SINGLE PLANT SELECTION
FOR YIELD IN BARLEY

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Statement

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

SUMMARY.

1. To be effective single plant selection methods for yield must estimate and allow for factors that influence the phenotypic expression of the genotype.

2. These factors are: (a) heterozygosity,
(b) genotype - environment interactions,
(c) interplant competition,
(d) differences in the micro-environment of plants.

3. An experiment was designed that it was hoped circumvented (a) and allowed some estimate of (b), (c) and (d).

The yields of individual plants in the F_3 generation of a barley cross were measured in 4 contrasting environments (2 densities and 2 nitrogen levels). 100 plants were then selected from the total yield range in each environment. The seed from the selected plants was increased in the F_4 and progeny tested in replicated plots in the F_5. The lines selected in any one of the four F_3 environments were tested in the same environment and in the alternate environment in the F_5 (e.g. lines selected in the F_3 at low density were tested in the F_5 at low density and at high density).

In the F_3, single plant grain yields, were assessed in a number of ways, some of which attempted to make allowance for the local environmental variation: response surfaces and moving means were used. The underlying assumption was that if the seeds were planted at random,

then the average yield of a group of contiguous plants could be used to estimate the yield potential within the group. Once the estimated mean yield of the individuals in the group was calculated then the performance of an individual was expressed as the difference between its actual yield and its (mean) yield as estimated from the group.

As well as grain yield a range of other plant characters were measured in both the F_3 and the F_5 generations. These included yield components, total dry matter yield above ground and certain vegetative characters (leaf length, leaf height and plant height).

4. The results confirmed the prevalent view that single plant selection, on the basis of yield, in early generations is not effective in selecting for yield in later generations. The experimental design permitted a partial analysis of this result. The genotype — environment interaction was very marked between the two years 1967 (F_3) and 1969 (F_5). At low density micro-environmental variation was also an important confounding factor. At high density and in the nitrogen experiment competition was important.

Of the other characters measured in the F_3 generation the vegetative morphological characters (leaf length, leaf height and plant height) were consistently effective in predicting the yield potential of lines tested at high nitrogen in the F_5. This was probably due to a causative relationship as the characters measured are known to influence the lodging resistance, and the efficiency of light and water use in pure stands. It was not possible to decide within this

experiment which of these factors was the more important. The vegetative characters were less influenced by genotype by environment interactions or by competition than was yield. As the characters were positively related to the yielding ability of phenotypes in pure culture at high nitrogen, they were better indicators of yield potential in future generations than was yield itself.

In this study indirect selection on a single plant basis was more successful than direct selection.

The implications of these results for selection practice in segregating populations are discussed.

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INTRODUCTION.

Effective single plant selection for yield in early generations would be of obvious benefit to the plant breeder as it would enable him to screen large numbers of genotypes with the minimum of time, effort, cost and space. However many authors consider that it is not effective (Allard 1960, Bell 1963, Elliott 1958, Harland 1949 and Harrington 1932). Their belief is based on the published data, and the intractability of the problems (see below for details) that confound single plant selection. However McGinnis and Shebeski (1968) question whether many of the experimental designs used adequately test the effectiveness of single plant selection. Further examination of the problem is therefore warranted.

Four possible causes for the low efficiency of single plant selection (Shebeski 1967) are:

(1) The effects of heterozygosity and consequent hybrid vigour on the performance of individuals in early segregating generations. This may lead to a false appraisal of the individual's worth.

(2) Large genotype-environment interactions. Selection must occur in a different generation to progeny testing and therefore in a different growing season, thus some interactions between genotypes and seasons are unavoidable. In addition selection often occurs at low density while the progeny are tested at commercial spacing. This introduces a possible genotype-density interaction.

(3) However if selection is carried out at any but very low densities, the relationship of the individual to its neighbours assumes great significance. Unless the yield of a plant in pure culture is positively correlated to its yield in mixed stands, selection of high yielding plants in a mixed population may be based on competitive ability rather than high yield.

(4) Each plant in a segregating population has its individual micro-environment. The micro-environment is not constant throughout a selection plot. The variation between the micro-environments of different plants may be sufficient to swamp the genetic differences between individual plants.

In this thesis, the problems involved in single plant selection for high yield are discussed in the light of the data available in the literature, and a project is described that attempts to assess and overcome these difficulties.

LITERATURE REVIEW.

(1) Introduction :

Allard (1960) notes that many of the plant breeders of the last century selected for yield on a single plant basis in the belief that the phenotype was inherited. However Vilmorin selected the best plants from within four varieties for 50 years and found there was no difference between the selected and unselected groups. An explanation for this was put forward by Johannsen (1903) who made the distinction between genotype and phenotype. He showed that the variation in a character, from one individual to another in a population, was governed by genotypic and environmental effects. Since then many workers have developed methods for measuring the genotypic and environmental variances and have expressed them as relative proportions of the total, or phenotypic variance, (Fisher 1918, Fisher et al. 1932, Wright 1920, Lush 1940, 1943, Robinson et al. 1949, Mather 1949, Warner 1952). Using one or more of these methods of partioning the variance, it has been shown often that the heritability of yield is low, that is that yield is strongly affected by the environment. (Grafius et al. 1952, Frey 1954, Rassmusson and Glass 1967 for barley; Liang and Walter 1968 for sorghum; Fonseca and Patterson 1968 for wheat; Mahmud and Kramer 1951, Bartley and Weber 1952, Weber and Moorthy 1952 and Johnson et al. 1955 for soybeans.)

In segregating populations genetic and environmental effects may so alter the phenotype of an individual that it is impossible to assess its genotype. The reasons for this will now be considered.

(2) Heterozygosity :

In the pedigree method of plant breeding selection is practiced in the F_2 and subsequent generations (Allard 1960). In these early segregating generations many loci are heterozygous. If dominance or overdominance results from this heterozygosity it may have a large effect on the phenotype. As heterozygosity cannot be maintained in a cereal variety, except by very special techniques, the heterozygous effect can lead to poor discrimination and evaluation of genotypes. In self pollinating crops there is no direct evidence on the importance of heterozygosity on selection. However hybrid vigour has often been reported in the literature for F_1 plants of self-pollinating species. (Immer 1941, Grafius 1959, Suneson and Riddle 1944, Suneson 1962, Severson and Rassmusson 1968 for barley; Briggle et al. 1968 a & b for wheat; for a review see Briggle 1963.)

The increased vigour attributable to heterozygosity falls rapidly with each cycle of selfing as the percentage of heterozygous loci falls. The problem for the plant breeder is to decide in which generation the effect of this unfixable vigour will be reduced to unimportant proportions.

In this project, selection was carried out in the F_3. Because of the lack of published information the choice was more or less arbitrary. But it was felt that by this generation the effects of heterozygosity would not adversely affect selection. There is some slight evidence for this in the literature. Atkins (1953 barley) studied the yields of 8 bulk populations for 4 generations (F_2 - F_5) and compared them with those of selections made in the F_2 and reselected in each generation on the basis of plant vigour and large heads free from disease. All the generations were compared in one season (1949). The experiment was repeated the following year, using the same material but advanced by 1 generation. The yields are given in table 1. It should be noted that there were no significant differences between the bulk or selected populations in 1950. Although not significant, the trends are the same as in 1949. In that year the yield of the bulks first fell and then at the F_5 rose again, until it was equal to the yield of both the F_2 bulk and the selections.

Table 1 :

Grain yield of bulk and selected lines of barley (Atkins 1953) (kgs/ha)*

	Bulk Population					Selected Lines			
Year	F_2	F_3	F_4	F_5	F_6	F_3	F_4	F_5	F_6
1949	2605 a(‡)	2240 bc	2227 c	2455 ab	-	2605 a	2521 a	2427 a	-
1950	-	2992 a	2842 a	2732 a	2934 a	-	2979 a	2999 a	2914 a

* All data throughout this thesis are presented in metric units, (including those quoted from the literature).

‡ In the same year yields having the same letter beneath them do not differ significantly.

It would appear that in the bulk F_2 heterozygosity caused the higher yield, which fell as heterozygosity decreased with inbreeding. During this period (F_3/F_4) there would be the maximum number of low yielding genotypes in the population, but these would be eliminated with successive cycles of natural selection so that the yield level would rise. As the selected lines were chosen for their vigour they were possibly heterozygous. Although the more heterozygous plants may have been chosen, in later generations the level of heterozygosity would fall gradually, causing a decline in yield. This occurred although the fall in yield in the selected lines was not significant. The selected F_3 had a 15% yield advantage over the bulk, which was significant at the 1% level; this had completely disappeared by the F_5. It appears that heterozygosity in this example has played a significant part in reducing the efficiency of selection in the F_2. But by the F_3 this factor appears to be of little importance as shown by the low F_3 bulk yield. A similar result has been obtained by Wiess et al. (1947) for soybeans, and Immer (1941) who found a similar fall in the yield of barley populations in successive generations until the F_4. He did not test later generations.

Although these three reports suggest that heterozygosity is not a problem in the F_3, there are two lines of research that suggest that it cannot be entirely disregarded.

Firstly, it has been shown that the hybrid advantage of an F_1 decreases with density (Severson and Rasmusson 1968). The F_1

plants were only slightly higher yielding than the parents at field spacing, but much higher at low rates of planting. Hybrid vigour may have a larger confounding effect if selection is carried out at low densities. However, no evidence for this effect was found in wheat by Briggle et al. (1967a and b).

Secondly, and more important, is the work of Allard and co-workers (reported by Jain and Allard 1960 and by Allard and Hansche 1964). They showed for populations of lima beans, barley and wild oats that the rate of change in the proportions of heterozygotes to homozygotes at certain loci within a population was slower than predicted, assuming equal selective advantage and a known percentage of out-crossing. The percentage of heterozygotes stabilised in later generations at a substantial and fairly constant level. The heterozygotes had a selective advantage over the homozygotes at those loci, and their persistence was probably related to their producing more seed. This higher yield would be picked out in any generation if plants are selected for yield and therefore heterozygosity could disrupt effective selection in any generation.

From the evidence available, no clear-cut conclusion can be drawn as to the importance of heterozygosity on selection. However, delaying selection until homozygosis is considered to have been reached may not in fact produce the desired results if the heterozygotes are at a selective advantage. The delay means that a large part of the population brought forward will be of little use and natural selection may eliminate many genotypes that are potentially high yielding in pure culture.

(3) Genotype-Environment Interaction :

If lines or varieties are gown at a series of sites for several seasons it is possible to partition the variance into components attributable to variety, sites and seasons, and their interactions. The first order interactions are the variety-site, the variety-seasons and the sites-seasons interactions, the second order is the variety-site-season interaction. Using an appropriate error it is possible to test for the significance of each of these terms. The methods for computing these variances and for testing them for significance have been presented by Comstock and Moll (1963).

From the analysis it is possible to test whether varieties respond to a changed environment in a similar linear fashion. If varieties do not a significant interaction occurs. When this happens it is not possible to draw any overall conclusions about the main effects as the varieties are no longer responding in a similar fashion. Such interactions have been reported in the literature for several crops, for example barley (Rasmusson and Lambert 1961), wheat (Ghandi et al. 1964), oats (Horner and Frey 1957), maize (Sprague and Federer 1951), soybeans (Johnson et al. 1955), and cotton (Miller et al. 1958 and 1962).

The work for this thesis was carried out at one site, thereby eliminating the possibility of a genotype-location interaction. Furthermore, although selection occurred in one year and progeny testing in another, no estimate of the genotype-years interaction was possible because selection was carried out on individual plants.

In a similar way it is possible to calculate a genotype-treatment (e.g. nutrient) interaction. If this is significant, the varieties under test are not responding linearly to the different treatments. Significant interactions have been found to occur for many cereals with a range of nutrient treatments. For example these have been found in barley (Reid et al. 1969), wheat (Jensen and Federer 1965, using the data of Isom 1954), and rice (Tanaka et al. 1964, Kwano and Tanaka 1968 and deDatta et al. 1968).

There is little relationship between the rankings of yield of cereal varieties grown at high and low densities. Significant interactions have been reported in barley (Immer 1941), wheat (Whitehouse 1953), sorghum (Koller and Scholl 1968), and maize (Griesbrecht 1969).

The important point which emerges from this survey is that plant density and soil nutrient status, factors of the environment easily manipulated by the plant breeder, have a profound but not uniform effect with different genotypes. It cannot be expected that lines selected for high yield under one set of conditions are necessarily high yielding under another. Genotype-environment interaction will therefore often severely limit the efficiency of selection should one attempt to select in one environment (including density, fertility level or climate) for performance in another.

(4) Competition : (A) In mixtures of varieties.

In segregating populations growing at normal field spacings, competition may have a large influence on the genotype-environment interaction. This was not the case in the examples already discussed where the different genotypes were grown in separate plots.

With the development of the bulk hybrid method of plant breeding considerable attention has been focussed on the importance of natural selection in segregating populations. The first person to show that genotypes may perform differently in pure culture (here the only competition is with identical genotypes) and in mixtures (here competition is with different genotypes) was Montgomery in 1912. He found that one variety dominated the mixture very rapidly, but this was not necessarily the highest yielding in pure culture. A similar result was obtained by Engledow (1925) and Klages (1936). In the latter case the result was due to differential disease resistance during the severe rust epidemic of 1935.

In what is probably the most complete experiment of this type Harlan and Martini (1938) grew a mixture of eleven varieties of barley, initially present in equal proportions, at ten sites in the U.S.A. for between four and eleven years. No conscious selection occurred during the experiment. Each year a census of the mixtures from each site was carried out on a space-planted subsample grown at one site. It was found that one or two varieties invariably and rapidly dominated the mixtures. Different varieties dominated at different sites. Six of the eleven varieties never became dominant.

The dominant varieties were often the local commercial strain. If plots of the individual varieties had been grown at each site, an estimate of yield in pure culture would have been obtained. This could then have been compared with the results from the mixture.

Since this study was published many similar ones have been reported. A common feature is the limited number of varieties used to make up the mixtures, and one variety rapidly became dominant. This was very often not the highest yielding variety in pure culture. For example Christian and Grey (1941) conclude that, in wheat mixtures, the yield of competing plants bears little relationship to pure stand performance. Laude and Swanson (1942) were able to explain the shift in their mixtures as being due to the differential winter survival of the varieties used. They note that competition may lead to the elimination of desirable types from a population and suggest that high yielding dwarf types would be at a severe disadvantage in a population containing many taller plants.

The most studied mixture has been that containing the barley varieties Vaughn, Atlas, Hero and Club Mariout. The early work on this mixture was reported by Suneson and Wiebe (1942) and Suneson (1949). They found that Atlas dominated the mixture although it was not as high yielding in pure culture as Vaughn nor as disease resistant. Vaughn was for practical purposes eliminated from the population. Since then a number of workers in California have tried to discover why this result occurred. In a study of competition between Vaughn and Atlas 46, a disease resistant back cross derivative of Atlas, and not strictly comparable with the original mixture. Lee (1960) found that competition became marked at jointing. This was associated with the development of the secondary root system. He suggested that greater root proliferation enabled Atlas 46 to compete more successfully for the available nutrients. The importance of light intensity on the two varieties has also been studied. The results showed that although reduced light had a marked effect on growth, it did not affect their relative competitive abilities (Edwards and Allard 1963). Hartman and Allard (1964) varied both the nitrogen and water status for these varieties grown in pots. Vaughn yielded more than Atlas both in pure culture and in the mixture. In the mixture the yield of Vaughn was depressed and that of Atlas increased, although not enough to reverse the actual yield rankings. This contradictory result is probably due to the plants being grown in pots and the difficulty of extrapolating from this situation to the field. In a recent paper, Allard and Adams (1969a) state that the average yield of Atlas has been higher than that of Vaughn for the past decade. This is in direct contrat to their relative performance reported two decades earlier (Suneson 1949). The most probable explanation is that yields quoted by Suneson were for the original Atlas whereas those of Allard and Adams were based on one or more of the disease resistance back cross derivatives. Suneson (1949) noted that the likely increase of Atlas 46 over Atlas in a bad year for disease was 15%. This would make it higher yielding on average than Vaughn.

Inter-specific mixtures of wheat have been studied by Pal et al. (1960). From their data they suggest that competitive ability is a desirable varietal character as it would help maintain varietal purity. Contaminating varieties would be suppressed and weed control would improve. This may be important in peasant agricultural systems, but where weed control and seed certification are the norm, high competitive ability may not be a desirable character. As already shown high yield in pure culture and ability to dominate mixtures are not necessarily related and in segregating populations this may lead to the elimination of desirable types.

Mutant forms of barley have been shown by Gustafsson and Nybom (1950) to have different competitive abilities. These workers found that some mutants although lower yielding, were more competitive. They also showed that the relative competitive ability varied between years. Wiebe et al. (1963) carried out a similar experiment using isogenic lines. They simulated various generations of a population by mixing isogenic lines and their hybrid in the expected ratios. They found competition caused a reversal in yield rankings of the lines in the mixtures and pure culture. However, Wiebe et al. (1963) stated: "This (result) is a paradox for the plant breeder. On the other hand if the rule has a degree of universality, it may explain why breeding for increased yield has proceeded so slowly". The paper is difficult to assess as the results are presented on a relative scale. When one line increases, the other must show a corresponding decrease. If they are correct in their conclusion, the finding has great significance for plant breeders.

Similar genotype-competition interactions have been reported in rice by Sakai (1955) and Jennings and de Jesus (1968). However Akihama (1968) found no interaction between competitive ability and environment. He suggests that competitive ability is independent of the environment.

In many of these studies a major weakness in design is the small number of lines used in the mixtures (Engledow, 1 mixture of two varieties; Klages, 3 mixtures of 2 varieties; Christian and Grey, 1 mixture of 2 varieties; Laude and Swanson, 2 mixtures of 2 varieties; Suneson, 2 mixtures of 4 and 5 varieties; Wiebe et al., 3 lines in various proportions; Gustafsson and Nybom, pairs of varieties and mutant lines; Sakai, 2 varieties; Jennings and de Jesus, 5 varieties in the mixture; Akihama, 2 varieties). If the varieties used differ markedly in their pure culture yield, then a very large genotype - competition interaction would be required to change their relative performance in mixtures. On the other hand, if the varieties chosen have a very similar yield in pure culture, then an unusually small interaction may have a very considerable impact on survival in a mixture. The result only reflects a sampling choice in the initial population. To have any general validity the sample of varieties would have to be large enough and be chosen at random to ensure that the result obtained was not due to the initial choice of varieties.

It is obvious that many of the experiments reported here do not meet this requirement. The results can be divided into two categories. Firstly, Harlan and Martini (1938) found that the local commercial variety tended to dominate the mixture. On the assumption that this would have been the highest yielding in pure culture, this suggests that yield in pure culture and competitive ability of individual genotypes are positively associated. This result is in contrast to that of many other workers (see above discussion) who found that the highest yielding lines in pure culture were eliminated in mixtures. These results show that no generalization can yet be made about the relationship between yield in pure culture and competitive ability. ✓ It is thought that the variety that dominates a mixture does so because it is highly competitive. From these results one can attempt to make some generalizations about what might occur in bulk hybrid populations.

The usual form of these predictions, as pointed out by Allard and Jain (1962) and Allard et al. (1968), is that, after several generations of inbreeding, the bulk would consist of a few highly competitive, high yielding, well adapted genotypes. But as ✓ already shown yielding ability in pure culture and competitive ability are not necessarily related. The conclusion that the bulks will be high yielding probably stems from Suneson's work (Suneson and Stevens 1953, Suneson 1956) on the yield of bulk populations, and not from a consideration of the work on mixtures. This latter would lead one to conclude that bulks would consist of a few highly competitive well adapted lines of unknown yielding ability.

On the basis of the questions raised by work on mixtures, Suneson (1949) discusses the validity of the bulk breeding method, and suggests that the classical concepts of what might be achieved by this method need revision. He concludes: "It seems important to learn more about the nature and importance of survival in competitive mixtures".

The bulk population experiments, to be considered next, do not in fact confirm the expectation that bulks in later generations will consist of a few highly competitive genotypes of varied yielding ability and a possible explanation for this discrepancy will have to be considered.

Competition : (B) In bulk hybrid populations.

Although the bulkpopulation method of breeding was used as early as 1908 by Nilsson-Ehle, (Akerman and Mackey 1948) it was not until the 1940s that breeders published on the survival of genotypes within these bulks.

The early work was concerned with the comparison between bulk and pure line breeding methods. The aim was to grow the bulks as cheaply and easily as possible until most loci were homozygous. This usually continued at least until the F_5 and more commonly until the F_6, F_7 or F_8. Selections were then made within the bulks and these compared with pure line selections from earlier generations. The work of Harlan et al. (1940) and Atkins (1953) on barley show that there was no difference between the two methods. High yielding lines had not been eliminated by competition. There was usually a sufficient range of genetic variation present for selection to be practised successfully for any character or combination of characters, (Adair and Jones 1946, rice). But Middleton and Chapman (1941, barley) noted that certain characters (smooth and hooded awns) were reduced to a very low frequency in the population.

Several workers have reported that different selection environments have tended to shift populations of the same initial material in different directions. For example, length of growing season varied with selection site (Adair and Jones 1946). The yield performance of bulks was markedly dependent on the site at which natural selection had occurred (Taylor and Atkins 1954). In contrast to this Reyes and Frey (1967) found that bulks grown at different densities did not show a genetic shift, and Oka and Lin (1958) obtained the same results with bulk populations grown at different fertility levels.

These results show that natural selection will alter populations. But the suggestion that only a few highly competitive genotypes (p.17) would survive, anticipated from work on mixtures is not correct. The most complete study of bulk populations has been on material developed by Suneson. These he called composite crosses because the populations were obtained from crosses between many parents. Composite cross populations therefore have a wide genetic base. In 1953, he and Stevens showed that certain characters, for example two row heads, hoods, smooth awns and black grains, decreased very rapidly with time in six populations. Some characters survived better at some sites than others. This result is similar to that obtained by Harlan and Martini (1938) for varieties.

The most controversial result, however, is their report on the yield trends of the composite crosses with advancing generations (Suneson and Stevens 1953 and Suneson 1956). The data for composite cross II as shown in Figure 1a is a copy of the results as presented by Suneson (1956). Figure 1b is from a table in the same paper.

Figure 1a shows a steady increase with time in the yield of Composite Cross II when compared with Atlas. There is some indication that the improvement only continues to the 20th generation. It is here that the control, Atlas, was replaced by Atlas 46. Figure 1b shows that, whilst there was some improvement in the performance of the composite cross with time, the yield of Atlas fell throughout the experiment. This would tend to exaggerate the gains of the composite cross when presented on a relative basis. Furthermore, the yield of both Atlas 46 and the composite cross fell very rapidly from about the 20th generation onwards. No explanation is offered for these decreases.

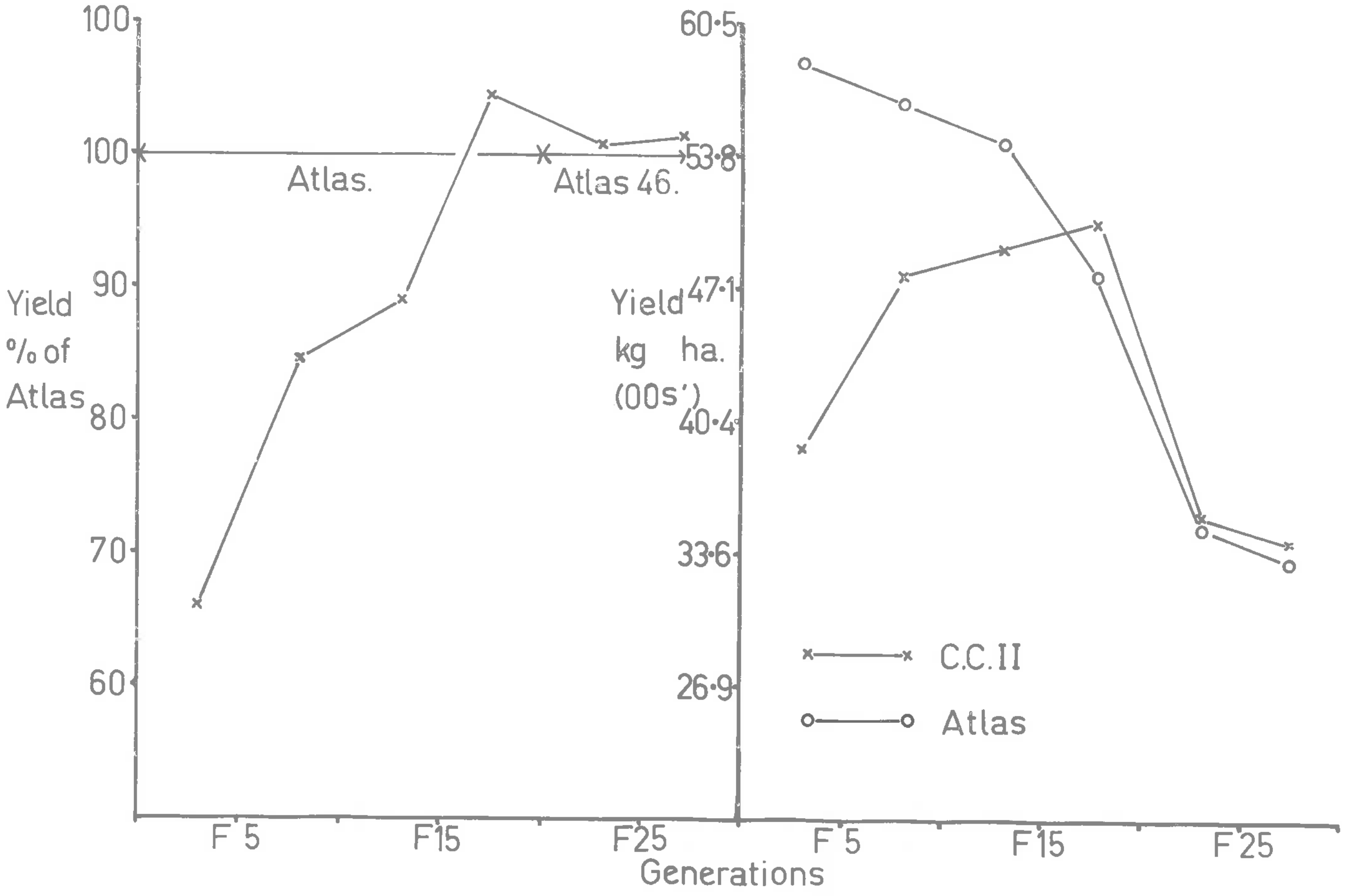
Although it is difficult to interpret what is happening

Figures 1a and 1b.

The relationship between the bulk yield of Composite Cross II and Atlas over generations (after Suneson 1956).

The relationship between Composite Cross II and Atlas.

a.) from a figure, Suneson 1956. b.) from a table, Suneson 1956.



within the composite cross, some significant results were obtained. Selections were made in the F_{12} (356 lines), the F_{20} (50 lines) and the F_{24} (66 lines). There were no high yielding lines in the F_{12} selections, there were 2 in the F_{20} and 10 from the F_{24}. Three of these latter had a yield advantage of 56% over Atlas 46. This suggests that natural selection has increased the proportion of high yielding genotypes.

The result is of considerable interest as it would imply that competition has worked in the opposite way from that commonly found in studies of mixtures. Two problems arise. Firstly, this result needed confirmation, and if confirmed, an explanation of how this difference in results occurred is required.

Using 63 random selections from the F_3, F_6 and the F_{13} generations of Composite Cross V Jain and Allard (Jain and Allard 1960, Jain 1961 and Allard and Jain 1962) showed that with time both the yield and the fitness of the population increased, in an approximately linear fashion. The yield was not, however, compared to that of the parents or Atlas. They further showed that the variance of two characters, heading date and height, decreased with time when compared with the between parent variance. It was however, much larger than the within parent variance. Selection was found to be both directional and stabilising for most characters. This suggests that there was a shift for characters whose means were not at the optimum for the environment; this shift was towards the optimum. For all characters studied there was an elimination of extreme types. Because of experimental difficulties, this work was conducted at 30.5 x 30.5 cm. spacing whereas Suneson worked with drill rows. As the authors point out, their conclusion cannot be compared unequivocably with those of Suneson because of a possible genotype - density interaction due to the low density used. No attempt was made to estimate the importance of this interaction. This work however, supports the contention of Suneson (1956) that the yield of the composite increased with time.

Adams and Allard (1969 a and b) measured the competitive ability of four barley varieties (the four used by Suneson in 1949) and four wheat varieties and eight selections from the F_{18} of Composite Cross V. The yield of varieties in pure culture was expressed as a percentage of one of the varieties, and the yield in mixture as a percentage of the yield of the individual variety in pure stand (percentages of percentages). This method of presentation is awkward to interpret. It is notable that in the three sets of comparisons, barley and wheat varieties and selections from the Composite Cross, the lowest yielding lines in pure culture showed the largest increase in yield under competitive conditions. In the case of the selections from the Composite Cross the highest yielding lines in pure culture showed the least relative change in yield. This was not as obvious in the case of the varieties, perhaps due to the inherent sampling errors that can be expected when small samples are used (c.f. p. 16).

This result suggests that the high-yielding lines in pure culture were the poorer competitors. There would appear to be an agreement here with the results from the majority of the mixture experiments.

Further evidence for this relationship between yielding and competitive ability is provided by some work on rice. Jennings and Herrera (1968),using bulk populations, found a negative association between yield and competitive ability.

The evidence therefore appears to have both confirmed the work of Suneson, namely that natural selection may concentrate high-yielding genotypes and also confirms that there is often a negative relationship between yielding ability and competitive ability. The conflicting results outlined above will be considered more fully in the next section.

Competition : (C) Theoretical considerations of natural selection in bulk populations.

As pointed out by Schutz et al. (1968) and Allard and Adams (1969 a and b) competitive ability,* measured by the relative performance of a variety in a mixture relative to its performance in a pure stand, is not a prime factor in ensuring survival in a bulk population. The determining factor is the ability to produce large

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* This definition of competitive ability, the ratio of the yield of a variety in a mixture, relative to its yield in pure culture is used throughout this thesis.

numbers of offspring in the next generation. A variety that can produce more seeds than its neighbours in a mixture, will dominate that mixture. This will occur even if, by the definition above, it is a poor competitor. The reasons for this are illustrated in figure 2.

Figure 2 represents a series of idealised relationships for a number of genotypes grown in two situations, firstly competing against the same genotypes (pure culture) and secondly competing against different genotypes (mixtures).

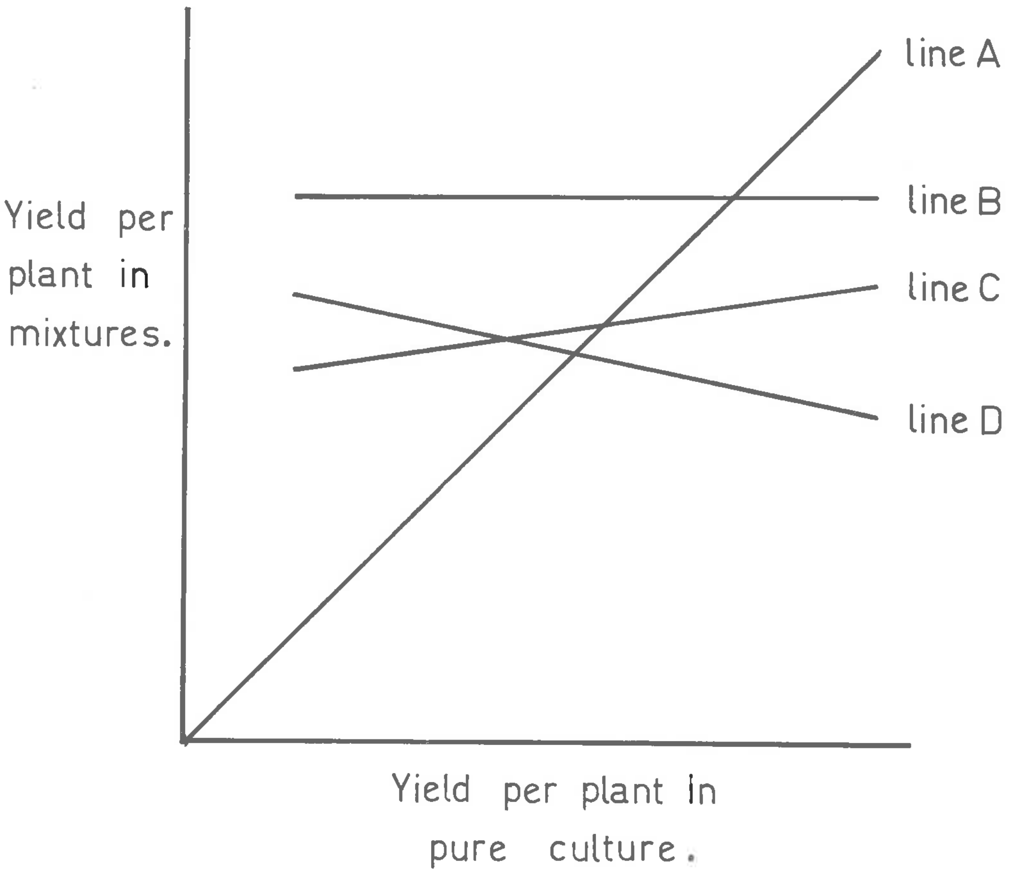
Line A has a slope of one. The different genotypes that lie on that line have the same yield in competition with other genotypes as they do when competing against themselves. That is to say that yield and competitive ability are independent. It is obvious that the high yielding genotypes will dominate any mixture as these genotypes will contribute more progeny to the mixture than will poorer genotypes. The same occurs, but more rapidly if yield and competitive ability are positively associated. The slope of the line would now be greater than one.

Line B has a zero slope. The yield of the different genotypes in the mixture is now the same, irrespective of their yield in pure culture. The high yielding genotypes in pure culture are poor competitors as the ratio of yield in the mixture to pure culture is less than one; the reverse is true of the low yielding genotypes. The proportions of the various genotypes in the mixture

Figure 2.

The theoretical relationships between a series of groups of genotypes grown in a mixture and as pure lines. This diagram was developed from the theoretical discussion of Schutz et al. (1968) and Allard and Adams (1969 a and b).

Hypothetical relationships between a series of genotypes grown as mixtures and as pure lines.(this figure is a development from the work of Schultz et al. 1968 and Allard and Adams 1969.)



depicted by line B will not change and the population will be at equilibrium.

Line C represents any line with a slope greater than zero but less than one. The high yielding genotypes in pure culture are again poor competitors and the low yielding genotypes good ones, as in case B; but because the high yielding genotypes still manage to produce more seed in the mixture than the low yielding genotypes the less competitive high yielding lines will dominate the mixture. This is despite their lower competitive ability. Their rate of domination will depend on the slope of line C, the steeper the slope, the faster the rate. Because the high yielding genotypes will dominate the mixture, the yield of the mixture will rise with successive generations as the low yielding genotypes are eliminated.

Line D has a negative slope. The yield of the low yielding genotypes in pure culture so improves relative to the high yielding genotypes when these are grown in competition that the former will dominate the mixture. The yield of the mixture would initially fall, and then stabilise at a low level.

In this discussion of Figure 2, the relationship between yield and competitive ability has been assumed to be perfect, with all the genotypes used falling exactly on the line. In practice, this would not occur. A large sample of genotypes would be expected to show some scatter. In addition, any one genotype would be expected to vary from its true genetic position in relation to the line, due to site, season, and individual neighbours. These variations would probably decrease the rate of change within a population, and would account for random fluctuations in all populations.

This simple model helps to explain the anomalous results already outlined, since it shows that it is possible for a population to improve with time, yet with the higher yielding genotypes less competitive than the low yielding ones. The populations used by Suneson and Allard and co-workers may be of type C, whereas that used by Jennings and Herrera may be of type D. The latter study would reflect an inverse relationship between yielding ability and height and a positive relationship between height and competitive ability.

In conclusion, it is clear that there is a competition between genotypes. Whether this will markedly hinder selection will depend on the relationship between yielding and competitive ability of the individuals in the population.

(5) Micro-Environmental Effects and Single Plant Selection :

It is not yet feasible to use vegatative propagation in cereals to provide replication of a single genotype in segregating generations. Because of the difficulties of replication and genetic variability, plant breeders have made little attempt to estimate micro-environmental effects. In a recent review LeClerg (1966) discusses the problems of experimental design in plant breeding in great detail, but although he states that the largest source of error is due to the lack of soil uniformity, he does not discuss its effect on single plant selection.

In 1938 Fairfield Smith considered soil heterogeneity and discussed the use of moving means to estimate its effects. Moving means provide an estimate of the average yield of a small area, and can be calculated if data are obtained as a series of contiguous samples. The most common measurement of this type is the population mean yield; however if, for example, there is a fertility trend down a row the mean yield of the row would not give any indication of this trend. One way of showing the trend would be to divide the row into a number of sections and obtain the mean yields of the sections. A better solution would be to use moving means, i.e. the mean of the first 3 samples in the row, then of samples 2-4 and so on until the end of the row is reached. In this way a continuous series of local means is obtained. These constitute the moving mean. The number of observations in the moving mean and the size of the basic unit are entirely arbitrary.

Fairfield Smith (1938) using moving means and a single variety presented a soil fertility map, expressed in terms of yield, which showed fluctuations of up to 100% in less than 5 feet. Reports of this range of variability are common in the literature (for a comprehensive catalogue of this work see Cochran 1937). Fairfield Smith used a plot containing six plants as his unit, but he noted that there was no reason why this should not be reduced to a single plant. Although he made this comment, the use of moving means to estimate local environmental effects was not adopted by plant breeders.

The efficiency of the moving mean as a measure of micro-environmental effects in segregating populations depends on two related problems: the moving mean must be calculated from a sufficient number of individuals to minimise any bias due to genetic effects, especially that due to the chance juxtaposition of several high or low yielding genotypes that would distort the average yield of any area. On the other hand the sample should be sufficiently small to reflect accurately the local environment. If a moving mean accurately reflects the micro-environmental effects, then a more precise relative assessment of individual genotypes will be possible.

A second approach is to use a polynomial function to calculate a surface of non-random variation. The function is basically one of regression in one or more dimensions of predetermined complexity. This technique is used in many fields, for example economics, chemical engineering, fertilizer rates, animal feeding trials. The method is used to optimise the effects of combinations of several factors on a particular process. In geology it is used to predict the spatial arrangement of ore bodies from a limited number of core samples (Field 1968). This approach is very similar to that proposed here, where the surface is used to estimate micro-environmental heterogeneity.

Field (1968) also discusses the use of moving means and double fourier analyses to estimate ore body shape. Fourier analysis has not been considered here as there is no reason to expect cyclic variation, although this may occur in geological studies where folded structures are encountered.

From this discussion it is apparent that improvements in selection may be possible using one of these techniques to estimate micro-environmental variation within a selection plot. This was attempted in this project and the results will be reported in a later section.

(6) Single Plant Selection Experiments for Yield :

(A) Introduction.

Possible reasons for the failure of single plant selection have been reviewed and all the factors considered, heterozygosity, genotype - environment interaction, competition and micro-environmental effects may each confound the relationship between individual performance and crop performance. It is reasonable to assume, that unless there is some control of these factors in a selection experiment then one or more of them will lower the efficiency of selection. They may so dominate an experiment as to render single plant selection futile.

Nearly all single plant selection experiments have been conducted to determine whether the plant breeder can define conditions in which selection for yield is effective. Commonly a range of nitrogen and density treatments have been used, as these are most easily controlled by the breeder. For certain characters the environment is vital in ensuring differentiation between genotypes (for example, if selection is for resistance to disease or lodging).

There are two approaches to the question of whether an optimal selection environment exists. One can use an environment that permits the maximum expression of the characters, as advocated by Frey (1964). Alternatively Donald (1962) and Hinson and Hanson (1962) consider such an environment bears little resemblance to commercial conditions, and suggest that selection should be carried out in an environment that closely resembles field practice.

To obtain data on this point, several selection experiments have been conducted to determine which procedure, if any, is valid.

(B) Selection at a range of densities.

Weber (1957) selected within 6 soybean crosses on the basis of yield and maturity at a range of densities and found no difference between the selections. This result is interesting as half the crosses were selected in the F_3 and half in the F_6 and both gave the same result, suggesting that heterozygosity was not an important problem, but that some other factor limited the efficiency of selection. A similar result was obtained by Shebeski (1967) and McGinnis and Shebeski (1968). They concluded that the selection for yield in the F_2 was not effective, although it appeared that the elimination of the very poor lines brought some overall improvement to the yield of the population.

Two oat populations were grown by Frey (1962) at low density and selections were made visually for good, random and poor plants. These selections were tested for two generations but there was no consistent difference between the groups in one cross and no significant differences between groups in the other. The number of lines used was small (10, 8 and 7 lines for the good, random and poor selections respectively). Three densities were used by Gotoh and Osansi (1959a) in an experiment on wheat. Twenty lines selected on the basis of high yield from each density, were tested at the high density. More good lines were present amongst those selected from the low density, than from the other two treatments.

Selection at wide spacing in a sugar beet cross (Hosokawa et al. 1964) was effective for either root weight or sucrose percentage, but as these workers did not overcome the strong negative association between these two characters, it is unlikely that selection for yield of sugar per hectare was effective.

Selection for high yield was not effective in any of these reports but all the experiments had design weaknesses. For example, in no experiment was any attempt made to estimate the micro-environmental effects in the selection generation, where local fluctuations may have had a large effect on single plant performance. However McGinnis and Shebeski went to great lengths to estimate localised effects in their test generation. This effort was ineffective as similar fluctuations in the previous generation were not estimated.

All these workers introduced a genotype - environment interaction as their selections were not tested in similar environments to those used during selection. Four authors used completely different environments for selection and yield testing (Hosokawa et al. 1964, Shebeski 1967, McGinnis and Shebeski 1968 and Frey 1962). The other two (Gotoh and Osanai 1959a and Weber 1957) tested their selections from several densities at a density which was identical to only one of their selection treatments. In some cases a control population was not grown so that one cannot tell whether selection had been effective (Weber 1957, Gotoh and Osanai 1959a, and Hosokawa et al. 1964).

The only unexpected result is that of Gotoh and Osanai (1959a). They claim that more good lines were found amongst selections from the low density treatment when selections were assessed at high density. The result must be viewed cautiously as only 20 lines were selected per treatment, or there may be no real improvement. From the data presented it is not possible to decide this point.

(C) Selection at different nutrient levels.

Gotoh and Osanai (1959b) selected at three levels of applied nitrogen and tested their selections at the same three levels. They claim that lines selected at lowest level of nitrogen were more widely adapted to fertilizer variations than were those selected at highest nitrogen level. It is difficult to accept this conclusion as the average yield of both groups of selections was similar at both high nitrogen (18.8 and 19.0 grams per plant) and at the low nitrogen (13.0 and 13.1 grams per plant). They also claim differences in heritability, calculated by the regression method, between lines selected in the various environments. These results were obtained without scaling to standard units as proposed by Frey and Horner (1957) and it is therefore impossible to make meaningful comparisons between the treatments.

A similar experiment was carried out by Frey (1964), who used stress and non-stress conditions. He found that selection, in the non-stress situation, was more effective for adaptation to a range of environments but that there was no difference in the average yields of the selections from the different environments.

Frey (1964) quotes Gotoh and Osanai (1959b) as supporting his own findings. "The data in this study (Frey 1964) support the first theory, i.e. a non-stress environment differentiates the adaptation reaction of oat strains better than a stress environment. Gotoh and Osanai also showed that the correlation between yields of varieties when tested under different fertility levels was higher for strains selected under high fertility than those selected under low fertility." It is difficult to reconcile this statement with the published one of Gotoh and Osanai (1959b). "Correlation coefficients in the 'a' derived line groups (selected at low N) were the highest in each test condition .... It is remarkable that h^2 value is highest in the 'a' condition. Consequently it seems likely that selection under the latter (fertility) condition was more effective than those under the 'b' (normal N) or 'c' (twice normal N) condition."

In both these reports the selections were tested in the same conditions as they were selected, thereby removing genotype-environment interaction, but no attempt was made to estimate the micro-environmental effects in the selection generation.

In the work reported here the control used was the population mean. The yield of any section of the population could then be compared with the population mean.

(D) Animal selection experiments.

Animal breeders have also been uncertain whether to select under optimal conditions or commercial conditions. Their experiments give a much clearer indication of the optimal selection environment and therefore merit consideration. Hammond (1947) takes the view that optimal conditions are preferable, on the basis that the rate of genetic advance will be faster when small differences in performance are apparent, thereby allowing more rigourous selection.

This view was challenged by Falconer and Latyszewski (1952) and Falconer (1952). These authors bred mice in two environments, in one they had an unrestricted diet, the "ideal" environment, in the other, food was limited providing a sub-optimal environment. The mice were selected on body weight at six weeks. After several generations some mice from each environment were transferred to the alternative environment. The results showed that when mice selected under ideal conditions were reared in a sub-optimal one, their growth was less than that of mice selected in those conditions. The reverse did not hold true. On examining the body tissue of the mice it was found that those selected and tested under optimal conditions had more fat tissue than the mice selected under sub-optimal and tested under optimal conditions. The authors suggest that, although the same objective selection criterion was used in both cases in fact selection occurred for two different components of body weight. In the optimal conditions selection was for food intake, whereas in the sub-optimal it was for conversion efficiency.

Similar results have been obtained with Drosophila (Robertson 1960) and for pigs (Fowler and Ensminger 1960, 1961 and Hale and Coey 1963). These results show very clearly that animal selection should be carried out in conditions as similar as possible to those used commercially.

These results raise three questions, in what ways does animal breeding differ from plant breeding, why are the animal breeding results so clear cut and what applicability do these results have for plant breeding?

Animal breeders, except those using Drosophila, work with relatively small populations. Because of the value of animals and their slow rate of reproduction breeders are unable to test and reject a large proportion or complete populations as is the practice of a plant breeder. Two important factors however favour the animal breeders, competition between animals for food can be eliminated and other factors of the environment can be closely controlled. It is probable that the removal of these two problems enables the animal breeder to select effectively, because the genotype - environment interactions are greatly reduced. This is a different situation from that facing the plant breeder. When growing plants at commercial spacing, he does not know whether a large plant is due to its inherent efficiency, to its being a better competitor than its neighbours and obtaining more than its share of growth limiting factors, or to its being in a more favourable than average micro-environment.

Although there are considerable uncertainties in extrapolating from the research in animal breeding work to plant breeding it would appear that if plant breeders hope to achieve comparable progress in the efficiency of selection, greater control of competition and the environment is needed.

(7) The Ideotype (*) Approach to Single Plant Selection for Yield :

In the study to be reported several characters were measured in addition to yield to determine if such measurements could aid the selection of high yielding genotypes. The characters could conceivably be more simply and more precisely assessed than yield itself.

As direct selection of single plants for yield has usually failed, it has been suggested that selection might be more effective if the breeder could identify high yielding genotypes indirectly (Donald 1968 a and b). Instead of selecting for yield he could select on some other plant character(s) that may be less influenced by heterozygosity, genotype - environment interactions, competition or micro-environmental effects. In this discussion model characters are defined as those which a breeder considers associated with yield potential and which are therefore worth including in his breeding objectives. The most obvious characters of this type are lodging and disease resistance.

Attempts to evaluate the relationship of plant characters to yield can be traced to the work of Engledow and his colleagues,

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(*) "The term 'ideotype' literally 'a form denoting an idea', is here proposed for biological models. In its broadest sense, an ideotype is a biological model which is expected to perform or behave in a predictable manner within a defined environment. More specifically, a crop ideotype is a plant model which is expected to yield a greater quantity or quality of grain, oil or other useful product when developed as a cultivar." (Donald 1968a) who divided yield into its components, plants per unit area, heads per plant, seeds per head and weight per seed, (Engledow and Wadham 1923, 1924 and Engledow 1925). It was hoped from this analysis to gain information on the effect of individual yield components on seed yield and to provide selection criteria for plant breeders. Frankel (1935) concluded that the results of this type of analysis were only of practical significance in the environment in which the experiment was conducted.

Breeding for yield components has gained some favour with plant breeders (Woodworth 1931, Grafius and Wiebe 1959). Donald (1962) states that at a conference in Canberra, plant breeders from various research stations nominated each of the different yield components as being the most important in determining cereal yield. In the same article, Donald points out that in placing emphasis on yield components plant breeders have been selecting for the final expression of yield. He further suggests (1962, 1968a) that if the supply of photosynthates that goes into yield is constant, then an increase in any one component must lead to a corresponding decrease in one or more of the other components. A negative relationship between yield components has often been reported (Frankel 1935, Adams 1967, Rasmusson and Cannell 1970).

Yield increases must therefore come from two possible sources, either the distribution of photosynthates must be altered, or their supply must be increased, or both.

The importance of the final distribution of photosynthates between economic and total yield has been stressed by Beavan (1947), Nicoporovic (1954) and Donald (1962), who called the relationship the Harvest Index. Donald (1962) noted that few breeders measure this ratio, and although it is empirical, it does offer a new approach to the problem of breeding for yield. The evidence of Beavan (ibid.), who found that there was a correlation between harvest index and yield, and of Sims (1963), who found that the difference between old and present day oat cultivars was not that the total crop weight had altered but rather that the harvest index had increased, support Donald's contention.

The second approach, namely to increase the supply of photosynthates, has recently come to the fore. This has depended on three developments in plant and crop physiology that permit the effect of canopy structure on photosynthesis to be analysed.

Individual leaves of temperate cereals have a photosynthetic response curve that approaches an asymptote at about 2000 foot candles (Loomis 1948, Rabinowitch 1951).

It is also known that although individual leaves become light saturated at relatively low light intensities, a crop responds to much higher light intensities (Boysen-Jensen 1932, 1949, Heinicke and Childers 1937, Thomas and Hill 1949, and Davidson and Philip 1956). Mutual shading within the canopy reduces the light intensity on the lower leaves. As the external light intensity increases, so the available light within the canopy increases, with a concomitant rise in the total photosynthesis on the crop. This occurs even though the upper leaves are light saturated (Donald 1963).

It was only with the discovery that the light intensity within the canopy fell in a predictable fashion approximating to Beer-Lambert's law (Monsi and Saeki 1953, Kasanga and Monsi 1954, Davidson and Philip 1956), that it was possible to analyse the effects of different canopy structures on the photosynthetic efficiency of a crop.

In a simplified model, three aspects of the canopy structure affect light penetration. These are the angle of the leaves to the incident light, and the vertical and horizontal distribution of the leaves. Wilson (1960) and Blackman (1961) show that the deeper light penetrates into a canopy, the greater the photosynthetic capacity of the crop. The depth of light penetration increases if the leaves are evenly dispersed both vertically and horizontally (Wilson 1960). Blackman (1961) suggests that narrow dissected leaves would be superior to round or cordate ones, but this is of little relevance to cereals. As the leaf angle increases from horizontal to vertical, so light from an overhead source penetrates further into a canopy (Wilson 1960). Light profiles within different canopy structures showing this effect have been presented by Blackman (1961) and Donald (1961).

The above discussion has been based purely on geometric considerations and as de Wit (1965) points out the model is very over-simplified. The use of computers now permits simulation studies involving a much larger range of factors. On the basis of his recent study he has shown that the earlier conclusions concerning the relationship of leaf angle to light interception need some modification depending on the angle of inclination of the sun.

This example, which shows how conclusions may have to be modified after further investigations, raises an important question on the use of models in plant breeding. A breeder would have to decide, often with limited data, on the usefulness of a particular character to his environment. He may then invest considerable time and effort in breeding for plant type. In a few years he may find that the evidence for his choice of characters was insufficient. This is the explanation for the reasonable but pragmatic attitude of many breeders that it is more efficient to select for yield itself.

However, apart from these theoretical studies on crop geometry, data are accumulating from field studies that suggest that canopy geometry might usefully be altered. The effect of leaf angle on light penetration has been shown to be important in elucidating the different yield potentials of wild and cultivated sugar beet (Watson and Witts 1959), of Japonica and Indica types of rice (Tanaka et al. 1966, Hayashi and Ito 1962), of isogenic lines of upright and normal-leaved maize (Pendleton et al. 1968) and of six barley varieties (Gardener 1966).

These results were obtained using different genotypes so that the yield differences may be due to other genetic factors rather than the characters studied. In two papers, by using a single genotype and physically altering the leaf angle, this problem has been overcome. Working with rice Matsushima et al. (1964) used paper clips to weigh down the leaves thereby decreasing their leaf angle. They found that at high densities the carbon assimilation of the plants with the paper clips on their leaves (i.e. low leaf angle) was only 65% of those without. At wide spacing no difference was detected. Similarly Pendleton et al. (1968), with corn, tied the leaves above the cob to the stem and compared this with the control. The plants with the tied up leaves yielded 14% more.

Besides using leaf canopy morphology as an explanation for yield differences between varieties, a group at Guelph, Canada, (Tanner et al. 1966), on the basis of Gardener's (1966) work, used it to predict yield. They rated 300 varieties of wheat, barley and oats on the basis of leaf angle and leaf width. They were able to identify all but two of the top fifty high yielding lines, and these two were easily explained exceptions. These workers further noted that compared with long leaved types, these high yielding lines were poor competitors with weeds (Tanner et al. 1966).

This work has led many authors to strongly recommend the incorporation of characters that affect canopy structure into breeding programmes (Jennings 1964, Beachell and Jennings 1965, Jennings and Beachell 1965, Stoskopf et al. 1963, Pendleton et al. 1968, and Donald 1968 a and b).

Other canopy characters that have been canvassed as potentially useful are net assimilation rate and efficiency of translocation (Lupton 1966). However, until some simple method of assessing these characters is available it is not feasible to use them as selection criteria. A more easily selected character is fewer nodes, and consequently fewer leaves per stem (Stoskopf et al. 1963 and Donald 1968 a and b). This would ensure a more even vertical dispersion of leaves, so allowing deeper light penetration.

Some workers suggest that the ability to tiller is very important. Various reasons have been proposed including weed suppression (Pal et al. 1960) and the rapid and complete interception of the incoming radiation (Asana 1965). These reasons are not always valid, for instance when herbicides can be used to control weeds. Mackey (1966) developed ideotypes based on yield components for different climatic regimes. In areas where there is a favourable environment he suggests that the factors limiting yield will be operative late in the crop's life cycle, for example during seed set and grain filling. In less favourable areas the important limitations to yield develop earlier and would affect tillering. He considers that in the less favourable areas tillering is the most important yield component. But this is not always true as rapid early tillering to ensure complete light interception and an adequate tiller number may be detrimental in dry environments. For example, prolific tillering would cause greater use of water early in the growing season. This may cause more severe water stress later and reduced yields. Several authors favour reduced or non-tillering plants.

Hurd (1969) suggests that in arid environments surplus tillers waste the available water. Stoskopf et al. (1963) suggests that if a non tillering type is grown it may be possible to predetermine the leaf area index that will be present at pollination, with consequent effects on leaf area duration after anthesis. (As most of the assimilates in the ear are produced during this period (Thorne 1966) the longer the leaf area duration the higher the yields.) Donald (1968 a and b) suggests that in single tiller plants there will be no competition between the developing ear and young tillers, allowing the development of a larger ear. Assimilates are not wasted in producing non-productive tillers which would also waste nutrients and water. In a pot experiment, using a cutting technique to control tiller number he obtained a clear increase in yield per tiller for the uniculm plant over multi-tillered plants (Donald 1968b). Compared with the experiments of Matsushima et al. (1964) and Pendleton et al. (1968) who altered leaf angle mechanically, removal of tillers is a very drastic approach to the problem. Unfortunately the only alternative is the use of iso-genic lines, and with these one cannot be certain that the lines differ only for the genes influencing the character involved.

It may never be fully possible to decide which tillering pattern is the more advantageous, although it would appear from present data that profuse tillering is a disadvantage, except in areas where chemical weed control is not practised. The problem of the number of ears limiting yield, raised by MacKey, can easily be overcome by increasing the seeding rate.

Various workers have advocated breeding for ear characteristics that would improve the photosynthetic capacity of this organ, for example glabrous glumes (Jennings and Beachell 1965), awned and upright ears (Donald 1968 a and b).

Although ideotype characters are at present in vogue and will have an increasing impact on plant breeding methods, they should be accepted with caution. Firstly, as already discussed, the breeder must decide if the character in which he is interested is applicable to the crop's environment. As Williams (1963) states, "The current emphasis upon light has been both timely and valuable, but there is need to guard against excessive stress on this factor. The crop is a great deal more than an abstract system of surfaces with an increasing tendency to self shading.".

A more serious criticism has however been raised by Finlay (1968). The acceptance of his argument depends upon the point which present yield has reached in relation to the absolute potential. Finlay argues that by defining and selecting for a model type we could be severely reducing the genetic variability available for further selection.

(8) Conclusions :

(1) Single plant selection for yield appears to have failed. This confirms the belief of many authors (Allard 1960, Elliott 1958, Bell 1963, Harland 1949, Harrington 1932).

(2) There are several factors which tend to reduce or destroy the predictive value of the yield of single plants in a heterogeneous population for performance in pure culture.

(3) No experiment on single plant selection has considered the effects of all these factors as a group on selection, and consequently no experiment has been designed to minimise them all.

(4) It would be worthwhile to reconsider the utility of single plant selection if the concept of ideotypes is useful and the characters proposed in a particular model prove to be less affected by the confounding factors.

This thesis describes a project re-examining the feasibility of single plant selection.

METHODS AND MATERIALS.

(1) Outline of the Experiment :

The experiment was designed to see whether single plant selection in the F_3 generation was successful in identifying genotypes that would be high yielding in pure stands in the F_5 generation.

The F_3 of a cross between two barley varieties (Proctor and C.1.3576) was grown in four contrasting environments (Fig. 3). These were two densities, at the same level of applied nitrogen (the density experiment), and two nitrogen levels at the same density (the nitrogen experiment). The environments provided contrasting competitive conditions. High yielding plants may be good competitors only in a particular environment, rather than in all situations.

The total yield range of the F_3 plants in each situation was divided into decile groups and selections were made at random within each group. Yield testing in a later generation would indicate whether the yield of an F_3 individual was attributable to its competitive ability in the mixture or whether it was a high yielding genotype.

The seed from the selected plants was increased in the F_4 and yield testing occurred in the F_5. Plants that had been selected in one environment were yield tested both in that environment and also in the alternate environment. For example plants selected at low nitrogen in the F_3 were yield tested at low and at high nitrogen in the F_5. This is shown diagramatically for all selection treatments in Figure 4.

(The seed from F_3 plants grown and selected in 1967 was increased by out-of-season plantings during the summer of 1967-8 (January - May). This out of season multipication was not fully successful. The F_5 yield trial in 1968 was therefore unsatisfactory because of inadequate seed supplies and the methods, results and discussion of that experiment are not included in the body of the thesis, but are given in appendix 1.)

New selections were made from the original F_3 populations and these were increased in the F_4 during the normal growing season of 1968. The F_5 yield testing was carried out in the normal growing season of 1969. The time sequence of all the generations is shown in Figure 5, with the main experiment shown on the left.

Several plant characters, other than yield, were measured on the F_3 plants to determine whether any of these gave a better indication, than did yield itself, of yield potential in future generations. These characters were again measured in the F_5 generation.

Figure 3

The F_3 selection environments

The selection environments.

Nitrogen Experiment.

Low Nitrogen
(0 kg/ha N.)
8 x 8 cm

and

High Nitrogen
(130 kg/ha N.)
8 x 8 cm

Density Experiment.

Low Density
(40x 40cm)
65 kg/ha N.

and

High Density
(4 x 4 cm)
65 kg/ha N.

Figure 4

Diagramatic outline of the experiment

Diagramatic Outline of the Experiment

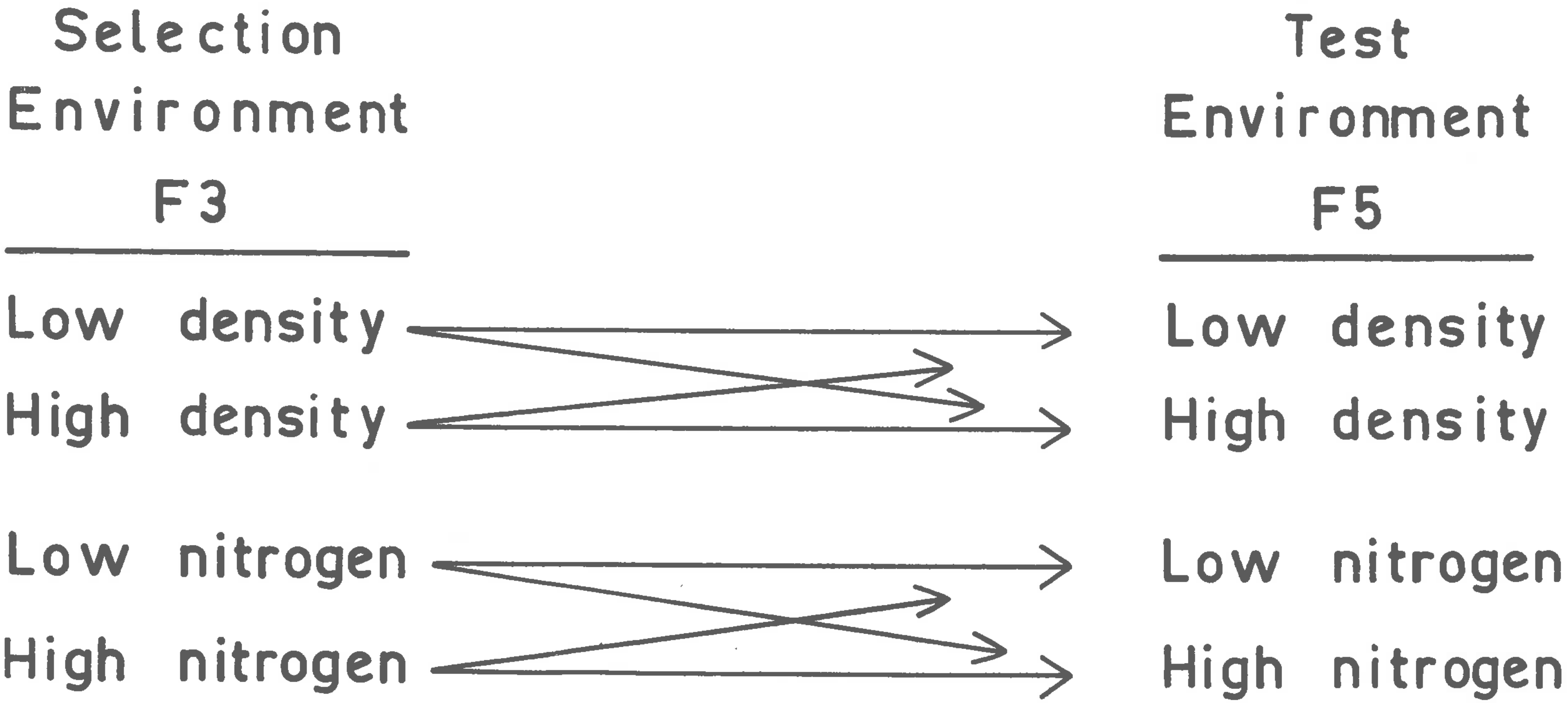
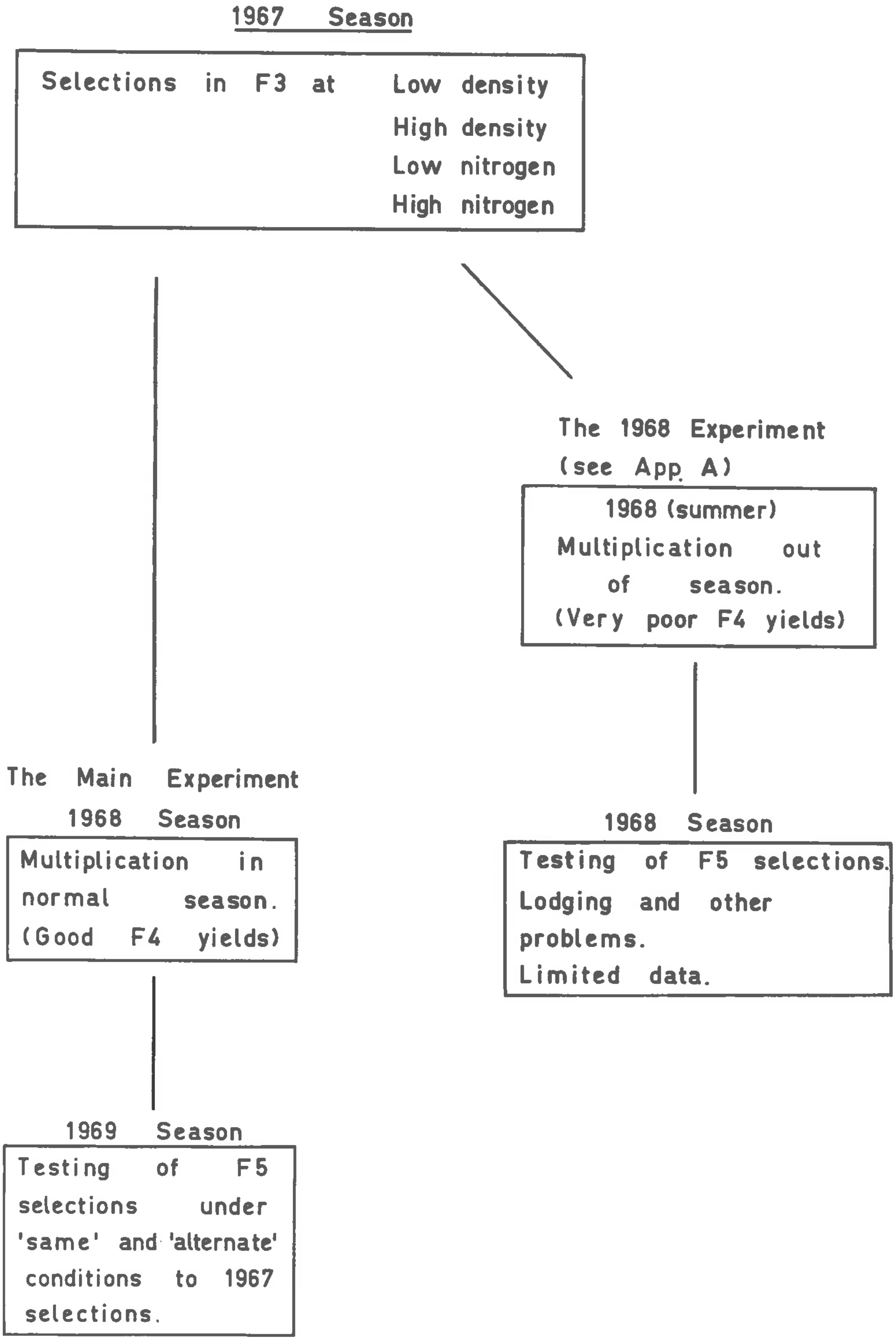


Figure 5

The sequence of the experiment

The Sequence of the Experiment



(2) Experimental Details :

(A) Site.

The experiments were carried out at the Waite Agricultural Research Institute, Adelaide, South Australia (34° 50' South, and 138° 38' East).

The soil is a red brown earth of the Urbrrae series (Litchfield 1951). Millington (1959) states that poor establishment of wheat on this soil is due to poor soil aeration following sowing. This is related to the amount of rainfall immediately after sowing, which affects the apparent soil density. The latter is also affected by the previous cropping sequence. Local experience suggests that establishment is enhanced if cultivation is kept to a minimum. Satisfactory seed beds were obtained using as little cultivation as possible.

The land use of the previous five years is given in table 2.

Table 2 :

Previous land treatment.

	Site 1967		Site 1968		Site 1969	
year	crop	fert.	crop	fert.	crop	fert.
1962	fallow	0	—	—	—	—
1963	fallow	0	wheat	super	—	—
1964	wheat	super(a)	fallow	0	lucerne	super
1965	fallow	0	wheat	super	lucerne	super
1966	wheat	super	peas(b)	super	lucerne	super
1967	experimental site		oats/ wheat(c)	super	fallow	0
1968	—	—	experimental site		oats	super
1969	—	—	—	—	experimental site	

(a) superphosphate applied at 108 kgs./ha.

(b) ploughed in in September.

(c) part of area was in oats, part in wheat, it was not a mixed crop.

The experiment always followed a cereal crop to ensure as low a level of soil nitrate as possible. Table 2 shows that, apart from phosphate, no inorganic fertilizer had been used on these sites. A basal dressing of 364 kg/ha superphosphate and 121 kg/ha potassium chloride (equivalent to 3 and 1 cwt/ac respectively) was used each year to ensure that these elements were readily available to the crop.

Nitrogen, as urea, was applied by hand to the plots at the appropriate rate immediately after emergence.

(B) Climatic data.

The climate of the experimental site is of the Mediterranean type, with cool wet winters and hot dry summers. The growing season extends through the winter and spring, from April/May till November/December, the actual length depending on the incidence and the total effective rainfall. The average rainfall for the period 1925 - 1969 was 619 mm (24.35 in) of which 517 mm (20.36 in) fell during the growing season, but the actual amount, in any one year can be very variable. The details of the rainfall and evaporation for the three years, 1967 - 1969, are given in table 3.

1967 was the driest year ever recorded at the Waite Institute, with only 326 mm (12.8 in) of rain. Rainfall exceeded the evaporation in only one month, July. To ensure that a grain yield was obtained under all treatments, both the nitrogen treatments and high density treatment were irrigated (75 mm (3 in) of water were added, 25 mm (1 in) at a time, at two week intervals during September and October). This water did not increase vegetative growth (figure 6), but ensured survival. No water was applied to the low density treatment which showed no apparent stress.

1968 was the wettest year recorded, with 821 mm of rain. The season was cold.

1969 had approximately average rainfall, 623 mm, although the growing season was a little drier than usual, due to a very dry October.

Table 3 :

Monthly rainfall and evaporation figures. (mm.)

	1967		1968		1969		Average 1925 - 1969	
Month	Rain	Evap.	Rain	Evap.	Rain	Evap.	Rain	Evap.
Jan.	16.5	201.0	40.4	238.2	10.7	233.8	22.1	217.1
Feb.	38.1	192.2	46.5	235.9	107.3	131.4	28.2	178.4
March	1.8	162.4	49.6	154.8	19.8	133.9	20.6	159.6
April	9.2	117.4	66.6	101.2	54.4	91.0	53.1	100.1
May	38.1	88.7	143.6	44.5	92.8	65.3	82.4	62.3
June	12.7	47.8	64.3	43.0	42.7	37.9	75.0	43.7
July	85.1	46.8	78.5	35.8	99.6	39.1	83.6	41.9
Aug.	57.2	58.5	112.1	44.5	55.9	76.7	72.2	56.4
Sept.	35.3	85.1	29.7	84.9	64.6	63.0	59.2	81.6
Oct.	15.0	147.4	88.5	111.8	2.3	132.4	52.6	117.2
Nov.	2.0	189.1	58.0	136.5	24.7	164.4	39.1	151.0
Dec.	14.7	209.1	42.7	194.2	47.8	168.0	30.2	188.6
TOTAL	325.7	1545.5	820.5	1425.3	622.6	1336.9	661.3	1397.9
TOTAL (ins.)	12.83	60.84	32.28	56.07	24.49	52.41	24.35	54.99

Figure 6

The F_3 low nitrogen plot in 1967

(Note the small leaf area and restricted growth.)

(C) The cross.

The barley cross Proctor x C.I.3576 was used in this study. Proctor is a north European variety of high malting quality and is late maturing in South Australia. Except in the most favourable seasons it is low yielding, sometimes failing to produce seed; using the terminology of Finlay and Wilkinson (1963) it is specifically adapted to high yielding conditions. C.I.3576 is a line from Egypt. Relative to the current commercial varieties it is always high yielding in South Australia, but has poor malting quality. It is a high yielding type having general adaptation (Finlay and Wilkinson 1963). From this cross a large number of high yielding lines have been isolated (Sparrow 1966). Its known potential made it eminently suitable for a study of single plant selection for yield.

(D) Seed source.

The cross was made in 1959 as part of the Waite Institute barley breeding programme and the F_1 was grown in pots in 1960. F_2 rows were grown in the field in 1962 and from this population, plants were selected at random. The ears from these plants were stored in tins. In 1967, after testing for germination percentage, which was 99%, the ears were threshed, the seed well mixed and a random sample taken for this study.

The F_3 was used in preference to the F_2 because the lower level of heterozygosity would lessen the possible confounding effects of hybrid vigour on selection.

(E) The F_3 generation (1967).

(a) Treatments.

Four contrasting selection environments were used. As indicated in figure 3 the F_3 was grown at two levels of applied nitrogen (0 and 130 kg N/ha) at a spacing of 8 x 8 cm, equivalent in area/plant to the commercial rate used in South Australia. The other two environments were two densities (40 x 40 and 4 x 4 cm). In this experiment the level of applied nitrogen was 65 kg N/ha. The areas of the F_3 selection plots were 14.0 m and 1.4 m square for the low and high density treatments respectively and 2.8 m square for each of the nitrogen treatments.

(b) Sowing method.

In an experiment where competition is being considered it is important that the plants be spaced as accurately as possible. The planting method must be quick and simple. A multiple dibber (c.f. Biffen and Engledow 1926) was used at the two higher densities (4 x 4 and 8 x 8 cm). The number of pegs per board depended on the number of plants per plot used in the F_5 generation (36 for the 8 x 8 cm and 64 for the 4 x 4 cm treatments). The boards were made accurately to butt against each other. This ensured quick and accurate alignment in the field. Each dibber board had a corresponding "female" board, with holes exactly matching the pegs. This prevented soil rising in lumps if the pegs did not come out cleanly. A seed was placed in each hole so made. This method gave constant interplant spacing and planting depth. To ensure even establishment the dibber holes, after planting, were filled with sand rather than soil.

At low density (40 x 40 cm) the ground was marked out and a few seeds were sown by hand at each point. At emergence the seedlings were systematically thinned to a single plant; the most northerly was always left. This ensured that no unconscious selection for either large or small seedlings occurred.

In each treatment the F_3 selection area consisted of 1225 plants (35 rows and 35 columns). The area was surrounded by 1 guard row in the low density plot (40 x 40 cm), by 6 guard rows in the nitrogen experiment (8 x 8 cm), and by 8 guard rows in the high density plot (4 x 4 cm). The seeds were sown on the 28th June.

(c) Plant growth in the F_3.

(i) Emergence and survival.

Light rain fell immediately after sowing and emergence was good. The percentage of plants that survived to harvest is shown in table 4.

Table 4 :

Percentage of F_3 plants surviving to harvest.

Density Experiment		Nitrogen Experiment	
Low D.(*)	High D.	Low N.	High N.
95%	87%	95%	92%

(*) The abbreviations D and N for density and nitrogen will be used throughout the thesis for all sub-headings in tables.

If a plant was missing, the neighbouring plants were at an advantage when compared with plants that had a complete set of neighbours. To avoid this effect, the plants surrounding 'missing plants' were not accepted as being available for selection. In table 5 (p.76) it is seen that the number of plants in the low nitrogen F_3 selection environment was less than in the other environments. This was not because of a large number of missing plants in this treatment, but because there was a well defined patch of high fertility within the plot. The affected part was excluded from the experiment, and this resulted in a reduced number of plants being available for selection.

(ii) Disease.

Disease was practically non-existent in 1967 and could not have affected selection.

(iii) Lodging.

To ensure that the lodging of plants did not affect plant performance in the high density and nitrogen treatments a string network was threaded between the plants. This precaution proved unnecessary because of the very dry season and consequent restriction of growth.

(d) Harvest.

The plants were pulled individually and taken to a laboratory for measurement and threshing. As the seed was required for the next generation only air dried seed yield and not oven dry weight was obtained. This measurement was made after the seed had been stored for a month in open packets.

(e) Characters measured.

The characters measured in the F_3 can be divided into three groups, yield (consisting of seed yield, biological yield [total dry matter yield above ground] and harvest index), yield components (ears per plant, seeds per ear and seed weight) and vegetative characters (leaf length, leaf height, and plant height).

(i) Yield.

Both the seed yield and the biological yield were measured. From these two characters it was possible to calculate the harvest index. Harvest index measures the proportion of the total dry matter that comprises the economic yield.

(ii) Yield components.

The number of fertile ears/plant and the 1000 grain weight were measured for each plant. From these and the seed yield it was possible to calculate the number of seeds/ear.

(iii) Vegetative characters.

Leaf length gives a crude measure of leaf area. Leaf area and disposition determine the light relations within the canopy, and consequently influence the photosynthesis of individual plants. Plants with long leaves will tend to shade their neighbours and to decrease the light available to them. The length of the penultimate leaf on the main stem was measured. All such leaves would be produced at a similar stage in the plants' life cycle and thus make it possible to compare different genotypes. This measurement was made in the field.

'Leaf height' was defined as the distance from the ground to the auricles of the penultimate leaf, and 'plant height' from the ground to the node at the base of the ear. Both these parameters are probably related to competitive ability and also affect the light distribution within the canopy. The measurements were made on mature plants. This only indicates final height and not necessarily the height when competition was most intense. But on average, one would expect the taller lines in a mixture to be at an advantage throughout the season.

(f) Micro-environmental variation in the F_3 (1967).

The phenotype of an individual plant will reflect both the genotype and the local environment. If the environment varies within the selection plot then it is not possible to say whether phenotypic differences are due to genotypic differences, or to variation in the local environment. Usually this problem is overcome by using replication. In single plant selection, where every genotype is different, this is not possible. However if the genotypes are planted at random, the average yield of a group of plants can be used to estimate local micro-environmental effects. By comparing the yield of the individual with this average it should be possible to account for some of the environmental variation. This has been attempted in two ways.

Firstly, a regression technique has been used to fit a three dimensional polynomial function (a response surface) to the yield values. The x and y axes are the coordinates of the individuals within the selection plot, and the z axis represents the calculated yield of the individual. The equation used is of the type

$$z = a + bx + cy + dx^2 + ey^2 + fxy + \text{----}$$

where bx and cy are the linear trends in the directions x and y, where dx^2 and ey^2 are the quadratic curvature terms; and where fxy indicates the direction of the squared terms in relation to the x and y axes, etc. This calculated yield reflects the average environmental effects at any point. The yield of an individual is compared with the calculated value for yield at that point. Positive differences signify high yielding genotypes,negative differences poor yielding genotypes. The differences may be measured either as actual or relative differences. The latter is conveniently expressed by subtracting the calculated yield from the recorded yield and dividing the result by the calculated yield.

The second approach has been to use a moving mean, (for description see p. 29) which also reflects local variation due to micro-environmental effects. The yield of individuals is compared with the moving mean at that point.

Further details of these techniques emerge in the 'Results' and the various problems associated with them will be reviewed in the Discussion.

(g) Selection method.

If the lines were ranked on the basis of uncorrected yield, it is likely that the high yielding lines would be those in the more favourable areas of the selection plot. To overcome this the lines were ranked on the basis of their relative deviation from the response surface. The ranked plants were stratified into groups, each containing 10% of the total number of genotypes. From within each of these groups ten lines were taken at random. This gave a total of 100 selections from each of the F_3 environments.

(F) The F_4 Generation (1968).

Each selected line was grown in a 1.5 m multiplication row. The number of seeds per row depended on the amount of seed available. No measurements were made on this material and no problems were encountered. The lines were harvested using a small plot harvester and there was sufficient seed from this generation to allow yield testing as crop communities in the F_5.

(G) The F_5 generation (1969).

(a) Treatments.

The treatments were the same as those used in the F_3, but lines selected in one environment, were tested in that environment and in the alternate environment (see figure 4).

(b) Sowing method and plot size.

The multiple dibbers used in the F_3 were again used. This method was accurate and relatively quick. There were 400 lines, 100 from each of 4 environments, grown in both the same and the alternate environment to the F_3 selection environment. With 3 replicates of each this made 2400 plots. In addition 624 parental plots were grown of which 576 were C.I.3576. This variety was used as a systematic control through the experimental design.

With so large a number of hand-planted plots it was not possible to have many plants within each test plot. Each plot contained 16 plants. At low density (40 x 40 cm) there were no border plants between plots. In the nitrogen experiment (8 x 8 cm) there was one border row of the same genotype for each plot, making two between the plots. This increased the numbers of plants of the same genotype that were sown from 16 to 36, of which 20 were border plants. At high density (4 x 4 cm) two border rows per plot were used, making a total of 64 plants, of which 48 were border plants.

With this arrangement a total of 162,724 plants were accurately planted. This included peripheral border rows around the outside of the blocks. The implications of the use of small plots in the F_5 yield trial is considered in the discussion.

The F_5 experiment was sown on 17th to 20th June.

(c) Plant growth in the F_5.

(i) Emergence and survival.

Emergence was good and stand survival was 92.5% over all treatments except low density, where multiple planting and thinning gave a stand of over 99%. Because of the high survival rate, and because yield was measured on a plot and not a plant basis, no correction was made for missing plants.

(ii) Disease.

Mildew was present in the crop, but was controlled with 'Benlate', a systemic fungicide. This was applied twice, in early August and in early September.

(iii) Lodging.

Following the experience of the previous year (see appendix 1), a wire network was used to prevent lodging. The size of the supporting wire grid was the same size as a plot. Two wire grids were used per block, one above the other at 45 and 70 cm from the ground. The uppermost had an additional string grid stretching from alternate corners. The supporting grids were placed above the crop, which grew up through the supports. As each plot had its own support and was well protected from its neighbouring plots (see figure 7), it was possible for an individual plot to lodge without falling on neighbouring plots and lodging them also (see figure 8).

(d) Harvest.

The whole crop, except the low density treatment, was pulled by hand and taken back to the laboratory for measurement. The low density treatment was threshed in the field.

(e) Characters measured.

The same characters were measured as had been measured in the F_3 (see pp. 64-65), with the addition of the date of anthesis. This was scored as the date on which 50% of the tillers in a plot had emerged awns. This method is used in South Australia as it is possible in a dry season for a plant to set seed without the ear emerging from the boot.

(f) The F_5 field arrangement.

In each F_5 test environment there were 200 selected lines, 100 from the same F_3 environment and 100 from the alternate F_3 selection environment. There were also 52 parental plots, 48 of C.I.3576 and 4 of Proctor. Because of the practical problems involved in measuring leaf length in a growing crop, a block could not be more than 6 test plots wide. On each side of the block there was a border plot. This meant that a block would be 42 plots long. This long narrow shape would increase the chances of soil variation increasing the error term. It was therefore decided to cut the blocks into halves and place them side by side, with a small path (60 cm wide) between them.

Figure 7

The wire supports in an F_5 high nitrogen plot. Only the cross wires are clearly visible.

Figure 8

Single plot lodging within the wire supports.

3.

The arrangement of the field trial is shown diagramatically in figure 9. The design was a split randomised block with three replications. Each split block contained 50 lines from each of the two selection environments (the same and the alternate environments of figure 9, the details are however, only shown for the same environment). The 50 lines were composed of 5 lines from each yield decile. These 5 lines were assigned to a split block at random. The plots of the control variety were arranged systematically, so that there was at least 1 control plot in every row and 4 in every column. The lines to be tested were assigned to the remaining plots at random. There were no significant differences between half blocks and the experiment was treated as a randomised block.

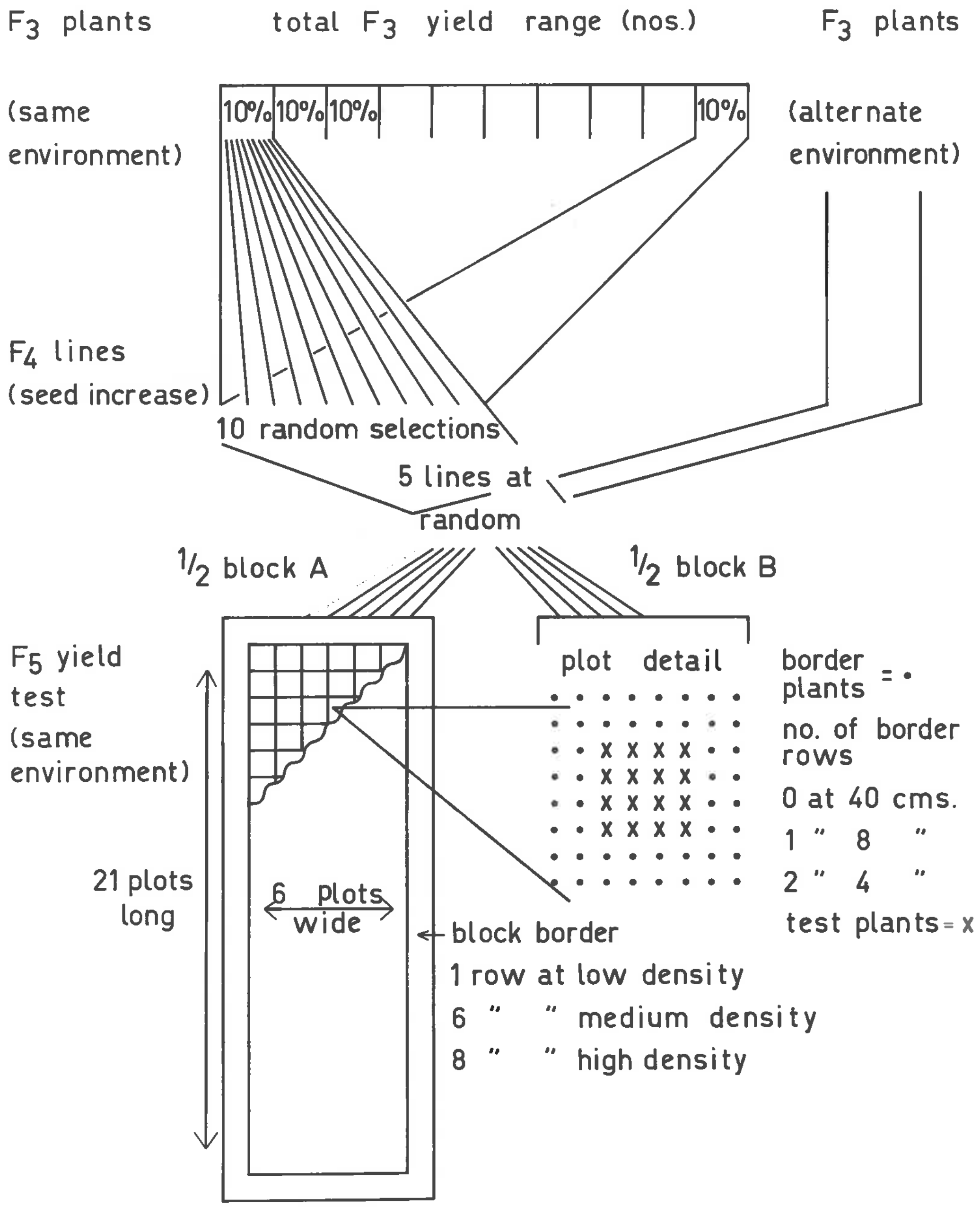
(g) Basic data.

The complete data obtained from the selected F_3 plants, and the corresponding data (mean of three replicates) from the F_5 progeny grown in both the same and alternate environments have been lodged in the library of the Waite Agricultural Research Institute. A small sample of the data, together with an explanation are given in appendix 2.

Figure 9

Diagramatic field plan of the F_5 yield trial.

Diagramatic field plan of the F_5 yield trial



RESULTS.

(1) Introduction :

It is emphasized that the F_3 data refer to single plants, whereas the F_5 data refer to mean values of three plots, i.e. to crop community values.

(2) Results :

(A) The mean values of the characters measured in the F_3 and in the F_5 for all environments.

The results for the F_3 are given in table 5 and for the F_5 in table 6.

There were no significant differences between the yields of lines selected in different environments but tested in the same environment. For example the average yield of lines selected (F_3) at low density and tested (F_5) at low density did not differ significantly from lines selected (F_3) at high density, but tested (F_5) at low density. This result was not surprising, however certain points do stand out clearly from these results (tables 5 and 6).

(1) The average yield per plant at low density was much greater than the average yield per plant of the other treatment. This was mainly due to an increase in the ears/plant, and to a lesser extent to increased seeds/ear and 1000 grain weight.

(2) In the nitrogen experiment yield was greater at high nitrogen than at low nitrogen in the F_3, but was depressed at high

nitrogen in the F_5. In the F_3 the yield increase at high nitrogen was associated with increased ears/plant. In the F_5 plots the high nitrogen treatment had more ears per plot, but fewer seeds/ear and a considerably lower 1000 grain weight. These latter two were sufficient to lower the average yield of the high nitrogen test plots to less than that of the low nitrogen plots.

(3) Leaf length was decreased in both the high density and low nitrogen treatments relative to the alternative treatments.

(4) Leaf and plant height were, on average, less at low density and low nitrogen levels.

(5) Biological yield showed a similar response to that of grain yield, but at high nitrogen in the F_5 the biological yield was slightly greater than that of the low nitrogen treatments, whereas grain yield was considerably less.

(6) Harvest index was reduced at both the high density and high nitrogen levels.

The above précis of the effects of treatments shows that there were large differences between treatments in both the F_3 selection and the F_5 test environments.

Table 5 :

The mean values of characters measured in the F_3.

DENSITY EXPERIMENT :

	Low Density (1161 observations)(*)	High Density (1060 observations)
Yield (gm/plant)	32.42	0.79
Ears/plant	31.87	1.41
Seeds/ear	24.04	14.59
1000 grain weight (gm)	42.53	38.74
Leaf length (cm)	21.22	16.18
Leaf height (cm)	39.28	65.13
Plant height (cm)	74.16	83.97
Biological yield (gm)	81.01	2.08
Harvest index (%)	39.93	37.83

NITROGEN EXPERIMENT :

	Low Nitrogen (741 observations)	High Nitrogen (1134 observations)
Yield (gm/plant)	1.65	2.93
Ears/plant	1.99	3.60
Seeds/ear	17.40	18.64
1000 grain weight (gm)	46.83	44.82
Leaf length (cm)	11.41	16.75
Leaf height (cm)	41.00	67.90
Plant height (cm)	66.12	89.51
Biological yield (gm)	3.76	7.76
Harvest index (%)	44.23	38.53

(*) The plant numbers available for selection varied with each treatment (c.f. p.63).

Table 6 :

The mean values of characters measured in the F_5.

DENSITY EXPERIMENT :

Selection environment (F_3)	Low Density		High Density	
Test environment (F_5)	Low D.	High D.	Low D.	High D.
Yield (gm/plot)	483.00(*)	11.91	460.49	11.37
Ears/plot	490.42	20.61	473.21	17.95
Seeds/ear	22.73	15.02	22.85	15.76
1000 grain weight (gm)	45.29	38.34	44.78	38.38
Leaf length (cm)	21.44	20.32	22.07	20.88
Leaf height (cm)	45.46	79.93	45.65	77.34
Plant height (cm)	79.01	104.63	79.53	105.23
Biological yield (gm)	1223.07	34.16	1201.95	32.85
Harvest index (%)	39.40	34.40	38.10	33.80
Maturity (‡)	5.82	4.38	5.83	4.44

NITROGEN EXPERIMENT :

Selection environment (F_3)	Low Nitrogen		High Nitrogen	
Test environment (F_5)	Low N.	High N.	Low N.	High N.
Yield (gm/plot)	43.44	35.07	44.10	36.03
Ears/plot	51.43	54.27	52.13	56.00
Seeds/ear	18.89	17.29	19.13	17.17
1000 grain weight (gm)	44.65	37.10	44.65	36.87
Leaf length (cm)	19.21	23.91	19.40	23.49
Leaf height (cm)	62.54	86.10	62.29	86.20
Plant height (cm)	98.23	114.49	98.58	113.98
Biological yield (gm)	118.70	121.47	119.10	123.20
Harvest index (%)	36.60	28.20	37.00	28.50
Maturity	5.48	5.31	5.61	5.49

(*) There were no significant differences between lines selected in different environments, but tested in the same environment.

(‡) Units were 1/2 weeks after an arbitrary date.

(B) Variability in the F_3 and in the F_5.

(a) Variability in the F_3 (1967).

Before proceeding to a presentation of the results of selection some consideration of the variability within the experiment is appropriate.

(i) Response surfaces.

As already discussed (p.29), any environmental variation within an F_3 selection plot may lead to a false appraisal of an individual's genetic worth. Two approaches to estimate and eliminate systematic environmental trends were used. First a response surface was generated. The yields were then measured from the response surface. These values may be expressed as either absolute, or as relative deviations from the response surface. Although the surface varies continuously over the plot, it is most easily visualised as a map with contours that depict the topography of the surface. Examples of these maps are shown in figures 10, 11, 12, 13 and 14.

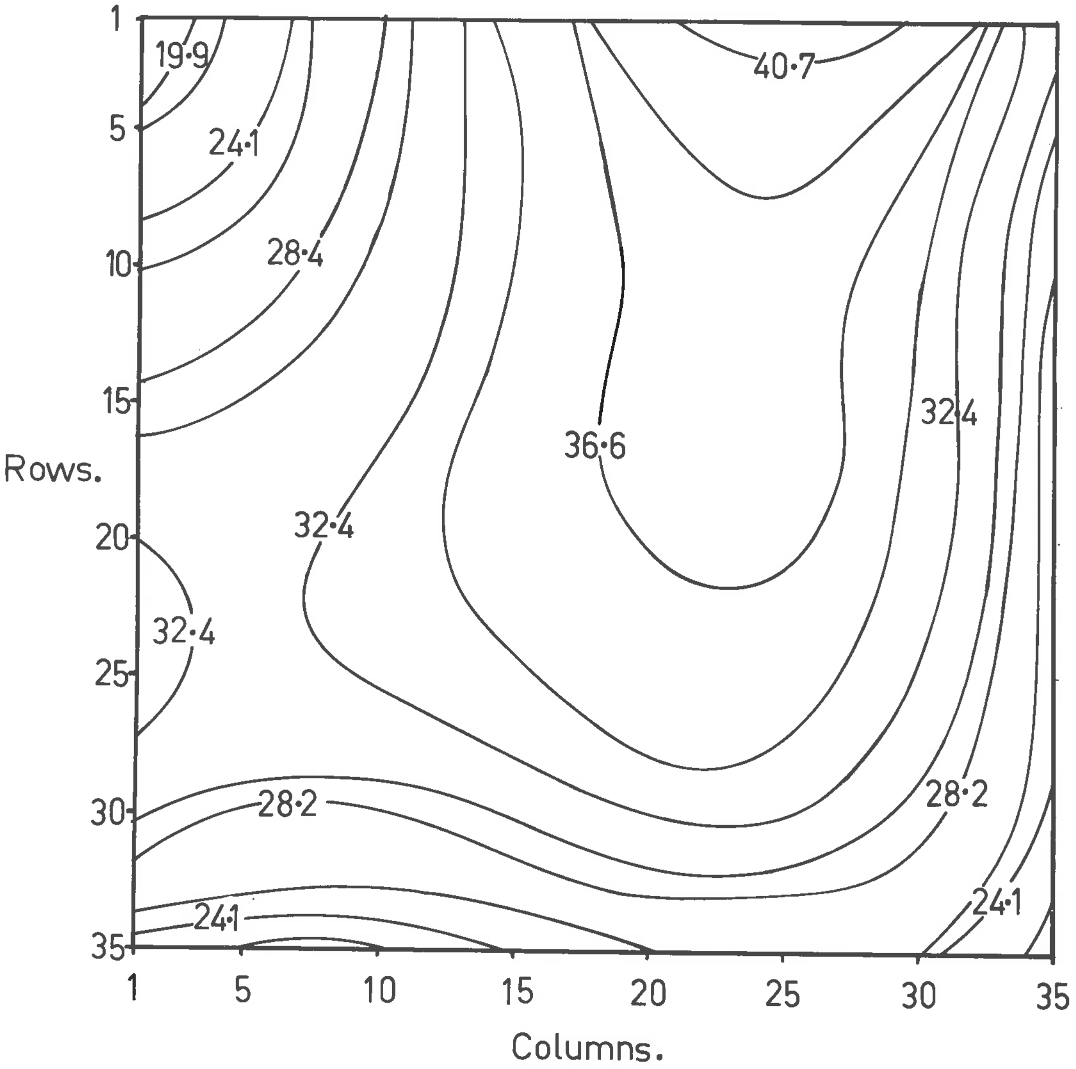
In order to compare these surfaces it was necessary to standardise the contour intervals so that, although the mean yields of the four treatments were very different, the contours would indicate, on each selection plot, the degree of non-random or systematic variation in comparable terms. This non-random variability was almost certainly associated with fertility trends within the selection plots. Two contour intervals were tried. First contours 1/5 of a standard deviation apart were used (figures 10, 11, 12 and 13). This interval has certain problems associated with it (see discussion) and therefore intervals of 10% of the mean yield were also used. Because the coefficient of variation for yield was approximately 50% for all treatments except the low density treatment, these two contour intervals were very similar (see table 7). In the low density treatment a contour interval of 1/5 of a standard deviation represented a much smaller yield difference than did a contour interval of 10% of the mean yield. Only in the latter treatment were the contour maps sufficiently different for both to be included (compare figure 10 with figure 14).

In the actual and relative deviations of yield from the calculated response surfaces some of the systematic environmental variation has been removed. The deviations were ranked and the genetic potential was considered to be related to the size of the deviation. A third ranking was also generated by obtaining the mean of the actual and relative rankings.

Figure 10

Yield response surface, low density F_3 selection environment, contours 1/5 St. Dev. apart (2.08 gm).

Yield response surface 40 x 40 cms. 65kg./ha. N.



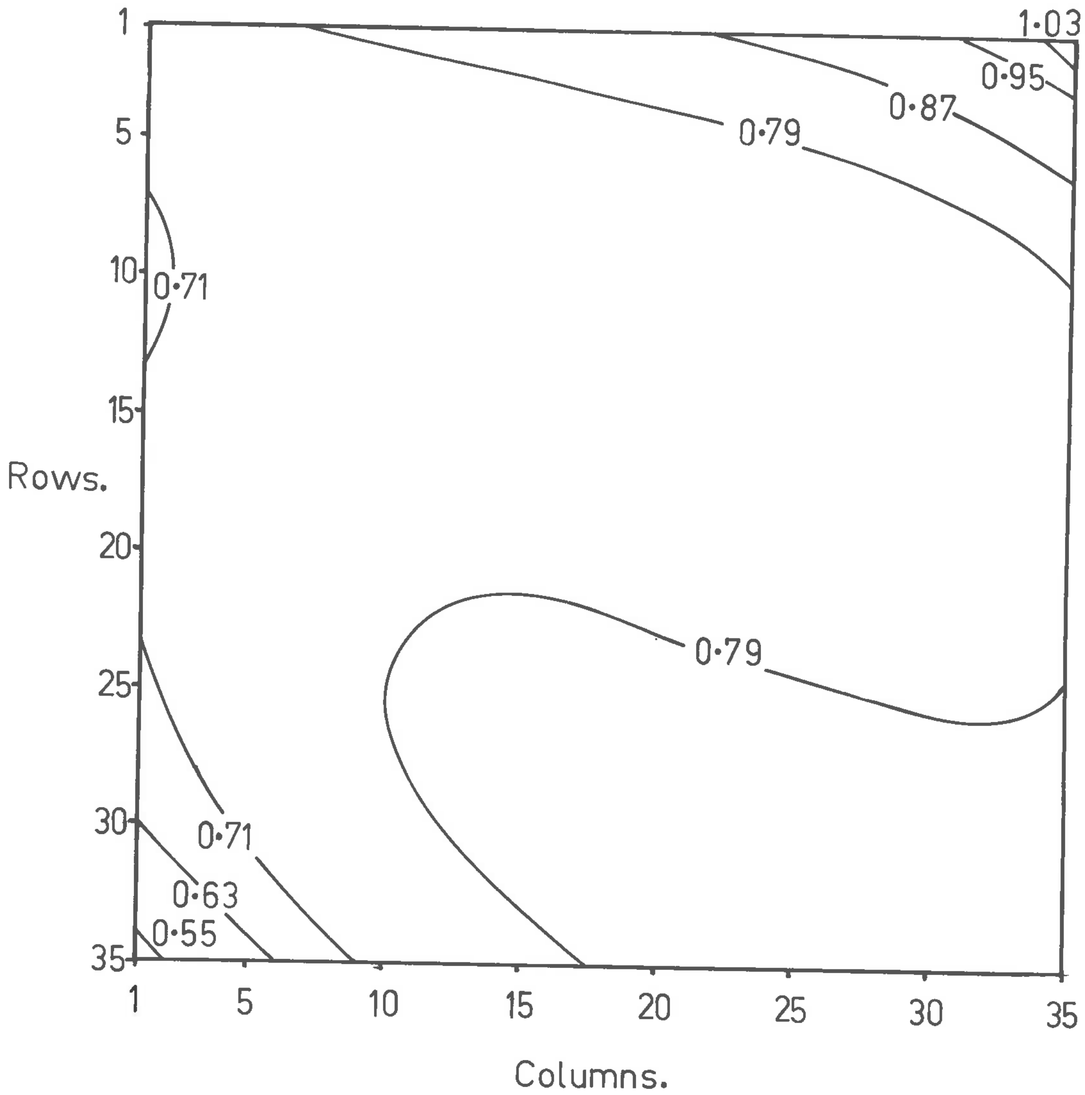
Mean yield = 32·4 grams.

Contour interval = 1/5 standard deviation (2·08 gm.)

Figure 11

Yield response surface. High density F_3 selection environment, contours 1/5 of a standard deviation apart (0.08 gm).

Yield response surface. 4 x 4 cms. 65 kg. / ha. N.



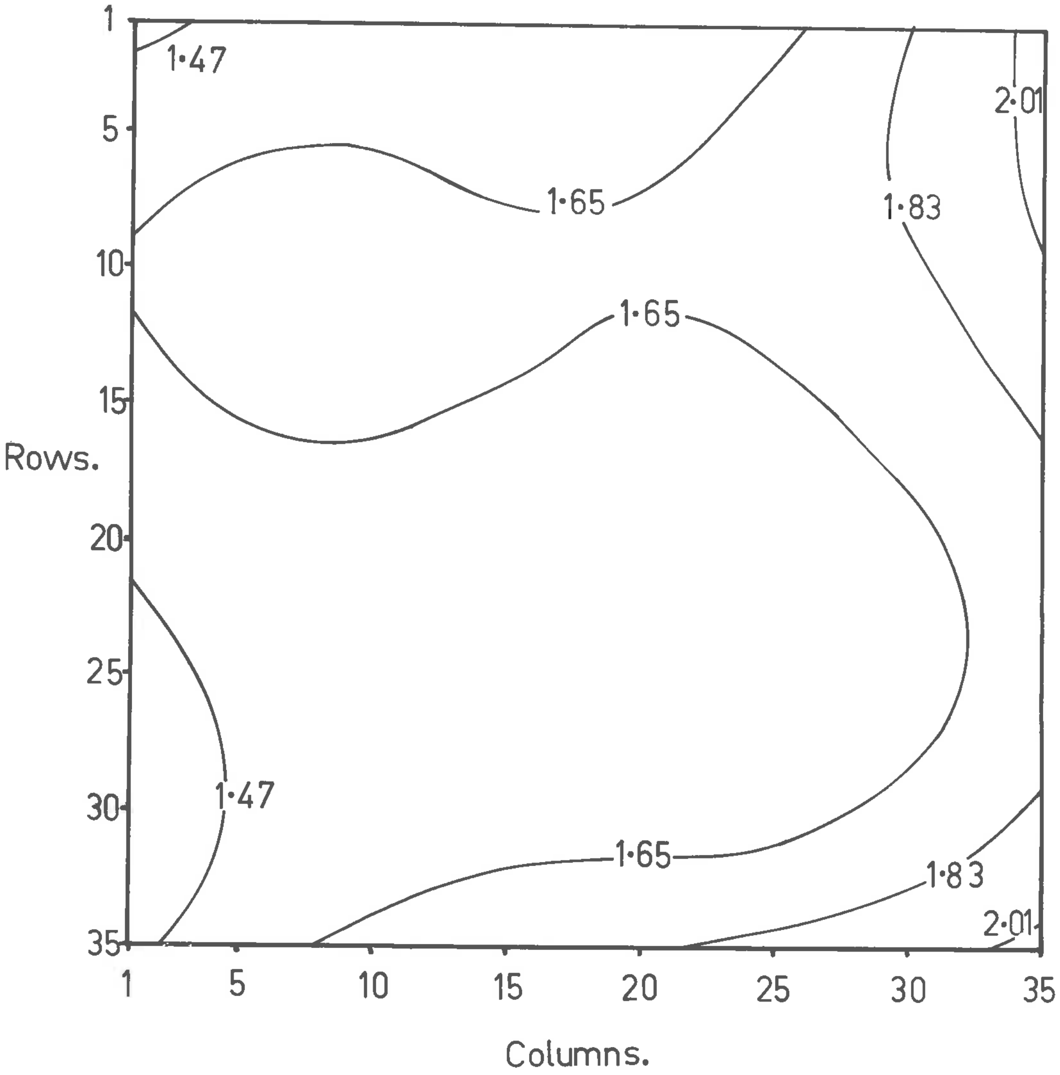
Mean yield = 0·79 grams.

Contour interval = 1/5 standard deviation. (0·08 gm.)

Figure 12

Yield response surface. Low nitrogen F_3 selection environment, contours 1/5 of a standard deviation apart (0.18 gm).

Yield response surface. 8 x 8 cms. 0 kg./ ha. N.



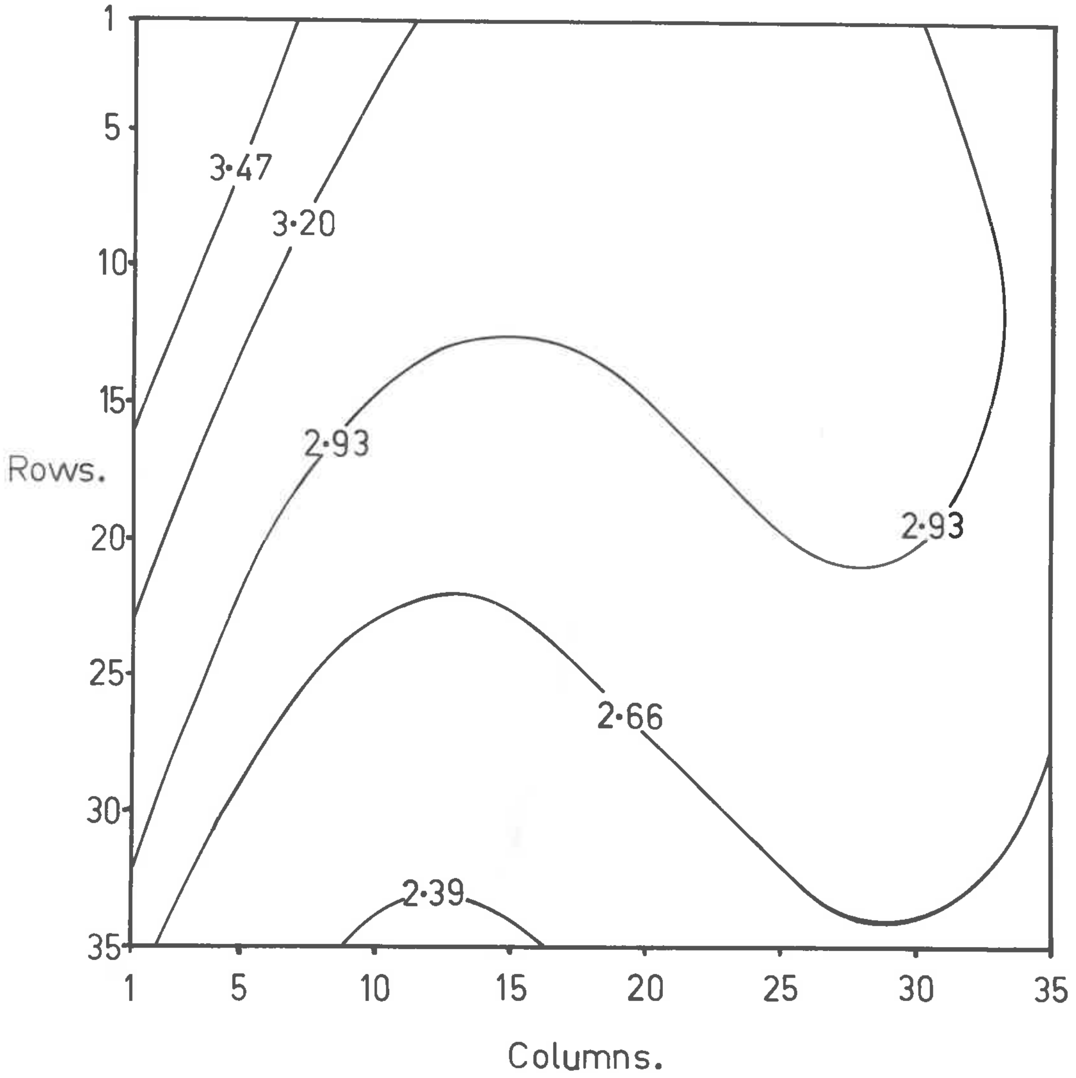
Mean yield = 1·65 grams.

Contour interval = 1/5 standard deviation. (0·18 gm.)

Figure 13

Yield response surface. High nitrogen F_3 selection environment, contours 1/5 of a standard deviation apart (0.27 gm).

Yield response surface. 8 x 8 cms. 130 kg./ha. N.



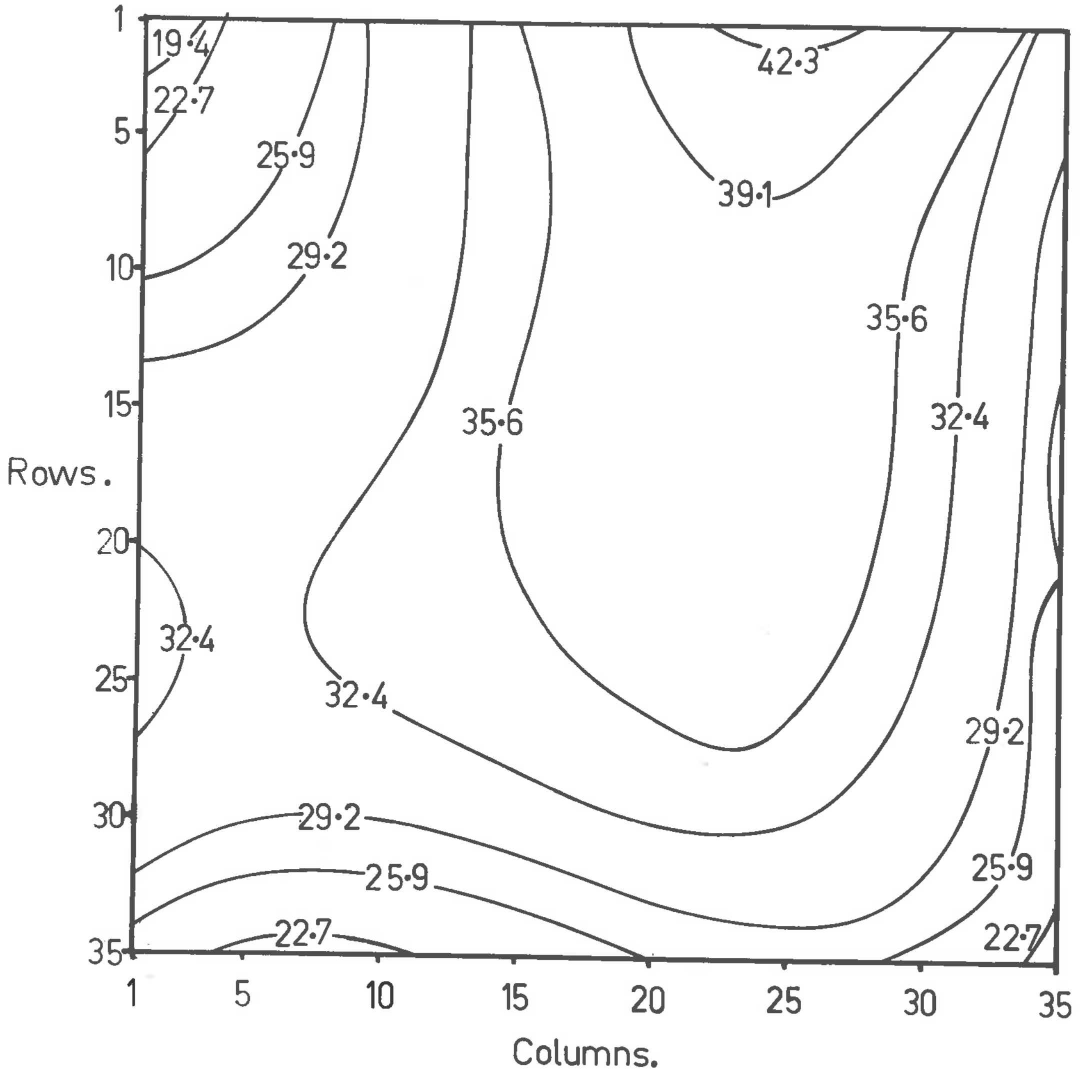
Mean yield = 2·93 grams.

Contour interval = 1/5 standard deviation. (0·27 gm.)

Figure 14

Yield response surface. Low density F_3 selection environment, contours 10% of the mean yield apart (3.24 gm).

Yield response surface. 40 x 40 cms. 65 kg./ha. N.



Mean yield = 32·4 grams.

Contour interval = 10% of mean yield (3·24 gm.)

Table 7 :

Mean yield, standard deviation, coefficient of variation, and contour intervals of the F_3 selection plots (see figures 10, 11, 12, 13, 14).

DENSITY EXPERIMENT :

	Low Density	High Density
Mean yield	32.4	0.79
S.D.	10.4	0.40
C.V.(*)	32.1	50.63
1/5 S.D.	2.1	0.08
10% of the mean yield	3.2	0.08

NITROGEN EXPERIMENT :

	Low Nitrogen	High Nitrogen
Mean yield	1.65	2.93
S.D.	0.90	1.35
C.V.	54.54	46.08
1/5 S.D.	0.18	0.27
10% of the mean yield	0.17	0.29

(*) The C.V. here included some genetic variance as well as random error, and this will be considered further in the discussion.

(ii) Moving means.

There are certain major limitations to response surfaces (see discussion) and in an attempt to overcome these moving means were also used to estimate trends. Moving means of 9, 25 and 49 plants were used (i.e. the test plant and 1, 2 or 3 surrounding rows of neighbours; these have been called moving means of side 3 (3 x 3 = 9), side 5 (5 x 5 = 25), and side 7 (7 x 7 = 49). The ideal size of the moving mean is one which covers the minimum area, but contains a sufficient number of individuals to ensure that the sample genetic mean approaches the population genetic mean. The three sizes of moving mean were used in an attempt to find an empirical solution to this problem. The deviations from the moving mean can again be measured in actual or relative units, and this gave 6 more estimates of F_3 genetic potential.

Using these various methods 10 estimates of yield were obtained for each F_3 selection environment. These were:

(1) Yield itself.
(2) Response surfaces (a) actual deviation
    (b) relative deviation
    (c) mean of actual and relative deviation.
(3) Moving means (a) actual deviations (i) side 3
        (ii) side 5
        (iii) side 7

(b) relative deviations (i) side 3
(ii) side 5
(iii) side 7.

As can be seen from figures 10, 11, 12, 13 and 14 the response surfaces showed considerable variation in the calculated yield over the plots. It is not useful to attempt similar figures for the moving means because local variation was such that extremely close and involved contours would be needed. However, the range in yields of the moving means increased as the number of plants contributing to the mean was decreased. The range of yields was usually greater than that obtained for response surfaces. This is illustrated in figure 18. Consideration of this figure, and of the differences and relative merits of response surfaces and moving means will be considered in the discussion.

The results from the response surfaces, moving means and coefficients of variation show that there was a large amount of variation in the F_3 and that a proportion of this was due to non-random variation. It may be expected that the partial estimation and removal of this non-random micro-environmental variation would improve the chances of single plant selection for yield being successful.

(b) Variability in the F_5 (1969).

The possibility of successful selection is increased if there are large consistent differences between the selected lines. The analyses of variance of the F_5 yields are given in tables 8 and 9.

It is seen that in the density experiment the lines differed significantly in all cases and in three out of four cases in the nitrogen experiment. There was a significant replicate effect for lines selected (F_3) and tested (F_5) at low density. This was due to the low values obtained in replicate 3 (see table 10).

Three points in the analysis of variance show that the chances of successful single plant selection for yield were restricted in particular sections of this study. The first was that there was a significant replicate effect throughout the nitrogen experiment although the differences between replicates were small (table 11). This was because there was a precise estimate of the replicate means (100 observations/replicate) and the very precise estimate of the error term (198 degrees of freedom). This allowed the detection of highly significant differences between replicates, even though the differences were not large. There was also a marked replicate by lines interaction, as indicated by the high coefficient of variation (tables 8 and 9). The low nitrogen treatment in the F_5 tended to suppress genetic differences in yield potential between lines. This suppression was total in the case of lines selected (F_3) and tested (F_5) at low nitrogen, and was considerable for lines selected (F_3) at high nitrogen and tested (F_5) at low nitrogen (lines only just significant at 5%, see table 9). For completeness the low nitrogen test (F_5) results have been included in the further analysis of the data, but this aspect must be borne in mind in the interpretation of the results.

Table 8 :

The analysis of variance of the F_5 yield data and the coefficients of variation in the density experiment.

Selection environment (F_3) Low Density

Test environment (F_5)		Low D.		High D.	
	D.F.	M.S.	f ratio	M.S.	f ratio
Reps.	2	58412.0	5.19 ** (a)	31.7	2.69 N.S.
Lines	99	16369.0	1.46 **	19.5	1.65 ***
Error	198	11248.0		11.8	
C.V.		22.0%		28.8%	

Selection environment (F_3) High Density

Test environment (F_5)		Low D.		High D.	
	D.F.	M.S.	f ratio	M.S.	f ratio
Reps.	2	23977.2	2.57 N.S.	25.7	1.88 N.S.
Lines	99	23661.4	2.53 ***	17.4	1.27 *
Error	198	9335.8		13.7	
C.V.		21.0%		32.5%	

(a) N.S. not significant
* significant at 5%
** " " 1%
*** " " 0.1%

This notation for statistical significance has been used throughout this thesis.

Table 9 :

The analysis of variance of the F_5 yield data and the coefficients of variation in the nitrogen experiment.

Selection environment (F_3) Low Nitrogen

Test environment (F_5)		Low N.		High N.	
	D.F.	M.S.	f ratio	M.S.	f ratio
Reps.	2	1037.8	10.26 ***	394.6	3.79 *
Lines	99	113.9	1.08 N.S.	358.2	3.44 ***
Error	198	104.7		104.1	
C.V.		23.6%		29.1%	

Selection environment (F_3) High Nitrogen

Test environment (F_5)		Low N.		High N.	
	D.F.	M.S.	f ratio	M.S.	f ratio
Reps.	2	939.8	8.53 ***	777.9	6.35 **
Lines	99	137.0	1.24 *(b)	491.2	4.01 ***
Error	198	110.1		122.5	
C.V.		23.7%		30.1%	

(b) This significance value interpolated from the tables of Fisher and Yates (1966).

Table 10 :

The yield of the three replicates selected (F_3) at low density and tested (F_5) at low density (gm/plot).

Selection environment (F_3) Low Density

Test environment (F_5) Low D.

Rep.1	Rep.2	Rep.3
499.9	493.8	455.3

L.S.D. at 5% = 29.7 gm.

The mean yield of lines selected (F_3) at the high density and tested (F_5) at low density which were not significantly different (see table 8) are given as a comparison.

Selection environment (F_3) High Density

Test environment (F_5) Low D.

Rep.1	Rep.2	Rep.3
478.4	451.1	451.6

L.S.D. at 5% = 27.1 gm. (*)

(*) N.B. In situations where the analysis of variance shows no significant differences, the use of L.S.Ds is not valid.

Table 11 :

The yield of the F_5 replicates tested at low nitrogen (gm/plot).

Selection environment (F_3) Low Nitrogen

Test environment (F_5) Low N.

Rep.1	Rep.2	Rep.3.
43.6	46.6	40.1

L.S.D. at 5% = 2.86 gm.

Selection environment (F_3) High Nitrogen

Test environment (F_5) Low N.

Rep.1	Rep.2	Rep.3.
43.2	47.5	41.6

L.S.D. at 5% = 3. 10 gm.

(C) The correlation of yield and the other characters measured in the F_3 with yield in the F_5.

(a) The correlation of F_3 yield with F_5 yield.

For each F_3 selection environment it was possible to correlate F_3 single plant yield with the corresponding F_5 plot yield in either the same or the alternate environment. None of these eight possible correlations was significant (table 12). However besides yield itself, other estimates of yield, nine in all, based on the response surfaces and the moving means were available for each F_3 selection environment. These estimates of F_3 single plant yield were also correlated with F_5 plot yield. None was significant (table 12). The lack of any correlation amongst the 80 correlations presented in table 12 is striking, but not completely unexpected as it must be remembered that the correlations shown in any one column are not independent and are related to the appropriate actual yield correlation.

To check whether the results obtained in the nitrogen experiment were due to a replicate by lines interaction, the F_3 yield rankings were correlated with each replicate separately. Again none of these comparisons was significant.

It was not possible within this experiment to determine directly whether there was a significant genotype by years interaction, but some indication of a genotype by treatment interaction was present in 1969. This was examined by correlating the yield of the different genotypes when grown in the same and the alternate environments in the F_5 (see table 13).

Table 12 :

(a) The correlations between the F_3 yield assessments and F_5 plot yields for the density experiment. (The actual values of the correlations are given in appendix 3.)

DENSITY EXPERIMENT.

Selection environment (F_3)	Low Density		High Density	
Test environment (F_5)	Low D.	High D.	Low D.	High D.
1 Actual yield	N.S.	N.S.	N.S.	N.S.
Yield deviations from the response surfaces.				
2 Actual deviations	N.S.	N.S.	N.S.	N.S.
3 Relative deviations	N.S.	N.S.	N.S.	N.S.
4 Mean of actual and relative deviations	N.S.	N.S.	N.S.	N.S.
Yield deviations from the moving means.				
5 Actual deviations, side 3	N.S.	N.S.	N.S.	N.S.
6 " " " 5	N.S.	N.S.	N.S.	N.S.
7 " " " 7	N.S.	N.S.	N.S.	N.S.
8 Relative deviations, side 3	N.S.	N.S.	N.S.	N.S.
9 " " " 5	N.S.	N.S.	N.S.	N.S.
10 " " " 7	N.S.	N.S.	N.S.	N.S.

Table 12 (cont.)

(b) The correlations between the F_3 yield assessments and the F_5 plot yields for the nitrogen experiment. (The actual values of the correlations are given in appendix 3.)

NITROGEN EXPERIMENT.

Selection environment (F_3)	Low Nitrogen		High Nitrogen	
Test environment (F_5)	Low N.	High N.	Low N.	High N.
1 Actual yield	N.S.	N.S.	N.S.	N.S.
Yield deviations from the response surfaces.				
2 Actual deviations	N.S.	N.S.	N.S.	N.S.
3 Relative deviations	N.S.	N.S.	N.S.	N.S.
4 Mean of actual and relative deviations	N.S.	N.S.	N.S.	N.S.
Yield deviations from the moving means.				
5 Actual deviations, side 3	N.S.	N.S.	N.S.	N.S.
6 " " " 5	N.S.	N.S.	N.S.	N.S.
7 " " " 7	N.S.	N.S.	N.S.	N.S.
8 Relative deviations, side 3	N.S.	N.S.	N.S.	N.S.
9 " " " 5	N.S.	N.S.	N.S.	N.S.
10 " " " 7	N.S.	N.S.	N.S.	N.S.

Table 13 :

The correlation between the F_5 performance in the same and alternate environments of lines derived from a single environment in the F_3.

DENSITY EXPERIMENT :

Selection environment (F_3)	Low Density	High Density
The two F_5 environments	Low D./High D.	Low D./High D.
Correlation coefficients of yields in the F_5 environments.	0.374 ***	N.S.

NITROGEN EXPERIMENT :

Selection environment (F_3)	Low Nitrogen	High Nitrogen
The two F_5 environments	Low N./High N.	Low N./High N.
Correlation coefficients of yields in the F_5 environments.	N.S.	0.343 ***

Two points emerge:

(1) There was a marked genotype by treatment interaction, which in the case of lines selected (F_3) at high density or low nitrogen destroyed any relationship between the relative performance of individual genotypes in the two F_5 environments.

(2) The fact that there were highly significant correlations between the two F_5 test conditions for genotypes selected (F_3) at low density and high nitrogen, but that no similar correlation was obtained for genotypes selected (F_3) at high density or low nitrogen, was not expected. There is no simple explanation for this result.

(b) The correlation of F_3 characters other than yield with F_5 yield.

In the F_3, characters other than yield were also measured. These were the yield components and certain vegetative characters which it was hoped would reflect the photosynthetic, physiological or competitive efficiency of a genotype.

The characters measured on single plants in the F_3 were correlated with F_5 yield. The results are shown in table 14. The following points should be noted for the density experiment.

(1) There were few significant correlations, and these accounted for only a very limited proportion of the total variation.

(2) Some of these results were not consistent; for example genotypes selected (F_3) at high density and tested (F_5) at low density had a negative correlation between leaf length and yield, whereas

those both selected (F_3) and tested (F_5) at low density had a positive correlation.

(3) Within this number of correlations (32), between one or two correlations would be expected to be significant at 5% by chance.

The results in the nitrogen experiment showed the following features:

(1) There were several highly significant correlations and the pattern tended to be consistent.

(2) There was a negative correlation between the height characters (F_3) and yield (F_5) at high nitrogen. This was independent of whether the lines were selected at high or low levels of nitrogen. This meant that short plants in the F_3 were higher yielding in the F_5 than the population as a whole, when grown at high levels of nitrogen. This is illustrated in figures 15 and 16. Both these figures show that if selection was for the shorter half of the F_3 population, the proportion of high yielding lines in the F_5 would have been increased relative to random selection.

(3) Seeds per ear in the F_3 showed a consistent negative correlation with yield in the F_5.

(4) F_3 leaf length was negatively correlated with F_5 yield at high nitrogen for lines selected (F_3) at low nitrogen.

(5) There were no significant correlations between F_3 characters and F_5 yield for lines selected (F_3) and tested (F_5) at low nitrogen. This result is no doubt associated with the lack of significant differences among the F_5 yields (see table 9).

Table 14 :

Correlation between F_3 single plant characters and F_5 plot grain yield.

DENSITY EXPERIMENT :

Selection environment (F_3)	Low Density		High Density	
Test environment (F_5)	Low D.	High D.	Low D.	High D.
Leaf length	0.244 *	0.230 *	-0.244*	N.S.
Leaf height	N.S.	N.S.	N.S.	N.S.
Plant height	N.S.	N.S.	N.S.	N.S.
Biological yield	N.S.	N.S.	N.S.	N.S.
Harvest index	N.S.	N.S.	N.S.	N.S.
Ears/plant	N.S.	-0.233 *	N.S.	N.S.
Seeds/ear	N.S.	N.S.	N.S.	N.S.
1000 grain weight	N.S.	0.290 **	N.S.	N.S.

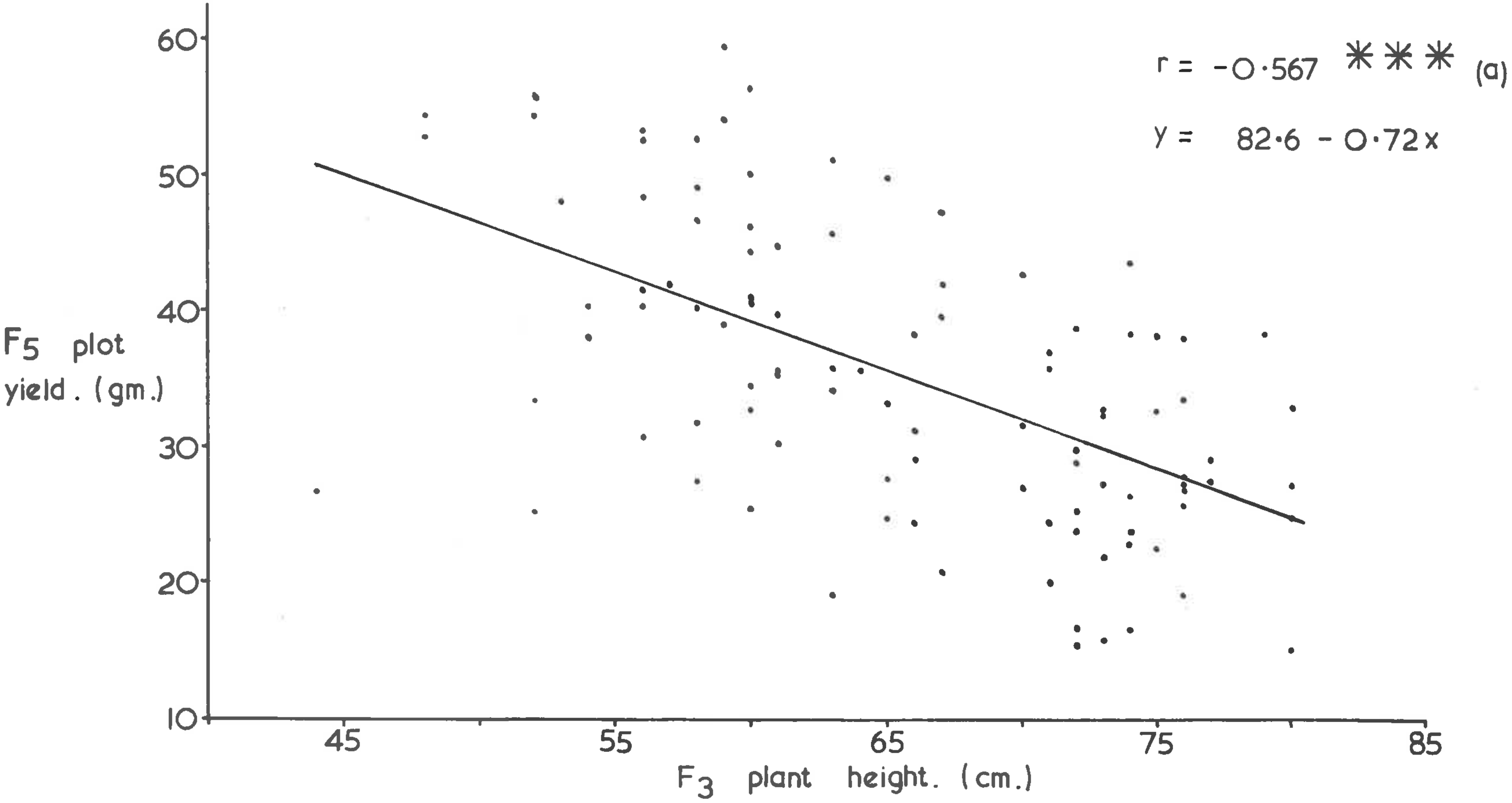
NITROGEN EXPERIMENT :

Selection environment (F_3)	Low Nitrogen		High Nitrogen	
Test environment (F_5)	Low N.	High N.	Low N.	High N.
Leaf length	N.S.	-0.296 **	N.S.	N.S.
Leaf height	N.S.	-0.439 ***	-0.232 *	-0.444 ***
Plant height	N.S.	-0.567 ***	-0.270 **	-0.531 ***
Biological yield	N.S.	N.S.	N.S.	N.S.
Harvest index	N.S.	0.441 ***	N.S.	N.S.
Ears/plant	N.S.	N.S.	N.S.	N.S.
Seeds/ear	N.S.	-0.268 **	-0.203 *	-0.296 **
1000 grain weight	N.S.	N.S.	N.S.	0.236 *

Figure 15

The relationship between F_3 plant height at low nitrogen and F_5 plot yield at high nitrogen.

The relationship between F_3 plant height at low N. and plot yield at high N.

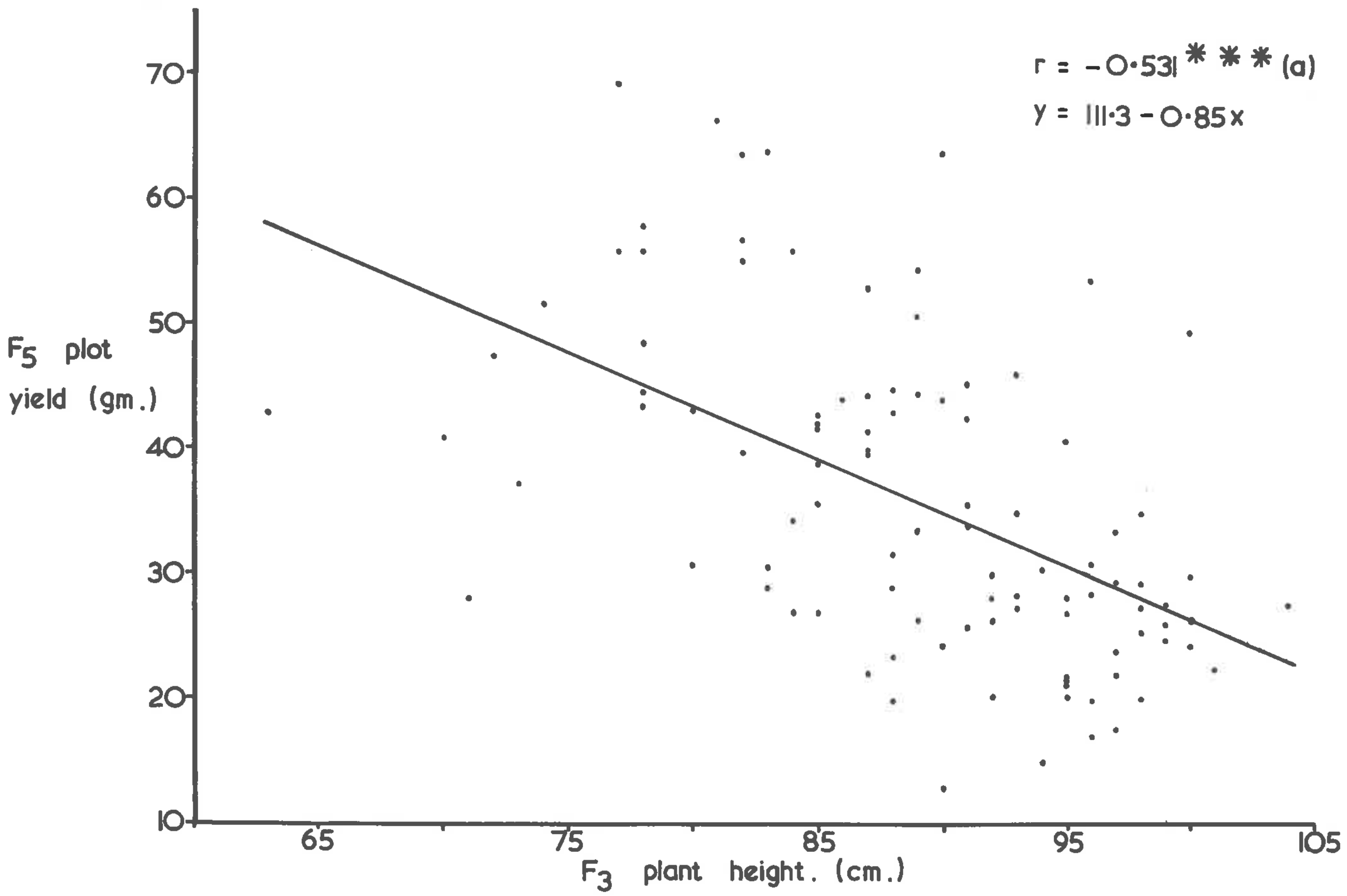


(a) correlation coefficient significant at 0·1%

Figure 16

The relationship between F_3 plant height and F_5 plot yield, both at high nitrogen.

The relationship between F_3 plant height and F_5 plot yield, both at high N.



(a) correlation coefficient significant at 0·1%.

(D) The correlation between characters measured on F_3 plants and the same characters measured on F_5 plots.

Because of the significant relationships between certain F_3 characters and F_5 yield it is appropriate to see if the characters themselves were related between generations. The results of these correlations are given in table 15. The following points are of interest:

(1) There are few statistically significant correlations between the morphological characters (leaf length, leaf height, and plant height) over generations in the density experiment. This contrasts markedly with the situation in the nitrogen experiment where all the morphological characters were significantly, and some very significantly, correlated between generations. These correlations occurred independently of whether the F_5 lines were grown in the same, or in the alternate environment.

(2) Some characters (leaf length, ears/plant and 1000 grain weight in the density experiment, and ears/plant in the nitrogen experiment) were correlated in one environment, but not in the other.

(3) 1000 grain weight was correlated over generations in all environments except when selected (F_3) and tested (F_5) at low density. This character has often been shown to be relatively insensitive to changes in the environment (Puckridge 1962, Donald 1963, and Rawson 1970). It would appear that this would apply between seasons as well as between treatments.

Table 15 :

The correlation between characters measured on F_3 plants and the same characters measured on F_5 plots.

DENSITY EXPERIMENT :

Selection environment (F_3)	Low Density		High Density	
Test environment (F_5)	Low D.	High D.	Low D.	High D.
Leaf length	0.299 **	N.S.	N.S.	0.288 **
Leaf height	N.S.	N.S.	N.S.	N.S.
Plant height	N.S.	N.S.	0.470 ***	0.236 *
Biological yield	N.S.	N.S.	N.S.	N.S.
Harvest index	0.348 ***	0.217 *	N.S.	N.S.
Ears/plant	N.S.	N.S.	N.S.	0.245 *
Seeds/ear	0.223 *	0.233 *	N.S.	N.S.
1000 grain weight	N.S.	0.256 **	0.234 *	0.333 ***

NITROGEN EXPERIMENT :

Selection environment (F_3)	Low Nitrogen		High Nitrogen	
Test environment (F_5)	Low N.	High N.	Low N.	High N.
Leaf length	0.251 *	0.408 ***	0.331 ***	0.298 **
Leaf height	0.434 ***	0.572 ***	0.587 ***	0.603 ***
Plant height	0.581 ***	0.644 ***	0.719 ***	0.595 ***
Biological yield	N.S.	N.S.	N.S.	N.S.
Harvest index	0.375 ***	0.406 ***	N.S.	N.S.
Ears/plant	N.S.	N.S.	N.S.	0.240 *
Seeds/ear	0.275 **	N.S.	N.S.	N.S.
1000 grain weight	0.266 **	0.271 **	0.325 ***	0.238 *

(4) Harvest index was correlated over generations in both the low nitrogen and the low density selection (F_3) treatments, independent of the test (F_5) environment. There was no correlation for lines selected (F_3) at the high density or nitrogen levels. The main difference between these two groups of treatments was that the low density and nitrogen levels had low leaf area indices compared with those grown at high density or nitrogen levels. (This is shown in figure 6 for the low nitrogen F_3 selection plot, at low density the distance between plants gave the same effect.)

(E) The correlation between yield and other characters in the same generation.

(a) In the F_3 generation (1967).

It has been shown (tables 14 and 15) that certain characters are correlated with both yield and with themselves in later generations. It is therefore pertinent to consider the relationship between these characters and yield in the same generation. The results for the F_3 generation are given in table 16. The following points stand out:

(1) Nearly all the characters measured were positively associated with yield; the only exception was harvest index in the low nitrogen environment.

(2) Of the yield components ears per plant was more important in determining yield than were seeds/ear or 1000 grain weight.

Table 16 :

The correlation between F_3 characters and F_3 yield.

DENSITY EXPERIMENT :

	Low density	High density
Leaf length	0.225 ***	0.445 ***
Leaf height	0.221 ***	0.404 ***
Plant height	0.563 ***	0.540 ***
Biological yield	0.923 ***	0.947 ***
Harvest index	0.425 ***	0.283 ***
Ears/plant	0.827 ***	0.694 ***
Seeds/ear	0.388 ***	0.532 ***
1000 grain weight	0.246 ***	0.295 ***

NITROGEN EXPERIMENT :

	Low nitrogen	High nitrogen
Leaf length	0.391 ***	0.320 ***
Leaf height	0.375 ***	0.069 *
Plant height	0.418 ***	0.166 ***
Biological yield	0.982 ***	0.942 ***
Harvest index	N.S.	0.153 ***
Ears /plant	0.825 ***	0.845 ***
Seeds/ear	0.482 ***	0.407 ***
1000 grain weight	0.305 ***	0.120 ***

Table 17 :

The correlation between F_5 characters and F_5 yield.

DENSITY EXPERIMENT :

Selection environment (F_3)	Low Density		High Density	
Test environment (F_5)	Low D.	High D.	Low D.	High D.
Leaf length	N.S.	N.S.	-0.205 *	N.S.
Leaf height	-0.266 **	N.S.	N.S.	N.S.
Plant height	-0.294 **	N.S.	N.S.	N.S.
Biological yield	0.834 ***	0.935 ***	0.898 ***	0.939 ***
Harvest index	0.737 ***	0.684 ***	0.770 ***	0.514 ***
Ears/plot	0.760 ***	0.432 ***	0.744 ***	0.404 ***
Seeds/ear	N.S.	0.313 **	N.S.	0.242 *
1000 grain weight	0.366 ***	0.571 ***	0.215 *	0.567 ***
Anthesis	-0.273 **	-0.588 ***	N.S.	-0.570 ***

NITROGEN EXPERIMENT :

Selection environment (F_3)	Low Nitrogen		High Nitrogen	
Test environment (F_5)	Low N.	High N.	Low N.	High N.
Leaf length	N.S.	-0.521 ***	N.S.	-0.430 ***
Leaf height	N.S.	-0.637 ***	-0.296 **	-0.494 ***
Plant height	N.S.	-0.730 ***	-0.243 *	-0.412 ***
Biological yield	0.773 ***	0.813 ***	0.799 ***	0.975 ***
Harvest index	0.432 ***	0.861 ***	0.582 ***	0.841 ***
Ears/plot	0.604 ***	0.888 ***	0.727 ***	0.881 ***
Seeds/ear	0.295 **	N.S.	0.285 **	0.326 ***
1000 grain weight	0.258 **	0.560 ***	0.290 **	0.605 ***
Anthesis	N.S.	-0.562 ***	-0.299 **	-0.568 ***

(b) In the F_5 generation (1969).

The correlations between the characters measured in the F_5 and yield in the F_5 are given in table 17. The following points are of interest:

(1) The vegetative characters (leaf length, leaf height and plant height) showed no consistent pattern in the density experiment, although the three significant correlations obtained were all negative, whereas in the nitrogen experiment there was a marked negative correlation between these characters and yield in the high nitrogen test environment (c.f. table 14).

(2) Of the yield components 1000 grain weight was more important than seeds/ear and in some cases, though not usually, more important than ears/plot (e.g. for lines tested at high density) in determining yield. Seeds/ear was not significantly correlated with yield in three comparisons; two of these were in the low density treatment.

(3) There was a high positive correlation between harvest index and yield, thus confirming the work of Beavan (1947) and Sims (1963).

(4) In most comparisons there was a marked negative correlation between date of anthesis and yield.

(5) Biological yield was always highly correlated with yield.

(F) Detailed analysis of the relationship between the vegetative characters (leaf length, leaf height and plant height) and yield in the nitrogen experiment.

The point which stands out clearly from the above results (tables 14, 15, 16 and 17) is the relationship between the vegetative characters and yield in the nitrogen experiment. Further examination of the data on these characters is therefore warranted. In table 18 the coefficients of variation of the vegetative characters are presented for all the F_3 selection plots. The analyses of variance of these characters for the nitrogen experiment are presented in table 19.

There are several points of interest in these two tables, especially when the results are compared with those presented in tables 7, 8 and 9.

(1) The coefficients of variation of the vegetative characters were very similar within each generation, and were much less than the corresponding coefficients of variation for yield.

(2) Most of the analyses of variance have a marked replicate effect. This was not surprising as the characters chosen were very responsive to the environment (c.f. the differences between treatments for these characters, tables 5 and 6, and the average values of the individual replicates table 20).

(3) The differences between genotypes within an F_5 treatment were all highly significant (c.f. table 9).

Table 18 :

The coefficients of variation of the vegetative characters (leaf length, leaf height, and plant height) in the F_3.

DENSITY EXPERIMENT :

	Low Density	High Density
Leaf length	16.2%	16.6%
Leaf height	15.4%	10.6%
Plant height	11.4%	11.0%

NITROGEN EXPERIMENT :

	Low Nitrogen	High Nitrogen
Leaf length	16.5%	15.2%
Leaf height	15.4%	11.0%
Plant height	14.6%	9.3%

Table 19 :

The analysis of variance of the F_5 vegetative data (leaf length, leaf height, and plant height) and the coefficients of variation in the nitrogen experiment.

Selection environment (F_3)			Low Nitrogen		
Test environment (F_5)		Low N.		High N.	
	D.F.	M.S.	f ratio	M.S.	f. ratio
Leaf length :					
Reps.	2	383.3	54.17 ***	126.0	36.44 ***
Lines	99	14.5	2.05 ***	14.3	4.14 ***
Error	198	7.1		3.5	
C.V.		13.9%		7.8%	
Leaf height :					
Reps.	2	5956.1	131.20 ***	15.5	0.63 N.S.
Lines	99	142.5	3.14 ***	133.9	5.44 ***
Error	198	45.4		24.6	
C.V.		10.8%		5.8%	
Plant height :					
Reps.	2	4372.0	56.74 ***	288.2	9.62 ***
Lines	99	272.0	3.53 ***	210.6	7.03 ***
Error	198	77.0		29.9	
C.V.		9.0%		3.7%	

Table 19 : (cont.)

Selection environment (F_3)		High Nitrogen			
Test environment (F_5)		Low N.		High N.	
	D.F.	M.S.	f ratio	M.S.	f ratio
Leaf length :					
Reps.	2	638.2	140.14 ***	180.0	179.96 ***
Lines	99	9.5	2.08 ***	14.4	2.59 ***
Error	198	4.6		5.6	
C.V.		11.0%		10.0%	
Leaf height :					
Reps.	2	6643.2	269.83 ***	65.4	1.26 N.S.
Lines	99	102.7	4.17 ***	119.9	2.31 ***
Error	198	24.6		51.9	
C.V.		8.0%		8.4%	
Plant height :					
Reps.	2	6154.9	205.00 ***	794.1	10.32 ***
Lines	99	213.0	7.09 ***	230.6	3.00 ***
Error	198	30.0		76.9	
C.V.		5.6%		7.7%	

Table 20 :

Average length (cm) of the vegetative characters per replicate (leaf length, leaf height and plant height) in the F_5 nitrogen experiment.

Selection environment (F_3) Low Nitrogen

Test environment (F_5) Low N.

	Rep.1	Rep.2	Rep.3	L.S.D. at 5%
Leaf length	21.3	18.9	17.4	0.71
Leaf height	71.1	60.3	56.2	1.89
Plant height	104.5	98.8	91.3	2.38
Selection environment (F_3)		Low Nitrogen		
Test environment (F_5)		High N.		
Leaf length	25.2	23.4	23.1	0.52
Leaf height	86.5	86.1	85.7	1.39
Plant height	116.4	113.8	113.3	1.53
Selection environment (F_3)		High Nitrogen		
Test environment (F_5)		Low N.		
Leaf length	22.1	18.9	17.1	0.60
Leaf height	71.4	60.0	55.6	1.39
Plant height	106.1	99.1	90.5	1.53
Selection environment (F_3)		High Nitrogen		
Test environment (F_5)		High N.		
Leaf length	25.0	22.7	22.6	0.66
Leaf height	87.1	85.8	85.7	2.33
Plant height	117.2	112.7	112.1	2.46

(G) Competitive relationships within the F_5 nitrogen experiment.

In the review of literature the relationship between the yield of plants in mixtures and their yield in pure culture was discussed. Idealised types of relationships were given in figure 2. In the F_5 nitrogen experiment each test plot was surrounded by a single border row of the same genotype. The test plot with its border row adjoined other bordered plots. The border rows were therefore competing partly with a different genotype (neighbouring border rows) and partly with a similar genotype (the test area). It was therefore theoretically possible to obtain an estimate of the yield per plant of the different genotypes when competing in mixtures (in the border) and in pure culture (in the test plot). Certain points must be emphasised. Firstly, the competition in mixtures was measured in a slightly unusual way. The borders of each plot had four adjacent competing genotypes. As there were three replicates of each genotype this meant that in the mixture every genotype was competing (on one side) with twelve different neighbours, which it was hoped would be approximate to the average competitive ability of this particular cross. Secondly, because the border rows were used, the estimate of yield in mixtures was not very precise as the borders were competing with the same (on the test plot side) as well as with different genotypes. It was thought however, that this would not affect the direction of any competitive ability/yield relationship, only its magnitude.

By harvesting the border rows as well as the F_5 test plots it was possible to obtain a crude estimate of the yield per plant in mixtures as well as yield per plant in pure culture. Using this approach the regressions of the relationship between yield in pure culture and yield in mixture were obtained for the nitrogen experiment (table 21). These are shown graphically in figure 17 for the high nitrogen F_5 test environment. From table 21 it is seen that all the regressions are significantly less than one, suggesting that the higher yielding genotypes in pure culture are less competitive than the lower yielding genotypes.

However, in each replicate, there were also 48 control plots (C.I.3576). These were put into 48 groups of three, made up to one plot, chosen at random, from each replicate. The 48 groups so obtained had yields in pure culture and in mixture that were directly comparable to those of the selected genotypes. The only difference was that the 48 values were all of the same genotype. The regression of the control plots was therefore calculated as a check on the method. The regression of the yield of the control variety in pure culture and the yield in mixture were also significantly less than one. Furthermore in one case, genotypes selected (F_3) and tested (F_5) at high nitrogen, the regression of the control variety was significantly less than that of the selections. These results will be considered again in the discussion.

Table 21 :

Regression analysis of yield in pure culture and yield in mixture of the genotypes selected (F_3) in the nitrogen experiment and the control plots (C.I.3576) when grown in the test generation (F_5).

Test environment. (F_5)	Regression equation of yield in pure culture and yield in mixture.	t for comparison with line of slope = 1.
Genotypes selected (F_3) at low nitrogen.		
Low N.	$Y = 0.39X + 1.85$	6.26***
S.E.	± 0.098	
High N.	$Y = 0.66X + 0.98$	8.12***
S.E.	± 0.054	
Genotypes selected (F_3) at high nitrogen.		
Low N.	$Y = 0.51X + 1.42$	5.57***
S.E.	± 0.047	
High N.	$Y = 0.71X + 0.87$	6.20***
S.E.	± 0.088	
Control plots (C.I.3576).		
Low N.	$Y = 0.46X + 1.99$	2.77**
S.E.	± 0.193	
High N.	$Y = 0.33X + 2.57$	4.29***
S.E.	± 0.156	

Table 21 (cont.) :

t values. (For comparing the slopes of the regressions of the selections with that of the corresponding control.)

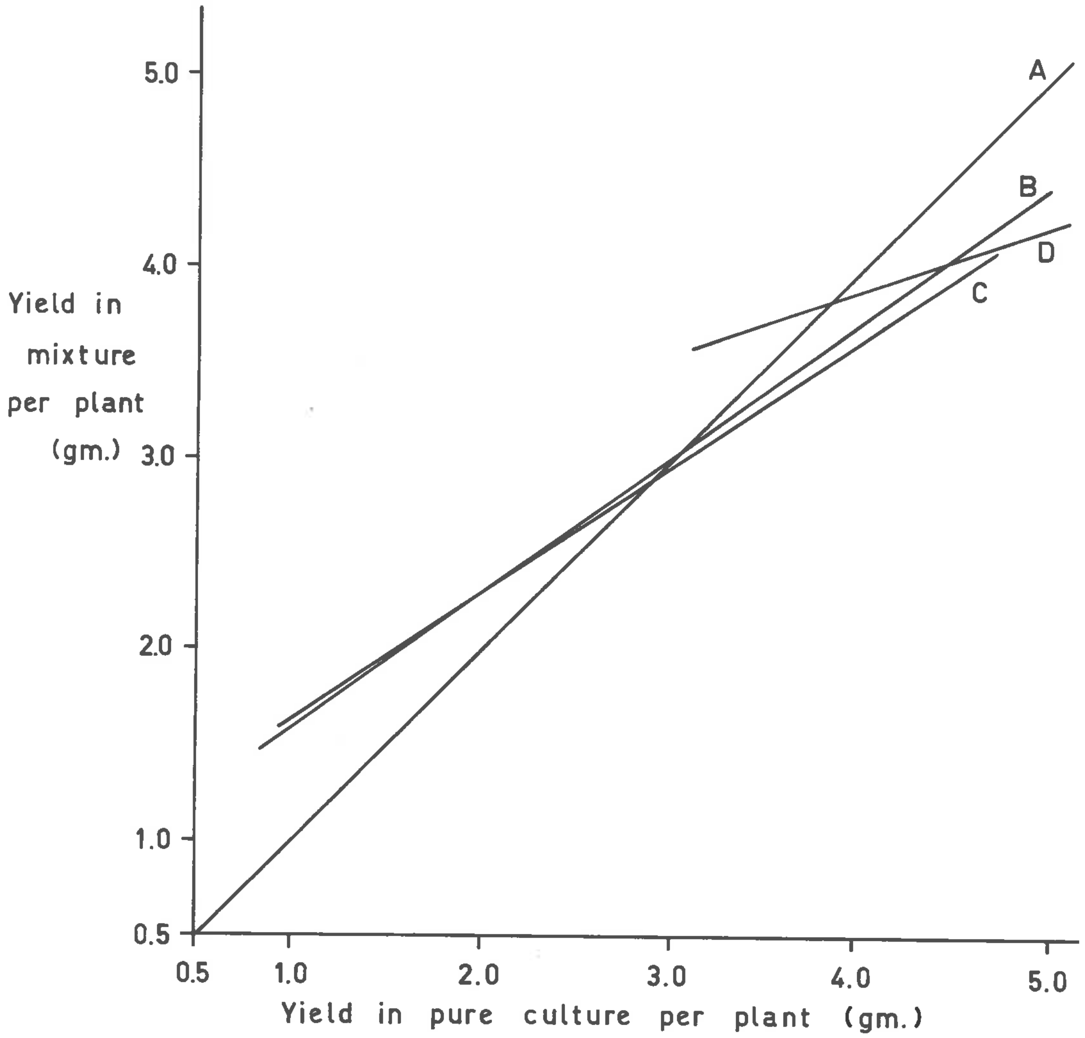
Selection environment (F_3)	Low Nitrogen	
Test environment (F_5)	Low N.	High N.
t value	0.07 N.S.	1.90 N.S.

Selection environment (F_3)	High Nitrogen	
Test environment (F_5)	Low N.	High N.
t value	0.24 N.S.	2.27 *

Figure 17

The relationship between yield in pure culture and yield in mixtures at high nitrogen.

The relationship between yield in pure culture and in mixtures at high N.



A is line of slope = 1

B is the regression of the high N selections, y = 0.71X + 0.874

C " " " " " low " " " " 0.66X + 0.977

D " " " " " control plots " " 0.33X + 2.571

DISCUSSION.

(1) Methodology :

Certain points of methodology call for consideration. They are:

(a) the use of response surfaces or moving means in estimating micro-environmental effects in mixed communites,

(b) the effect of plot size in the experiment described in this thesis,

(c) the procedure for analysis of F_5 yield.

(A) Response surfaces and moving means.

In cereals vegetative propagation is not yet a practical proposition and therefore single plants in segregating generations cannot be replicated. If different genotypes are grown in a variable environment it is not possible to estimate the micro-environmental variance. If, for example, there is a fertility trend within a plot, this may lead to false appraisal of an individual's worth. It is therefore important to consider possible means of estimating and removing as much of the environmental variability as possible. This was the purpose of fitting response surfaces and moving means.

The response surfaces fitted were polynomial functions that related the position of the individual plants within the F_3 selection plot to their yield. The position coordinates, x and y, were the independent variables, and the yield of the individuals (z) was the dependent variable. The technique involved the simultaneous fitting of a multiple regression to the x and y axes of the plot, producing a response surface in three dimensions x, y and the estimated yield. This equation can be represented as a contour map, which shows the calculated mean yield over the selection plot (see figures 10, 11, 12, 13 and 14).

Theoretically the ideal surface would be one that estimates all the environmental variation, without removing the genetic variation. However, in single plant selection it is impossible to estimate the genetic and environmental proportions of the variance. It is therefore impossible to decide objectively what number of terms should be included in the regression equation. Two empirical approaches to this problem are possible:

(1) is to calculate progressively higher order terms of the polynomial until there is no statistical improvement in the fit of the surface. This was done, and except at low density, the cubic expressions did not differ significantly from the quadratic. However, the former were used because it was presumed that they gave a slightly more accurate description of the actual situation. In the low density treatment there was an improvement using the cubic expression, but because the computer (C.D.C.6400) had inadequate memory for storage and calculation, it was not possible to go to fourth order expressions to determine whether these differed significantly from the cubic expression. Two points need emphasis; as variation can be very localised (see later discussion) a very large number of terms may be

needed to account for the micro-environmental variation. Also, if the actual pattern of variation is complex, then there is no reason to expect that by increasing the number of terms from the quadratic to the cubic, the fit of the equation will be usefully improved.

(2) Another approach, not used in this experiment because the magnitude of the micro-environmental variation was not anticipated, would be to plant a standard variety as a recurrent control. The surface would then be fitted to this variety. The major problem is that, unless the control had adequate borders, competition would be very important in determining its yield. On the other hand if it is bordered, then the distance between the control plants and the test plants will be increased. As large changes in the micro-environment can occur over short distances, this will reduce the precision of the fitted surface in relation to the total environment.

Once the equation to be used has been decided there are still two limitations to the use of response surfaces. The surface is less well defined near the borders of the experimental plot as no information is available beyond the perimeter. Furthermore even if the equation gives an adequate description of the environment in one situation it is not necessarily adequate in another. The terms of the equation have no biological significance.

These problems are illustrated in figure 18. This shows a cross section of the low density F_3 selection plot, with the yields of individual plants in a column of the plot and the corresponding section of the response surface depicted. In the overlays the corresponding moving means (to be referred to later) are shown. The moving means show that the average yield of plants in the first few rows (rows 1 - 5) is rising. The surface on the other hand shows yield as falling rapidly. This occurs because the cubic surface is not only affected by the yields of plants in the individual column, but by every other plant in the F_3 selection plot. If an equation containing more terms had been used the surface might have shown the same trend as the moving means.

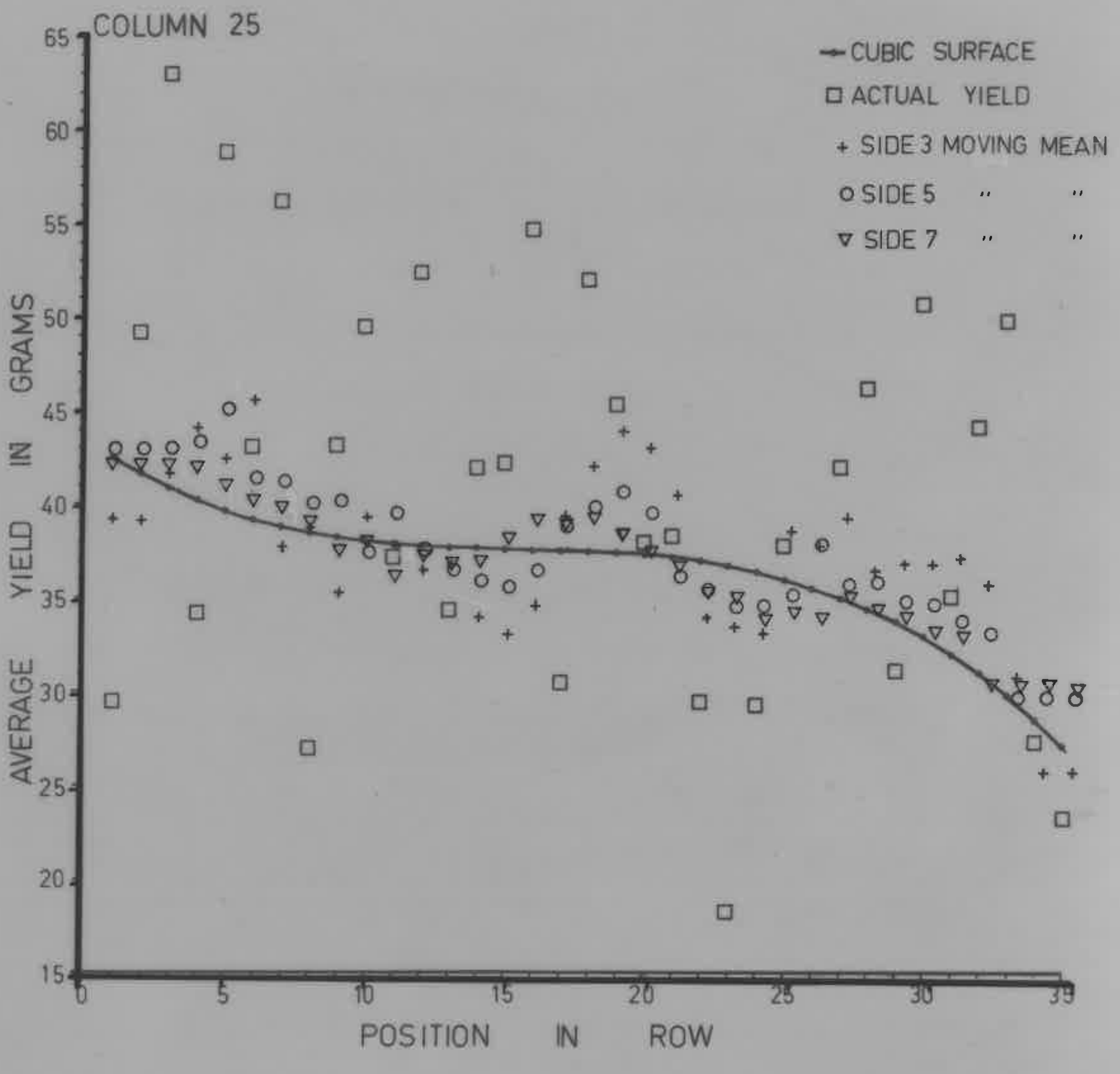
The above discussion concerns the theoretical problems associated with response surfaces. Another more practical problem is how to depict different surfaces so that they may be compared. For example, what contour interval should be used so that the non-random variation within a plot can be compared with that of another plot, even though the plots have been planted at different densities and have very different mean yields. On a relative basis the scale used must be comparable.

A possible contour interval would be some fraction of the standard deviation. This is a scale based on variability. It was used in figures 10, 11, 12 and 13 showing the surfaces for the F_3 selection plots where the contours are at intervals of 1/5 of a standard deviation. Using this scale the F_3 response surfaces are not completely comparable because the coefficients of variation were not the same (see table 7). This would tend to decrease the contour

Figure 18

A cross section of the low density yield response surface. The figure also shows the actual yields, and in the overlays the three moving means.

40 x 40 cms. 60 lbs. NITROGEN.



interval, relative to the mean yield, in treatments having a low coefficient of variation, in this experiment the low density F_3 selection plot. This treatment had more contours than the others (compare figure 10 with figures 11, 12 and 13), not because it was inherently more variable, but because of scaling effects. To overcome this problem the contours were re-drawn at intervals of 10% of the mean yield. (It should be noted that in treatments having a coefficient of variation of approximately 50%, contour intervals of 10% of the mean closely approximate to 1/5 of a standard deviation, see table 7.) In the low density F_3 selection environment a contour interval of 10% of the mean increased the distance between contours by 56% relative to the contour interval of 1/5 st. dev. Only in this case (low density F_3 selection plot) were the contour intervals (1/5 of st. dev. V. 10% mean yield) sufficiently different to be worth showing as a separate figure. Figure 14 shows the response surface of this plot with contour intervals of 10% of the mean yield. This figure should be compared with figure 10.

Even using this contour interval (compare figures 11, 12, 13 with 14) the low density F_3 selection plot had more contours and a more complex surface than the other environments. This result was not surprising, as on a statistical basis, one would expect a greater range of variation over a larger area. But, the low density F_3 selection plot also had a low coefficient of variation (see table 7) compared with the other F_3 treatments. It is important to consider what this means.

The coefficients of variation of the F_3 plots will include variation due to genetic differences between individuals, to systematic environmental variation and to random variation. It is reasonable to assume that the proportion of the genetic variation is constant in each treatment, and that the genotype - environment interaction will either be constant in all treatments, or increase at low density, where the genotypes will be better able to express their full potential (Frey 1964).

Among the F_3 selection plots, a greater proportion of the total variance was due to systematic environmental effects in the low density plot than in the others, (c.f. discussion of surfaces above). Therefore it would appear that more of the variance at low density is due to genotype - environment interaction and to systematic variation than can be explained by these factors in the other F_3 selection environments. But these other environments, low and high nitrogen and high density, have larger coefficients of variation, and therefore on a relative basis more variability.

This increased variability must be due to greater random variation. The factor which fits this situation is competition between plants. This factor was more than sufficient to compensate for the decrease in micro-environmental effects that would occur with the reduction in area used. An increase in the coefficient of variation with increasing density and competition has also been found by Stern (1965) using subterranean clover.

Perhaps surprisingly table 12 (and tables A1 and A3 appendices 1 and 3) show that the use of response surfaces to obtain estimates of F_3 yield potential did not provide a better estimate for predicting future performance than did yield itself. One reason for this was that the cubic surface was severely limited in its responsiveness to localised variation. If there were small areas of poor ground surrounded by larger good areas, the surface would make little allowance for the poorer patches. This results from the limitations imposed by the order of the polynomial used in fitting the equation.

A solution to this problem would be to estimate variation within smaller areas than the whole plot. It was therefore decided to use moving means. One needs a small sample to estimate effects over a minimum area, but a large enough sample to ensure that the sample genetic mean approaches the population genetic mean. In an attempt to find an empirical solution to this problem three sizes of unweighted moving means were used. These consisted of 9, 25 and 49 plants (sides 3, 5 and 7), where the test plant was the centre of the sample unit..

Two problems associated with the use of moving means were how to allow for the effects of missing plants and also how to estimate the calculated values at the edges of the selection plot where the yields of plants making up the guard rows were not measured.

As no test plant used was immediately adjacent to a missing plant (c.f. p.63) the problem of missing plants did not arise when moving means of side 3 were used. When moving means of side 5 or 7 (25 or 49 plants) were used, there may have been some missing plants in the outer surrounding rows. The effect of these were ignored and the calculated yield obtained from the actual number of surviving plants. Because of the large numbers of plants in the average (25 or 49) and because the neighbouring plants would compensate for missing plants, the errors of this method would be minimal.

At the edge of a selection plot, although there were border rows these were not harvested, no information was available as to the yield of some of the plants adjacent to a test plant normally included in the moving mean. Two methods of estimating the calculated yield of test plants at the edge of a plot were possible, either one could use the closest complete estimate, which would not be strictly applicable to the test plant being considered, or one could calculate the moving mean using the neighbours on three sides only. This estimate of the moving mean would be less reliable than those obtained for test plants further from the periphery of the F_3 selection plot. Both these methods of estimating the calculated yield have disadvantages but for computational reasons the former was used in this study.

It is pertinent to consider how the methods of ranking F_3 yield (yield itself and response surfaces and moving mean estimates) differed from each other.

Firstly, actual yield is a measurement of the phenotype, where no account is taken of micro-environmental effects; all the other methods of ranking F_3 yield took some account of these effects.

Secondly, it was possible to measure the deviations from the response surfaces and from the moving means either as an actual or as a relative deviation. The relative deviations would take into account the average yield of an area and would allow more accurate comparison between areas. For example, if two individuals from within the same selection plot had the same actual deviation from the response surface, but in one case the value of the calculated yield was half that of the other, then although on an actual deviation basis both plants had the same yield, on a relative basis one would be much superior to the other as some account had been taken of the fact that the area in which it was growing was lower yielding.

A comparison of the moving means and response surfaces may be made from figure 18, which shows a single section through the low density F_3 selection plot. Similar results occurred in the other F_3 selection environments, but only one example is given. It shows the actual yield, the response surface, and in the overlays the three moving means. The following points are apparent:

(1) The data shown are in two dimensions, while the surface and the moving means include information in a third dimension at right angles to the figure.

(2) The surface takes into account all the other plants in the plot, whereas the moving means consider only immediately adjacent plants.

(3) The range in the actual yields was very much greater than the variation in the response surface or the moving means.

(4) By definition the cubic response surface is seen in any single transect (x or y axis) as a smooth curve with two points of inflection. The surface gives some indication of the trend across the area, but its limitations are clearly indicated by the moving means. These show that there were systematic fluctuations that the surface was not able to accommodate.

(5) The fluctuations in the moving means were more frequent and of greater amplitude as the size of the sample for the moving mean decreased (49 to 25 to 9 plants). This is to be expected as the smaller the number of plants contributing to the moving mean the smaller the area sampled and the greater the effect of local good or poor patches. There is also a greater chance of the small samples containing more than an average proportion of genetically superior or inferior plants.

The moving means show that the response surface used in this study was an oversimplification of the (systematic) environmental effects. It would appear that a polynomial of the sixth or seventh power would have been more appropriate than the cubic one used. Because of computational limitations the moving mean was a simpler way of obtaining a similar result. The moving mean approximates to a series of localised surfaces.

For a response surface to be effective the equation used must be sufficiently complex to allow for any systematic trends within the plot. Because, in using a moving mean no equation is fitted to the data, but only local averages are obtained, the moving means are more flexible and no prior knowledge is needed as to the complexity of the trends present. Moving means will therefore always reflect local environmental variation independent of its complexity whereas response surfaces will only do this if by chance the equation used contains the appropriate number of terms to account for the variation present.

(B) The choice of plot size.

As already pointed out (p.68) there were only 16 test plants per F_5 plot, with various numbers of border rows, the actual number depending on the density. The relationship between yield performance and plot size is very important when extrapolation to field conditions is sought.

Several authors (Ross and Miller 1955, Torrie 1962, Jellum et al. 1963, Frey 1965, Jensen and Robson 1969) have compared "micro plots" with field plots. The yield ranking of varieties grown in micro plots corresponded moderately well with the yield ranking obtained from field plots. Frey has the widest experience of the use of "micro" plots and he (1965) concludes that they are efficient for early generation testing but that final yield evaluation should be carried out in field plots.

The most commonly observed result in all the reports was a substantial increase (2-5 times) in the coefficient of variation of "micro plots" as compared with field plots. The coefficients of variation of the F_5 plots were given in tables 8 and 9. The coefficients were high (21.0% to 32.5%), but in an adjoining field R.P. Johnston (unpublished data) obtained a coefficient of variation of 27% for field plots. This was in close agreement with a five year average of 26% obtained by D.H.B. Sparrow and K.W. Finlay at the Waite Institute (unpublished data). These values suggest that "micro plots", despite their high coefficient of variation, were as efficient as field plots in this agricultural environment. The overall conclusion must be that there is very large, localised soil variation on the red brown earth of the Waite Institute; this severely limits the efficiency of early generation selection in cereals.

(C) The F_5 analysis.

The relationship between the number of replicates needed to detect a significant difference between variety or treatment means with different coefficients of variation have been tabulated by Hoblyn (1931). Some of this table is shown in table 22.

Table 22 :

The relationship between the number of replicates, the coefficient of variation and the size of differences detected at the 5% level (Hoblyn 1931). The number of replicates required to detect a specified difference is given in the body of the table.

	Coefficients of variation		
Difference	20%	25%	30%
10%	32	50	72
20%	8	12	18
30%	5	6	8
40%	4	4	5
50%	3	3	4

From table 22 it is seen that if the coefficient of variation is of the order of 25% as in this study, then a very large number of replicates is needed to detect a relatively small difference (10-20%) between lines.

It should be noted that to plant the F_5 yield trial required 48 man days (12 people for 4 days); any further increase in the size of the experiment was not feasible. Therefore were there other ways in which the number of replicates might have been increased?

100 lines were chosen from each selection environment. If this had been reduced to 50 lines then it would have been possible to

double the number of replicates without increasing the total size of the experiment. In most selection experiments for yield (see pp. 32-37) only the high yielding single plants were selected; however as already pointed out, (pp. 12-28) there is no reason to assume that the yield of single plants in mixtures and the yield of the same genotypes in pure culture are positively associated. If they are not, then selection of high yielding single plants would not be effective. To obtain data on the relationship between competitive ability and yield in pure culture, the total yield range had to be evenly sampled. To ensure an adequate sample of the range, a large number of lines was needed. It is thought that the use of only 50 selections from each F_3 environment would not have been adequate as this would have meant only limited sampling from each yield decile (5 lines/decile). This size of sample greatly increases the chance of a result being due to sampling effects and not a true result (c.f. discussion on p. 16).

An alternative would have been to plant the experiment by machine, so making it possible to plant more replicates. The F_3 generation was hand planted on the square to ensure even spacing and competition. If this had been machine planted, the F_3 single plant yields would have been confounded by variable spacing within the row. Once it was decided to avoid these problems by hand planting on the square in the F_3, it was necessary to plant the F_5 yield trial the same way and thus minimise the genotype - treatment interaction.

With hind sight it is possible to suggest a programme that would have enabled more F_5 replicates to be planted. It has been shown (tables 12 and 14 and later in the discussion) that in the density experiment there was little relationship between any F_3 characters and F_5 yield. On the other hand clear relationships between F_3 and F_5 were shown in the nitrogen experiment. This experiment was conducted at approximately commercial spacing, suggesting that selection should be carried out at this spacing. If this had been done and the density experiment had been eliminated, then it would have been possible to double the number of replicates in the nitrogen experiment. But when the experiment was designed these results could not have been anticipated.

In retrospect another solution may have been to imitate as closely as possible normal field spacing in the F_3. Instead of using square planting the plants could have been grown in rows with accurate spacing within the rows. The F_5 test plots could have been machine planted to those specifications. As the average density in the F_5 test plots would have been the same, local variations within the plots would not have biased the results as areas of lower than average density would have been compensated for by areas of greater than average density within the same plot (Fairfield Smith 1937). This would have enabled more replicates to be used in the F_5 yield trial.

(2) Discussion of the Results :

(A) The correlation of F_3 yield with F_5 plot yields.

With the development of various methods of estimating F_3 single plant yield it was possible to compare these yields with F_5 yield; as already indicated (table 12, p. 94) not one of the correlations was significant. (But it must be remembered that these estimates are not independent, c.f. p. 93.) However, this result is in agreement with the consensus of plant breeding opinion (see Introduction p. 1 and Review of literature pp. 3-49) that single plant selection for yield is not possible. Furthermore there is no indication from this study that F_3 plant selection in an environment similar to the F_5 plot environment is any more (or any less) effective than F_3 selection in an environment which contrasts with the plot environment of the F_5.

If the level of heterozygosity in the F_3 was the reason for the lack of relationship between F_3 and F_5 performance, then, from the design of the experiment, it is not possible to make any progress in analysing the results. The experiment was based on the assumption that heterozygosity would not be an overwhelming problem in the F_3 generation, and it would appear from the literature (c.f. pp. 5-9) that this was a reasonable assumption. Also, if heterozygosity was the major factor disrupting selection, it could be expected to have a similar effect on the vegetative characters (leaf height, leaf length, plant height). This was not the case (see table 15). Therefore it would appear that although heterozygosity may have had some confounding effect, it was insufficient of itself to account for the total failure of F_3 selection on the basis of single plant yield.

The difficulties of selection in one environment for performance in another, with inherent genotype - environment effects have been partially overcome in this study by testing in an environment (density or N level) as similar as possible to that used for selection. Nevertheless it is possible that the lack of correlation was attributable to other genotype-environment interactions, such as genotype-seasons interaction between 1967 and 1969 (c.f. table 3). Although the importance of the genotype-season interaction may be considerable (p. 10) in a field experiment of this type, it was both unavoidable and unmeasurable on the selected genotypes. Some indication of its magnitude can however be obtained indirectly. Table 13 shows the correlation between the yield of the F_5 lines when tested in the same and in alternate environments. In two cases there was no correlation, while in the other two cases the correlation, although highly significant, only accounted for 12% and 14% of the variation.

A second source of evidence comes from the Waite Institute breeding programme. In the same seasons as the F_3 and the F_5 (1967, 1969) generations were grown, late generation selections of the same cross as was used in this study (Proctor x C.I.3576) were grown in replicated plots. There was no correlation between the yields of 47 lines grown in 1967 and the same 47 lines grown in 1969 (D.H.B. Sparrow unpublished data). However, because the average yield per unit area of these 47 lines was much lower than that of the F_3 selections used in this study, a second comparison was made, this time among 22 lines from a similar cross (Bonus x C.I.3576) which had a similar yield in 1967 to the F_3 selection plots. Again there was no relationship between the performance of the 22 lines in 1967 and in 1969 (K.W. Finlay unpublished data).

These results clearly show that there was a large genotype-seasons interaction between 1967 and 1969, the F_3 and the F_5 years of this study. This interaction of itself may have been sufficient to destroy any relationship between the yield of single plants in the F_3 and the yield of plots in the F_5.

The low density F_3 selection environment was used to minimise competition between individuals. Yet even then it proved not possible to select effectively in the F_3 for yield at low density in the F_5. This strongly suggests that micro-environmental factors so affect plant performance that they also may have been sufficient to destroy any correlation between the F_3 and F_5 performance.

It is important to obtain some indication of the scale of the micro-environmental effects that occur between adjacent plants. This is best done by considering the variation that occurred over 40 cm in the high density treatment. Figure 11 (p. 81) of the high density response surface shows that the mean yield per plant can be expected to vary by 30% in 40 cm (0.6 of a standard deviation within a distance of 11 plants). Yet this method (response surface) of assessment under-estimates local variation (p.128) and it is instructive to consider assessment based on the moving means. An extreme set of results is presented in table 23.

Table 23 :

Moving mean variation in F_3 plant yield (gm) found over 40 cm in the high density environment (column 20 rows 21-31).

Moving mean

	21	22	23	24	25	26	27	28	29	30	31
Side 3 9 plants	0.53	0.44	0.63	0.58	0.78	0.71	0.80	0.87	0.92	1.00	1.12
Side 5 25 plants	0.52	0.67	0.65	0.75	0.85	0.92	0.86	0.95	0.96	1.01	1.06
Side 7 49 plants	0.65	0.65	0.71	0.76	0.83	0.85	0.90	0.85	0.95	1.00	0.94

The plot mean yield was 0.79 gm/plant. The range of values of moving means of sides 3, 5 and 7 respectively over a distance of 40 cm was equal to 87%, 68% and 44% of the mean of the whole F_3 plot, a very large micro-environmental change within a short distance.

This degree of non-random environmental variation would have been quite sufficient to destroy any correlation that may have existed between the yield of single F_3 plants and F_5 progeny plots at low density.

Therefore a serious limitation to the use of either response surfaces or moving means at low density is that the area is not sampled closely enough to estimate local variation accurately. But in both the high density F_3 selection environment and in the nitrogen experiment the area was sampled more closely and the estimate of local variation should have been correspondingly better. However, competition has greatly increased the coefficients of variation in those treatments (high density and high and low nitrogen) where competition was potentially important (p. 124). Therefore the effects of competition would be expected to confound the estimates of yield potential in pure culture that were obtained from yield in a close spaced F_3 population.

The failure of single plant selection on the basis of yield in this study is not surprising when one considers the several major factors which operated against effective selection. It would seem that genotype-season interaction, micro-environmental effects, and competition were sufficient to destroy any correlation that might exist. This result confirms and analyses the contention that selection for crop yield, based on single plant yield in early generations, is not possible.

One must therefore turn to the possibility of selection on the basis of characters other than yield which are indicative of yield in pure culture.

(B) The use of F_3 characters other than yield as selection criteria for yield in later generations.

In the F_3 the yield components, and several characters that may be associated with photosynthetic, physiological or competitive efficiency were measured. These characters have been correlated with F_5 yield and the results were given in table 14.

In the density experiment there were few significant correlations and these were not consistent. However the negative correlation between ears per plant at low density in the F_3 and plot yield at high density in the F_5 supports Hurd's (1969) contention that selection at wide spacing should be for poorly tillered plants if they are to be grown under field conditions in a semi-arid environment.

In the nitrogen experiment there were two sets of results that were consistent and need detailed consideration. There were negative correlations between the F_3 vegetative characters (leaf length and leaf and plant height) in either selection environment (high or low N) and yield in the high nitrogen test environment. Thus tall long leaved F_3 plants tended to have low yielding progeny in the F_5. There was also a consistent negative relationship between seeds/ear in the F_3 and yield in the F_5.

Four points concerning the vegetative characters stand out.

Firstly there was a positive association between these characters and yield in the F_3 (see table 16).

Secondly the vegetative characters were inherited from the F_3 to the F_5 (see table 15).

Thirdly there was a negative correlation between the characters in the F_3 and yield in the F_5 at high nitrogen (see table 14).

Fourthly there was a negative relationship, within the F_5 high nitrogen environment, between these characters and yield (see table 17).

It is important to find an hypothesis that accounts for these results.

In the mixed F_3 community the taller, longer leaved, and probably more competitive plants yielded more than the more dwarf, short leaved plants, which would be susceptible to competition. This result is similar to that of Jennings and Herrera (1968) who found that in a segregating population the short plants yield less than tall plants.

The short plants in the F_3 had short progeny in the F_5. This means that effective selection for plant height was possible. This result has often been reported for cereals in the literature (Vogel et al. 1956, 1963, Liang and Walter 1968, Frey 1959, Patterson et al. 1963, Threlkeld 1962, Lebsock 1963, Anon 1962, Jain and Upadhyay 1964). The level of nitrogen had little influence on the relative expression of this character (table 15).

Short plants in the F_3 gave rise to higher yielding progeny in the F_5 than did tall plants (see table 14). Also the high yielding F_5 lines were themselves short (table 17). This suggests that there is some intrinsic advantage for short plants when grown at high nitrogen. There are three major reasons why short plants may be at an advantage in this circumstance.

Short plants are more resistent to lodging. This will enable them to respond better than tall plants to high levels of nitrogen (Vogel et al. 1963, Porter et al. 1964, Woodward 1966). In the high nitrogen experiment lodging was important, (see fig. 8) but due to the wire supports a lodged plot did not affect neighbouring plots. If a plot lodged this clumped all the stems and ears together in a corner of the supporting grid. The less favourable light relations within the clump would have caused lower yields of tall lines susceptible to lodging.

Although lodging may explain the results alternative explanations are possible. Choudry and Allen (1966) found that short plants tended to have short leaves and Fowler and Rassmusson (1969) showed that leaf area was inherited. These results were confirmed in this experiment (see tables 24 and 15).

TABLE 24 :

The correlation between leaf length and plant height in the nitrogen experiment.

(a) F_3 in 1967.

	Low Nitrogen	High Nitrogen
Leaf length/plant height	0.603 ***	0.286 ***

(b) F_5 in 1969.

	Low N.	High N.	Low N.	High N.
Leaf length/plant height	0.635 ***	0.518 ***	0.641 ***	0.332 ***

On average one would expect that short leaves would be more upright, as the bending moment of the weight of the leaf is less. The crop canopy of short upright lines would have many of the features put forward by Wilson (1960), Blackman (1961), Stoskopf et al. (1963), Jennings (1964), Jennings and Beachell (1965), Beachell and Jennings (1965), Pendelton et al. (1968) and Donald (1962 and 1968 a & b), (c.f. Ideotype Plants pp. 40-48) as being inherently more efficient at converting solar energy into dry matter when grown in pure stands. The difference in yield between tall and short lines may be related in part, or even wholly to this and not necessarily to a greater resistance to lodging.

Plant morphology may also affect the moisture use of a crop. Luebs and Laag (1969) and Fischer and Kohn (1966a), in environments similar to South Australia, showed that increasing the level of nitrogen increased the leaf area of barley and wheat and that this increased the water loss. Thus lines with short leaves and stature would be expected to use water less rapidly than tall long leaved lines. This may have enabled the short upright types to continue photosynthesis for longer, either by increasing the length of time between flowering and senescence or by allowing photosynthesis to continue longer during the day before wilting occurred.

Short upright types therefore have three potential advantages over tall floppy leaved types, namely (a) they are more lodging resistant, (b) they would use light more efficiently, and (c) they would use water more efficiently. Within this experiment it was not possible to decide on the relative importance of these factors on yield. However all these factors would increase the amount of photosynthesis after ear emergence.

Thorne (1966) reviewing the physiological aspects of grain yield, concluded that yield is proportional to leaf area duration after ear emergence. Fischer and Kohn (1966b) found a high correlation between leaf area duration after flowering and yield in wheat in Australia. Although the high yielding F_5 plots had shorter leaves (table 17) this was compensated by more ears per unit area, and consequently more leaves. Also the high yielding plots flowered earlier. As grain filling occurs in increasingly dry conditions (see table 3 for rainfall and evaporation during September - November) all lines usually ripen at about the same time, except when occasional late rains benefit late maturing lines. With this exception, the length of time for grain filling is determined by the date of anthesis. The high yielding lines had a longer period of grain filling, and although they had shorter leaves, they had more of them. Therefore the results of this thesis do not conflict with the contention of Thorne (1966) and Fischer and Kohn (1966b) outlined above.

(C) Competitive ability and yielding ability.

The other main point that develops from these results on vegetative morphology and yield concerns the relationship between competitive ability in mixtures and the yielding ability of different genotypes in pure culture.

Certain authors (Wiebe et al. 1963, Jennings and Aquino 1968, Jennings and de Jesus 1968, Jennings and Herrera 1968, Donald 1968 a and b), suggest that there is a negative relationship between competitive ability in mixtures and yield in pure stands. In table 16 (p.105) it was shown that there was a positive correlation between characters that were considered to be indicative of competitive ability, (long leaves and tall plants) and yield in the F_3. However, in the F_5 at high nitrogen levels this situation was reversed (table 17, p.106). This suggests that the characters that were advantageous in a mixture were disadvantageous in pure culture. An attempt was made to examine this relationship in 1969; the border rows of the F_5 plots were harvested and it was possible to compare the relative performance of the genotypes both in pure culture (the central sample) and in competition with other genotypes (the borders of the plot).

All the regressions had a slope significantly less than 1 (table 21, p.115-6). This would mean that the higher yielding genotypes were poorer competitors than the lower yielding genotypes. But, as already pointed out, (p.114) to use the control plots to check this result showed that the regression of yield in pure culture against yield in mixtures was again significantly less than one in the control; in one comparison (with genotypes selected and tested at high nitrogen) the regression of the control plots was significantly less than that of the selections. This would mean that the competitive ability of the control variety changed with its yield. Though not impossible, this is unlikely and therefore other explanations must be sought.

Engledow and Ramiah (1930) found that yield per unit area of wheat was closely related to the number of plants per foot of row, and suggested that a considerable reduction in yield occurred because of local areas of low density. The inadequacies of this hypothesis were established by Fairfield Smith (1937). He showed that areas of higher than average density must on average be surrounded by areas of less than average density. The loss of yield associated with the areas of low density was compensated by the immediately surrounding areas of higher density.

This argument needs only slight modification to explain the results obtained in this experiment. Any plot growing in better than average soil would on average be surrounded by plots that were not on such good soil. Thus a high yielding sample area would be likely to have a lower yielding border. This, in the analysis used, would make the genotype appear to be of less than average competitive ability. The hypothesis similarly predicts the borders being higher yielding than the sample area when the sample area was low yielding.

This approach seems to explain adequately the results obtained with the control plots, and seriously undermines the technique of using border rows as a means of assessing the competitive ability of high or low yielding genotypes. This could only be determined with further experimentation. Nevertheless short plants with short leaves were lower yielding within the F_3 mixture, but higher yielding as pure cultures in the F_5 plots. This conforms with the view that poor competitors in mixtures are higher yielding in pure culture.

It is appropriate to consider why effective selection for yield was possible in the F_3 on the basis of vegetative morphology, but not on the basis of yield itself. The coefficient of variation for yield was less in the low density selection environment than in the other environments. It is suggested that this increase in the coefficient of variation at high densities is due to competition. Competition has not increased the coefficients of variation for the morphological characters (compare those for low density with the other F_3 selection environments, table 18, p.108). It therefore seems that competition had little confounding effect on the expression of these characters.

The nitrogen level had little effect on the relative expression of the vegetative characters. There are two sources of evidence for this. Table 15 shows that these characters were correlated between the F_3 and the F_5 generations in either the same or the alternate environment. In the F_5 the level of nitrogen therefore had little effect on the relative ranking of the genotype. The analysis of variance of the morphological characters (table 19, p.110-111) shows that although there was a large and very significant replicate effect in all the treatments, the error term was small. Thus the ranking of varieties by morphology did not change much between replicates. This was in marked contrast to yield (c.f. tables 8 and 9).

Morphological characters are therefore less affected by competition, genotype-season interaction and genotype-treatment interaction than is yield. It seems likely that, in this study, because of the relationship between vegetative morphology and yield, and the ability to select on the basis of morphology, it is possible to select indirectly for yield, where it is not possible to select directly in mixtures for yield on the basis of yield.

The other consistent result for characters measured in the F_3 and yield in the F_5 (table 14, p.99) was the negative correlation between seeds/ear in the F_3 nitrogen experiment and yield two generations later (table 14). This negative correlation is probably associated with the negative correlation for height. If competition was critical at the time of ear initiation, then one would expect that short plants would be at a competitive disadvantage, and have small ears. Some indication of this is obtained from table 25 (p.148) which shows the correlations between the vegetative characters and the yield components in the F_3 nitrogen experiment. It is apparent that there was a higher correlation between the vegetative characters and seeds/ear than between the vegetative characters and the other yield components. This suggests

Table 25 :

The correlations between the vegetative characters and yield components in the F_3 generation of the nitrogen experiment.

	Low Nitrogen (739 d.f)	High Nitrogen (1134 d.f)
Leaf length :		
Ears/plant	0.217 ***	0.262 ***
Seeds/ear	0.520 ***	0.388 ***
1000 gr. wt.	0.293 ***	-0.134 ***
Leaf height :		
Ears/plant	0.174 ***	N.S.
Seeds/ear	0.576 ***	0.448 ***
1000 gr. wt.	0.249 ***	-0.130 ***
Plant height :		
Ears/plant	0.170 ***	-0.070 *
Seeds/ear	0.680 ***	0.545 ***
1000 gr. wt.	0.396 ***	-0.083 **

that competition was most important when ear size was being determined. In Mediterranean environments light intensities are low during the period of ear initiation. The shorter plants in the F_3 therefore had fewer seeds/ear. The alternative hypotheses for this result are thus

(i) that the genetically small plant had genetically small ears and

(ii) that the small plants in the F_3 have small ears because they are less competitive than their taller neighbours, and therefore have less assimilates available for floret initiation.

The data support the second hypothesis, for if the first were correct then one would anticipate that the short high yield plants in the F_5 would have few seeds/ear. In fact in three out of four cases (table 17, p.106) in the nitrogen experiment F_5 yield was correlated with seeds/ear. It therefore appears that the negative relationship between seeds/ear in the F_3 and seed yield in the F_5 nitrogen experiment was due to competitive effects in the F_3 and not genetic effects.

(D) <u>The correlation between plant characters in the F_3 and F_5 generations.</u>

In the density experiment there are some positive relationships between vegetative characters in the F_3 and F_5 (table 15, p.103), but no consistent pattern is present. The difference between these results and those of the nitrogen experiment is difficult to explain. It appears that there was a genotype-season interaction in the density experiment, but not in the nitrogen experiment. This is an unsatisfactory explanation as it does not identify the underlying causes, only the end result; there is however no indication from the data available what the cause might be.

Harvest index was significantly correlated over generations, and in both the same and the alternate environment for the low density and low nitrogen selection environments (table 15, p. 103). These two environments had two factors in common. First competition for light between genotypes would not have been severe in either of these environments. Figure 6 shows the low nitrogen F_3 selection plot during grain filling and it is obvious that light was not an important limiting factor. At low density the distance apart between plants would ensure the same adequacy of light. Also both these selection environments had higher harvest indices than occurred in either high density or high nitrogen environments (table 5, p.76). The inheritance of harvest index needs further study to elucidate the results obtained here.

Of the remaining correlations only 1000 grain wt. was consistent. This character was correlated over generations in all comparisons except for those lines selected and tested at low density. As already pointed out this character is only slightly affected by the environment, and this seems to apply between seasons as well as between treatments.

Seeds/ear shows some correlation between the F_3 and the F_5 for lines selected at low density and tested at either high or low density. The correlation is however low and only accounts for some 5%

of the total variation. In the nitrogen experiment a significant inter-generation correlation was found for lines selected and tested at low nitrogen. This was the only environment that did not show a significant negative correlation between F_3 seeds/ear and F_5 yield (table 14, p.99). This confirms the suggestion made earlier (p.149) that the above negative correlations were not due to genetic effects, but to competitive relationships.

(E) The correlation between F_5 plant characters and F_5 yield.

In the density experiment the F_5 vegetative characters (leaf length, leaf height and plant height) did not show a consistent relationship with F_5 yield (table 17, p.106), although any significant correlations were negative (c.f. results of N experiment discussed p.139).

Not unexpectedly there was a high degree of association between biological yield and yield and between most of the yield components with yield. The exception to this was seeds/ear. In both low density test (F_5) situations there was no relationship between seeds/ear and yield. This may have been due to there being little competition in this environment so that each selection was fully able to express its potential. Yield for all genotypes would then be determined by the ability to produce fertile ears and large seeds. There are no data available that either confirm or disprove this hypothesis, and this warrants further study. In the nitrogen experiment there was one instance where there was also no correlation (lines selected (F_3) at low and tested (F_5) at high nitrogen). This result is very anomalous and no explanation is available as to why this should have occurred.

Of the other yield components in the F_5, ears per plant was more highly correlated with yield in the low density environment than at high density (0.744 and 0.760 as against 0.404 and 0.432). Although seeds per ear was not correlated with yield at low density, both it and 1000 grain weight were correlated at high density. The results not unexpectedly show that at low density yield was mainly determined by the number of ears per plant, whereas at high density this factor was less important, and the relative importance of seeds per ear and seed weight increased.

There was also a marked negative correlation between yield and maturity. This increased at high density.

In the nitrogen experiment the results were very similar to those of the density experiment, except that the differences between treatments were less. However the results for 1000 grain weight and maturity mirrored the density results. These characters were more important in the high leaf area treatments. This suggests that the finish to the growing season was more critical in determining seed weight in those environments which would potentially use more water. (c.f. the data of Luebs and Laag 1969 and Fischer and Kohn 1966 a and b showing greater water loss from treatments having a high leaf area index.) This explains the importance of early flowering under these conditions as it would enable grain filling to occur while the moisture relations of the crop were more favourable.

(3) General Discussion of the Results and Implications for Plant Breeding :

(A) Introduction.

In this experiment single plant selection on the basis of yield was not effective in identifying the high yielding genotypes. One must decide whether this result indicates that it is not possible ever to select on this basis, or whether the procedure would in other circumstances have a greater chance of success.

(B) Heterozygosity.

If heterozygosity was the reason for the failure of selection, then by not selecting till later generations, effective selection would then be assured. However this would appear to be a relatively minor component of the problem and that other causes of failure predominate.

(C) Genotype-environment interaction.

Genotype-environment interactions can have a large effect on (a genotype's) performance. Data from the Waite Institute breeding programme showed that there was no correspondence between the performance of barley genotypes in 1967 and in 1969. It is not surprising that single plant selection was not effective, when a genotype-seasons interaction of this magnitude was operative. The importance of this interaction is liable to be greater on single plants than on replicated plots, where local micro-environmental effects are less important.

It would seem that there is little hope of single plant selection on the basis of yield being effective in situations where successive seasons are very different from each other.

Genotype-treatment interactions were also large. This suggests that selection should always be carried out at commercial densities and fertility levels. It has been shown often (LeClerg 1966) that large fluctuations in the micro-environment occur over very short distances. This result was repeated in this experiment. Because at low density the sampling of the environment is relatively infrequent, there is no effective way of estimating and allowing for soil heterogeneity. The scale of the soil variation at low density is so large that the performance of a plant is dominated by the environment. This will seriously bias estimates of an individual's genetic worth. If the density of the selection environment is increased three things occur.

(1) The growing conditions are more similar to those found in commercial practice. The genotype-treatment interaction is therefore less.

(2) The environment is sampled more frequently and a better appraisal of the micro-environmental variation is obtained. This can be allowed for in estimating the genetic potential of a particular phenotype.

(3) The competitive ability on an individual becomes very significant in determining its performance in relation to other genotypes.

Therefore, although at commercial densities treatment interactions are removed and it is possible to obtain a better estimate of micro-environmental variation, it is the relationship between competitive ability in mixtures and yielding ability in pure culture, for any population, that will determine whether single plant selection on the basis of yield, for yield in future generations, will be effective.

(D) Bulk populations.

Using the relationship, proposed on pages 24-28, it is possible to predict what would happen, over generations, to populations having different yield/competitive relationships.

If the slope of the line relating yield in pure culture to yield in mixtures (see fig. 2, p. 26) was positive, then over generations, the average yield of the population would rise as the genotypes that yielded less in both pure culture and in mixtures were eliminated. If the slope of the relationship was zero then no change in the yield or composition of the population would occur. If it was negative, the yield of the population would be expected either to rise or to remain constant as the proportion of genotypes that were highly competitive, and consequently high yielding in mixtures but low yielding in pure culture, increased. At an undefined critical point the percentage of these would be sufficient to cause mutual suppression and the yield of the population, with further cycles of natural selection, would fall.

Using a carefully conducted yield trial it would be possible to discover whether the yield of segregating populations relative to control varieties, was changing. The direction and magnitude of the changes would indicate the type of competitive ability/yield relationships of the population. With this information a rational approach to single plant selection on the basis of yield within these populations could be formulated. For example, if the yield of the population increased steadily with time, this would indicate that the genotypes that were both high yielding in mixtures and in pure culture were being retained. Within this type of population single plant selection for high yielding phenotypes should, on average, be effective in increasing the percentage of high yielding genotypes.

If the slope of the relationship between yield and competitive ability was zero, then single plant selection on the basis of yield would be equivalent to random selection. This would seem to be the case in the experiment reported here.

If the slope of the relationship was negative this would indicate that selection of the low yielding phenotypes would be effective in selecting for genotypes that would be high yielding in pure culture. This conclusion is similar to that of Wiebe et al. (1963) and provides an explanation for his conclusion.

Besides allowing rational consideration of how to select effectively within populations the suggested relationship also permits some discrimination between populations. If the yield of a bulk population is increasing with time, then selection within that population may be delayed without the loss of genotypes that would be high yielding in pure culture from the bulk population. The proportion of these high yielding genotypes will increase with time.

If on the other hand the yield of the bulk is decreasing, but there are desirable characters within the population, it is important that selection should occur in early generations for low yielding individuals which have the other desirable characters.

In all other cases where selection is for yield, any bulk population that has either a constant yield with time, or a falling yield, should be discarded.

The above theoretical discussion, concerning selection within bulk populations for yield in pure culture has not, as far as I am aware, been tested in practice. If successful, it would provide a rational method for handling these populations. To ensure success sowing must be accurate so that the yield of individuals is not confounded by varying distances between plants. This requirement should not be difficult to obtain using precision planting techniques.

(E) Breeding for variable environments.

Because single plant selection can only occur in one environment, this will tend to pick out genotypes suited to that particular environment. Single plant selection cannot be used to select for ability to perform well ower a range of environments. If this is required selected lines must be tested over a range of sites to select those lines that are adapted to a range of environments.

Single plant selection as a positive selection technique, will be most effective in very uniform environments, for example in glass house crops (c.f. discussion of differences between animal and plant selection experiments, p.38).

(F) Density for selection.

In this discussion it has been pointed out that selection should be at commercial densities. This may not be absolutely correct, but on the basis of present evidence, is more likely to be successful than any other density. In any crop the yield per unit area initially increases linearly with increasing density. As competition occurs so the total dry weight of the individual starts to fall. This continues to the point where any increase in plant numbers is exactly balanced by a corresponding decrease in plant weight. Donald (1963) gave many examples of this relationship and showed that for a very wide range of densities there was little change in biological yield, although (in some cases) seed yield fell slowly with increasing density past an optimum.

Farmers tend to sow their crops at a high density as an insurance against the possible loss of individuals. The use of commercial densities may thus cause an unnecessary increase in the confounding effects of competition. It would seem that the optimum density for selection is the lowest at which the maximum grain yield per unit area is obtained. At this density the plants' environment is similar to crop conditions, but competitive effects will be lessened, a good estimate of micro-environmental effects would also be obtained.

(G) Indirect selection for yield.

The results showed that in some environments indirect selection for yield was more effective than direct selection. This raises two points. Firstly why was indirect selection effective in one environment and not in the others, and secondly what implications do the results have for single plant selection.

It was found that there was a significant negative correlation between F_3 vegetative characters and F_5 yield at high nitrogen levels. The characters suggest differences in lodging resistance, net photosynthetic efficiency of the canopy and water use. These characters would be of major importance in situations where plants were tall and had high leaf area indices.

This relationship did not apply at low density where the main factor limiting yield was the lack of ears per unit area. This character was not correlated over generations (table 15, p. 103) and therefore indirect selection was not effective. At low nitrogen the level of available nitrogen was the chief limitation to growth and grain yield. There was little reason to expect that the morphological characters used in this experiment would indicate which plants were more efficient at absorbing or utilizing nitrogen and which would be at an advantage. Indirect selection therefore would not be effective.

In the high density situation the plants were tall and there was a high leaf area index, therefore one might expect the characters that were effective in predicting yield at high nitrogen to be effective here. However there was some evidence that the high density treatment was also nitrogen deficient as the plots looked a paler green, even though 65 kg. N per ha. was applied to the plots. It would seem that competition for nitrogen, or the interaction between competition for nitrogen and for light, was sufficient to destroy any relationship between yield and morphology.

The reasons why the morphological characters used were successful in predicting yield in pure culture at high nitrogen whether selected at high or low nitrogen are firstly that they were related to the plants ability to perform well at high nitrogen. Short plants were not so liable to lodge. There would be better light relations within the canopy, and therefore more photosynthesis throughout the growing season. Also the leaf area index was possibly less with a consequent reduction in water loss. The short plants flowered earlier and therefore had a longer and more favourable grain filling period. Also the vegetative characters used were little affected by competition, and had only small genotype-season, or genotype-treatment interactions. They were inherited.

The results of indirect selection show that it could be a way of improving the efficiency of selection for yield in either a bulk or a pedigree breeding programme. The problem lies in defining characters that are indicative of future performance. In this study the characters chosen affected the light and lodging relationships of individuals. It would now be possible to screen F_2 populations on the basis of plant height. All short plants could be retained, or perhaps only those short plants that were high yielding. The advantage of this system is that very large populations could be screened, and only those having the desired characters need be retained. The proportion of high yielding genotypes within the population would be increased thereby and so improve the breeders' chances of identifying high yielding lines.

It is important that plant breeders and crop physiologists should consider other characters that may be of potential use in the early screening of populations, and test them to see if they are effective. This need not be a laborious process, for if the character is simple to score, then selection is rapid. Selected lines may then be tested as a bulk and the yield compared with that of the unselected population. If indirect selection was effective, then the selected lines will be higher yielding than the bulk. Using studies of this type it would be possible to assess a range of characters with little effort. In this way the plant breeder would be able to test out the ideas of the crop physiologists without committing himself to a major breeding programme based on ideotype characters before these had been adequately tested for his specific crop and environment.

CONCLUSIONS.

(1) Single plant selection in the F_3, on the basis of yield, was not effective in this experiment. Further analysis suggests that the reasons for this result vary with the environment:

(A) The genotype-seasons interaction was very important in all the environments used. This was measured indirectly, as it was not possible to estimate the genotype-seasons interaction using the F_3 individuals.

(B) In non-competitive situations, (low density) it was not possible to measure the local soil variation with any precision. As the micro-environmental variation can be large over short distances (40 cm) this means that the phenotype will not be indicative of genotype.

(C) In competitive situations (high density and high and low nitrogen), where a more precise estimate of localised variation is obtained, localised variation was no longer the major confounding factor, competition was more important.

(D) Points (B) and (C) above show why the use of response surfaces and moving means to estimate environmental effects in the F_3 were not effective. At low density the estimate of the local variation was not precise, and when the density of planting was increased, competition became more important than local micro-environmental variation.

(E) Heterozygosity did not appear to be a major confounding factor in this experiment, although little data were available to confirm this.

(F) Because it is not possible to estimate and allow for the genotype-seasons interaction, at low density for the micro-environmental variation, and at high density for the competitive effects, when selecting on the basis of yield it is unlikely that single plant selection for yield will ever be effective, unless there is a positive relationship between the yield of the genotypes in pure culture and in mixture (see (4) below).

(2) Indirect selection for yield, on the basis of vegetative characters (leaf length, leaf height and plant height), was more successful than direct selection in the nitrogen experiment, when the selected lines were tested at high nitrogen.

(A) Short plants with upright leaves were more efficient than tall plants with floppy leaves in the high nitrogen F_5 test environment. Further analysis suggests the possible reasons for this result were:

(a) potentially less lodging susceptible,
(b) potentially more efficient photosynthetically,
(c) potentially used water more efficiently,
(d) earlier and therefore had a longer and more favourable grain filling period.

It was not possible within this experiment to differentiate between these.

(B) The vegetative characters were less affected by

(a) competition,

(b) genotype-season interaction,

(c) genotype-treatment interaction,

than was yield. As there appears to be a causitive relationship between plant type and yield in pure culture, it was therefore possible to select more effectively on the basis of plant type in mixtures, than it was on the basis of yield.

(3) The data indicated a negative relationship between competitive ability and yield in the nitrogen experiment. This was demonstrated by the fact that high yielding F_3 individual plants had tall, long leaved plants, whereas in pure culture in the F_5, at high nitrogen, high yield was associated with short statured, short leaved plants. Unfortunately the comparison of the yield of the borders, with the yield of the central test area, to confirm this relationship proved inadequate.

(4) A technique is proposed for estimating the average competitive relationships within a population. Using this it should be possible to predict whether a bulk population would be expected to improve with time. If it does improve with time then the yield in pure culture is positively associated with yield in mixtures. In this circumstance alone, single plant selection should prove effective.

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APPENDIX 1.

The 1968 F_5 Experiment.

Figure 5 of the sequence of the experiment shows that there was an F_4 summer multiplication followed by an F_5 yield trial in 1968. This was not a successful experiment, and will only be reviewed briefly.

Methods and Materials.

The details of the site, the season, the cross, the seed source and the F_3 generation were given in the methods and materials section of the thesis, and will not be repeated.

(1) The F_4 generation (January - May 1968).

In an attempt to save time, an out of season multiplication generation was grown during the summer of 1968. This was sown on the 18th January. In the next two months there were 28 days having a maximum shade temperature above 32°C (90°F) of which three were over 43°C (110°F). The early lines did not tiller and came rapidly into head. Anthesis occurred during hot weather and little or no seed was set. The mid season lines produced moderate quantities of seed and the late lines failed to mature as the season 'broke' early and it was cold and wet in April and May. The sample of seed available for planting in the F_5 was not representative of the original F_3 population. Both the early and late lines had been eliminated. In the case of the high density F_3 selection environment only three lines from the lower half of the yield range survived into the F_5.

(2) The F_5 generation (1968).

(a) The treatments, planting method, plot size, and harvest, were the same as those used in the 1969 F_5 yield trial. The characters measured were the same as those measured in the F_3 selection generation.

(b) Plant growth in the F_5 (1968).

(i) Emergence and survival.

The seed used was discoloured and shrivelled and emergence was poor. Survival to harvest was 74% over all treatments.

(ii) Diseases.

Mildew may have affected the accuracy of the 1968 results.

(iii) Lodging.

A string network similar to that in the F_3 was used. This support proved to be inadequate and severe lodging occurred. An attempt was made to pull the plants up by using wires threaded through the crop but this failed.

(c) The F_5 field arrangement.

In the density experiment seed was available for two replicates. These contained 47 lines from the low density and 44 lines from the high density F_3 selection environments. In the nitrogen experiment seed was available for only one replicate. This contained 51 lines from the low nitrogen and 72 lines from the high nitrogen F_3 selection environment. The experimental design was a randomised block.

Results.

The 1968 F_5 yield trial had many limitations, which were outlined in the last section. Because of these, the analysis of the results has been confined to a comparison of the F_3 characters and the F_5 yield. The results are given in table A1.

TABLE A1 :

Correlations between F_3 plant characters in 1967 and F_5 plot yield in 1968.

Density experiment.

Selection environment (F_3)	Low Density		High Density	
Test environment (F_5)	Low D.	High D.	Low D.	High D.
Yield	N.S.	N.S.	N.S.	N.S.
Actual deviation from surface	N.S.	N.S.	N.S.	N.S.
Relative " " "	N.S.	N.S.	N.S.	N.S.
Ears/plant	N.S.	N.S.	N.S.	-0.333 *
Seeds/ear	N.S.	N.S.	N.S.	0.294 *
1000 grain weight	0.299 *	0.443 **	N.S.	N.S.
Biological yield	N.S.	N.S.	N.S.	N.S.
Harvest index	N.S.	N.S.	N.S.	N.S.
Leaf length	N.S.	N.S.	N.S.	N.S.
Leaf height	N.S.	N.S.	N.S.	0.335 *
Plant height	N.S.	N.S.	N.S.	N.S.

TABLE A1 (cont.) :

Nitrogen experiment.

Selection environment (F_3)	Low Nitrogen		High Nitrogen	
Test environment (F_5)	Low N.	High N.	Low N.	High N.
Yield	0.299 *	0.290 *	0.249 *	N.S.
Actual deviation from surface	0.302 *	0.284 *	0.278 *	N.S.
Relative " " "	0.314 *	0.284 *	0.276 *	N.S.
Ears/plant	0.306 *	N.S.	N.S.	N.S.
Seeds/ear	0.294 *	0.347 *	0.249 *	N.S.
1000 grain weight	N.S.	0.282 *	N.S.	N.S.
Biological yield	0.291 *	N.S.	0.257 *	N.S.
Harvest index	N.S.	N.S.	N.S.	N.S.
Leaf length	N.S.	N.S.	0.271 *	N.S.
Leaf height	N.S.	0.359 **	N.S.	N.S.
Plant height	N.S.	0.302 *	N.S.	N.S.

The following points are of interest:

(1) The density results are similar to those obtained in 1969, in that they show little significance or consistency.

(2) In the nitrogen experiment there was a significant positive correlation between F_3 and F_5 yield in three out of four cases (c.f. table 12).

(3) The use of actual or relative deviations from the response surface did not improve these correlations.

(4) The correlations between morphological characters and yield were all positive (c.f. table 14).

(5) There was a positive correlation between seeds/ear and seed yield in three out of four cases.

The results pointed out in (2), (4) and (5) above are in direct contrast with the 1969 nitrogen experiment results (table 14). The implications of this will be considered in the discussion, but it must be remembered that the results reported here have several major experimental weaknesses.

Discussion.

In the nitrogen experiment in 1968 there was only one replicate, the results therefore cannot be interpreted with confidence. This apart, it is interesting to note the contrast with the 1969 results. F_3 yield was positively correlated with F_5 yield in three out of four comparisons. The response surface however had no effect in improving the F_3/F_5 yield correlations. This was not surprising, because as pointed out on page 138, competition will have an important confounding effect at this density, and this would compensate for any reduction in the micro-environmental effects that the surface might account for.

Of the morphological characters leaf and plant height were positively correlated with yield in the F_5, for lines selected at low and tested at high nitrogen. This result is in contrast to the 1969 result, where all lines tested at high nitrogen had negative correlations with these morphological characters (table 14). The result also agrees with the correlations within the F_3 (table 16), of morphology and yield.

It would appear that in 1968 at high nitrogen competitive ability and yield were positively associated. Perhaps the reason for this was that in 1968 the high nitrogen treatment lodged severely, and the taller plots on average suffered less from the smothering effects of lodging than the shorter plots.

A similar explanation fits the reversal in correlation that occurred between seeds per ear in the F_3 and yield in 1968 and 1969. The results showed that plots derived from the more competitive F_3 plants were at an advantage in 1968 and therefore yielded more.

APPENDIX 2.

A sample of the basic data lodged with the library of the Waite Agricultural Research Institute.

The order of the data. (Treatments.)

The data from each F_3 selection environment is followed by the corresponding data for the F_5 derived lines in the same environment and then for the F_5 derived lines in the alternative environment. The order of the treatments is shown below:

F_3	Plants from the low nitrogen selection environment	3 pages
F_5	Lines from F_3 low N tested at low N (same)	3 pages
F_5	Lines from F_3 low N tested at high N (alt.)	3 pages
F_3	Plants from the high nitrogen selection environment	3 pages
F_5	Lines from F_3 high N tested at high N (same)	3 pages
F_5	Lines from F_3 high N tested at low N (alt.)	3 pages
F_3	Plants from the low density selection environment	3 pages
F_5	Lines from F_3 low D tested at low D (same)	3 pages
F_5	Lines from F_3 low D tested at high D (alt.)	3 pages
F_3	Plants from the high density selection environment	3 pages
F_5	Plants from F_3 high D tested at high D (same)	3 pages
F_5	Plants from F_3 high D tested at low D (alt.)	3 pages
	TOTAL	36 pages

The order of the data. (Within treatments.)

For each set of data (treatments) there were 100 plants (for the F_3) or 100 derived lines (for the F_5). On the first and second pages of each set of data there is information on 33 plants or lines and on the third page there is information on 34 plants or lines. The F_3 data refers to a single plant, whereas the F_5 data is the mean of three replicates.

On each page there is the following information for each plant or derived line:

Line name : A code for identifying plants and their derived lines.

Leaf length (cm) : The length of the penultimate leaf on the main stem, in the case of F_3 plants, and the mean of four plants per replicate chosen at random, in the case of F_5 lines.

Leaf height (cm) : The height of the auricles of penultimate leaf on the main stem from the ground, the conditions the same as for leaf length.

Plant height (cm) : The height of the node at the base of the ear from the ground, the conditions the same as for leaf length.

Biological yield (Biol. yield) (gm) : The total dry matter yield of the plant or plot.

Ears/plant : The number of ears per plant or per plot.

Grain yield (gm) : The seed yield per plant or per plot.

Harvest index (%) : The grain yield/biological yield x 100.

Seeds/ear : The seed number/ears/plant or /plot.

1000 gr. wt. (gm) : The weight of 1000 grains.

Maturity (Mat.) : Applies only to F_5 plots and measured in half weeks from an arbitrary date.

Table A2 shows a small sample of the original data. It contains the first page of the F_3 low nitrogen selection environment data and the corresponding data for the F_5 derived lines in the same and alternative environments.

TABLE A2 :

F_3 data Low Nitrogen (0 kgs N/Ha) - Sheet I

Line name	Leaf length cm	Leaf ht. cm	Plant ht. cm	Biol. yield gm	Ears/ plant	Grain yield gm	Harvest index %	Seeds/ ear	1000 grain wt.
0111	8.7	37	60	2.1	1	1.0	47.6	20.0	50.0
0112	11.1	36	60	3.2	2	1.4	43.7	14.5	48.3
0122	9.4	42	63	1.8	1	0.8	44.4	17.0	47.1
0130	11.6	39	65	3.5	2	1.5	48.4	15.5	48.4
0212	7.4	31	52	4.5	3	2.3	51.1	14.7	52.3
0213	12.0	39	66	2.2	1	1.0	45.6	20.0	50.0
0225	10.3	36	58	5.3	3	2.6	49.1	17.7	49.1
0231	11.3	50	76	5.5	2	2.3	41.8	22.5	51.1
0425	14.9	45	70	3.4	2	1.5	44.1	19.0	39.4
0426	7.8	32	48	1.0	1	0.5	50.0	11.0	45.5
0527	12.8	46	72	3.2	2	1.4	43.7	15.5	45.2
0531	12.6	50	76	7.2	3	3.3	45.8	22.6	48.5
0728	12.0	48	76	4.4	1	1.0	22.7	19.0	52.6
0734	10.5	42	67	1.7	1	0.7	41.2	13.0	53.8
0835	10.8	35	52	2.9	3	1.1	37.9	9.7	37.9
0931	11.8	41	61	3.0	2	1.5	50.0	15.0	50.0
1032	12.9	51	76	6.7	3	2.8	41.8	18.3	50.9
1135	15.7	45	71	6.4	3	3.4	53.1	23.0	49.3
1432	11.9	44	66	1.6	1	0.7	43.7	15.0	46.7
1535	14.3	38	61	2.1	1	1.0	47.6	22.0	45.5
1930	12.1	45	71	5.9	3	2.5	42.4	18.0	46.3
1932	11.2	34	56	6.2	4	3.2	51.6	16.0	50.0
2106	10.4	41	58	3.7	2	1.7	45.9	15.5	54.8
2107	8.4	36	58	3.2	2	1.6	50.0	16.5	48.5
2108	14.7	31	61	3.2	2	1.3	41.9	14.5	44.8
2109	15.0	45	75	7.5	4	3.4	45.3	19.5	43.6
2131	11.6	42	66	1.7	1	0.8	47.1	17.0	47.1
2204	11.0	43	67	1.7	1	0.8	47.1	16.0	50.0
2209	11.4	47	73	1.8	1	0.5	27.8	18.0	27.8
2210	13.7	46	79	4.8	2	2.1	43.7	19.5	53.8
2211	10.2	41	61	3.1	2	1.5	48.4	18.5	40.5
2227	10.9	36	66	4.9	3	1.9	38.8	15.3	41.3
2231	11.9	35	63	3.0	2	1.3	43.3	13.5	48.1

TABLE A2 (cont.) :

F_5 Plot data (F_3 Low N, F_5 Low N) - Sheet I

Line name	Leaf length cm	Leaf ht. cm	Plant ht. cm	Biol. yield gm	Ears/ plot	Grain yield gm	Harvest index %	Seeds/ ear	1000 grain wt.	Mat.
0111	14.5	46.8	84.5	89.2	70.0	38.2	42.8	12.2	45.2	3.0
0112	20.3	65.2	107.9	123.2	49.7	45.2	36.7	20.1	46.0	6.0
0122	23.0	71.7	110.3	117.3	51.0	39.1	33.3	17.5	43.9	6.0
0130	21.8	69.7	107.5	135.9	51.7	48.0	35.3	21.6	43.1	6.0
0212	15.9	58.7	95.8	136.1	68.3	50.6	37.2	17.8	42.8	6.3
0213	18.7	66.4	109.4	108.7	42.3	42.5	39.1	20.8	48.1	5.3
0225	15.4	50.7	85.4	114.0	65.3	49.7	43.6	17.4	43.7	3.0
0231	19.4	64.0	101.2	122.7	47.0	43.1	35.2	20.8	44.6	6.0
0425	22.7	66.9	99.3	106.6	47.3	32.3	30.3	15.8	43.6	6.0
0426	18.8	55.1	88.8	126.4	59.0	50.3	39.8	18.5	46.4	4.7
0527	20.4	67.5	106.4	99.0	42.7	35.9	36.3	18.7	45.1	5.7
0531	20.8	72.2	106.2	161.9	61.7	52.7	32.5	20.6	41.5	5.3
0728	20.8	70.4	108.8	150.5	56.3	44.2	29.3	17.6	44.6	6.0
0734	18.9	69.7	103.2	151.1	62.3	50.5	33.4	19.3	44.3	6.0
0835	17.4	54.0	96.5	114.1	55.0	43.7	38.3	16.8	47.7	6.0
0931	21.4	54.7	94.2	126.3	58.3	49.4	39.1	18.0	47.0	4.3
1032	22.1	71.6	105.5	110.1	36.3	35.3	32.0	21.4	42.5	6.0
1135	21.4	55.7	86.3	144.7	61.3	55.3	38.2	19.2	48.7	5.7
1432	19.9	64.5	101.9	122.1	52.7	42.0	34.4	22.3	36.6	5.7
1535	20.7	56.8	91.7	114.8	59.0	47.4	41.3	17.6	45.6	6.0
1930	19.3	69.8	105.7	138.8	51.7	46.7	33.7	21.4	42.6	5.7
1932	17.4	54.4	85.6	122.6	59.0	46.4	37.8	17.1	45.6	3.7
2106	17.7	55.8	83.8	116.5	58.0	49.8	42.8	17.8	48.8	3.3
2107	15.5	51.3	85.4	98.9	54.3	41.1	41.5	15.4	49.7	3.7
2108	18.1	68.6	104.8	128.7	47.3	39.3	30.5	21.0	40.0	6.0
2109	17.4	62.3	92.0	79.5	44.0	30.5	38.3	17.1	39.9	5.3
2131	20.3	68.7	107.4	132.3	49.7	48.9	36.9	22.2	45.6	6.0
2204	18.9	66.0	104.7	100.0	39.0	38.4	38.4	21.4	46.5	6.0
2209	20.5	68.7	112.2	132.4	52.3	50.4	38.1	21.0	46.4	5.7
2210	18.5	64.4	102.2	122.3	55.7	42.7	34.9	18.9	42.2	5.7
2211	17.8	62.9	90.2	125.9	56.7	53.1	42.2	22.5	41.7	6.3
2227	19.3	64.9	106.4	129.5	50.3	49.2	38.0	20.5	47.6	6.0
2231	19.8	59.1	95.2	132.7	59.7	44.4	33.4	15.0	49.8	5.7

TABLE A2 (cont.) :

F_5 Plot data (F_3 Low N, F_5 High N) - Sheet I

Line name	Leaf length cm	Leaf ht. cm	Plant ht. cm	Biol. yield gm	Ears/ plot	Grain yield gm	Harvest index %	Seeds/ ear	1000 grain wt.	Mat.
0111	19.9	76.9	105.2	132.5	81.7	44.4	33.5	14.3	37.5	2.7
0112	25.8	91.7	123.3	106.9	38.3	25.5	23.8	18.0	35.0	6.0
0122	24.8	89.2	121.7	80.4	26.7	19.1	23.8	18.3	33.7	6.3
0130	24.1	92.7	126.5	86.5	35.3	24.7	28.6	17.2	39.7	5.3
0212	22.4	64.1	96.4	104.1	61.7	25.2	24.2	12.4	31.7	6.0
0213	25.2	93.0	123.4	96.9	43.7	24.5	25.3	16.2	34.7	6.0
0225	21.7	74.6	107.0	129.2	81.0	40.1	31.1	12.7	39.9	3.3
0231	24.7	92.2	118.1	81.7	29.0	19.1	23.4	15.9	37.3	6.7
0425	28.1	89.7	118.2	150.6	61.0	42.6	28.3	18.6	37.7	5.7
0426	24.9	83.7	111.4	147.4	60.0	54.4	36.9	20.5	44.5	4.0
0527	24.8	87.2	123.7	74.9	26.7	15.3	20.4	17.0	33.1	6.0
0531	23.4	88.6	120.7	129.1	50.3	38.0	29.5	19.7	38.2	6.0
0728	25.7	87.8	119.7	116.6	47.3	25.7	22.1	14.9	35.7	5.7
0734	23.1	86.5	114.5	126.1	64.3	40.2	31.9	15.7	40.0	5.7
0835	21.7	81.9	110.0	118.0	56.7	33.4	28.3	15.4	38.4	6.3
0931	21.5	80.0	109.1	122.5	53.7	36.1	29.4	14.5	46.0	3.7
1032	27.3	95.3	121.7	97.9	41.3	26.9	27.4	17.7	36.2	6.0
1135	24.5	87.7	107.2	136.4	63.3	37.0	27.1	15.8	37.2	5.7
1432	23.0	85.3	109.7	129.4	59.0	38.3	29.6	16.2	40.2	6.0
1535	24.7	81.7	107.8	127.2	65.7	39.7	31.2	16.4	36.6	5.3
1930	25.3	93.9	120.3	89.3	32.0	24.5	27.5	20.5	39.5	6.0
1932	21.6	77.3	108.4	154.7	79.3	52.5	33.9	16.8	39.3	3.7
2106	19.3	76.0	101.3	134.6	75.0	49.0	36.4	15.1	43.4	2.0
2107	19.1	75.2	105.1	154.4	73.7	52.6	34.1	16.5	43.5	2.7
2108	26.1	92.9	121.3	115.6	47.0	30.2	26.1	17.9	35.8	6.0
2109	25.2	85.2	114.1	127.6	66.0	38.2	29.9	16.1	36.3	4.7
2131	26.0	90.0	121.0	109.3	44.0	29.1	26.6	17.5	36.6	6.3
2204	26.1	92.5	121.7	90.5	34.7	20.9	23.1	16.1	36.2	6.0
2209	26.7	93.3	126.2	73.2	25.7	16.7	22.8	18.6	34.5	6.7
2210	23.9	83.3	121.8	141.3	56.0	38.4	27.1	18.6	36.7	5.7
2211	23.4	83.0	106.3	116.1	60.7	35.3	30.4	17.2	34.2	6.7
2227	24.7	90.3	123.7	77.7	39.0	20.4	26.2	16.0	33.1	6.0
2231	22.4	76.1	107.7	123.5	60.7	35.8	29.3	15.6	38.5	6.0

APPENDIX 3.

TABLE A3 :

The values of the non-significant correlations given in table 12.

DENSITY EXPERIMENT :

Selection environment (F_3)	Low Density		High Density	
Test environment (F_5)	Low D.	High D.	Low D.	High D.
Actual yield	0.13	-0.08	0.00	-0.01
Yield using the response surfaces :				
Actual deviation	0.09	-0.00	0.00	-0.02
Relative deviation	0.11	0.03	-0.02	-0.02
Mean of act. and rel. dev.	0.08	0.01	-0.04	0.06
Yield using the moving means :				
Actual deviation side 3	0.07	0.00	-0.03	-0.03
" " " 5	0.10	0.01	-0.02	-0.02
" " " 7	0.09	0.01	-0.01	-0.01
Relative deviation side 3	0.09	0.02	-0.05	-0.06
" " " 5	0.11	0.03	-0.01	-0.00
" " " 7	0.10	-0.01	-0.01	-0.01

TABLE A3 (cont.) :

The values of the non-significant correlations given in table 12.

NITROGEN EXPERIMENT :

Selection environment (F_3)	Low Nitrogen		High Nitrogen	
Test environment (F_5)	Low N.	High N.	Low N.	High N.
Actual yield	-0.02	-0.00	0.02	-0.03
Yield using the response surfaces :				
Actual deviation	-0.07	-0.01	0.03	0.05
Relative deviation	-0.07	-0.01	0.05	0.08
Mean of act. and rel. dev.	-0.02	0.08	0.01	0.05
Yield using the moving means :				
Actual deviation side 3	-0.06	-0.01	0.02	0.08
" " " 5	-0.03	-0.02	0.01	0.06
" " " 7	-0.02	-0.02	0.04	0.07
Relative deviation side 3	-0.05	-0.02	0.03	0.08
" " " 5	-0.03	-0.03	0.01	0.06
" " " 7	-0.02	-0.01	0.05	0.08