SELECTION FOR YIELD AND OTHER CHARACTERS IN WHEAT

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SUMMARY

Aspects of selection for yield and other characters in wheat were investigated using lines derived from the F_2, F_3, F_4 and F_5 generation of two wheat crosses, all lines being obtained by random pedigreed selection. The lines were grown in plots at two sites over two years. In the first year, only F_2 and F_3 derived lines were available, but in the second year the F_2 to F_5 was grown. Single plants in the F_2, F_3 and F_4 were also studied in one year. The other characters measured were plant height, heading date, harvest index, flour yield and pearling resistance (a measure of grain hardness).

Correlations between generations, and the variance within lines for each generation were determined. Selection in different generations was simulated on the data. These results assessed the effectiveness of selecting in the F_2 to F_4 in one environment, for performance in the same and different environments. The most efficient breeding method could then be devised.

The conclusions from the study were:-

1. Correlations between lines in one generation, and the mean of lines derived from them in a following generation, increased as the generations were advanced.

2. Correlations between consecutive generations were higher than those between generations two or three generations apart.

3. The correlations between generations were lower for grain yield than for other characters.

4. Correlations between F_2 and F_5 derived lines, which indicate the effectiveness of selecting F_2 lines, varied from 0.10ns to 0.49^{**} for grain yield, when lines from both generations were grown in the same environment. Selecting the best 20 per cent of the F_2 derived lines gave

F_5 lines that exceeded random selection by 8 to 20 per cent. These lines were 14 to 23 per cent better than the mid-parent in one cross, but were less than the mid-parent in the other cross.

5. Correlations between the F_2 and F_5 for flour yield were 0.65^{**} to 0.70^{**}. The F_5 derived lines obtained by selecting the best 20 per cent F_2 derived lines had flour yields of 58 and 60 per cent for the two crosses, compared with mid-parental values of 54 and 58 per cent.

6. It was suggested from these results that the degree of homozygosity in a particular generation determines the predictive value of that generation.

7. As the generations were advanced and greater homozygosity was achieved, the variability within lines was reduced. It was suggested that more accurate predictions of the performance of homozygous lines may be obtained by delaying testing until an appropriate level of homozygosity and homogeneity is achieved.

8. The rate of decrease in variability within lines was the same for grain yield as for the simply inherited characters. This was contrary to theoretical expectation. If yield is governed by many genes it should take more generations of selfing to achieve uniformity.

9. The genetic variance of the F_2 generations as measured by the difference in variance between the parents and F_2's, was smaller than expected on the basis of quantitative genetic theories. The magnitude of this variance may be underestimated, because the environmental variance, as estimated from the parents, may be larger than the environmental variance component of the F_2.

10. Contrary to some theoretical proposals, the same improvement in yield will be obtained by selecting in early or late generations. While high yielding genotypes may be lost by delaying selection, this is counteracted by the better predictive value of late generations due to their greater homozygosity and homogeneity.

11. Correlations between years of lines from the same or different generations were low and often non-significant for grain and flour yield, whereas correlations for plant height, heading date and pearling resistance were high. Response to selection for grain yield, measured in a different year, was little better than random selection. The effect of different sites also reduced the improvement from selection for grain yield. Selection for grain and flour yield should be based on performance at a number of sites in different years.

12. Selection for improvement of grain yield using harvest index was no more effective than selection for yield directly, when considered across years.

Aspects of choosing suitable sites for testing crossbred material were investigated. The relationship between sites in the states of South Australia and Victoria, and the whole of Australia were examined using data from the state Departments of Agriculture and the Australian Interstate Wheat Variety Trials. Principal component analyses were used to investigate the grouping of sites based on similarities of varietal performance. Conclusions from these investigations were:-

1. Subregions within the Australian wheat area could be defined, these being northern, southern and western regions. The differences between extreme sites in Australia in one year were greater than the differences between years for any one site.

2. No subregions could be detected within South Australia or the main wheat areas of Victoria. The differences in the sites between years in these regions were generally greater than the differences between sites within one year. In favourable years most sites gave similar results, but in stress years each site was different.

3. Sites that represent contrasting environments within a breeding region should be chosen for testing lines in the early generations.

Performance at these sites in one year will give only a limited indication of performance in different years, and trials in several years are necessary. The effects of different years for one region could probably be obtained in one year by choosing appropriate sites elsewhere in Australia.

On the basis of all results, it was concluded that the most effective method of improving yield should be to isolate lines in an early generation e.g. the F_2, and select these on the basis of tests at different sites in different years. In this system, lines from early generations are tested, not for theoretical reasons proposed in the literature, but to enable testing across environments as soon as possible.

STATEMENT OF ORIGINALITY

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

Bryan Whan

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INTRODUCTION

In recent years the efficiency of traditional breeding methods for improving grain yield, such as the pedigree method, has been questioned. These methods often rely on the ability of a breeder to recognize the high yielding genotypes, but this ability is apparently limited. The wheat crop in Australia has undergone a relatively high level of improvement, and further increases in yield may be harder to achieve. It is apparent that if improvement is to continue, more objective methods of selection are required. Developments of sowing and harvesting equipment and computer systems over the past decade have made it possible to test large numbers of lines for yield. New breeding methods, based on yield measurement rather than observation, can therefore be developed.

Theoretical considerations suggest that selection for yield should be carried out in as early a generation as possible, because the proportion of plants with the most desirable combination of genes, in a homozygous or heterozygous state, decreases rapidly with advancing generations. In addition, selection in early generations should be the most efficient method, as only the best lines are retained through the segregating generations. However, when this method has been assessed experimentally, results have been inconsistent, and the advantage over other methods has not been as great as expected.

Past experiments that have assessed the value of selecting lines from early generations have usually compared an early generation with only one later generation. In addition, genotype x year interactions have often confounded the results. These experiments have answered some specific questions regarding selection for yield in a particular generation, but there is a need for a comparison of the value of selection for yield in various generations.

This thesis investigates aspects of selection for grain yield, and other characters, with particular emphasis on comparing the effectiveness of selecting in early generations with later generations. The studies have included the effects of selecting and testing in different years and at different sites, as well as in identical environments. The results were used to assess the theories that have formed the basis for some important breeding methods.

These studies should provide information so that the most effective method of breeding for yield can be devised.

Chapter 1

LITERATURE REVIEW

INTRODUCTION

The pedigree, bulk and single seed descent methods of breeding, and their variations, are reviewed with respect to their suitability for yield improvement. It is concluded on theoretical and experimental grounds that they are inefficient, as they do not allow intense selection for yield until later generations. A theoretical basis of breeding for yield is presented, and the proposition is discussed that yield testing and selection must be commenced in the earliest possible segregating generation to prevent the loss of high yielding genotypes.

Testing plots of lines in the early segregating generations gives good results in some situations, but the advantage over other methods is not as great as expected on theoretical grounds. It is suggested that the main reasons for poor correlations between assessments of early and late generation lines are the degree of heterozygosity and the level of heterogeneity present in early generations. The variability of characters in successive generations of selfing, and its implications regarding the success of a breeding method, are discussed.

VALUE OF COMMON BREEDING METHODS FOR YIELD IMPROVEMENT

The common methods for breeding self pollinating crops have been described frequently (Akerman and MacKey 1948; Harrington 1952; Hayes, Immer and Smith 1955; Elliot 1958; Poehlman 1959; Allard 1960; Andrus 1963; Heyne and Smith 1967). These methods will be discussed with respect to their suitability for yield improvement in cereals.

1. PEDIGREE METHOD

The pedigree method, also referred to as the line method (Heyne and Smith 1967), has been popular in the past (Shebeski 1967), but in recent years other methods such as early generation yield testing and single seed descent have increased in importance (Hurd 1977). The pedigree method involves selecting plants with the desirable combination of characters in the F_2. The progenies of these selected plants are grown, and further selection is practised in succeeding generations until uniformity is reached, usually about the F_5 or F_6 generation (Hayes, Immer and Smith 1955; Poehlman 1959). This method can provide information on the genetics of the material, but it has the disadvantages that it is expensive and requires detailed note-taking and recording of pedigrees (Love 1927; Harrington 1952; Elliot 1958).

The success of the pedigree method relies on the ability of a breeder to identify superior genotypes as single plants, either visually or from measurement. While this is possible for simply inherited characters, the ability of breeders to identify high yielding lines as single plants appears to be extremely limited.

Effectiveness of visual selection of single plants for yield improvement

Many recent studies have demonstrated that little gain in yield occurs from visual selection of plants or plots. Selectors have often shown little ability to select the highest yielding lines or appreciably increase the population mean (Shebeski 1967; Townley-Smith, Hurd and McBean 1973). In other cases, selectors have visually selected high yielding plants in F_2, but these did not give high yielding F_3 plots (McGinnis and Shebeski 1968), or if F_3 plot yields were increased the increase was not large enough to give worthwhile improvements (Knott 1972). Even under ideal conditions where plots were grown with adjacent controls, the ability of individual selectors to identify the highest yielding plots in an experiment was limited, although the average yield of selected plots was improved (Briggs and Shebeski 1970). Frey (1962) classified F_2 and F_3 oat plants as good or poor yielders but this assessment was ineffective in predicting the yield of their progenies. However, visual selection on F_5 progeny rows was more effective than on single plants. In contrast with this, Boyce, Copp and Frankel (1947) found that eye selection of plots was not as successful as that of plants. Studies in barley and soybean have shown that, while some improvement is obtained with visual selection, it is small, and is effective only for discarding the low yielding genotypes (Hanson, Leffel and Johnson 1962; Atkins 1964; Kwon and Torrie 1964).

A preconceived opinion of the desirable plant type is important in visual selection (Boyce, Copp and Frankel 1947). Townley-Smith, Hurd and McBean (1973) showed that two technicians selected higher yielding plants than three wheat breeders, because the wheat breeders were biased towards characters that had no relation to yield. When more than one selector agrees on a particular selection there is a greater chance of improvement (Boyce, Copp and Frankel 1947; McGinnis and Shebeski 1968; Briggs and Shebeski 1970). It has been generally suggested that when selecting visually, a low selection intensity should be used to ensure that the high yielding genotypes are retained (Briggs and Shebeski 1970; Townley-Smith, Hurd and McBean 1973). But Boyce, Copp and Frankel (1947) found that eye selection of single plants was more successful the higher the intensity of selection, because the few best plants were more obvious, and bias due to personal opinion was less improtant.

It must be concluded from these studies that visual selection for yield is little better than random selection. As the pedigree method of breeding relies on visual selection, there must be little chance of conscious yield improvement using this method.

And yet, one wonders why, until recent years, so many successful varieties have been produced using the pedigree method. Most of the studies discrediting visual selection have been fairly recent using modern breeding material. In 1947, Boyce, Copp and Frankel (1947) using crosses of older varieties showed that visual selection could be partly effective, and that selection by eye was as successful as selection by weight in raising the mean yields of progenies. However, they recognized the complexities and uncertainties of the process. In diverse oat populations, Stuthman and Steidl (1976) had some success with visual selection, and in the comparatively unimproved crop, triticale, Salmon and Larter (1976) reported that visual selections were superior to a random sample, and selectors were able to identify high yielding lines. It would appear that visual selection, and breeding methods such as the pedigree method that rely on visual selection, may give improvement when a crop is relatively unimproved, but when a crop has reached a high level of development, as is the situation with most cereals, more sophisticated and objective methods are necessary to gain further significant improvements in yield.

Effectiveness of single plant measurements for yield improvement

If visual selection of single plants is ineffective, can improvements be made by measuring their yields? Some authors have been successful. Comparatively high correlations have been obtained between single plant yields in F_2 and plot or row yields in F_3, e.g. 0.47^{**} to 0.66^{**} reported by Chowdhry and Sabir (1973), and up to 0.87^{**} reported by Skorda (1973).

Johnston (1972) obtained a correlation of 0.61^{**} between F_4 single plants of barley and the same lines in F_6 plots. In another experiment he simulated an F_2 by mixing 100 homozygous barley varieties and obtained a correlation of 0.56^{**} between single plant yields in the mixture and yields of the varieties in pure stands. However, both of Johnston's experiments avoid the segregation between F_2 and F_3 which could cause poor correlations between these two generations. By arranging the barley varieties in different patterns in the simulated F_2, Johnston showed that the mean competition from neighbouring varieties was relatively uniform, as the yield of a particular variety was not altered by changing the varieties with which it was competing. Johnston concluded that selection within a mixture based on single plant yield was effective, but it was even more effective when the mean of a variety across replications was used.

Phung (1976) compared single wheat plants in F_4 with their pure stands in F_6, and also showed that when a large number of replications was included (48) a high correlation ($r = 0.75^{**}$) was obtained. However, when single replications were analysed, as would be the case in F_2 single plant selection, the correlations varied from -0.29ns to 0.70^{**}.

Boyce, Copp and Frankel (1947) had varied success by selecting the highest yielding F_2 plants, as they increased the yield of F_3 plants in some families of a cross, but not in other families.

It has been suggested that grain yield per head might give a better prediction of F_4 plot performance than yield per plant (Alessandroni and Scalfati 1973), as the yields of F_2 heads were more highly correlated with F_4 plot yields than were the yields of F_2 plants. However, the correlation between F_2 heads and F_4 plots was still very low ($r = 0.18^{**}$). Although the authors concluded that early selection for yield per head should be promising for obtaining higher yielding genotypes, the expected improvement could only be slight.

The magnitude of the environmental variation and low heritabilities obtained when yield is measured on single plants makes selection for yield on F_2 plants ineffective (Palmer 1952; Fiuzat and Atkins 1953; Chebib, Helgason and Kaltsikes 1973). In fact, the environmental variance associated with single plant determinations are, in many cases, larger than the genetic variances which exist in the segregating material (Chebib, Helgason and Kaltsikes 1973). The most important controllable non-genetic factors are plant spacing, seed size, and genotypic competition. Chebib, Helgason and Kaltsikes (1973) suggested that the efficiency of single plant selection could be doubled by sowing uniform seed under close spacing. Christian and Gray (1941) also suggested eliminating some variation due to interplant competition by sowing only seed of approximately the same weight in one plot.

Variation due to micro-environmental factors such as soil heterogeneity, which are not controllable by the breeder, also reduces the efficiency of single plant yields as a selection criterion (Hamblin 1971; Johnston 1972; Phung 1976). Fasoulas devised the "honeycomb method of selection" (Fasoulas 1973, 1976; Fasoulas and Tsaftaris 1975), which involves growing the plants in a hexagonal arrangement widely spaced, and he claims this overcomes the effects of soil heterogeneity and interplant competition. While this method might improve the accuracy of the actual plant selection in the F_2 or F_3, no evidence is given on whether selected F_2 plants will perform well as pure stands in yield tests in later generations. Fasoulas claims that plants selected under non-competitive conditions will give the same results when grown under commercial density in pure stands, but this view is in conflict with those of many other authors (Engledow 1925; Suneson and Wiebe 1942; Hinson and Hanson 1962; see also review by Johnston 1972).

2. BULK OR POPULATION METHOD

The bulk or population method consists of growing the material in a bulk plot, usually from the F_2 to about the F_6 generation, followed by head or plant selection in the F_6 (Hayes, Immer and Smith 1955). This method was being used in Sweden by Nilsson-Ehle as early as 1908 (Akerman and MacKey 1948), and was later described by Love (1927) and Florell (1929). Florell used it effectively for yield improvement in a breeding program, and suggested that it would be an important method for selection for disease resistance and winder hardiness.

Because of the ease with which crosses can be grown in bulk, a greater number can be handled than with the pedigree method (Hayes, Immer and Smith 1955). The bulks may be carried through to homozygosity without any selection, but a higher proportion of the population will be undesirable than with the pedigree method which, in theory at least, would have eliminated more of the undesirable types.

Often some artificial selection is imposed on the populations during the segregating generations to increase the frequency of the desirable phenotypes. This may involve roguing poor individuals, selecting for winter hardiness by exposing to cold, for maturity by sowing at appropriate sites, or for disease resistance by creating artificial epiphytotics or sowing in infected areas (Florell 1929; Akerman and MacKey 1948; Elliot 1958).

In the bulk method, selection is delayed until the majority of the hybrid population is homozygous. The number of generations required depends on the number of genes involved (Florell 1929). For five pairs of genes a bulk population would contain, in theory, 14.2 per cent heterozygous individuals in the F_6 and 7.8 per cent in the F_7. With 10 pairs of genes there would be 26.3 per cent heterozygotes in the F_6 and only about 1 per cent in the F_{11}. The effect of outcrossing reduces the effects of segregation to some extent and causes a slight reduction in the rate of approach to homozygosity (Palmer 1952).

The disadvantage of the method is that the best genotypes, which are rare, are probably lost, because only a small sample of the population can be grown over the segregating generations. This is further considered in a section dealing with the theoretical aspects of breeding for yield. Akerman and MacKey (1948) claimed that the effective variation in a population is not lost as long as sufficiently large populations are grown, but this conclusion was based on the assumption that a cross might segregate for only 10 genes. If the parents in a cross differ by only one gene for yield on each chromosome of wheat, and this almost certainly is an under estimate, a cross would segregate for 21 genes for yield. In this case more than 4×10^{12} plants must be grown in the F_2 if all the different possible recombinants have a chance to occur (Allard 1960). Because of segregation, the frequency of the ideal combination is lower when full homozygosity is reached (1 plant in 2×10^6), but this would only occur if the segregation was not limited in earlier generations. The population required to allow complete segregation could not be maintained in practice, and the variation obtained at homozygosity must be limited. It must therefore be assumed that the highest yielding lines are not present in the F_6-F_8 populations.

Early generation testing in bulk populations

The bulk method lends itself ideally to early generation yield tests so, if these tests were effective predictors of the performance of lines which could be derived from them, whole populations could be culled or selected in an early generation. A number of experiments have suggested that yield tests of early generation bulk populations are useful in predicting later generation performance. These have included evaluations on barley (Harlan, Martini and Stevens 1940; Immer 1941; Smith and Lambert 1968), wheat (Harrington 1940), soybeans (Torrie 1958*b*, Leffel and Hanson

1961), and dry bean, *Phaseolus vulgaris* (Hamblin and Evans 1976).

Harrington (1940) claimed that early generation bulks were measuring heterosis, and the ones with the greatest degree of heterosis would give the greatest number of high yielding selections. In his experiments, F_3 bulks showed less heterosis than F_2 bulks, so he concluded that F_3's were not as valuable as the F_2's, and might have supplementary value only. He made this conclusion even though the crosses ranked almost identically in both the F_2 and F_3 yield tests. If heterosis was the important criteria to be measuring in early generation bulks, it would be expected that F_1 yields would be of value in predicting later generation performance. However, the use of F_1 performance has not been reliable for predicting cross potential in barley or soybeans (Immer 1941; Weiss *et al.* 1947; Kalton 1948).

In many instances where bulk populations were good predictors of the value of crosses, results showed that the performance of parents was also valuable. This has been shown for wheat (Fowler and Heyne 1955), barley (Grafius, Nelson and Dirks 1952; Smith and Lambert 1968), soybeans (Leffel and Hanson 1961), and for dry beans (Hamblin and Evans 1976).

Although there are a number of experimental results supporting the value of yield testing early generation bulks, there are many others that conflict with this conclusion. Again these studies have included wheat (Fowler and Heyne 1955; Lupton and Whitehouse 1957), oats (Atkins and Murphy 1949), barley (Grafius, Nelson and Dirks 1952; unpublished data of Lambert quoted by Taylor and Atkins 1954), and soybeans (Weiss *et al.* 1947; Kalton 1948).

While many studies have shown that early generation bulks have no value in predicting cross potential, the same experiments have often shown that characters more simply inherited than yield, such as maturity, height, lodging, and test weight can be quite reliably assessed in early generation bulks (Weiss *et al.* 1947; Fowler and Heyne 1955).

A number of explanations have been proposed to explain why yields of early generation bulks might not give good predictions of late generations. These include:-

1. No yield differences being apparent in the bulks due to lack of variability between parents (Fowler and Heyne 1955).

2. The effects of different seasons and different levels of disease (Weiss *et al.* 1947; Atkins and Murphy 1949), so that testing in the early generation is in a different environment to the later generation.

3. The effects of natural selection. If the early generation bulks are grown under conditions which cause major changes in the population structure due to intense selection pressure from, for example, abnormal years or disease conditions, the early generations are not likely to be representative of the yields of selections made later from the populations (Taylor and Atkins 1954).

4. The effects of competition. The yield of a genotype in a mixture of segregants might not be correlated with its yield when grown in pure stand (Suneson and Wiebe 1942). Competitive differences could explain why sometimes high yielding bulks do not always give the highest yielding selections (Atkins and Murphy 1949), as the high yielding selections might be poor competitors.

3. MASS-PEDIGREE METHOD

To overcome some of the disadvantages of the pedigree and bulk methods, Harrington (1937) proposed that the methods be combined in the mass-pedigree method. An essential feature is that crosses are carried in bulk until a season favourable for selection occurs. Then plant selections are taken and progeny tested the following year. Desirable progenies can be bulked, reselected again, or carried in separate bulks, depending on the following seasons.

A problem associated with this method is how to rationally decide whether the environment experienced in a year is suitable for selection.

4. COMPOSITE CROSS OR COMPLEX BULK METHOD

This method, devised by Harlan and Martini (1929), is an extension of the bulk population method. A diverse germplasm is created by combining many different crosses, and sometimes incorporating male sterile lines (Suneson 1956; Suneson and Stevens 1953). By continued intercrossing within the composite, numerous recombinations are obtained (Suneson and Wiebe 1962). The composite cross population that results is grown for many generations in the area of contemplated use to subject the progeny to natural selection (Suneson 1956). Hence it has been referred to as an evolutionary breeding method. Fifteen generations has been suggested as the most desirable number of generations of natural selection. Thereafter, conventional selection and testing can be used, natural selection can be continued in the bulk, or selected recombinants can be recrossed.

When a mixture of varieties is grown year after year the relative proportions of the varieties change, indicating that they have different competitive abilities (Harlan and Martini 1938; Suneson and Wiebe 1942). Similarly, specific characters of genotypes in composite crosses exhibit differential survival, and some environments are more selective than others (Suneson and Stevens 1953; Jain 1961; Suneson 1964; Johnson and Singh 1971). Using five marked loci, Jain (1961) showed that at some loci as many as 10 to 13 per cent of individuals may be heterozygous even after 18 generations. Other loci behaved as expected, and heterozygotes were halved each selfing generation. The increased heterozygosity could not be explained solely by outcrossing, and Jain and Allard (1960) concluded that natural selection favoured heterozygotes at such loci.

Harlan, Martini and Stevens (1940) compared nearly 3000 selections taken from the F_8 of a composite cross involving 379 crosses, and the same number of selections taken from individual bulks of the same 379 crosses. They concluded that the composite cross method was at least equal to the bulk method.

A number of composite crosses of barley have been developed, some of which have been grown for 37 generations (Suneson and Stevens 1953; Suneson 1956; Suneson 1964). Yield improvement has been obtained within these composites due to natural selection, and it has been shown in one composite cross that wider adaptability is also obtained (Finlay 1971; Lohani 1970). However, Hamblin and Morton (1977) suggested that caution is needed in interpreting the data on composite crosses, as they concluded from experiments on bulk populations of beans (*Phaseolus vulgaris*) that there is a greater chance of producing improved varieties from a large number of simple crosses than from a small number of more complex ones. This is supported to some extent by the published data on Composite Cross XII (Suneson 1956) in which two varieties, Atlas and Vaughn, contribute 50 per cent of the genes. Although this composite cross increased in yield relative to a check variety over 11 generations, it is likely that at least as good a result would have been achieved more quickly from the simple Atlas* Vaughn cross, as four successful barley varieties have been developed from this cross (Suneson 1956). It is possible that yield improvement within a composite cross will be obtained through natural selection only if low yielding crosses are involved (Lohani 1970; Hamblin 1977).

5. MASS SELECTION METHOD

Some of the disadvantages of the bulk method may be overcome by increasing the frequency of the desirable genotypes through mass selection. Mass selection involves some form of phenotypic selection within a genetically heterogeneous population without resorting to progeny tests (Romero and Frey 1966). The sample of retained plants or seeds is bulked to propagate the next generation. In practice, this method is usually repeated for several generations. Characters may be modified by mass selection directly, or indirectly through correlated characters.

Mass selection has been used to improve yield through increased seed size in wheat (Derera and Bhatt 1972, 1973; Bhatt and Derera 1973*a*), to improve grain size, test weight, seed shape, seed colour and appearance, maturity, height, and disease resistance in wheat (Derera, Bhatt and Ellison 1974), to improve yield, heading date and seed weight, and reduce height in oats (Romero and Frey 1966; Frey 1967; Chandhanamutta and Frey 1973; Geadelmann and Frey 1975), to modify oil and protein content in soybeans (Hartwig and Collins 1962; Fehr and Weber 1968; Smith and Weber 1968), to increase hard seed in clovers (Bennett 1959; Weihing 1962), to alter seed size in barley and soybeans (Bal, Suneson and Ramage 1959; Fehr and Weber 1968), and to increase leaf weight in tobacco (Matzinger and Wernsman 1968). Mass selection is a very common method utilized in breeding cross pollinated crops, e.g. it has been used to improve yield and other characters in maize (Gardner 1961; Lonnquist, Cota and Gardner 1966; Genter 1976).

Although mass selection can result in improvement of characters with high heritability, the effectiveness of improving yield indirectly by selection for an associated character will depend on both the heritability of the selected attribute and the genetic correlation between yield and the selected character (Romero and Frey 1966).

6. SINGLE SEED DESCENT

If homozygosity has to be achieved before yield testing becomes efficient, it might be an advantage to advance the generations as quickly as possible. Single seed descent, sometimes called the modified pedigree or the random method, was first suggested by Goulden (1941) to obtain large numbers of homozygous lines in two years after making a cross. A comparable pedigree method would need five years. Segregating generations are rapidly advanced without selection, growing three generations per year, and only one or two progeny from each plant are taken in each successive generation. By growing the seedlings closely spaced in sand with minimum nutrients, a large number of plants can be grown in a small area (Grafius 1965).

Application of the method to soybean, oat, and wheat breeding has been discussed by Brim (1966), Kaufmann (1971), and Knott and Kumar (1975) respectively. Selection during the segregating generations can be carried out for characters of high heritability, e.g. height, maturity, disease resistance, shatter resistance and seed quality, as these characters can be effectively selected on a single plant basis (Brim 1966). Selection for characters of low heritability, such as yield, would be ineffective.

Some theoretical aspects of selection in the single seed descent method have been discussed by Baker (1971). Using computer simulation techniques, Snape and Riggs (1975) looked at the theoretical changes in the mean and variance of a segregating population under single seed descent and found that the direction and magnitude of these changes depended on the genetics of the character under consideration. When dominance is present and is directional for the increasing allele, a fall in the generation mean will occur, whereas if there is no dominance little change will occur. Genotypic variance will always increase from the F_2 to F_6 except when the character is influenced by complementary gene interactions. For situations where heterosis is exhibited, notably when systems of dispersed genes and complementary gene interactions are displayed, the population of F_6 lines obtained will fall well below the expectations of the F_2, and a greater genetic advance would be expected by using the normal pedigree method.

However Snape and Riggs concluded that other advantages might warrant the use of the single seed descent method.

While single seed descent does permit homozygous lines to be obtained quickly, it suffers from the same disadvantages as the bulk method in that valuable variation could be absent when selection for yield is commenced.

THEORETICAL CONSIDERATIONS IN BREEDING FOR YIELD

Various authors have considered the quantitative genetic theory that underlies breeding for yield (Van der Kley 1955; Allard 1960; Shebeski 1967; Shebeski and Evans 1973), and as some important methods of breeding for yield improvement have been proposed as a consequence of these theories, it is worthwhile considering them in detail.

Shebeski (1967) indicated that it was essential to select for yield in the earliest possible generation so that rare valuable genotypes could be detected and isolated. These genotypes occur at a higher frequency in the earlier generations. If one considers an example of a cross between two parents which differ by 25 independent genes for yield, only 0.075 per cent of the F_2, or 1 plant in 1330, may be expected to contain all 25 of the desirable genes in either the homozygous or the heterozygous condition. The consequence of this is that at least 1330 plants would have to be grown for the chance occurrence of one containing all the desirable alleles.

If selection is delayed until later generations, the proportion of plants containing all the 25 desirable genes is greatly reduced, e.g. only 1 plant in 1.8 million at F_4, or 1 plant in 15.6 million by F_6.

All methods which delay selection until later generations must therefore suffer from the disadvantage that the most desirable genotypes are lost during the multiplication phases, as it is not possible to maintain the plant population necessary to retain them.

In the 25 gene example, the most probable genotype for the F_2 plant with the desired genes would be homozygous for 8 and heterozygous for 17 of the desired genes. Since the homozygous desirable genes are fixed, the critical F_3 arising from this F_2 may be thought of as an F_2 population stemming from a cross in which the parents differ by 17 genes and, therefore, 0.75 per cent, or 1 plant per 133, could be expected to possess all desirable alleles. So the number of plants grown in the F_3 and subsequent generations is also important to retain the desirable genotype.

An important assumption in this theory is that the yield of a heterozygote may be used to predict the yield of segregates that will be obtained from it.

The opposing view is that the phenotype of a heterozygous plant is not a useful guide (Van der Kley 1955), and it has been suggested that selection for yield should be delayed until later generations when the genotypes are approaching homozygosity (Lupton and Whitehouse 1957; Allard 1960). If selection for yield is delayed until late generations, it is only possible to assess a small proportion of the possible genotypes. For example, if there were 25 independently segregating factors in the cross, a total of 33.6 million different genotypes could be possible at homozygosity. Apparently the advantage of dealing with homozygous lines must be weighed against the risk of losing the superior genotypes.

The above considerations assume that the "ideal" will be the only useful genotype in the hybrid population, but other combinations short of perfection will be useful and relatively common (Palmer 1953). Lines selected from any hybrid population most likely belong in this latter category. If the parents differed by 20 independent genes for yield, individuals homozygous for 16 or more plus genes could be valuable. While only one individual in 2^{20} will have all the plus genes combined when homozygous, 4845 in 2^{20} individuals will have 16 of the plus genes combined. Palmer suggested crossing together high yielding progeny from the same cross to eventually give the ideal combination, as there would be a good chance that these lines would complement each other.

YIELD TESTING OF LINES FROM EARLY GENERATIONS IN PLOTS

Shebeski's proposal that selection for yield should commence on F_2 derived lines to prevent potentially valuable genotypes from being lost, has important implications. If this view is accepted, breeding methods such as the bulk and single seed descent cannot be efficient, as they delay conscious selection for yield and randomly discard the majority of the population during the segregating generations. Similarly, as the pedigree method usually relies on visual selection for yield on a single plant basis, no objective selection for yield can be practised with this method until late generations. When these methods are used therefore, it is likely that the most desirable genotypes are lost before any yield testing has been carried out. If it was possible to select for yield on a single plant basis, isolating high yielding lines in early generations would be easy. As yield testing plants appears to be ineffective, the logical solution is to yield test, in plots, lines derived from the single plants (Fiuzat and Atkins 1953; Knott 1972).

Following his conclusions that yield testing must be carried out in as early a generation as possible, Shebeski (1967) suggested a method based on yield testing F_3 plots derived from F_2 plants. The effectiveness of this method has been studied by comparing the yields of F_2 derived lines in small F_3 plots, with related F_4 derived lines grown in F_5 plots. Briggs and Shebeski (1971) found a positive relationship in only one of three years studied ($r = 0.83^{**}$), the correlations in the other two years being non-significant. However these poor results can be partly explained by the fact that only the high yielding lines were carried on from the F_3, giving a narrow range of yield, not typical of the true population. De Pauw and Shebeski (1973) obtained a correlation of 0.56^{*} between F_2 derived lines and related F_4 derived lines. They also compared F_2 derived lines grown as F_3 plots with related F_4 bulk means, and obtained a correlation of 0.59^{**}.

McKenzie and Lambert (1961) studied the effectiveness of testing the yield of F_2 derived lines in the F_3 generation, by comparing their yields with those of related F_4 derived lines grown in F_6 plots. The yields of families in the F_3 and F_6 generations showed little association in one cross ($r = 0.31^{**}$), although a useful association was found in another cross ($r = 0.54^{**}$).

In a similar comparison in two wheat crosses, Knott and Kumar (1975) obtained low correlations between the yields of F_3 and F_5 rows ($r = 0.29^{**}$ and $r = 0.14^{**}$). They concluded that although selection based on F_3 yields would have some effect, it is doubtful if it would be worth the labour involved.

The above studies (Briggs and Shebeski 1971; De Pauw and Shebeski 1973; McKenzie and Lambert 1961; Knott and Kumar 1975) have all compared generations grown in different years so are confounded by the effects of genotype x year interactions. Better comparisons could be expected if the generations being compared were grown in the same year.

F_2 derived lines can also be tested in F_4 and later generation yield trials by multiplying seed in the F_3, perhaps with selection for simply inherited characters in the F_2 and F_3 (Frey 1954). This has been called the F_2 progeny method by Lupton and Whitehouse (1957) and Whitehouse (1953), who suggested that it was desirable to select in the F_2 and F_3 generations for simply inherited characters, and delay selection for yield and quality until the genotypes approach homozygosity. Of course, this philosophy of delaying selection for yield conflicts somewhat with the ideas of Shebeski and colleagues presented earlier. Frey (1954) tested this method using two barley crosses, and concluded that the performance of F_2 derived lines tested in F_5 gave a reasonably good indication of the yield of the F_3 derived lines selected from them. The F_2 derived lines did not differ significantly for yield in one cross, but in the other cross a yield test of F_2 derived lines was successful in identifying lines giving superior F_3's.

In his breeding program, Hurd (1969) carried out yield tests from F_4 to F_8, and his results suggest that the yield tests were successful in isolating high yielding lines.

The use of F_2 or F_3 derived lines for early generation tests seems to have been fairly successful in soybean breeding. Thorne, Weber and Fehr (1970) reported that selection of the highest yielding F_5 lines based on F_2 or F_3 derived line performance was successful, selection based on F_3 derived lines being the more successful. These results must be treated with caution, as the F_2 and F_3 derived lines were simulated by mixing appropriate F_5 sister lines, so important variability would be lost and the effects of heterozygosity ignored. In 16 comparisons between F_3 and F_5 derived lines, Thorne (1974) obtained 13 significant correlations ranging from 0.46^{**} to 0.85^{**}. Selection of the four highest yielding F_3 derived lines would have successfully isolated high yielding F_5 lines.

Lupton and Whitehouse (1957) considered the time taken to produce a true breeding line of known yielding capacity could be reduced by at least two years if yield testing and normal pedigree selection were carried out concurrently. In this method, known as the pedigree-trial method, normal pedigree selection is carried out in each generation, but plants remaining in a row after selections have been taken,are bulked for yield testing. This is not a new method, as similar schemes were used by Nilsson-Ehle as long ago as 1910 (Akerman and MacKey 1948) and by Breakwell at Roseworthy in 1938 (Breakwell and Hutton 1939). This scheme has also been proposed for use in soybeans by Raeber and Weber (1953).

To improve the efficiency of selection by using replication, and to enable widely adaptable F_3 lines to be identified, Shebeski and Evans (1973) proposed a method of growing F_3 lines in replicated head hills at a number of sites. To test the value of this method, they compared it with the pedigree method and early generation yield tests in F_3 plots, using three crosses. In one cross all three methods were effective in recovering lines outyielding the control, in another none was effective, and in the third, the hill plot method was better than the pedigree method and slightly better than the F_3 plot method (Seitzer 1974).

A COMPARISON OF VARIOUS METHODS FOR YIELD IMPROVEMENT

While numerous breeding methods have been proposed and comparisons made on theoretical grounds, only a few valid comparisons have been made experimentally between alternative procedures. Valid comparisons are difficult to make due to the size of the experiments that are involved, and also the most suitable method will depend on the particular set of circumstances and breeding objectives.

With regard to yield improvement, there appears to be little difference between the pedigree, bulk, or single seed descent methods. In 18 comparisons between the pedigree and bulk methods in six soybean crosses, the yields of F_6 lines were similar for the two methods in all cases except two (Torrie 1958*a*). In the two exceptions the bulk method was superior. The single seed descent and bulk methods have been compared in wheat and soybeans (Empig and Fehr 1971; Tee and Qualset 1975), but there were no consistent differences between the two methods for generation means or genetic variances, particularly when competition effects in the population were not important. If segregation occurs for a character that has competitive influence on the population, such as height, there may be a genetic shift with advancing generations when the bulk population is used, but this is avoided with the single seed descent method.

Computer simulation has been used by some authors to compare breeding methods, and simulation using actual experimental data has been used in this thesis to investigate various aspects of selection. The pedigree, bulk and single seed descent methods have been compared using simulated data (Casali and Tigchelaar 1975*b*), and this has shown that the most appropriate method probably depends on the heritability of the character involved. Pedigree selection was the most effective at high heritabilities (50-75%), whereas at low (25%) and very low (10%) heritabilities, mass selection and single seed descent respectively yielded the best single F_6 line. Single seed descent retained the greatest variability for line selection in F_6. It was suggested that pedigree or mass selection for highly heritable characters in F_2 and F_3, followed by single seed descent then selection in the F_6 for characters of low heritability, should maximize progress for most breeding situations. Field studies with tomatoes support this suggestion (Casali and Tigchelaar 1975*a*).

Of particular interest in this review are comparisons of the pedigree, bulk and single seed descent methods with yield testing lines derived from early generations. Frey (1968) collected complete data from F_2 and F_3 derived lines of two barley and one oat cross. Using portions of these data he simulated selection to compare the testing of early generation lines with the bulk and single seed descent methods. Testing of early generation lines gave a greater expected genetic gain than the other two methods for grain yield and plant height in barley and oats, and grain weight per volume in barley. The bulk and single seed descent methods gave equal gains. The degree of superiority of testing early generation lines was related to the heritability of the trait in question. With low heritability the expected genetic gain from the early generation testing was more superior than when the heritability was high. With barley, 40 to 50 per cent of the expected genetic gain from the early generation testing resulted from the F_3 derived line test, but most of this gain was due to exploiting genotypic variance among selected F_2 families. With oats, much of the expected genetic gain from the F_3 derived lines was due to exploiting genotypic variances among F_3 derived lines within F_2 families.

Using two wheat crosses, Knott and Kumar (1975) also compared early generation yield testing and single seed descent, but concluded that any advantage of testing early generation lines over single seed descent did not warrant the extra work involved. The best 20 per cent of lines based on F_3 yields were compared in the F_5 with the 20 per cent highest yielding single seed descent lines in the F_6. The yield tested lines were reselected in the F_3. In each cross, the single seed descent lines were at least as good as the yield tested lines. On this basis Knott and Kumar suggested selecting for highly heritable characters in the F_2 and possibly the F_3, carrying these lines through to F_5 or F_6 by single seed descent, then yield testing. While recognizing that this method might lose the best genetic combinations, they felt there was no alternative if selection for yield was not effective.

Testing of early generation lines in soybeans has been compared with the bulk method (Raeber and Weber 1953), with the bulk and pedigree methods (Voigt and Weber 1960; Luedders, Duclos and Matson 1973), and with the single seed descent and pedigree methods (Boerma and Cooper 1975).

Raeber and Weber (1953) compared the five highest and five lowest yielding lines based on F_3 and F_4 yield tests with 10 phenotypically superior plants from an F_5 bulk and 40 random plants from the F_5 bulk, in four crosses. Comparisons in F_6 experiments showed that the high yielding lines from early generations and the superior lines from the bulk were equal in yield, and these were superior to the random bulk lines, which were superior to the low yielding lines from early generations.

Voigt and Weber (1960) found that yield evaluation in the F_4 produced significantly higher yields in the F_5 compared with the bulk and pedigree methods, although the differences were small (averages of 3031, 2990 and 2970 kg/ha respectively). A greater number of lines exceeded the cross mean and control yields with the early generation test than the other methods.

Luedders, Duclos and Matson (1973) found no significant differences between testing of F_3 and F_4 derived lines, the pedigree and two bulk methods, although the complete bulk and early generation testing methods retained a few more superior lines than the maturity bulk (a bulk of lines based on maturity) and pedigree methods. Similarly, Boerma and Cooper (1975) did not find consistent differences between early generation testing, single seed descent or the pedigree methods, and the highest yielding lines from all methods were superior to the parents in some crosses but not others. They concluded that single seed descent was the most efficient method as it required less effort and resources.

CONSIDERATIONS REGARDING THE EFFECTIVENESS OF YIELD TESTING LINES IN EARLY GENERATIONS

Although there is good theoretical evidence to suggest that yield testing of lines in early generations should give good progress and should be more efficient than the pedigree, bulk or single seed descent methods, disappointing results have been obtained from the many experiments discussed above designed to evaluate early generation testing of lines. A number of explanations for the failure to recognize high yielding lines in early generations can be suggested.

1. Many experiments (e.g. Briggs and Shebeski 1971; Thorne, Weber and Fehr 1970) have used small populations. For early generation testing to be effective, large populations must be tested to ensure the superior genotypes are included (Shebeski 1967).

2. The experiments that have compared early generation tests with later generations have compared the two generations in different years e.g. McKenzie and Lambert (1961); Briggs and Shebeski (1971); De Pauw and Shebeski (1973); Knott and Kumar (1975). Genotype x environment interactions may confound the comparisons in such cases.

3. As well as experimental inaccuracies, interplant and interplot competition can be important in giving poor relationships between early and late generations (Leffel and Hanson 1961).

It is proposed in this thesis that the major factors causing poor comparisons between early and late generation lines are the degree of heterozygosity and the level of heterogeneity in early generations. These could influence results in a number of ways.

1. Early generation plants, being heterozygous, might be heterotic, and their yields would then be poor predictors of the yields of pure lines isolated from them (Allard 1960; Leffel and Hanson 1961).

2. If early generation lines are tested in plots, the plot might be extremely heterogeneous. The value of any plot yield or measurement might then have little meaning as it is a summation of the performance of many individual genotypes. This might be further biased if the different genotypes differ in their competitive abilities.

3. Segregation after the generation of testing might lead to individuals which are extremely different to those that were tested.

If these arguments apply to the testing of early generation progeny, they will also apply to the testing of unselected bulks, but to a much greater extent.

The effects that heterozygosity and heterogeneity have on the relationship between different generations, and hence the predictive value of early generations, form the basis of the experimental work in this thesis. As an introduction to this, the theories of quantitative genetics pertaining to the variability of characters in successive generations will be discussed. This will be followed by a review of the small amount of experimental work on this subject, which highlights some of the problems involved.

VARIABILITY OF CHARACTERS IN SUCCESSIVE GENERATIONS OF SELFING

In self-pollinated species the proportion of heterozygosity for each gene pair is reduced by one-half in each generation (Allard 1960; Heyne and Smith 1967). The proportion of homozygous plants in a population after m generations of self fertilization when the number of independently inherited gene pairs is n, is given by the formula $((2^m-1)/2^m)^n$ (Allard 1960). With 5 independent gene pairs, 24 per cent of the population will be homozygous at all 5 loci in the F_3, 51 per cent will be homozygous in the F_4, 72 per cent in the F_5, and 85 per cent by the F_6. With 25 independent genes, only 4 per cent of the population will be homozygous at all 25 loci in the F_4, 20 per cent in the F_5, 45 per cent in the F_6, and it is not until the F_9 that 90 per cent are homozygous. From this consideration it follows that simply inherited characters will be fixed fairly quickly, so early generation tests of progeny should be valid. But with more complex characters such as yield, the early generations may still be quite heterozygous, and this might affect the value of testing early generation lines.

Information on the variability of characters over a number of generations, and the rate of approach to uniformity, is limited. It has been suggested that there may be considerable character fixation for yield in the F_2 (Thorne, Weber and Fehr 1970), and Frey (1968) reported results from a barley cross that showed little variation for yield after the F_2. These results are surprising, as this could only happen if yield was governed by only a few genes, and this is unlikely. A high degree of fixation for yield may be apparent by the F_4 (Weiss, Weber and Kalton 1947; Raeber and Weber 1953; Thorne, Weber and Fehr 1970), and relative homozygosity has been reported in the F_5 (Raeber and Weber 1953). Mahmud and Kramer (1951) calculated that detectable segregation occurred until F_5 for yield, and F_8 for maturity in soybeans, but as these were extrapolations from F_4 data their validity may be queried.

Depending on their heritability, different characters approach homozygosity at different rates. Seed size, protein content and oil content in soybeans are almost homozygous after the F_3 (Thorne, Weber and Fehr 1970). Plant height has appeared uniform after the F_2 in barley (Frey 1954, 1968), while in soybeans and oats considerable variation has still existed after the F_3 (Frey 1968; Thorne, Weber and Fehr 1970).

The variation of yield within lines is greatest in early generations, so it is often suggested that greatest emphasis should be placed on the earliest selections, or that selection among lines would be more beneficial than selection within lines (Weiss, Weber and Kalton 1947; Akerman and MacKey 1948).

Considering the basis of quantitative genetics, there are a number of features of selfed populations that should apply to pedigree data (East 1916).

1. F_1 populations from homozygous parents should be as uniform as the parents.

2. The variability of the F_2 population from such a cross should be much greater than that of the F_1 or parents.

3. When a significant number of F_2 individuals are available, the parental types should be recovered.

4. In certain cases, some F_2 individuals may show a greater deviation than is found in the frequency distribution of either parent.

5. Individuals from various points on the frequency curve of an F_2 population should give F_3 populations differing markedly in their modes and means.

6. Individuals either from the same or from different points on the frequency curve of an F_2 population should give F_3 populations of diverse variabilities extending from that of the original parent to that of the F_2 generation.

7. In generations succeeding the F_2, the variability of any family may be less, but never greater than the variability of the population from which it came.

East (1916) demonstrated that most of these principles held for corolla length in tobacco, which is relatively unaffected by environment, but no such detailed work has been carried out in many generations on a complex character like yield.

One of the basic assumptions of quantitative genetics and practical breeding programs in self pollinated crops is that the variability obtained in an F_2 is far greater than that of the parents. However, when yield is measured on a single plant basis, results have shown that the variability of the parents and F_2's are often similar in magnitude, or if the F_2 variability is greater, it is not significantly so (Immer 1942; Palmer 1952; Chebib, Helgason and Kaltsikes 1973; Phung 1976; Hamblin 1977). Large differences in variances between parents and F_2's have sometimes been reported (Mahmud and Kramer 1951), but when proper account is taken of differences in the means, the variation of parents and F_2's is again similar. It seems that the yield of an F_2 plant is determined very largely by factors of the environment (Immer 1942), and genetic potential may be masked. No work has been reported on making such comparisons in plots, rather than on plants, to overcome these limitations.

It is apparent that there is a lack of general understanding of the behaviour of yield as a character in successive generations of selfing and selection. An understanding of the variability of yield in successive generations, and the manner in which it approaches homozygosity, is important in forming a basis on which to develop the most successful breeding methods. These aspects are considered in the experimental work.

PHENOTYPIC STABILITY IN RELATION TO DEGREE OF HETEROZYGOSITY

There is evidence that heterozygotes exhibit a greater phenotypic stability than homozygotes when exposed to a spectrum of environmental conditions, and this may partly explain why little or no differences between the variation of parents and F_2's have been reported in the literature. It was also found in the experimental work of this thesis, which compared the variability of parents and different generations of the progeny, that this difference in stability between heterozygotes and homozygotes explained aspects of the results obtained. It is therefore necessary to review the literature on this subject.

There are two ways by which a variety can achieve stability (Allard and Hansche 1964). Individuals themselves may be well buffered, or the population may be made up of a number of different genotypes each adapted to a different range of environments.

a) Individual buffering

Individual buffering can be a feature of heterozygotes in animals (Lerner 1954; Dobzhansky and Levene 1955). For example, in *Drosophila pseudo-obscura* individuals heterozygous for the second chromosome had greater stability with respect to viability over a broad range of environments than the homozygotes (Dobzhansky and Levene 1955). Similarly, individual buffering is associated with heterozygosity in outbreeding plants. This has been shown in individual races of *Mimulus* and *Potentilla* (Hiesey 1963), and in maize (Shank and Adams 1960; Rowe and Andrew 1963).

Although there is a consistency of evidence for the greater stability of heterozygotes in outbreeding species, the evidence for inbreeding species is conflicting (Lewis 1954; Jinks and Mather 1955; Williams 1960). Griffing and Langridge (1963) used the species *Arabidopsis thaliana* to study buffering in inbreeding species. They used this plant because it has a short life cycle and can be grown in test tubes under controlled environments. In these studies, heterozygous F_1 and F_2 populations had a greater mean growth and a greater stability of phenotypic expression over a range of temperatures than the homozygotes.

Individual buffering for the heterozygote appears to be more striking under stress conditions. In *Arabidopsis thaliana* the greater stability of heterozygotes was mainly due to their superiority at the highest temperatures (Griffing and Langridge 1963). In lima beans, F_1 hybrids differ little from their parents in number of seeds produced in favourable environments, but in unfavourable years the F_1 hybrid may yield twice as much as the better homozygous parent (Allard and Hansche 1964). Also in lima beans, Allard and Workman (1963) used marker genes in populations to show that homozygotes and heterozygotes contributed equal numbers of progeny to the next generation when seed yields were high, but in poor years the heterozygotes sometimes contributed more than twice as many offspring to the next generation as the corresponding homozygote.

b) Population buffering

While it can be difficult to explain individual buffering, population buffering can be easily explained biologically as being a result of interactions between different genotypes within a population (Allard and Hansche 1964). If a small change of environment does not suit one component, then another component may compensate.

In the self pollinating species wheat, barley and lima beans, heterogeneous and heterozygous bulk hybrid populations have outyielded pure line varieties when considered over a range of environments (Allard 1961, 1967; Finlay 1964; Qualset 1968). While pure lines might have the highest (or lowest) yield in certain environments, heterogeneous bulks have greater stability over a range of environments (Allard 1961, 1967). The regression coefficient of variety yield on site mean yield has also been used to show that F_2 or later generation bulk barley populations have a greater stability than their pure line parents (Finlay 1964; Rasmusson 1968). Using soybeans, Byth and Weber (1968) showed that heterogeneous F_2 derived lines were more stable across environments than homogeneous F_5 derived lines.

As with individual buffering, the increased stability through population buffering is largely due to the accentuated superiority of the bulks in the unfavourable environments (Finlay 1964).

In maize, double crosses are more stable than single crosses, as measured by smaller variety x location and variety x year interactions (Sprague and Federer 1951), or by smaller coefficients of variability (Jones 1958). Because of this stability, double crosses yield better when averaged over many seasons, even though the highest yield in any one situation might be from a single cross. It has also been shown that in grain sorghum three-way hybrids are slightly more stable than single crosses (Patanothai and Atkins 1974).

Small changes in heterozygosity and heterogeneity, even between generations, can be important. Bhatt and Derera (1973*b*) compared F_2 derived lines with F_3 derived lines, and F_3 derived lines with F_4 derived lines, and showed that the higher levels of heterogeneity were either superior or equal to the lower levels for grain yield, grain weight, flour yield and flour protein.

While there is a large amount of evidence showing that heterozygous bulks have better performance and stability than their parents, it is not without exception. Busch, Hammond, and Frohberg (1976) compared the F_2's and F_3's of 28 hybrid wheat populations with their 8 parents in five to six environments. The bulks were similar in yield to the mid-parents across environments, even in stress environments, and they did not differ in stabilities.

If population buffering is due to an interaction between different genotypes within a population, buffering should also be a character of mixtures of varieties as well as heterozygous populations. While in many situations mixtures have greater stability than pure varieties (Allard 1961, 1967; Simmonds 1962; Pfahler 1964; 1965*a*; Frey and Maldonado 1967; Qualset and Granger 1970), in some situations mixtures have been either less stable or no more stable than varieties (Clay and Allard 1969; Rasmusson 1968). In other situations results have been inconsistent (Pfahler 1965*b*). Stability of mixtures appears to be dependent on the nature of the environments under study (Frey and Maldonado 1967), the relative frequencies of genotypes within the populations (Qualset and Granger 1970), and the particular combinations in the mixtures (Simmonds 1962; Early and Qualset 1971). Mixtures might have greater stability than varieties to macro-environmental differences such as different sites and years, but they might not be more stable to micro-environmental variation such as variation within one location (Early and Qualset 1971).

While mixtures of pure lines might be more stable than pure lines over a range of environments in many circumstances, their stability is not as effective as bulk hybrids (Allard 1961, 1967). The superior stability of hybrids over simple mixtures appears to be associated, not with heterosis, but with the ability of a large number of different genotypes to exploit particular ecological sites to their own particular advantage (Allard 1961).

Chapter 2

INTRODUCTION TO EXPERIMENTAL WORK

It was suggested in the literature review that breeding methods such as the pedigree, bulk, or single seed descent methods might not be the most efficient for yield improvement, as they do not allow intense selection for yield until late generations. Testing of progeny from early generations, in plots, has been suggested as an alternative, but results often have been disappointing. The major factors that reduce the relationship between the plot yield of an early generation line and the performance of the selections from it might be the degree of heterozygosity and heterogeneity of the early generation lines.

The experiments in this thesis investigate aspects of selection for yield and other characters in wheat, with particular emphasis on the effectiveness of testing lines in early generations. The specific objectives are as follows:

1. To study the correlations between lines derived from all generations up to F_5, to assess the value of each generation in predicting the performance of the near-homozygous lines. The efficiency of using each generation for selection can then be determined. This is reported in chapter 4.

2. To assess the improvement obtained if different selection intensities are applied in various generations, and the effects of delaying selection from early to late generations. Selection was simulated on a computer using the data from a number of experiments. This is described in chapter 5.

3. To study the variability of characters having either a high or low heritability in each generation after random, pedigreed selection, and to measure the reduction of genetic variability within lines as generations are advanced. This study tests the hypothesis raised in the literature review that variability and the degree of heterozygosity of a character in each generation might be the most important factors determining the success or failure of early generation selection. If uniformity and homozygosity are not achieved until a late generation, it might be desirable to delay selection. This aspect was studied on single plants and in plots, and is reported in chapter 6.

The above objectives were studied by comparing large numbers of pedigreed but randomly selected lines from the F_2, F_3, F_4 and F_5 generations of two wheat crosses. All experiments were conducted in the field at several sites in South Australia.

Grain yield was the major character studied. Two characters, plant height and heading date, thought to be different from yield in heritability, were included for comparison. Harvest index was studied in some experiments because of the suggestion that it is associated with yield (Singh and Stoskopf 1971; Fischer 1975; Donald and Hamblin 1976; Bhatt 1976, 1977). It may be more useful in early stages than yield of single plants (Syme 1972; Fischer and Kertesz 1976) or microplots (Fischer and Kertesz 1976). Flour yield and grain hardness were studied because of the emphasis placed on milling quality in recent years. Estimates of heritability for milling yield, which vary from 35.5% (Everson and Seeborg 1958) to 83% (Briggle *et al.* 1968), and estimates of expected genetic gain, indicate that good progress should be possible by selecting for high milling yield in early generations. However, correlations of flour yields of F_3 and F_5 plots have been poor and inconsistent (Briggs and Shebeski 1971), with significant correlations between generations being obtained in only one of three years. Clearly, more information is required on flour yield in early generations to formulate efficient selection techniques.

A conclusion drawn during the experimental program was that crossbred lines should be tested at a number of sites in a number of years, as genotype x year and genotype x location interactions were important in developing new cultivars. It is necessary to choose objectively the sites used in a breeding program, but little information is available on which to base a decision in terms of number or location of the sites in Australia. This topic was investigated using data from the Australian Interstate Wheat Variety Trials, and variety experiments conducted by the South Australian and Victorian Departments of Agriculture. This topic is reported in chapter 7.

Chapter 3

GENERAL METHODS AND MATERIALS

As many of the methods and materials are common to all experiments, these will be described only in this chapter. Other methods that are specific to experiments will be described in the separate chapters.

In this thesis, the terms "derived lines" and "families" are used frequently and are defined as follows. An F_2 derived line is a line derived from a single F_2 plant, irrespective of the generation in which it is tested. Similarly, an F_3 derived line is a line derived from a single F_3 plant. It is inferred that the line has been carried in bulk since the single plant, and has not been reselected.

An F_2 family includes all lines which can be traced back to a single F_2 plant, including all reselections. An F_2 family might include a number of F_3, F_4 and F_5 derived lines, and an F_3 family might include F_4 and F_5 derived lines.

The experiments involved growing lines derived from the F_2, F_3, F_4 and F_5 generations, and comparing the variances of lines in these generations, and correlating the performances between the generations.

a) CROSSES

Two wheat crosses were used.

1. DX39 * Mexico 8156
2. Olympic * DX39

DX39 and Mexico 8156 are semidwarf lines introduced from CIMMYT (Mexico) and selected in Victoria. Olympic is a commercial variety of standard height grown widely in Victoria. It will be seen later that these varieties are well adapted to South Australian conditions. DX39 and Olympic have soft grain and Mexico 8156 has a hard grain. The pedigrees of these parents are:-

DX39	Nainari 60 * Mexico 8156 * Lerma Rojo 64^2* Sonora 64
Mexico 8156	Penjamo 62 * Gabo 55
Olympic	Baldmin * Quadrat

The widely grown Australian wheat, Gabo, is the progenitor of both Gabo 55 and Nainari 60.

The two crosses were made in the semidwarf wheat breeding program in Victoria, and were considered typical of the crosses used in that and other programs in Australia.

The DX39 * Mexico 8156 cross was chosen as being a cross between parents of similar type, and in which it was expected that there would be fewer genes segregating for yield, maturity and plant height than in the second cross. Note that Mexico 8156 is also one of the parents of DX39. In contrast, Olympic * DX39 was a cross of widely differing parents, and more segregation was expected for yield, maturity and plant height.

b) SELECTION OF RANDOM LINES, AND SEED PRODUCTION

Details of the isolation of lines, and seed production are as follows:-

1974 winter	F_2 plants were chosen at random from rows at the State Research Farm, Werribee, Victoria.
1974/75 summer	Random F_2 lines were sown in pots in the glasshouse and space planted in a birdproof enclosure at the Waite Agricultural Research Institute, Adelaide, to give F_3 lines.

1975 winter

The 1975 experiments involved sowing the F_2 and F_3 derived lines as F_3 and F_4 plots.

One F_3 derived line for each F_2 family was randomly chosen to be further selected to give F_4 derived lines. These were actually taken as heads from separate F_4 rows sown for the purpose.

1975/76 summer

The F_4 derived lines were sown as head hills in a birdproof enclosure at the Waite Agricultural Research Institute for seed multiplication. One F_4 derived line for each F_2 family was chosen to be further selected, and seeds of these were also space planted to give F_5 derived lines.

1976 winter

The 1976 experiments involved sowing F_2, F_3, F_4 and F_5 derived lines as F_4, F_5, F_6 and F_6 plots respectively. The F_2 and F_3 derived lines came from seed harvested from the 1975 experiment, the F_4 derived lines came from the head hills sown in summer, and the F_5 derived lines came from the single plants sown in summer.

The scheme for producing the pedigreed, random lines is illustrated in figure 3.1 for one F_2 family. Thirty-six such F_2 families were produced for each cross. Only one F_3 and F_4 derived line was carried on for each F_2 family, as the physical limitations of growing the required number of plots prevented carrying more than this. It was considered better from an analytical viewpoint to maintain a large number of F_2 families, each with one line carried through to F_5, than to carry on a number of lines in each generation but with few F_2 families.

The actual number of lines compared in each experiment varied, and these details will be included in the description of the individual experiments.

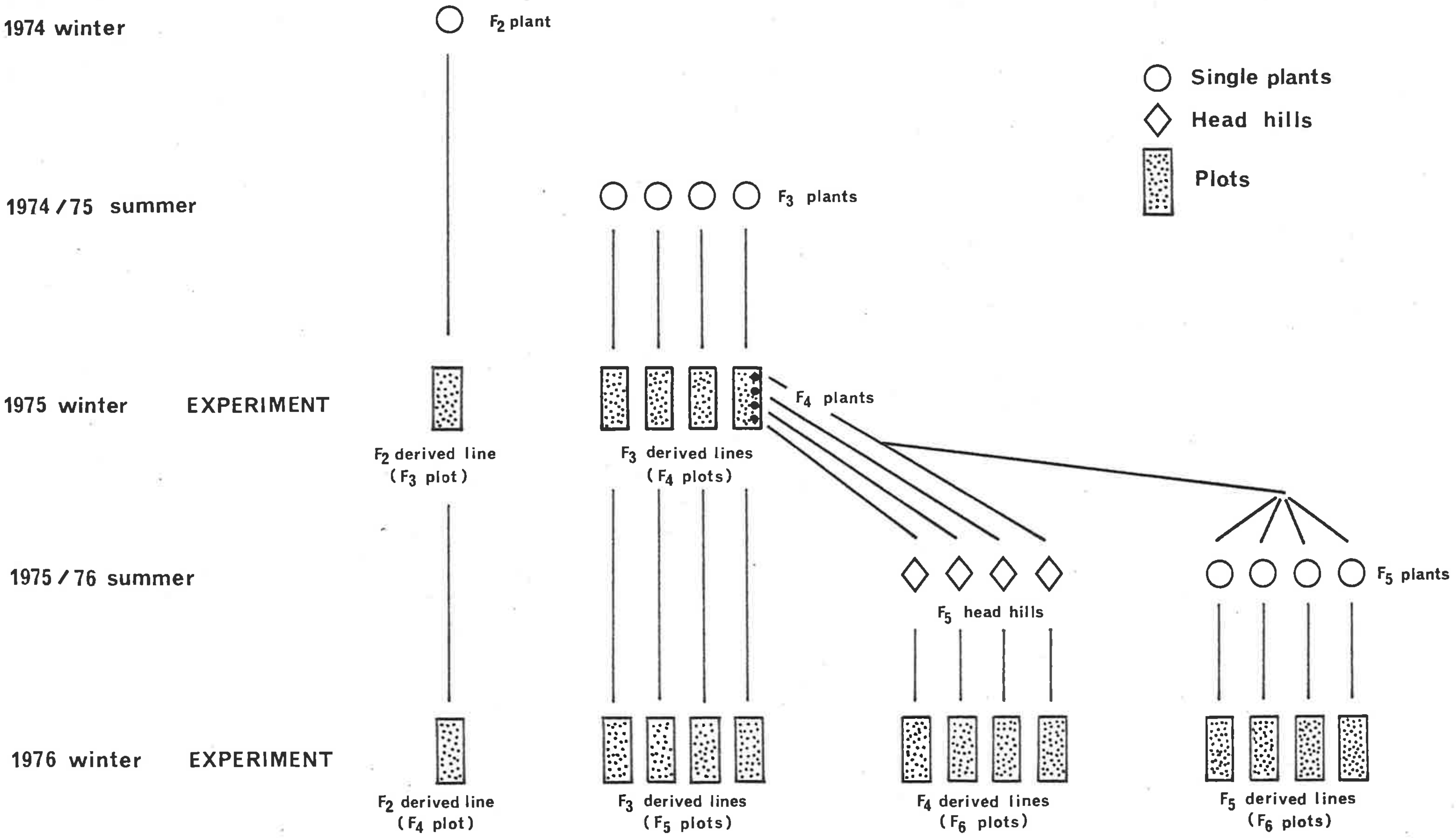


Figure 3.1: Method of producing pedigreed random lines in F_2 to F_5 generations, illustrated for one F_2 family only.

c) SITES

The experiments in 1975 were sown at Roseworthy Agricultural College and a private farm at Saddleworth (Tuela, of Mr. R. Coleman), and in 1976 at Roseworthy Agricultural College and Mortlock Experiment Station (University of Adelaide).

1. Soil types

(i) Roseworthy Agricultural College, 1975.

The soil of this site is classified by French, Matheson and Clarke (1968) as a loamy Mallee soil, but Nicolson (personal communication) describes it more specifically as a calcareous, solonized, brown earth with a sandy loam top soil.

(ii) Roseworthy Agricultural College, 1976.

This soil was a red-brown earth with a loamy top soil (French, Matheson and Clarke 1968), and is classified as Dr 2-33 by Northcote (1960, 1974).

Although the soil types of the two sites at Roseworthy are classified in different major soil groups, these sites are closely related agriculturally and according to native vegetation.

(iii) Saddleworth 1975.

This site had a dark grey self-mulching soil that cracks when dry, and has been classified as a clayey, red-brown earth (French, Matheson and Clarke 1968). Agriculturally, this site is quite distinct from the Roseworthy sites, as the soil has a high capacity for moisture retention and crops are sown later.

(iv) Mortlock Experiment Station 1976.

This site was on undulating land with a soil classified as shallow brown soil over rock (Mulcahy 1954). The top soil was brown stony loam with a weak crumb structure.

2. Seasonal conditions

The climate at the sites is of the Mediterranean type, with cool, wet winters and hot dry summers. The normal growing season is 6 to 8 months of the autumn, winter and spring, and extends from May or June to November or December.

The 1975 growing season had below average rainfall in the autumn and early winter, particularly in June, but this was followed by good rains in late winter and spring (table 3.1). The wet spring favoured the development of *Septoria tritici*, but disease incidence appeared similar on all lines.

The 1976 season in South Australia was characterised by a severe drought until October. The site at Roseworthy was particularly dry and the experiments were sprinkler irrigated throughout the growing season. While the rainfall at Mortlock was less than average, it was satisfactory for growth. Some patches of rhizoctonia *(Rhizoctonia solani)* and take-all (*Gaeumannomyces graminis)* were evident in one experiment at Mortlock.

In both years of these experiments it was not possible to sow until mid June or early July, so the growing seasons were short, extending for 6 months only.

Despite some incidence of disease and a dry season at Roseworthy in 1976, the yields obtained in these experiments were fully comparable with those normally experienced in these regions.

d) MEASUREMENTS

1. Single plant experiments

All single plants were individually pulled and the following measurements taken:-

TABLE 3.1

Rainfall at Roseworthy Agricultural College, Saddleworth and Mortlock Experiment Station in 1975 and 1976, compared to the average

Month	Roseworthy			Saddleworth		Mortlock	
	Average 1883-1976	1975	1976	Average 1872-1976	1975	Average 1967-1976	1976
January	21	14	12	20	11	33	2
February	19	2	21	22	0	39	21
March	20	67	2	23	40	28	9
April	38	10	9	40	11	36	13
May	50	71	12	57	61	65	19
June	54	8	38	59	4	53	41
July	48	64	20	58	71	69	18
August	52	31	33	63	64	85	51
September	45	69	31	54	73	61	54
October	42	90	63	44	123	61	103
November	27	17	35	31	18	35	57
December	24	6	14	26	15	18	12
Total	440	449	290	497	491	582	400

(i) Plant height - was measured on the tallest stem from the base of the plant to the tip of the spike, excluding awns.

(ii) Plant weight - weight of total plant, above ground.

(iii) Grain weight

(iv) Harvest index - calculated as (grain weight/plant weight) x 100.

2. Plot experiments

The following measurements were taken, some being taken from one site only in each year.

(i) Heading date. Heading date was measured on a year day basis, for example January 1 = day 1 and December 31 = day 365. A plot was defined as being in head when 75 per cent of the plants had heads emerged from the boot.

(ii) Plant height. Plant height was measured as the height from ground level to the tip of the spikes of the majority of plants in the plot.

(iii) Harvest index. Harvest index was determined on randomly chosen plots from the 1975 experiments at Roseworthy. A sample, 1 row x 0.5m was cut from the plot prior to harvest for this determination.

(iv) Grain yield. The grain was weighed after harvesting with a stripper type harvester.

(v) Grain hardness. Grain hardness was determined using the pearling resistance test (Chesterfield 1971) on 5g of wheat in 1975 and 10g in 1976.

(vi) Flour yield. Flour yields were determined on a Brabender Quadrumat Junior mill using the small scale method developed by Whan (1974). A sample size of 10g was used in 1975, and 15g in 1976. This method involves milling hard wheats at a moisture content one per cent higher than the soft wheats, and very hard wheats two per cent higher than the soft wheats. The soft wheats can be milled at any suitable moisture content. The hardness groups are defined according to a particle size index (P.S.I) test (Symes 1961) which is adjusted to a standard scale.

The values of some varieties on this standard scale are Emblem 11.9, Falcon 12.5, Gabo 14.3, Halberd 15.7, Stockade 15.8, Gamenya 21.5, Summit 27.7, Olympic 28.7 and Insignia 30.9. Soft wheats, by definition, have a standardised P.S.I greater than 20.5, hard wheats have a P.S.I. 12.5 to 20.5, and very hard wheats have a P.S.I. less than 12.5. Pearling resistance values were used to group the different wheats, by establishing the relationship between pearling resistance and the standardised P.S.I. for the particular experiment using a set of 10 standard varieties grown for this purpose. The correct pearling resistance values that corresponded to the standardised P.S.I. values of 12.5 and 20.5 could then be established.

As only a single milling on each sample was possible, a bulk Halberd was milled approximately every tenth sample to enable adjustment for possible variations during the milling.

e) ANALYSIS OF DATA

The experiments involved large numbers of plants or plots; in 1975 there were 8,640 plots and 6,300 plants, and in 1976, 11,200 plots. Additional records had to be kept of many rows, head hills and plants needed for seed production in several seasons and years. The analysis of data and production of records was possible only through the extensive use of the computer. Programs were written, using FORTRAN IV language, to construct the trials, print field books and other listings, to print harvest bag labels, to manipulate, sort and adjust the data where necessary, to statistically analyse the data, to graph the results, and to simulate various selection schemes. Statistical analyses were also carried out using the statistical packages, SPSS (Statistical Package for the Social Sciences) (Nie *et al.* 1975), and Statscript (Lamacraft 1973). The University of Adelaide CDC 6400 computer was used for all purposes.

In the text that follows, statistical significances will be denoted in the conventional manner, * for significance at the 5% level, and ** for significance at the 1% level.

Chapter 4

THE RELATION BETWEEN WHEAT LINES DERIVED FROM THE F_2, F_3, F_4 AND F_5 GENERATIONS FOR GRAIN YIELD, FLOUR YIELD AND OTHER CHARACTERS

INTRODUCTION

For maximum efficiency and progress in breeding for any character, selection should be carried out in as early a generation as possible so that only the best lines are retained for further testing. However, testing the performance of lines in early generations is of little value if their results do not indicate the performance of the selections which could be taken from those lines in later generations. Selection for simply inherited characters in early generations has been successful, but the value of selection for complex characters such as yield is not as clear. Testing F_2 progeny as F_3's is the earliest stage that lines within a cross can be tested for yield in plots.

Results of yield testing F_2 derived lines as F_3 or F_4 plots have been inconsistent (Frey 1954; McKenzie and Lambert 1961; Briggs and Shebeski 1971; DePauw and Shebeski 1973; Knott and Kumar 1975), and often poor correlations have been obtained with later generations. But often these experiments have compared the early generation with only one later generation and intermediate comparisons have not been made. In other cases, the generations have been grown in different years so the interaction between genotype and environment could have affected the correlations. Comparisons of testing progeny in early generations with other methods such as the pedigree, bulk and single seed descent have also been inconsistent

(Raeber and Weber 1953; Voigt and Weber 1960; Frey 1968; Luedders, Duclos and Matson 1973; Boerma and Cooper 1975; Knott and Kumar 1975).

If the heterozygosity and variability within an F_2 derived line cause a poor relationship between it and the lines selected from it, it might be more desirable to test progeny from later generations e.g. F_3 and F_4. We would expect to get closer associations between performances in two late generations than between two early generations, as greater homozygosity would have been achieved.

This chapter describes experiments that determine the relationship between lines derived from the F_2, F_3, F_4 and F_5 generations of the two wheat crosses, for a number of characters. The relationship between different generations can be compared and the effect of increasing homozygosity and decreasing heterogeneity within lines established. The optimum generation to commence testing for each character can then be determined.

METHODS AND MATERIALS

EXPERIMENT I - RELATIONSHIP BETWEEN F_2 AND F_3 DERIVED LINES IN PLOTS, 1975

F_2 and F_3 derived lines from the two crosses were sown in plots of 2 rows, 2 metres long in a completely randomized design at Roseworthy and Saddleworth. The distance between rows within a plot was 18cm and between plots 30cm. For each cross 36 F_2 derived lines were included (table 4.1), forming the basis of 36 F_2 families. For 14 of the F_2 families 70 F_3 derived lines were included, and for the other 22 F_2 families, 15 F_3 derived lines. This experiment was combined with another designed to measure the variability of the two generations. The 70 F_3

TABLE 4.1

Origin and number of lines in experiment I (1975)

Generation of lines (generation from which derived)	Number of lines	Origin of lines		
		No. of crosses	No. of F_2 derived lines for each cross	No. of F_3 derived lines for each F_2 derived line
F_2	72 (40)+	2	36 (20)	
F_3	2620(410)	2	14 (7) 22 (13)	70 (20) 15 (5)

+ Numbers in parenthesis indicate number of lines measured for harvest index, pearling resistance and flour yield.

derived lines were required for these latter determinations.

All plots were sown from the seed of a single plant, so the F_2 and F_3 derived lines were sown as F_3 and F_4 plots respectively. The experimental error was greater at Saddleworth than at Roseworthy, due to weed infestation, soil variability and harvesting problems, and greater emphasis will be placed, therefore, on the Roseworthy results.

Grain yield, heading date, mature plant height, harvest index, pearling resistance, and flour yield were measured at Roseworthy, and grain yield was measured at Saddleworth. Harvest index, pearling resistance and flour yield were determined on a sub sample of plots only, these being chosen randomly within each group of lines (table 4.1).

As the experiments involved a large number of plots, it occupied an area sufficiently large to be subject to the problems of environmental variation and soil heterogeneity. The experiments were designed to take account of this variation. The variety Wariquam was sown every fifth plot as an indicator of the variability of yield over the experimental area. However, its yields were not used for adjustment; a moving mean was found to be more efficient in accounting for environmental variation within each site. The evidence for using moving means and the justification for adjusting yields in this manner is fully discussed in chapter 6. The moving mean was calculated from the grain yields of a number of entries on either side of the plot being adjusted. The entry was then adjusted by multiplying its yield by the proportion (site mean/moving mean). Neither check plots nor the yield of the entry being adjusted were included in the moving mean. A mean of 14 entries,7 either side of the one being adjusted, was used for the moving mean at Roseworthy, and a mean of 16 entries was used at Saddleworth, as these gave the most effective reduction of residual variance (chapter 6).

Correlations and regressions between lines derived from F_2 and F_3 generations were calculated by comparing the F_2 derived lines (F_3 plots) with the average of the corresponding F_3 derived lines (F_4 plots) (figure 4.1).

EXPERIMENT II - RELATIONSHIP BETWEEN F_2, F_3, F_4 AND F_5 DERIVED LINES IN PLOTS, 1976

F_2, F_3, F_4 and F_5 derived lines from the two crosses were sown in plots of 4 rows, 2.5 metres long at Roseworthy and Mortlock. The distance between rows within a plot was 15cm and between plots 30cm. For each cross families of lines derived from 36 F_2 lines were sown, the numbers included in each generation being shown in table 4.2.

Only one F_3 and F_4 derived line was carried on to later generations. Because of a shortage of seed, some F_2 families could not be represented by F_5 derived lines at Mortlock - the F_5 derived lines of only 30 or 32 of the 36 F_2 families for the two crosses could be included. The same F_2 and F_3 derived lines were sown at both sites, but some F_4 derived lines and all the F_5 derived lines were different at each site. The F_2, F_3, F_4 and F_5 derived lines were sown as F_4, F_5, F_6 and F_6 plots respectively.

To obtain the best comparisons within each family of lines, the lines were sown in nested groups, in a similar manner to a split plot design. The experiment was subdivided into crosses, the crosses were subdivided into F_2 families, and each F_2 family was subdivided into lines from the F_3, F_4 and F_5. Lines and groups were randomly arranged within each level of subdivision. Hence the lines being compared were sown in proximity in the experiment. To overcome differences between groups due to environmental variation across the experimental site, all yields were adjusted according to a grid control of the variety Wariquam sown every fifth plot. The two neighbouring grid controls for each entry were averaged, and the yield of the entry multiplied by the proportion (site mean/mean of the two neighbouring controls).

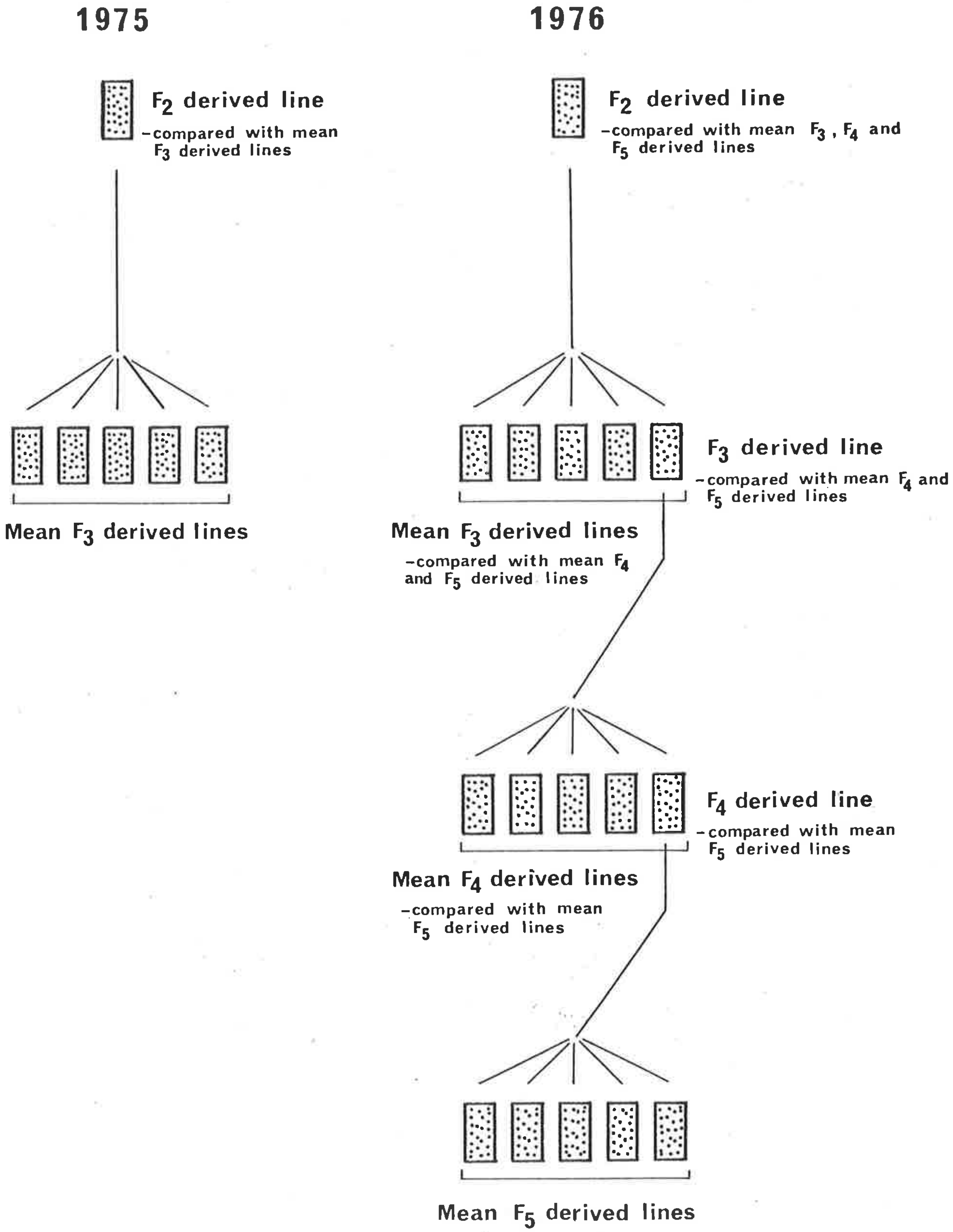


Figure 4.1: An illustration of the comparisons made between generations in 1975 and 1976.

The lines within only one F_2 family are shown. For each cross, 36 such F_2 families were included.

TABLE 4.2

Origin and number of lines in experiment II (1976)

Generation of lines (generation from which derived)	Number of lines	Origin of lines				
		No. of crosses	No. of F_2 derived lines for each cross	No. of F_3 derived lines for each F_2 derived line	No. of F_4 derived lines for each F_3 derived line	No. of F_5 derived lines for each F_4 derived line
F_2	72 (40)[+]	2	36 (20)[+]			
F_3	R[Ø] 720 (120) M[Ø] 360	2	36 (20)	R 10 (3) M 5		
F_4	360 (120)	2	36 (20)	1 (1)	5 (3)	
F_5	216 (120)	2	36 (20)	1 (1)	1 (1)	3 (3)

[+] Numbers in parenthesis indicate number of lines measured for pearling resistance and flour yield - at Roseworthy only.

[Ø] R and M indicate numbers included at Roseworthy and Mortlock respectively. Where not indicated, the same numbers were included at both sites.

Yield, heading date and plant height were measured at Mortlock, and yield, pearling resistance and flour yield were measured at Roseworthy. Pearling resistance and flour yield were determined on a sub sample of plots randomly chosen from each group of lines (table 4.2).

Correlations and regressions between lines derived from the different generations were calculated (figure 4.1). Regressions were calculated, in addition to the correlations, because the slope of the regression indicates the response in the later generation that will be obtained from selection in the earlier generation. The earlier generation was always considered the independent variable.

Comparisons were made within the two crosses, and for the two crosses pooled. The latter comparison was made because in some situations breeders do not select within crosses but consider all their materials.

RESULTS

A. COMPARISONS WITHIN ONE YEAR

1. Grain Yield

The correlations between the yields of single lines in one generation, and the mean yield of lines derived from them in the next generation, increased with advancing generations (table 4.3). It will be recalled that all the generations were grown together in one season, and the results are not influenced by seasonal differences. As an example of increasing correlations, the values at the bottom of the table for the two crosses pooled and averaged over the two sites, increased from $r=0.51^{**}$ for the F_2 line/F_3 mean comparison to $r=0.68^{**}$ for the F_3 line/F_4 mean to $r=0.78^{**}$

TABLE 4.3

Relationship between F_2, F_3, F_4 and F_5 derived lines for two wheat crosses, 1976

Grain Yield

All coefficients are significant at the 1% level unless indicated otherwise:- * $P < 0.05$, ns not significant.

Site	Cross		Association of single lines in one generation with mean of lines derived from them in a following generation						Association of mean of lines in one generation with mean of corresponding derived lines in a following generation		
			F_2 line with mean F_3 lines	F_3 line with mean F_4 lines	F_4 line with mean F_5 lines	F_2 line with mean F_4 lines	F_3 line with mean F_5 lines	F_2 line with mean F_5 lines	Mean F_3 lines with mean F_4 lines	Mean F_4 lines with mean F_5 lines	Mean F_3 lines with mean F_5 lines
Roseworthy	DX39*Mex 8156	r[+]	0.62	0.61	0.77	0.32ns	0.29ns	0.22ns	0.57	0.44	0.24ns
		b[+]	_0.33_	_0.60_	_0.69_	_0.28ns_	_0.28ns_	_0.20ns_	_0.96_	_0.44_	_0.41ns_
	Olympic *DX39	r	0.43	0.58	0.60	0.28ns	0.43	0.33*	0.52	0.60	0.37*
		b	_0.35_	_0.44_	_0.51_	_0.26ns_	_0.41_	_0.38_*	_0.59_	_0.75_	_0.52_*
	Two crosses pooled	r	0.59	0.62	0.69	0.38	0.34	0.25*	0.61	0.46	0.28*
		b	_0.38_	_0.59_	_0.59_	_0.36_	_0.32_	_0.23_*	_0.89_	_0.45_	_0.41_*
Mortlock	DX39*Mex 8156	r	0.50	0.61	0.82	0.41*	0.53	0.49	0.60	0.81	0.61
		b	_0.40_	_0.44_	_0.60_ _(n=30)_	_0.42_*	_0.33_ _(n=30)_	_0.38_ _(n=30)_	_0.75_	_0.66_ _(n=30)_	_0.74_ _(n=30)_
	Olympic *DX39	r	0.41*	0.48	0.67	0.11ns	0.44	0.10ns	0.49	0.71	0.45
		b	_0.30_*	_0.43_	_0.58_ _(n=32)_	_0.08ns_	_0.46_ _(n=32)_	_0.08ns_ _(n=32)_	_0.52_	_0.82_ _(n=32)_	_0.54_ _(n=32)_
	Two crosses pooled	r	0.44	0.57	0.75	0.28*	0.49	0.28*	0.56	0.76	0.53
		b	_0.35_	_0.44_	_0.59_ _(n=62)_	_0.26_*	_0.37_ _(n=62)_	_0.26_* _(n=62)_	_0.65_	_0.72_ _(n=62)_	_0.64_ _(n=62)_
Average of 2 sites	DX39*Mex 8156	r	0.57	0.71	0.88	0.43	0.47	0.42	0.66	0.69	0.45
		b	_0.46_	_0.55_	_0.62_	_0.47_	_0.30_	_0.38_	_0.89_	_0.57_	_0.51_
	Olympic *DX39	r	0.46	0.60	0.71	0.29ns	0.37*	0.17ns	0.57	0.60	0.38*
		b	_0.38_	_0.48_	_0.63_	_0.23ns_	_0.41_*	_0.18ns_	_0.54_	_0.84_	_0.50_*
	Two crosses pooled	r	0.51	0.68	0.78	0.39	0.42	0.29*	0.62	0.63	0.42
		b	_0.41_	_0.53_	_0.61_	_0.37_	_0.33_	_0.28_*	_0.73_	_0.64_	_0.51_

[+] r and b are the correlation and regression coefficients respectively

n=36 for the comparisons of separate crosses and n=72 for comparisons of the two crosses pooled, unless indicated otherwise.

for the F_4 line/F_5 mean. Similarly, the regression coefficients were 0.41^{**}, 0.53^{**} and 0.61^{**}.

Correlations for the four independent sets of observations (i.e. for the two crosses at each site) all showed the same general trend. The increase in the correlations with advancing generations, was significant for the four independent sets of correlations, as, using the binomial distribution, the probability of obtaining this pattern, and no other, is 0.016.

The experiment in the previous year (1975) which, of course, compared fewer generations, gave results for Roseworthy (table 4.4) which were in general agreement with the results for 1976 (table 4.3). The correlations between F_2 derived lines and the mean of the F_3 lines derived from them were a little higher in 1975, particularly when compared with the Mortlock results in 1976. On the other hand, the regression coefficients were consistently higher in 1976. The correlation and regression coefficients between the F_2 and F_3 derived lines at Saddleworth in 1975 were low and usually not significant, indicating the greater environmental variability at this site.

Correlations and regressions between generations two generations apart were lower than comparisons between consecutive generations (table 4.3).

Again the associations between later generations were closer than between earlier generations, for example the correlations for the two crosses pooled, averaged over the two sites were $r=0.39^{**}$ for the comparison of F_2 lines with the mean of the corresponding F_4 lines derived from the and $r=0.42^{**}$ for the comparison of F_3 lines with the mean of the F_5 lines.

Lastly, when the correlations and regressions were calculated between lines three generations apart, that is between F_2 derived lines and the mean of the corresponding F_5 lines derived from them, the values were generally lower again, and some were not significant. These correlations

TABLE 4.4

Relationship between F_2 and F_3 derived lines (F_3 and F_4 plots) for two wheat crosses, 1975

All coefficients were significant at the 1% level unless indicated otherwise:- * $P < 0.05$; ns not significant

Character		DX39 * Mexico 8156	Olympic * DX39	Two crosses pooled
Grain Yield				
Roseworthy	r^+	0.64	0.65	0.63
	b^+	*0.32*	*0.26*	*0.28*
Saddleworth	r	0.25ns	0.26ns	0.27*
	b	*0.10ns*	*0.09ns*	*0.10**
Average 2 sites	r	0.57	0.62	0.60
	b	*0.30*	*0.30*	*0.31*
Harvest Index	r	0.61	0.55	0.68
	b	*0.39*	*0.38*	*0.45*
Heading date	r	0.87	0.93	0.92
	b	*0.93*	*0.93*	*0.96*
Plant Height	r	0.91	0.94	0.93
	b	*0.87*	*0.83*	*0.85*
Pearling Resistance	r	0.95	0.62	0.95
	b	*1.04*	*0.73*	*0.90*
Flour Yield	r	0.50	0.86	0.76
	b	*0.36*	*0.76*	*0.63*

For comparisons of the separate crosses, n=36 for grain yield, heading date and plant height, and n=20 for harvest index, pearling resistance, and flour yield. For comparisons of the two crosses pooled n=twice these numbers.

+ r and b are the correlation and regression coefficients respectively.

have practical implications as they indicate that the value of yield testing F_2 lines, varied from r=0.10ns to $r=0.49^{**}$.

One aspect of the above is that each comparison is between a single line in one generation and a mean of lines derived from it in a following generation. In the absence of replication - the single lines were grown as single plots - inaccuracies in the determination of the yield of the single line can lower the correlations and regressions. Although this is usually the situation confronting the plant breeder, it is of interest to compare the means of lines in one generation with the means of lines in a following generation. The mean of a group of F_3 lines can be considered a replicated result of the F_2 line from which it was derived. A correlation between this mean and the mean of F_4 or F_5 derived lines may then be calculated. Similarly, the mean of the F_4 derived lines can be considered a replicated result of the F_3 line from which it was derived, and a correlation calculated with the mean of F_5 derived lines.

Correlations and regressions calculated in this way were higher than the corresponding comparison when the single lines were used (table 4.3). For example, for the two crosses pooled, averaged over the two sites, the correlations between F_3 means and F_4 means was 0.62^{**} compared to 0.39^{**} for the F_2 line with the F_4 mean, the correlation between F_4 means and F_5 means was 0.63^{**} compared to 0.42^{**} for the F_3 line with the F_5 mean, and the correlation between F_3 means and F_5 means was 0.42^{**} compared to 0.29^{**} for the F_2 line with the F_5 mean. Apparently the use of means improved the correlations. The improvement was greater for Mortlock than Roseworthy indicating a greater need for replication in experiments at that site. This is also expected from its greater environmental variation (see chapter 6).

It is to be expected that the correlation between the mean of F_3 lines and the mean of F_4 lines would be lower than the correlation between the individual F_3 line and the mean of the F_4 lines, as the F_3 mean includes lines that could have very different yields. Similarly, a lower correlation is expected for other corresponding comparisons. This occurred consistently at Roseworthy, but at Mortlock the two correlations were similar for all comparisons. It appears that the yields of individual lines were subject to greater environmental variation at Mortlock, as the genetic differences within groups of lines were relatively less important. This supports the proposition that there is a greater need for replication at Mortlock.

Most correlations between generations in 1976 were higher for the cross DX39 * Mexico 8156 than for Olympic * DX39, although in 1975, the correlations were the same for the two crosses.

2. Heading Date

The principles established in the comparisons between generations for grain yield also apply generally for heading date (table 4.5). The correlations between a single line in one generation and the mean of lines derived from it in a following generation increased with advancing generations. Correlations between consecutive generations were greater than between generations two apart, and these in turn were greater than between generations three apart.

Correlations between the means of lines in one generation and the means of the corresponding derived lines in following generations were always higher than the corresponding comparisons involving just the single line e.g. F_3 mean/F_4 mean compared with F_2 line/F_4 mean.

The regressions did not always follow the same patterns as the correlations.

In all cases the correlations and regressions were much higher than similar associations for grain yield. The results for the two crosses were similar. The correlations between F_2 and F_3 derived lines in 1975 (table 4.4) were higher than in 1976 (table 4.5).

TABLE 4.5

Relationship between F_2, F_3, F_4 and F_5 derived lines for two wheat crosses, Mortlock 1976

Heading date

Cross		Association of single line in one generation with mean of lines derived from it in a following generation						Association of mean of lines in one generation with mean of corresponding derived lines in a following generation		
		F_2line with mean F_3lines	F_3line with mean F_4lines	F_4line with mean F_5lines	F_2line with mean F_4lines	F_3line with mean F_5lines	F_2line with mean F_5lines	Mean F_3 lines with mean F_4lines	Mean F_4 lines with mean F_5lines	Mean F_3 lines with mean F_5lines
DX39*Mex8156	r^+	0.70	0.82	0.89	0.57	0.71	0.42*	0.81	0.93	0.67
	b^+	0.79	0.83	0.90 (n=30)	0.85	0.73 (n=30)	0.71* (n=30)	1.07	0.98 (n=30)	0.91 (n=30)
Oly*DX39	r	0.69	0.90	0.91	0.56	0.67	0.44*	0.67	0.85	0.44*
	b	0.77	0.97	0.77 (n=32)	0.94	0.69 (n=32)	0.63* (n=32)	1.02	0.80 (n=32)	0.57* (n=32)
Two crosses pooled	r	0.69	0.86	0.89	0.56	0.69	0.43	0.72	0.89	0.54
	b	0.78	0.91	0.81 (n=62)	0.90	0.70 (n=62)	0.66 (n=62)	1.02	0.88 (n=62)	0.72 (n=62)

+ r and b are the correlation and regression coefficients respectively.

n=36 for comparisons of separate crosses and n=72 for comparisons of the two crosses pooled, unless indicated otherwise

* All coefficients are significant at the 1% level except these, which are significant at the 5% level.

3. Plant Height

In contrast with the results for yield and heading date, the correlations and regressions between lines derived from consecutive generations for plant height were similar for each comparison, with little or no increase in coefficients with advancing generations (table 4.6). Correlations and regressions between lines two or three generations apart were generally similar, but less than comparisons between consecutive generations.

Correlations and regressions between the means of lines in one generation and the mean of the corresponding lines in a following generation were higher than the corresponding comparisons involving only the single line e.g. F_3 mean/F_4 mean compared with F_2 line/F_4 mean. An increase in correlations between generations when generations were advanced was more apparent when the means rather than single lines were used.

The actual values of the correlations and regressions for plant height were higher than for yield or heading date. Again an effect of the years was present and the correlations between F_2 and F_3 derived lines in 1975 were higher than in 1976.

4. Harvest index

Harvest index was measured in 1975 on the material at Roseworthy. The correlations between F_2 and F_3 derived lines for harvest index were generally similar to those for yield (table 4.4), but the regression coefficients were higher for harvest index than for yield.

Harvest index and yield of the plots were not correlated, either for the same generation or between different generations (table 4.7). This surprising result may be a consequence of the material under consideration. Lines that headed later and were taller had lower harvest indices (table 4.8), but these lines had the highest grain yields.

TABLE 4.6

Relationship between F_2, F_3, F_4 and F_5 derived lines for two wheat crosses, Mortlock 1976

Plant height

All coefficients are significant at the 1% level

Cross		Association of single line in one generation with mean of lines derived from it in a following generation						Association of mean of lines in one generation with mean of corresponding derived lines in a following generation		
		F_2line with mean F_3lines	F_3line with mean F_4lines	F_4line with mean F_5lines	F_2line with mean F_4lines	F_3line with mean F_5lines	F_2line with mean F_5lines	Mean F_3 lines with mean F_4lines	Mean F_4 lines with mean F_5lines	Mean F_3 lines with mean F_5lines
DX39*Mex8156	r^+	0.84	0.80	0.85	0.78	0.71	0.73	0.87	0.88	0.89
	b^+	*0.86*	*0.71*	*0.82* *(n=30)*	*0.88*	*0.64* *(n=30)*	*0.93* *(n=30)*	*0.96*	*0.92* *(n=30)*	*1.04* *(n=30)*
Olympic*DX39	r	0.82	0.79	0.87	0.64	0.55	0.60	0.67	0.83	0.59
	b	*0.82*	*0.74*	*0.86* *(n=32)*	*0.65*	*0.58* *(n=32)*	*0.59* *(n=32)*	*0.68*	*0.93* *(n=32)*	*0.63* *(n=32)*
Two crosses pooled	r	0.83	0.80	0.86	0.71	0.67	0.65	0.78	0.87	0.76
	b	*0.84*	*0.73*	*0.85* *(n=62)*	*0.78*	*0.63* *(n=62)*	*0.76* *(n=62)*	*0.84*	*0.93* *(n=62)*	*0.87* *(n=62)*

+ r and b are the correlation and regression coefficients respectively

n=36 for comparisons for separate crosses and n=72 for comparisons of the two crosses pooled, unless indicated otherwise

TABLE 4.7

Correlations between harvest index and grain yield of F_2 and F_3 derived lines grown at Roseworthy 1975

All correlations are not significant at 5% level

Cross	Harvest Index	Yield	
		F_2 line	Mean F_3 lines
DX39 * Mexico 8156	F_2 line	0.41	0.16
	Mean F_3 lines	0.06	-0.03
Olympic * DX39	F_2 line	-0.27	-0.01
	Mean F_3 lines	-0.32	-0.15
Two crosses pooled	F_2 line	0.04	0.15
	Mean F_3 lines	-0.13	0.01

n=20 for comparisons of separate crosses and n=40 for comparisons of the two crosses pooled.

TABLE 4.8

Correlations of grain yield and harvest index vs heading date and plant height for F_2 and F_3 derived lines grown in plots at Roseworthy 1975

Comparison	Generation in which compared	DX39* Mex8156	Olympic * DX39	Two crosses pooled
Grain yield vs heading date	F_2 F_3	0.20 0.38*	0.59** 0.64**	0.45** 0.41**
Harvest index vs heading date	F_2 F_3	-0.59** -0.69**	-0.47* -0.71**	-0.51* -0.67**
Grain yield vs plant height	F_2 F_3	0.38* 0.49**	0.62** 0.69**	0.50** 0.50**
Harvest index vs plant height	F_2 F_3	0.25 -0.28	-0.34 -0.17	-0.08 -0.30

n=20 and 36 for harvest index and yield respectively for comparisons of separate crosses, and n=twice these numbers for comparisons of the two crosses pooled

* $P < 0.05$; ** $P < 0.01$

Calculating a correlation between the yield and harvest index of the same plant or plot is based on questionable statistical grounds (Donald and Hamblin 1976), but such results are often reported. This query is applicable when correlating the yield and harvest index for the same generation, but not when correlating harvest index in one generation with the yield of lines in the next generation.

5. Pearling resistance

The correlations and regressions between all generations for pearling resistance were high, even between the individual F_2 derived lines and the mean of F_5 derived lines (tables 4.4 and 4.9). The associations were not as close for the Olympic * DX39 cross, but this was due to less variation for pearling resistance in this cross as the grain of both parents are soft. The magnitude of the correlations and regressions between generations for pearling resistance were higher than for any other character studied.

While correlations between generations generally increased as generations were advanced, the increases were small and the trend was not consistent in comparisons between a single line in one generation and the mean of lines in the next generation.

Comparisons involving the mean of lines in one generation with the mean of the corresponding lines in a following generation were very similar to the corresponding comparisons involving only the single line.

6. Flour Yield

The correlations and regressions for flour yield between a single line in one generation and the mean of lines derived from it in a following generation increased with advancing generations (tables 4.4 and 4.10). Correlations and regressions between generations two and three

TABLE 4.9

Relationship between F_2, F_3, F_4 and F_5 derived lines for two wheat crosses, Roseworthy 1976

Pearling resistance

All coefficients are significant at the 1% level

Cross		Association of single line in one generation with mean of lines derived from it in a following generation						Association of mean of lines in one generation with mean of corresponding derived lines in a following generation		
		F_2line with mean F_3lines	F_3line with mean F_4lines	F_4line with mean F_5lines	F_2line with mean F_4lines	F_3line with mean F_5lines	F2line with mean F_5lines	Mean F_3 lines with mean F_4lines	Mean F_4 lines with mean F_5lines	Mean F_3 lines with mean F_5lines
DX39*Mex8156	r^+ b^+	0.91 *1.01*	0.98 *1.03*	0.97 *0.88*	0.89 *1.16*	0.91 *0.97*	0.84 *1.11*	0.86 *1.00*	0.92 *0.93*	0.78 *0.92*
Olympic*DX39	r b	0.74 *0.62*	0.90 *0.98*	0.77 *0.64*	0.70 *0.70*	0.81 *0.85*	0.79 *0.76*	0.84 *1.01*	0.90 *0.87*	0.84 *0.97*
Two crosses pooled	r b	0.93 *1.04*	0.98 *1.00*	0.97 *0.88*	0.92 *1.13*	0.94 *0.95*	0.90 *1.11*	0.92 *1.01*	0.95 *0.95*	0.88 *0.97*

+ r and b are the correlation and regression coefficients respectively

n=20 for comparisons of separate crosses, and n=40 for comparisons of the two crosses pooled

TABLE 4.10

Relationship between F_2, F_3, F_4 and F_5 derived lines for two wheat crosses, Roseworthy 1976

Flour Yield

All coefficients are significant at the 1% level

Cross		Association of single line in one generation with mean of lines derived from it in a following generation						Association of mean of lines in one generation with mean of corresponding derived lines in a following generation		
		F_2line with mean F_3lines	F_3line with mean F_4lines	F_4line with mean F_5lines	F_2line with mean F_4lines	F_3line with mean F_5lines	F_2line with mean F_5lines	Mean F_3 lines with mean F_4lines	Mean F_4 lines with mean F_5lines	Mean F_3 lines with mean F_5lines
DX39*Mex8156	r+	0.62	0.85	0.80	0.63	0.84	0.70	0.83	0.91	0.90
	b+	*0.76*	*0.58*	*0.71*	*0.73*	*0.65*	*0.91*	*0.77*	*1.02*	*0.94*
Olympic*DX39	r	0.69	0.87	0.93	0.66	0.89	0.65	0.78	0.88	0.78
	b	*0.71*	*0.81*	*0.92*	*0.73*	*0.88*	*0.77*	*0.83*	*0.94*	*0.89*
Two crosses pooled	r	0.74	0.86	0.88	0.75	0.87	0.73	0.85	0.91	0.87
	b	*0.74*	*0.74*	*0.82*	*0.77*	*0.77*	*0.77*	*0.87*	*0.94*	*0.91*

+ r and b are the correlation and regression coefficients respectively

n=20 for comparisons of separate crosses, and n=40 for comparisons of the two crosses pooled generations apart were similar to associations between consecutive generations.

Correlations and regressions between the means of lines in one generation and the means of corresponding lines in a following generation were generally higher than the corresponding associations involving just the single line.

In all cases the correlations and regressions between generations for flour yield were high, even between the F_2 and F_5 generations. These coefficients were higher than similar comparisons for grain yield and heading date, and were similar in magnitude to the correlations and regressions obtained for plant height.

B. COMPARISONS BETWEEN YEARS AND SITES

The effect of different years on early generation tests as predictors of performance in late generations, can be seen by comparing the results for 1975 and 1976. And the difference between Mortlock and Roseworthy in any one year illustrates the effect of different sites.

1. Grain yield

The correlations for grain yield between F_2 and F_3 derived lines grown at Roseworthy in 1975 and the F_3, F_4 and F_5 derived lines grown at Roseworthy and Mortlock in 1976 were, with some exceptions, low and non-significant (table 4.11). The results between the two years were correlated in some instances for Olympic * DX39, particularly at Roseworthy. The correlations decreased as the number of generations separating the generations increased. Although not presented, the corresponding comparisons between results at Saddleworth in 1975, or the average of Roseworthy and Saddleworth in 1975, and the results in 1976 gave similar correlations, although they were generally weaker. Correlations between years were

TABLE 4.11

Correlations between F_2 and F_3 derived lines grown in 1975 at Roseworthy, and F_3, F_4 and F_5 derived lines grown in 1976 at 2 sites

Grain Yield

The mean F_3, F_4 and F_5 lines are the means of a number of lines

Cross	Roseworthy 1975	1976 sites								
		Roseworthy			Mortlock			Average of 2 sites		
		Mean F_3 lines	Mean F_4 lines	Mean F_5 lines	Mean F_3 lines	Mean F_4 lines	Mean F_5 lines	Mean F_3 lines	Mean F_4 lines	Mean F_5 lines
DX39*Mex8156	F_2line	-0.13	-0.29	0.09	-0.14	-0.07	0.01	-0.15	-0.16	0.03
	Mean F_3lines	-0.21	-0.34*	0.07	-0.17	-0.07	0.03 (n=30)	-0.20	-0.17	0.07
Olympic*DX39	F_2line	0.36*	0.34*	0.23	0.43**	0.05	0.04	0.45**	0.17	0.14
	Mean F_3lines	0.66**	0.39*	0.43**	0.49**	0.14	0.15 (n=32)	0.60**	0.27	0.31
Two crosses pooled	F_2line	0.12	0.00	0.16	0.18	0.00	0.03	0.19	0.00	0.10
	Mean F_3lines	0.12	-0.13	0.23*	0.21	0.05	0.11 (n=62)	0.21	0.00	0.21

n=36 for comparisons of separate crosses and n=72 for comparisons of the two crosses pooled, unless indicated otherwise

* $P < 0.05$; ** $P < 0.01$

sometimes significant for Olympic * DX39, but not the other cross.

Harvest index is less influenced by environmental changes than yield (Fischer and Kertesz 1976; Donald and Hamblin 1976), so it may be a criterion of value in selection for yield if it is more stable across locations and years. But harvest indices of F_2 and F_3 derived lines grown in 1975 were not correlated with the yields of the F_3, F_4 and F_5 derived lines grown in 1976 (table 4.12).

Yield results from the different sites in any one year were more closely correlated than between years, and the correlations across sites were often significant (table 4.13). However, the small magnitude of the correlations indicates that agreement across sites is not always good.

2. Heading date and plant height

For both heading date and plant height, the results of the F_2 and F_3 derived lines in 1975 were highly correlated with the F_3, F_4 and F_5 derived lines in 1976 (tables 4.14 and 4.15). The correlations decreased as the number of generations separating the generations increased. Agreement between years was better for plant height than for heading date.

3. Pearling resistance

The number of lines that could be compared between years for pearling resistance and flour yield was only 10 for the DX39 * Mexico 8156 cross and 12 for Olympic * DX39. The correlations were affected by these small numbers and were not often significant.

The correlations for pearling resistance between F_2 and F_3 derived lines in 1975 and the F_3, F_4 and F_5 derived lines in 1976 (table 4.16) were significant for DX39 * Mexico 8156, but not for Olympic * DX39, although all coefficients were positive. The low correlations for Olympic * DX39 were due to the small variation for pearling resistance present in this cross of two soft grained varieties. The correlations for both

TABLE 4.12

Correlations between harvest index of F_2 and F_3 derived lines grown in 1975 at Roseworthy, and yield of F_3, F_4 and F_5 derived lines grown in 1976 at 2 sites

Cross	Roseworthy 1975	1976 sites								
		Roseworthy			Mortlock			Average of 2 sites		
		Mean F_3 lines	Mean F_4 lines	Mean F_5 lines	Mean F_3 lines	Mean F_4 lines	Mean F_5 lines	Mean F_3 lines	Mean F_4 lines	Mean F_5 lines
DX39*Mexico 8156	F_2line	0.00	-0.07	-0.07	0.11	0.18	0.18	0.09	0.12	0.12
	Mean F_3lines	0.18	0.23	-0.04	0.39	0.42	0.32	0.38	0.40	0.15
							(n=16)			
Olympic*DX39	F_2line	0.11	-0.09	-0.30	-0.26	0.01	-0.12	-0.18	-0.03	-0.24
	Mean F_3lines	-0.31	-0.08	-0.05	-0.48*	-0.13	-0.09	-0.48	-0.16	-0.13
							(n=17)			
Two crosses pooled	F_2line	-0.07	-0.15	-0.13	0.01	0.11	0.05	-0.01	0.04	-0.02
	Mean F_3lines	-0.13	0.02	-0.03	0.07	0.21	0.12	-0.02	0.18	0.03
							(n=33)			

n = 20 for comparisons of separate crosses and n=40 for comparisons of the two crosses pooled, unless indicated otherwise.

* $P < 0.05$

TABLE 4.13

Correlations of F_2, F_3, F_4 and F_5 derived lines between Roseworthy and Saddleworth in 1975 and between Roseworthy and Mortlock in 1976

Grain Yield

Cross		Correlation with same lines at different site	Correlations with succeeding generations at different site		
			Mean F_3 lines	Mean F_4 lines	Mean F_5 lines
	Roseworthy 1975	Saddleworth 1975			
DX39*Mexico8156	Individual F_2line	0.20_{**}	0.38^{*}		
	Mean F_3lines	0.65			
Olympic*DX39	Individual F_2line	0.08	0.46^{**}		
	Mean F_3lines	0.74			
Two crosses pooled	Individual F_2line	0.12_{**}	0.43^{**}		
	Mean F_3lines	0.73			
	Roseworthy 1976	Mortlock 1976			
DX39*Mexico8156	Individual F_2line	0.22_{**}	0.34^{*}	0.26_{*}	0.30 (n=30)
	Individual F_3line	0.55_{**}	0.35^{*}	0.49_{**}	0.26_{**}(n=30)
	Individual F_4line	0.60 (n=30)		0.55	0.63 (n=30)
	Mean F_3lines$_{+}$	0.49^{**}_{**}		0.46^{**}	0.35 (n=30)
	Mean F_4lines^{+}	0.48			0.33 (n=30)
Olympic*DX39	Individual F_2line	0.13	0.37^{*}	0.23	0.26 (n=32)
	Individual F_3line	0.31_{**}	0.23	0.17	0.12_{*}(n=32)
	Individual F_4line	0.48 (n=32)		0.08	0.35 (n=32)
	Mean F_3lines$_{+}$	0.50^{**}		0.21	0.18 (n=32)
	Mean F_4lines^{+}	0.05			0.17 (n=32)
Two crosses pooled	Individual F_2line	0.19_{**}	0.26^{*}_{*}	0.21_{**}	0.24 (n=62)
	Individual F_3line	0.42_{**}	0.24	0.34_{**}	0.17 (n=62)
	Individual F_4line	0.54 (n=62)		0.34	0.45 (n=62)
	Mean F_3lines$_{+}$	0.36^{**}_{*}		0.29^{*}	0.21 (n=62)
	Mean F_4lines^{+}	0.28			0.19 (n=62)

n=36 for comparisons of separate crosses and n=72 for comparisons of the two crosses pooled, unless indicated otherwise.

+ Lines contributing to this mean are not always common between the 2 sites. Mean F_5 lines were not included because all lines were different between the 2 sites.

$* \; P < 0.05$; $** \; P < 0.01$

TABLE 4.14

Correlations between F_2 and F_3 derived lines grown in 1975 at Roseworthy, and F_3, F_4 and F_5 derived lines grown in 1976 at Mortlock

Heading Date

Cross	Roseworthy 1975	Mortlock 1976		
		Mean F_3 lines	Mean F_4 lines	Mean F_5 lines
DX39*Mexico8156	F_2 line Mean F_3 lines	0.80 0.83	0.67 0.73	0.62 0.69 (n=30)
Olympic*DX39	F_2 line Mean F_3 lines	0.79 0.85	0.52 0.58	0.45 0.43* (n=32)
Two crosses pooled	F_2 line Mean F_3 lines	0.73 0.75	0.56 0.61	0.49 0.51 (n=62)

n=36 for comparisons of separate crosses and n=72 for comparisons of the two crosses pooled, unless indicated otherwise.

*All coefficients are significant at the 1% level except these, which are significant at the 5% level.

TABLE 4.15

Correlations between F_2 and F_3 derived lines grown in 1975 at Roseworthy, and F_3, F_4 and F_5 derived lines grown in 1976 at Mortlock

Plant Height

All coefficients are significant at the 1% level

Cross	Roseworthy 1975	Mortlock 1976		
		Mean F_3 lines	Mean F_4 lines	Mean F_5 lines
DX39*Mexico8156	F_2 line	0.79	0.78	0.68
	Mean F_3 lines	0.88	0.85	0.79 (n=50)
Olympic*DX39	F_2 line	0.84	0.70	0.64
	Mean F_3 lines	0.90	0.73	0.68 (n=32)
Two crosses pooled	F_2 line	0.81	0.74	0.68
	Mean F_3 line	0.89	0.80	0.76 (n=62)

n=36 for comparisons of separate crosses and n=72 for comparisons of the two crosses pooled, unless indicated otherwise.

TABLE 4.16

Correlations between F_2 and F_3 derived lines grown in 1975 at Roseworthy, and F_3, F_4 and F_5 derived lines grown in 1976 at Roseworthy

Pearling resistance

Cross	1975	1976		
		Mean F_3 lines	Mean F_4 lines	Mean F_5 lines
DX39*Mexico8156	F_2 line	0.86**	0.63*	0.63*
	Mean F_3 lines	0.87**	0.72*	0.68*
Olympic*DX39	F_2 line	0.39	0.17	0.19
	Mean F_3 lines	0.55	0.28	0.26
Two crosses pooled	F_2 line	0.92**	0.78**	0.81**
	Mean F_3 lines	0.92**	0.82**	0.82**

n=10 for DX39 * Mexico 8156 cross; n=12 for Olympic * DX39 cross; n=22 for two crosses pooled.

* P < 0.05

** P < 0.01

crosses generally decreased as the number of generations separating the generations increased.

4. Flour yield

The correlations for flour yield between F_2 and F_3 derived lines in 1975 and the F_3, F_4 and F_5 derived lines in 1976 were low and not significant (table 4.17). Agreement between years was better for DX39 * Mexico 8156 than for Olympic * DX39.

DISCUSSION

The effect of heterozygosity on the correlations across generations

For the characters grain yield, heading date, and flour yield, correlations and regressions between lines in consecutive generations increased as the generations were advanced, but for plant height and pearling resistance there was little or no increase in correlations between the later generations.

In the instance of a character determined by many genes, e.g. grain yield, the proportion of plants and loci that are homozygous will be small in early generations, but will increase with successive generations. Therefore, although the effects of segregation will be large in early generations this will decrease with advancing generations, and correlations between generations will increase. In contrast, for characters determined by few genes, e.g. plant height and pearling resistance, there will be a high proportion of lines and loci homozygous in early generations and high correlations will be obtained. Because further segregation is relatively less important, the increase in correlations will be only slight. It is

TABLE 4.17

Correlations between F_2 and F_3 derived lines grown in 1975 at Roseworthy, and F_3, F_4 and F_5 derived lines grown in 1976 at Roseworthy

Flour yield

All correlations are not significant at 5% level

Cross	1975	1976		
		Mean F_3 lines	Mean F_4 lines	Mean F_5 lines
DX39*Mexico8156	F_2 line Mean F_3 lines	0.47 0.29	0.52 0.10	0.40 0.05
Olympic*DX39	F_2 line Mean F_3 line	0.20 0.21	-0.21 -0.19	-0.08 0.05
Two crosses pooled	F_2 line Mean F_3 line	0.28 0.11	0.08 -0.14	0.12 0.00

n=10 for DX39 * Mexico 8156 cross; n=12 for Olympic * DX39 cross; n=22 for two crosses pooled.

expected that fewer genes are involved in the inheritance of flour yield and heading date than for grain yield, so it is understandable that higher correlations were obtained between early generations for these characters than for grain yield. Correlations still increased with advancing generations as greater homozygosity was achieved.

For all characters, correlations between consecutive generations were higher than those between generations two or three generations apart. This is to be expected if segregation is occurring.

It appears that the degree of homozygosity of a character in a particular generation is a factor that determines the correlation between generations, and the predictive value of the material.

The value of testing lines from early generations

The correlation between single lines derived from the F_2 and the corresponding lines derived from the F_5 is of particular concern to the breeder as it indicates the value of early testing. Selection among F_2 derived lines should be the most efficient selection method as only the best lines are retained through the segregating generations, and Shebeski (1967) suggested it is essential to select for yield at this stage to avoid losing potentially high yielding lines. F_2 derived lines gave a good prediction of later generations for characters such as plant height, heading date, pearling resistance and flour yield. The high regressions coefficients also indicated that selection in F_2 would have given good responses in the F_5. The situation for grain yield is much less favourable. In some instances only, will valuable responses be obtained by selecting among F_2 derived lines. This matter was investigated further, and the actual response to selection will be considered in chapter 5. If selection of F_2 derived lines does not give good results in later generations then, regardless of theory, selection for yield might have to be deferred until lines are less heterozygous and more homogeneous.

Explanation for higher correlations in 1975

For grain yield, heading date and plant height, the correlations between F_2 and F_3 derived lines were higher at Roseworthy in 1975 than at either site in 1976. This might be due to these lines being grown as F_4's and F_5's in 1976, whereas in 1975 they were grown as F_3's and F_4's directly from single plants. The extra generation of bulking in 1976 would allow more segregation so creating greater variability within plots, which could cause poorer relationships between the two generations. Also, some degree of natural selection may have caused changes in the populations.

Importance of replication

Usually when lines derived from single plants are tested in early generations it is possible to have a single determination only of each line, unless some bulk increase of seed has been attempted. More accurate predictions can be made from the means of several plots than from single plots. This will be more important at variable sites, such as at Mortlock. In these experiments, the yield of a particular line was more accurately assessed by using the average of a number of lines derived from it. In a breeding program, this could be achieved by bulking lines over a generation to give enough seed for replication and testing at several sites.

Effects of different sites and years on effectiveness of selection

While associations between generations for grain yield in one year and site might be considered satisfactory to warrant selection in early generations, the poor correlations between years, and to a lesser extent between sites, indicates that site and year effects must be prime considerations in a breeding program. Similarly, the high correlations between the F_2 and F_5 generations for flour yield indicate that good progress could be achieved by selecting in early generations, but the poor correlations of lines between years reflect the great environmental influence on flour yield. It is of no value making selections for high yield or high flour extraction in early generations if genotype x environment interactions are so great that lines developed from the selection will not be superior in other sites or seasons. It is therefore important that selection for grain yield and flour yield are based on data from different locations and years. Genotype x environment interactions were not large for heading date, plant height or pearling resistance, and there was good agreement of results across years.

While the growing conditions of the two years contrasted in many respects, it is difficult to know if these conditions are commonly experienced in South Australia. Comparisons between years in South Australia and Victoria are presented in chapter 7. They indicate that large differences between successive years are common within these states. Even if normal differences between successive years are not as great as between 1975 and 1976, the effects of different years always will be important.

Value of selection for harvest index to improve yield

Some authors have suggested that the harvest index of single plants or microplots might be better than other characters in predicting grain yield in later generations. These suggestions have been the result of a number of findings.

1. There has been an increase in yield with successive releases of new cereal cultivars and this has been associated with an increase in harvest index (Van Dobben 1962; Sims 1963, 1968; Cannell 1968; Chandler 1969).

2. Genetic variability exists for harvest index (Singh and Stoskopf 1971; Bhatt 1976).

3. Harvest index responds to selection (Bhatt 1977).

4. Harvest index of single plants has been highly correlated with yields in plots (Fischer 1975; Fischer and Kertesz 1976) and yields in International trials (Syme 1972), whereas the yields of single plants have not.

5. Harvest index is rather stable to environmental changes such as population type and plant density (Fischer and Kertesz 1976; Donald and Hamblin 1976). Results will also be presented in chapter 6 to show that harvest index is less influenced by environment than yield. If harvest index is less subject to genotype x environment interaction, the harvest index at one site in one year should be a predictor of the harvest index, and hopefully yield, at other sites in other years.

The results obtained on harvest index provide information on the value of selection in early generations for harvest index to give an improvement in yield in late generations, and whether it will be more effective than selection for yield in small plots. Harvest index in early generations was not correlated with yield at the same site in the same year, and it was not as good as yield in predicting the yield of late generations, when considered across years. This can be partly explained by the influence of heading date and plant height on harvest index and yield. Later and taller lines tended to have higher yields but lower harvest indices. Syme (1972) also found that late ear emergence was closely associated with low harvest index.

It is concluded that selection for harvest index in early generations is not more valuable than selection for yield itself.

The recommended breeding method

While the principle still holds of yield testing in as early a generation as possible, of foremost consideration is the greater accuracy of yield determinations over a number of sites and years. It is considered that the best method of selecting for yield is to isolate lines in an early generation (F_2 or F_3), increase seed over the next generation, and then grow the lines at a number of sites, preferably with replication. The effect of different years might possibly be represented to a small degree by choosing contrasting sites in one year, but the effect of different years can only be completely resolved by repeating the trials, after some selection of the better lines, in successive years.

The problems of genotype x environment interaction that apply to grain yield also apply to flour yield, so it would be desirable and convenient to test simultaneously for flour yield.

Chapter 5

RESPONSE TO SELECTION FOR GRAIN YIELD, FLOUR YIELD AND OTHER CHARACTERS IN THE F_2, F_3 AND F_4 OF TWO WHEAT CROSSES

INTRODUCTION

The associations between generations were compared in chapter 4, at the same site or in different sites in the one year, and in different years. Responses to selection in various generations and situations can be predicted from these correlations and regressions, but it is more meaningful to know the actual response to selection. This would give a better indication of the improvement expected in a breeding program.

Even though lines from late generations are more highly correlated than lines from early generations, due to their greater homozygosity, it does not necessarily follow that selection in late generations will give a greater improvement. The genetic variability and generation means might be reduced, so that selection in, say, the F_4 would be no better than in the F_2.

There are opposing views on the quantitative genetic theory that underlies selection for characters which are complexly inherited, such as grain yield. One is that the phenotype of the heterozygote is not a reliable guide to the lines which might be derived from it (Van der Kley 1955; Allard 1960). In addition, as the proportion of homozygotes in early generations is very small, selection should be delayed until late generations when it is greater. Advocates of the bulk and single seed descent methods support these concepts.

The opposing view is that expressed by Shebeski (1967) and referred to in the discussion of chapter 4. This assumes that the most desirable gene combination can be identified even in the heterozygote. The essential point of this view is that the proportion of plants with the most desirable combination of genes decreases rapidly with advancing generations, so if these are not selected in the earliest possible generation, even if heterozygous, they will be lost. Furthermore, the populations grown in later generations must be relatively large to reduce the possible loss of the best genotypes.

As these views have far reaching consequences, it would be of benefit to compare selection under the two schemes. It would also be of interest to test Shebeski's (1967) hypothesis that the best genotypes are irretrievably lost if selection is delayed.

The complete data from a number of experiments involving F_2, F_3, F_4 and F_5 derived lines were utilized in simulating various selection procedures. As all lines were randomly chosen, the response to selection in any generation could be measured from the data in all succeeding generations. This technique was used to investigate the following aspects of selection and breeding methods.

1. To determine the actual levels of improvement resulting from selection in different generations, at different sites, and in different years, as predicted in chapter 4.

2. To test if the best lines are irretrievably lost if selection is delayed. Selections from late generations e.g. F_4 would then be lower yielding than selections from early generations e.g. F_2.

3. To compare the response of grain and flour yield to selection with the more highly heritable characters plant height, heading date and pearling resistance. Also to compare the improvement in grain yield by direct selection for yield or from selection for harvest index.

METHODS AND MATERIALS

Simulated selection was undertaken on the results of the experiments described in chapter 4, which involved plots of F_2 and F_3 derived lines in 1975, and F_2, F_3, F_4 and F_5 derived lines in 1976, all lines being randomly chosen. Data were from Roseworthy in 1975, and Roseworthy and Mortlock in 1976.

For each cross, the data from 36 F_2 families were available for grain yield and plant height, and from 20 F_2 families for flour yield, pearling resistance and harvest index. It will be recalled that, in these experiments, one line in each generation was randomly chosen to be carried on to the next generation for further random pedigreed selection (figure 4.1). Therefore, if selection is simulated on F_3 or F_4 derived lines, it is implied that lines were randomly carried in the previous generations.

A single line in each generation could be compared with the mean of a number of lines derived from it in the next generation. In this way a number of F_2 derived lines were selected, and their response measured in the next generation using the means of the F_3 lines derived from them. The response to selecting F_2 derived lines was also measured in the F_4 and F_5, assuming lines in these generations to be randomly continued after the selection. Similarly, response to selecting F_3 derived lines was measured using the means of F_4 and F_5 derived lines, and response to selecting F_4 derived lines measured using the means of the F_5 derived lines.

Selection was also simulated using the means of derived lines in each generation rather than the individual lines (figure 4.1). The mean of the F_3 derived line originating from a single F_2 line can be regarded as a "replicated" value of the performance of the F_2 line, so selection can be carried out on the basis of these means. Responses were measured using the means of F_4 and F_5 derived lines. Similarly selection was simulated among the means of F_4 derived lines. In the same way that 7 lines were selected from 36 to give a 20 per cent selection on individual F_2 or F_3 lines, 7 lines were selected from the 36 when selection was undertaken using the F_3 or F_4 means. A greater accuracy, and therefore greater response, is expected from selection on means than from selection on single lines.

Selection was simulated using a FORTRAN IV program and the CDC SORT/MERGE package program on the CDC 6400 computer. Values for the material being selected were sorted into an ascending or descending order, whichever was relevant for the character being selected, and the best lines selected according to a predetermined selection intensity. The results for these lines in the following generations were then calculated. Random selection was similarly simulated in several runs. Five random runs were performed and the results averaged. The values for the simulated selection were expressed in absolute terms, and as a percentage of the random selection. The following selection schemes were investigated.

1. Response to selection for grain yield, flour yield, pearling resistance and plant height measured at the same site as the site of selection, in the same year. Also estimated was the effect on grain yield of selection intensities of 10, 20 and 30 per cent.

2. Response to selection for grain yield measured at a different site in the same year, using a selection intensity of 20 per cent.

3. Response to selection for grain yield and plant height measured in a different year, using a selection intensity of 20 per cent.
The effect of selecting for harvest index in early generations, in one year, on response to grain yield in following generations in the next year was also studied. It was not possible to determine the response to selection for flour yield or pearling resistance in a different year due to the small number of lines that were tested in both years.

Selection was for high and low grain yield, high flour yield, pearling resistance and harvest index, and short plants. It is appreciated that, when selecting for pearling resistance or plant height in practice, selection is often for intermediate types, but the directional selection is the clearest way of illustrating the response to selection of these characters.

Selection was simulated within crosses, and within the two crosses pooled to form one population.

RESULTS

Generation averages for grain yield

At Mortlock, but not at Roseworthy, there was generally a decrease in the mean grain yield with advancing generations (table 5.1). This is suggestive, possibly, that high yielding lines were being lost.

A. LEVEL OF IMPROVEMENT ACHIEVED BY SELECTING IN VARIOUS GENERATIONS

I. IMPROVEMENT MEASURED AT THE SAME SITE AS THE SITE OF SELECTION, IN THE SAME YEAR.

a) Grain yield

1. *Mortlock*

Selection of F_2, F_3 and F_4 derived lines for grain yield at Mortlock resulted in good improvements in succeeding generations when all were grown at Mortlock in the same year (table 5.2 to 5.4). Tables 5.2, 5.3 and 5.4 present the responses obtained by selecting at 10, 20 and 30 per cent intensities, but it will be the selection at 20 per cent intensity that will be considered in detail. The effects of selecting at the different intensities will be considered at the end of the section. When

TABLE 5.1

Grain yield averages for different generations of two wheat crosses at two sites in 1976

Site	Generation[+] and data averaged	Generation averages		
		DX39* Mex8156	Oly* DX39	Two crosses pooled
Mortlock	Individual F_2 lines[ø]	475	480	477
	Individual F_3 lines	506	467	487
	Individual F_4 lines	455	464	459
	Mean F_3 lines[ø]	503	460	481
	Mean F_4 lines	479	456	467
	Mean F_5 lines	448	427	438
Roseworthy	Individual F_2 lines	309	341	325
	Individual F_3 lines	310	334	322
	Individual F_4 lines	310	339	325
	Mean F_3 lines	307	334	320
	Mean F_4 lines	307	348	328
	Mean F_5 lines	310	322	321
Average of 2 sites	Individual F_2 lines	392	410	401
	Individual F_3 lines	408	401	404
	Individual F_4 lines	371	394	383
	Mean F_3 lines	405	397	401
	Mean F_4 lines	393	402	398
	Mean F_5 lines	374	366	370

[+] Generation is the generation in which lines were derived.

[ø] Individual F_2, F_3 and F_4 lines were the progenitors of a number of lines giving the F_3, F_4 and F_5 means respectively.

TABLE 5.2

Effect of selecting for grain yield in different generations at Mortlock in 1976 on improvement in succeeding generations at the same site.

Selection intensity of 10%

Values are grams per plot with, in parenthesis, the percentage of random selection.

Cross	Generation+ and data selected	Improvement in generation of selection	Improvement in succeeding generations+		
			F_3	F_4	F_5
DX39 * Mexico 8156	Individual F_2 lines	678 *(141)*	610 *(114)*	590 *(116)*	651 *(146)*
	Individual F_3 lines	831 *(179)*		660 *(139)*	653 *(153)*
	Individual F_4 lines	751 *(136)*			613 *(119)*
	Mean F_3 lines	704 *(141)*		621 *(125)*	764 *(178)*
	Mean F_4 lines	750 *(160)*			641 *(142)*
	Mean F_5 lines	670 *(158)*			
Olympic * DX39	Individual F_2 lines	668 *(152)*	569 *(135)*	497 *(115)*	445 *(111)*
	Individual F_3 lines	630 *(135)*		467 *(103)*	461 *(105)*
	Individual F_4 lines	661 *(143)*			526 *(123)*
	Mean F_3 lines	612 *(128)*		524 *(111)*	582 *(140)*
	Mean F_4 lines	613 *(128)*			589 *(128)*
	Mean F_5 lines	627 *(139)*			
Two crosses pooled	Individual F_2 lines	678 *(143)*	595 *(125)*	512 *(111)*	478 *(113)*
	Individual F_3 lines	769 *(158)*		569 *(123)*	586 *(134)*
	Individual F_4 lines	721 *(153)*			553 *(128)*
	Mean F_3 lines	688 *(139)*		582 *(119)*	602 *(135)*
	Mean F_4 lines	697 *(148)*			619 *(132)*
	Mean F_5 lines	660 *(139)*			

+ Generation is the generation in which lines were derived.

Parental values:- Mexico 8156 - 332
Mid-parental value - 436
DX39 - 540
Mid-parental value - 544
Olympic - 548

Average of 3 parents - 473

TABLE 5.3

Effect of selecting for grain yield in different generations at Mortlock in 1976 on improvement in succeeding generations at the same site.

Selection intensity of 20%

Values are grams per plot with, in parenthesis, the percentage of random selection.

Cross	Generation[+] and data selected	Improvement in generation of selection	Improvement in succeeding generations[+]		
			F_3	F_4	F_5
DX39 * Mexico 8156	Individual F_2 lines	644 *(132)*	560 *(107)*	569 *(123)*	536 *(120)*
	Individual F_3 lines	765 *(163)*		591 *(126)*	586 *(133)*
	Individual F_4 lines	675 *(149)*			593 *(133)*
	Mean F_3 lines	660 *(129)*		593 *(123)*	583 *(126)*
	Mean F_4 lines	672 *(151)*			595 *(140)*
	Mean F_5 lines	610 *(133)*			
Olympic * DX39	Individual F_2 lines	646 *(138)*	518 *(115)*	497 *(113)*	454 *(108)*
	Individual F_3 lines	606 *(127)*		498 *(101)*	496 *(103)*
	Individual F_4 lines	628 *(133)*			539 *(126)*
	Mean F_3 lines	576 *(122)*		502 *(115)*	480 *(117)*
	Mean F_4 lines	580 *(129)*			563 *(132)*
	Mean F_5 lines	581 *(140)*			
Two crosses pooled	Individual F_2 lines	646 *(134)*	537 *(113)*	515 *(112)*	488 *(115)*
	Individual F_3 lines	695 *(152)*		538 *(118)*	499 *(116)*
	Individual F_4 lines	651 *(149)*			553 *(130)*
	Mean F_3 lines	625 *(127)*		575 *(119)*	537 *(117)*
	Mean F_4 lines	627 *(132)*			561 *(129)*
	Mean F_5 lines	595 *(141)*			

[+] Generation is the generation in which lines were derived.

Parental values:- Mexico 8156 - 332
Mid-parental value - 436
DX39 - 540
Mid-parental value - 544
Olympic. - 548

Average of 3 parents - 473

TABLE 5.4

Effect of selecting for grain yield in different generations at Mortlock in 1976 on improvement in succeeding generations at the same site.

Selection intensity of 30%

Values are grams per plot with, in parenthesis, the percentage of random selection.

Cross	Generation$^+$ and data selected	Improvement in generation of selection	Improvement in succeeding generations$^+$		
			F_3	F_4	F_5
DX39 * Mexico 8156	Individual F_2 lines	616 *(128)*	548 *(102)*	560 *(105)*	522 *(104)*
	Individual F_3 lines	707 *(144)*		552 *(114)*	494 *(107)*
	Individual F_4 lines	613 *(139)*			533 *(120)*
	Mean F_3 lines	622 *(125)*		574 *(122)*	521 *(118)*
	Mean F_4 lines	624 *(133)*			564 *(127)*
	Mean F_5 lines	566 *(126)*			
Olympic * DX39	Individual F_2 lines	621 *(125)*	511 *(112)*	468 *(100)*	449 *(101)*
	Individual F_3 lines	582 *(124)*		489 *(107)*	483 *(117)*
	Individual F_4 lines	592 *(129)*			502 *(117)*
	Mean F_3 lines	552 *(120)*		502 *(110)*	479 *(112)*
	Mean F_4 lines	559 *(125)*			516 *(120)*
	Mean F_5 lines	538 *(129)*			
Two crosses pooled	Individual F_2 lines	618 *(134)*	530 *(112)*	514 *(113)*	482 *(117)*
	Individual F_3 lines	648 *(133)*		527 *(111)*	483 *(110)*
	Individual F_4 lines	604 *(131)*			517 *(117)*
	Mean F_3 lines	591 *(122)*		541 *(116)*	503 *(116)*
	Mean F_4 lines	591 *(124)*			540 *(124)*
	Mean F_5 lines	552 *(124)*			

$^+$ Generation is the generation in which lines were derived.

Parental values:- Mexico 8156 - 332

Mid-parental value - 436

DX39 - 540

Mid-parental value - 544

Olympic - 548

Average of 3 parents - 473

the top 20 per cent of lines were selected from the cross DX39 * Mexico 8156, the actual yields obtained in the F_5 derived lines varied from 536g/plot to 595 g/plot, depending on the generation of selection (last column, top section of table 5.3). Although these yields were less than the yields of the lines in the generation of selection, they represent considerable improvement when compared to the mid-parental value for the cross (436g/plot). In addition, they were 20 to 40 per cent better than the random selections.

The F_5 derived lines obtained by selecting the best 20 per cent in the Olympic * DX39 cross were lower yielding than those from the DX39 * Mexico 8156 cross. While this is partly due to the lower yields of the lines in the generation of selection, it also reflects the lower correlations between generations (table 4.4), as the improvement over random selection was also less. However, some improvement was achieved in the F_5 derived lines, as all selected groups were considerably better than random selection, and the top yielding groups either approached or exceeded the mid-parent. When the two crosses were pooled, the level of improvement was intermediate between that of the separate crosses.

The yields of the selected lines in the generation after selection were considerably less than in the generation of selection, an indication of the degree of association between the two generations. The yields of the selected lines were often further reduced when they were advanced at random through the following generations. As an example, the best 20 per cent of individual F_2 derived lines from the two crosses pooled at Mortlock had a yield of 646 g/plot when selected, but this was reduced to 537 g/plot in the generation after selection (table 5.3). This yield was further reduced to 515 g/plot in the F_4 and 488 g/plot in the F_5. This reduction in the generations following selection, was fairly consistent over the different crosses, selection intensities and sites.

When the best lines were selected on a basis of the means of lines derived from them, the yields in succeeding generations were higher than when the individual lines only were used (tables 5.2 to 5.4). For example, the yield of F_5 derived lines from the best 20 per cent of F_3 derived line means for the DX39 * Mexico 8156 cross was 583 g/plot (26 per cent better than random selection), whereas the F_5 derived lines from the best 20 per cent of individual F_2 derived lines was only 536 g/plot (20 per cent better than random selection) (table 5.3). This was consistent over the crosses and selection intensities.

As the selection intensity was increased from 30 per cent to 10 per cent, the level of improvement increased (tables 5.2 to 5.4). The improvement obtained from the 10 per cent selection intensity was high, particularly for DX39 * Mexico 8156. The F_5 lines of this cross were more than 200 g/plot higher yielding than the mid-parent, and often 40 to 50 per cent better than random selection. While the improvement in yield was not as great when 30 per cent of the best lines were selected, the increases over the mid-parent and random selection were still valuable, particularly for DX39 * Mexico 8156.

2. *Roseworthy*

The improvement in grain yield obtained at Roseworthy, as indicated by the percentage of random selection (tables 5.5 to 5.7), was generally not as good as at Mortlock. However, considerable progress could still be expected from selection, as F_5 lines were generally about 11 per cent higher yielding than those randomly selected, at a 20 per cent selection intensity (table 5.6).

There was little absolute difference in grain yield between the two crosses at Roseworthy, although, as Olympic * DX39 had a higher mid-parental value, the selections from this cross did not often reach this level. Selections from DX39 * Mexico 8156 almost always exceeded the

TABLE 5.5

Effect of selecting for grain yield in different generations at Roseworthy in 1976 on improvement in succeeding generations at the same site.

Selection intensity of 10%

Values are grams per plot with, in parenthesis, the percentage of random selection.

Cross	Generation[+] and data selected	Improvement in generation of selection	Improvement in succeeding generations[+]		
			F_3	F_4	F_5
DX39 * Mexico 8156	Individual F_2 lines	415 *(148)*	336 *(113)*	360 *(116)*	344 *(115)*
	Individual F_3 lines	406 *(128)*		395 *(125)*	358 *(112)*
	Individual F_4 lines	430 *(136)*			372 *(117)*
	Mean F_3 lines	363 *(117)*		409 *(132)*	337 *(105)*
	Mean F_4 lines	414 *(122)*			362 *(109)*
	Mean F_5 lines	431 *(131)*			
Olympic * DX39	Individual F_2 lines	406 *(120)*	363 *(112)*	365 *(108)*	361 *(114)*
	Individual F_3 lines	433 *(134)*		410 *(116)*	372 *(116)*
	Individual F_4 lines	424 *(122)*			361 *(112)*
	Mean F_3 lines	384 *(114)*		382 *(114)*	353 *(111)*
	Mean F_4 lines	410 *(116)*			370 *(118)*
	Mean F_5 lines	393 *(122)*			
Two crosses pooled	Individual F_2 lines	414 *(121)*	350 *(108)*	354 *(103)*	343 *(106)*
	Individual F_3 lines	425 *(129)*		407 *(124)*	355 *(113)*
	Individual F_4 lines	429 *(132)*			373 *(118)*
	Mean F_3 lines	381 *(123)*		387 *(118)*	356 *(111)*
	Mean F_4 lines	415 *(128)*			370 *(119)*
	Mean F_5 lines	420 *(133)*			

[+] Generation is generation in which lines were derived.

Parental values:- Mexico 8156 - 282
DX39 - 348
Olympic - 411

Mid-parental value - 315
Mid-parental value - 380

Average of 3 parents - 347

TABLE 5.6

Effect of selecting for grain yield in different generations at Roseworthy in 1976 on improvement in succeeding generations at the same site.

Selection intensity of 20%

Values are grams per plot with, in parenthesis, the percentage of random selection.

Cross	Generation+ and data selected	Improvement in generation of selection	Improvement in succeeding generations+		
			F_3	F_4	F_5
DX39 * Mexico 8156	Individual F_2 lines	402 *(129)*	337 *(110)*	349 *(115)*	360 *(111)*
	Individual F_3 lines	389 *(125)*		345 *(107)*	363 *(109)*
	Individual F_4 lines	419 *(131)*			384 *(116)*
	Mean F_3 lines	357 *(119)*		365 *(120)*	339 *(110)*
	Mean F_4 lines	400 *(139)*			366 *(116)*
	Mean F_5 lines	409 *(124)*			
Olympic * DX39	Individual F_2 lines	397 *(114)*	353 *(107)*	364 *(105)*	348 *(109)*
	Individual F_3 lines	410 *(122)*		383 *(110)*	341 *(106)*
	Individual F_4 lines	415 *(125)*			345 *(105)*
	Mean F_3 lines	379 *(113)*		379 *(111)*	356 *(108)*
	Mean F_4 lines	402 *(117)*			360 *(116)*
	Mean F_5 lines	382 *(117)*			
Two crosses pooled	Individual F_2 lines	399 *(130)*	345 *(109)*	357 *(112)*	354 *(112)*
	Individual F_3 lines	400 *(124)*		376 *(114)*	363 *(111)*
	Individual F_4 lines	417 *(126)*			363 *(111)*
	Mean F_3 lines	369 *(115)*		380 *(114)*	346 *(108)*
	Mean F_4 lines	402 *(125)*			361 *(111)*
	Mean F_5 lines	396 *(121)*			

+ Generation is generation in which lines were derived

Parental values:- Mexico 8156 - 282
Mid-parental value - 315
DX39 - 348
Mid-parental value - 380
Olympic - 411

Average of 3 parents - 347

TABLE 5.7

Effect of selecting for grain yield in different generations at Roseworthy in 1976 on improvement in succeeding generations at the same site.

Selection intensity of 30%

Values are grams per plot with, in parenthesis, the percentage of random selection.

Cross	Generation^{+} and data selected	Improvement in generation of selection	Improvement in succeeding generations^{+}		
			F_3	F_4	F_4
DX39 * Mexico 8156	Individual F_2 lines	386 *(122)*	329 *(105)*	323 *(104)*	335 *(106)*
	Individual F_3 lines	373 *(123)*		342 *(112)*	351 *(109)*
	Individual F_4 lines	393 *(124)*			382 *(117)*
	Mean F_3 lines	348 *(113)*		358 *(118)*	339 *(110)*
	Mean F_4 lines	380 *(126)*			362 *(113)*
	Mean F_5 lines	391 *(123)*			
Olympic * DX39	Individual F_2 lines	387 *(115)*	349 *(105)*	362 *(104)*	344 *(108)*
	Individual F_3 lines	392 *(121)*		372 *(108)*	342 *(111)*
	Individual F_4 lines	404 *(119)*			346 *(105)*
	Mean F_3 lines	369 *(111)*		358 *(104)*	320 *(103)*
	Mean F_4 lines	392 *(111)*			350 *(107)*
	Mean F_5 lines	370 *(116)*			
Two crosses pooled	Individual F_2 lines	387 *(116)*	341 *(107)*	350 *(107)*	342 *(106)*
	Individual F_3 lines	382 *(117)*		359 *(108)*	350 *(108)*
	Individual F_4 lines	401 *(124)*			364 *(114)*
	Mean F_3 lines	360 *(112)*		365 *(110)*	335 *(103)*
	Mean F_4 lines	388 *(117)*			355 *(110)*
	Mean F_5 lines	381 *(116)*			

$^{+}$ Generation is generation in which lines were derived.

Parental values:- Mexico 8156 - 282
Mid-parental value - 315
DX39 - 348
Mid-parental value - 380
Olympic - 411

Average of 3 parents - 347

mid-parental value, even at the 30 per cent level of selection. Increasing the intensity of selection had a less dramatic influence on the improvement obtained at Roseworthy than at Mortlock. In fact, the yields of the generations following the generation of selection were often higher when 20 per cent of lines were selected than when only 10 per cent were selected.

At Roseworthy, selection based on individual lines and selection based on the means of lines derived from them, gave similar results. This was in contrast to the greater improvement obtained using means at Mortlock. Again this supports previous conclusions about the greater need for replication at Mortlock.

3. *Average of Mortlock and Roseworthy*

When the best 20 per cent of lines were selected based on the average yields from Mortlock and Roseworthy, the yields of the F_5 lines were 5 to 29 per cent better than random selection for DX39 * Mexico 8156, 1 to 24 per cent better than random selection for Olympic * DX39, and 4 to 18 per cent better than random selection for the two crosses pooled (table 5.9). The actual yields considerably exceeded the mid-parent for DX39 * Mexico 8156, and the selected lines from this cross were generally higher yielding than those from Olympic * DX39. Selected lines from Olympic * DX39 did not reach the level of the mid-parent, although the mid-parental value for this cross was comparatively high.

The level of improvement increased as the intensity of selection was increased (tables 5.8 to 5.10), although the response to increasing selection intensity was not as great as that obtained by using the data from Mortlock by themselves.

b) Plant height

The difference between selecting characters with low or high heritability can be illustrated by comparing the selection for high grain

TABLE 5.8

Effect of selecting for grain yield in different generations on improvement in succeeding generations, using the average of Roseworthy and Mortlock in 1976.

Selection intensity of 10%

Values are grams per plot with, in parenthesis, the percentage of random selection.

Cross	Generation⁺ and data selected	Improvement in generation of selection	Improvement in succeeding generations⁺		
			F_3	F_4	F_5
DX39 * Mexico 8156	Individual F_2 lines	516 *(125)*	476 *(117)*	480 *(129)*	456 *(129)*
	Individual F_3 lines	600 *(155)*		506 *(131)*	431 *(119)*
	Individual F_4 lines	573 *(152)*			492 *(131)*
	Mean F_3 lines	519 *(132)*		481 *(124)*	403 *(117)*
	Mean F_4 lines	562 *(150)*			476 *(131)*
	Mean F_5 lines	513 *(133)*			
Olympic * DX39	Individual F_2 lines	511 *(130)*	456 *(117)*	427 *(109)*	390 *(105)*
	Individual F_3 lines	518 *(137)*		433 *(110)*	392 *(105)*
	Individual F_4 lines	523 *(135)*			416 *(114)*
	Mean F_3 lines	483 *(120)*		456 *(112)*	406 *(110)*
	Mean F_4 lines	471 *(118)*			439 *(118)*
	Mean F_5 lines	481 *(129)*			
Two crosses pooled	Individual F_2 lines	518 *(125)*	453 *(113)*	436 *(107)*	415 *(114)*
	Individual F_3 lines	571 *(139)*		463 *(117)*	405 *(106)*
	Individual F_4 lines	557 *(152)*			458 *(127)*
	Mean F_3 lines	517 *(127)*		456 *(116)*	431 *(120)*
	Mean F_4 lines	529 *(131)*			456 *(120)*
	Mean F_5 lines	505 *(130)*			

⁺ Generation is the generation in which lines were derived.

Parental values:- Mexico 8156 - 307
Mid-parental value - 376
DX39 - 444
Mid-parental value - 462
Olympic - 479

Average of 3 parents - 410

TABLE 5.9

Effect of selecting for grain yield in different generations on improvement in succeeding generations, using the average of Roseworthy and Mortlock in 1976.

Selection intensity of 20%

Values are grams per plot with, in parenthesis, the percentage of random selection.

Cross	Generation⁺ and data selected	Improvement in generation of selection	Improvement in succeeding generations⁺		
			F_3	F_4	F_5
DX39 * Mexico 8156	Individual F_2 lines	492 *(129)*	459 *(112)*	455 *(113)*	451 *(120)*
	Individual F_3 lines	559 *(140)*		467 *(117)*	399 *(105)*
	Individual F_4 lines	528 *(150)*			474 *(129)*
	Mean F_3 lines	499 *(123)*		449 *(113)*	411 *(107)*
	Mean F_4 lines	522 *(135)*			455 *(120)*
	Mean F_5 lines	495 *(127)*			
Olympic * DX39	Individual F_2 lines	498 *(118)*	438 *(111)*	434 *(108)*	391 *(101)*
	Individual F_3 lines	490 *(117)*		443 *(108)*	414 *(112)*
	Individual F_4 lines	505 *(126)*			410 *(110)*
	Mean F_3 lines	461 *(119)*		436 *(112)*	380 *(105)*
	Mean F_4 lines	463 *(119)*			426 *(124)*
	Mean F_5 lines	461 *(122)*			
Two crosses pooled	Individual F_2 lines	496 *(123)*	445 *(112)*	432 *(107)*	408 *(108)*
	Individual F_3 lines	530 *(125)*		449 *(108)*	393 *(104)*
	Individual F_4 lines	517 *(133)*			440 *(116)*
	Mean F_3 lines	482 *(120)*		461 *(117)*	405 *(110)*
	Mean F_4 lines	493 *(123)*			435 *(118)*
	Mean F_5 lines	479 *(129)*			

⁺ Generation is the generation in which lines were derived

Parental values:- Mexico 8156 - 307
Mid-parental value - 376
DX39 - 444
Mid-parental value - 462
Olympic - 479

Average of 3 parents - 410

TABLE 5.10

Effect of selecting for grain yield in different generations on improvement in succeeding generations, using the average of Roseworthy and Mortlock in 1976.

Selection intensity of 30%

Values are grams per plot with, in parenthesis, the percentage of random selection.

Cross	Generation+ and data selected	Improvement in generation of selection	Improvement in succeeding generations+		
			F_3	F_4	F_5
DX39 * Mexico 8156	Individual F_2 lines	475 *(122)*	442 *(107)*	439 *(107)*	427 *(111)*
	Individual F_3 lines	530 *(134)*		455 *(121)*	400 *(109)*
	Individual F_4 lines	491 *(135)*			459 *(122)*
	Mean F_3 lines	477 *(120)*		462 *(124)*	402 *(112)*
	Mean F_4 lines	493 *(134)*			436 *(122)*
	Mean F_5 lines	461 *(122)*			
Olympic * DX39	Individual F_2 lines	486 *(119)*	423 *(108)*	422 *(108)*	385 *(108)*
	Individual F_3 lines	471 *(117)*		430 *(108)*	420 *(118)*
	Individual F_4 lines	487 *(120)*			421 *(115)*
	Mean F_3 lines	448 *(115)*		419 *(104)*	374 *(101)*
	Mean F_4 lines	456 *(116)*			431 *(123)*
	Mean F_5 lines	444 *(119)*			
Two crosses pooled	Individual F_2 lines	482 *(117)*	435 *(106)*	426 *(106)*	401 *(108)*
	Individual F_3 lines	503 *(126)*		442 *(110)*	407 *(110)*
	Individual F_4 lines	491 *(124)*			435 *(116)*
	Mean F_3 lines	463 *(117)*		438 *(111)*	388 *(106)*
	Mean F_4 lines	474 *(119)*			439 *(120)*
	Mean F_5 lines	454 *(122)*			

+ Generation is the generation in which lines are derived.

Parental values:- Mexico 8156 - 307
Mid-parental value - 376
DX39 - 444
Mid-parental value - 462
Olympic - 479

Average of 3 parents - 410

yield (tables 5.2 to 5.10) with the selection for short plants (table 5.11). The response to selection for short plants was extremely good. For example, for DX39 * Mexico 8156, selected lines had values from 64 to 70cm in the generations after selection, whereas the mid-parental value was 86cm. Only a little of the improvement gained in the generation of selection was lost in the generations following selection, and the height of lines in succeeding generations, even of F_5 derived lines, was very close to the height of the lines in the generation of selection.

The heights of selected lines were always less than the mid-parents, and they were up to 25 per cent shorter than lines randomly selected.

c) Pearling resistance

The response to selection for harder grain (higher pearling resistance) was extremely good (table 5.12), and the improvement obtained in the generation of selection was maintained in all succeeding generations. Selected lines from DX39 * Mexico 8156 were 12 to 25 per cent harder than randomly selected lines in the F_5, at a 20 per cent selection intensity, and the mid-parental value was greatly exceeded. Even though Olympic * DX39 involved two soft parents, an increase in grain hardness was still obtained in this cross. Selected lines had a pearling resistance of 45 to 46 in the F_5 compared to 40 for the mid-parent, and these lines were 8 to 12 per cent harder than randomly selected lines.

d) Flour yield

The response to selection for higher flour yield was also extremely good, as the improvement obtained in the generation of selection was usually maintained in succeeding generations (table 5.13). The 20 per cent of lines selected had flour yields in later generations of 58 to 61

TABLE 5.11

Effect of selecting for short plants in different generations at Mortlock in 1976 on improvement in succeeding generations at the same site.

Selection intensity of 20%

Values are cm.with, in parenthesis, the percentage of random selection.

Cross	Generation+ and data selected	Improvement in generation of selection	Improvement in succeeding generations+		
			F3	F4	F5
DX39 * Mexico 8156	Individual F2 lines	67.9 *(76)*	67.3 *(78)*	65.7 *(76)*	65.4 *(77)*
	Individual F3 lines	62.1 *(73)*		70.2 *(82)*	70.3 *(80)*
	Individual F4 lines	66.4 *(74)*			66.7 *(77)*
	Mean F3 lines	66.0 *(79)*		65.7 *(79)*	63.8 *(75)*
	Mean F4 lines	64.8 *(79)*			64.7 *(78)*
	Mean F5 lines	66.7 *(79)*			
Olympic * DX39	Individual F2 lines	72.9 *(81)*	73.3 *(84)*	81.0 *(92)*	79.7 *(89)*
	Individual F3 lines	71.4 *(81)*		76.2 *(88)*	84.2 *(99)*
	Individual F4 lines	77.9 *(87)*			77.9 *(88)*
	Mean F3 lines	69.4 *(79)*		75.4 *(85)*	80.4 *(92)*
	Mean F4 lines	71.2 *(83)*			76.3 *(85)*
	Mean F5 lines	76.4 *(86)*			
Two crosses pooled	Individual F2 lines	70.4 *(80)*	70.3 *(84)*	73.3 *(86)*	74.0 *(87)*
	Individual F3 lines	64.6 *(74)*		69.1 *(80)*	70.6 *(82)*
	Individual F4 lines	70.7 *(80)*			71.8 *(82)*
	Mean F3 lines	67.5 *(81)*		69.5 *(83)*	70.5 *(83)*
	Mean F4 lines	66.5 *(77)*			66.9 *(76)*
	Mean F5 lines	70.1 *(84)*			

+ Generation is the generation in which lines were derived.

Parental values:- Mexico 8156 - 96.3
Mid-parental value - 85.7
DX39 - 75.0
Mid-parental value - 87.5
Olympic -100.0

Average of 3 parents - 90.4

TABLE 5.12

Effect of selecting for harder grain (higher pearling resistance) in different generations at Roseworthy in 1976 on improvement in succeeding generations at the same site.

Selection intensity of 20%

Values are % pearling resistance with, in parenthesis, the percentage of random selection.

Cross	Generation$^+$ and data selected	Improvement in generation of selection	Improvement in succeeding generations$^+$		
			F_3	F_4	F_5
DX39 * Mexico 8156	Individual F_2 lines	61.2 *(118)*	60.2 *(115)*	61.9 *(116)*	61.2 *(114)*
	Individual F_3 lines	61.5 *(117)*		62.8 *(116)*	61.3 *(112)*
	Individual F_4 lines	63.9 *(131)*			62.2 *(125)*
	Mean F_3 lines	60.8 *(114)*		62.8 *(119)*	61.3 *(118)*
	Mean F_4 lines	63.1 *(120)*			61.4 *(115)*
	Mean F_5 lines	62.9 *(123)*			
Olympic * DX39	Individual F_2 lines	46.9 *(112)*	43.8 *(107)*	43.3 *(107)*	45.0 *(108)*
	Individual F_3 lines	43.9 *(111)*		45.9 *(111)*	45.6 *(108)*
	Individual F_4 lines	46.0 *(112)*			45.2 *(108)*
	Mean F_3 lines	45.1 *(110)*		45.9 *(113)*	46.2 *(112)*
	Mean F_4 lines	45.9 *(113)*			45.6 *(110)*
	Mean F_5 lines	46.6 *(112)*			
Two crosses pooled	Individual F_2 lines	58.4 *(130)*	59.2 *(131)*	60.9 *(137)*	60.2 *(135)*
	Individual F_3 lines	59.9 *(140)*		61.6 *(139)*	61.0 *(136)*
	Individual F_4 lines	62.2 *(132)*			61.2 *(127)*
	Mean F_3 lines	59.5 *(125)*		60.6 *(128)*	60.2 *(126)*
	Mean F_4 lines	61.6 *(137)*			61.0 *(134)*
	Mean F_5 lines	61.4 *(129)*			

$^+$ Generation is the generation in which lines were derived.

Parental values:- Mexico 8156 - 62.4
Mid-parental value - 49.3
DX39 - 36.1
Mid-parental value - 40.0
Olympic - 43.8

Average of 3 parents - 47.4

TABLE 5.13

Effect of selecting for flour yield in different generations at Roseworthy in 1976 on improvement in succeeding generations at the same site.

Selection intensity of 20%

Values are % flour extracted with, in parenthesis, the percentage of random selection.

Cross	Generation+ and data selected	Improvement in generation of selection	Improvement in succeeding generations+		
			F_3	F_4	F_5
DX39 * Mexico 8156	Individual F_2 lines	57.9 *(104)*	57.9 *(104)*	57.2 *(102)*	58.1 *(104)*
	Individual F_3 lines	59.6 *(105)*		58.1 *(103)*	58.6 *(103)*
	Individual F_4 lines	58.9 *(105)*			58.1 *(103)*
	Mean F_3 lines	59.1 *(104)*		58.1 *(103)*	58.9 *(103)*
	Mean F_4 lines	58.6 *(103)*			58.6 *(103)*
	Mean F_5 lines	58.9 *(105)*			
Olympic * DX39	Individual F_2 lines	60.6 *(103)*	59.9 *(102)*	60.1 *(102)*	60.0 *(103)*
	Individual F_3 lines	61.0 *(106)*		60.8 *(104)*	60.9 *(105)*
	Individual F_4 lines	61.0 *(104)*			61.3 *(104)*
	Mean F_3 lines	60.8 *(104)*		60.5 *(104)*	60.4 *(104)*
	Mean F_4 lines	60.8 *(104)*			60.9 *(105)*
	Mean F_5 lines	61.3 *(106)*			
Two crosses pooled	Individual F_2 lines	59.8 *(105)*	59.0 *(103)*	59.2 *(104)*	59.1 *(103)*
	Individual F_3 lines	60.3 *(106)*		59.5 *(103)*	59.7 *(104)*
	Individual F_4 lines	60.2 *(105)*			59.7 *(103)*
	Mean F_3 lines	60.0 *(105)*		59.3 *(103)*	59.5 *(103)*
	Mean F_4 lines	60.1 *(105)*			60.2 *(105)*
	Mean F_5 lines	60.2 *(105)*			

+ Generation is the generation in which lines were derived.

Parental values:- Mexico 8156 - 53.7
Mid-parental value 53.8
DX39 - 53.9
Mid-parental value 58.2
Olympic - 62.4

Average of 3 parents - 56.7

per cent compared with mid-parental values of 54 and 58 per cent. These increases, which were 3 to 5 per cent better than lines randomly selected, represent a substantial improvement for flour yield. Similar levels of improvement were obtained by selection in all generations.

II IMPROVEMENT MEASURED AT A DIFFERENT SITE TO THE SITE OF SELECTION WHEN GROWN IN THE SAME YEAR

Grain yield

The performance of the later generations of lines selected at one site, was generally better at that site than elsewhere (compare table 5.14 with 5.3, and table 5.15 with 5.6). For example, the improvements obtained at Roseworthy in the F_3, F_4 and F_5 of DX39 * Mexico 8156 were 337, 349 and 360 g/plot when the best 20 per cent individual F_2 derived lines were selected at Roseworthy (table 5.6), but 308, 324 and 333 g/plot when the lines were selected at Mortlock (table 5.15). An exception was when the best individual F_2 derived lines of DX39 * Mexico 8156 or the two crosses pooled selected at Roseworthy gave a greater improvement at Mortlock, than F_2 lines selected at Mortlock (tables 5.3 and 5.14).

Selection at Roseworthy gave a greater improvement at Mortlock, than the improvement obtained at Roseworthy by selecting at Mortlock. The improvement obtained at one site by selecting at the alternate site was satisfactory for DX39 * Mexico 8156, as the mid-parent was exceeded and the yields were considerably better than random selection. However, for Olympic * DX39 selection at another site was less effective, as the lines in succeeding generations at the alternate site were often no better than random selections, and the yields were considerably less than the mid-parent.

TABLE 5.14

Effect of selecting for grain yield in different generations at Roseworthy in 1976 on improvement in succeeding generations at a different site, Mortlock, in the same year.

Selection intensity of 20%

Values are grams per plot with, in parenthesis, the percentage of random selection.

Cross	Generation⁺ and data selected Roseworthy 1976	Improvement in generation of selection	Improvement in succeeding generations⁺ at Mortlock in 1976		
			F_3	F_4	F_5
DX39 * Mexico 8156	Individual F_2 lines	402 *(131)*	592 *(118)*	588 *(120)*	590 *(129)*
	Individual F_3 lines	389 *(124)*		613 *(124)*	560 *(122)*
	Individual F_4 lines	419 *(134)*			592 *(130)*
	Mean F_3 lines	357 *(118)*	528 *(109)*	564 *(127)*	501 *(115)*
	Mean F_4 lines	400 *(129)*		601 *(131)*	546 *(134)*
	Mean F_5 lines	409 *(120)*			543 *(120)*
Olympic * DX39	Individual F_2 lines	397 *(117)*	494 *(104)*	491 *(104)*	467 *(108)*
	Individual F_3 lines	410 *(123)*		464 *(102)*	426 *(99)*
	Individual F_4 lines	415 *(122)*			461 *(108)*
	Mean F_3 lines	379 *(116)*	509 *(113)*	447 *(98)*	445 *(101)*
	Mean F_4 lines	402 *(114)*		457 *(107)*	431 *(104)*
	Mean F_5 lines	382 *(121)*			469 *(108)*
Two crosses pooled	Individual F_2 lines	399 *(125)*	543 *(112)*	540 *(114)*	523 *(119)*
	Individual F_3 lines	400 *(123)*		511 *(110)*	471 *(105)*
	Individual F_4 lines	417 *(128)*			511 *(119)*
	Mean F_3 lines	369 *(114)*	524 *(104)*	515 *(105)*	475 *(101)*
	Mean F_4 lines	402 *(123)*		529 *(111)*	474 *(105)*
	Mean F_5 lines	396 *(124)*			481 *(107)*

⁺ Generation is the generation in which lines were derived.

Parental values :-		Roseworthy	Mortlock
	Mexico 8156	282	332
	DX39	384	540
	Olympic	411	548

	Roseworthy	Mortlock
Mid-parental value -	315	436
Mid-parental value -	380	544

TABLE 5.15

Effect of selecting for grain yield in different generations at Mortlock in 1976 on improvement in succeeding generations at a different site, Roseworthy, in the same year.

Selection intensity of 20%

Values are grams per plot with, in parenthesis, the percentage of random selection.

Cross	Generation$^+$ and data selected Mortlock 1976	Improvement in generation of selection	Improvement in succeeding generations$^+$ at Roseworthy in 1976		
			F_3	F_4	F_5
DX39* Mexico 8156	Individual F_2 lines	644 *(132)*	308 *(103)*	324 *(106)*	333 *(106)*
	Individual F_3 lines	765 *(149)*		335 *(109)*	358 *(112)*
	Individual F_4 lines	675 *(143)*			351 *(109)*
	Mean F_3 lines	660 *(141)*	330 *(107)*	324 *(108)*	353 *(108)*
	Mean F_4 lines	672 *(147)*		371 *(122)*	328 *(101)*
	Mean F_5 lines	610 *(134)*			353 *(108)*
Olympic * DX39	Individual F_2 lines	646 *(128)*	333 *(101)*	352 *(103)*	318 *(100)*
	Individual F_3 lines	606 *(133)*		377 *(111)*	354 *(110)*
	Individual F_4 lines	628 *(146)*			333 *(102)*
	Mean F_3 lines	576 *(126)*	344 *(101)*	345 *(97)*	318 *(97)*
	Mean F_4 lines	580 *(122)*		331 *(95)*	310 *(94)*
	Mean F_5 lines	581 *(135)*			338 *(110)*
Two crosses pooled	Individual F_2 lines	646 *(143)*	323 *(101)*	342 *(106)*	330 *(105)*
	Individual F_3 lines	695 *(145)*		355 *(112)*	367 *(117)*
	Individual F_4 lines	651 *(148)*			344 *(108)*
	Mean F_3 lines	625 *(131)*	332 *(104)*	326 *(99)*	338 *(105)*
	Mean F_4 lines	627 *(133)*		342 *(105)*	314 *(97)*
	Mean F_5 lines	595 *(136)*			346 *(109)*

$^+$ Generation is the generation in which lines were derived.

		Mortlock	Roseworthy
Parental values:-	Mexico 8156	- 332	282
	DX39	- 540	348
	Olympic	- 548	411

	Mortlock	Roseworthy
Mid-parental value	- 436	315
Mid-parental value	- 544	380

III IMPROVEMENT MEASURED IN A DIFFERENT YEAR TO THE YEAR OF SELECTION

a) Grain Yield

Selection in one year did not result in high yields in succeeding generations the next year (table 5.16). Yields of the selected lines in the second year were little better than random selections, and were usually lower yielding than the mid-parent.

When individual F_2 derived lines were selected in 1975, a considerable amount of the improvement gained by these lines was lost in the F_3 derived lines in the same year. For example, the best 20 per cent of individual F_2 derived lines from the DX39 * Mexico 8156 cross yielded 293 g/plot (32 per cent better than random selection), but the F_3 lines derived from them measured in the same year yielded only 215 g/plot (14 per cent more than random selection).

b) Plant height

In contrast to selection for grain yield, selection for plant height in one year was very effective in obtaining improvement in succeeding generations in the next year (table 5.17). The decrease in plant height was much greater than that obtained from random selection, and represented a considerable reduction below the mid-parent. The improvement obtained from selecting in a different year was comparable with that obtained from selecting at the same site in the same year (tables 5.11 and 5.17).

c) Harvest index

Selecting for grain yield using harvest index in the previous year was ineffective (table 5.18), and the yields of the selected lines in the year following selection were no better than randomly selected lines. The yields obtained were usually lower than when selection in the previous

TABLE 5.16

Effect of selecting for grain yield in different generations at Roseworthy in 1975 on improvement in succeeding generations at Roseworthy in 1976.

Selection intensity of 20%

Values are grams per plot with, in parenthesis, the percentage of random selection.

Cross	Generation$^+$ and data selected Roseworthy 1975	Improvement in generation of selection	Improvement in succeeding generations$^+$			
			Roseworthy 1975	Roseworthy 1976		
			F_3	F_3	F_4	F_5
DX39 * Mexico 8156	Individual F_2 lines	293 *(132)*	215 *(114)*	308 *(100)*	272 *(85)*	346 *(105)*
	Mean F_3 lines	231 *(117)*		305 *(102)*	290 *(100)*	335 *(107)*
Olympic * DX39	Individual F_2 lines	329 *(152)*	205 *(113)*	353 *(105)*	383 *(109)*	336 *(105)*
	Mean F_3 lines	218 *(125)*		356 *(105)*	361 *(102)*	355 *(109)*
Two crosses pooled	Individual F_2 lines	315 *(157)*	213 *(118)*	344 *(107)*	334 *(101)*	332 *(102)*
	Mean F_3 lines	226 *(124)*		324 *(102)*	315 *(97)*	335 *(106)*

+ Generation is the generation in which lines were derived.

		1975	1976
Parental values:-	Mexico 8156	- 238	282
	DX39	- 214	348
	Olympic	- 294	411

	1975	1976
Mid-parental value	- 226	315
Mid-parental value	- 254	380

TABLE 5.17

Effect of selecting for short plants in different generations at Roseworthy in 1975 on improvement in succeeding generations at Mortlock in 1976.

Selection intensity of 20%

Values are cm with, in parenthesis, the percentage of random selection.

Cross	Generation+ and data selected Roseworthy 1975	Improvement in generation of selection	Improvement in succeeding generations+			
			Roseworthy 1975	Mortlock 1976		
			F_3	F_3	F_4	F_5
DX39 * Mexico 8156	Individual F_2 lines	63.6 *(80)*	63.0 *(81)*	67.7 *(81)*	65.4 *(79)*	65.4 *(78)*
	Mean F_3 lines	63.0 *(79)*		67.7 *(80)*	65.4 *(77)*	65.4 *(78)*
Olympic * DX39	Individual F_2 lines	67.9 *(78)*	67.4 *(81)*	71.7 *(84)*	77.0 *(89)*	77.3 *(87)*
	Mean F_3 lines	66.9 *(82)*		70.4 *(84)*	78.4 *(90)*	78.3 *(87)*
Two crosses pooled	Individual F_2 lines	65.4 *(81)*	65.4 *(84)*	70.7 *(86)*	71.9 *(85)*	73.3 *(85)*
	Mean F_3 lines	64.4 *(82)*		68.9 *(82)*	69.6 *(83)*	69.8 *(84)*

+ Generation is the generation in which lines were derived.

Parental values:-		1975	1976
	Mexico 8156	84.4	96.3
	DX39	68.3	75.0
	Olympic	96.6	100.0

	1975	1976
Mid-parental value	76.4	85.7
Mid-parental value	82.5	87.5

TABLE 5.18

Effect of selecting for harvest index in different generations at Roseworthy in 1975 on improvement for grain yield in succeeding generations at Roseworthy in 1976.

Selection intensity of 20%

Values are grams per plot for yield and % for harvest index with, in parenthesis, the percentage of random selection.

Cross	Generation^{+} and data selected Roseworthy 1975 (harvest index)	Improvement in generation of selection Harvest index	Improvement in succeeding generations^{+}				
			Roseworthy 1975		Roseworthy 1976		
			Harvest index F_3	Grain yield F_3	Grain yield F_3	F_4	F_5
DX39 * Mexico 8156	Individual F_2 lines	45.0 *(121)*	37.8 *(107)*	184 *(94)*	324 *(101)*	315 *(100)*	320 *(99)*
	Mean F_3 lines	39.7 *(106)*		190 *(102)*	335 *(102)*	345 *(99)*	340 *(101)*
Olympic * DX39	Individual F_2 lines	38.7 *(111)*	35.3 *(105)*	169 *(91)*	327 *(94)*	353 *(102)*	319 *(101)*
	Mean F_3 lines	36.1 *(109)*		158 *(89)*	307 *(90)*	351 *(103)*	328 *(103)*
Two crosses pooled	Individual F_2 lines	43.1 *(118)*	37.1 *(106)*	179 *(96)*	320 *(95)*	325 *(97)*	311 *(97)*
	Mean F_3 lines	38.9 *(114)*		191 *(108)*	321 *(99)*	332 *(98)*	325 *(101)*

$^{+}$ Generation is the generation in which lines were derived.

Parental values:-		HI 1975	GY 1975	GY 1976
	Mexico 8156	- 42.4	238	282
	DX39	- 41.0	214	348
	Olympic	37.2	294	411

	HI 1975	GY 1975	GY 1976
Mid-parental value	- 41.7	226	315
Mid-parental value	- 39.1	254	380

year was based on yield itself.

Selecting the F_2 derived lines with the best harvest indices was also ineffective in improving grain yield of F_3 derived lines at the same site in the same year, as the yields of the F_3 derived lines were no higher than randomly selected lines.

B. EFFECT OF DELAYING SELECTION FOR GRAIN YIELD ON THE POSSIBLE POTENTIAL FOR IMPROVEMENT

The effect of delaying selection can be studied by comparing the response to selection in each generation. In these comparisons the response to selection in any generation is measured by the actual yield obtained in the next generation. The yields of any further generations cannot be used to indicate the potential available from the selected lines, as the lines in succeeding generations were derived from one randomly chosen line only, so further selection could not be carried out within the original selected group.

As an illustration, consider the 20 per cent selection at Mortlock in 1976, for the DX39 * Mexico 8156 cross (table 5.3). The improvement obtained by selecting the best individual F_2 derived lines can be measured by the yield of the corresponding F_3 derived lines, which is 560 g/plot. When selection was delayed one generation, and the best F_3 derived lines selected, the yield of the selected lines in the following generation was 591 g/plot. When the best individual F_4 derived lines were selected the average yield of the F_5 derived lines was 593 g/plot. Similarly, the effect of selecting using the means of lines from the F_3 and F_4, rather than the individual F_2 or F_3 derived lines, can be assessed by the yields obtained in the following generations (592 and 595 g/plot respectively).

Results of the simulated selections at different selection intensities and different sites, presented in tables 5.2 to 5.10, indicate that lines selected in late generations have the potential to give rise to lines that are just as high in yield as lines resulting from selection in early generations. While in some instances lines selected in early generations were higher yielding than lines selected in late generations, in other instances the reverse was true. The overall trend is best summarized by averaging the yields obtained by selecting in different generations for all selection intensities and sites in 1976 (table 5.19). The yields of selected lines in the generation after selection were the same, regardless of the generation in which they were selected.

If the aim was to select for low yield,the effect of delaying selection was quite different to the situation when selection was for high yield (table 5.20). Selection in late generations, e.g. F_4, gave a greater reduction in yield in the next generation, and therefore greater change, than selection in an early generation, e.g. F_2.

DISCUSSION

The yield improvement obtained by selecting in an early generation is related to the correlations and regressions obtained between the generations, as presented in chapter 4, e.g. at Mortlock the correlations between F_2 and F_3 derived lines for the DX39 * Mexico 8156 cross was 0.49^{**} while for Olympic * DX39 it was 0.10ns. Consequently, the improvement obtained in the F_5 by selecting F_2 derived lines was much greater in the first cross (20 per cent greater than random) than in the second (8 per cent greater than random). It is important to note that, in some instances,

TABLE 5.19

Effect of selecting for high grain yield in different generations on the yield obtained in the next generation.

Average of simulated selection at 10, 20 and 30 per cent intensities at Mortlock, Roseworthy and the average of these 2 sites, in 1976.

Cross	Generation+ and data selected	Yield in generation of selection (g/plot)	Yield of selected lines in generation+ after selection (g/plot)
DX39*Mexico8156	Individual F_2 lines	514	455
	Individual F_3 lines	573	479
	Individual F_4 lines	541	478
	Mean F_3 lines	505	479
	Mean F_4 lines	535	472
Olympic*DX39	Individual F_2 lines	513	442
	Individual F_3 lines	504	436
	Individual F_4 lines	515	430
	Mean F_3 lines	474	440
	Mean F_4 lines	483	449
Two crosses pooled	Individual F_2 lines	515	448
	Individual F_3 lines	547	459
	Individual F_4 lines	532	451
	Mean F_3 lines	497	465
	Mean F_4 lines	513	460

+ Generation is the generation in which lines were derived.

TABLE 5.20

Effect of selecting for low grain yield in different generations on the yield obtained in the next generation.

Average of simulated selection at 10, 20 and 30 per cent intensities at Mortlock, Roseworthy and the average of these 2 sites in 1976.

Cross	Generation[+] and data selected	Yield in generation of selection (g/plot)	Yield of selected lines in generation[+] after selection (g/plot)
DX39*Mexico8156	Individual F_2 lines	259	355
	Individual F_3 lines	251	320
	Individual F_4 lines	259	306
	Mean F_3 lines	317	334
	Mean F_4 lines	290	338
Olympic*DX39	Individual F_2 lines	311	367
	Individual F_3 lines	301	345
	Individual F_4 lines	281	295
	Mean F_3 lines	313	341
	Mean F_4 lines	317	301
Two crosses pooled	Individual F_2 lines	279	360
	Individual F_3 lines	272	325
	Individual F_4 lines	266	299
	Mean F_3 lines	312	334
	Mean F_4 lines	296	323

+ Generation is the generation in which lines were derived.

while the correlations were low, the improvement from selection was quite valuable e.g. the correlation between the F_2 and F_5 derived lines for the two crosses pooled, at Mortlock, was only 0.28^*, but when the best 20 per cent of lines were selected for yield, the F_5 derived lines from these were 15 per cent better than random selection and they also exceeded the average of the three parents.

When selection is carried out in an early generation, e.g. among F_2 derived lines, the important consideration is the response to this selection in a late generation, e.g. the F_5, when lines are approaching homozygosity. In the simulated selection schemes considered here, the selected lines could not be reselected, and the available data enabled each selected line to be continued with one random line only. This caused a loss of variability for grain yield, and the gain from selection was often reduced in the generations following selection. One random line was not sufficient to maintain the yield improvement. In practice, the selected group would be continued with many lines, probably with further selection, and we would expect the gain to be maintained. The yields obtained in the generation after selection were the same for all generations selected. It appears that it is of little consequence ultimately in what generation selection for yield is practised. A decision on when to commence selection for yield can therefore be based on other factors.

Value of replication

Because the seed supply is limited, selection for grain yield in early generations is often based on single plots of the lines. These plots are subject to a large experimental error as they are not replicated. Better responses to selection were obtained at Mortlock when selection was based on the means of a number of lines than with the individual lines, suggesting that some form of replication is desirable. A greater selection efficiency may result from smaller, replicated plots, or from delaying a generation enabling a multiplication of seed for replicated experiments of large plots. This would be particularly suitable if the additional multiplication could be undertaken out of season.

Response to selection

Responses to selection for grain yield when improvement was measured at the same site and in the same year as the selection, suggest that good progress for yield should be possible through selection. Better progress would be achieved in some crosses than in others. Selecting the best 20 per cent of lines from DX39 * Mexico 8156 gave F_5 lines that exceeded the mid-parent by 36 per cent, and the highest yielding parent by 10 per cent.

However, when the effect of different years is considered, the response to selection for yield in early generations, e.g. among F_2 derived lines, is poor. Yields of lines from succeeding generations in the year after selection were usually lower than the mid-parent, and were little better than random selection. Obviously, the overwhelming factor to be considered in developing a breeding method for yield improvement is the influence of different years. The effect of different sites in the one year was not as great as the effect of different years, but it is still an important factor reducing the effectiveness of selection. Selection at one site will give various responses at other sites depending on the similarities between the sites. Methods of testing to represent the effect of years and sites must be a prime consideration in a breeding program. This illustrates the complexities of selecting for grain yield. Selection for this character was very different from selection for simply inherited characters such as plant height, which give extremely good and predictable responses, even between years.

Selection for harvest index, instead of grain yield, in early generations did not overcome the problem of the environmental influence on yield. Selection for harvest index on F_2 derived lines was no more effective in improving yield in succeeding generations in the next year, than selection for yield directly.

The responses to selection for flour yield indicate that considerable improvement in flour yield is possible. Lines with higher flour yields were obtained from Olympic * DX39 than from DX39 * Mexico 8156. This reflects the good milling qualities of the Olympic parent. It was not possible in these simulation experiments to determine the effects of different years on selection for flour yield, but previous results (chapter 4) indicate that the large influence of the environment would have reduced the response to selection in different years.

Implications of results on theories of breeding

The strongest argument for selecting for grain yield in early generations is that the frequency of the best genotypes rapidly decreases with advancing generations (Shebeski 1967; Shebeski and Evans 1973). It follows that, if population size is constant, a late generation e.g. F_4 which has not been selected for yield previously, should have a lower potential to give high yielding genotypes than an early generation e.g. F_2. The potential of each generation to give high yielding genotypes was determined in these experiments by selecting in each generation and measuring the yield obtained in the generation after selection. If the effect of delaying selection was to irretrievably lose the highest yielding genotypes, selection in later generations would give lines that were lower yielding than those obtained by selection in early generations. However, this was not obtained. Improvements in yield in the generation after selection were the same regardless of the generation of selection. This response to selection was the same, even though in some instances the generation mean yield overall had decreased by the later generations.

While it is still feasible that delaying selection reduces the frequency of high yielding genotypes, this disadvantage is counteracted by the greater homozygosity and predictability of selection in the later generations.

If low yield was an objective, the frequency of low yielding genotypes should increase with advancing generations, and selection from late generations should be more effective. The results obtained support this suggestion, as the response to selection increased as selection was delayed from F_2 to F_4.

Practical arguments for testing in early generations

Although these results indicate that the improvement obtained by selecting in late generations is just as effective as in early generations, there are still arguments for selecting for grain yield in early generations. They are:-

1. A more efficient use of resources would result from selecting early and retaining only a proportion of the population (e.g. 20per cent). The improvement could be continued by further selection in later generations.

2. It would enable testing in many sites and years from an early stage. The testing across environments must be the prime consideration in a breeding program. By starting in early generations, selection will be practised for high yield stability across environments.

Chapter 6

THE VARIABILITY OF PEDIGREED LINES DERIVED FROM SUCCESSIVE GENERATIONS OF TWO WHEAT CROSSES, FOR GRAIN YIELD, FLOUR YIELD AND OTHER CHARACTERS

INTRODUCTION

It was proposed, after reviewing the literature, that the predictive value of early generation plots was determined by the degree of heterozygosity and the variability of the character being tested, in that generation. These factors could influence results in two ways.

1. If the plots are heterogeneous, due to segregation, the plot yield will be a sum of yields of many different genotypes. Therefore, the plot yield can not indicate the value of the best genotypes. Competition between genotypes may further decrease the predictive value of the measurement.

2. Segregation after the plot trial might produce genotypes that are quite different from those in the original population.

If these factors are important, the plots in early generations are unreliable indicators of the performance of the genotypes which could ultimately be obtained from them. However, these problems could be avoided if a plot assessment was delayed until an appropriate degree of homozygosity and homogeneity was achieved.

This chapter examines the variability of a number of characters in pedigreed lines derived from the F_2, F_3, F_4 and F_5 generations of two wheat crosses, tracing the decline in genotypic variance within families. The relative magnitudes of variances in each generation may be indicative of the most appropriate generation in which to commence selection for a particular character.

In these experiments the variability of lines grown as plots and single plants were measured in the F_2, F_3, F_4 and F_5 generations of two wheat crosses for grain yield, heading date, plant height, harvest index, pearling resistance and flour yield. Theoretical considerations, discussed in the literature review, indicate that the genetic variability within families should decrease more rapidly as generations are advanced for characters controlled by few loci, than for characters controlled by many loci.

METHODS AND MATERIALS

EXPERIMENT I - VARIABILITY OF LINES GROWN AS SINGLE PLANTS

a) Single plants at commercial density

The three parents, the F_2's, and F_3 and F_4 lines obtained by random pedigreed selection of the two wheat crosses were sown in rows 4.5 metres long and 20cm apart. The rows were cut back to 3.5 metres prior to harvest. For each cross 14 F_3 lines, originating from F_2 plants, and 14 F_4 lines were included, the 14 F_4 lines being derived from 7 F_3 lines each with 2 F_4 lines. Three rows of each parent and F_2, and one row of each F_3 and F_4 line were sown, giving a total of 71 rows (one parent being common to the two crosses).

The rows were sown with a cone seeder at a density three times that required in the treatment. The plants were thinned after emergence, using a marked rod, to 3cm spacing between plants, a density equivalent to commercial rates. This method of sowing was used to simulate as closely as possible, commercial conditions, and to overcome the problems associated with handsowing.

The plants were pulled when they had matured, and measurements were taken of grain yield, plant height and plant weight. Harvest index was calculated from grain yield and plant weight. For each row, 75 random plants were processed.

b) Plants at low density

The parents and F_2's of the two crosses were also sown at low density, to give comparative measurements when the plants were grown under minimum competition. Pairs of seeds were hand sown at 30cm intervals in rows 5 metres long and 36cm apart. Seedlings were thinned after emergence to give single plants at each position. Eight rows were sown side by side for each entry.

At maturity the plants were pulled and grain yield, plant height and plant weight were measured. Harvest index was calculated.

EXPERIMENT II - VARIABILITY OF LINES GROWN IN PLOTS, 1975

The three parents, and F_2 and F_3 derived lines obtained by random pedigreed selection of the two crosses were sown in plots 2 rows x 2 metres in a completely randomized design, at Roseworthy and Saddleworth. For each cross, 130 F_2 derived lines and 980 F_3 derived lines were included, the 980 F_3 derived lines being derived from 14 F_2 derived lines each with 70 F_3 derived lines (table 6.1).

All plots, except the parents, were sown from the seed of a single plant, so the F_2 and F_3 derived lines were sown as F_3 and F_4 plots respectively. Identical lines were sown at the two sites. The variety Wariquam was sown in a grid every fifth plot as a control variety to indicate environmental variability within the experimental area.

TABLE 6.1

Origin and number of lines in experiment II (plots 1975)

Generation of lines from crosses (generation) from which derived)	Number of lines or plots	Origin of lines				
		Crosses			Parents	
		No. of crosses	No. of F_2 derived lines for each cross	No. of F_3 derived lines for each F_2 derived line	No.of Parents	No. of plots per parent
Parents	390 (60,210)				3	130 (20,70)+
F_2	260 (40,140)	2	130 (20,70)			
F_3	1960(280,280)	2	14 (7,7)	70 (20,20)		

+ Numbers in parenthesis indicate number of lines measured for harvest index (first figure) and pearling resistance and flour yield (second figure).

Grain yield, heading date, mature plant height, harvest index, pearling resistance and flour yield were measured at Roseworthy, and grain yield was measured at Saddleworth. Harvest index, pearling resistance and flour yield were determined on a restricted number of plots chosen at random within each group (table 6.1).

EXPERIMENT III - VARIABILITY OF LINES GROWN IN PLOTS, 1976

The three parents, and F_2, F_3, F_4 and F_5 derived lines obtained by random pedigreed selection were sown in plots 4 rows x 2.5 metres at Roseworthy and Mortlock, but F_5 derived lines were not included at Mortlock. The same lines were sown at both sites, where possible, so that means over the two sites could be analysed. The origin and number of lines included are indicated in table 6.2. The F_2, F_3, F_4 and F_5 derived lines were sown as F_4, F_5, F_6 and F_6 plots respectively. The variety Wariquam was sown in a grid every fifth plot as a control variety.

Grain yield, heading date and plant height were measured at Mortlock, and grain yield, pearling resistance and flour yield were measured at Roseworthy. Pearling resistance and flour yield were determined on a restricted number of plots chosen randomly from each group (table 6.2).

ADJUSTMENT OF GRAIN YIELD OF PLOTS, EXPERIMENTS II AND III

In experiments II and III the plot yields of all entries were adjusted to account for site variability. The following adjustements were calculated, and the effectiveness of each determined by examining the average coefficient of variation of the three parents. The most effective method should be the one that gives the lowest coefficient of variation for the parents. Comparisons were made between:-

TABLE 6.2

Origin and number of lines in experiment III (plots 1976)

Generation of lines from crosses (generation from which derived)	Number of lines or plots	Origin of lines						
		Crosses					Parents	
		No. of crosses	No. of F_2 derived lines for each cross	No. of F_3 derived lines for each F_2 derived line	No. of F_4 derived lines for each F_3 derived line	No. of F_5 derived lines for each F_4 derived line	No. of parents	No. of plots per parent
Parents	390 (210)						3	130 (70)[+]
F_2	260 (140)	2	130 (70)					
F_3	1400 (280)	2	14 (7)	50 (20)				
F_4	R[ø] 840 (280) M[ø] 560	2	14 (7)	1 (1)	R 30 (20) M 20			
F_5	R 420 (105)	2	14 (7)	1 (1)	1 (1)	R 15 (15)		

[+] Numbers in parenthesis indicates number of lines measured for pearling resistance and flour yield.

[ø] R and M indicate numbers included at Roseworthy and Mortlock respectively. Where not indicated, the same numbers were included at both sites.

1. No adjustment.

2. Adjustment of trial entries using the average of the two neighbouring Wariquam controls. The yield of an entry was multiplied by the proportion (site average/average of the 2 neighbouring controls) to give adjusted values.

3. Adjustment using four controls. The same as 2 above, except the four neighbouring controls in the bay were used i.e. the two controls either side of the entry.

4. Adjustment using a moving mean of various sizes. For each entry, the mean of a number of entries on either side was calculated, e.g. with a moving mean of size 10 the average values of the five entries either side of the one being adjusted would be calculated. The yield of the entry and grid controls were not included in the moving mean. Each entry was adjusted by multiplying by the proportion (site average/moving mean for that entry). Moving means of sizes 2 to 26 were compared.

In the above methods of adjustment, each entry is expressed as a proportion of the neighbouring controls or moving mean, and then multiplied by the site average to retain the units as grams per plot. Expressing yields as a percentage of controls or moving means is advocated and used by many authors (e.g. Shebeski 1967; Briggs and Shebeski 1970, 1971; Knott 1972; Skorda 1973; DePauw and Shebeski 1973; Knott and Kumar 1975).

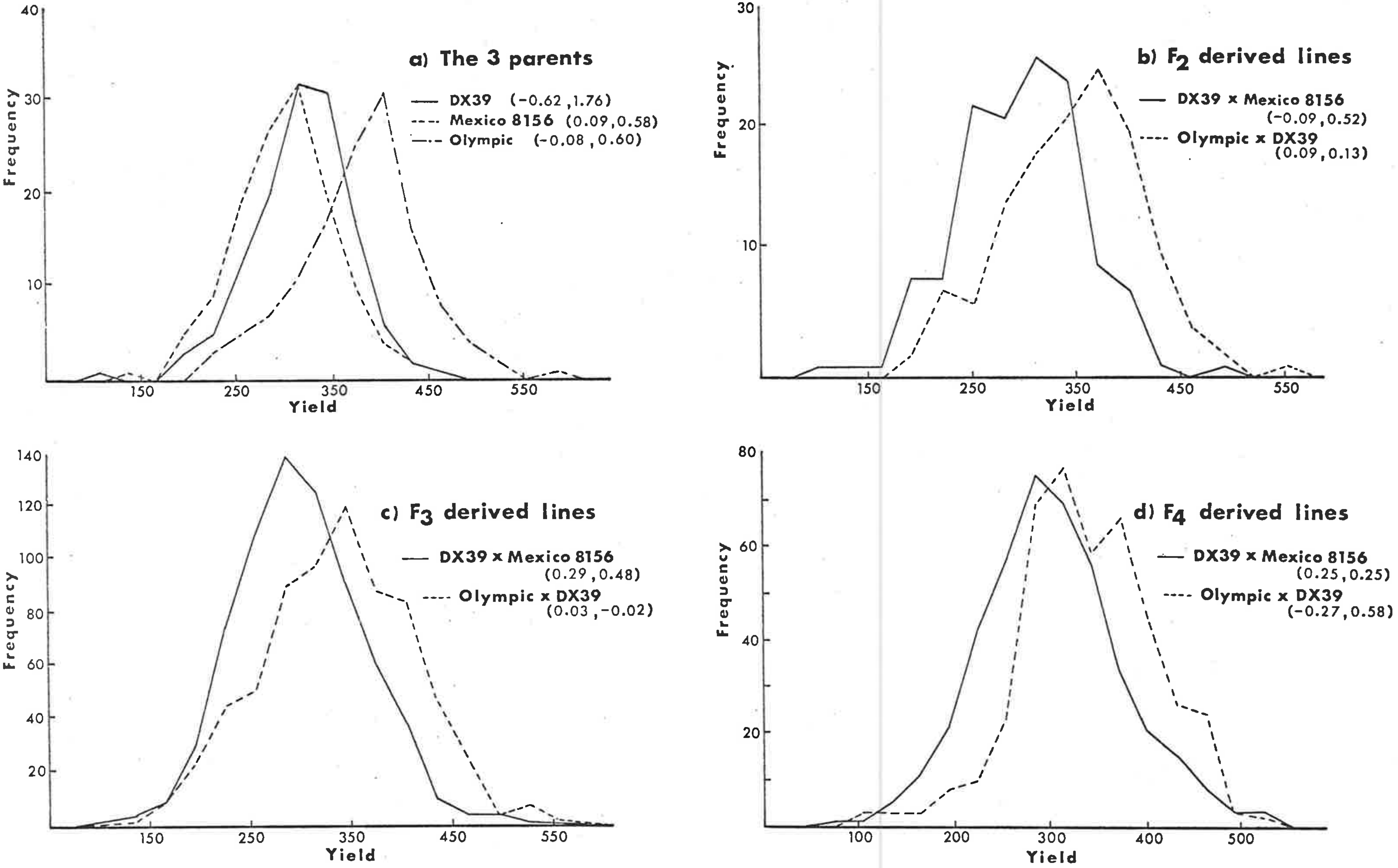
It was found that adjusting the yields in this way was more effective than adjustment in an additive manner,which uses the difference between the entry and the neighbouring controls.

A criticism of using yields expressed as a percentage of controls or moving means is that, being a ratio, the distribution may not be normal. This is not a valid criticism of the data in these experiments, as the adjusted data were quite normal, as illustrated by examples in figure 6.1, and the adjusted data did not depart from normality any more than the unadjusted data.

Figure 6.1

Frequency distributions for grain yield of the parents and F_2, F_3 and F_4 derived lines at Roseworthy 1976.

The skewness and kurtosis for each graph are indicated in parenthesis.


a) The 3 parents
DX39 (-0.62 ,1.76)
Mexico 8156 (0.09,0.58)
Olympic (-0.08 , 0.60)
Frequency
40
30
20
10
150
250
350
450
550
Yield
b) F2 derived lines
DX39 x Mexico 8156
(-0.09,0.52)
Olympic x DX39
(0.09,0.13)
Frequency
30
20
10
150
250
350
450
550
Yield
c) F3 derived lines
DX39 x Mexico 8156
(0.29,0.48)
Olympic x DX39
(0.03 ,-0.02)
Frequency
140
120
100
80
60
40
20
150
250
350
450
550
Yield
d) F4 derived lines
DX39 x Mexico 8156
(0.25,0.25)
Olympic x DX39
(-0.27,0.58)
Frequency
80
60
40
20
100
200
300
400
500
Yield

The results showed similar trends for analyses of unadjusted and adjusted yields. However, trends were more significant when the data were adjusted, and the environmental variation was reduced.

STATISTICAL PROCEDURES FOR COMPARING THE GENERATIONS

The variability of the parents, F_2's, and lines from succeeding generations were compared using variances and coefficients of variation. Data from each generation were also subjected to a hierarchal analysis of variance so the variation due to different levels of subdivision, e.g. between crosses, between F_2's within crosses, between F_3's within F_2's, and between F_4's within F_3's, could be analysed. The expected mean squares for this analysis of variance are illustrated for the F_4 single plant data in table 6.3(a).

Broad sense heritabilities for all characters were calculated using the variance components from the hierarchical analyses of variance for each cross separately (table 6.3(b)). In the example shown, the genetic variance would be estimated from the between F_2 variance component, σ^2_{F2}. Environmental variances, σ^2_e, were estimated in two ways:-

1. The "error" variance component, which would be the "between F_3 within F_2" variance component, σ^2_{F3}, in the example shown.
2. The average variance of the two parents for each cross.

TABLE 6.3

Expected mean squares for the hierarchal analyses of variance

a) Analysis of variance including the two crosses, illustrated by the F_4 single plant data

Source of variation	Degrees of freedom	Mean squares	Expected mean squares
Between crosses	a - 1	MS_C	$\sigma^2_{F_4} + d\sigma^2_{F_3} + cd\sigma^2_{F_2} + bcd\sigma^2_c$
Between F_2 within crosses	a (b-1)	MS_{F_2}	$\sigma^2_{F_4} + d\sigma^2_{F_3} + cd\sigma^2_{F_2}$
Between F_3 within F_2	ab (c-1)	MS_{F_3}	$\sigma^2_{F_4} + d\sigma^2_{F_3}$
Between F_4 within F_3	abc(d-1)	MS_{F_4}	$\sigma^2_{F_4}$
Total	abcd -1		

b) Analysis of variance for the separate crosses used to calculate broad sense heritabilities, illustrated by the F_3 plot data

Source of variation	Degrees of freedom	Mean squares	Expected mean squares
Between F_2	a - 1	MS_{F_2}	$\sigma^2_{F_3} + b\sigma^2_{F_2}$
Between F_3 within F_2	a (b-1)	MS_{F_3}	$\sigma^2_{F_3}$
Total	ab - 1		

RESULTS

EFFECTIVENESS OF DIFFERENT METHODS OF ADJUSTMENT OF YIELD IN PLOTS

The different methods of adjusting the grain yields of trial entries were compared at four sites spread over two years. In all cases a moving mean reduced the site variability to the greatest extent, as indicated by the average coefficient of variation of the three parents (table 6.4). The optimum moving mean size was 14 at Roseworthy in 1975, 16 at Saddleworth in 1975, and 10 at Roseworthy and Mortlock in 1976. Using small moving means of 2 or 4 sometimes increased the variation compared with the unadjusted data, as exceptional values then had a large influence in adjustment. Using four grid controls was better than only two in 1975, but there was little difference in 1976.

On the basis of these results, the yields in these experiments were adjusted using a moving mean, the optimum size for each experiment being used.

VARIABILITY OF DIFFERENT CHARACTERS IN SUCCESSIVE GENERATIONS

The magnitudes of the means and variances were sometimes positively related, so coefficients of variation (CV) are also presented. Significance tests have been performed on important variance ratios, but these should be treated with caution where the magnitudes of the means differ greatly. A one-tailed test was used to test the significance of variance ratios, as the hypothesis being tested was whether one variance was significantly greater than the other.

1. Grain yield

The yields from Saddleworth in 1975 were more variable than at the other sites (table 6.4), and these data will not be presented.

TABLE 6.4

Effectiveness of different methods of adjusting the yield of trial entries to correct for site variation

Method of adjustment	Average coefficient of variation of 3 varieties (total of 390 plots)			
	Roseworthy 1975	Saddleworth 1975	Roseworthy 1976	Mortlock 1976
No adjustment	26.8	30.5	21.9	23.9
Two grid controls	26.6	33.8	18.3	20.8
Four grid controls	25.1	30.1	18.6	20.2
Moving means:- size 2	37.2	38.7	19.6	25.3
size 4	28.3	30.9	17.3	20.8
size 6	25.4	29.5	17.1	20.3
size 8	25.1	28.4	17.0	20.1
size 10	24.4	27.5	16.9	19.6
size 12	24.4	27.4	17.3	20.1
size 14	23.9	27.2	17.7	20.1
size 16	24.2	27.1	17.6	19.8
size 18	23.9	27.2	17.6	20.0
size 20	23.9	27.2	17.6	20.0
size 22	24.1	27.1	17.6	20.1
size 24	23.9	27.2	17.7	20.2
size 26	24.0	27.2	17.7	20.2

The environmental variability, as estimated by the average coefficient of variation of the three parents, was much greater for the yield of single plants than for the yield of plots, particularly for the single plants at commercial density where interplant competition would have occurred (tables 6.5 to 6.10). The environmental variability of plants at low density (table 6.5) was only two-thirds that of plants at commercial density (table 6.6). The environmental variability of the four row plots in 1976 was less than the two row plots in 1975 (tables 6.7 to 6.9).

The F_2 generations were always more variable than the average of the respective parents (tables 6.5 to 6.10). In several instances (plants at low density DX39 * Mexico 8156 (table 6.5), Roseworthy plots 1975 Olympic * DX39 (table 6.7), and Mortlock plots 1976 Olympic * DX39 (table 6.9)) the variance of the F_2 was not significantly greater than the average variance of the two parents, but this was apparently due to the parents having a larger variance due to a higher mean, as is shown by the differences in the coefficients of variation.

The variability of each generation after pedigreed selection can be seen by comparing the averages of the within line variances for each of the generations. When the grain yields of lines were assessed on single plants, the F_3 and F_4 generations were significantly less variable than the F_2, and as uniform, or almost as uniform, as the parents (table 6.6).

When grain yields were measured in plots (tables 6.7 to 6.10), lines from the F_3 and F_4 were generally less variable, on average, than the F_2, and there was a steady trend to greater uniformity with advancing generations. The results from Roseworthy in 1976 were an exception, as the F_3, F_4 and F_5 still maintained the same amount of variability as the F_2 (table 6.8). The average variabilities of lines from the F_3, F_4 and F_5 were greater than the parents in all plot experiments when compared using coefficients of variation.

TABLE 6.5

The variability of 3 parents and 2 F_2's for grain yield, plant height and harvest index measured on plants at low density, Roseworthy 1975.

Character	Parents					F_2			
	Parent	Number	Mean	Variance	C.of V.	Number	Mean	Variance	C.of V.
Grain yield (g/plant)	DX39	145	19	29^a	28	122	18	56^a	41
	Mexico 8156	145	28	75	31				
	Average		24	52	30				
	Olympic	139	23	49	30	93	23	126^b	48
	DX39	145	19	29	28				
	Average		21	39^b	29				
	Average of 3 parents or $2F_2$'s		23	51	30		21	91	45
Plant height (cm)	DX39	145	66	10	5	122	72	97^c	14
	Mexico 8156	146	89	19	5				
	Average		78	15^c	5				
	Olympic	139	98	18	4	93	82	150^d	15
	DX39	145	66	10	5				
	Average		82	14^d	5				
	Average of 3 parents or $2F_2$'s		84	16	5		77	124	15
Harvest index (%)	DX39	145	33	25	16	122	35	42^e	19
	Mexico 8156	140	36	19	12				
	Average		35	22^e	14				
	Olympic	137	28	22	17	92	30	41^f	21
	DX39	145	33	25	16				
	Average		31	24^f	17				
	Average of 3 parents or $2F_2$'s		32	22	15		33	42	20

Variances followed by the same letter are significantly different, $P < 0.05$

TABLE 6.6

The variability of grain yield of 3 parents and successive generations of 2 wheat crosses measured on single plants at commercial density, Roseworthy 1975.

Parents (n=225)				F_2 (n=225)			F_2 family number	F_3 - within F_2lines (n=75)			F_4 - within F_3lines (n=75)		
Parent	Mean (g/plant)	Variance	CV	Mean (g/plant)	Variance	CV		Mean (g/plant)	Variance	CV	Mean (g/plant)	Variance	CV
							DX39 * MEXICO 8156						
DX39	1.2	0.4	51										
				2.0	1.6^{abc}	63	1	2.2	1.3	51	3.0	2.0	48
Mexico 8156	2.5	1.6	49								1.1	0.2	44
							2	1.9	0.8	45			
Average	1.9	1.0^{a}	50				3	1.8	1.3	64	1.1	0.2	44
											1.5	0.5	48
							4	2.2	1.1	46	1.9	0.9	49
											2.0	0.8	45
							6	2.2	1.5	54	1.5	0.7	57
											2.2	1.7	58
							7	2.9	2.0	49			
							9	1.1	0.4	54	1.3	0.3	45
											1.4	0.5	49
							11	1.7	0.3	33	1.6	0.5	42
											1.9	0.7	43
							13	1.8	0.6	45	2.0	0.8	43
											1.7	0.8	55
							15	2.2	1.0	46			
							16	2.0	1.1	53			
							17	2.6	0.9	36			
							18	2.5	1.3	46			
							19	1.2	0.3	45			
Average								2.0	1.0^{bd}	48	1.8	0.8^{cd}	48
Variance of family means									0.3			0.2	
Statistics for all lines pooled								2.0	1.2	54	1.8	1.0	56
							OLYMPIC * DX39						
Olympic	2.7	1.4	44										
				2.1	2.5^{fgh}	74	5	1.4	0.4	44	2.1	1.3	54
DX39	1.2	0.4	51								1.9	1.0	52
							7	1.1	0.2	42			
Average	2.0	0.9^{fi}	48				8	2.3	1.4	52	2.6	1.7	50
											2.2	1.8	60
							10	2.1	0.9	45	2.3	1.8	59
											2.0	1.1	53
							13	1.6	0.8	56			
							15	1.1	0.4	56			
							16	2.3	1.3	49			
							17	1.3	0.5	56			
							18	1.4	0.8	61			
							19	1.3	0.7	63	1.5	0.8	61
											1.0	0.3	60
							20	1.8	1.4	67			
							21	2.2	0.9	43	1.9	1.2	57
											2.4	0.8	38
				Average of F_2's			22	1.8	1.4	66	2.2	1.7	59
Average of 3 parents	2.2	1.1	48	2.1	2.1	69					2.4	1.7	56
							23	1.3	0.5	57	1.0	0.3	52
											2.2	1.2	50
Average								1.6	0.8^{g}	54	2.0	1.2^{hi}	54
Variance of family means									0.2			0.3	
Statistics for all lines pooled								1.6	1.0^{j}	61	2.0	1.4^{j}	61

Variances followed by the same letter are significantly different, $P < 0.05$

TABLE 6.7

The variability of grain yield in plots of 3 parents and successive generations of 2 wheat crosses, Roseworthy 1975.

	Parents (n=130)			F_2 (n=130)			F_2 family number	F_3 - within F_2 lines (n=70)		
Parent	Mean (g/plot)	Variance (x10^{-1})	CV	Mean (g/plot)	Variance (x10^{-1})	CV		Mean (g/plot)	Variance (x10^{-1})	CV
DX 39 * MEXICO 8156										
DX39	214	264	24.0							
				225	396^{ab}	28.0	1	213	308	26.1
Mexico 8156	238	300	23.0				2	167	256	30.2
							3	225	424	28.9
Average	226	282^{a}	23.5				4	192	215	24.2
							5	208	363	29.0
							6	184	239	26.5
							7	207	210	22.1
							8	200	312	27.9
							9	164	202	27.4
							10	259	412	24.8
							11	180	192	24.3
							12	200	206	22.7
							13	180	262	28.4
							14	185	361	32.5
							Average	198	283^{b}	26.8
							Statistics for all lines pooled	198	337	29.4
OLYMPIC * DX39										
Olympic	294	528	24.7							
				194	412^{cd}	33.1	1	197	439	33.6
DX39	214	264^{c}	24.0				2	151	157	26.2
							3	165	186	26.2
Average	254	396	24.4				4	204	257	24.9
							5	152	219	30.8
							6	181	360	33.1
							7	137	327	41.6
							8	194	238	25.1
							9	205	230	23.4
							10	174	295	31.2
Average of 3 parents	249	364	23.9	Average of F_2's			11	166	328	34.6
				209	404	30.6	12	144	173	28.9
							13	160	372	38.2
							14	162	243	30.5
							Average	171	273^{d}	30.6
							Statistics for all lines pooled	171	316	32.9

Variances followed by the same letter are significantly different, $P < 0.05$

TABLE 6.8

The variability of grain yield in plots of 3 parents and successive generations of 2 wheat crosses, Roseworthy 1976.

Parents (n=130)				F_2 (n=130)			F_2 family number	F_3- within F_2lines (n=50)			F_4- within F_3lines (n=30)			F_5- within F_4lines (n=15)		
Parent	Mean (g/plot)	Variance ($x10^{-1}$)	CV	Mean (g/pl)	Variance ($x10^{-1}$)	CV		Mean (g/pl)	Variance ($x10^{-1}$)	CV	Mean (g/pl)	Variance ($x10^{-1}$)	CV	Mean (g/pl)	Variance ($x10^{-1}$)	CV
							DX39 * MEXICO 8156									
DX39	319	267	16.2	301	387^{aij}	20.7	1	295	243	16.7	265	356	22.5	258	361	23.3
Mexico 8156	301	294	18.0				2	282	661	28.9	247	334	23.4	248	246	20.0
							3	331	439	20.0	332	816	27.2	316	364	19.1
Average	310	281^{abcd}	17.1				4	325	334	17.8	300	409	21.3	302	331	19.0
							5	283	346	20.8	285	259	17.9	280	406	22.7
							6	290	269	17.9	340	250	14.7	325	409	19.6
							7	297	348	19.9	305	569	24.7	337	357	17.7
							8	263	500	26.9	298	315	18.8	303	484	22.9
							9	294	273	17.8	283	371	21.5	266	162	15.1
							10	290	298	18.8	250	457	27.0	253	407	25.2
							11	280	291	19.3	306	198	14.6	288	698	29.1
							12	299	388	20.8	288	420	22.5	290	150	13.4
							13	331	345	17.7	405	547	18.3	376	808	23.9
							14	339	320	16.7	333	400	19.0	353	390	17.9
Average								300	361^{b}	20.0	303	407^{c}	21.0	300	399^{d}	20.6
Variance of family means								52^{no}			168^{n}			149^{c}		
Statistics for all lines pooled								300	403^{kl}	21.2	303	551^{ik}	24.5	300	513^{jl}	23.9
							OLYMPIC * DX39									
Olympic	380	399	16.6	349	437^{em}	18.9	1	367	378	16.8	336	302	16.3	351	489	19.9
DX39	319	267	16.2				2	335	358	17.8	341	408	18.8	335	195	13.2
							3	339	367	17.9	421	266	12.3	374	550	19.9
Average	350	333^{eh}	16.4				4	374	259	13.6	360	359	16.6	329	285	16.2
							5	294	436	22.5	347	382	17.8	321	422	20.2
							6	326	684	25.3	355	690	23.4	365	751	23.8
							7	285	638	28.0	279	217	16.7	266	472	25.9
							8	360	522	20.1	327	542	22.5	324	300	16.9
							9	367	392	17.1	367	243	13.4	350	238	13.9
							10	346	698	24.2	349	605	22.3	387	370	15.7
Average of 3 parents	333	320	16.9	Average of F_2's			11	308	490	22.7	292	398	21.6	305	241	16.1
				325	412	19.8	12	292	402	21.7	315	299	17.4	294	391	21.3
							13	339	667	24.1	301	437	21.9	272	469	25.2
							14	362	644	22.2	369	303	14.9	367	263	14.0
Average								335	495^{hfg}	21.0	340	389^{f}	18.3	331	388^{g}	18.7
Variance of family means								91			133			140		
Statistics for all lines pooled								335	571^{m}	22.5	340	501	20.8	331	495	21.2

Variances followed by the same letter are significantly different, $P < 0.05$

TABLE 6.9

The variability of grain yield in plots of 3 parents and successive generations of 2 wheat crosses, Mortlock 1976

	Parents (n=130)			F_2 (n=130)			F_2	F_3 - within F_2lines (n=50)			F_4 - within F_3lines (n=20)		
Parent	Mean (g/plot)	Variance ($x10^{-1}$)	CV	Mean (g/pl)	Variance ($x10^{-1}$)	CV	family no.	Mean (g/pl)	Variance ($x10^{-1}$)	CV	Mean (g/pl)	Variance ($x10^{-1}$)	CV
							DX39 * MEXICO 8156						
DX39	497	686	16.7	406	1097^{ab}	25.8	1	408	1097	25.7	338	653	23.9
Mexico 8156	349	616	22.5				2	390	1447	30.8	367	957	26.7
							3	499	674	16.5	488	2025	29.1
Average	423	651^{acd}	19.6				4	403	1036	25.3	393	871	23.8
							5	354	921	27.1	314	716	26.9
							6	448	893	21.1	539	587	14.2
							7	373	858	24.8	354	948	27.5
							8	323	829	28.2	357	329	16.1
							9	485	870	19.2	489	514	14.7
							10	401	1075	25.9	356	559	21.0
							11	324	665	25.2	310	662	26.3
							12	453	692	18.4	377	878	24.9
							13	389	886	24.2	495	1196	22.1
							14	511	979	19.4	482	857	19.2
							Average	411	923^{c}	23.7	404	840^{bd}	22.6
							Variance of family means		364			595	
							Statistics for all lines pooled	411	1245	27.1	404	1355	28.8
							OLYMPIC * DX39						
Olympic	485	916	19.7	400	794^{e}	22.3	1	341	595	22.6	291	437	22.7
DX39	497	686	16.7				2	271	385	22.9	268	474	25.7
							3	399	673	20.6	413	519	17.5
Average	491	801	18.2				4	474	814	19.0	388	499	18.2
							5	372	577	20.4	389	913	24.6
							6	386	834	23.7	298	601	26.0
							7	396	899	23.9	394	981	25.1
							8	417	514	17.2	348	525	20.8
							9	409	477	16.9	431	1094	24.3
							10	378	1135	28.2	439	447	15.2
				Average of F_2's			11	382	731	22.4	387	102	8.3
Average of 3 parents	443	739	19.6	403	946	24.1	12	321	599	24.1	249	306	22.2
							13	420	804	21.3	424	491	16.5
							14	375	427	17.4	357	1096	29.3
							Average	382	676	21.5	363	606^{e}	21.2
							Variance of family means		232			391	
							Statistics for all lines pooled	382	879	24.6	363	942	26.8

Variances followed by the same letter are significantly different, $P < 0.05$

TABLE 6.10

The variability of grain yield in plots of 3 parents and successive generations of 2 wheat crosses, average of 2 sites 1976 (Roseworthy and Mortlock)

Parents (n=130x2)				F_2 (n=130x2)			F_2 family number	F_3 - within F_2lines (n=50x2)			F_4 - within F_3lines (n=20x2)$^+$		
Parent	Mean (g/plot)	Variance (x10^{-1})	CV	Mean (g/pl)	Variance (x10^{-1})	CV		Mean (g/pl)	Variance (x10^{-1})	CV	Mean (g/pl)	Variance (x10^{-1})	CV
							DX39 * MEXICO 8156						
DX39	408	246	12.2										
				353	437^{abij}	18.7	1	351	320	16.1	302	216	15.4
Mexico 8156	325	237	15.0				2	336	730	22.5	300	378	20.5
							3	415	351	14.3	398	716	21.3
Average	367	242^{acd}	13.6				4	364	418	17.8	342	381	18.1
							5	318	459	21.3	301	302	18.3
							6	369	268	14.0	431	226	11.0
							7	335	417	19.3	334	371	18.3
							8	293	411	21.9	329	273	15.9
							9	389	375	15.7	386	199	11.6
							10	345	424	18.9	304	205	14.9
							11	302	291	17.9	298	334	19.4
							12	376	253	13.4	340	321	16.7
							13	360	291	15.0	448	491	15.6
							14	425	367	14.3	406	324	14.0
							Average	356	384^{ce}	17.3	351	338^{bde}	16.6
							Variance of family means		149			276	
							Statistics for all lines pooled	356	515^{ik}	20.2	351	575^{jk}	21.7
							OLYMPIC * DX39						
Olympic	433	391	14.5										
				375	384^{fg}	16.5	1	354	289	15.2	315	146	12.1
DX39	408	246	12.2				2	303	160	13.2	309	109	10.7
							3	369	300	14.8	413	243	11.9
Average	421	319^{f}	13.4				4	424	286	12.6	369	277	14.3
							5	333	297	16.4	378	146	10.1
							6	356	380	17.3	331	385	18.7
							7	341	444	19.5	339	358	17.6
							8	388	305	14.2	342	371	17.8
							9	388	243	12.7	403	394	15.6
							10	362	639	22.1	392	372	15.6
Average of				Average of F_2's			11	345	404	18.4	329	131	11.0
3 parents	389	291	13.9	364	411	17.6	12	307	203	14.7	283	177	14.9
							13	380	456	17.8	356	267	14.5
							14	369	355	16.2	364	265	14.2
							Average	359	340^{h}	16.1	352	259^{gh}	14.2
							Variance of family means		105			140	
							Statistics for all lines pooled	359	431	18.3	352	385	17.6

$^+$ Some groups of F_4 derived lines did not have the full 20 lines at both centres

Variances followed by the same letter are significantly different, $P < 0.05$

While the averages of the lines showed these trends, the variability of individual lines in each generation differed considerably (tables 6.7 to 6.10). Many lines were quite uniform, compared with the parents, as early as the F_3, whereas other lines from the F_4 or F_5 were more variable than the F_2. Although the parents were considered uniform, many lines, even in the F_3, appeared much more uniform. This occurred in all experiments involving both single plants and plots.

The total cross variability for each generation, in contrast to the variability within lines, can be assessed, firstly by pooling the data for all lines, and secondly from the variance of family means in each generation. There was a general trend for the total variability to increase with advancing generations when grain yield was measured in plots (tables 6.8 to 6.10), but no increase in total variability was evident when grain yield was measured on single plants (table 6.6).

The hierarchal analyses of variance (table 6.11) show that most of the variation for grain yield was between lines of the generation analysed, e.g. if lines from the F_5 were analysed, then most of the variation was between F_5 lines within F_4 lines. This generally accounted for 60 to 80 per cent of the total variation. Some of this would be genetic variation, but a high proportion would be environmental.

As the generation analysed was advanced, the variation of the lowest level in the analysis of variance, i.e. between lines in the generation analysed, was generally reduced in comparison with the higher levels. For example, considering the average of the two sites in 1976, the percentages of total variation for the levels "between F_3 within F_2" and "between F_4 within F_3" were 75 and 61 per cent respectively. This indicates the greater uniformity that was achieved with advancing generations and increased homozygosity. There were some exceptions, the F_5 data from Roseworthy in 1976 and the single plant data.

TABLE 6.11

Hierarchal analysis of variance of grain yield of lines from different generations of 2 wheat crosses in a number of experiments.

Experiment	Site	Generation+ analysed	source of variation	Degrees of freedom	Mean squares	F	Variance components	% of total variance
Single plants 1975	Roseworthy	F_3^{+}	Between crosses	1	80.9	4.8^{*}	0.06	5
			Between F_2 within crosses	26	16.8	18.5^{**}	0.21	18
			Between F_3 within F_2	2072	0.9		0.91	77
		F_4	Between crosses	1	17.7	0.7	0.00	0
			Between F_2 within crosses	12	24.7	2.1	0.09	7
			Between F_3 within F_2	14	11.9	11.9^{**}	0.15	12
			Between F_4 within F_3	2068	1.0		1.00	82
Plots 1975	Roseworthy	F_3	Between crosses	1	349140	8.9^{**}	316	8
			Between F_2 within crosses	26	39193	14.1^{*}	520	14
			Between F_3 within F_2	1932	2780		2780	77
Plots 1976	Roseworthy	F_3	Between crosses	1	44221	12.4^{**}	581	11
			Between F_2 within crosses	26	3581	8.4^{**}	631	12
			Between F_3 within F_2	1372	428		4282	78
		F_4	Between crosses	1	29014	6.4^{*}	583	10
			Between F_3 within crosses	26	4514	11.3^{**}	1372	23
			Between F_4 within F_3	812	398		3984	67
		F_5	Between crosses	1	12611	5.2^{*}	485	7
			Between F_4 within crosses	26	2432	5.0^{**}	1296	19
			Between F_5 within F_4	392	488		4884	73
Plots 1976	Mortlock	F_3	Between crosses	1	30999	2.1	230	2
			Between F_2 within crosses	26	14916	18.7^{**}	2823	26
			Between F_3 within F_2	1372	799		7995	72
		F_4	Between crosses	1	24233	2.5	513	4
			Between F_3 within crosses	26	9861	13.6^{**}	4569	37
			Between F_4 within F_3	532	722		7228	59
Plots 1976	Average of 2 sites 1976	F_3	Between crosses	1	293	0.0	0	0
			Between F_2 within crosses	26	6339	17.5^{**}	1196	25
			Between F_3 within F_2	1372	362		3619	75
		F_4	Between crosses	1	54	0.0	0	0
			Between F_3 within crosses	26	3874	13.0^{**}	1950	39
			Between F_4 within F_3	486	299		2988	61

+ Data for each generation were measured using lines derived from that generation

* $P < 0.05$; ** $P < 0.01$

2. Heading date

The F_2 generations were much more variable than the parents for heading date (tables 6.12 and 6.13), the differences being significant. The average variability of lines from the F_3 and F_4 was significantly reduced with advancing generations, but lines from the F_4 were still significantly more variable than their parents. A number of individual lines were as uniform as the parents by the F_3, whereas the variability of others was increased. In some instances, lines from the F_3 and F_4 were significantly more variable than the original F_2. The total population variability was increased with advancing generations (table 6.13).

Analyses of variance of F_3 data showed that 62 to 65 per cent of the variation in the heading date of F_3's was attributable to variation between F_3 lines within F_2's (table 6.14). A greater degree of uniformity had been obtained by the F_4, as only 23 per cent of the total variance was between F_4 lines within F_3's. This indicates the degree of fixation that occurred for heading date by the F_3.

3. Plant height

The environmental variability for plant height measured on single plants at commercial density was about twice that for height measured on plants at low density, or in plots (tables 6.5, 6.15 to 6.17). Height of spaced plants and plots were equally variable.

The variability of plant height in the F_2 was always significantly greater than the parents. The variability of the F_2 compared with the parents was proportionally greater when measured in plots or on plants at low density, than when measured on single plants at commercial density. The average variability of lines from the F_3 and F_4 was significantly reduced with advancing generations, but uniformity was not achieved by the F_4, as the average variability of lines in this generation was still significantly more variable than the parents. The approach to uniformity of

TABLE 6.12

The variability of heading date in plots of 3 parents and successive generations of 2 wheat crosses, Roseworthy 1975.

Parents (n=130)				F_2 (n=130)			F_2 family number	F_3- within F_2lines (n=70)		
Parent	Mean (days)	Vari-ance	CV	Mean (days)	Vari-ance	CV		Mean (days)	Vari-ance	CV
DX39 * MEXICO 8156										
DX39	276	3.1	0.6							
				277	34.0^{ae}	2.1	1	278	1.2	0.4
Mexico 8156	278	1.7	0.5				2	282	82.7	3.2
							3	277	8.4	1.1
Average	277	2.4^{ab}	0.6				4	278	2.8	0.6
							5	284	98.9	3.5
							6	276	4.5	0.8
							7	280	90.6	3.4
							8	283	89.6	3.4
							9	275	5.0	0.8
							10	296	4.5	0.7
							11	274	6.2	0.9
							12	274	6.1	0.9
							13	278	3.0	0.6
							14	277	2.5	0.6
						Average		279	29.0^{b}	1.5
						Statistics for all lines pooled		279	58^{e}	2.7
OLYMPIC * DX39										
Olympic	282	1.0	0.4							
				279	54.5^{c}	2.6	1	288	7.2	0.9
DX39	276	3.1	0.6				2	281	56.1	2.7
							3	281	65.7	2.9
Average	279	2.1^{cd}	0.5				4	283	67.9	2.9
							5	273	3.8	0.7
							6	278	40.7	2.3
							7	275	5.9	0.9
							8	283	80.3	3.2
							9	281	80.4	3.2
							10	280	76.6	3.1
				Average of F_2's			11	277	49.4	2.5
Average of 3 parents	278	1.9	0.5	278	44.3	2.4	12	279	60.6	2.8
							13	281	78.3	3.2
							14	282	86.7	3.3
						Average		280	54.3^{d}	2.5
						Statistics for all lines pooled		280	66.2	2.9

Variances followed by the same letter are significantly different, $P < 0.05$

TABLE 6.13

The variability of heading date in plots of 3 parents and successive generations of 2 wheat crosses, Mortlock 1976.

Parents (n=130)				F_2 (n=130)			F_2 family number	F_3 - within F_2 lines (n=50)			F_4-within F_3 lines (n=20)		
Parent	Mean (days)	Variance	CV	Mean (days)	Variance	CV		Mean (days)	Variance	CV	Mean (days)	Variance	CV
DX39 * MEXICO 8156													
DX39	293	1.6	0.4	295	17.7^{abcmn}	1.4	1	296	3.1	0.6	298	4.2	0.7
Mexico 8156	296	1.4	0.4				2	298	36.6	2.0	294	1.7	0.5
							3	295	7.1	0.9	297	13.4	1.2
Average	295	1.5^{aef}	0.4				4	296	3.2	0.6	296	1.5	0.4
							5	301	31.3	1.9	315	0.7	0.3
							6	294	3.7	0.7	293	1.5	0.4
							7	297	42.1	2.2	309	5.1	0.7
							8	298	40.0	2.1	307	38.5	2.0
							9	293	5.3	0.8	293	2.5	0.5
							10	307	6.7	0.9	309	8.4	0.9
							11	292	4.0	0.7	298	42.6	2.2
							12	293	3.6	0.7	294	2.0	0.5
							13	297	5.1	0.8	297	3.5	0.6
							14	296	3.2	0.6	296	3.6	0.7
Average								297	13.9^{bde}	1.1	300	9.2^{cdf}	0.8
Variance of family means									14.6^{p}			50.3^{p}	
Statistics for all lines pooled								297	27.2^{mo}	1.8	300	55.8^{no}	2.5
OLYMPIC * DX39													
Olympic	298	0.7	0.3	296	26.2^{ghi}	1.7	1	298	2.8	0.6	299	0.9	0.3
DX39	293	1.6	0.4				2	297	21.5	1.6	299	24.3	1.7
							3	297	25.2	1.7	303	5.6	0.8
Average	296	1.2^{gkl}	0.4				4	298	23.7	1.6	294	2.3	0.5
							5	290	4.6	0.7	290	4.9	0.8
							6	295	14.0	1.3	295	6.5	0.9
							7	291	6.7	0.9	292	2.5	0.5
							8	296	30.0	1.9	301	30.4	1.8
							9	295	31.9	1.9	298	41.3	2.2
							10	296	26.3	1.7	297	19.7	1.5
				Average of F_2's			11	294	16.1	1.4	293	2.3	0.5
Average of 3 parents	296	1.3	0.4	296	21.9	1.6	12	294	28.4	1.8	299	20.1	1.5
							13	295	19.9	1.5	288	4.2	0.7
							14	298	29.9	1.8	296	8.8	1.0
Average								295	20.1^{hjk}	1.5	296	12.4^{ijl}	1.1
Variance of family means									6.3^{q}			17.2^{q}	
Statistics for all lines pooled								295	25.5	1.7	296	27.9	1.8

Variances followed by the same letter are significantly different, $P < 0.05$

TABLE 6.14

Hierarchal analysis of variance of heading date of lines from different generations of 2 wheat crosses in two experiments

Experiment	Site	Generation analysed[+]	Source of variation	Degrees of freedom	Mean squares	F	Variance components	% of total variance
Plots 1975	Roseworthy	F_3[+]	Between crosses	1	243	0.2	0	0
			Between F_2 within crosses	26	1594	38.3**	22	35
			Between F_3 within F_2	1932	42		42	65
Plots 1976	Mortlock	F_3	Between crosses	1	752	1.4	0.3	1
			Between F_2 within crosses	26	519	30.6**	10.0	37
			Between F_3 within F_2	1372	17		17.0	62
		F_4	Between crosses	1	1761	2.6	3.9	8
			Between F_3 within crosses	26	676	62.5**	33.3	69
			Between F_4 within F_3	532	11		10.8	23

[+] Data for each generation were measured using lines derived from that generation

[*] $P < 0.05$; ** $P < 0.01$

TABLE 6.15

The variability of plant height of 3 parents and successive generations of 2 wheat crosses measured on single plants at commercial density, Roseworthy 1975

Parents (n=225)				F_2 (n=225)			F_2 family number	F_2 - within F_2 lines (n=75)			F_4 - within F_3 lines (n=75)		
Parent	Mean (cm)	Variance	CV	Mean (cm)	Variance	CV		Mean (cm)	Variance	CV	Mean (cm)	Variance	CV
DX39 * MEXICO 8156													
DX39	58	38	10.6										
				71	115^{ablm}	15.0	1	77	124	14.4	87	54	8.4
Mexico 8156	84	66	9.7								73	91	13.1
							2	70	142	17.0			
Average	71	52^{ade}	10.2				3	69	138	16.9	54	37	11.2
											59	24	8.3
							4	75	97	13.1	72	159	17.5
											83	79	10.7
							6	69	134	16.8	63	147	19.3
											79	34	7.4
							7	88	54	8.4			
							9	55	88	17.1	55	25	9.1
											60	36	9.9
							11	88	37	6.9	80	40	7.9
											90	62	8.7
							13	72	140	16.4	76	102	13.3
											60	43	11.0
							15	70	94	13.8			
							16	77	231	19.7			
							17	80	46	8.5			
							18	71	138	16.7			
							19	55	37	11.0			
Average								73	107^{cd}	14.1	71	67^{bce}	11.1
Variance of family means									95			148	
Statistics for all lines pooled								73	193^{l}	19.1	71	206^{m}	20.3
OLYMPIC * DX39													
Olympic	96	67	8.5										
				76	191^{fghn}	18.2	5	74	132	15.6	82	73	10.4
DX39	58	38	10.6								74	86	12.5
							7	54	24	9.1			
Average	77	53^{fjk}	9.6				8	88	104	11.6	93	163	13.7
											90	89	10.5
							10	89	126	12.5	89	149	13.8
											86	116	12.6
							13	72	120	15.1			
							15	74	149	16.6			
							16	83	64	9.6			
							17	71	91	13.4			
							18	70	191	19.7			
							19	70	204	20.6	76	96	12.9
											59	101	16.9
							20	80	130	14.3			
							21	87	96	11.2	85	75	10.2
											83	29	6.4
Average of 3 parents	79	57	9.6	Average of F_2's 74	153	16.6	22	77	285	21.9	92	231	16.5
											100	145	12.1
							23	62	95	15.7	61	77	14.4
											76	63	10.5
Average								75	129^{gij}	14.8	82	107^{hik}	12.4
Variance of family means									99			138	
Statistics for all lines pooled								75	221	19.8	82	230^{n}	18.5

Variances followed by the same letter are significantly different, $P < 0.05$

TABLE 6.16

The variability of plant height in plots of 3 parents and successive generations of 2 wheat crosses, Roseworthy 1975.

Parents (n=130)				F_2 (n=130)			F_2 family number	F_3- within F_2lines (n=70)		
Parent	Mean (cm)	Vari-ance	CV	Mean (cm)	Vari-ance	CV		Mean (cm)	Vari-ance	CV
				DX39 * MEXICO 8156						
DX39	68	7	3.9	80	108^{abg}	13.1	1	80	68	10.3
Mexico 8156	84	8	3.3				2	77	127	14.6
							3	75	80	12.0
Average	76	8^{ac}	3.6				4	81	75	10.7
							5	86	101	11.7
							6	71	79	12.6
							7	90	51	7.9
							8	95	63	8.3
							9	63	13	5.7
							10	98	13	3.6
							11	89	20	5.0
							12	79	66	10.3
							13	75	93	12.9
							14	63	41	10.2
						Average		80	64^{bc}	9.7
				Statistics for all lines pooled				80	170^{g}	16.3
				OLYMPIC * DX39						
Olympic	97	8	3.0	84	116^{deh}	12.7	1	97	48	7.2
DX39	68	7	3.9				2	89	64	9.0
							3	80	95	12.3
Average	83	8^{df}	3.5				4	84	112	12.7
							5	78	66	10.5
							6	74	71	11.4
							7	61	32	9.2
							8	91	78	9.7
							9	90	90	10.6
							10	91	82	10.0
				Average of F_2's			11	78	38	7.9
Average of 3 parents	83	8	3.4	82	112	12.9	12	94	71	8.9
							13	78	105	13.1
							14	82	30	6.7
						Average		83	65^{ef}	9.9
				Statistics for all lines pooled				83	153^{h}	14.9

Variances followed by the same letter are significantly different, $P < 0.05$

TABLE 6.17

The variability of plant height in plots of 3 parents and successive generations of 2 wheat crosses, Mortlock 1976.

Parents (n=130)				F_2 (n=130)			F_2 family number	F_3 - within F lines (n=50)			F_4 - within F lines (n=20)		
Parent	Mean (cm)	Variance	CV	Mean (cm)	Variance	CV		Mean (cm)	Variance	CV	Mean (cm)	Variance	CV
DX39 * MEXICO 8156													
DX39	66	10	4.8	80	85^{abcmn}	11.6	1	81	72	10.6	87	82	10.5
Mexico 8156	82	23	5.8				2	77	126	14.5	80	35	7.4
							3	74	83	12.4	81	21	5.6
Average	74	17^{aef}	5.3				4	80	83	11.5	82	35	7.2
							5	82	81	10.9	97	35	6.1
							6	72	92	13.4	65	31	8.7
							7	85	61	9.2	92	41	6.9
							8	90	41	7.1	89	30	6.1
							9	64	17	6.4	65	5	3.5
							10	90	27	5.8	91	17	4.5
							11	84	39	7.5	88	14	4.2
							12	77	72	11.0	82	35	7.2
							13	76	100	13.3	62	14	6.1
							14	63	34	9.3	62	6	4.1
Average								78	66^{bde}	10.2	80	29^{cdf}	6.3
Variance of family means									67			143	
Statistics for all lines pooled								78	127^{mo}	14.4	80	161^{no}	15.8
OLYMPIC * DX39													
Olympic	91	16	4.4	80	82^{ghipq}	11.3	1	88	53	8.3	95	41	6.7
DX39	66	10	4.8				2	82	58	9.3	84	59	9.2
							3	79	68	10.5	88	41	7.3
Average	79	13^{gkl}	4.6				4	78	68	10.5	78	38	7.9
							5	72	39	8.7	72	14	5.2
							6	71	72	12.0	77	38	8.0
							7	61	37	10.0	61	22	7.7
							8	85	56	8.8	91	73	9.4
							9	84	85	11.0	84	86	11.0
							10	85	70	9.9	78	45	8.6
Average				Average of F_2's			11	71	43	9.2	69	13	5.2
of 3 parents	80	16	5.0	80	83	11.5	12	89	84	10.3	92	75	9.4
							13	75	53	9.8	78	22	6.0
							14	77	56	9.7	81	24	6.1
Average								78	60^{hjk}	9.9	81	42^{ijl}	7.7
Variance of family means									60			89	
Statistics for all lines pooled								78	115^{p}	13.7	81	123^{q}	13.8

Variances followed by the same letter are signficantly different, $P < 0.05$

TABLE 6.18

Hierarchal analysis of variance of plant height of lines from different generations of 2 wheat crosses in a number of experiments.

Experiment	Site	Generation[+] analysed	Source of variation	Degrees of freedom	Mean squares	F	Variance components	% of total variance
Single plants 1975	Roseworthy	F_3[+]	Between crosses	1	3266	0.4**	0	0
			Between F_2 within crosses	26	7293	61.7	96	45
			Between F_3 within F_2	2072	118		118	55
		F_4	Between crosses	1	63759	3.5**	44	16
			Between F_2 within crosses	12	17976	4.1**	91	33
			Between F_3 within F_2	14	4425	51.1	58	21
			Between F_4 within F_3	2069	87		87	31
Plots 1975	Roseworthy	F_3	Between crosses	1	4793	0.7**	0	0
			Between F_2 within crosses	26	7200	107.7	102	60
			Between F_3 within F_2	1932	67		67	40
Plots 1976	Mortlock	F_3	Between crosses	1	7	0.0**	0	0
			Between F_2 within crosses	26	3175	50.2	62	50
			Between F_3 within F_2	1372	63		63	50
		F_4	Between crosses	1	10	0.0**	0	0
			Between F_3 within crosses	26	2320	65.4	114	76
			Between F_4 within F_3	532	36		36	24

[+] Data for each generation were measured using lines derived from that generation

* $P < 0.05$; ** $P < 0.01$

individual lines varied, as many lines were as uniform as the parents in the F_4 or even the F_3. The total cross variability was greatly increased with advancing generations (tables 6.15 to 6.17).

The greater degree of uniformity of F_4 lines within F_3's, compared with the F_3 lines within F_2's, is also indicated in the hierarchal analyses of variance (table 6.18). Analysis of lines derived from the F_3 showed that 40 to 55 per cent of the variation was attributed to variation between F_3 lines within F_2's, but when the F_4 derived lines were analysed, variation between F_4 lines within F_3's accounted for only 24 to 31 per cent of the total variation. Considerable fixation for plant height had occurred apparently by the F_3.

4. Harvest index

The environmental variability was much lower for harvest index (tables 6.5, 6.19 and 6.20) than for grain yield (tables 6.5 to 6.10). Harvest index of the parents was less variable when measured from plots (table 6.20) than when measured on single plants (table 6.19). Plants at low density (table 6.5) were slightly more variable than plants at commercial density.

The F_2 was significantly more variable than the parents, except for the Olympic * DX39 cross in plots at Roseworthy in 1975 (table 6.20). In that situation Olympic was more variable than the other parents and the F_2 was significantly more variable than the second parent of the cross, DX39. The variability of lines in successive generations was reduced, and when measured on single plants, the average variability of F_4 lines was not significantly greater than the parents (table 6.19). As with the other characters, the degree of uniformity varied considerably between different lines. In contrast to other characters, the total population variability for harvest index was not consistently increased with successive generations (tables 6.19 and 6.20).

TABLE 6.19

The variability of harvest index of 3 parents and successive generations of 2 wheat crosses measured on single plants at commercial density, Roseworthy 1975.

Parents (n=225)				F2 (n=225)			F2 family number	F3 - within F2 lines (n=75)			F4 - within F3 lines (n=75)		
Parent	Mean (%)	Variance	CV	Mean (%)	Variance	CV		Mean (%)	Variance	CV	Mean (%)	Variance	CV
							DX39 * MEXICO 8156						
DX39	41	27	12.7										
				43	34^{abj}	13.6	1	44	13	8.0	45	12	7.6
Mexico 8156	44	22	10.6								40	25	12.5
							2	37	42	17.3			
Average	43	25^{ad}	11.7				3	39	23	12.3	38	27	13.7
											41	23	11.6
							4	41	19	10.4	42	16	9.4
											44	17	9.4
							6	40	28	13.2	41	22	11.5
											45	15	8.6
							7	40	54	18.1			
							9	39	74	22.0	37	13	9.8
											35	21	12.8
							11	44	12	8.0	45	65	18.1
											42	13	8.6
							13	42	34	14.0	41	22	11.5
											38	21	12.0
							15	49	26	10.4			
							16	36	65	22.5			
							17	46	16	8.8			
							18	45	19	9.6			
							19	37	23	12.8			
						Average		41	32^{cd}	13.4	41	22^{bc}	11.2
						Variance of family means			15			10	
						Statistics for all lines pooled		41	44^{j}	16.0	41	31	13.5
							OLYMPIC * DX39						
Olympic	41	25	12.3										
				37	48^{efg}	18.9	5	40	27	12.9	37	27	14.0
DX39	41	27	12.7								39	11	8.5
							7	41	16	9.8			
Average	41	26^{ei}	12.5				8	39	69	21.2	40	18	10.6
											40	47	17.5
							10	36	28	14.6	38	34	15.3
											38	26	13.4
							13	37	31	15.0			
							15	35	49	20.2			
							16	40	25	12.6			
							17	39	33	14.9			
							18	26	43	25.1			
							19	31	27	17.0	35	28	15.2
											33	36	18.0
							20	41	21	11.3			
							21	37	23	13.0	37	27	14.1
											40	8	7.3
Average of 3 parents				Average of F2's			22	34	78	25.9	37	29	14.4
	42	25	11.9	40	41	16.3					38	14	9.8
							23	35	28	15.0	37	60	21.0
											41	12	8.4
						Average		36	35^{fhi}	16.3	38	27^{gh}	13.4
						Variance of family means			18			5	
						Statistics for all lines pooled		36	51	19.7	38	31	14.6

Variances followed by the same letter are significantly different, $P < 0.05$

TABLE 6.20

The variability of harvest index in plots of 3 parents and successive generations of 2 wheat crosses, Roseworthy 1975.

	Parents (n=20)			F_2 (n=40)			F_2 family number	F_3- within F_2 lines (n=20)		
Parent	Mean (%)	Variance	CV	Mean (%)	Variance	CV		Mean (%)	Variance	CV
DX39 * MEXICO 8156										
DX39	41	7	6.5	39	21^{a}	11.7	1	39	10	8.2
Mexico 8156	42	8	6.5				2	32	47	21.6
Average	42	8^{ab}	6.5				4	38	13	9.3
							7	35	23	13.5
							10	32	9	9.2
							11	38	10	8.4
							14	38	14	9.7
Average								36	18^{b}	11.7
Statistics for all lines pooled								36	25	13.9
OLYMPIC * DX39										
Olympic	37	18	11.4	34	17^{c}	12.3	3	31	23	15.5
DX39	41	7^{cd}	6.5				5	36	6	6.7
Average	39	13	9.0				6	35	15	11.0
							7	35	13	10.5
				Average of F_2's			8	35	17	11.7
Average of 3 parents	40	11	8.1	36	19	12.0	9	35	16	11.3
							11	35	15	10.9
Average								35	15^{d}	11.1
Statistics for all lines pooled								35	17	11.9

Variances followed by the same letter are significantly different, $P < 0.05$

TABLE 6.21

Hierarchal analysis of variance of harvest index of lines from different generations of 2 wheat crosses in two experiments

Experiment	Site	Genertion$^+$ analysed	Source of variation	Degrees of freedom	Mean squares	F	Variance components	% of total variance
Spaced plants 1975	Roseworthy	F_3^+	Between crosses	1	13329	11.4**	11.6	19
			Between F_2 within crosses	26	1169	34.7**	15.1	25
			Between F_3 within F_2	2072	34		33.7	56
		F_4	Between crosses	1	5794	7.6*	4.8	13
			Between F_2 within crosses	12	763	2.6*	3.1	9
			Between F_3 within F_2	14	297	12.1**	3.6	10
			Between F_4 within F_3	2068	25		24.6	68
Plots 1975	Roseworthy	F_3	Between crosses	1	146	1.2	0.2	1
			Between F_2 within crosses	12	123	7.5**	5.3	24
			Between F_3 within F_2	265	16		16.4	75

$^+$ Data for each generation were measured using lines derived from that generation

* $P < 0.05$; ** $P < 0.01$

Like grain yield, the greatest contribution to the total variation of harvest index came from between lines of the generation being analysed (table 6.21), e.g. when the F_3 data were analysed, 56 to 75 per cent of the total variation came from between F_3 lines within F_2's. The proportion of variation of harvest index contributed by these lowest levels were less than, or in one case equal to, the corresponding variation for grain yield (compare table 6.11 and 6.21).

5. Pearling resistance

The F_2 generations were significantly more variable than their parents for pearling resistance (tables 6.22 and 6.23). The F_2 of the DX39 * Mexico 8156 cross was much more variable than the other cross as it involves parents with soft and very hard grain. The F_3, F_4 and F_5 showed a trend to uniformity, and this was particularly obvious for DX39 * Mexico 8156. However, the F_5 was still significantly more variable than the parents. The total cross variability increased significantly in successive generations for DX39 * Mexico 8156, but no increase was evident for Olympic * DX39.

The approach to uniformity of pearling resistance is also clear from the hierarchal analyses of variance (table 6.24). A high degree of homozygosity had been achieved by the F_4, as when the F_5 lines were analysed, only 5 per cent of the total variation was attributable to variation between F_5 lines within F_4's. The variation between crosses was much more important for pearling resistance than other characters, as the magnitude of the variation generated was quite different for each cross.

6. Flour yield

The variability of the F_2's was significantly greater than the parents for flour yield (tables 6.25 and 6.26). The F_3, F_4 and F_5

TABLE 6.22

The variability of pearling resistance of 3 parents and successive generations of 2 wheat crosses grown in plots, Roseworthy 1975.

	Parents (n=70)			F_2 (n=70)			F_2 family number	F_3-within F_2 lines (n=20)		
Parent	Mean (%)	Variance	CV	Mean (%)	Variance	CV		Mean (%)	Variance	CV
DX39 * MEXICO 8156										
DX39	39.3	1.4	3.0	53.3	36.9^{a}	11.4	1	54.7	28.4	9.7
Mexico 8156	61.1	2.6	2.7				2	53.1	64.3	15.1
Average	50.2	2.0^{ab}	2.9				4	52.5	33.2	11.0
							7	52.2	34.6	11.3
							10	56.5	43.5	11.7
							11	51.0	29.1	10.6
							14	53.4	50.5	13.3
						Average		53.3	40.5^{b}	11.8
						Statistics for all data pooled		53.3	41.5	12.1
OLYMPIC * DX39										
Olympic	40.0	2.2	3.7	44.2	5.9	5.5	3	43.5	6.4	5.8
DX39	39.3	1.4	3.0				5	43.5	3.7	4.4
Average	39.7	1.8^{cd}	3.4				6	44.3	4.4	4.7
							7	44.8	19.9	9.9
				Average of F_2's			8	42.9	2.6	3.7
Average of 3 parents	46.8	2.1	3.1	48.8	21.4	8.5	9	43.3	6.2	5.7
							11	43.5	8.6	6.7
						Average		43.7	7.4^{d}	5.8
						Statistics for all lines pooled		42.7	7.4	6.2

Variances followed by the same letter are significantly different, $P < 0.05$

TABLE 6.23

The variability of pearling resistance of 3 parents and successive generations of 2 wheat crosses grown in plots, Roseworthy 1976.

Parents (n=70)				F_2 (n=70)			F_2 Family number	F_3- within F_2lines (n=20)			F_4- within F_3lines (n=20)			F_5- within F_4lines (n=15)		
Parent	Mean (%)	Vari-ance	CV	Mean (%)	Vari-ance	CV		Mean (%)	Vari-ance	CV	Mean (%)	Vari-ance	CV	Mean (%)	Vari-ance	CV
DX39 * MEXICO 8156																
DX39	35.4	2.1	4.1	49.5	47.0^{abcdr}	13.9	2	47.8	25.4	10.6	40.5	4.3	5.1	40.7	2.7	4.1
Mexico 8156	61.6	2.9	2.8				5	56.6	23.3	8.5	58.0	6.1	4.3	59.0	2.4	2.6
							8	43.0	3.2	4.1	44.4	2.2	3.3	41.8	5.5	5.6
Average	48.5	2.5^{aghi}	3.4				10	51.3	56.0	14.6	54.9	45.1	12.2	62.3	1.9	2.2
							11	49.2	46.1	13.8	51.5	40.0	12.3	59.7	5.7	4.0
							13	42.2	3.8	4.6	40.4	3.7	4.7	40.4	5.4	5.8
							14	49.0	41.5	13.2	48.8	60.6	16.0	39.7	3.6	4.8
Average								48.4	28.5^{beg}	9.9	48.4	23.2^{cfh}	8.3	49.1	3.9^{defi}	4.2
Variance of family means									24.1^{q}			47.8			112.1^{q}	
Statistics for all lines pooled								48.4	47.9^{st}	14.3	48.4	63.5^{su}	16.4	49.1	100.2^{rtu}	20.4
OLYMPIC * DX39																
Olympic	42.0	1.8	3.2	40.6	5.9^{jkvwx}	6.0	1	42.1	1.9	3.3	40.4	3.2	4.5	40.9	6.0	6.0
DX39	35.4	2.1	4.1				2	44.6	12.6	8.0	45.3	5.5	5.2	44.5	6.1	5.5
							4	42.9	37.7	14.3	42.7	3.4	4.3	42.1	5.7	5.7
Average	38.7	2.0^{jnop}	3.7				5	38.4	25.4	13.1	38.8	4.4	5.4	38.0	2.3	4.0
				Average of F_2's			6	39.5	16.1	10.2	37.4	4.9	5.9	39.5	4.0	5.1
Average of 3 parents	46.3	2.3	3.4	45.1	26.5	10.0	10	42.0	5.4	5.5	42.2	4.5	5.0	42.2	2.0	3.3
							11	39.5	6.7	6.6	38.7	1.6	3.3	38.4	4.7	5.6
Average								41.3	15.1^{lmn}	8.7	40.8	3.9^{klo}	4.8	40.8	4.4^{mp}	5.0
Variance of family means									4.9			7.7			5.4	
Statistics for all lines pooled								41.3	18.8^{v}	10.5	40.8	10.4^{w}	7.9	40.8	8.9^{x}	7.3

Variances followed by the same letters are significantly different, $P < 0.05$

TABLE 6.24

Hierarchal analysis of variance of pearling resistance of lines from different generations of 2 wheat crosses in two experiments

Experiment	Site	Generation[+] analysed	Source of variation	Degrees of freedom	Mean squares	F	Variance components	% of total variance
Plots 1975	Roseworthy	F_3[+]	Between crosses	1	6534	179.0**	46.4	65
			Between F_2 within crosses	12	37	1.5	0.6	1
			Between F_3 within F_2	266	24		23.9	34
Plots 1976	Roseworthy	F_3	Between crosses	1	3555	12.2**	23.4	40
			Between F_2 within crosses	12	291	13.4**	13.5	23
			Between F_3 within F_2	265	22		21.6	37
		F_4	Between crosses	1	4099	7.5*	25.6	39
			Between F_3 within crosses	12	546	40.2**	26.8	41
			Between F_4 within F_3	264	14		13.6	21
		F_5	Between crosses	1	3470	4.0	24.9	29
			Between F_4 within crosses	12	870	210.6**	58.0	67
			Between F_5 within F_4	195	4		4.1	5

[+] Data for each generation were measured using lines derived from that generation

* $P < 0.05$; ** $P < 0.01$

TABLE 6.25

The variability of flour yield of 3 parents and successive generations of 2 wheat crosses grown in plots, Roseworthy 1975

Parent	Parents (n=70) Mean (%)	Parents (n=70) Variance	Parents (n=70) CV	F_2 (n=70) Mean (%)	F_2 (n=70) Variance	F_2 (n=70) CV	F_2 family number	F_3- within F_2lines (n=20) Mean (%)	F_3- within F_2lines (n=20) Variance	F_3- within F_2lines (n=20) CV
DX39* MEXICO 8156										
DX39	57.4	1.1	1.8							
				58.5	4.4^{a}	3.6	1	58.1	4.9	3.8
Mexico 8156	56.7	1.0	1.8				2	56.7	7.5	4.8
							4	58.3	3.6	3.2
Average	57.1	1.1^{ab}	1.8				7	59.3	2.4	2.6
							10	58.5	1.4	2.0
							11	59.4	2.5	2.6
							14	56.8	1.6	2.2
Average								58.2	3.4^{b}	3.0
Statistics for all lines pooled								58.2	4.2	3.5
OLYMPIC * DX39										
Olympic	63.1	1.5	2.0							
				59.5	4.2^{ce}	3.5	3	57.7	9.8	5.4
DX39	57.4	1.1	1.8				5	57.1	2.7	2.9
							6	55.4	4.5	3.8
Average	60.3	1.3^{cd}	1.9				7	55.2	4.9	4.0
				Average of F_2's			8	60.0	3.3	3.1
Average of 3 parents	59.1	1.2	1.9	59.0	4.3	3.6	9	59.8	2.3	2.5
							11	59.1	4.4	3.5
Average								57.8	4.6^{d}	3.6
Statistics for all lines pooled								57.8	7.8^{e}	4.8

Variances followed by the same letters are significantly different, $P < 0.05$

TABLE 6.26

The variability of flour yield of 3 parents and successive generations of 2 wheat crosses grown in plots, Roseworthy 1976.

Parents (n=70)				F$_2$ (n=70)			F$_2$ family number	F$_3$- within F$_2$lines (n=20)			F$_4$- within F$_3$lines (n=20)			F$_5$- within F$_4$line (n=15)		
Parent	Mean (%)	Vari-ance	CV	Mean (%)	Vari-ance	CV		Mean (%)	Vari-ance	CV	Mean (%)	Vari-ance	CV	Mean (%)	Vari-ance	CV
DX39 * MEXICO 8156																
DX39	56.6	1.5	2.2	57.4	3.6^{abcd}	3.3	2	57.5	2.2	2.6	58.0	2.4	2.7	58.2	1.1	1.8
Mexico 8156	54.0	0.7	1.5				5	58.0	1.6	2.2	57.4	4.7	3.8	58.1	1.1	1.8
							8	56.7	3.0	3.0	56.9	1.5	2.1	57.1	0.3	1.0
Average	55.3	1.1^{afg}	1.9				10	56.6	1.9	2.5	56.4	1.3	2.1	55.3	1.4	2.1
							11	58.2	0.9	1.6	56.9	1.6	2.3	56.4	3.6	3.3
							13	56.0	3.2	3.2	57.4	1.4	2.1	56.9	1.3	2.0
							14	56.7	1.3	2.0	56.7	3.1	3.1	56.7	1.3	2.0
Average								57.1	2.0^{bef}	2.4	57.1	2.3^{cg}	2.6	57.0	1.4^{de}	2.0
Variance of family means								0.7			0.3			1.0		
Statistics for all lines pooled								57.1	2.5	2.8	57.1	2.5	2.7	57.0	2.2	2.6
OLYMPIC * DX39																
Olympic	61.9	1.1	1.7	58.8	2.7^{hij}	2.8	1	58.8	1.5	2.1	58.1	0.8	1.5	57.5	1.5	2.1
DX39	56.6	1.5	2.2				2	59.0	1.0	1.7	58.6	1.4	2.0	58.9	2.6	2.7
							4	59.3	2.9	2.9	59.8	1.3	1.9	58.6	3.9	3.4
Average	59.3	1.3^{hkl}	1.9				5	58.6	2.0	2.4	58.3	1.6	2.1	57.5	1.7	2.2
				Average of F$_2$'s			6	57.1	1.8	2.4	56.2	2.4	2.8	57.9	1.2	1.9
Average of 3 parents	57.5	1.1	1.8	58.1	3.2	3.1	10	57.8	4.1	3.5	57.4	3.7	3.4	57.5	2.2	2.6
							11	58.9	0.9	1.6	58.3	1.5	2.1	59.0	1.1	1.8
Average								58.5	2.0^{ik}	2.4	58.1	1.8^{j}	2.2	58.1	2.0^{l}	2.4
Variance of family means								0.6			1.2			0.5		
Statistics for all lines pooled								58.5	2.5	2.7	58.1	2.8	2.9	58.1	2.3	2.6

Variances followed by the same letter are significantly different, $P < 0.05$

TABLE 6.27

Hierarchal analysis of variance of flour yield of lines from different generations of 2 wheat crosses in two experiments

Experiment	Site	Generation analysed[+]	Source of variation	Degrees of freedom	Mean squares	F	Variance component	% of total variance
Plots 1975	Roseworthy	F_3[+]	Between crosses Between F_2 within crosses Between F_3 within F_2	1 12 266	13 51 4	0.3 12.8**	0.0 2.3 4.0	0 37 63
Plots 1976	Roseworthy	F_3	Between crosses Between F_2 within crosses Between F_3 within F_2	1 12 265	137 13 2	10.9** 6.2**	0.9 0.5 2.0	26 15 59
		F_4	Between crosses Between F_3 within crosses Between F_4 within F_3	1 12 264	71 15 2	4.7 7.4**	0.4 0.7 2.0	13 21 66
		F_5	Between crosses Between F_4 within crosses Between F_5 within F_4	1 12 195	72 11 2	6.4* 6.6**	0.6 0.6 1.7	20 22 58

[+] Data for each generation were measured using lines derived from that generation

* $P < 0.05$;   ** $P < 0.01$

gradually became more uniform, with the exception of the F_5 for the Olympic * DX39 cross which increased in variability from the F_4 (table 6.26). The F_5 of DX39 * Mexico 8156 was almost as uniform as the parents, but the F_5 of Olympic * DX39 was still significantly more variable. The hierarchal analyses of variance (table 6.27) do not indicate any trend to uniformity, and it is possible that environmental variation might have masked genetic trends. The total cross variability for flour yield did not increase with advancing generations.

A comparison of the decrease in variability within lines for different characters

The average within line variance in the different generations compared to the parents is summarized for all characters in table 6.28. The data that best illustrates the overall results have been used in this summary. While there was a general reduction in the average within line variance as generations were advanced, lines from the F_4 were still more variable than the parents, usually significantly so, for all characters measured in this generation. Even lines from the F_5 were more variable than the parents for pearling resistance and flour yield. The rate of decrease in variability within lines was similar for all characters.

The uniformity of lines from the F_4 can also be compared for the different characters, by examining the percentage of the total variation attributable to variation between F_4 lines within F_3's. These percentages were 23% for heading date, 24% for plant height, 21% for pearling resistance, 66% for flour yield,and 59 to 67% for grain yield. The much higher values for grain yield and flour yield indicate that either these characters approach uniformity at a slower rate than the other characters, or else the relatively large variation of F_4 lines within F_3's for these characters includes a larger environmental component. The trends in table 6.28 suggest that the latter alternative is more probable.

TABLE 6.28

Average variability of 3 parents and successive generations of 2 wheat crosses after random pedigreed selection, for a number of characters grown in plots.

The parents are averages of 2 parents; the F_3 and F_4 are averages of 14 or 7 lines derived from these generations (14 for yield, heading date and plant height, 7 for harvest index, pearling resistance and flour yield).

Character	Experiment	Cross[ø]	Parents			F_2			F_3- within F_2lines			F_4- within F_3lines			F_5- within F_4lines		
			Mean	Vari-ance	CV	Mean	Vari-ance	CV	Mean	Vari-ance	CV	Mean	Vari-ance	CV	Mean	Vari-ance	CV
Grain yield (gm/plot)	Average of 2 sites, 1976	1	367	$^{+}242^{acd}$	13.6	353	437^{ab}	18.7	356	384^{ce}	17.3	351	338^{bde}	16.6			
		2	421	319^{f}	13.4	375	384^{fg}	16.5	359	340^{h}	16.1	352	259^{gh}	14.2			
Heading date (days)	Mortlock 1976	1	295	1.5^{aef}	0.4	295	17.7^{abc}	1.4	297	13.9^{bde}	1.1	300	9.2^{cdf}	0.8			
		2	296	1.2^{gkl}	0.4	296	26.2^{ghi}	1.7	295	20.1^{hjk}	1.5	296	12.4^{ijl}	1.1			
Plant height (cm)	Mortlock 1976	1	74	17^{aef}	5.3	80	85^{abc}	11.6	78	66^{bde}	10.2	80	29^{cdf}	6.3			
		2	79	13^{gkl}	4.6	80	82^{ghi}	11.3	78	60^{hjk}	9.9	81	42^{ijl}	7.7			
Harvest index (%)	Roseworthy 1975	1	42	8^{ab}	6.5	39	21^{a}	11.7	36	18^{b}	11.7						
		2	39	13	9.0	34	17	12.3	35	15	11.1						
Pearling resistance (%)	Roseworthy 1976	1	48.5	2.5^{aghi}	3.4	49.5	47.0^{abcd}	13.9	48.4	28.5^{beg}	9.9	48.4	23.2^{cfh}	8.3	49.1	3.9^{defi}	4.2
		2	38.7	2.0^{jnop}	3.7	40.6	5.9^{jk}	6.0	41.3	15.1^{lmn}	8.7	40.8	3.9^{klo}	4.8	40.8	4.4^{mp}	5.0
Flour yield (%)	Roseworthy 1976	1	55.3	1.1^{afg}	1.9	57.4	3.6^{abcd}	3.3	57.1	2.0^{bef}	2.4	57.1	2.3^{cg}	2.6	57.0	1.4^{de}	2.0
		2	59.3	1.3^{hkl}	1.9	58.8	2.7^{hij}	2.8	58.5	2.0^{ik}	2.4	58.1	1.8^{j}	2.2	58.1	2.0^{l}	2.4

[ø] Cross 1 is DX39 * Mexico 8156 ; cross 2 is Olympic * DX39

[+] Variances of grain yield are multiplied by 10^{-1}
Variances from the same experiment followed by the same letter are significantly different, $P < 0.05$

BROAD SENSE HERITABILITIES FOR DIFFERENT CHARACTERS

The estimation of broad sense heritabilities for grain yield gave similar results for the two methods of calculation (table 6.29), but for the other characters, higher estimates were obtained when environmental variance was estimated using the average variance of the two parents.

In most instances heritabilities increased as generations advanced.

Heritabilities of heading date, plant height and pearling resistance were much higher than for grain yield or flour yield, particularly when the environmental variance was estimated from the parents. The heritability of plant height measured on single plants was lower than when measured in plots. Heritabilities of harvest index were higher than for grain yield, but not as high as heading date or plant height. The heritability of pearling resistance for Olympic * DX39 measured at Roseworthy in 1975 was exceptionally low, but this was due to a lack of variation in this cross, as both parents were soft.

The average heritabilities calculated from plots, using the parents to estimate the environmental variance, were 90% for heading date, 88% for plant height, 68% for pearling resistance, 39% for flour yield, and 25% for grain yield. The heritability of harvest index in plots was 54% for one cross but only 16% for the other. The average heritabilities of grain yield and harvest index measured on single plants and using the parents to estimate the environmental variance were 19% and 37% respectively.

The expected genetic advance for grain yield measured in plots generally increased as the generation of selection was advanced (table 6.30).

TABLE 6.29

Broad sense heritabilities (%) in different generations of 2 wheat crosses for a number of characters measured at 3 sites in 2 years.

The heritabilities in columns A are based on an environmental component estimated from the error variance. The heritabilities in columns B are based on an environmental component estimated from the average variance of the 2 relevant parents.

Character	Data used for calculation site and derived generation of lines)	DX39*Mexico8156		Olympic*DX39	
		A	B	A	B
Grain Yield	Roseworthy 1975 - F_3	17	17	15	10
	Saddleworth 1975 - F_3	4	6	7	8
	Av. Ros & Sad 1975 - F_3	12	16	15	13
	Roseworthy 1976 - F_3	11	14	14	20
	- F_4	28	36	24	27
	- F_5	24	30	19	29
	Mortlock 1976 - F_3	27	35	25	21
	- F_4	40	46	37	31
	Av.Ros & Mort 1976 - F_3	27	37	22	24
	- F_4	43	51	34	30
	Single plants - F_3	19	20	18	18
Heading Date	Roseworthy 1975 - F_3	52	93	19	86
	Mortlock 1976 - F_3	51	90	23	83
	- F_4	84	97	57	93
Plant height	Roseworthy 1975 - F_3	64	94	56	92
	Mortlock 1976 - F_3	50	80	50	82
	- F_4	83	90	67	87
	Single plants - F_3	46	64	43	65
Harvest index	Roseworthy 1975 - F_3	32	54	13	16
	Single plants - F_3	29	34	33	39
Pearling resistance	Roseworthy 1975 - F_3	3	38	1	3
	Roseworthy 1976 - F_3	45	90	22	69
	- F_4	66	95	66	79
	- F_5	97	98	54	73
Flour yield	Roseworthy 1975 - F_3	22	48	45	74
	Roseworthy 1976 - F_3	21	33	20	29
	- F_4	7	13	39	47
	- F_5	41	47	14	20

TABLE 6.30

Expected genetic advance for grain yield by selecting the 20 per cent highest yielding lines in different generations of 2 wheat crosses.

The heritabilities used were based on an environmental component estimated from the average of the 2 relevant parents.

Data used for calculation (site and derived generation of lines)		DX39 * Mexico 8156		Olympic * DX39	
		Expected genetic advance in grams per plot	Expected genetic advance in % of the generation mean	Expected genetic advance in grams per plot	Expected genetic advance in % of the generation mean
Roseworthy 1975	- F_3	14	7	10	6
Roseworthy 1976	- F_3	11	4	18	5
	- F_4	33	11	25	7
	- F_5	27	9	28	8
Mortlock 1976	- F_3	48	12	30	8
	- F_4	71	17	47	13
Av. Ros. & Mort. 1976	- F_3	32	9	21	6
	- F_4	51	14	28	8

DISCUSSION

Adjustment of grain yield of plots to account for environmental variation within a site

Plant breeders often use a system of regular check plots arranged in a grid pattern in their trials. It is assumed that these controls reflect the micro-environmental variation and can be used to adjust the yields of intervening crossbreds. Briggs and Shebeski (1968) contend that frequent controls are essential for efficient selection for yield, and control plots as frequent as one in every three have been suggested (Shebeski 1967). In the present experiments, a moving mean was more effective than grid controls in accounting for the site variation. This finding is in agreement with other results (Knott 1972; Townley-Smith and Hurd 1973). Seif, Lind and Martin (1974) also found that using grid controls produced only small reductions in experimental error. As the use of grid controls requires 20 to 30 per cent more plots in a trial, it is often difficult to justify their use. A greater gain in efficiency would be achieved by extra replication or reduced experimental area. However, the use of grid controls will still have value in trials when not all plots are harvested, or where entries are not randomized, e.g. when lines from each cross are grown together to enhance selection within and between crosses, or when a group of selections are used to assess the performance of a family.

When yields were adjusted using a moving mean, the optimum number of plots included in the mean varied from 10 to 16 depending on the plot size and site. If this method was used in plant breeding experiments, the optimum size of moving mean could be determined by testing which size gives the greatest reduction in environmental variance. This could be measured by a conventional analysis of variance if the entries are replicated, or, if replication is not possible, by an analysis of a number of plots of one variety.

Environmental variability

For all characters, environmental variability was less for plots than for single plants, plants at low density being less variable than plants at commercial density. Four row plots were less variable than two row plots. This was particularly evident for grain yield, and the importance of accurate, and preferably replicated assessments of yield is obvious.

Heritabilities of different characters

Caution must be used when interpreting the broad sense heritabilities, as the estimation of the environmental variation could have been biased. Environmental variance estimated using the "error" variance component could be overestimated, as it might have contained a significant genetic component. This was particularly apparent for heading date, plant height and pearling resistance, and to a lesser extent harvest index and flour yield. All gave lower heritabilities with this method, particularly in the early generations when the genetic portion of the "error" variance component could have been relatively large. For these characters, it is more realistic to use the parental variation for estimates of environmental variability. For grain yield, there was little difference between the two methods of calculation. In fact, in some cases, the environmental variance was greater when estimated from the parents than the "error" variance component. The variance of parents can also be an overestimation of environmental variation when compared to heterozygous material, and this will be discussed later.

Plant height, heading date and pearling resistance were highly heritable characters, whereas grain yield and flour yield were much less heritable. Harvest index was more heritable than yield, although the heritabilities for harvest index were not as high as other published values (Rosielle and Frey 1975; Bhatt 1976, 1977).

The heritability of all characters increased with advancing generations. If the phenotypic variance is constant over generations, a greater response to selection would be expected in late generations. This is very evident in the expected genetic advances for grain yield. This conclusion supports the findings of previous chapters.

Comparative variability of parents and F_2's

For all characters, the variance of the F_2 exceeded the mean variance of the parents, usually at a significant level. The F_2 was more variable than the parents for simply inherited characters such as heading date, plant height and pearling resistance. For grain yield and flour yield, the differences were less, even though significant. The differences in variability between the parents and F_2's were greater for flour yield than for grain yield.

Differences in variability between parents and F_2's for grain yield were greater than those obtained by other authors, who used single plants (Immer 1942; Palmer 1952; Phung 1976). However, the differences were not great, particularly when it is considered that a basic assumption in a wheat breeding program is that variability in an F_2 is far greater than in the parents or homozygous lines. It is to obtain variability that the cross is made. This assumption is also basic to the theory of quantitative genetics (East 1916; Babcock and Clausen 1927).

The comparatively small difference in variability for grain yield appears to be due to the large influence of environment which masks the expression of genetic variability. When grown at a commercial density, competition between individual plants in early stages of growth may determine their yield. This environmental factor may be more important than genetic factors, and it will occur in the parents and the F_2's. When competition was not present, as with the plants at low density, the differences between parents and F_2's were greater, although environmental variability was still large. Other factors such as micro-environmental variation, must also be important in determining the variation in yield of single plants.

The small differences in variability between the parents and F_2's for grain yield suggest that the genetic variance in the F_2 is small. However, in concluding this, it is assumed that the environmental variance component in the F_2 is equal to the environmental variance measured by the parents. This assumption may not be correct. Heterozygous individuals and heterogeneous populations are more stable over differing environments than homozygotes or pure lines (Allard 1961, 1967; Griffing and Langridge 1963; Finlay 1964; Qualset 1968). Therefore, the estimation of environmental variance using the parents may be greater than the environmental variance component in the F_2, as the F_2 lines, being heterozygous and heterogeneous, will be buffered to environmental variation over the site, whereas the parents, being homozygous, will give larger reactions to site variation. This suggestion is further supported by the fact that often F_3 lines were more uniform for grain yield than the parents, even though still highly heterozygous. The difference in variability between the parents and F_2's, therefore, may not give a true indication of the magnitude of the F_2 genetic variance.

If homozygous varieties are less stable to environmental changes than heterozygous lines, using varieties as grid controls would not give an adequate picture of site variation for adjustment of intervening heterozygous lines. The varieties and heterozygous lines could react differently to environmental variation over the site. It has already been demonstrated that using grid controls of a variety is of limited value in reducing site variation, and this could partly be due to the grid controls reacting differently to the entries being adjusted. Further work is required to investigate whether mixtures or bulks might give a getter picture of site variation than homozygous varieties.

Comparative variability as homozygosity is approached

As the generations were advanced, the average variability of pedigreed lines from each generation was reduced. This was shown by averaging the variabilities of individual lines, and by the hierarchal analyses of variance. However, all characters were still not as uniform as the parents, on average, by the F_4 or F_5. Even when parents differ by only three genes, as could be the case for heading date, plant height or pearling resistance, theoretically 33 per cent of individuals could still be heterozygous at some loci in the F_4 (Knight 1968). Some degree of variability could therefore be expected for these characters in the F_4, and this was obtained in these experiments.

If parents differ by many genes, as is often suggested for grain yield, the rate of decrease in variability within lines should be slower than for plant height, heading date or pearling resistance. If the parents differed by 25 genes for yield, theoretically only 4 per cent of individuals would be homozygous in the F_4, compared to 67 per cent if the parents differed by only three genes (Knight 1968). It would not be until the F_7 that 67 per cent of individuals would be homozygous for yield, if 25 genes were involved. However, when measured in plots, the rate of decrease in variability within lines for grain yield was similar to all other characters. There are two possible explanations for this.

1. There may be only a few important genes segregating for yield in these crosses. The parents may actually differ by many more genes for yield, but these may have only small effects, possibly too small to be detected.

2. The uniformity of lines from each generation was assessed by comparing them with the variance of the parents, which, being genetically uniform, was used to estimate the environmental variance. It has been previously demonstrated that the variance of parents for yield may be an overestimate of the environmental variance applicable to heterozygous

material. This would therefore give the impression that uniformity is achieved in an earlier generation than is actually occurring. This argument is supported by the fact that a number of lines from the F_3 were more uniform than the parents.

It is possible that both these explanations apply.

Applications of variability results

It was envisaged that the most efficient early generation selection would occur when the character being selected was relatively uniform. There would be minimal bias in a plot in the absence of variability, and the effect of segregation after the generation of testing would be reduced. It is difficult to be certain of when adequate uniformity has been achieved, as complete uniformity is not essential. Furthermore, while on average there is a steady trend to uniformity, many individual lines become uniform before the average.

For grain yield, it might not be essential to have genetic uniformity before selection is commenced. In fact, it might be more desirable to retain some variability to make use of the greater buffering capacity of heterogeneous populations. It might only be necessary to attain uniformity of plant height, heading date and agronomic type, to avoid bias caused by variability in these characters.

This argument can be extended to fixed lines and varieties. Traditionally, genetic uniformity of all characters has been an aim in developing a variety. But by aiming for complete genetic uniformity for grain yield in a variety, we might be creating varieties that are poorly buffered. While it is necessary to have homogeneity for plant height, maturity, agronomic type and quality characteristics to satisfy market and seed requirements of a variety, it might not be necessary to have complete homogeneity for grain yield. By retaining some variability, the variety as a crop might be more stable and higher yielding.

Total population variability

Although the variability within the pedigreed lines decreased with advancing generations, the total cross variability increased for all characters, except harvest index and flour yield. This increased genetic variability is a result of the heterozygotes segregating to give genotypes not present in the earlier generation. With arithmetic gene action, no dominance and no gene interaction, the theoretical variance when segregation has ceased should be double that of the F_2 (Wright 1921). With other genetic systems an increase in variance will still be obtained, theoretically, but it might not be as great (Palmer 1952).

Use of harvest index

As grain yield, particularly on single plants, is greatly influenced by environment, the use of harvest index in selecting for yield improvement has been suggested (Singh and Stoskopf 1971; Syme 1972; Fischer 1975; Bhatt 1976, 1977; Donald and Hamblin 1976; Fischer and Kertesz 1976). It has been shown that variation for harvest index exists (Singh and Stoskopf 1971; Bhatt 1976), and the heritability of harvest index is high (Rosielle and Frey 1975; Bhatt 1976, 1977). The results on harvest index reported here agree with these points in that harvest index was less influenced by environment than grain yield, it was easier to detect genetic variation in harvest index, and the heritability of harvest index was higher than grain yield. However, these points simply suggest that harvest index might be simpler to work with than yield. The critical question is whether selection for harvest index in early generations will give a greater improvement of yield of homozygous lines in late generations than selection for yield directly. Results from chapters 4 and 5 indicate that it will not.

Chapter 7

AN ANALYSIS OF SITES USED FOR TESTING ADVANCED WHEAT LINES IN AUSTRALIA, AND ITS IMPLICATIONS FOR PLANT BREEDING PURPOSES

INTRODUCTION

An early testing of lines at a number of sites in a number of years is a prime consideration when devising a breeding method (see chapters 4 and 5). A question that arises from the findings in these chapters is how does a breeder choose sites for testing crossbred material in the various stages of a breeding program?

Within any region devoted to a crop it is customary to find subregions with different environments or cultural practices. A variety that does well in one subregion will not necessarily do well in another, and variety x environment interactions will occur. The performance of the cultivars themselves will be the best indicator of the existence of regions and subregions. Analyses of the performance of varieties at different sites has been used to divide some states or regions in the U.S.A. into subregions for variety recommendations for oats, corn and cotton (Horner and Frey 1957; McCain and Schultz 1959; Abou-El-Fittouh, Rawlings and Miller 1969).

Various statistical techniques have been used to group locations with similar environments, using the performance of crop varieties. Regions of adaptation have been defined by grouping sites which gave the greatest reduction in genotype x location interaction (Horner and Frey 1957; McCain and Shultz 1959; Liang, Heyne and Walter 1966) and similar sites have been grouped using cluster analysis (Abou-El-Fittouh, Rawlings and Miller 1969) and correlations between pairs of locations (Guitard 1960). The value of pattern analysis to characterize the value of test sites has been demonstrated recently in Queensland (Australia) using the performance of soybeans at four sites in two years (Shorter, Byth and Mungomery 1977).

It is usual to find that variety x year interactions are greater than variety x location interactions (Rasmusson and Lambert 1961; chapters 4 and 5 of this thesis), and using principal component analysis, Goodchild and Boyd (1975) showed that between season variation of yield in the Western Australian wheat belt was greater than within season variation. It is essential, therefore, that investigations to examine the choice of sites should include an assessment of the effects of different years.

This chapter examines a number of questions regarding the choice of sites for testing crossbred lines in various stages of development.

1. Could the wheat growing areas of Australia be divided into a number of subregions based on the different performance of varieties, and hence should sites be chosen to represent these subregions?

2. Will the differences between subregions, or sites representing the subregions, be consistent between years?

3. How many sites are required to test adequately crossbred material over a region or subregion?

4. Can locations be chosen in one year to reflect the variation in a particular subregion over several years?

These questions were examined using data from the variety testing programs conducted by the Departments of Agriculture in South Australia and Victoria, and data from the Australian Interstate Wheat Variety Trials. These data were subjected to principal component analyses to detect the similarity of sites in South Australia, two areas of Victoria, and the whole of Australia, in a number of years.

METHODS

THE DATA

Principal component analyses were carried out on data from four situations.

1. Australian wheat belt

Twelve sites over the whole of the Australian wheat growing area were examined using data from the Australian Interstate Wheat Variety Trials for 1974, 1975 and 1976 (figure 7.1).

These trials, at sites in Western Australia, South Australia, Victoria, New South Wales and Queensland, assess advanced breeding material contributed by breeders from throughout the region. The objectives of these trials are to allow testing of advanced lines in the environments experienced in all states before possible registration as a variety, and to provide the opportunity for breeders to study and use useful breeding lines. These trials also provide the opportunity to carry out studies of adaptation.

A group of varieties is grown in this trial in two consecutive years, at 6 or 7 sites in the first year and up to 15 sites in the second year. The 12 sites used in these analyses were chosen because they were common between the years.

2. South Australian wheat belt

Ten sites in South Australia were analysed using data from the advanced variety experiments of the South Australian Department of Agriculture for 1974, 1975 and 1976 (figure 7.2).

These experiments, which include up to 22 sites over the South Australian wheat belt, are used to evaluate advanced breeding lines and

Figure 7.1: Location of experimental sites used in the Australian Interstate Wheat Variety Trials.

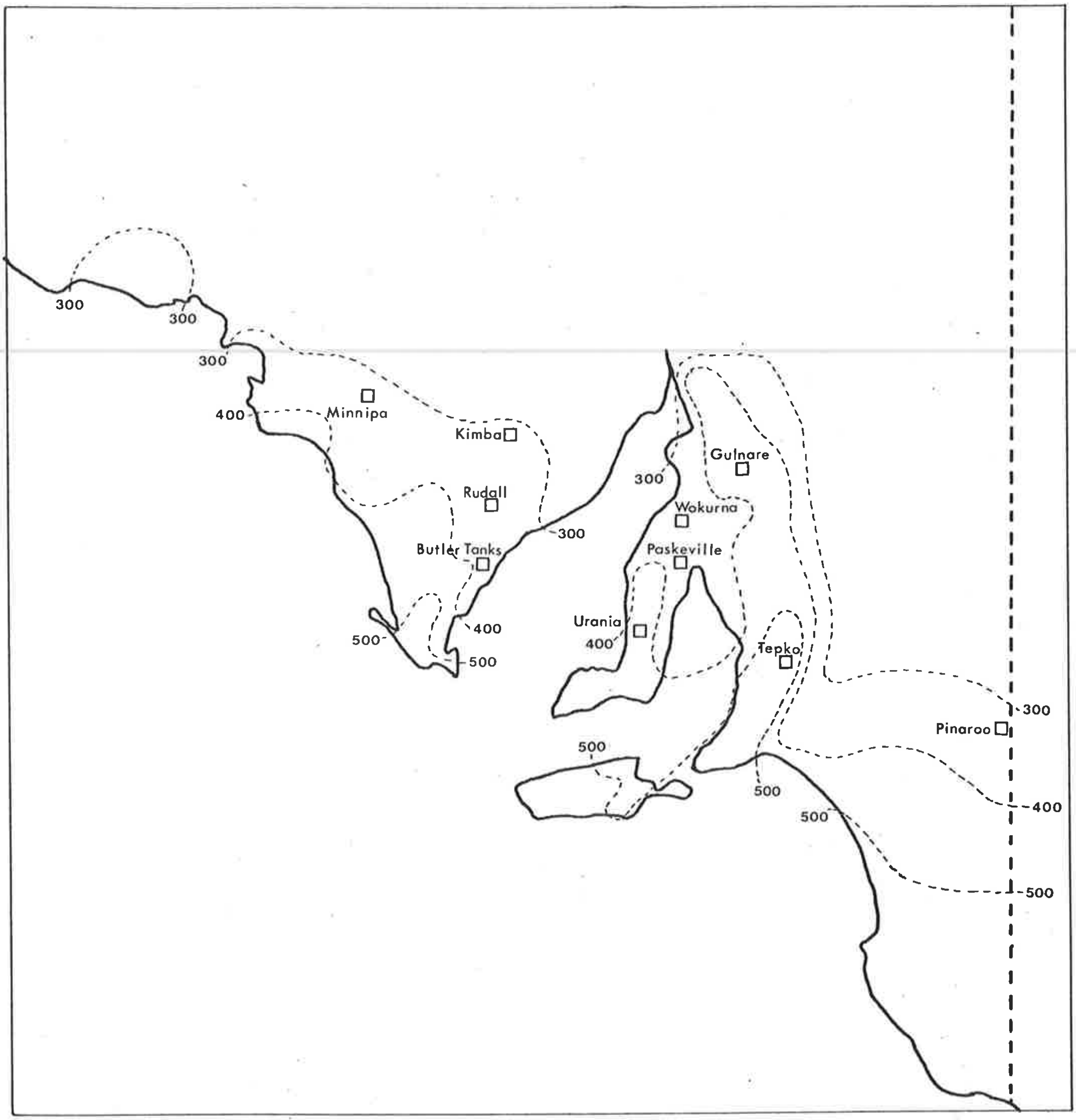


Figure 7.2: Location of experimental sites used in the variety experiments of the South Australian Department of Agriculture. Isohyets are mean annual rainfall (mm).

to formulate variety recommendations. The 22 sites are chosen on the basis of local experience, with rainfall and soil type being the main criteria. The only objective basis for choosing these sites on varietal performance has been when testing at some sites was terminated if it was apparent that these sites give the same results as others.

3. Zones 3 and 4 of Victoria

In Victoria, wheat variety recommendations are made for eight zones, these zones being separated on a basis of their protein content (McCann and Mullaly 1971). Data from the advanced variety experiments of the Victorian Department of Agriculture were used to examine the similarity of sites within zones 3 and 4, and within zones 1 and 2 (figure 7.3). Zones 3 and 4 cover the Wimmera area, and most of this area is suitable for soft wheats only, as the crops grown are low in protein. Zones 1 and 2 includes the Mallee area, and because of the higher protein content of crops in these zones, hard or soft wheats can be grown.

Up to 32 sites are included in the Victorian experiments, these being chosen to represent local variations within a zone, mainly based on experience and soil type. As with the South Australian experiments, testing at some sites were discontinued when it was apparent they gave similar results to other sites, and this is the only objective basis of choosing sites in these experiments, based on varietal performance.

Eight sites in the years 1973 to 1976 were examined for zones 3 and 4.

4. Zones 1 and 2 of Victoria

Nine sites in zones 1 and 2 were analysed for 1971 and 1972, and ten sites were analysed for 1974, 1975 and 1976 (figure 7.3). The same sites were included in 1975 and 1976, but one or two sites were different in the other years.

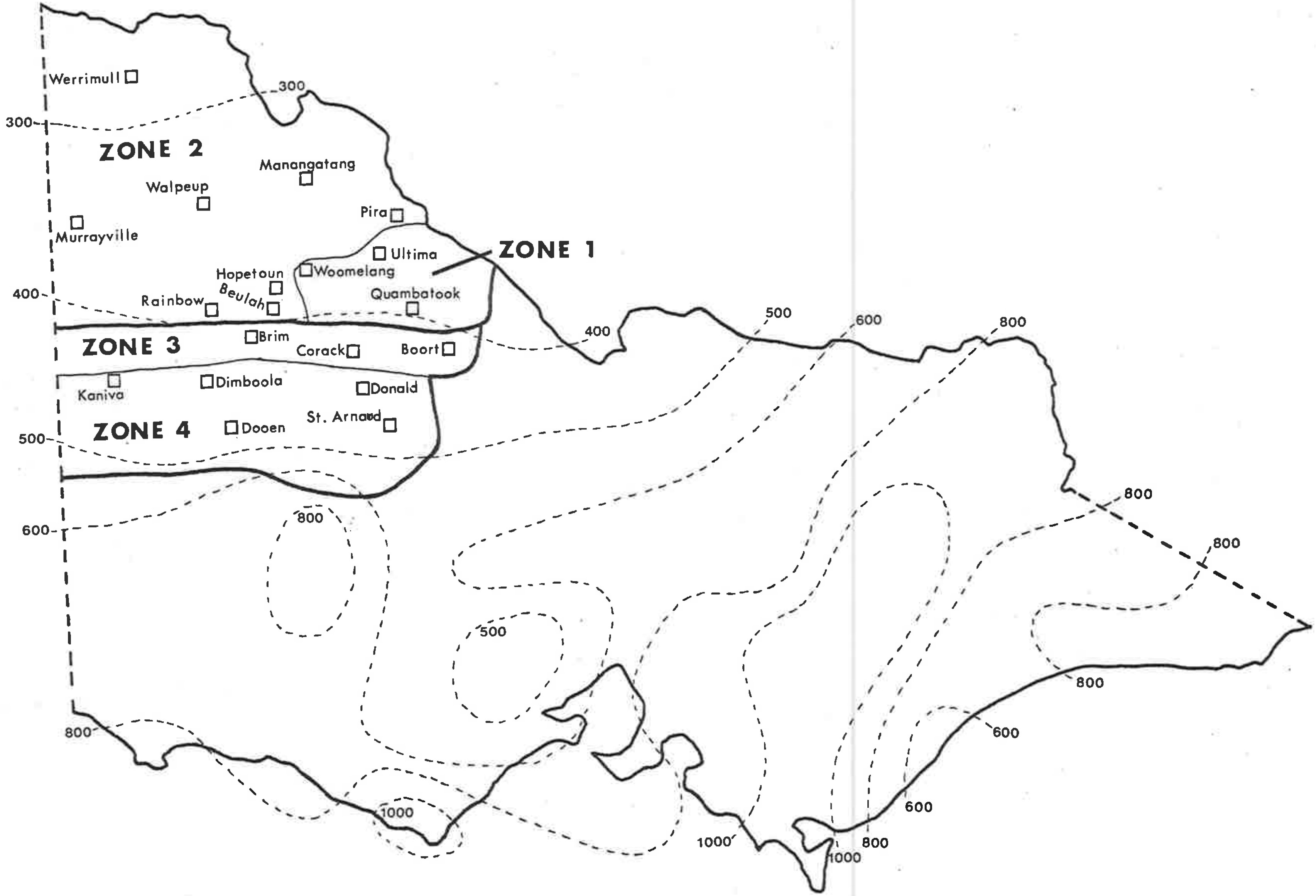


Figure 7.3: Location of experimental sites used in the variety experiments of the Victorian Department of Agriculture. Isohyets are mean annual rainfall (mm).

A randomized block design with four replications was used in all these experiments, except in Victoria where six replications were sometimes used. Plot sizes varied from 6 to 50sq m in the Interstate Wheat Variety Trials, from 14 to 58 sq m in the South Australian experiments, and from 43 to 72 sq m in the Victorian experiments.

For each of the four situations two types of analysis were carried out.

A. Analysis of individual years

The relationships between sites in individual years were compared to determine if similarities and dissimilarities were consistent over years. Because the experiments were designed to provide data for assessing potentially new varieties, inferior lines were discarded after each year's trial. It was therefore not easy to obtain data which included a large set of varieties grown at all sites in a number of years. While it would have been desirable to have a complete set of common varieties between years, it was considered even more desirable to include as many varieties as possible in each year.

A substantial number of the varieties were grown between years. Analyses were carried out on these common varieties alone, and results obtained were similar to the whole set of varieties. Because the accuracy of the analyses was greater using the extra varieties, they will be described.

The conclusions drawn in this section result from analyses over many years. The effect of not using complete sets of common varieties between years would be minimal.

B. Analysis of two years combined

The effects of different years or sites were analysed using data from two years combined. In these analyses, only values for varieties at all sites over the two years were used. Because of the nature of the data, these analyses sometimes included less sites and varieties than the analyses of individual years.

PRINCIPAL COMPONENT ANALYSIS

Fox (1977) compared a number of univariate and multivariate methods for their value in characterizing the sites in the Australian Interstate Wheat Variety Trials in 1975. These included regression analysis, cluster analysis, correlations, analysis of ranks at different sites, and principal component analysis. He concluded that the principal component method was the most effective method for grouping similar sites on varietal performance.

Principal component analysis transforms a given set of variables into a new set of composite variables or principal components, which have certain properties (Holland 1969).

1. The derived components are uncorrelated with each other.

2. They are linear functions of the original variates.

3. The total variation in the derived components is equal to the total variation in the original variates, so that no information concerning differences is lost.

4. The first component accounts for the largest possible proportion of the total variation, the second accounts for the largest possible portion of the remainder, and so on. Consequently the first few components may explain most of the variance of the data.

No particular assumption about the underlying structure of the variables is required (Kim 1975). The technique is valuable for reducing numerous variables to a few which account for most of the variation (Ehrenberg 1975).

Scaling problems are eliminated in the analysis, as variates are standardized by dividing each by its standard deviation. The resulting covariance matrix is the same as the correlation matrix. After extraction of the principal components, rotation is used to give a simpler and more meaningful pattern of variables.

In the analyses described here, the first two components accounted for most of the variation, so only these will be generally considered.

RESULTS

1. AUSTRALIAN WHEAT BELT

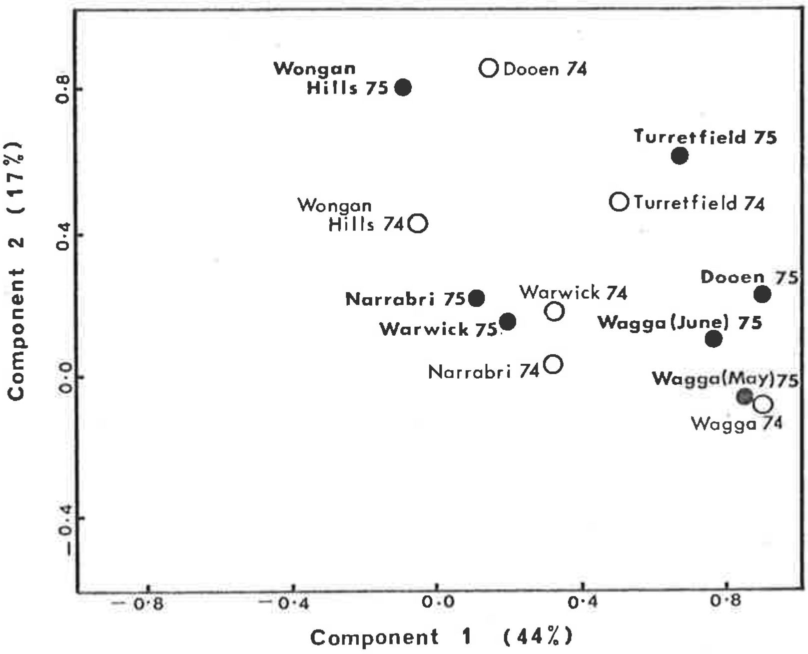
The locations of the 12 sites were indicated in figure 7.1. In 1974 two experiments were conducted at Wagga, one sown in May and the other in June. The similarity of sites is evident from the grouping in figure 7.4, where the first two components are presented. Analyses combining the sites over two consecutive years indicated that most sites assessed the varieties similarly over the two years (figures 7.4a and 7.4b). Exceptions were Dooen and Turretfield between 1975 and 1976, and Dooen between 1974 and 1975. The same general trend is indicated in the correlations between years for each site (table 7.1). In these analyses, the differences between sites were apparently greater than the differences between years.

When individual years were considered,the sites showed considerable differences (figures 7.4c to 7.4e). This is also clear from the correlation matrix between sites for 1975,which is presented as an example (table 7.2). While overall, the sites were dissimilar, some sites were grouped indicating that they were similar. In 1975 these groups were distinct, and consisted of northern sites (Narrabri, Warwick and Pirrinuan), southern sites (Wagga, Dooen, Turretfield, Urania and Nangari) and western sites (Wongan Hills and Merredin). The Gums (in the north), and Walpeup (in the south) were exceptions, being grouped with the western

Figure 7.4

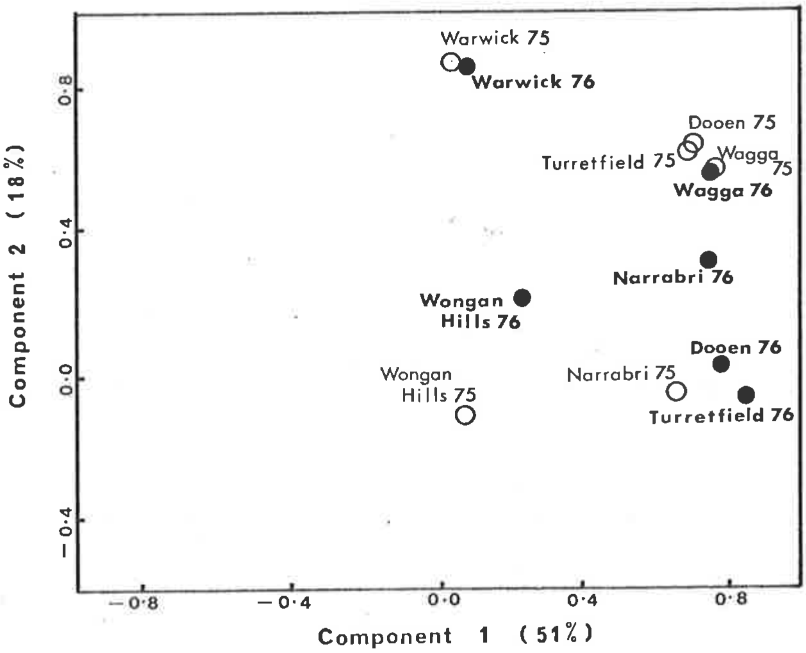
Australian Interstate Wheat Variety Trials 1974 to 1976. Arrangement of sites according to the first two components from principal component analyses.

Percentage of total variation attributable to each component is indicated in parenthesis on the axes.



a) 1974 and 1975 combined,

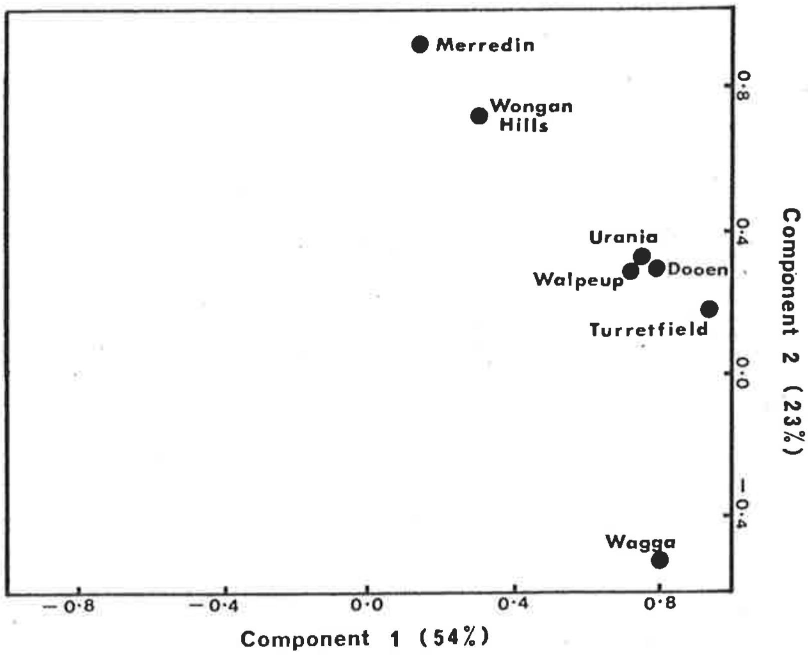
using 20 varieties



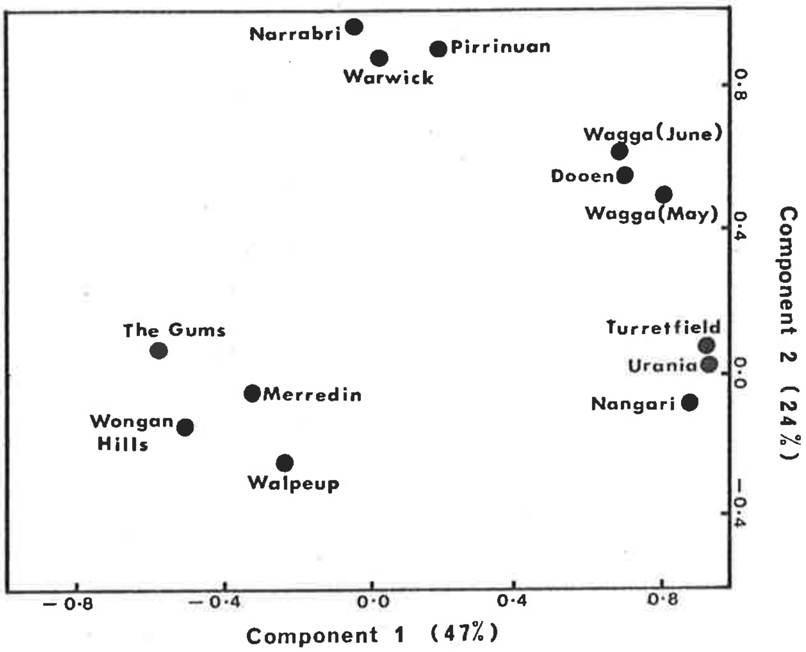
b) 1975 and 1976 combined,

using 20 varieties

c) 1974, using 18 varieties



d) 1975, using 22 varieties



e) 1976, using 20 varieties

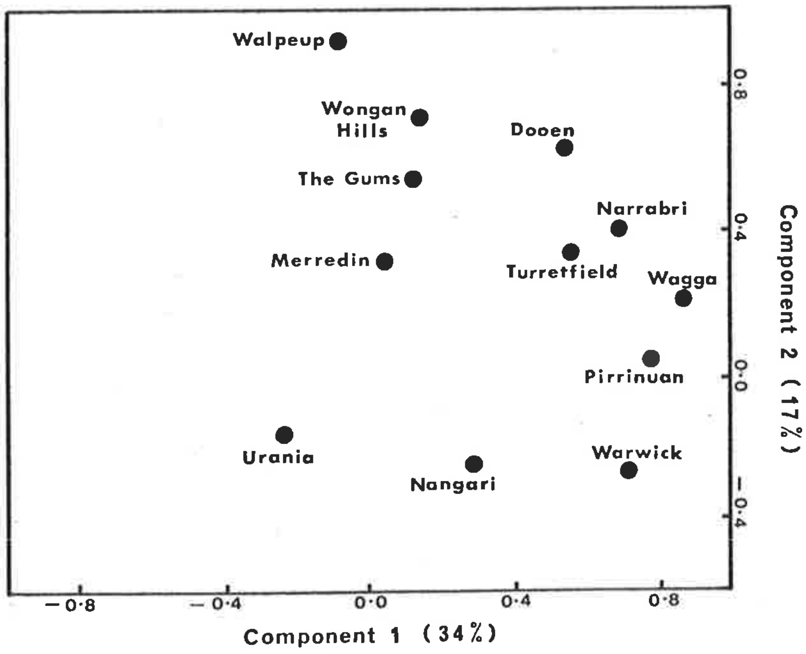


TABLE 7.1

Australian Interstate Wheat Variety Trials - correlations between years

Site	Correlations between two years	
	1974 and 1975 (n=20)	1975 and 1976 (n=20)
Turretfield	.61**	.44*
Dooen	.37	.58**
Wagga - May	.80**	.84**
Wagga - June	.69**	
Warwick	.62**	.53*
Narrabri	.33	.50*
Wongan Hills	.51*	.46*

* P < 0.05 ; ** P < 0.01

TABLE 7.2

Australian Interstate Wheat Variety Trials - correlations between sites
1975

Sites	Nangari	Urania	Turretfield	Dooen	Wagga - May	Wagga - June	Pirrinuan	Warwick	Narrabri	The Gums	Merredin	Wongan Hills
Nangari	-											
Urania	.73**	-										
Turretfield	.70**	.90**	-									
Dooen	.49*	.75**	.81**	-								
Wagga - May	.65**	.75**	.83**	.92**	-							
Wagga - June	.49*	.60**	.67**	.78**	.90**	-						
Pirrinuan	.16	.18	.18	.53*	.55**	.73**	-					
Warwick	.10	.05	.08	.54**	.46*	.42*	.75**	-				
Narrabri	-.17	.02	.05	.50*	.45*	.59**	.88**	.79**	-			
The Gums	-.28	-.67**	-.72**	-.57**	-.48*	-.33	.00	.20	.01	-		
Merredin	-.15	-.42*	-.56**	-.63**	-.39	-.12	.08	-.12	.00	.74**	-	
Wongan Hills	-.42*	-.54**	-.35	-.45*	-.54**	-.44*	-.21	-.01	-.19	.49*	.17	-
Walpeup	-.37	-.06	-.09	.04	-.18	-.35	-.43*	-.32	-.18	-.45*	-.62**	-.30

n=22 for all comparisons

* P < 0.05 ; ** P < 0.01

sites. However, Walpeup was negatively correlated with The Gums, Wongan Hills and Merredin (table 7.2), and it was heavily weighted on the third component. When the first and third, or the second and third components were considered, Walpeup appeared as a separate site and was not grouped with the western sites.

In 1974 the sites were also grouped on western and southern sites, except that Wagga was different to the rest of the southern sites. Northern sites could not be included in the 1974 analysis.

Distinct groups were not obvious in 1976 as all sites were dissimilar to one another. However, Merredin, Wongan Hills, The Gums and Walpeup were more closely associated with each other than with the other sites, and Warwick and Pirrinuan were closely associated.

2. SOUTH AUSTRALIAN WHEAT BELT

The locations of the 10 sites throughout the South Australian wheat belt were indicated in figure 7.2. The three years considered in the analyses were characterized by good rainfall in 1974, a dry autumn and winter but wet spring in 1975, and severe drought until October (late spring) in 1976.

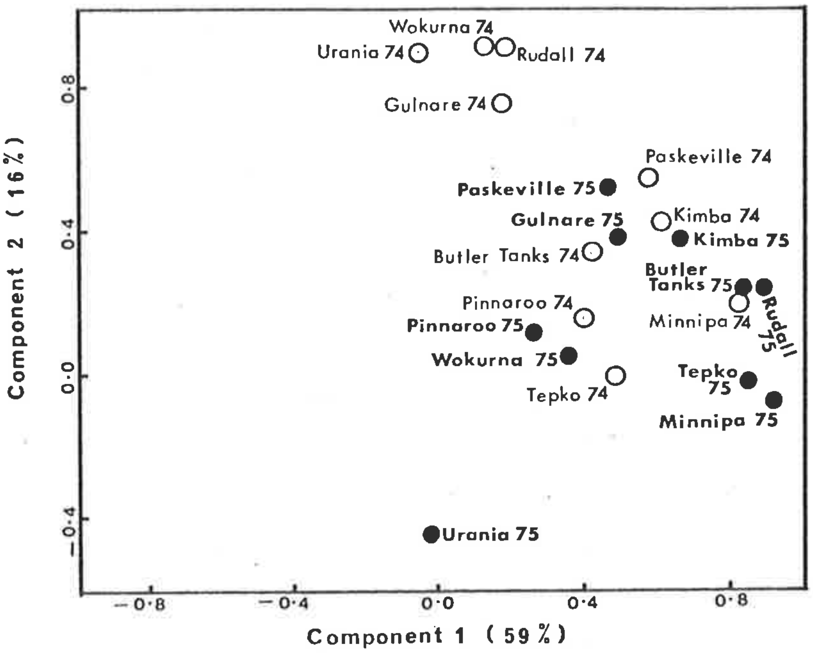
There was a clear separation of the sites in each year for the analyses involving 1974 and 1976 (figure 7.5b), and for 1975 and 1976 (figure 7.4c). The differences between years were greater than the differences between sites, as sites within any year were more similar than any site between years. The difference between 1974 and 1975 was not as great (figure 7.5a), as some sites showed similarities between years. However, Urania, Wokurna and Rudall were quite different in these two years.

The poor comparisons between years are also evident from the correlations (table 7.3). The correlations were generally higher between 1974 and 1975 than between 1974 and 1976 or between 1975 and 1976, a result

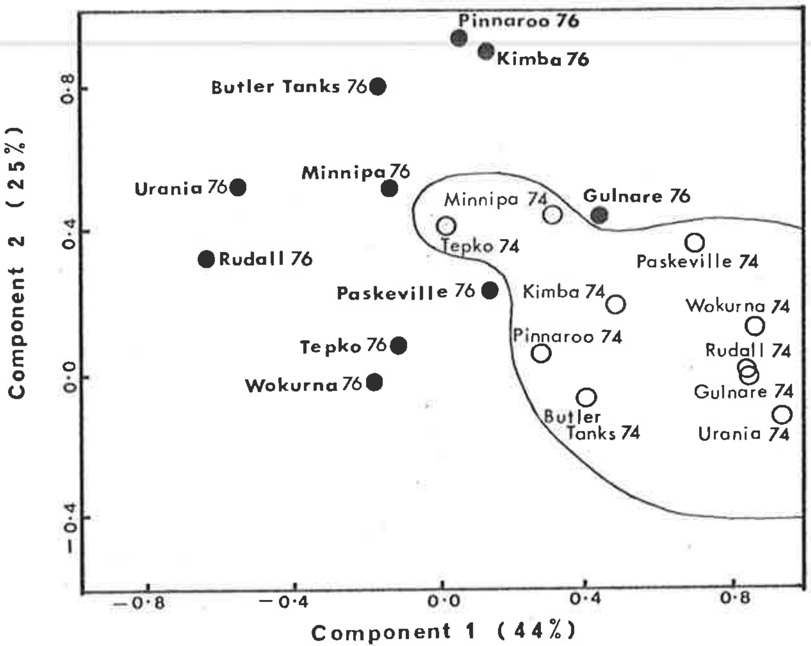
Figure 7.5

Variety experiments for South Australia 1974 to 1976. Arrangement of sites according to the first two components from principal component analyses.

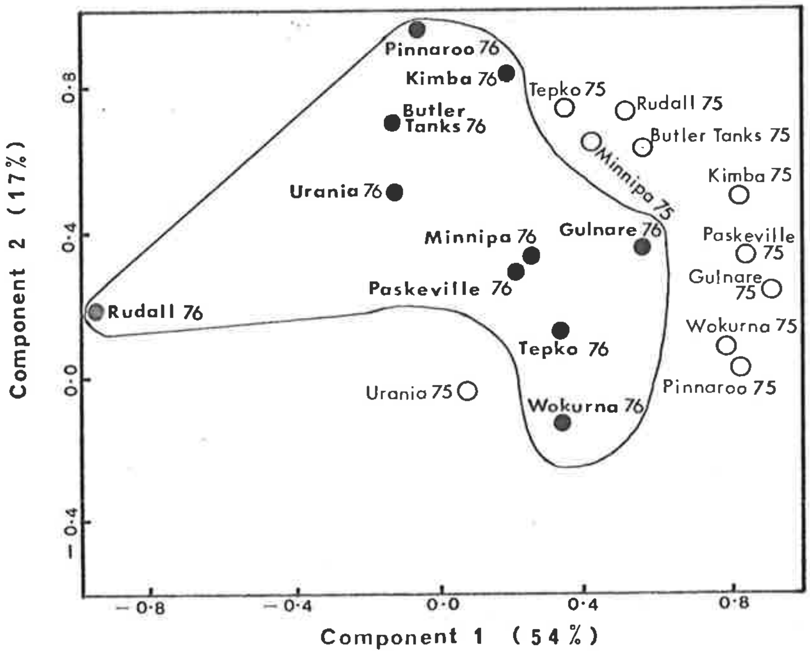
Percentage of total variation attributable to each component is indicated in parenthesis on the axes.



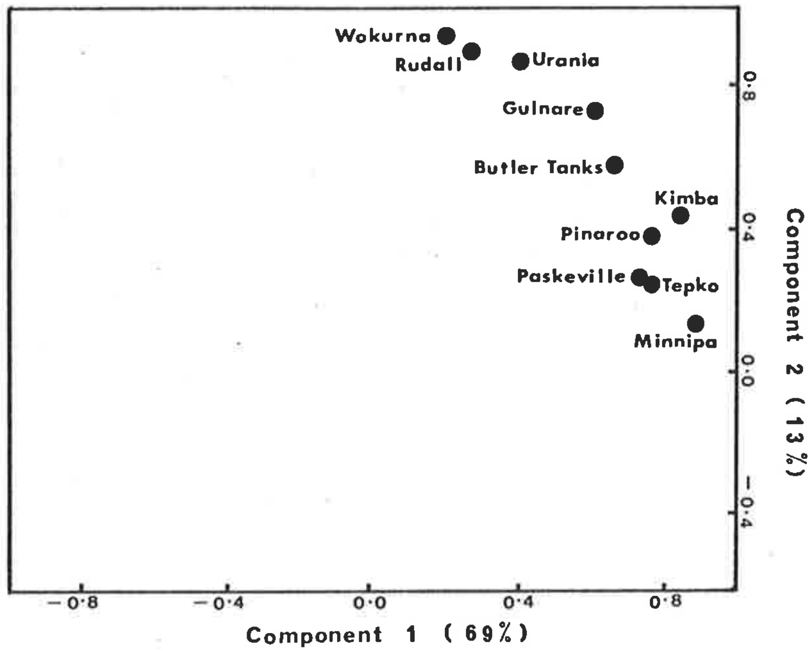
a) 1974 and 1975 combined,
using 9 varieties



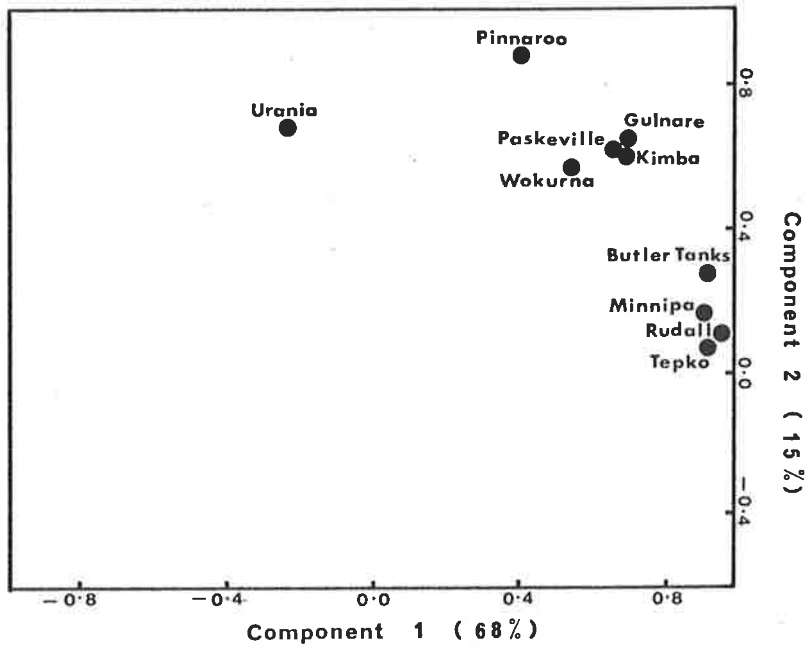
b) 1974 and 1976 combined,
using 9 varieties



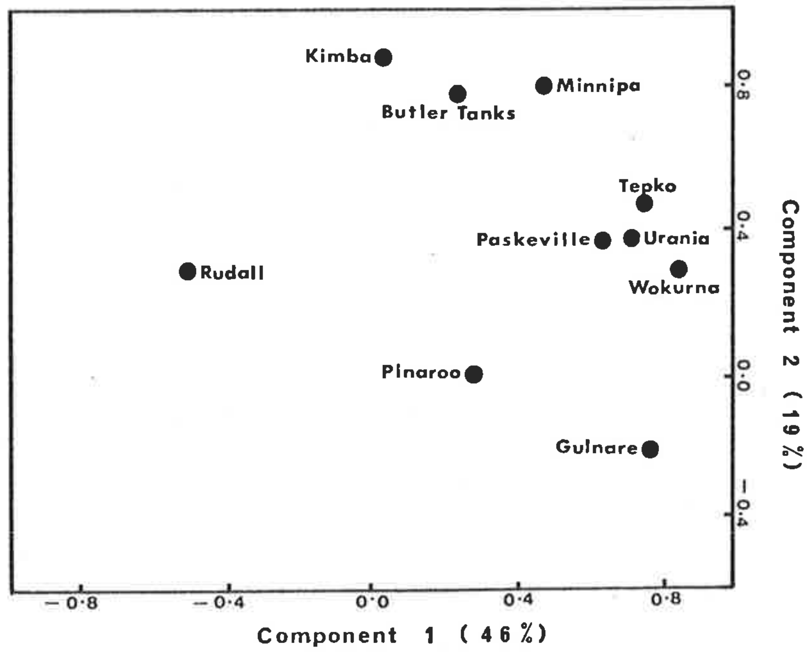
c) 1975 and 1976 combined,
using 9 varieties



d) 1974,
using 12 varieties



e) 1975,
using 9 varieties



f) 1976,
using 17 varieties

TABLE 7.3

Variety experiments for South Australia - correlations between years

Site	Correlations between two years		
	1974 and 1975 (n=9)	1974 and 1976 (n=9)	1975 and 1976 (n=9)
Tepko	.72*	.71*	.54
Rudall	.33	-.52	-.39
Minnipa	.91**	.45	.60
Butler Tanks	.62	.16	.67*
Wokurna	.21	-.28	.56
Paskeville	.87**	.33	.63
Kimba	.65	.34	.67*
Gulnare	.72*	.58	.72*
Pinnaroo	.60	.27	-.01
Urania	-.41	-.49	.26

* P < 0.05 ; ** P < 0.01

TABLE 7.4

Variety experiments for South Australia - correlations between sites 1975

Sites	Tepko	Rudall	Minnipa	Butler Tanks	Wokurna	Paskeville	Kimba	Gulnare	Pinnaroo
Tepko	-								
Rudall	.93**	-							
Minnipa	.89**	.87**	-						
Butler Tanks	.89**	.92**	.92**	-					
Wokurna	.49	.52	.60	.55	-				
Paskeville	.62	.71*	.60	.83**	.60	-			
Kimba	.63	.76*	.71*	.79*	.69*	.88**	-		
Gulnare	.63	.75*	.66	.79*	.82**	.91**	.88**	-	
Pinnaroo	.41	.43	.52	.61	.82**	.81**	.77*	.87**	-
Urania	.03	-.05	.03	.05	.01	.19	.22	.15	.43

n=9 for all comparisons

* P < 0.05 ; ** P < 0.01

which supports the principal component analyses. These results indicate that agreement between years for sites in South Australia is not good.

The differences between sites were much greater in 1976 than in either 1974 or 1975 (figures 7.5d to 7.5f).

There was no consistency in the pattern of sites with respect to their similarities in the three years (figures 7.5d to 7.5f) e.g. Wokurna, Rudall and Urania were similar in 1974 but appeared quite different in other years.

3. ZONES 3 AND 4 OF VICTORIA

Zones 1 to 4 of Victoria, and the locations of sites were indicated in figure 7.3. In addition to the analyses presented here, it was possible to carry out a number of additional analyses of zones 3 and 4, and zones 1 and 2. Those presented here are typical examples illustrating the general trends obtained.

The two years 1974 and 1975 were quite different in zones 3 and 4 as there was a distinct separation of the sites in the two years on the principal components (figure 7.6b), and the correlations were low (table 7.5). In contrast, 1973 and 1974 were similar, as many sites were similar for the two years using principal component analysis (figure 7.6a), and the correlations of sites between years were often high (table 7.5). The year effects between 1974 and 1975 were greater than the differences between sites, whereas the differences between sites were greater than the differences between the years 1973 and 1974.

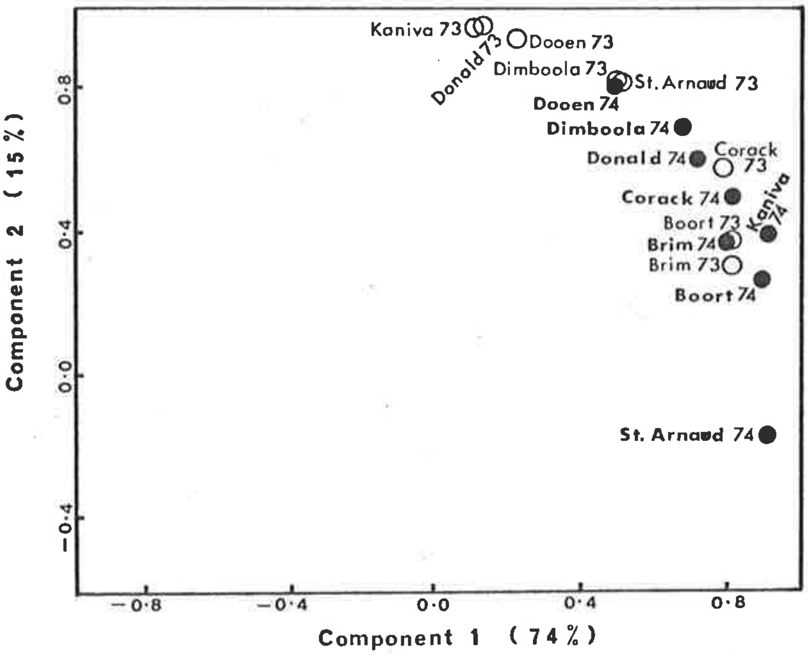
Growing conditions in the years 1974 and 1975 were different, as 1974 was wet, and 1975 was dry in autumn and winter, and very wet in spring. Conditions in 1973 and 1974 were similar as both were wet years. Stem rust, *Puccinia graminis* occurred extensively in 1973.

Other analyses, not presented here, showed that there were major differences between 1975 and 1976, giving a separation of sites between the years, similar to figure 7.6b. Conditions in 1971 and 1972 also caused a

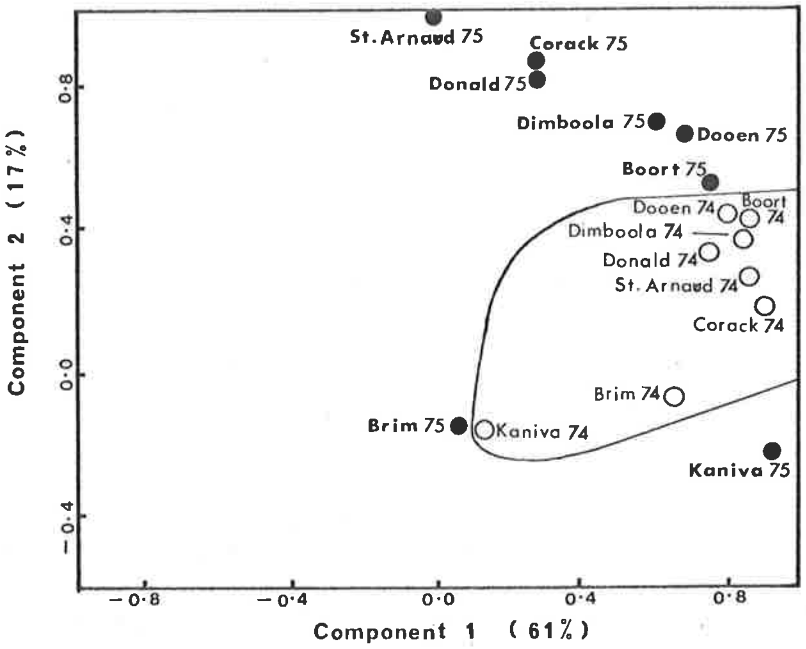
Figure 7.6

Variety experiments for Victoria, zones 3 and 4, 1973 to 1976. Arrangement of sites according to the first two components from principal component analyses.

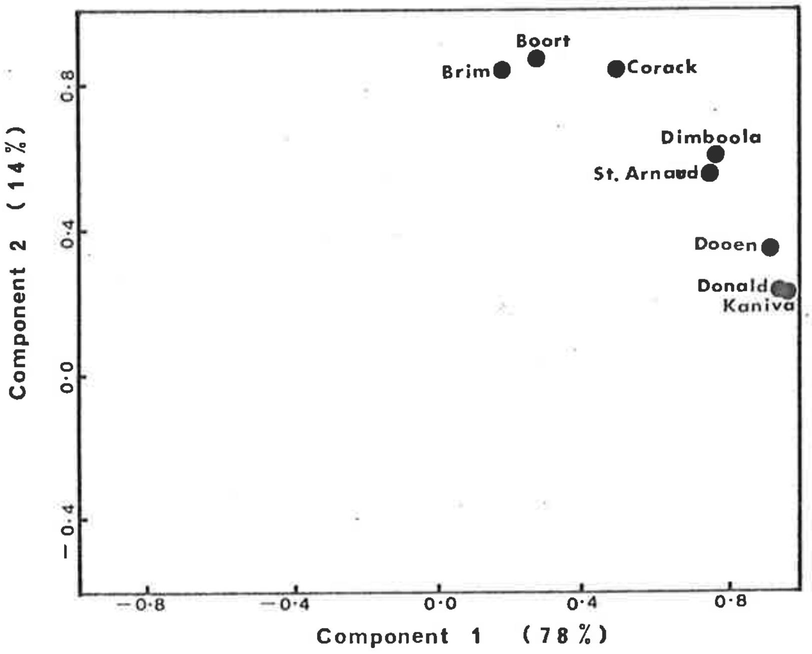
Percentage of total variation attributable to each component is indicated in parenthesis on the axes.



a) 1973 and 1974 combined, using 10 varieties

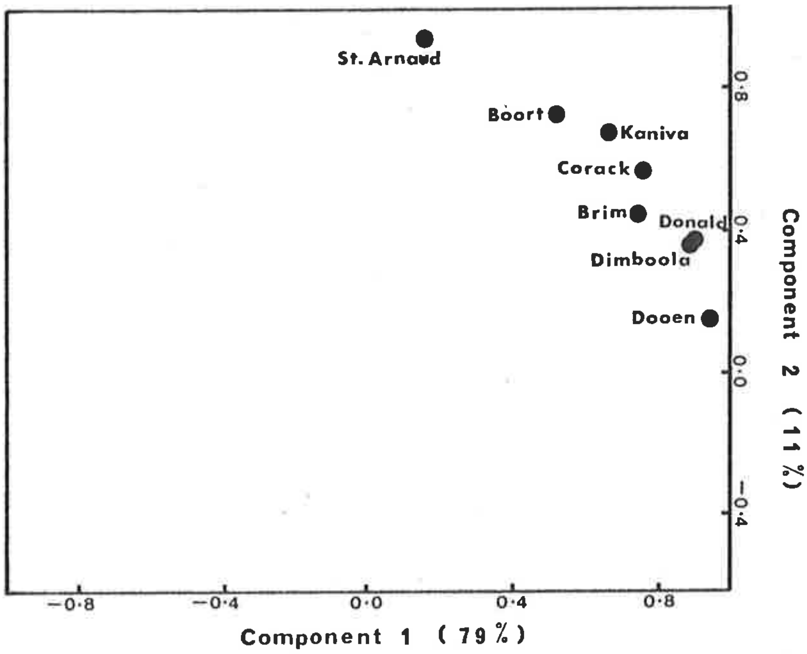


b) 1974 and 1975 combined, using 6 varieties

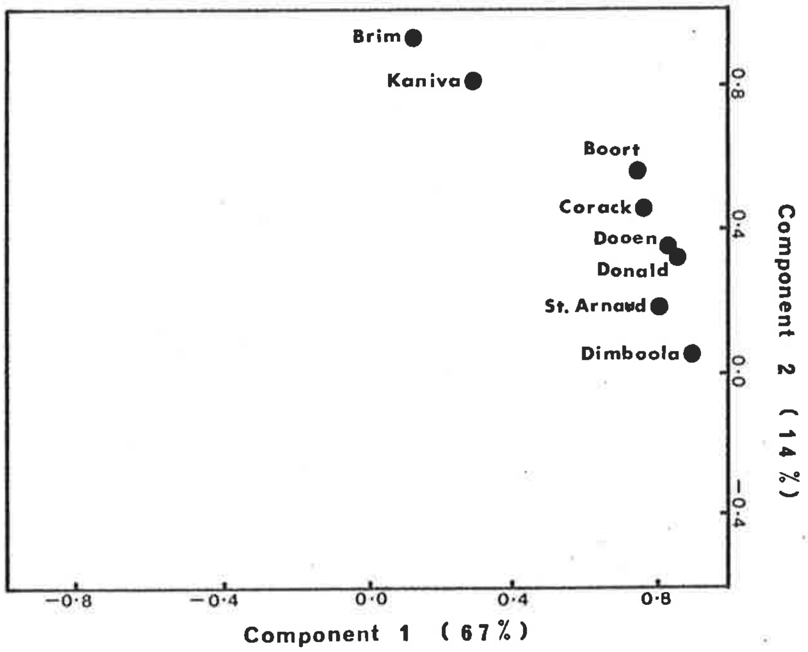


c) 1973, using 10 varieties

d) 1974,
using 12 varieties



e) 1975,
using 14 varieties



f) 1976,
using 10 varieties

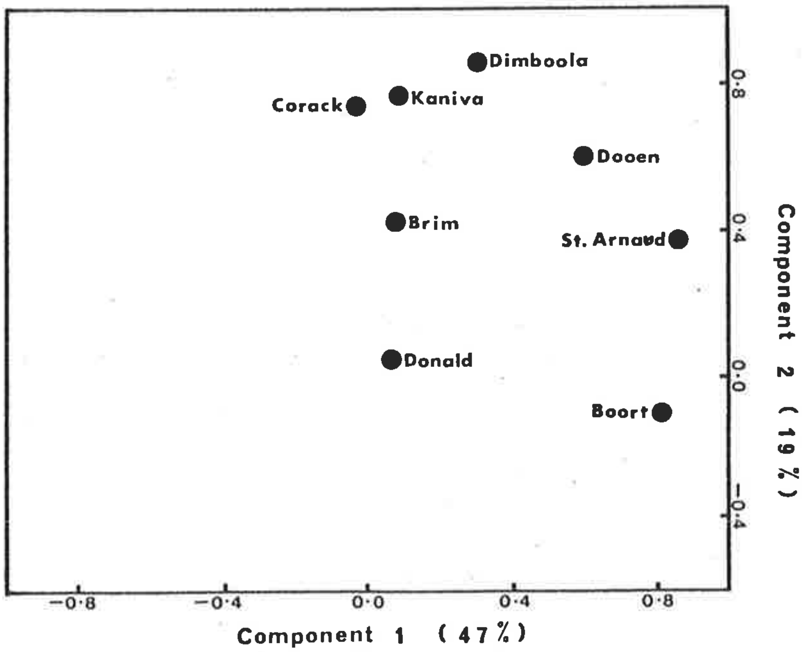


TABLE 7.5

Variety experiments for Victoria, zones 3 and 4 - correlations between years

Site	Correlations between two years	
	1973 and 1974 (n=10)	1974 and 1975 (n=6)
Brim	$.71^{*}$	-.60
Kaniva	.48	.11
Boort	$.78^{**}$	.79
Corack	$.90^{**}$	.27
Dooen	$.78^{**}$	$.85^{*}$
Donald	$.71^{*}$	.68
St. Arnaud	.34	.30
Dimboola	$.87^{**}$	$.90^{*}$

* P < 0.05 ; ** P < 0.01

TABLE 7.6

Variety experiments for Victoria, zones 3 and 4 - correlations between sites 1975

Sites	Brim	Kaniva	Boort	Corack	Dooen	Donald	St. Arnaud
Brim	-						
Kaniva	$.65^{*}$	-					
Boort	$.58^{*}$	$.67^{**}$	-				
Corack	$.60^{*}$	.43	$.83^{**}$	-			
Dooen	.37	$.68^{**}$	$.76^{**}$	$.72^{**}$	-		
Donald	.41	.51	$.81^{**}$	$.80^{**}$	$.79^{**}$	-	
St. Arnaud	.44	.17	$.71^{**}$	$.79^{**}$	$.58^{*}$	$.78^{**}$	-
Dimboola	.09	.48	$.68^{**}$	$.61^{*}$	$.89^{**}$	$.71^{**}$	$.58^{*}$

n=14 for all comparisons

* P < 0.05 ; ** P < 0.01

grouping of sites between years, although the differences between these years were not as great.

Within any one year, many sites in zones 3 and 4 gave similar results, as they were comparatively closely grouped on the principal components (figures 7.6c to 7.6f). An exception was 1976, which was a severe drought year, when sites were generally dissimilar (figure 7.4f).

There did not seem to be any consistent pattern of sites over the four years. With the exception of 1976, the yields of the varieties at most sites were closely correlated, with perhaps two or three sites giving somewhat different results. Thus, in 1975 all sites except Brim and Kaniva were closely associated, and this is also apparent from the correlation matrix between sites for this year (table 7.6). In 1974 all sites except St. Arnaud were very similar, and in 1973 all sites except Brim, Boort and Corack were similar.

Similar results to those presented here have been obtained with other analyses e.g. sites within 1970 and 1972 were dissimilar as in 1976, and in 1971 all sites were similar.

4. ZONES 1 AND 2 OF VICTORIA

The years considered in the analyses were characterized by a good year climatically in 1971, a very dry year in 1972, very wet years in 1973 and 1974, a dry autumn and winter but wet spring in 1975, and a very dry year in 1976.

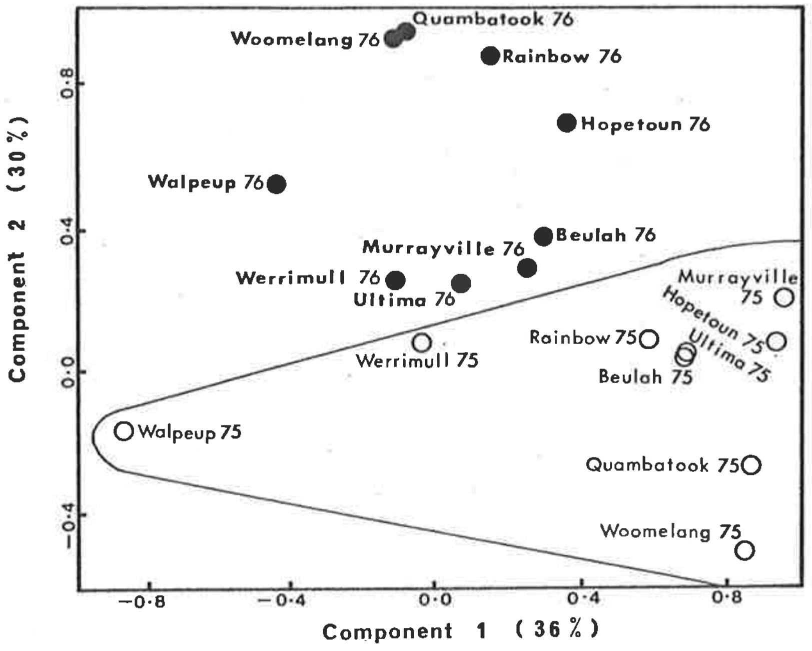
The analysis of the sites in 1975 and 1976 combined showed that the differences in the two years were great, greater than the differences between the sites in one year (figure 7.7a). The correlations between years for the sites also shows poor agreement between the two years (table 7.7). Other analyses, involving other pairs of years, also indicated that the differences between years were important.

When the years were considered individually, the sites in zones 1 and 2 were very similar in some years while in other years they were

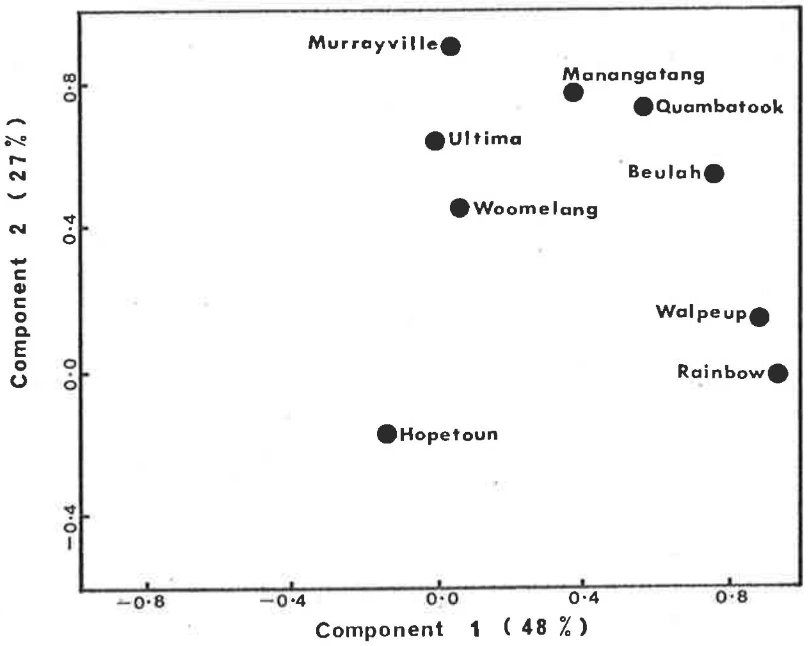
Figure 7.7

Variety experiments for Victoria, zones 1 and 2, 1971, 1972, 1974, 1975 and 1976. Arrangement of sites according to the first two components from principal component analyses.

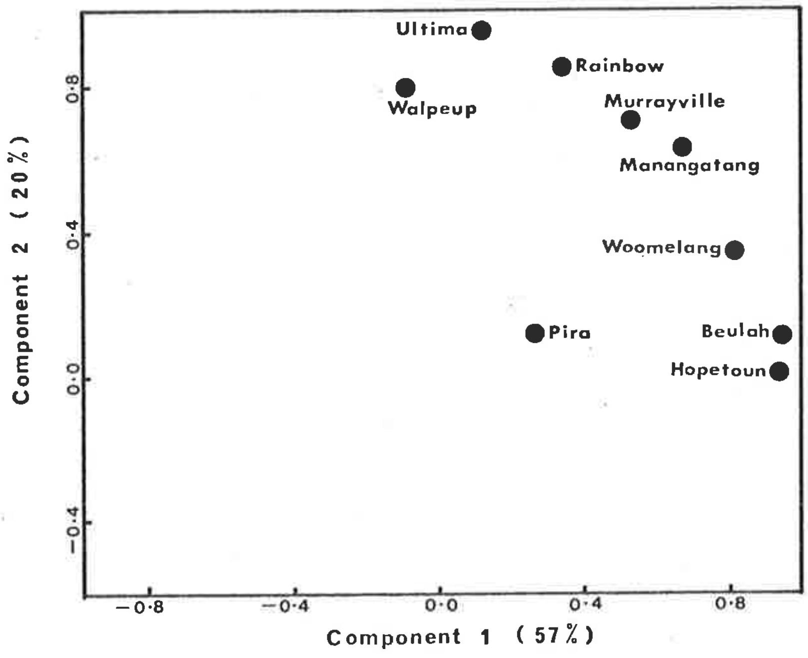
Percentage of total variation attributable to each component is indicated in parenthesis on the axes.



a) 1975 and 1976 combined,
using 9 varieties

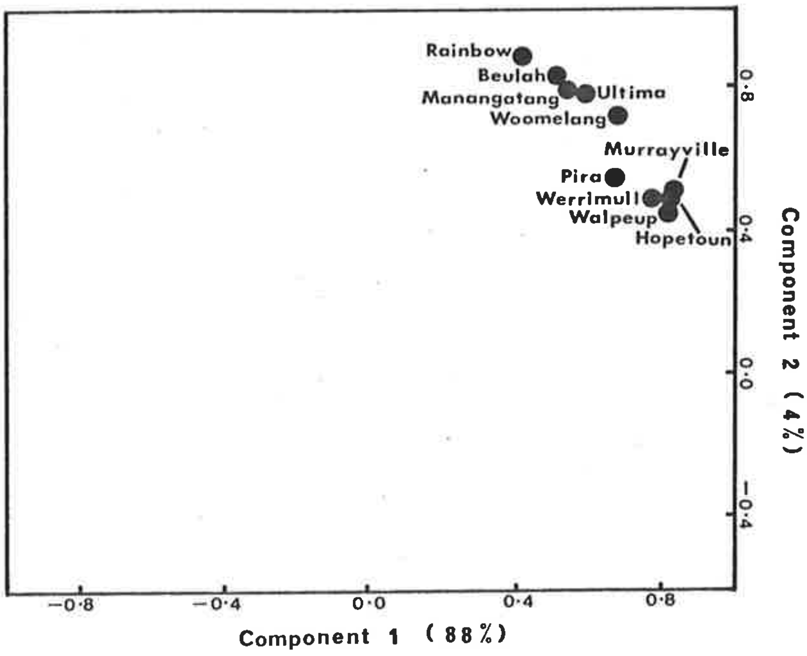


b) 1971,
using 10 varieties

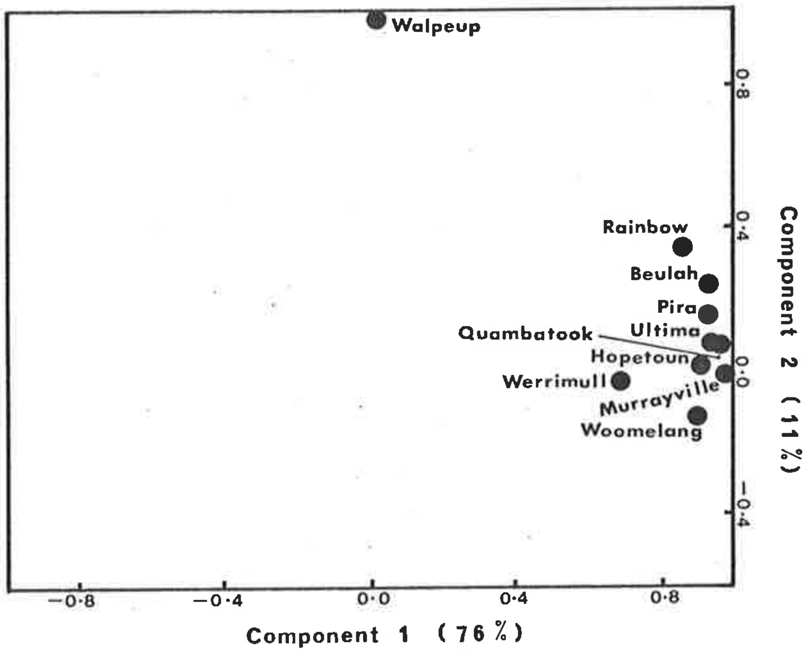


c) 1972,
using 11 varieties

d) 1974 ,
using 7 varieties



e) 1975 ,
using 13 varieties



f) 1976 ,
using 12 varieties

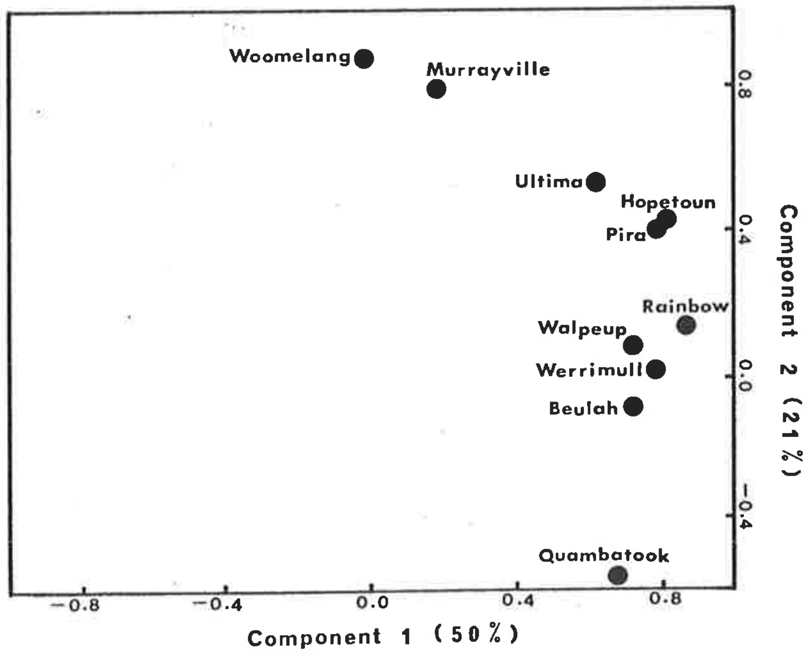


TABLE 7.7

Variety experiments for Victoria, zones 1 and 2 - correlations between years

Site	Correlations between 1975 and 1976 (n=9)
Woomelang	-.59
Werrimull	.35
Murrayville	.40
Hopetoun	.37
Quambatook	-.20
Ultima	.66
Beulah	-.03
Rainbow	.19
Walpeup	.46

All correlations are not significant at the 5% level

TABLE 7.8

Variety experiments for Victoria, zones 1 and 2 - correlations between sites

1975

Sites	Woomelang	Werrimull	Murrayville	Hopetoun	Quambatook	Ultima	Pira	Beulah	Rainbow
Woomelang	-								
Werrimull	.52	-							
Murrayville	.87**	.66*	-						
Hopetoun	.87**	.39	.93**	-					
Quambatook	.89**	.74**	.95**	.84**	-				
Ultima	.83**	.67*	.93**	.88**	.92**	-			
Pira	.80**	.62*	.93**	.91**	.87**	.91**	-		
Beulah	.84**	.59*	.94**	.91**	.90**	.88**	.97**	-	
Rainbow	.72**	.65*	.86**	.75**	.91**	.86**	.81**	.85**	-
Walpeup	-.06	.00	.02	.04	.10	.11	.18	.27	.35

n=13 for all comparisons

* P < 0.05 ; ** P < 0.01

quite different. All sites in 1974, and all sites except Walpeup in 1975 gave very similar results (figures 7.7d and 7.7e, table 7.8). In 1976 many sites gave very different results, particularly Woomelang, Murrayville and Quambatook (figure 7.7f). In 1971 there were considerable differences between sites, with Walpeup, Rainbow and Hopetoun being quite different to the others (figure 7.7b). In 1972 the sites experienced different conditions with Walpeup, Ultima, Rainbow, Hopetoun and Pira forming the extremes (figure 7.7c).

While there did not appear to be any clear and consistent pattern in the distribution of sites in the different years, Walpeup was often quite different from the other sites, or was the extreme in a range of different sites. Rainbow also was often an extreme site in a range.

DISCUSSION

Definition of subregions

There is evidence from the Australian Interstate Wheat Variety Trials that subregions occur within the Australian wheat belt. To confirm this conclusion, analyses of more years is required, but it appears these subregions consist of northern sites, southern sites and western sites. An exception was The Gums which, although a northern site geographically, was grouped with the western sites in the two years considered. The grouping of sites was not distinct in 1976 as many areas were subject to drought. The effect that stress years have on the relationships is discussed in more detail later. It was not uncommon for a site in one subregion to resemble sites in another subregion in some years e.g. Walpeup was typical of southern sites in 1974, it was different to all other sites in 1975, and it was closely associated with the western sites in 1976.

The occurrence of subregions within Australia is probably caused by large differences in weather patterns between these areas, whereas within any particular subregion the general weather conditions are similar.

No subregions could be detected within South Australia or the two main wheat areas of Victoria, as there was not a consistent pattern of sites within these regions. Exceptions to this were Walpeup and Rainbow which often gave different results to the other sites in zones 1 and 2 in Victoria. Although the sites in both states were selected largely on soil type, this apparently had no influence on the performance of the sites. Rasmusson and Lambert (1961) similarly concluded that the state of Minnesota (U.S.A.) could not be divided into subregions on the performance of barley varieties, as there was only a small variety x location interaction in tests over that state.

Effects of different years and locations, and the implications in testing

When small regions are considered, such as the South Australian wheat belt or zones in Victoria, the difference between years in usually greater than the difference between sites. The agreement of sites between years is often not good, particularly between years that contrast climatically. In favourable seasons, most sites in any one of these small regions generally give similar results, although some sites might be atypical. In unfavourable or "stress" years, such as 1976, it was common for the sites to be dissimilar. This may be caused by stress occurring at different stages of plant development at the different sites, and varieties will be affected differently according to their maturity.

In contrast to the situation for small regions, there were large differences in the sites over the whole of the Australian wheat belt because the differences between sites in any one year were greater than the differences in sites between years.

The effects of genotype x year interactions cause problems when the yields of early generation lines in one year are used to predict the performance of homozygous lines obtained from them in future years (chapters 4 and 5). It was concluded in chapters 4 and 5 that year and site effects should be the prime considerations in a breeding method, and it was suggested that early generation lines should be selected on the basis of tests at a number of sites in different years. Also advanced lines must be tested a minimum of four or five years before release as a variety, so testing in both early and advanced stages of a breeding program may be reduced if the effects of different years could be obtained in one year by the choice of contrasting sites.

Although a range of conditions could be obtained in one state e.g. Walpeup, Dooen, Kaniva and Hopetoun in Victoria, the differences between these sites would not be as great as the differences obtained between years.

By choosing appropriate sites over Australia, the effects of different years might be obtained in one year, because the differences between sites are greater than the differences between years, over this region. Dooen, which is typical of zones 3 and 4 in Victoria, was similar to Wagga and different to Wongan Hills in 1975, but in 1976 it was similar to Wongan Hills (figure 7.4). Therefore results from Wagga and Wongan Hills in 1975 would have reflected the results that could be obtained at Dooen in 1975 and 1976. Testing large numbers of breeders' lines over Australia is not practical at present, but with further work a breeder may be able to choose, say, two sites that would adequeately indicate the effects of different years in his state. Such a proposition could then be feasible, possibly by cooperation between breeders.

Number of sites

One critical question that confronts plant breeders is how many sites are required to adequately evaluate the performance of crossbred material in a region? In favourable years, when conditions over the region are uniform and all sites give similar results, very few sites would be required. However, in years when growing conditions vary greatly and sites give different results, a large number of sites would be required to give a good representation of the region. An optimum number of sites must be chosen to give reliable results in all years, and it is possible to calculate the optimum number of plots, years and locations for a particular set of circumstances using variance component estimates (Rasmusson and Lambert 1961; Liang, Heyne and Walter 1966; Liang and Walter 1966; Campbell and Lafever 1977). However, this number depends on the stage of testing. Obviously many sites are required in advanced stages of testing, but only a few sites can be handled efficiently in trials of early generation material. Analyses such as those carried out here may help breeders to make a more objective choice of sites for use in early stages, to give the suitable range of conditions.

The need for more data

A striking feature that became clear in these investigations was that, although the testing of crossbred material at different sites in different years is important in a breeding program, very little data on varietal performance are available to investigate the differences between sites and the best method of choosing sites. The data used in these analyses are the most extensive available, and yet it was difficult to get information on many varieties at enough sites over many years. Even the Australian Interstate Wheat Variety Trials, which has as one of its aims to provide data for studies such as these, did not enable comparisons to be made involving the same varieties over a number of years for all sites.

While up to 15 sites are included in the advanced stage of this trial, a particular set of varieties is grown at all these sites in one year only.

It was not possible to attempt to explain the relationships between sites apparent in these analyses, because detailed information on climate, disease incidence, nutrient status, moisture reserves etc. were not available for the experiments.

There remains a need for further investigations into the choice of sites, particularly what environmental and management factors characterize a site, and what specific factors cause the large differences in performance between different sites in some individual years and between the same sites in different years. While these studies would be involved, this should be considered in relation to the economies they could provide. If the efficiency of variety testing could be improved by having fewer sites or more rapid release of varieties, the initial effort and expense may be worthwhile.

Valuable information could be obtained immediately, with very little extra effort, by an expansion of existing variety experiments. Testing in the Interstate Wheat Variety Trials could be extended to include testing of each group of varieties at the complete 15 sites in a second year, and variety experiments in each state could possibly retain a group of lines over years instead of deleting those which are inferior. Supporting data on climate, disease incidence, soil types, nutrient status etc. would help explain differences between sites, and there is already a trend to obtain more of this type of data.

The statistical techniques are available to study the problems concerning the choice of sites, but adequate field data are needed.

Chapter 8

GENERAL DISCUSSION AND CONCLUSIONS

Chapter 4 of this thesis considered the correlations between the F_2 to F_5 generations, and the value of selecting in each generation was predicted. The actual response to selection was reported in chapter 5. The results of these two chapters were related to the variability within lines, presented in chapter 6. The importance of selecting for yield on the basis of performance in different environments was emphasized in chapters 4 and 5, and aspects of choosing sites for variety testing were examined in chapter 7. The major findings of these chapters will now be integrated.

The value of using the performance of F_2 derived lines to predict the performance of near-homozygous lines in the F_5 can be assessed from the correlations between these generations. For grain yield, these correlations varied from 0.10ns to 0.49^{**}, when lines from both generations were grown in the same environment. Satisfactory improvement in the F_5 was possible by selecting the best F_2 derived lines. Correlations were high for plant height, heading date, pearling resistance, and flour yield, and selecting F_2 derived lines gave good improvement in the F_5.

As the generations were advanced and greater homozygosity achieved, the correlations between lines in one generation and the mean of lines derived from them in a following generation increased. In addition, the heritability increased, and the variability within lines decreased.

Therefore, better predictions of the performance of homozygous lines will be obtained by testing lines from late generations than from early generations. Plots will be more homogeneous, and the extent of segregation after the plot trial will be reduced. However, this does not mean that greater improvements will be obtained by selecting in late generations, as genetic variability and generation means might be reduced by the late generations.

It is desirable to attain some homozygosity and homogeneity for plant height, heading date and agronomic type before selection for yield is commenced, to avoid bias caused by variability in these characters. However, it might not be necessary to achieve a very high level of homozygosity and homogeneity for yield itself. By retaining variability for yield, the selected lines may benefit from a greater buffering capacity.

Correlations between early generation lines in one year and lines from later generations in the next year were low for grain and flour yield. Response to selection for grain yield measured in the following year was little better than random selection. The effect of different sites also reduced the improvement from selection. In contrast, correlations between years for plant height, heading date and pearling resistance were high. It is concluded that selection for grain and flour yield should be on the basis of performance at a number of sites, in different years.

Harvest index was less influenced by environment than grain yield, it was more highly heritable, and it was easier to detect genetic variation in harvest index than yield. But selection for harvest index in early generations was no more effective in improving grain yield in later generations in the next year, than selecting for yield directly.

Contrary to some theoretical proposals, it is of little consequence in what generation selection for yield is practised. The same improvement will be obtained by selecting in early or late generations.

While delaying selection may reduce the frequency of the best genotypes in the breeder's population, this is counteracted by the fact that better predictions of the performance of homozygous lines are obtained in late than in early generations. The decision on when to commence selection for yield can therefore be based on other factors.

The requirement of selecting over different environments should be a major consideration, and it is concluded that lines from early generations should be tested, not for theoretical reasons proposed in the literature, but to enable testing across environments as soon as possible. Selection for flour yield should be carried out concurrently with selection for yield, as environmental influences are important for this character also.

It is concluded that the best method of selecting for grain yield is to isolate lines in an early generation e.g. the F_2, increase seed over the next generation, and then grow the lines at a number of sites. Choosing appropriate sites is important for greatest efficiency. Contrasting sites should be chosen representative of the breeding region. With present knowledge, the only objective way to choose these sites is on the basis of existing variety experiments. The effect of different years can be simulated to a limited extent only, using contrasting sites in one year within a state or breeding region. It is therefore necessary to repeat trials in successive years. The effects of different years for one region could perhaps be indicated in one year by choosing appropriate sites elsewhere in Australia, but at present this is not practical for large numbers of breeder's lines.

A reflection on the experiments

It is worthwhile reflecting on the experiments of this thesis, and considering whether they could have been improved.

The approach adopted was to use large numbers of lines, with only one replication at each site. Different sites were used in preference to two replications at one site, to give some safeguard, and to assess the effect of different environments. Shortage of seed and the excessive number of plots that would be involved, prevented more than two plots of each line being grown. It was considered that large numbers were necessary, so that the populations were indicative of those confronting a plant breeder. The experiments were concerned with determining the means and variances of families of lines. It was considered preferable to have a large number of lines, each of one replication, contributing to these statistics, than to have a small number but with a number of replications. Large numbers are essential to obtain reliable measurements of variances.

An alternative approach would have been to have fewer lines, but with a number of replications. While this would have overcome some of the problems associated with environmental variation, the small number of lines would be a severe limitation, and results would be less applicable to the true plant breeding situation. In addition, plot sizes would have been smaller.

In these experiments, the environmental variation was estimated using the variance of a number of plots of the parents. However, it was suggested that this might give an overestimate when related to heterozygous material. Better estimates of the environmental variation applicable to heterozygous material might be obtained from a number of plots of F_2 bulks. The experiments could have been improved, therefore, by including F_2 bulks of each cross.

Speculations and suggestions for future studies

It was suggested that the environmental variation is overestimated in relation to heterozygous material when measured using the variance of a variety, because pure lines are less stable to environmental changes than heterozygous lines. This had implications in assessing the genetic variance of an F_2, in evaluating the rate of decrease in variability within lines with advancing generations, in calculating heritabilities, and in the effectiveness of using varieties as control plots. It would be worthwhile studying these aspects using more appropriate estimates of environmental variance e.g. the variance of plots of an F_2 bulk. Further work is also required to assess the stability over an experimental site of material differing in degree of heterogeneity and heterozygosity.

The within line variance for grain yield decreased with advancing generations at a rate faster than expected if the crosses were segregating for a large number of genes for yield. While this may have been partly due to the variance of the parents being used to indicate uniformity, it was also suggested that it may indicate that there were comparatively few major genes that give measurable differences segregating in these crosses for yield. It cannot be disputed that there would be very many genes segregating for yield, but many of these may give differences that are too small to be detected with present methods. As the number of important genes segregating for yield in a cross has important implications in interpreting quantitative genetic theories, this warrants further investigation.

A considerable amount of work has accumulated which advocates improving yield by selecting for harvest index in early generations. Many of these studies have not looked directly at the value of selecting for harvest index, but have considered aspects such as the increase in harvest index of successive releases of new cereal cultivars, and the genetic variability and heritability of harvest index. Comparisons of harvest index and yield have been made, but have generally been restricted to comparisons within groups of varieties. The investigations on harvest index in this thesis were concerned with selecting for grain yield through harvest index within crosses, so they were more applicable to the breeding situation. Further work of this nature, involving more crosses, is required. Donald and Hamblin (1976) suggested that harvest index may be a valuable criterion for early generation selection among spaced plants. This needs to be investigated within crosses, rather than within groups of varieties.

An important finding of this thesis is that selecting for grain yield in a late generation, after randomly maintaining the population, will give the same improvement as selecting in an early generation. Consequently, the same improvement might possibly be obtained from single seed descent or the bulk methods, than by testing in early generations. This needs to be tested using large populations, either by direct comparison of the methods or by simulating the different methods using appropriate data.

A recommendation arising from these studies is that lines from early generations should be tested in different sites and years. Although more evidence is required, it was suggested that the effects of different years in one state could be obtained in one year, by choosing appropriate sites over Australia. However, this is not possible for large numbers of early generation lines, at present. A proposal that could possibly be considered is whether a national breeding program in Australia would have merit. International testing of material from The International Maize and Wheat Improvement Centre (CIMMYT), Mexico, is now common, and in recent years there has been a trend in Australia for cooperation between states in the National Rust Control Program, the Interstate Wheat Variety Trials, and the growing of an elite crossing nursery and a Septoria nursery. The value of a national program that could grow early generation lines at a number of sites over Australia is perhaps worthy of consideration. Selected lines would be widely adaptable, and should maintain their performance in different years. These could then be distributed to breeders in different states.

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