increase in the variance ratio for varieties, none was better than that using weights proportional to distances, and using linear gradients between check plots.

McClelland also stated that adjustment would not be useful unless all varieties responded in the same way to changes in the environment. In Experiment 1 in 1970 the mean yields of the 100 varieties was greater than the mean of the grid plots in Rep 1 but steadily declined until in Rep 4 the mean of the 100 varieties was less than the mean of the grid plots. Clearly the 100 varieties had not responded to changes in the environment in the same way as the Clipper grid plots. If there had been no replication this would have brought about misleading results as varieties which were inferior to the grid plots in one part of the experimental area were superior in other areas. However, the fact that there were four replicates appears to have overcome this problem.

The final assumption discussed by McClelland was that there should be a positive correlation between check and test plot yields. If no such correlation existed the adjustment of plot yields would be of no value. Correlations between the yields of grid plots and the yields of adjacent test plots were 0.26 and 0.85 for Experiment 1 in 1970 and Experiment 2 respectively. Both these correlations were very highly significant and the adjustment of plot yields reduced error mean squares and increased the variance ratio for treatment effects.

Various factors contributed to the lower correlation in 1970. One was that the correlation between grid plots and the adjacent experimental plots is influenced by both genotypic and environmental effects. If the range of genotypes in an experiment is large, as in Experiment 1, a lower correlation would be expected than if the range of genotypes was smaller, as in Experiment 2. A second was that the extent of environmental variation clearly influences the size of the correlation. In an extremely uniform site no correlation would be expected as the yields of adjacent plots would reflect only genotypic differences. Conversely in a site with large environmental variation the yields of adjacent plots would tend to be similar because of the large environmental effect and a high correlation would be expected. Since it has been suggested that environmental variation was much larger in 1971 (e.g. from the coefficients of variation) than in 1970, it follows that the correlation between grid plots and adjacent experimental plots was larger in 1971 than in 1970.

In these experiments the grid plots provided an effective method of adjusting yields and it is believed this technique is capable of estimating the localised environmental variation which occurs within large plant breeding experiments. From inspection of the plot results, it is considered that the irregular variation at Aldinga in 1971 could not have been estimated effectively by a lattice design.

b) <u>The use of machine harvested yields</u>

Although there was a loss of approximately 25% of the potential yield from machine harvesting, it is the machine harvested yields that have been used, except in the comparison of the means of characters measured in mixture and in pure stand (Tables 15 and 30, pp. 73 and 97). There were several reasons for this choice:

i) The hand harvested samples could not be adjusted using the grid plot technique as this requires equal spacing of the grid plots and the samples were taken at random. If grid plots are not equally spaced the weighting factors used in the smoothing process introduce bias and in addition the use of a linear gradient between grid plots is invalid. If the precise location of the samples were known, it might have been possible to use this technique.

ii) The mean yields of varieties based on hand harvested samples were very highly correlated with the means based on machine harvesting (0.88*** in 1970 and 0.72*** in 1971). Furthermore there was no evidence of interaction between varieties and the method of harvesting in either year. Apparently the relative yields of varieties were estimated satisfactorily by either method of harvesting.

iii) The correlation between yield in mixture and hand harvested yield in 1970 was 0.50*** which was very similar to that with adjusted machine harvested yield (0.54***). However in Experiment 2 differences between lines for hand harvested yields were barely significant (Table 27, pg. 90) and the success of this experiment was dependent on the adjustment of yield to give a better assessment of pure stand yield.

C. General Discussion

The most important finding was that the yields of genotypes in a heterogeneous population were positively correlated with the yields of the same genotypes grown in pure stands. Simulated truncation selection indicated that it was possible to select within the heterogeneous populations on the basis of single plant yields, for yield in pure stand (Tables 14 and 29, pp. 70 and 95).

This conclusion does not conform with the commonly held belief that single plant selection for yield in pure stand is not effective (McGinnis and Shebeski (1968) and Hamblin 1971)).

However it can be explained by examining the effects referred to in the literature review.

1. Interactions due to Plant Density

Throughout this study a constant plant density of 165 plants per square metre was used and the possibility of genotype x density interaction did not arise. In contrast, the F2 generation studied by McGinnis and Shebeski (1968) was grown at a density of approximately 3.2 per square metre while their F3 generation was grown at a density of approximately 147 plants per square metre.

2. The Confounding Effects of Competition

It was apparent from the results of both Experiments 1 and 2 that yield in mixture was positively correlated with yield in pure stand, however the correlations, although very highly significant, accounted for only 25% of the variation in Experiment 1 and 36% of the variation in Experiment 2. Furthermore the yields of some varieties when grown in mixture were very different from their yields in pure stand. It was possible that this had been brought about by the difference between intergenotypic competition in mixture and intragenotypic competition in pure stand.

Experiment 1a was designed to determine whether competition had brought about the different yields in mixture of three varieties which had very similar yields in pure stand but this experiment was a failure. The environmental variation was so extreme that no meaningful interpretations could be made.

Because of the failure of Experiment 1a, attempts were made to obtain indirect estimates of the effects of competition in Experiment 1. If the competitive ability of the varieties in this experiment could be measured, the contribution of competition to the relationship between yield in mixture and yield in pure stand could be evaluated. In the literature review the difficulty in relating competitive ability, measured in terms of yield, to yield itself, was discussed. Similar difficulties would arise if competitive ability was measured in terms of any character which was highly correlated with yield.

The best independent estimate of competitive ability that could be obtained was from the number of tillers which was not correlated with yield either in mixture or pure stand but which did appear to reflect the effects of competition. The ratio of tiller number in mixture to tiller number in pure stand was calculated for each variety. This ratio was then included as an independent variable in the stepwise regression analysis in an attempt to reduce the large proportion of unexplained variation in the multiple regression of characters from the mixture plots on yield in pure stand (Table 19, pg. 78).

The results of this new stepwise regression analysis are presented in Table 34.

This shows that competitive ability measured from tiller number did contribute to the relationship between performance in

Table 34

Stepwise regression of characters in mixture on yield in pure stand, Experiment 1, 1970

Variable entered in equation	Multiple R	Multiple R^2	Increase in R^2	F to enter equation
Yield in mixture	0.539	0.290	0.290	40.1
Straw weight	0.592	0.351	0.060	9.0
Flag height	0.637	0.405	0.055	8.8
Height	0.692	0.478	0.073	13.3
Tiller ratio	0.717	0.514	0.036	6.8

mixture and in pure stand but it was a small contribution and accounted for only 3.6% of the total variation.

In Experiment 2 (Table 34) over 60% of the variation in pure stand yields was explained by variation in yield and straw weight in mixture and it was clear that intergenotypic competition had not been an important effect in this experiment.

Thus it appears that although competition influenced the yields of single plants in mixture the effect was not large enough to conceal the correlation between yield in mixture and in pure stand. Furthermore there was no evidence that competitive ability was correlated with yield in pure stand. This reinforces the conclusion reached earlier (page 13) that the negative relationships reported by Akihama (1967), Jennings and Aquino (1968) and

Donald (1968) may be artifacts brought about by the definition of competitive ability.

If one assumes that:

i) the direction of the response to competition is not correlated with yield in pure stand,

and

ii) a genotype which alters its share of the resources of nutrients, moisture or light by virtue of its competitive attributes, increases or decreases its yield by an amount proportional to its pure stand yield (de Wit, 1961), rather than by an absolute amount (McGilchrist, 1965), it follows that the relationship between yield in mixture and yield in pure stand will be fan-shaped on a graph. Good competitors which are high yielding in pure stand will show a greater increase in yield than good competitors which are low yielding in pure stand, when grown in competitive situations. Similarly, high yielding, poor competitors will suffer relatively more from competition than low yielding, poor competitors.

This speculation is supported by the apparent fan-shaped distributions in Figs. 4, 5, and 8.

It is clear that if a distribution such as that shown in Fig. 4 is general, studies conducted with two-component mixtures could be biased seriously by sampling from this population.

Samples could be chosen in which a genotype with low pure stand yield suppressed a high yielding genotype when grown in a simple mixture. Sampling of this nature could account for the results of Wiebe et al (1963) and of Sandfaer (1970). Both these studies showed that a low yielding barley genotype suppressed a high yielding genotype in a mixture, although in Sandfaer's study this occurred in only one of several two-component mixtures.

The general conclusions of Allard (1960) and Allard and Hansche (1964) that genotypes which survive in mixed populations tend to have high yields in pure stand, is supported by the results of these experiments. Consequently it is suggested that in most crosses, competition should not be a major factor influencing the efficiency of single plant selection for yield in pure stand. Exceptions will undoubtedly occur such as that reported by Jennings and Aquino (1968) where tall, leafy plant types shaded the potentially high yielding short, erect leafed genotypes in bulked generations of a rice cross. Nevertheless they were able to overcome this problem by hand rogueing and similar approaches could be used where gross morphological differences exist in the progeny of a cross.

3. Genotype x Environment Interaction

Hamblin (1971) suggested that genotype x environment interaction involving different seasons may have been one of the major causes contributing to his failure to select effectively for yield on a single plant basis. Since McGinnis and Shebeski (1968) also conducted their experiment in different seasons, genotype x environment interaction could have been a factor contributing to the lack of correlation between the yield of single F2 plants and F3 plots.

Genotype x environment interactions involving sites and seasons were avoided in this study by growing both the mixture and pure stand plots at the same site in a single season. However, Experiment 1 was grown at the Waite Institute in 1969 and at Aldinga in 1970 and the results for these two environments can be compared. Although this comparison involved both sites and seasons, yields in the two environments were highly correlated (Table 22). It is clear that these two seasons were more alike than those in which Hamblin's experiments were grown and it is believed that genotype x environment interaction was not a major factor in this study.

Furthermore the correlations between yield in mixture in one year and yield in pure stand in the other year were both very highly significant and similar to those within years. This suggests that single plant selection would have been effective in either season for yield in pure stand in the other season. It is concluded that although genotype x environment interaction is a major problem in most breeding programmes, it is not necessarily large enough to invalidate the use of single plant yields as a selection criterion.

4. The Confounding Effects of Heterozygosity

Heterozygosity was not a factor in Experiment 1 which was designed to avoid the complication by using homozygous varieties. In Experiment 2 however, it was possible that some of the lines were high yielding in the F4 mixtures due to heterozygosity.

This does not appear to have occured as the correlation between F4 yield in mixture and F6 yield in pure stand was higher (0.61***) than the like correlation in Experiment 1 (0.56*** and 0.54*** in 1969 and 1970 respectively). Nevertheless it is true that selection on the basis of single F4 plants was not as effective as selection on the basis of the mean yield in the F4 of each line (Table 28). It may be concluded that the use of 30 F4 plants from each F3-derived line allowed a realistic assessment of the mean yield of each line but segregation within lines contributed to the relative ineffectiveness of selection on a single plant basis. The yield of each line in the F6 generation is expected to approximate the mean yield of all possible segregates from that line, while the yield of individual segregates in the F4 would be distributed about this mean. Consequently the use of 30 F4 plants from each line can be looked upon as a progeny test of the F3 plant which evaluates satisfactorily the mean yield in the F6 of segregates derived from that line.

5. Micro-Environmental Variation

The correlations presented in Table 11 between single plant yields in mixture and yield in pure stand, clearly illustrate the problems of micro-environmental variation. The highest correlation between yield in mixture and in pure stand was obtained when based upon the mean of two years results (0.657***), that is, when yield was based upon the most extensive data available. When yield in mixture was measured on a single plant of each variety the correlations were much lower and occasionally were not significant.

It may be concluded that the yield of a single plant is not a very accurate estimate of the genotype and that micro-environmental variation influences the relationship between the yields of single plants in heterogeneous populations and their yields in pure stand. In Experiment 1, the effects of micro-environmental variation could be overcome to some degree by replication of single plants of the same genotype, but usually this is not possible when selecting, for example, in the F2 generation.

The methods proposed by Hamblin (1971) to overcome micro-environmental variation could not be evaluated adequately. His method of adjusting yields using the 'moving mean' depends on a local estimate of yield which is not biased by the genotypes included in the mean. Consequently the local mean must be based on a large enough number of plants to ensure that the genotypic effect approximates the population mean. On the other hand the number must be small enough to account for irregular variation.

In the present study a sample which was large enough to eliminate genotypic bias was, in fact, a large proportion of the plot and therefore approximated the plot mean. The deviation of the yield of a single plant from the moving mean was therefore similar to its deviation from the plot mean and in the normal analysis of variance this would be taken as a replicate effect.

Another difficulty was encountered towards the ends of rows. When calculating a moving mean in these positions, very few plants contributed to the mean and the possibility of genotypic bias was increased. For example, when calculating moving means based on three plants on each side of the central plant and three plants in adjacent rows immediately opposite the central plant, there should be 12 plants contributing to each mean. However the mean for the last location in a row is based on only seven plants. Since the mixtures were grown in 5-row plots there were 10 locations at which the moving mean was based on only seven plants. It is believed that this contributed to inaccurate assessment of the moving means at the ends of plots and to the failure of this method of yield adjustment in the small plots used in this experiment.

Both of these difficulties would be overcome to some degree if larger plots were used. Hence the methods suggested by Hamblin remain as potential methods of overcoming the problem of micro-environmental variation but no evidence in their favour could be found in this study.

If single plant yield can be used as a selection criterion there are several situations in which more emphasis could be placed on them in breeding programmes. In most breeding programmes seed from single plants is increased to provide adequate seed for yield testing. Selection could be practised in this increase generation by testing a number of single plants from each line. This would be similar to the technique used in Experiment 2 when each F3-derived line was progeny tested in the F4 generation. It would also be possible to test single plants from each line at a number of sites and this would reduce the problem of genotype x environment interaction due to different sites. If, for each line, a number of single plants were tested at several sites the mean yield should be a useful estimate of the line and adequate seed would be obtained for larger plots in the following season.

Similar techniques could also be used in breeding methods, such as single seed descent, which require an increase generation before full scale yield tests are commenced.

C. Conclusions

1) In both experiments there was a positive correlation between yield in a complex mixture and yield in pure stand. It is believed that this result was established for the following reasons:

i) Although there was some evidence that competition between genotypes influenced the yields of single plants in mixture, it was concluded that this effect was of minor importance. Furthermore there was no evidence that competition favoured genotypes with either high or low yields in pure stand. It is believed that the negative correlations between competitive ability and yield in pure stand reported by other authors, may be artifacts brought about by the definition used for competitive ability.

ii) It is possible that heterozygosity in early generations could lead to poor assessment of the genotypic value of individual plants. However in Experiment 2, each F3-derived line was evaluated by testing 30 F4 plants and this evaluation was highly correlated with F6 yield. Consequently it was concluded that heterozygosity did not have a confounding effect in this experiment.

iii) Although it was suggested that genotype x environment interactions should not necessarily be considered when evaluating single plant selection for yield, it was shown that no large interaction occurred in the two years of Experiment 1. Yield in mixture in one year was positively correlated with yield in pure stand in the other year and it was concluded that in these two environments genotype x environment interaction was not a major problem.

iv) Efforts were made to obtain accurate assessments of the genotypes in both mixture and pure stand. Extensive replication was used in the mixtures and a method of yield adjustment based on a grid of control plots was used in addition to replication, in pure stand. It was believed that the grid plot technique improved the assessment of genotypes in pure stand and that it estimated irregular variation which would not have been estimated adequately by a lattice design.

In spite of the improvement achieved in the assessment of genotypes, it was concluded that micro-environmental variation remained as a major source of error. It was felt that this type of variation was the main effect limiting the correlation between yield in mixture and yield in pure stand.

2) The results of these experiments support the conclusions of Allard and Hansche (1964) that survival in heterogeneous

populations was usefully associated with yield in pure stand . It was shown that, in general, high yielding genotypes in the mixture were also high yielding in pure stand and since grain yield is a large component of fitness in barley it is the high yielding genotypes that would eventually dominate if the mixture were grown for a number of generations.

3) Simulated truncation selection on the basis of single plant yields was effective, but it was evident that the accuracy with which a genotype was assessed was a major factor determining the effectiveness of selection. In the present study the best estimate of yield in mixture was based on a large number of replicates, but it is clear that replication is not possible if selection is attempted on the basis of individual plant yields. Nevertheless alternative methods of estimating micro-environmental variation were proposed by Hamblin (1971) and these may improve assessments of genotypes in mixture. Although these methods could not be evaluated satisfactorily in these experiments, it is believed that they warrant further study.

ACKNOWLEDGMENTS

The investigations reported in this thesis were carried out under the supervision of Dr. R. Knight and Dr. D.H.B. Sparrow. I appreciate the guidance and encouragement they gave during the experimental phase and in the preparation of this thesis.

I would also like to thank Miss S. Chambers and Mr. R. Lamacraft for advice in the biometrical and computing fields.

Many members of the Agronomy Department gave valuable assistance with field work and I appreciate, in particular, the help of Miss A. Trumble, Mr. S. Jantke, Mr. M. Howe and Mr. D. Hatchard.

Finally I am deeply grateful for the constant support from my wife whose encouragement helped greatly in moments of despair.

VI. BIBLIOGRAPHY

AKIHAMA, T. 1967.- Estimation of competitive ability and its relation to fitness in rice hybrid populations. Jap. J. Breed. 17:262-265.

ALLARD, R.W. 1960.- Principles of Plant Breeding. John Wiley & Sons Inc.

ALLARD, R.W. and ADAMS, J. 1969.- Population studies in predominantly self-pollinating species. XIII. Intergenotypic competition and population structure in barley and wheat. Am. Nat., 103:621-645.

ALLARD, R.W. and BRADSHAW, A.D. 1964.- Implications of genotype-environment interactions in applied plant breeding. Crop Sci., 4:503-508.

ALLARD, R.W. and HANSCHE, P.E. 1963.- Population and biometrical genetics in plant breeding. Proc. XI Int. Cong. Genet., The Hague, The Netherlands, 3:665-680.

ALLARD, R.W. and HANSCHE, P.E. 1964.- Some parameters of population variability and their implications in plant breeding. Adv. Agron., 16:281-325.

ALLARD, R.W. and JAIN, S.K. 1962.- Population studies in predominantly self pollinated species. II. Analysis of quantitative genetic changes in a bulk-hybrid population of barley. Evolution, 16:90-101.

ALLARD, R.W. and WORKMAN, P.L. 1963.- Population studies in predominantly self pollinating species. IV. Seasonal fluctuations in estimated values of genetic parameters in lima bean populations. Evolution, 17:470-480.

BELL, G.D.H. 1963.- Breeding techniques - general techniques. Barley Genetics I. Wageningen, 295-302.

BLUM, A. 1970.- Effect of plant density and growth duration on grain sorghum yields under limited water supply. Agron. J., 62:333-336.

BRIGGLE, L.W. 1963.- Heterosis in wheat - a review. Crop Sci., 3:407-412.

BRIGGLE, L.W., COX, E.L. and HAYES, R.M. 1967.- Performance of a spring wheat hybrid, F2, F3 and parent varieties at five population levels. Crop Sci., 7:465-470.

BRIM, C.A., JOHNSON, H.W. and COCKERHAM, C.C. 1959.- Multiple selection criteria in soybeans. Agron. J., 51:42-46.

BRUCE, A.B. 1910.- The Mendelian theory of heredity and the augmentation of vigour. Science, 32:627-628.

CALDWELL, B.E., WEBER, C.R. and BYTH, D.E. 1966.- Selection value of phenotypic attributes in soybeans. Crop Sci., 6:249-251.

CANNELL, R.Q. 1968.- The yielding capacity of cereal crops. J. Univ. Newcastle-upon-Tyne agric. Soc., 22:3-6.

CARLETON, A.E. and FOOTE, W.H. 1968.- Heterosis for grain yield and leaf area and their components in two six rowed barley crosses. Crop Sci., 8:554-557.

CLAY, R.E. and ALLARD, R.W. 1969.- A comparison of the performance of homogeneous and heterogeneous barley populations. Crop Sci., 9:407-412.

COCHRAN, W.G. and COX, G.M. 1962.- Experimental designs. John Wiley and Sons Inc.

DAVENPORT, C.B. 1908.- Degeneration, albinism and inbreeding. Science, 28:454-455.

DEMIRLICAKMAK, A., KAUFMAN, M.L. and JOHNSON, L.P.V. 1963.- The influence of seed size and seeding rate on yield and yield components of barley. Can. J. Pl. Sci., 43:330-337.

DIXON, W.J. (ed) 1968.- BMD Biomedical Computer Programs. Univ. Calif. Publs Automatic Computation No. 2.

van DOBBEN, W.H. 1965.- Systems of management of cereals for improved yield and quality. IN: The growth of cereals and grasses. (ed. F.L. Milthorpe and J.D. Levins) Butterworths, London.

DONALD, C.M. 1968.- The breeding of crop ideotypes. Euphytica, 17:385-403.

DONALD, C.M. 1963.- Competition among crop and pasture plants. Adv. Agron., 15:1-118.

EAST, E.M. 1908.- Inbreeding in corn. Rept. Connecticut Agric. Expt. Stn. for 1907, pp. 419-428.

EBERHART, S.A. and RUSSELL, W.A. 1966.- Stability parameters for comparing varieties. Crop Sci., 6:36-40.

EFROYMSON, M.A. 1962.- Multiple regression analysis. IN: Mathematical methods for digital computers. (Ed. Ralston, A. and Wilf, H.S., Wiley & Sons).

ELLIOT, F.C. 1958.- Plant breeding and cytogenetics. McGraw Hill Book Company.

ENGLEDOW, F.L. 1925.- Investigations on yield in the cereals II. J. agric. Sci. Camb., 15:125-146.

FINLAY, K.W. 1963.- A semi-automatic seed drill for experimental plots. J. agric. Engng Res., 8:41-47.

FINLAY, K.W. and WILKINSON, G.N. 1963.- The analysis of adaptation in a plant breeding programme. Aust. J. agric. Res., 14:742-745.

FOWLER, W.L. and HEYNE, E.G. 1955.- Evaluation of bulk hybrid tests for predicting performance of pure line selections in hard red winter wheat. Agron. J., 47:430-434.

FRANKEL, O.H. 1947.- The theory of plant breeding for yield. Heredity, 1:109-120.

GARDENER, C.J. 1972.- Environmental responses of barley genotypes. Ph.D. thesis. Univ. Adelaide.

GARDNER, C.O. 1961.- An evaluation of mass selection and seed irradiation with thermal neutrons on yield of corn. Crop Sci., 1:241-245.

GRANHALL, I. 1946.- On heterosis effects in Triticum vulgare. Hereditas, 32:297-293.

GIESBRECHT, J. 1969.- Effects of population and row spacing on the performance of four corn (Zea mays L.) hybrids. Agron. J. 61:439-441.

GRAFIUS, J.E. 1965.- A geometry of plant breeding. Michigan State University, Research Bulletin 7.

GRAFIUS, J.E., NELSON, W.L. and DIRKS, V.A. 1952.- The heritability of yield in barley as measured by early generation bulked progenies. Agron. J. 44:253-257.

GUITARD, A.A., NEWMAN, J.A. and HOYT, P.B. 1961. The influence of seeding rate on the yield components of wheat oats and barley. Can. J. Pl. Sci., 41:751-758.

GYAWALI, K.K., QUALSET, C.O. and YAMAZAKI, W.T. 1968.- Estimates of heterosis and combining ability in winter wheat. Crop Sci., 8:322-324.

HAMBLIN, J. 1971.- Single plant selection for yield in barley. Ph.D. thesis. Univ. Adelaide.

HARDING, J., ALLARD, R.W. and SMELTZER, D.G. 1966.- Population studies in predominately self pollinated species IX. Frequency-dependent selection in Phaseolus lunatus. Proc. Nat. Acad. Sci. U.S., 56:99-104.

JENNINGS, P.R. and AQUINO, R.C. 1968.- Studies on competition in rice. III. The mechanism of competition among phenotypes. Evolution, 22:529-542.

JENNINGS, P.R. and HERRERA, R.M. 1968.- Studies on competition in rice. II. Competition in segregating populations. Evolution, 22:332-336.

JENNINGS, P.R. and DEJESUS, Jr., J. 1968.- Studies on competition in rice. I. Competition in mixtures of varieties. Evolution, 22:119-124.

JOHNSON, H.W. and BERNARD, R.L. 1963.- Soybean genetics and breeding. IN. The Soybean (ed. A.G. Norman) Academic Press, pp. 1-70.

JOHNSTON, T.D. 1971.- The effects of plant density and fertilizer application on yield components in 3 marrow-stem kale (Brassica oleracea L.) varieties. J. agric. Sci., Camb. 77:83-90.

KIRBY, E.M.J. 1967.- The effect of plant density upon the growth and yield of barley. J. agric. Sci., Camb. 68:317-324.

KNIGHT, R. 1960.- The growth of cocksfoot (Dactylis glomerata L.) under spaced plant and sward conditions. Aust. J. agric. Res., 11:457-472.

HARLAN, H.V. and MARTINI, M.L. 1938.- The effect of natural selection in a mixture of barley varieties. J. agric. Res., 57:189-199.

HARLAND, S.C. 1949.- Methods and results of selection experiments with Peruvian Tanguis cotton. Pt. I. A survey of present methods of cotton breeding and a description of the 'mass pedigree system'. Emp. Cott. Grow. Rev., 26:163-174.

HARRINGTON, J.B. 1932.- Predicting the value of a cross from an F2 analysis. Can. J. Res., 6:21-37.

HARRINGTON, J.B. 1952.- Cereal breeding procedures. FAO Development Paper No. 18.

HAYES, H.K. 1925.- Control of soil heterogeneity and use of the probable error concept in plot breeding studies. Bull. Minn. agric. Exp. Stn., 30:1-21.

HAZEL, L.N. 1943.- The genetic basis for constructing selection indexes. Genetics, 28:476-490.

HAZEL, L.N. and LUSH, J.L. 1942.- The efficiency of three methods of selection. J. Hered. 33:393-399.

HINSON, K. and HANSON, W.D. 1962.- Competition studies in soybeans. Crop Sci., 2:117-123.

HORNER, T.W. and FREY, K.J. 1957.- Methods for determining natural areas for oat varietal recommendations. Agron. J., 49:313-315.

LAMACRAFT, R.R. 1969.- STATSCRIPT: A programming language for statistical data-processing in the biological sciences. Proc. 4th Aust. Computer Conf., Adelaide, South Aust.

LAZENBY, A. and ROGERS, H.H. 1964.- Selection criteria in grass breeding. II. Effect on Lolium perenne of differences in population density, variety and available moisture. J. agric. Sci. Camb., 62:285-298.

LECLERG, E.L. 1966.- Significance of experimental design in plant breeding. IN. Plant Breeding (ed. K.J. Frey) Iowa State University Press, pp. 243-313.

LEFFEL, R.C. and HANSON, W.D. 1961.- Early generation testing of diallel crosses of soybeans. Crop Sci., 1:169-174.

LEHMAN, W.F. and LAMBERT, J.W. 1960.- Effects of spacing of soybean plants between and within rows on yield and its components. Agron. J., 52:84-86.

LITCHFIELD, W.H. 1951.- Soil survey of the Waite Agricultural Research Institute, Glen Osmond, South Australia. C.S.I.R.O. Aust. Div. Soil, Divl. Rep. 2/51.

LOHANI, S.N. 1970.- The effects of natural selection on the yield and adaptation of genotypes in composite cross populations. Ph.D. thesis. Univ. Adelaide.

McCLELLAND, C.K. 1926.- New methods with check plots. J. Am. Soc. Agron., 18:566-575.

McGILCHRIST, C.A. 1965.- Analysis of Competition experiments. Biometrics 21:275-985.

McGINNIS, R.G. and SHEBESKI, L.H. 1968.- The reliability of single plant selection for yield in the F2. Proc. 3rd Int. Wheat Genet. Sym. Canberra, Aust. Acad. Sci., 410-416.

PENDLETON, J.W. and DUNGAN, G.H. 1960.- The effect of seeding rate and rate of nitrogen application on winter wheat varieties with different characteristics. Agron. J., 52:310-312.

PENDLETON, J.W. and SIEF, R.D. 1961.- Plant population and row spacing studies with brachytic 2 dwarf corn. Crop Sci., 1:433-435.

PLAISTED, R.L. and PETERSON, L.C. 1959.- A technique for evaluating the ability of selections to yield consistently in different locations or seasons. Am. Potato J., 36:381-385.

PROBST, A.H. 1945.- Influence of spacing on yield and other characters in soybeans. J. Am. Soc. Agron., 37:549-554.

RASMUSSEN, D.C. and LAMBERT, J.W. 1961.- Variety x Environment interactions in barley variety tests. Crop Sci., 1:261-262.

RENNIE, G.K. 1957.- Experiments on seed rates, nitrogen rates for spring barley 1952-3-4. Expl Husb., 2:12-17.

ROSENQUIST, C.E. 1931.- Hybrid vigour in wheat (Triticum vulgare). J. Am. Soc. Agron., 23:81-105.

ROBINSON, H.F., COMSTOCK, R.E. and HARVEY, P.H. 1951.- Genotypic and phenotypic correlations in corn and their implications in selection. Agron. J., 43:282-287.

SAKAI, K. 1965.- Contributions to the problem of species colonization from the viewpoint of competition and migration. IN: The Genetics of Colonizing Species (eds. Baker, H.G. and Stebbins, G.L.) Adacemic Press, New York, pp. 215-240.

SAKAI, K. 1957.- Studies on competition in plants. VII. Effects on competition of a varying number of competing and non-competing individuals. J. Genet., 55:227-234.

SAKAI, K. and IYAMA, S. 1966.- Studies on competition in plants and animals XI. Competitive ability and density response in barley. Jap. J. Breed. 16:1-9.

SALMON, S.C. 1951.- Analysis of variance and longtime variety tests of wheat. Agron J., 43:562-570.

SAMMETA, K.P.V. and LEVINS, R. 1970.- Genetics and ecology. A. Rev. Genetics, 4:469-488.

SANDFAER, J. 1970.- An analysis of the competition between some barley varieties. Danish Atomic Energy Commission. Riso Rep. No. 230.

SCHUSTER, W. and SPENNEMANN, F. 1964.- Untersuchungen uber den Einfluss der Standweite auf die Variabililitat einiger Eigenschaften von verschiedenen Sojabohnensorten (Glycine soja. L.). Zuchter, 34, 262-272.

SCHUTZ, W.M., BRIM, C.A. and USANIS, S.A. 1968.- Intergenotypic competition in plant populations. I. Feedback systems with stable equilibria in populations of autogamous homozygous lines. Crop Sci., 8:-1-66.

SEVERSON, D.A. and RASSMUSSEN, D.C. 1968.- Performance of barley hybrids at four seeding rates. Crop Sci., 8:339-341.

SHEBESKI, L.H. 1967.- Wheat and breeding. Proc. Canadian Centennial Wheat Sym. (ed. K.F. Neilsen), Modern Press, Saskatoon, pp. 249-272.

SHEHATA, A.H. and COMSTOCK, V.E. 1971.- Heterosis and combining ability estimates in F2 flax populations as influenced by plant density. Crop Sci., 11:534-536.

SHULL, G.H. 1908.- The composition of a field of maize. Rept. Am. Breeders Assoc., 4:296-301.

SIEMANS, L.B. 1963.- The effect of varying row spacings on the agronomic and quality characteristics of cereals and flax. Can. J. Pl. Sci., 43:119-130.

STICKLER, F.C., AHMED, M.K. and MAMBRY, J.L. 1964.- Response of certain winter wheat varieties to stand density. Trans. Ka. Acad. Sci., 67:405-417.

SUNESON, C.A. 1956.- An evolutionary plant breeding method. Agron. J. 48:188-191.

TERMUNDE, D.E., SHANK, D.B. and DIRKS, V.A. 1963.- Effects of population levels on yield and maturity of maize hybrids grown on the Northern Great Plains. Agron. J., 55:551-555.

THOMAS, V.J. 1970.- A mathematical approach to fitting parameters in a competition model. J. appl. Ecol., 7:487-496.

THORNE, G.N. 1966.- Physiological aspects of grain yield in cereals. IN: The growth of cereals and grasses (ed. F.L. Milthorpe and J.D. Levins) Butterworths, London, pp. 88-105.

UPADHYAYA, B.R. and RASMUSSEN, D.C. 1967.- Heterosis and combining ability in barley. Crop Sci., 7:644-647.

VOIGT, R.L. and WEBER, C.R. 1960.- Effectiveness of selection methods for yield in soybean crosses. Agron. J., 52:527-530.

WALTON, P.D. 1971.- The use of factor analysis in determining characters for yield selection in wheat. Euphytica, 20:416-421.

WARD, W.T. 1966.- Geology, geomorphology and soils of the south-western part of County Adelaide, South Australia. C.S.I.R.O. Aust., Soil Publ., No. 23.

WHITEHOUSE, R.N.H., THOMPSON, J.B. and RIBEIRO, M.A.M. 1958.- Studies on the breeding of self pollinating cereals. 2. The use of a diallel cross analysis in yield prediction. Euphytica, 7:147-169.

WIEBE, G.A., PETR, F.C. and STEVENS, W. 1963.- Interplant competition between barley genotypes. Statistical Genetics and Plant Breeding. Nat. Acad. Sci., Nat. Res. Council. Publ. No. 982, pp. 546-555.

WILLIAMS, W. 1959.- Heterosis and the genetic concept of complex characters. Nature, 184:527-530.

De WIT, C.T. 1961.- Space relationships within populations of one or more species. Symp. Soc. Exp. Biol. 15:314-329.

YOUNG, S.S.Y. 1961.- A further examination of the relative efficiency of three methods of selection for genetic gains under less restricted conditions. Genetics Res., 2:106-121.