IMPROVING WHEAT BY COMPOSITE CROSSES BASED ON 'CORNERSTONE' NUCLEAR MALE STERILITY

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by

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SUMMARY

The utilization of composite crosses in wheat breeding was investigated by using a composite cross based upon 'Cornerstone' male-sterility. The composite was established by crossing seven Australian wheats to a homozygous male-sterile 'Cornerstone' stock. It was propagated through seed harvested from steriles only in the F_2 and subsequent generations.

Two composite populations were grown concurrently. A 'Random' series was propagated through seed from randomly chosen steriles while a 'Selected' series was propagated through the progenies of steriles less than 100 cm high selected for long heads and high spikelet number. In each generation 10 seeds from each 100 chosen steriles were used to establish the next composite population.

Height, number of tillers, and the headlength, spikelet number, grain number and yield of the longest head of each individual plant were measured in the first three generations of each series. Their fertility/sterility classification was also recorded. The ratio of fertiles to steriles departed from expected ratios and was probably caused by differential wind-borne pollen transmission. Significant differences in the average expression of some characters between fertiles and steriles occurred in the first composite generation, but the differences decreased in subsequent generations. The differences may have been caused by genes initially linked to the male-sterile (*Ms 1C*) locus. The correlations between characters changed significantly over three composite generations. The trends in correlations suggested that competition between fertile pollinators was intensif~~ying~~ied the association of characters which favoured pollinator effectiveness such as height and high numbers of florets per plant.

The yields of bulked progenies of fertiles from the first seven generations of each composite series did not have any significant trend and were significantly less than the best parents and commercial check varieties. Therefore visual selection of male-sterile parents in each generation was ineffective. Selection of S_0 fertile plants for

The method
used for

morphological characters and yield components to increase yield ~~was~~ were either ineffective or of ~~so~~ little value ~~that it would be an inefficient~~ as a selection procedure.

Comparison of the yields of some S_0-derived S_2 lines with parents and S_1 and S_2 bulks demonstrated that S_2 progeny testing of individual S_0 fertile plants would identify high-yielding S_0-derived families. This would probably be an effective selection procedure. The best S_0-derived families could be reselected in later near-homozygous generations or used to reconstitute composite populations in a recurrent procedure.

After three cycles of outcrossing in the composite cross, 90 $F_3(S_2)$-derived F_5 families were derived from the Random and Selected series and the distributions of their yields were compared at three sites with a Control population of F_5 families derived directly from the seven F_1s which were used to construct the composite populations. The means of the distribtions of the populations did not generally differ greatly at each site. The most obvious aspect of the results was the presence of high-yielding 'tails' in the Random and Selected distributions which contained lines equal to or significantly exceeding the highest yielding parents and commercial checks. Sister-lines occurred ~~so~~ frequently in these 'tails' at each site that an analysis of probabilities suggested that intermating and recombination within the two series of composite crosses had generated S_0 genotypes from which high-yielding S_2-derived families had descended. None occurred in the 'Control' sample of equal size.

Samples from the extremes of the distributions of F_5 lines were compared in the next year as F_6 lines. The high-yielding 'tails' and strong correlation of sister lines were again evident, especially in the Selected series.

A small sample of the highest yielding lines were compared with some of the highest yielding parents and commercial checks for two more seasons. Some lines were consistently higher yielding, but unsuitable for commercial production in Australia because of red grain colour and unacceptable associations of quality characteristics. Strong correlations of quality characteristics also occurred within sets of F_3-derived sister lines.

It was concluded from the experimental programme that composites based on 'Cornerstone' nuclear male-sterility in which outcrossing is enforced for a few generations would be a useful component of a wheat improvement programme. They would generate useful variation which could be identified if the composite were partitioned into families derived from S_0 individuals or early-generation segregants.

STATEMENT

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

I consent to this thesis being made available for photocopying and loan if applicable if accepted for the award of the degree.

IAN D. KAEHNE
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1. INTRODUCTION

Many procedures have been proposed for breeding wheat and other autogamous species (FREY, 1975). It is unlikely that a comprehensive comparison of the various procedures will be achieved because of physical constraints. Therefore, in studies which compare breeding methodologies many procedures must be excluded after arbitarily choosing *a priori* those procedures which will be used in a particular study. In this study the improvement of wheat by composite crosses based on 'Cornerstone' male-sterility (DRISCOLL, 1977, 1978) focusses attention upon bulk breeding methods, selection in early segregating generations and F_3 progenies within F_2-derived families. In the latter method, a large experiment compared the F_3 progenies derived from the composite with equivalent derivatives from two-parent crosses. The composite population was propagated through the progenies of male-steriles only. Within these physical restraints, this study reviews the relationship between composite crosses and other breeding methods and investigates the efficiency of using a composite cross based on 'Cornerstone' male-sterility as a component of wheat improvement.

2. LITERATURE REVIEW

2.1 Introduction

The fundamental purpose of using male nuclear male-sterility in wheat composites is to increase outcrossing in each generation and thereby create a large number of recombinants between the parental genomes. FREY (1975) emphasised that composites involving enhanced outcrossing should generate greater genotypic variation in inbreeding species which, in turn, would assist crop improvement if associated with effective methods of selecting superior homozygous genotypes.

In this review I will survey crop improvement methods from the perspective of using composite crosses based on male-sterility for the enhancement of outcrossing and I will define the role and potential of composites in wheat breeding. Commencing with breeding methods characterised by minimal outcrossing and selection within inbreeding progenies I will proceed to methods involving increasing emphasis on outcrossing and broad parental bases, in which the creation of variation and selection are attempted simultaneously. I will emphasise the effect of this progression of methodologies on the genetic structure of the breeding populations and the effectiveness of selecting new homozygous genotypes with improved yield.

2.2 The Prediction of the Yield of Crosses from Parental Performance

The initial problem for the breeder of an autogamous species in which there is a large array of potential parents, such as wheat, is the choice of those parents which will give the greatest gain. Usually the number of parents chosen and the number of two-parent crosses made is a small portion of the total possible number. If the performance of a variety were a reliable indicator of its potential as a parent, the breeder's chance of success could be improved. His breeding strategy would primarily involve yield trails (ia) to choose parental varieties and emphasis upon comparing hybrid families from two-parent crosses would be reduced.

Undoubtedly the occurrence of high-yielding arrays in progenies of high-yielding parents (BROWN, WIEBEL AND SEIF, 1966; DYCK and

BAKER, 1975) reflects the common practice of using adapted high-yielding varieties as a major part of a parent set, but it does not assist the breeder to identify those poor yielding varieties with high potential as parents (BUSCH, JANKE and FROHBERG, 1974; GYAWALI, QUALSET and YAMAZAKI,1968; HARLAN, MARTINI and STEVENS, 1940; STUTHMAN and STUCKER, 1975; WHITEHOUSE, THOMPSON and DO VALLE RIBEIRO, 1958). Low yielding parents can have high general or specific combining ability in early generations (F_1 and F_2) and produce high-yielding segregants in later generations. It is probable that many potentially valuable parents are never used because their poor adaptation or yield precludes them from small sets of chosen parents. Poor yielding parents will not be commonly used unless procedures are developed to expeditiously introduce them into breeding programmes and reliable methods are derived to efficiently identify and select high-yielding families and segregants from their descendants.

Introducing genes from many parents into a breeding programme by using nuclear male-sterile parents is one relatively fast method of generating individual two-parent crosses or composites for yield assessment, selection and continuing recombination. Emphasis can them be moved from the restrictions imposed by a small set of parents to methods of identifying high-yielding families and segregants.

2.3 Using Bulked Progenies of Crosses to Identify Useful Parents and Crosses

A simple method of gaining information on the genetic value of a parent is measurement of the yield of the F_1 and bulks of the subsequent generations. However, in wheat considerable heterosis is usually expressed in the F_1 but is less pronounced in the F_2 and later generations (BHULLAR, GILL and KEHRA, 1979; BUSCH, LUCKEN and FROHBERG, 1971; LUPTON and WHITEHOUSE, 1957). Also, the magnitudes of heterotic effects and the rates of inbreeding depression significantly differ between crosses (CREGAN and BUSCH, 1978). Consequently the unknown effects of heterosis in any cross seriously reduce the effectiveness of using F_1 yields to identify superior crosses. In oats, SAMPSON (1972) concluded F_1 yields did not predict the F_2 and F_3 yields in 21 crosses. SIKKA, JAIN and PARMAR (1959) found in 12 wheat crosses there were considerable changes in rank of some crosses from the F_1 to the F_3.

The yields of bulks of the F_2 and succeeding generations are a more reliable indicator of high-yielding crosses (CREGAN and BUSCH, 1977; HARRINGTON, 1940; IMMER, 1941) but they may also be questionable because of year to year variation of the relative yields of bulks (LUPTON and WHITEHOUSE, 1957). They do not indicate the magnitude of segregation in later generatons (LUPTON, 1961). The relative yields of F_3, F_4, and F_5 bulks of all possible crosses between ten winter wheats studied by FOWLER and HEYNE (1955) did not predict the crosses from which the highest proportion of superior segregants were obtained. Therefore, superior genotypes may remain undetected within advanced bulks which are approaching homozygosity. A sampling procedure within the bulks is required to identify the highest-yielding segregants.

Competition between individual plants within a bulk strongly affects relative fitness and may change the frequency of particularly high-yielding segregants. TEE and QUALSET (1975) found increased height from the F_3 to F_6 in one of two wheat crosses and BUSCH and LUIZZI (1979) reported a shift towards tallness from the expected proportion of semi-dwarf plants in an F_5 bulk of spring wheat. Such shifts and competitive effects in homogeneous populations may affect the frequency of the genotypes with highest yield, but their selection is probably not precluded by elimination through competition.

Although it may be argued that bulk testing of progenies may not indicate the cross from which the highest yielding segregant would be obtained, a strong case can be made for the use of early generation bulk progeny tests to estimate parental general and specific combining abilities. Consequently, bulks may predict those families from which it is most likely to obtain high-yielding advanced generation bulks and inbred lines (BHULLAR, GILL and KHEHRA, 1979; BUSCH, HAMMOND and FROHBERG, 1976; BUSCH, JANKE and FROHBERG, 1974; CREGAN and BUSCH, 1977). Generally in these studies the F_1 was the least reliable indicator, but the F_2 and succeeding generations had acceptable predictive value. Most studies are based on a small set of parents in the initial diallel set. It could be argued that the indicated value of early-generation bulk testing is strongly biased by the members of the parent array. The array should be sufficiently large to remove bias introduced by the parent samples. Therefore, the strongest case for the predictive value of early-generation bulk yields is possibly presented by HARLAN *et al* (1940) who found in a 28-parent diallel of barley that the crosses which produced the highest proportion of outstanding selections were those with the highest yielding bulks.

Nuclear male-sterility presents the opportunity to efficiently create a large array of crosses by crossing known parents over a set of male-sterile lines or creating a panmictic population in which seed is harvested from open-pollinated male-steriles. These proce~~e~~dures would provide an extremely large array of indiviuals which may be regarded as F_1's. (If the panmictic population has been propagated for more than one generation the designation S_0, by convention, would be more precise than F_1). In a study with soybean, LEFFEL and HANSON (1961) concluded that bulk testing early generations derived from individuals resulting from extensive cycles of intermating would identify families from which the most desirable segregants would be obtained. In wheat crosses and composites a similar procedure could be followed. The F_1 and subsequent bulk progenies of a given male-sterile female could assess the parental value of that female (and the male pollen donors, if identified). Bulks could also be derived from F_1 (S_0) and subsequent generations. In yield trials high-yielding families could be identified from which high-yielding segregants may be obtained, provided that the early-generation bulks have significant predictive value.

The high numbers of F_1 or S_0 individuals which can be produced using nuclear male-sterile females, especially in panmictic composite populations, permits a larger number of S_0-derived families to be compared than would be expected from a conventional crossing programme. The eventual variance of inbreds within the highest yielding bulks is not indicated by a bulk's performance and it would be beneficial to identify as early as possible not only the early-generation bulk families which are high-yielding, but also those segregants within bulks which will produce high-yielding lines in later generations. It is important in a programme based on a potentially large number of F_1 (S_0)-derived lines to remain focused upon testing for difference between a large number of S_0-derived families rather than upon differences between inbred segregants within a few families.

2.4 The Effectiveness of Selection Within Early Generations of Inbreeding

The rapid fixation of genotypes during inbreeding would suggest that a high proportion of desirable genic association reponsible for high-yielding homozygous segregants should be fixed in the homozygous condition in discrete subfamilies by the F_3 and F_4 (S_2 and S_3) generations. HARRINGTON (1937) proposed sampling an F_3 bulk population and testing the F_4 progenies to identify high yielding subfamilies.

Partition at the F_2 or F_3 also permits an estimate of the variance within a family. Total reliance upon early-generation bulk yields may result in the rejection of bulks containing high-yielding segregants. ATKINS and MURPHY (1949) found in oats that high-yielding F_6 and F_7 segregants could be derived from low yielding F_2 to F_6 bulk progenies. LUPTON (1961) extended his prediction of cross performance from F_1 and F_2 bulks by growing F_3 and F_4 progenies of randomly selected F_2 plants. He found that this breeding procedure which he named the 'F_2-progeny method" not only identified the F_3 and F_4 families expressing segregation for high yield, but also high-lighted the importance of the variance of the F_2-derived families in obtaining high-yielding segregants from F_1 and F_2 bulks. A variation of the F_2-progeny method was described by BREAKWELL and HUTTON (1939) and named by LUPTON and WHITEHOUSE (1957) the 'pedigree-trial system'. In this system a subfamily was carried forward through a selected individual while its sister plants were used for field trials. This procedure is only effective if there are high genotypic correlations between all individuals in the subfamily.

In wheat, SHEBESKI (1967) found significant correlations of the ranks of F_3 and F_4 bulks derived from single F_2 plants and proposed that early-generation (F_2) selection enabled a higher chance of detecting families carrying desirable genes in either the homozygous or heterozygous condition. The number of desirable genes retained in a given proportion of the F_2 population is approximately twice the number retained in the same proportion of the F_4 and subsequent populations because of the higher frequency of heterozygotes in the F_2. However, SHEBESKI (1967) emphasised that large populations are necessary, even in the F_2, to retain a small number of independent desirable genes. O'BRIEN, BAKER and EVANS (1978) found greater gains could be achieved for equal effort by selection between F_3 lines rather than selection at F_5 within F_3's. SNEEP (1977) also supports Shebeski's argument and recommends F_3 yield trials of F_2 progenies to increase the chance of retaining desirable alleles. He suggests that multiple crosses before choosing F_2 plants would not be significant because increasing the number of desirable genes decreased the chance of detecting families carrying those genes. He did not allow for the greater opportunity for recombination between many contributing genomes before inbreeding and the consequential higher chance of obtaining recombinants between desirable genes at non-independant loci.

A number of studies have shown that F_2-progeny testing may not always have high reliability, but other methods such as pedigree, single-seed descent or selection within advanced lines have not generally been superior. BRIGGS and SHEBESKI (1971) found discouraging ranking relationships between F_3 and F_5 yield but they found the 'best' yielding lines in F_5 were derived from the highest-yielding F_3 lines. Therefore, the early-generation selections of greatest potential would possibly be retained although line x year interactions are significant. WHAN, RATHJEN and KNIGHT (1981) also found poor correlations between F_2 to F_5 generations in F_2-derived families and they suggested that year to year interactions and heterozygosity in early generations restrict effective F_2-progeny testing to only some crosses. However, selection for yield from later generation bulks was not more effective (WHAN, KNIGHT and RATHJEN, 1982). The later generations would be expected to contain high-yielding homozygous segregants but they occur at such low frequencies that the highest yielding lines detected are no better than those isolated from high-yielding F_2-derived progenies. KNOTT and KUMAR (1975) found an F_3-progeny scheme equivalent to single-seed descent for detecting high-yielding wheat lines but the F_3-progeny scheme reduced the frequency of low yielding lines in advanced generations. In soybean, BOERMA and COOPER (1975a, 1975b) and IVERS and FEHR (1978) also found the F_2-progeny method equivalent to bulk, pedigree and single-seed descent methods.

The efficiency of early-generation selection is not increased by selection between individual F_2 plants (DePAUW and SHEBESKI, 1973; KNOTT, 1972; McGINNIS and SHEBESKI, 1968). HAMBLIN, KNIGHT and ATKINSON (1978) concluded single plant selection was ineffective in barley because of genotype x year interactions caused by competitive interactions in the population of selected single plants (HAMBLIN and DONALD, 1974). However, the relative frequency of high-yielding F_2 plants and bulk F_2 performance in a 6-parent barley diallel permitted ST-PIERRE and JENSEN (1972) to detect crosses which produced high-yielding segregants. Visual selection of individual early-generation plants is also ineffective, but visual selection of individuals within visually superior populations may be better than random choice (BRIGGS and SHEBESKI, 1970; THAKARE and QUALSET, 1978).

A serious deficiency of testing early-generation subfamilies is the inability to predict the genotype x environment interaction of a single inbred homozygote from the performance of its bulk progenitor family. Where early generation bulks are unreliable there is strong justification for the single-seed descent method of selection (KAUFMANN,1971; KNOTT, 1979). JINKS and POONI (1981a) argued that selection between inbreds should be delayed until near homozygosity to avoid the effects of residual heterozygosity in early generation individuals. They found family selection at the F_3 useful for identifying the progenitors of high-yielding inbreds. They had argued earlier (JINKS and POONI, 1976) that at the level of crosses there is no reason to go beyond the F_2 of an inbreeding programme without a reasonably clear idea of the value of a cross. If this is so, the genetic interaction ultimately responsible for high-yielding inbreds must be strongly reflected in the very heterozygous F_2 bulk. However, breeding experience would suggest advancement to F_3 lines to gain an estimate of within-cross variance is useful (LUPTON, 1961).

The genetic interactions responsible for the phenotypic expression of high yield in successive generations of an inbreeding family will undoubtedly be complex and specific to that family. Consequently, unequivocal results have not been forthcoming from comparative studies of breeding strategies (MAYO, 1980) due to the lack of theory to predict the genotype x environment interactions in inbreeding families and the changes in genetic interactions from early to late inbreeding generations. BUSCH, LUCKEN and FROHBERG (1971) found both simple and complex interactions responsible for high-yielding segregants in three wheat crosses. Simulation studies have demonstrated the strong effects of relatively simple genetic interactions. For example, SNAPE and RIGGS (1975) demonstrated that different interactions produced different distributions in F_2 populations yet, near homozygosity, the F_6 distributions were similar. Consequently, selection of F_2-derived lines may choose families which do not have a greater chance of producing superior inbreds. Simple interactions may also produce skewness in the distributions of inbreds derived from an F_1 (FISHER, IMMER and TEDIN, 1932, MATHER, 1943). Complementary and duplicate interactions may cause positive and negative skewness respectively (CHOO and REINBERGS, 1982; POONI, JINKS and CORNISH, 1977; JINKS and POONI, 1981b; SNAPE and RIGGS, 1975) and kurtotic effects may result from genetic interactions and linkage disequilibria (CHOO and REINBERGS, 1982; JINKS and POONI, 1981b).

Mass selection in early generations has been successfully used to select for characters with high heritability (CHANDHANAMUTTA and FREY, 1973; FREY, 1967; ROMERO and FREY, 1966). CASALI and TIGCHELAAR (1975) demonstrated by simulation that high heritability assisted mass and pedigree selection but single-seed descent was superior for characters with lower heritability, such as yield. They did not simulate the F_2 progeny or similar methods but the ineffectiveness of single plant selection in the F_2 for yield in wheat indicates the ineffectiveness of mass selection for yield in early generations.

In summary, partitioning inbreeding families in early generations and yield testing subfamilies has been found a reliable method of detecting progenitor families of high-yielding segregants. At the genic level this method has a higher chance of retrieving useful genes and identifies at an early stage subfamilies carrying useful genetic interactions. The efficiency of selection may be decreased if genetic interactions responsible for high yields in early generations are lost as inbreeding proceeds. A further deficiency is the lack of predictablity of genotype x environment interaction of ultimately selected inbreds. Nevertheless partitioning, particularly the 'F_2-progeny method' has been found equivalent or superior to other breeding methods. Its principle advantages have been to overcome the ineffectiveness of mass or visual selection between individual F_2 or F_3 plants and estimate the yielding potential and variance within a cross by the F_3 generation to enable early rejection of inferior crosses and subfamilies.

In wheat crosses and composites based upon outcrossings of nuclear male-sterile females, emphasis could be moved from partitioning a relatively small number of crosses into F_2-derived families to partitioning large arrays of crosses or selections from panmictic populations into F_1 (or S_0-) derived families. The best families, which are equivalent to cross bulks could be further partitioned into F_2-(or S_1-) derived subfamilies to detect the inbreeding lines most likely to produce high-yielding inbreds.

2.5 Composite Crosses in Plant Breeding

The Effectiveness of the Composite Cross Breeding Method

Composite crosses of autogamous species are populations formed by mixing derivatives from more than one cross and maintaining the population by growing successive generations of seed. The conceptual basis ~~of~~ for using composite populations of crosses between inbreds is the enlargement of the pool of variability beyond that of a bulked single cross and simultaneously achieving a higher level of heterozygosity and heterogeneity than is possible by mixing the parental inbred lines (SUNESON and STEVENS, 1953). A significant level of outcrossing between individuals within the composite is also usually implied. The methods of establishing composite cross are varied. They are exemplified by SUNESON and STEVENS (1953) who established six composites by mixing F_1's in a bulk, bulking multiple crosses of F_1's, multiple crossing an array of parents until one F_1 was achieved, and crossing parents onto a common male-sterile parent. The initial concept of composite crosses implied natural cross-pollination within the population. The concept has been enlarged to embrace varying degrees of control or selection upon the parent plants which will contribute seed to the next generations and manipulation of the parent plants to enhance the level of hybridization within the composite (SUNESON, 1945; DRISCOLL, 1981).

The usefulness of composite crosses in plant improvement is determined by their capacity to produce a bulk or derived selections which exceed the yield of both the parents of the composite and commercially grown varieties. The results from early barley composites were inconclusive. In Composite Cross II (CCII) SUNESON and STEVENS (1953) found after twelve generations no random selections outyielded the check 'Atlas'. Only after about twenty generations did the composite bulk exceed the yield of 'Atlas'. Therefore, the composite method may be considered effective but other breeding methods might have been expected to produce lines exceeding 'Atlas' in less time. The method of establishment of composites affected their rate of yield increase. CC II had been based on the bulk of a large diallel of 2-parent crosses containing both adapted and unadapted agents. In three other composites (CC V, CC XII, and CC XIV) the yield exceeded CC II in early generations and they achieved equivalence with 'Atlas'in ten to twelve generations (SUNESON, 1956). These composites were based on a multiple cross, crosses to a common F_1 of known parental worth, and adapted varieties crossed with a nuclear male-sterility factor included in the population to enhance outcrossing. The efficiency of composite-based plant improvement therefore, increased if the parentage was narrower, contained a high proportion of adapted lines with known parental value and the chance of recombination between the parental genomes was increased by multiple crossing or male-sterile assisted outcrossing. Increasing yields during successive generations of a composite are not axiomatic.

In field beans HAMBLIN (1977) found no increase by F_6 in a composite based on high-yielding lines.

Most barley composites eventually stabilised for yield and some exceeded the best commercial varieties but individual lines selected from composites seldom exceeded commercial checks. The interactions within composites are complex; the advanced generation bulks have higher yield stability than their component lines and resynthesis of a bulk from a sample of its components may not reproduce a population with stability and yield equal to the sampled composite bulk (ALLARD, 1967). LOHANI (1976) found that a composite (CC XVI) based on selections from earlier composites did not increase yield and he concluded that a similar yield limit occurred in many composites after natural selection even though the diversity of initial parentage may influence the rate of yield increase in early generations. Therefore, composite crosses which rely upon natural selection and natural outcrossing, even when assisted by male-sterility, are generally an ineffective breeding strategy. Those having high yield are identified only after about ten generations and selections from them are usually inferior to both the bulk and commercial check varieties.

The Genetic Effects in Composite Crosses

The phenotypic associations of characters can change significantly during the propagations of a composite (BAL, SUNESON and RAMAGE, 1959). In CC V increased yield was correlated with increased fitness determined by seed number per plant (JAIN, 1961).

A prominent genetic characteristic of composites is the maintenance of a higher level of heterozygosity than expected after many generations of inbreeding at very low levels of natural outcrossing. For example, JAIN (1961) found heterozygote frequencies of 10 to 13 percent at some loci after 18 generations. Consequently composites probably contain a high proportion of heterozygosity which contributes to their fitness as a population, but reduces the chance of extracting high yielding inbred segregants from them. Heterozygosity is maintained during inbreeding at loci in which homozygotes are at a disadvantage (HAYMAN and MATHER, 1953).

The selective forces within composite crosses can also produce strong gametic phase disquilibria. ALLARD (1977) detected significant disequilibria between four loci in early generations of two composites and found they increased to 50% and 80% of the theoretical maxima by advanced (26th and 41st) generations. Consequently it is reasonable to conclude that strong selective forces act within composites to generate and maintain a co-adapted population of genotypes which interact to raise the population fitness to a stabilised level. Consequently reconstituting a composite population from a sample of its components would not be expected to achieve the yield level of the sampled composite until the optimum interactions are restored. Furthermore, it is most unlikely that inbreds derived from partially heterozygous individuals contributing to the fitness of a heterogeneous composite population would be expected to produce high yielding homzygotes when grown in a homogeneous population.

The Theoretical Consequences of Outcrossing in Composite Crosses

Composite crosses may appear an attractive method to produce new recombinations of many alleles and generate improved genic combinations but the genetic consequences of the composite cross procedure may be inimical to the plant breeder's aim of isolating superior inbred recombinants.

ALLARD and HANSCHE (1964) considered the consequences of a number of factors on the likelihood of desirable alleles being retained in and selected from gene pools created by composite crosses. In a composite of many parents, desirable alleles carried by a few parents occur at an initially low frequency. If such a composite is propagated through a small number of parents the most frequent (and possibly least desirable) alleles will tend to become rapidly fixed in the population and, conversely, the desired alleles will be lost. For example, if an allele at initial frequency 0.1 and no advantage (W++ = W+- = W-- =1.0) were propagated through 10 parents per generation (N = 10), 51% are expected to be lost, even with random mating, by the fifth generation.

The loss through drift is reduced if the parent population is increased but at N = 50, 18% are still [illegible] lost. ALLARD and HANSCHE extended this model to more complex initial allelic arrangements but generally found with small parent populations that fixation occurred in 10 to 20 generations, genotypic response was erratic and that greater advance was only possible by intercrossing better fixed lines or using higher values of N. A close similarity of results between random mating and only 5% outcrossing were maintained throughout their study and linkage effects (r = 0.1 and 0.5) were relatively unimportant.

The implications of these results are serious in composites with many parents. Although a breeder may wish to create extremely diverse gene pools with a wide parental base, it is doubtful whether a high proportion of the rarer alleles are retained unless the population size is large. An alternative strategy involving many composite with smallar parent sets concurrently selected and maintained through a reasonable large parent populations (N = 100) in each composite may retain a higher proportion of a given allele and also identify the parent sets with greatest potential.

Outcrossing permits the retention of heterozygotes in a population. Without heterozygote advantage in a large population, their frequency (f_H) [illegible] is given by:

$$f_H = 2\ pq\ (\frac{2t}{1+t})$$

Where p,q = initial frequencies of two alleles at a locus
t = proportion of outcrossing

It is seen that when t approaches 1, f_H is high and determined by initial frequencies but when t approaches 0, f_H is trivially small and heterozygote advantage ($W+- > W++$ and $W+-$) is necessary to maintain a significant level of alleles in heterozygote loci in a population (ALLARD, JAIN and WORKMAN, 1966). When heterozygous selective advantage is high equilibria may be reached in a few generations. In lima beans ALLARD and HANSCHE (1964) estimated the selective values at 3 loci (parental segments) in the heterozygous condition were twice either homozgote ($W+- = 1.0$, $W++ = W-- = 0.50$)

and with 5 % outcrossing equilibria were reached in 4 to 5 generations. Strong heterozygote advantage was also detected in barley JAIN (1960). Because intermediate expressions are most common in barley for a number of fitness components, JAIN (1966) suggested that an excess of repulsion phase linkage disequilibria may be responsible for heterozygote advantage in composite populations. It seems reasonable to assume that a similar structure of heterozygote advantage could be found in wheat composites.

The means and variances of a number of fitness traits in composites generated either by natural outcrossing (ALLARD and JAIN, 1962) or outcrossing enchanced by male-sterility (JAIN, 1966) suggest that composite populations move to a genetic architecture with heterozygous families near the population mean. The residual heterozygosity in families after many generations suggests that homeostasis may be operative (LERNER 1954) or intermediate phenotypes may be fittest, irrespective of levels of heterozygosity.

In summary, the probable genetic structure of composites is a population of relatively heterozygous individuals maintained in that state by heterozygote advantage even though natural outcrossing may be quite low. The heterozygous advantage may be associated with repulsion phase linkage disequilibria and intermediate values for fitness components. The population probably achieves its overall fitness by complex interactions which arise through strong selective forces in the early generations of propagation. The selective forces probably eliminate many alleles through genetic drift and erosion if the composite is propagated through a small number of parents. The fate of any allele is therefore strongly dependent upon the fitness and competitive ability of the genotypes in which it occurs.

Inter-plant Competition in Composites and Bulks

The fitness of an individual in a heterogeneous composite or bulk population is not usually determined by alleles and genotypes which produce high yielding homozygotes in monoculture. ALLARD and ADAMS (1969) cite an example of 2-row types becoming fixed in a barley composite although six-row pure line selections were superior. Plant height is a strong determinant of competitive ability. In rice, competition dependent upon height may eliminate the most desirable high-yielding dwarf genotypes (JENNINGS and AQUINO, 1968). KHALIFA and QUALSET (1974) found a tall genotype, which is low-yielding in monoculture, increased in frequency in a bulk mixture with a high yielding dwarf variety and reduced the yield of the bulk. Furthermore, the competitiveness of the two genotypes were frequency dependent but changed in opposing ways. Decreased frequency favoured the tall variety but disadvantaged the short.

Although the effects of frequency dependence are only measureable and meaningful in mixtures where the competitors are identifiable, it is reasonable to assume that an analogous process may ~~be~~ occur~~ing~~ in a segregating bulk population. However, the magnitudes of frequency dependence and fitness will differ between families of segregants (PHUNG and RATHJEN, 1976). The frequency dependence and fitness or parents in mixtures will probably not be of predictive value in bulks of crosses between those parents. KALIFA and QUALSET (1975) found in a wheat cross between a low-yielding tall variety and a high-yielding dwarf that dwarf genotypes were eliminated but the bulk yield increased and intermediate height segregants exceeded in monoculture the yields of both parents. ALLARD and ADAMS (1969) argued that if the frequency of heterozygotes in a population is inversely related to their reproductive success they would be maintaine~~e~~d indefinitely even when outcrossing is very infrequent.

Competition between individuals in bulks has a significant effect upon estimating genetic parameters and therefore estimates made in bulks probably have little predictive value for pure line isolates from the bulk (HAMBLIN and ROSIELLE, 1978).

In summary, competition between the individuals in a composite population may eliminate or reduce the frequency of desirable alleles and genotypes. The interaction of competition with frequency of genotypes and with the level of heterozygosity also bring into serious question the usefulness of composites as sources of superior inbred segregants, particularly if the composite is propagated for many generations.

Utilizing Nuclear Male-Sterility in Composite Crosses

SUNESON (1945) proposed using nuclear male-sterility in composite crosses for barley improvement. He suggested crossing fertile parents to a homozygous male-sterile and harvesting in the F_2 and a few subsequent generations only steriles to generate more recombinants between the parents than would occur by natural outcrossing. In two barley composites containing a nuclear male sterility factor, CC XIV and CC XV, the progenies of all plants, both fertile and sterile, were bulked in each generation (JAIN and SUNESON, 1963). The proportion of male-sterile (*ms ms*) individuals declined but the rate of diminution was slower than expected without selection. JAIN and SUNESON deduced from the percentage seed-set on steriles that outcrossing and the consequent maintenance of heterozygosity would be significant while the frequency of male-steriles was about 0.10 to 0.20. In these composites this condition pertained for five to ten generations indicating that male-steriles were being retained at a higher frequency than their initial frequency and relative seed-set would suggest. JAIN and SUNESON (1964) proposed that an increase in the outcrossing rate of male-steriles as they become rarer contributed to their prolonged retention. After five to ten generations the effectiveness of the male-sterile factor was marginal and almost equivalent to natural outcrossing. Consequently, harvesting the progenies of both fertile and sterile plants into a bulk in a composite containing a male-sterility factor quickly reduces the level of heterozygosity from that which would be achieved if only steriles were harvested.

Propagation through a bulk of all plants or bulk of progenies of steriles only produced different outcomes in barley. JAIN and SUNESON (1966) found the between- and within-family components of variability were greater in a series of populations generated only through the progeny of outcrossed male-steriles than in populations generated by outcrossing levels approaching natural outcrossing without assistance from male sterility. However, the mean fitness of the continuously outcrossed series was lower. They concluded that the higher rates of recombination and greater levels of heterozygosity achieved with continuous outcrossing facilitated by male-sterility do not translate into increased fitness in a bulk-propagated outcrossing composite cross.

In an outcrossing series, JAIN (1966) found that in addition to increased levels of heterozygosity there were greater levels of genetic polymorphism. The selective values of segments at given loci were significantly influenced by the method of propagation and character associations did not develop as in the selfing series of CC II and CC V (BAL, SUNESON and RAMAGE, 1959). This suggests that continuous out-crossing causes disruption of linkage associations.

If male-sterility were to promote the formation of multiple heterozygotes with fitness advantage, then in composites maintained for many generations with a low level of outcrossing a few multiple heterozygotes may be expected. However, JAIN and QUALSET (1976) observed that the frequency of individuals heterozygous at many linked loci decreased with increasing numbers of generations. Therefore, the role of genetic polymorphisms in composite crosses, while undoubtedly of adaptive significance, is not understood (JAIN, 1971).

The enhanced level of outcrossing permitted by nuclear male-sterility in composites probably increases the rate of genetic drift beyond the high levels observed in composites having a low outcrossing level (ALLARD and HANSCHE, 1964). Consequently, relatively long segments of intact parental genome could be lost while other segments with genes of high selective advantage rapidly increase their frequency in the population. Therefore, male-sterility may assist strong selective forces, eliminate gene segments and preclude their role in enhanced recombination.

In composites propagated through the progeny of male-steriles strong selective advantage would be expected for genes determining high pollen donation and female receptivity. Loci linked to those genes may therefore, be affected by undesirable genetic drift. Selection between male-steriles for seed set or other traits would introduce another opportunity for a change of gene frequency. Therefore, the best management strategy for maximising recombination and minimising genetic drift in a composite may be controlled outcrossing between a large number of randomly chosen pairs of parents. Even at this level of control it would be likely that non-random assortment would occur because of non over-lapping periods of pollen production and stigma receptivity in some pairs.

Assortative matings between individuals with overlapping periods of maturity probably will decrease genetic variation, promote associations between characters and increase the frequency of homozygosity at loci linked to those determining maturity time (BREESE 1956; GREGORIUS 1980a). If assortative mating is only partial, genes which are not completely linked will tend towards independent association. However, at a relatively low assortative rate and with moderate linkage values, the effect of assortative mating can be significant for many generations (GREGORIUS, 1980b).

Although the use of male-sterility to enhance outcrossing and recombination seems an attractive method for increasing the effectiveness of composite crosses there is no evidence that the chance of selecting high yielding inbred derivatives is increased. On the contrary, the evidence suggests an intensification of processes leading to an interacting population of more heterozygous genotypes which maintain a stable fitness level unable to increase to levels equivalent to well adapted parental varieties.

SUNESON (1945) ~~had~~ proposed two al~~ternative~~ ways of using male-sterility in population improvement; composite crosses including male-sterility which are propagated for many generations or pedigree selection 'after about three seasons of continuous random natural crossing'.

A population propagated similarly to the second alternative is the basis of the experimental programme reported in this dissertation. DRISCOLL (1981) described its establishment. The composite involves a γ-ray induced nuclear male-sterile stock, 'Cornerstone', and seven other parental varieties. Three cycles of outcrossing and propagation of the composite through seed harvested from selected steriles only is followed by random inbreeding within families to obtain near homozygous segregants for yield trials. DRISCOLL proposes such 'managed' composites, with selection of steriles only at each cycle, as method of accumulating minor genes which contribute to particular characters. DOGGETT (1968) named the process of selecting steriles only from a composite 'female choice' selection to differentiate it from mass selection which could include the progenies of both sterile and fertile plants. The use of male-sterility to impose a short series of outcrossing before reverting to a conventional selection programme within inbreeding families differs fundamentally from the evolutionary concepts proposed by SUNESON (1956). In the former, emphasis is placed upon maximising recombination and imposing selection simultaneously for a limited period while in the latter natural selection and outcrossing (with or without assistance from male-sterility) are relied upon to effect population improvement after a relatively large number of generations.

The overall conculsion of this review is that composites reliant upon natural selection have been an ineffective means of generating higher yielding bulks or inbred derivatives. They have tended to rapidly evolve a complex interactive genetic structure from which the chance of extracting superior inbreds is less than that in conventional two parent crosses. DRISCOLL'S proposal again focuses attention upon enhanced recombination, but attempts to minimise natural selection and maintain deliberate selection for desirable agronomic characters.

2.6 Factors affecting Seed-Set on Male-Sterile Wheat Plants

The utilisation of male-sterility in wheat composites is dependent upon sufficient levels of cross-pollination on sterile plants. Fertilisation of all steriles is also desirable to minimise the genetic drift of desirable alleles linked with those causing low seed-set. The percentage of florets fertilised on male-sterile wheat plants pollinated by wind borne pollen is less than on fertile pollinator plants. In wheat, KHERDE, ATKINS, MERKLE and PORTER (1967) reported a range of 2% to 61% and JOHNSON and SCHMIDT (1968) 46 to 82%. If similar variation occurred in wheat composites, considerable genetic drift would occur and increase the risk of losing alleles associated with low seed-set. The drift could be counteracted by randomly selecting equal numbers of seeds from each fertilised male sterile.

Factors in both the sterile and fertile pollinators determine the level of cross pollination. De VRIES (1971) suggests that the opening of glumes, the duration of opening of a floret, the awness of the lemma and the size of the stigma all influence the degree of fertilisation on male steriles. The extension of the stigma beyond the lemma and palea (WILSON, 1968) and the duration of receptivity of the stigma (IMRIE, 1966) are probably also important factors.

The pollen shedding capacity of fertile pollinators is also determined by many factors. De VRIES (1971) suggested that pollinator effectiveness may depend upon the number of pollen grains per anther, dehiscence, the mass, density and dimensions of pollen grains and pollen viability. BERRI and ANAND (1971) found that in 22 wheat varieties anther size was correlated with pollen grains per anther and with pollen grains shed. Pollen shedding was also strongly correlated with filament length and plant height. JOPPA, McNEAL and BERG (1968) found percentage anther extursion, pollen grains per anther and tillers per plot accounted for 92 to 96% of variation in pollen shedding, which had a threefold variation within spring wheats. CAHN (1925) and KHAN, HEYNE and ARP (1973) also reported significant variation in pollen grains per anther in wheat. In BERRI and ANAND's data there is a strong suggestion that shorter filament lengths occur in many dwarf wheats and JOHNSON and SCHMIDT (1968) remarked that semi-dwarfs, as a group, shed less pollen than taller varieties. However, the data of BERRI and ANAND suggests that sufficient variation for filament length and higher pollen number per anther occurs in dwarf spring wheats to select for high rates of pollen shedding. Highly significant correlations between pollen grains per anther and anther length in spring wheat (De VRIES, 1974) would facilitate selection for pollen shedding by selection for the easily measured characters, anther length and extrusion. ATASHI-RANG and LUCKEN (1978) found significant general and specific combining ability effects for both anther length and extrusion in spring wheat.

The evidence from field studies contradicts the proposition that anther size and extrusion may be principal factors in improving pollen shedding. De VRIES (1972, 1973) found no simple relationships between anther extrusion and pollen contribution to the surrounding field from five spring wheats. GHIASI, LUCKEN and HAMMOND (1982) did not detect a significant change in the frequency of anther extrusion in a bulk population carrying a cytoplasmic male-sterility factor after four cycles of selection, yet anther extrusion was increased by direct selection.

The level of cross pollination depends upon synchronization of pollen release with stigma receptivity. De VRIES (1973) found the duration of pollen release varied form approximately 4 to 19 days be~~tween~~ for five spring wheats. Environmental changes may differentially affect pollen donors (WELSH and KLATT, 1971). BITZER and PATTERSON (1967) observed maximum seed set on steriles flowering at peak pollen levels and exposed for 4 to 5 days, however, KHAN, HEYNE and ARP (1973) found a sterile exposed for one day had the same percentage seed set as continuously exposed checks. Therefore, one day of overlapping pollen shedding and stigma receptivity may be sufficient to achieve optimum seed set on a male sterile plant.

The relative height of a pollen donor and its distance from a receptive male sterile are possibly important factors in cross pollination in a composite population. De VRIES (1972) recorded higher pollen concentrations 20 cm below shedding heads than above them and pollen density declined rapidly more than 1m from the pollen source. The density gradients will be significantly skewed by prevailing winds (BITZER and PATTERSON, 1967).

In summary, in composite crosses of wheat considerable assortative mating between synchronously flowering fertiles and steriles and selective advantages for tall pollinators and the most receptive male-steriles are expected. The influence of anther size and extrusion is less certain, but in composites containing dwarf spring wheats there is the possibility of low pollen shedding from some parents. Other factors which may possibly affect the pattern of cross pollination are tiller numbers per plant, duration of flowering, glume tenacity, pollen grains per anther and environmental effects on pollen viability and stigma receptivity. All these factors could contribute to significant shifts away from random mating and cause considerable genetic drift. It is reasonable to except that unimpeded cross pollination would tend to increase the frequencies of tall pollinators with high pollen shedding capacity and male-steriles with a high receptive capacity. The most significant cause of genetic drift may be differences in seed set between male steriles. The frequencies of genes associated with low seed set would be expected to fall rapidly. This effect could be offset by harvesting equal numbers of seeds from each male-sterile. The differences in pollen donor effectivenss could be also reduced by paired crosses between donors and male-steriles but non-overlapping flowering periods prevent the complete correction of assortative mating between synchronously flowering plants. Intervention into natural cross pollination within a composite changes the purpose of the composition process away from the evolutionary viewpoint (SUNESON, 1956) and towards an emphasis upon recombination (DRISCOLL, 1981; SUNESON, 1945). However, higher degrees of intervention change the concept of composites from populations in which panmictic processes are inferred to an elaboration of diallel and multiple crossing.

2.7 The Relationship between Yield and Yield Components in Wheat

In Sections 2.3 and 2.4 it was concluded that selection for individual plant yield in the F_1 and the early segregating populations of a cross is ineffective. Selection for high expression of yield components is another avenue to achieve yield improvement provided that the expression of components in a plant is correlated with its yield.

If the expression of yield components in heterozygous individuals in early inbreeding generations were correlated with yield of homozygous progenies derived from the heterozygotes, then selection for yield components could precede progeny tests for yield. Significant correlations would be particularly useful in composite cross breeding methods to select plants for crossing or harvesting from within the composite population. If nuclear male-sterility is involved in the composite, characters other than seed yield per plant or head could be used to select male-sterile parents.

The association between yield and its components in populations of homozygotes

Plant yield is the result of contributions by many individual plant components. Reported studies have tended to include many characters, obviously to increase the chance of detecting the most indicative. The dilemma of choice is exemplified by comparing four studies in inbred lines. NASS (1973) and SYME (1972) measured 27 characters, 8 in common, and found only one, harvest index, signifcant in both studies. SYME found eleven other characters and NASS found two, yield per spike and grains per spike, significantly associated with yield. SCOTT, DOUGHERTY and LANGER (1977) found grains per spikelet, not considered by either NASS or SYME, useful in selection. In barley BRIGGS, FARIS and KELKER (1978) found grains per spike, grain weight, earliness and height reliable, but they did not measure harvest index or yield per spike. Overall, harvest index and components closely related to yield, such as yield per spike and grains per spike, may be the most useful.

The predictability of selection for yield by correlation with yield components is questionable. RASMUSSON and CANNELL (1970) found that responses to selection using components differed between two barley crosses and they suggested the reliability of characters may interact with environmental factors. ADAMS (1967) postulated it is difficult to establish optimum character criteria because of compensatory relationships between components which are expressed as negative correlations. Furthermore oscillatory compensation during component development, e.g. high spike number may reduce grain number which may in turn increase grain weight, would reduce the effectiveness of any one character ADAMS and GRAFIUS (1971). Developmental and compensatory interactions reduce the effectiveness of combining extreme expressions of characters from two parents (KNOTT and TALUKDAR, 1971). Therefore, a high correlation between yield and one of its components in a parent may be less reliable in its hybrid progeny.

In summary, although studies on limited sets of inbreds may identify significant associations of yield and its components, the reliability of these associations within other populations is probably reduced by different levels of developmental and compensatory interactions unique to each population. In addition, in heterogeneous populations of inbreds inter-plant competition would undoubtedly diffentially influence the development of each genotype.

The effectiveness of selection for yield using yield components in inbreeding populations

The inconclusive pattern of associations between yield and its components in inbreds is also found in studies of inbreeding populations.

Comparisons between studies highlight the specific relationships usually found between yield and its components in each specific cross. In a cross 'Thatcher' x 'Lemhi', McNEAL (1960) found a strong correlation between spikes per F_2 plant and their F_3 progeny yields (0.973). In contrast, selection from the F_2 to F_8 for spikes per plant in another cross involving 'Thatcher' reduced yield per area. However, selection for grain weight and grains per spike was effective in both studies. McNEAL (1960) also found that spikelets per spike and grains per plant were correlated with yield in the F_2 and F_3 but selection for these characters in the F_2 did not increase F_3 yield. These studies of two sister crosses involving 'Thatcher' highlight the specificity of response within crosses to selection for yield components. Yield tests in each cross during early inbreeding generations would be needed to identify reliable characters, yet at this level the F_2 progeny test has been found a reliable direct indicator of yield performance.

Selection for yield per spike has been found effective for increasing yield by DERERA and BHATT (1972), NASS (1978) and ALESSANDRONI and SCALFATI (1973) in the F_2 generation of wheat and by GEADELMANN and FREY (1975) in a near homozygous bulk of oats. However, McVETTY and EVANS (1980a) only found yield per spike reliable in one of three crosses, which emphasised again the specificity of response to characters within crosses and the risks in generalization.

Similar inconsistent results are found with harvest index. SINGH and STOSKOPF (1971) found selection for harvest index improved yield, and BHATT (1980) in his review of early generation selection criteria for yield in wheat concluded that harvest index, in particular, deserved attention. In contrast, NASS (1980) found selection by harvest index of little value and McVETTY and EVANS (1980b) only found it useful in a selection index including plant height and total plant biomass. WHAN, KNIGHT and RATHJEN (1982) found selection by harvest index no more effective than selection for yield directly.

The only reasonable conclusion which can be drawn from these studies is that any yield components which assist selection in a cross are so specific to that cross that their general application would probably be ineffective. Conversely, pooled estimates are unlikely to assist selection or identify the most effective components in individual crosses. There is a strong inducement to conclude that some characters such as grain yield per spike, grain number per spike and harvest index may have general reliability because of their significant association with yield in many studies and the intuitive opinion that components so closely related to yield per area must be reliable. However, the high frequency of effectiveness of these three characters in the reviewed studies could be the result of a fortuitous sampling of crosses. Nevertheless, of all the characters studied, grain yield per spike and grain number per spike would seem the most promising.

There are no studies of selection for yield using yield components in composite cross populations. Because the genetical evidence suggests a considerable degree of heterozygosity is present in composites, particularly if they contain a nuclear male-sterility factor, it might be argued that selection within composites would be as inconclusive as in studies of small set of crosses. However, the genetical structure of composites may alter the effectiveness of selection from that found in small sets of single crosses. It could be postulated that the panmictic processes within composites would reduce the specific effects found in 2-parent crosses because specific linkage relationships would be reduced. Consequently the effectiveness of selection may improve. In contrast, the reliability of selection relative to single crosses may be reduced as a genotypic structure and inter-plant competition unique to each composite develop in the panmictic process.

If it were found that single plant selection in composites for yield components was significant it could be used in conjunction with progeny yield tests to increase the chance of detecting high-yielding progenies. Also, selection for yield components could be used to select parents for the next generation of the composite. A specific application of this approach would be to select male-sterile parents which are either naturally outcrossed or pollinated by fertiles also selected for high expression of reliable yield components.

The effectiveness of selection for yield using characters of the F_1

If all individuals in a composite population~~s~~ were progeny of nuclear male-steriles in the prece~~e~~ding generation then every plant in the composite would be the result of an outcross (S_0). Although there are no reports on selection for yield using components among S_0 individuals in composites of autogamous cereals, an indication of its effectiveness may be obtained from studies involving the F_1 generation. Both S_0 and F_1 individuals approximate a zero level for their inbreeding coefficient, particularly if the relevant composite is large and parents of the F_1 are unrelated.

The degree of heterosis in yield components varies between crosses and is generally not correlated with the degree of inbreeding depression from the F_1 to the F_2 (BHULLAR, GILL and KHEHRE, 1979; BRIGGLE, COX and HAYES, 1967; BRIGGLE, PETERSEN and HAYES, 1967; PARODA and JOSHI, 1970). SIKKA, JAIN and PARMAR (1959) found the ranking of F_1 yield components did not predict the ranking of F_3 bulks in twelve crosses made to a common parent. Consequently, selection in the F_1 for yield through expression of yield components would probably be ineffective.

The heritabilities of yield components in the F_1 may be generally higher than for yield. SIKKA, JAIN, and PARMAR (1959) found the ranks of three yield components, grains per primary spike, grain weight and primary spike length were consistent from F_1 to F_3. FONSECA AND PATTERSON (1968) found the ~~heribailities~~ heritabilities of the number of spikes and grains per spike in the F_1 of a 7-parent wheat diallel were higher than for yield. The number of spikes, grain per spike and grain weight were correlated with plant yield but significant negative correlations occurred between the three yield components, reflecting the lack of strong expression for all three components in any parent. Crosses with high and specific combining effects for yield also tended to have high combining effects for grains per spike and grain weight.

We may cautiously conclude from these studies that selection for some yield components in the F_1 may effectively increase their expression in later generations in contra~~c~~st to the lower predicat~~i~~bility of yield per plant. The greater reliability of selection for yield components may reflect a simpler genetic control than for yield. WALTON (1969) and HSU and WALTON (1970) found ear length, spikes per plant, spikelets per spike, grain number per spike and grain weight were under predominantly additive control with some dominance effect. In contra~~c~~st~~s~~, yield is usually inherited in a more complex manner possibly reflecting the complex interactions which occur between the relatively simply inherited components.

Translation of these results from studies involving the F_1 to composites comprised of S_0 indiviiduals would suggest that selection amongst S_0 individuals may effectively increase the expression of the selected yield components but it is unlikely that an increase in bulk yield will also occur. Nevertheless, indirect selection for yield using the 'female-choice' method (DOGGETT, 1968; DRISCOLL, 1981) has appeal because of its lower cost. Therefore its effectiveness should be tested. The effects of the panmictic process in composites (enforced in the case of propagation through male-sterile parents) are unknown.

The effects of dwarfing genes on yield and yield components

The *gai* dwarfing genes have been found to not only influence height but grain number. SYME (1970) suggested that the higher harvest index and higher yielding ability of the semi-dwarf wheats 'Mexico 120' and 'WW-15' resulted form their ability to set more grains relative to chaff and straw production than tall wheats. HOLMES (1973) concluded that the yielding potential of the semi-dwarf wheat 'Pitic 62' is not directly associated with a shorter culm but with a higher number of grains per spike. GALE and LAW (1976, 1977) found that the yield difference between F_3 families homozygous for either the dwarfing gene *Gai 2* or the recessive *gai 2* in a cross between Maris Hobbit (dwarf) and Chinese Spring (tall) could be attributed to higher grain number rather than grain weight. Consequently yield per spike was correlated with plant yield.

In addition to the direct effect of dwarfing *gai* genes on grain number, they allow exploitation of other genes with pleiotropic effects for height and yield. GALE and LAW (1976, 1977) found a positive correlation between height and yield in the three genotypic classes for dwarfness ($Gai_2\ Gai_2$; $Gai_2\ gai_2$ and $gai_2\ gai_2$) in three crosses. They suggested that selection for tall dwarfs in families homozygous for *Gai* may successfully exploit this relationship. LAW, SNAPE and WORLAND (1978) suggested that there is a strong positive association between height and yield in wheat but that selection against lodging while attempting to increase yield has caused dispersal of the genetic variation for height and yield. The dwarfing genes would allow maximum expression of the influence on yield of the 'height-yield' genes and selection by height could be a principal criterion for selection for yield.

The probable effectiveness of selection for yield in composites by using yield components.

The preceding review of effectiveness of selection for yield by using yield components has indicated two general conclusions. The effectiveness of selection for yield seems to decline as the level of heterozygosity is increased and selection for characters closely related to yield such as yield per spike, grains per spike and grain weight appear to be the most effective.

The lower effectiveness of selection associated with heterozygosity is particularly serious if selection is attempted in composite populations. In panmictic populations with partial outcrossing the level of heterozygosity of individuals would be unknown. It is probable that the highest expression of yield components may occur in the most heterozygous plants exhibiting expression analogous to high levels of F_1 heterosis. The confounding effects of varying level of heterozygosity can only be removed by inbreeding selected families to homozygosity (in which case yield could be measured directly) or ensuring that all individuals in the composite are S_0 i.e. the progeny of an outcross in the previous generation. However, in the latter case, selection would be expected to be least effective because the S_0 population would have the highest level of heterozygosity. Selection between S_0 individuals for more than one generation would probably increase the expression of yield components by intensifying genetic interactions but may not increase yield. The panmictic process in composites would be expected to reduce bias introduced by linkage associations within the parents of the composite. However, the genetic relationships generated by continued selection within the composite at the S_0 level may be equally intense and reduce the effectiveness of selection for yield. The relative magnitude of these effects is not known.

The personal preference for particular characters by those studying the relationship between yield and its components has resulted in no character being common to all the studies reviewed. The frequent report of a positive association with a frequently studied character draws attention away from those infrequently studied. Nevertheless an overview suggests that yield per spike, grains per spike and grain weight are most consistently related to yield at all the levels of heterozygosity. Other characters, though less frequently measured, seem to be associated with yield only in specific crosses. Therefore, greatest reliability probably remains with yield per spike, grains per spike and grain weight. This conclusion has serious consequences for composites propagated through male-steriles. Partial seed-set on the steriles does not permit selection using these apparently most reliable characters. Therefore characters independent of seed set, such as headlength and spikelets per spike, must be employed. The studies reviewed have shown that these characters are not reliable. Selection for yield using height in populations homozygous for a dwarfing gene is a probable exception to this general conclusion. Indeed, a selection procedure involving yield per spike, grains per spike, grain weight and height in a composite homozygous for a dwarfing gene may be promising.

In conclusion, it is most unlikely that selection for yield using yield components would be effective in composite crosses. The likelihood of success will probably be least in 'female choice' selection where S_0 female parents are chosen using characters independent of seedset.

2.8 The Limitations Imposed by Inbreeding on Genotypic Improvement

Genotypic improvement resulting from the reassortment of genes contributed by parents to a cross of an autogamous species is a common occurence. Reassortment is dependent upon the linkage relationships between loci. In the absence of selection during inbreeding genes on different chromosomes, or separated sufficiently on the same chromosome, can randomly assort but as linkage between loci increases the opportunity for recombination of parental genes decreases.

The effects of gene distribution between parents and the distribution of independent alleles on selection in inbreeding populations.

When genes assort randomly the binomial distribution can be used to calculate the probability of fixation of a given number of favourable alleles in a genotype (BAILEY and COMSTOCK, 1976). If one parent initially has a high proportion of the favourable alleles it is unlikely that random assortment will fix any superior genotypes in a reasonable sample. For example, BLISS and GATES (1968) calculated that if one parent contained 25 of 30 favoured independent alleles only 0.0056 of segregants would contain more than 25. Furthermore, if two parents contain more than 25 favoured independent alleles between them it is unlikely that fixed lines could be isolated containing all the favoured alleles.

Consequently, if one wishes to accumulate large numbers of alleles from two parents into one genotype it would be necessary to intercross segregants which jointly carry all the desired alleles (if they could be identified) and reselect for greater accumulation. These procedures will be discussed in detail later in this review.

The likelihood of retrieving and accumulating favoured alleles decreases as their heritability decreases. In a simulation of 10 generations of selection with 15 to 60 independent alleles, six levels of heritability and selection intensities ranging from 0.05 to 0.50 MARANI (1975) found the mean genotypic progress was 67% of the maximum theoretical gain at $h^2 = 1.0$ but only 48% at $h^2 = 0.25$. He found that the effects of loci number and selection intensity were also pronounced. His study emphasised the reduction from maximum possible gain which results from genic fixation during inbreeding. The fixation levels ranged from 83% to33% and the greatest responses usually occurred at intermediate selection intensities (0.20, 0.25). Where many additive genes controlled a character, high selection intensities (0.05 and 0.10) were most effective, but fixation levels were still only moderate because of the predominance of the effects of inbreeding.

Fixation at levels less than the theoretical maximum in breeding populations under selection is a direct result of insufficient individual plants being grown in the F_2 and subsequent generations to retain at least one plant carrying all the favoured genes. If n independent loci are segregating in the F_2, $(\frac{1}{2})^n$ of the population would be homozygous but only $(\frac{1}{4})^n$ would be homozygous for all desired alleles. Although the proportion of the F_2 carrying at least one of each desired allele is much greater $(\frac{3}{4})^n$, this proportion also becomes very small as n increases, e.g. $(\frac{3}{4})^7 = 0.133$ (SHEBESKI, 1967).

If all the desired alleles are to be retained, individuals carrying them must be selected in early generations because the expected proportion of individuals carrying n desired alleles decreases to:

$$\left(\frac{2^{x-1} + 1}{2^{x}}\right)^{n} \qquad (1)$$

by the F_x generation (after SHEBESKI, 1967). Therefore, for example, at F_6 and $n = 7$, $(1) = 9.69 \times 10^{-3}$; i.e. only 7.26% of the F_2 value (0.133).

The rapid decrease of (1) to a limiting value of $(\frac{1}{4})^n$ is a direct result of segregation increasing the proportion of desired homozygotes at each locus to $\frac{1}{2}$.

The expected proportion of plants homozygous for all desired alleles at F_x is (VAN DER KLEY, 1955):

$$\left(\frac{2^{x-1} - 1}{2^{x}}\right)^{n} \qquad (2)$$

Therefore, for the previous example, at F_2 and $n = 7$ $(2) = 6.103 \times 10^{-5}$ but at F_6, $(2) = 6.256 \times 10^{-3}$. (2) approaches the limit $(\frac{1}{2})^n$ from below. $((\frac{1}{2})^7 = 7.813 \times 10^{-3})$. Consequently, selection in early segregating populations for individuals carrying desired alleles is likely to be more successful than selection within a population permitted to inbreed randomly to fixation (BLISS and GATE, 1968).

The effects of linkage on the response to selection in inbreeding populations.

The two important relationships between linked genes in the parents of an inbreeding population are their recombination values and the distribution of coupling and repulsion phase relationships. NELDER (1952) and CURNOW (1978) derived the genotypic frequencies at each generation of inbreeding from the coupled parental configuration $\frac{AB}{ab}$. At fixation the proportion of the coupled homozygotes (AABB and aabb) are $\frac{1}{2(1 + 2r)}$ and those of the repulsion homozygotes are $\frac{r}{(1 + 2r)}$ where r is the recombination value between loci. For an F_1 in repulsion, $\frac{Ab}{aB}$, the frequencies of coupling and repulsion at fixation are interchanged. The most critical aspects of this result are the initial genotypic configuration and the recombination value.
For example, when
$r = 0.05, \frac{1}{2(1 + 2r)} = 0.4545$ and $\frac{r}{1 + 2r} = 0.0455$, i.e. only 9.1% of segregants at fixation are recombinants. At F_x, the proportion of double heterozygotes remaining from an initial repulsion phase heterozygote $\frac{Ab}{aB}$ is (BENNETT, 1954a):

$$(\frac{1}{2})^{x-1}(1 - 2r + 2r^2)^{x-1}$$

The extreme values, $(\frac{1}{2})^{x-1}$ when r = 0 and $(\frac{1}{4})^{x-1}$ at independent assortment (r = 0.5), indicate the strong effect close linkage has on maintaining the initial double heterozygote configuration.

HALDANE and WADDINGTON (1931) emphasised that the expected increase in recombinants is small after about 5 generations. They extended their analysis to the three linked loci, $\frac{AbC}{aBc}$, and showed that the proportion of double crossover homozygotes $\frac{ABC}{ABC}$, at fixation is

$$\frac{1}{2} \left(\frac{2p}{1 + 2p} + \frac{2q}{1 + 2q} + \frac{2r}{1 + 2r} \right)$$

where p,q and r are the recombination values between AB, BC and AC respectively. Inequality of p and q further reduces the chance of obtaining AABBCC. NARAIN (1965) developed a generalised theory demonstrating that the linkage effects increase as the number of linked loci increases.

A further consideration in the effects of linkage is the extent of reinforcement or opposition between alleles at linked loci (MATHER and JINKS, 1971). If reinforcement occurs between coupled alleles then the effect of linkage on the means and variances of phenotypic expression will be greater than if the linked genes have opposing action. MATHER and JINKS emphasised that coupling and repulsion are mechanical relationships whereas reinforcement and opposition of these phases ~~is~~ are phenotypically expressed.

The principles of recombination between loci during inbreeding have been extended to the multilocus case by computer simulation. BAILEY and COMSTOCK (1976) found that tighter linkage caused retention of a higher proportion of parental configuations and that the frequency of desired genotypes was reduced severely if a high number of effective crossovers was required. When a high proportion of desired alleles are linked in one parent, thereby increasing the likelihood that they are in coupling, the chance of retaining desired alleles is greater than under independent assortment and is enchanced by close linkage. However, when the distribution of desired alleles between parents becomes very uneven, not even close linkage can retain in coupling sufficient alleles for fixed segregants to equal the genetic value of the superior parent. The effectiveness of truncated selection is dependent upon the initial configuration and intensity of linkage. BAILEY and COMSTOCK (1976) found that linkage increased the retention of desired alleles in coupling during truncated selection from the F_2 but if they were linked in extreme repulsion, truncation resulted in lower frequencies of desired recombinants than under independent assortment. Both effects were intesified by closer linkage. BLISS and GATES (1968) found that the realised gains from truncated selection were reduced by close linkage if the initial F_1 contained a randomly generated configuration of desired alleles. The linkage effects predominated and could not be overcome by reduced selection pressure or increased population size.

Computer simulation of the multilocus case has reinforced the general conclusions from two and three loci: linkage tends to increase the frequency of parental genotypes found in fixed lines and inbreeding limits the chance for meaningful crossovers to occur in segregating lines.

When the distribution of desired alleles between parents is so unbalanced that segregants superior to the best parent are unlikely to be retrieved even with assistance from strong coupling (BAILEY and COMSTOCK, 1976; BLISS and GATES, 1968), backcrossing must be invoked with the best parent used recurrently. Although the number of loci which retain genes from both parents during backcrossing is reduced by ½ each generation, loci linked to the locus of the desired donor allele will tend to remain heterozygous and it will require an average of $\frac{1}{r}$ generations for the desired allele and a linked undesirable allele r recombination units apart to be separated (CROW and KIMURA, 1970). Consequently a large segment of chromosome linked to the donor allele would be retained (STAM and ZEVEN, 1981). For example, they found 38 cM of a 200 cM chromosome would be retained after 6 generations. Often, the superiority of one parent is suspected and the effects of the few alleles in the inferior parent are not easily identified. In this case, BAILEY (1977) and REDDY and COMSTOCK (1976) proposed one or more backcrosses to the superior parent followed by selection during inbreeding to increase the likelihood of retaining genes from the superior parent. SUNESON and STEVENS (1953) observed that a process similar to backcrossing may have occurred in CC II. They found many segregants resembled the best adapted, i.e. superior parents. In general, in composites with few parents and a low frequency of outcrossing there is a risk that alleles from the superior parent may rapidly increase in frequency before the limited opportunities for meaningful crossovers have recombined the initial parental genomes. Consequently the level of genetic recombination in composites with a low outcrossing frequency may be intermediate between the genetic behavior of a panmictic population and inbreeding 2-parent crosses or be similar to inbreeding progenies of a limited backcross series. Therefore, genetic improvement in such composites would tend to be limited by the strong effects of rapid approach to homozygosity and retention of closely linked configurations of alleles as found in inbreeding populations.

2.9 The Genetical Consequences of Consecutive Cycles of Intermating the Progeny of Two or More Parents

In the preceeding section the strong restraint imposed by inbreeding was shown to reduce the opportunity for meaningful crossovers between closely linked loci to such an extent that new recombinations would be rarely detected in a reasonable sample of inbred homozygous segregants derived from an F_1 by inbreeding. From an evolutionary perspective the limitations imposed by inbreeding tend to retain genomes assembled by natural selection, but they do not permit the rapid reassortment of genes required for increasing the phenotypic value of crop plants. Interposed cycles of intermating, after the inital cross and before inbreeding is permitted, will allow greater opportunity for reassortment of linked genes.

The effects of consecutive cycles of outcrossing on linked genes

At Hardy-Weinberg equilibrium the gametic frequencies of linked loci are the products of gene frequencies. If the gametic frequencies depart from equilibrium, the departure, D, defined as:

$D = p_1\ p_2 \cdot q_1 q_2 - p_1\ q_2 \cdot p_2 q_1$

where $f(A) = p_1$, $f(B) = p_2$, $f(a) = q_1$, $f(b) = q_2$

is a measure of gametic linkage disequilibrium (GEIRINGER, 1944, 1945). Therefore, in a cross of two parents forming a double heterozygote in repulsion $\frac{Ab}{aB}$, the gametic linkage equilibrium will approach a maximum value as the intensity of linkage between a and b increase. if the progeny of this cross are randomly intermated for n generations, the recursive value of D is:

$$D^{(n)} = (1 - r)^n D^{(0)}$$

where r is the recombination value between the loci and $D^{(o)}$ is the initial disequilibrium (ALLARD, JAIN and WORKMAN, 1966). The limiting value of $D^{(n)} = 0$. Therefore, a number of cycles of random intermating in the progeny of the F_1, $\frac{Ab}{aB}$, will increase the chance of obtaining the non-parental recombinant homozygote, AABB, after inbreeding. KIMURA (1963) and BENNETT (1954b) extended this argument to three loci and any number of linked factors respectively, and found consecutive intermatings also reduced disequilibria in multiloci cases.

In addition to gametic disequilibrium, the zygotes which contribute gametes to a population may be a non-random sample of all possible zygotes. Random consecutive outcrossing also dissipates this zygotic association (ALLARD, JAIN and WORKMAN, 1966; WEIR and COCKERHAM, 1973).

Unless outcrossing is maintained at 100% in composites of inbreeding species by retaining seed from male-sterile or hand-pollinated emasculated plants only,the proportion of outcrossing will be low and the progeny from each generation will be the result of both outcrossing and inbreeding (self-pollination). In the one locus case as the number of generations approaches ∞, the proportions of homozygotes at the limit is $s/(2-s)$, and of heterozygotes $2(1-s)/(2-s)$, where s is the proportion of selfing (NARAIN, 1966). In the multilocus case, the degree of linkage between loci enters the description of both the rate of inbreeding and the limiting values of homozygosity and heterozygosity. NARAIN (1966) found with two loci that increased selfing at constant linkage increased inbreeding and inbreeding increased as linkage tightened.

The trends in the relationships of linked genes are also dependent upon the selective values of the zygotic genotypes. The changing fitness levels in composites and bulks indicate~~s~~ that selection may be a critical determinant of the fate of genes and parental linkage groups. ALLARD, JAIN and WORKMAN (1966) summarised the results of simulations involving varying levels of selfing in models of genic interaction and selection between zygotes. In contrast to the dissipation of gametic and zygotic associations with no selfing or selection, they found there was a general tendency for close linkage to maintain gametic linkage disequilibria and zygotic associations at equilibrium. JAIN (1968) found that these effects were produced in finite populations also, unless the number of individuals per generation was so small that genic dispersion resulted from random genetic drift. The results from various simulation models are usually quite specific, but the following conclusions are of particular relevance to breeding by using composites:

1) dispersal effects are insignificant if the population size exceeds 100 or if loci are very tightly linked
2) tight linkage and a high proportion of self-pollination generated higher levels of repulsion phase gametic disequilibria in models of intermediate genotypic optima and heterotic effects
3) at low levels of self pollination non-random genic associations are only maintained by very tight linkages
4) the rate of fixation of loci is strongly determined by the mode of selection and population size.

Consequently, partial selfing significantly retards the dissipation of gametic and zygotic associations of genes, particularly in the presence of selection between zygotes. Indeed, in populations where selfing exceeds 90% the restriction on recombination resulting from inbreeding and selection is sufficient to bind together and increase the frequency of interacting genes (ALLARD, 1975). These processes probably generate the co-adapted and partially heterozygous individuals responsible for increasing and maintaining fitness in composite crosses of predominantly self-pollinating species.

The effects of consecutive cycles of outcrossing on the length of intact segments of parental genome

An alternative approach to examine the effects of continuous outcrossing after the F_1 generation on a cross between two inbred parents is to estimate the length of intact parental chromosome segments. HANSON (1959a) found the average segment lengths of intact parental chromosome in the gametes of an F_1, assuming independence of recombination between all positions in chromosome, were 39.3, 63.2 and 86.5 map units long for chromosomes of 50, 100 and 200 centimorgans length, respectively. He concluded that those lengths, particularly in shorter chromosomes, preclude significant amounts of recombination between parental genomes during meiosis. HANSON (1959b) therefore continued his analysis to consider the effectiveness of n repeated cycles of intermating on reducing the length of intact parental segments. He found that with repeated cycles, the expected average intact segment length approximated $\frac{100}{n}$ centimorgans after six to eight cycles. For the above examples, after three intermating cycles the expected lenghts are 25.9, 31.7 and 33.3 centimorgans respectively. Therefore, for long chromosomes, consecutive intermating cycles considerably reduce the length of intact segments. However, in all cases considerable average lengths remain.

HANSON (1959c) extended his analyses by taking into account recombinations between homozygous and heterozygous chromosome pairing at the point of crossover. A reduction in linkage block length is effected by recombinations at points heterozygous with respect to progenitor chromosome types, but recombinations of homozygous segments reshuffle previous breaks. Their average effect is the same as if the recombinations had not occurred. These non effective crossovers have the effect of preserving linked parental gene sequences which are longer than the length of intact parental chromosomes. These adjustments to the above example increase the lengths of parental sequence to 31.6, 43.2 and 49.1 centimorgans, respectively.

HANSON (1959d) then calculated the expected average length of parental segment which would remain in a random intermating population resulting from crossing two or more parents in all combinations at the first intermating followed by random crosses in succeeding generations. In the first intermating the greatest reduction of parental sequence occurs and is independent of the number of parents because only pairs (equivalent to a population with only two parents) are intermated. In subsequent generations the effect of increasing the number of parents is not as great as the number of intermating cycles. An infinite parental array is little more effective than 10 parents and there is little advantage in greater than four parents. In the above examples after three intermatings with ten parents the average sequence length are 25.9, 31.7 and 33.2 centimorgans, respectively. In the ten parent case inbreeding after three intermating cycles gives 19.6, 21.5 and 21.7 centimorgans, respectively. In summary, HANSON's analyses indicates that in composite crosses intermated for a number of cycles and then inbred without selection to homozygosity, there is little advantage gained from more than four to ten parents and after three or four cycles of intermating further significant reductions of parental sequence require many intermating generations. Therefore the principal effect of large parent sets and many intermating cycles is the creation of genotypes with many parental contributors rather than an accelerated break up of parental gene sequences. It is of interest that after many intermating cycles followed by inbreeding that the intact sequence length is effectively independent of original chromosome length and sequences from two-parent crosses are only approximately twice the length of sequences in inbreds derived from an infinite parental array.

The effects of small population size on the effectiveness of continuous intermating

As the size of a breeding population is reduced, there is an increasing chance for matings between near relatives and hence a higher likelihood that a pair of allelic genes in any individual are identical by descent (SVED, 1971). The most extreme case is a completely inbreeding population. FRANKLIN (1977), using an analysis based on 'junctions' in either homozygous or heterozygous chromosome segments, showed that on inbreeding, the expected length of heterozygous segment after n generations of inbreeding in a chromosome of length l is

$$n (1 - e^{-2nl})$$

which reduces to n as n becomes large. The corresponding increase of homozygous segments, $(1 - n)$, which results in complete homozygosity in approximately 5 to 15 generations under self-fertilization is considerably extended by sib-mating a pair of offspring per cycle. In this case, the maximum likelihood of complete homozygosity occurs at the thirty-fourth generation (BENNETT, 1953) thus indicating that sib-mating two progeny per generation markedly reduces the fixation effects of inbreeding and for practical breeding is as effective as a random mating population.

In intermating populations larger than 2 individuals per generation a decline in mean homozygosity occurs at a locus with two alleles but the approach to homozygosity is so gradual that populations of 20 or more intermating individuals may be considered as infinite for practical breeding purposes (STAM, 1980; SVED, 1971). In contrast, when more than two alleles per locus are present in a small intermating population, a rapid loss of alleles can occur. LATTER and NOVITSKI (1969) found with N individuals per generation initially carrying 2N alleles, that the number of alleles declined in small random mating populations (N = 5 to 40) to about 2.8 per locus after 1.4N generations. Although loss of alleles would be slower in larger populations, appreciable losses would occur as the number of alleles approaches 2N. Therefore there may be little long term advantage in composites based on large numbers of unrelated parents.

Intermating will only be useful if, in addition to retaining as many alleles as possible, opportunity is given for recombination between closely linked loci. KARLIN, McGREGOR and BODMER (1967) emphasised that rare recombinants between closely linked loci will only occur in large populations and the mean number of generations before the desired recombinant event occurs may be very large. In a small population, fixation of close parental linkages is likely to occur before a recombination event. Close linkage has a greater effect than directional selection on increasing homozygosity (GILL and CLEMMER, 1966). In a large simulated population (N = 500) with moderately close linkage (r = 0.1) between 10 loci, heterozygosity fell very little in 40 generations (ALLARD and HANSCHE, 1965). They also found that the mean length of parental sequence fell rapidly in the first 5 generations but stabilised by approximately 25 generations. This result corresponds with HANSON (1959d). In addition, provided that strong heteroygote advantage was present, the number of genotypes generated and mean length of residual parental genome approached panmictic values at only 5% outcrossing. Consequently, obligatory outcrossing of each individual may not be necessary in large composites to achieve significant reassortment of parental genomes.

In summary, propagation of an intermating population, such as a composite involving enforced outcrossing, through a small number of individuals (N) per generation will be detrimental. In small populations, fixation of close parental linkages is expected before a recombinant event and a rapid loss of alleles is expected, particularly when the number of alleles approaches 2N. However, even if alleles are retained in populations where N is much larger than the number of parents, recombination between closely linked loci may not occur for many generations.

When these conclusions are combined with those of the previous section, an optimum procedure for using composite crosses in breeding emerges. No more than approximately 10 parents or intermating beyond approximately 5 to 10 generations are advantageous and the composite should be propagated through a large number of outcrossed individuals per generation (possibly > 100). A larger parent pool and prolonged intermating will not achieve a greater disruption of parental genomes for practical purposes and a smaller number of individuals per generation would result in unacceptably high loss of alleles and rates of genetic fixation. In addition, it has been previously argued that probable strong selective forces within the composite must be counteracted to retain the initial parental gene frequencies or, alternatively, selection should be practiced for individuals which will aid achievement of the goal of the composite cross. Nuclear male-sterility is a valuable tool to efficiently achieve intermating and obtain seed from outcrossed male-sterile plants.

The effect of a small number of intermating cycles on response to selection in a cross of two homozygous parents

The distribution and linkage relationships between desired alleles in the two parents of a single cross are almost always not known. We have seen previously that no superior segregant can be expected in a reasonable sample of inbred derivatives if the distribution of desired alleles is very unbalanced (BAILEY and COMSTOCK, 1976). Where balance occurs, intermating is advantageous if the desired alleles have predominantly repulsion phase associations in the F_1.

The ratio of the variance of inbreds derived from an intermated F_2 (V_1) to the variance of inbreds derived directly from the F_2 (V_0) in a two-locus repulsion phase heterozygous F_1, $(\frac{01}{10})$, is

$$\frac{V_1}{V_0} = \frac{5 - 2r}{4}$$

where r is the recombination value (PEDERSON, 1974). Therefore the limiting value of $\frac{V_1}{V_0}$ for repulsion is 1.25 as r approaches 0. In contrast, $\frac{V_1}{V_0}$ for coupling, i.e. F_1, $(\frac{11}{00})$, is always less than 1. PEDERSON extended his analysis to 8 linked loci and found that where repulsion phase linkages predominated, intermating was advantageous with maximum values of $\frac{V_1}{V_0}$ being near 1.2. However, in configurations involving mixed repulsion and coupling, there was little change in $\frac{V_1}{V_0}$ from 1.0. Two cycles of intermating in general approximately doubled significant $\frac{V_1}{V_0}$ gains. BLISS and GATES (1968) found by simulation that intermating the F_2 from an extreme repulsion phase F_1 removed a negative bias in additive variance, thereby assisting selection of superior segregants.

BOS (1977) defined the advantage of intermating as the increase in the frequency of the desired genotype ($a_1a_1b_1b_1$) at homozygosity. In a population derived directly by inbreeding from a double heterozygote F_1 in repulsion, $\frac{a_1\ b_2}{a_2\ b_1}$, the frequency of $a_1a_1b_1b_1$ is:

$$F = \frac{r}{1 + 2r}$$

When the F_2 is intermated the frequency is

$$F^* = \frac{5r - 2r^2}{4(1 + 2r)}$$

and the pertinent ratio

$$\frac{F^*}{F} = \frac{5 - 2r}{4}$$

with a maximum value of 1.25 at r = 0. However, this advantage is illusionary. To achieve this advantage as r approaches 0, large populations would be required. For example, at r = 0.01,

$$F^* = \frac{0.0122}{0.0098} = 1.245$$

but it is seen that the actual increase is only 24 in 10,000. If the ratio of $\frac{F^*}{F}$ is developed from BOS's paper for an F_1 in coupling,

$\frac{a_1b_1}{a_2b_2}$, the ratio is:

$$\frac{F^*}{F} = \frac{2 - r + 2r^2}{2}$$

which has maxima of 1.0 at r = 0 and 0.5 and a minimum value 0.94 at r = 0.25. This result complements PEDERSON's analysis of variance ratios. BAKER (1968) demonstrated that at least 30 pairs of F_2 plants must be crossed in 2- and 9-loci models to ensure that the potential increment of desired recombinants is not offset by losses through genetic drift.

PEDERSON (1974) found that where intermating was beneficial, truncated selection from F_3 families was equally effective for increasing the frequency of desirable genotypes. In the special case of maximum repulsion, $\frac{101010...}{010101...}$, STAM (1977) found the maximum advantage with selection occurred when selected F_4 individuals were intermated.

Because the genetic configuration of desired alleles in the F_1 is generally unknown, the applicability of intermating is uncertain. However, the models of PEDERSON, BOS and STAM are restricted to additive and dominance effects and two-parent crosses. This may be a serious weakness and tend to deflate the usefulness of intermating if epistatic and other interactive effects are important and the involvement of more than two parents significantly increases the frequency of useful genic interactions. However, the useful recombinants may be only detected if selection is practiced in large populations.

2.10 The Use of Additional Intermating in Breeding Self-Pollinated Species

In this section additional intermating will be defined as crossing descendants from a cross of two homozygous parents before the descendants approach closely to homozygosity. Therefore the extremes of intermating range from crosses between F_1 individuals to crosses in any generation approaching homozygosity. Intermating usually implies crosses between F_1, F_2 and F_3 or, in the case of composites, S_0, S_1 or S_2 individuals.

If an individual's breeding history is represented by O for any prece~~d~~ding outcrossing event and by I for any inbreeding event, then the breeding histories can be denoted symbolically. For example, intermating an F_1 for one more cycle, followed by inbreeding to generate F_3 individuals, is represented as: O_2I_2. This annotation simplifies and clarifies comparisons between breeding strategies. A further elaboration indicates random choice (R) or selection (S) in each generation. In the above example, if F_3 individuals were selected and the breeding cycle repeated, the programme would be represented as:

$O_{2R}I_{IR}I_{IS}O_{2R}I_{IR}I_{IS}$ ... etc.

A number of intermating schemes have been proposed. For example ATHWAL and BORLAUG (1967) proposed a broad-based composite involving a male-sterility factor to give flexibility to a programme of the general form $O_xI_yO_xI_y$ where x,y > 1. The specific case, $O_{IR}I_{IS}O_{IR}I_{IS}$ would be an S_1 progeny test recurrent selection programme. COMPTON (1968) suggested recycling n/2 random F_5 individuals from n/2 crosses between n parents, i.e. $O_{IR}I_{4R}O_{IR}$, etc., but this strategy would eliminate many genes and recombinants by drift (BAKER, 1968; YONEZAWA and YAMAGATA, 1978).

JENSEN (1970, 1978) proposed the 'diallel selective mating scheme' in which the scheme is established by diallel matings with small sets of parents and selected individuals from any inbreeding generation are recycled as parents. JENSEN criticised conventional breeding for its small parental base, limited disruption of parental linkages and restriction of recombination to within the initial cross. In contrast his proposal allows simultaneous input of parents, greater opportunity to disrupt parental linkages, freeing of genetic variability and fostering of desired recombinants by selection. He suggests intermating selected male-steriles with selected fertile pollinators for a number of generations. CHOO, CHRISTIE and REINBERGS

(1979) proposed intermating selected doubled haploids. This process removes error caused by residual heterozygosity, yet permits frequent intermating by reducing the inbreeding process to one generation.

Intermating permits greater genetic reassortment between parents, accelerated disruption of parental linkages, and selection and recycling more frequently than in conventional breeding. Most studies of intermating in autogamous species emphasise one of these aims.

Intermating to achieve greater genetic variability

In studies of intermating F_2 wheat plants there have not been consistent effects. Intermating F_2 plants did not change means and variances in crosses studied by SNAPE (1978) and NANDA, HAZARIKA and GILL (1981). In contrast, GILL, BAINS, SINGH and BAINS (1973) and SINGH an DWIVEDI (1978) reported the means of a number of characters were greater in the progenies of intermated F_2 plants and variances and covariances were significantly altered. Intermating can shift genotypic correlations in the direction required to increases the frequency of desired recombinants (VERMA, KOCHHAR and KAPOOR, 1979) but may also disrupt useful character associations. For example, RANDHAWAN and GILL (1978) found intermating F_2 individuals increased the grain protein content of the top 15% of lines but this response was correlated with a decline in yield, grains per spike and grain weight. Intermating may also decrease the mean expression of characters. REDDEN and JENSEN (1974) found that the green tiller number and grain weight were smaller in progenies of intermated F_2's than in the F_1 and F_3.

Studies with soybean, cotton and tobacco have also elucidated the beneficial effects of intermating. GATES, WEBBER and HORNER (1960) found repulsion phase linkages among the genes controlling yield and height in soybean. They suggested intermating to disrupt these linkages, followed by partitioning the population and inbreeding to detect lines expressing useful recombinants. HANSON, PROBST and CALDWELL (1967) intermated an F_3 bulk of 56 crosses and increased genetic variability beyond that derived from the initial two-parent crosses. They demonstrated that combining genes from more than two parents before inbreeding can be beneficial. In cotton, MILLER and

RAWLINGS (1967a) found intermating for six generations shifted genotypic correlations in a cross of two contrasting inbreds towards values expected nearer to linkage equilibrium. However, in most individual traits the genetic variance was decreased. They concluded that intermating provided a more profitable source for selections and could be used to introduce genes from an unadapted parent into a breeding programme. MEREDITH and BRIDGES (1971) reduced a negative genotypic correlation between two economically important characters of cotton, lint yield and fibre strength, by two cycles of intermating after the F_3 in a two-parent cross. In tobacco, intermating decreased the yield and leaf width after each of five intermatings, but the magnitude of detrimental changes was so small that they could be offset by one generation of selection (HUMPHREY, MATZINGER and COCKERHAM, 1969; MATZINGER, MANN and ROBINSON, 1960).

Intermating is differentiated from evolutionary composite crosses in plant breeding methodology by its smaller parent base, high degree of control in the mating process, and its emphasis upon a small number of consecutive cycles of outcrosses. However, these aspects of intermating correspond closely with the more recent concept of composites in which intensive out-crossing is enforced for only a few generations in a population with a relatively small parental base (DRISCOLL, 1981). Studies of intermating suggest that if such composites were propagated for a few generations without selection there would be shifts in the mean expression of characters (both positive and negative) and generally a decline in genotypic correlations which would improve simultaneous selection of negatively correlated characters and probably assist the incorporation of unadapted varieties into a breeding programme. However, random intermating may dissipate high and desirable genotypic correlation. Therefore, simultaneous intermating and selection may be a more efficient breeding procedure (DOGGETT, 1972; DRISCOLL, 1981; JENSEN, 1978).

Intermating in conjunction with selection in self-pollinated species

The conventional breeding method ($0_1 I_n$ where $n \simeq 5$) has been criticised because it tends to accumulate only a portion of many desired genes (BAILEY and COMSTOCK, 1976; PALMER, 1953), uses a small parental base (McPROUD, 1979) and allows little effective recombination (JENSEN, 1970). Consequently many breeding strategies involving a higher frequency of outcrossing and reduction of the inbreeding component have been proposed for autogamous species and can be illustrated using the notation defined earlier. For example, from the classification by HALLAUER (1981):

(1) Phenotypic (mass) recurrent selection (usually $0_{1R}I_{1S}$or $0_{1R}I_{2S}$)

(2) Progeny evaluation and continuous outcrossing e.g. composites with selection (0_{1S} 0_{1S} etc.) Eventually this process must revert to $0_{1}I_{nS}$ to detect superior inbreds.

(3) The diallel selective mating scheme

$$\begin{tikzcd}
0_{1S} \arrow[r] \arrow[d] & 0_{1S} \arrow[r] \arrow[d] & 0_{1S}I_{nS} \\
I_{nS} & I_{nS} &
\end{tikzcd}$$

with new stocks being added to any outcrossing stage.

(4) S_1 (0_{1S} I_{1S}) and half-sib progeny ($0_{1S}0_{1S}$ etc.) recurrent selection.

Further complexities are added by an array of bulk and family structures. HALLAUER emphasised that reducing the I phase reduces the time per cycle and has merit if selection in early generations is effective. If the outcrossing phase exceeds 0_1, the benefits of intermating are increased but cycle time is increased and consecutive outcrossings would only be justified by a greater long-term gain per generation.

Intermating has been used in conjunction with selection to improve characters in wheat and many other autogamous species. In wheat, McNEAL, McGUIRE and BERG (1978) increased protein percentage by intercrossing F_3 selections and reselecting in the F_4 i.e. $0_{1}I_{1R}I_{1S}0_{1}I_{2R}I_{1S}$, but grain yield decreased in almost all families. Therefore, undesirable negative correlations must be counteracted, particularly if frequent intermating accelerates the response to selection of a particular character. REDDEN and JENSEN (1974) found that intensified intermating, $0_{1}I_{1S}0_{2S}I_{2S}$ enabled a greater increase in tiller number than truncated selection, $0_{1}I_{4S}$, in both wheat and barley. Their study also showed that intermated series involved more parents than truncated selection in the high-tillering selections, thereby emphasising that more frequent intermating can exploit useful genes from a broader genetic base.

In sorghum, successful selection strategies using frequent intermating are well established. DOGGETT and EBERHART (1968) proposed using nuclear male-sterility in a progeny test scheme such as $0_{1R}I_{1R}(I_{1S})0_{1R}I_{1R}(I_{1S})$ in which remnant seed from the I_{1R} generation is used in the succeeding intermating cycle. Therefore, both yield tests and intermatings would be done with I_1 i.e. S_1 (or F_2) families. The fertile S_1 plants permit yield assessment and the male-sterile S_1 segregants are used for intermating. In contrast to wheat and barley, the seed-set on male-sterile sorghum plants intermingled with male-fertile pollen donors is not less than on male-fertile plants for practical breeding purposes. Therfore the seed-set on male-sterile S_0 (F_1) sorghum plants can be used for selection for yield. DOGGETT (1972) used this character to advantage in three selection strategies involving frequent intermating; 'S_1 testing ', 0_{1R} $I_{1R}(I_{1S})$,0_{1R} etc. (as above), 'female choice' mass selection, $0_{1S}0_{1S}$ etc., 'alternating female choice and selfed plant mass selection', $0_{1S}I_{1S}0_{1S}I_{1S}$. The 'female choice' scheme relies entirely upon the yield of S_0 (F_1) plants, while the other schemes test inbred $S_1(F_2)$ lines. DOGGETT'S study did not allow exact comparisons of the schemes but all effectively increased yields by approximately 20% in two cycles. 'S_1 testing' appeared to be the most successful and 'female-choice' the least. Valid comparisons of three selection strategies were conducted by JAN-ORN, GARDNER and ROSS (1976) who found S_1 family selection, $0_{1R}I_{1R}(I_{1S})$,$0_{1R}I_{1R}(I_{1S})$ the most effective, fullsib family selection, $0_1(I_{1S})0_1(I_{1S})$, intermediate, and half-sib family selection, also $0_1(I_{1S})0_1(I_{1S})$ the least effective. The latter two scheme differed in their selection of parents for outcrossing; in the full-sib scheme both the male and female parents of each outcross were selected while in the half-sib scheme the selected female parent was open-pollinated by surrounding males. JAN-ORN *et al.* suggested half-sib selection be used only for highly heritable traits. In other studies with sorghum ECKEBIL, ROSS, GARDINER and MARANVILLE (1977) found S_1 progeny selection using male-sterility was effective in populations with a broad genetic base including exotic parents. SINGH (1977) recognised the potential for using nuclear male-sterility and a number of elaborations of full-sib and S_1 progeny tests to introduce alien sorghums into breeding populations.

These results present a strong challenge to wheat breeders. The success of the S_1 progeny test in all four sorghum studies suggest that a wheat breeding strategy be attempted in which the S_1 progenies (F_2) of randomly chosen S_0 (F_1) plants be used to select for yield and full-sib crosses be made between fertiles and male-steriles in the highest yielding S_1 lines. If a nuclear male-sterility factor is used, the partial seed set on male-steriles in the S_1 will introduce error into yield determination, but in practice this error may not significantly interfere with yield comparisons between S_1's. Consecutive selection at the S_1 (F_2) level of inbreeding may be ineffective if the S_1 yields are not indicative of high yield in S_1-derived inbreds. However, S_1 selection is at the same inbreeding level as the successful 'F_2-progeny' scheme (LUPTON, 1961). The effectiveness of the S_1 test could be checked by testing more advanced inbreds (S_2; S_3) in a supplementary programme. This would be required to isolate superior inbred homozygotes from the S_1 progeny test programme. These concepts align closely with the 'diallel mating system' of JENSEN (1970, 1978). The beneficial influence of exotic parents in the sorghum breeding strategies of ECKEBIL *et al.* (1977) support JENSEN's proposition that frequent intermating in conjunction with selection and full-sib mating may successfully exploit unadapted parent in wheat breeding, even though conventional wheat breeding (0_1I_N) seldom uses exotic parents successfully.

Evidence supporting the use of frequent intermating has been obtained with soybean. BRIM and STUBER (1973) proposed recurrent selection procedures to improve yield in soybean with the notation $0_1I\ _1(I_{1S})$ by using S_1 progeny, full-sib and half-sib schemes. They emphasized the advantage of using nuclear male-steriliy in these procedure to facilitate outcrossing between S_1 (F_2) individuals. KENWORTHY AND BRIM (1979) found the S_1-progeny test variant of the above scheme increased yield in each of three cycles without significant effects on other seed traits. However, MILLER and FEHR

(1979) needed to use stratification and selection indices to avoid inbreeding of relatives and undesirable genetic drifts when using an S_1-progeny scheme to select for lower oil and higher protein content in soybean. Significant responses may be possible with small populations using the S_1 progeny test strategy. BRIM and BURTON (1979) found little difference between effective population sizes of 10 and 30 while selecting for seed protein content. They also found (BURTON and BRIM, 1981) a half-sib selection procedure, $O_{1S}I_{1S}O_{1S}I_{1S}$ etc., effectively increased oil content. Although small populations and the half-sib technique were successful in selecting for oil and protein content they may not be as effective in selection for yield which probably has a lower heritability. The results from soybean again indicate that frequent intermatings in conjunction with selection may be beneficial in wheat breeding.

Intermating has also been used successfully in cotton. MILLER and RAWLINGS (1967b) observed a linear response in lint yield in three cycles of selection using the strategy, $O_{1R}I_{1R}I_{1S}O_1R$ etc. They observed decreasing correlations between yield and other characters of the high-yielding parent, suggesting that consecutive intermatings were disrupted coupling phase linkages. The third cycle selection exceeded the response of conventional breeding (O_1I_{4S}) and the F_1 between the parents. Therefore, cyclical intermating and selection may generate and retain genetic interactions in partial homozygotes (S_2 or F_3) superior to those in the heterozygous F_1. In tobacco, LEGG, MATZINGER and MANN (1965) deduced from variances in an intermated 8-parent synthetic that intermating selected unrelated S_1 lines would more effectively improve yield than mass selection or pedigree selection between or within families. Because leaf yield in tobacco can be determined before flowering, mass selection can be used in a continuous outcrossing procedure $O_{1S}O_{1S}$ etc. Using this method MATZINGER and WERNSMAN (1968) reported a linear response for four cycles. Selection for leaf alkaloid content before flowering also permitted MATZINGER, WERNSMAN and COCKERHAM (1972) to achieve significant gains from two cycles of a full-sib progeny test in which both parents of each intermating cycle were selected.

Shorter selection cycles in autogamous species and the use of nuclear male-sterility to assist female choice, half-sib, full-sib and S_1-progeny selection procedures has tended to converge the breeding strategies of autogamous species with those employed in cross-pollinated crops. The following examples from the extensive literature on corn (*Zea mays*) breeding are pertinent to this section of the review.

SPRAGUE and BRIMHALL (1950), SPRAGUE, MILLER and BRIMHALL (1952) and SPRAGUE (1966) found S_1-progeny testing gave greater gains per generation for oil content of the kernel than truncated selection during selfing. They consequently advocated more frequent intermating to increase the rate of genetic gain. This result corresponds with the observations reported in this section. In the 'modified ear-to-row' selection scheme (COMPTON and BAHADUR, 1977; WEBEL and LONNQUIST, 1967) a half-sib progeny of a selected plant (equivalent to the progeny of a selected outcrossed male-sterile in an autogamous species) is yield tested. The parents of the next generation of half-sibs are chosen from within the highest yielding half-sib families. Both studies found this procedure more effective than mass selection. In autogamous species the equivalent of this scheme may have greater promise than 'female-choice' mass selection, particularly where imcomplete seed-set on male-steriles does not allow determination of S_0 yield. The half-sib progeny of an outcrossed male-sterile is analogous to a set of F_1's with a common parent. Therefore, half-sib progenies would provide an estimate of the general combining ability of the male-sterile parent. Intercrossing selected fertiles and male-steriles from half-sib progenies would allow recombination between the genomes of superior male-steriles and initiate another cycle of selection. Although the F_1 of a 2-parent cross is not a reliable guide to its capacity to provide superior inbreds (Section 2.3) a family of $S_0(F_1)$ individuals with a common male-sterile parent may reliably identify S_1 (F_2) progenies from which superior inbreds may be selected.

S_1-progeny test developments in corn breeding relevant to improvement of autogamous species are: selecting within S_1 progeny to initiate new intermating cycles (HORNER, 1963), using the increased variance in the S_1 to achieve greater genetic gain (HORNER, 1968) and using the S_1 to emphasise additive rather than heterotic effects which probably predominate in S_0 individuals (LONNQUIST and LINDSEY, 1964; CRESS, 1967). Alternating cycles of outcrossing and inbreeding with selection between S_1 families would allow improvement of a composite while maintaining a high frequency of outcrossing (DARRAH, EBERHART and PENNY, 1978). Exotic germplasm could be effectively introduced (MOLL and SMITH, 1981). At this point the concepts of corn improvement are coincident with the results of ECKERBIL, ROSS, GARDNER adn MARANVILLE (1977) who successfully exploited exotic germplasm in sorghum. The advocacy of S_1 and S_2 progeny tests for improvement of partially inbred grain legumes (RACHIE and GARDNER, 1975) and sorghum (GARDNER, 1977) could be extended to encompass other autogamous species such as wheat.

The first step in testing the efficency of S_1-progeny procedures in wheat should be selection of high-yielding S_1 (F_2) families and testing their stability in the S_2 (F_3). It has been concluded previously (Section 2.6) that imcomplete sed-set on male-steriles in wheat precludes using characters dependent upon seed-set (yield per spike, grains per spike, grain weight) to reliably select S_0 parent plants. Therefore interuption of intermating with alternating generations of S_1 yield tests may increase the efficiency of the composite breeding process in wheat, as found in sorghum (DOGGETT, 1972). Computer simulations suggest that S_1-progeny tests are more effective than mass (female choice) and half-sib methods but that additive variance declines more rapidly. (CHOO and KANNENBERG, 1979a, 1979b, 1981b). However, in the long term the loss of additive variance may be compensated for by greater real gains than would be achieved by mass (female choice) selection.

The integration of selection with intermating could move emphasis from the disruption and recombination of parent genomes to selection for desirable characters and selection against undersirable genetic changes. Consequently the purpose of each population in a composite cross breeding programme must be defined: is it to assist in the selection of new commercial varieties, in which some new variants may be detrimental, or to explore the limits of potential variation. HARLAN (1956) described new variants produced in barley composites. Once such characters have evolved, they in turn, may be introduced into composite breeding as 'alien' germplasm. For example, the branched spike of *Triticum turgidum* increased grain number but decreased grain weight in crosses with *T. aestivum*, but recurrent selection involving alternating intermating and selection may dissipate this negative correlation and permit exploitation of increased grain number.

In summary, this section has emphasised the beneficial effects of intermating for a small number of generations, particularly if more than two inital parents are involved. This evidence reinforces the argument for composite breeding populations based on a small number of parents and a limited number of intermating generations. In addition, the effectiveness of selection in conjunction with intermating presents a powerful argument for augmentation of composite breeding with intermittent generations of selection. In wheat breeding these avenues are yet to be explored.

2.11 The Genetical Behaviour of Outcrossing Populations

In Section 2.9 the immediate genetical consequences of imposing outcrossing on the progeny of inbred parents was reviewed. If outcrossing were pursued for many generations in such populations the influence of the initial homozygous parents would decrease and the genetical structure of the population would change to one resembling that of an outcrossing species. Therefore, the genetical relationships of outcrossing populations would probably indicate the likely genetical changes in long term composites initiated from a set of homozygous parents.

The expected response to selection in outcrossing populations

The extensive literature describing the theoretical outcome of selection in outcrossing populations indicates the most likely genetical developments in a panmictic composite under selection.

Computer simulation of multi-loci models in large populations initially at linkage equilibrium generally demonstrate that the response to selection is determined by interactions between selection intensity, the degree of linkage, heritability, and mode of genetic action. If the selection intensity and heritability are both relatively high, the response to selection is rapid and genetic variance also rapidly declines, resulting in little response after approximately 10 generations. Dominant alleles increase the response to selection but rapidly decrease genetic variance. High selection intensities may also interact with close linkage to drag poor alleles into fixed lines before recombination between desired and undesired genes can occur. At low selection intensities, the responses are slower but the genetic gain usually reaches levels similiar to those under intense selection. However, the number of generations required to achieve similar gains with low selection intensities are usually of the order of 30 to 200. Consequently, in plant breeding high selection intensities seem a practical requirement (BELLMAN and AHRENS, 1966; CHOO and KANNENBERG, 1981a; MARTIN and COCKERHAM, 1960; YOUNG, 1966). QURESHI, KEMPTHORNE and HAZEL (1968) and YOUNG and SKAVARIL (1976) found that these general conclusions were valid in populations greater than approximately 50 provided that linkage was not closer than r = 0.05. Even in very large populations close linkage (r= 0.005) reduced gains to less than those under independent assortment (BELLMAN and AHRENS, 1966).

The practical implications of these results for composite breeding are that direct selection will probably accumulate genes controlling relatively simply inherited characters of high heritability within a few generations. Useful gains in multi-genic characters with low heritability (e.g yield) would not occur within a practical time span. Therefore alternative selection strategies would be required.

If selection is applied to populations smaller than approximately 50 per generation the effects of linkage, initial genetic disequilibria and the mode of action of desired genes become critical in the response achieved. Generally in small finite populations definite phases of responses are observed for linked loci. At close linkage realised gains are less than theoretical maxima because desired alleles are eliminated before effective crossovers can occur or the small populations cause their exclusion and loss (LATTER, 1965a, 1965b, 1966b; QURESHI and KEMPTHORNE 1968; QURESHI, KEMPTHORNE and HAZEL, 1968). However, in most models there is significant gain by 10 generations which is either intensified or reduced by the dominance or recessiveness of desired alleles respectively (ROBERTSON 1970a; QURESHI, 1968; WRIGHT, 1977). Close linkage in small populations may also generate repulsion phase equilibria and high levels of segregation at individual loci (HILL and ROBERTSON, 1966; LATTER, 1966a). If composites are maintained through small populations these results again emphasise the loss of alleles by genetic drift and also emphasis that desired alleles are more likely to be in undesirable repulsion phase with close linkage, thereby reducing the chance of retrieving them in one individual after inbreeding.

Extremely high initial levels of genetic disequilibria are expected in composite populations established by intermating unrelated homozygous parents. In small populations the initial disequilibria will probably affect the eventual fixation genotypes, particularly for closely linked loci (KARLIN and McGREGOR, 1968; OHTA, 1968). ROBERTSON (1977) emphasised that whole chromosomes carrying valuable alleles may be eliminated if they initially pair with a chromosmoe of very low genetic worth. Therefore, the most critical factors determining the success of a given composite may be the genetic structure of the first generation of intermatings, the size of the early generations and the intensity of selection. Initially high levèls of repulsion phase disequilibria between desired alleles will delay response to selection until sufficient recombinants are formed to approach zero disequilibria. Then close linkage in the coupling phase will assist selection (BODMER and PARSONS, 1962; FELSENSTEIN, 1965; ROBERTSON, 1970a). Departures from Hardy-Weinberg and linkage equilibria may also reduce the effectiveness of selection (BULMER, 1976).

In summary, the results of theoretical studies of selection in small populations emphasise the need for large populations and a number of generations with low selection intensity (random intermating) to enable significant recombination and disruption of repulsion phase linkage to occur. These conclusions complement those from studies of intermated progenies derived from two or more inbred parents and propagated through very small populations (ALLARD and HANSCHE, 1965; KARLIN, McGREGOR and BODMER, 1967; LATTER and NOVITSKI, 1969; STAM, 1980; SVED, 1971); see Section 2.9. Both approaches emphasise that the initial parent array should not be large and that a minimum population size of 50, and preferably 100, is desirable.

ROBERTSON (1960, 1970b) proposed that the optimum selection intensity would be 0.50 to achieve maximum responses in large populations and the optimum proportion to select to achieve the maximum possible advance after n generations in populations of size T was a function of n/T and increased to 0.50 at n/T = 8. FRANKHAM (1977) found good agreement with this function with selection in *Drosophila* at low values of n/T, i.e. large populations, but when T was small the model did not agree. FRANKHAM suggested that small populations exposed the effects of strong major genes, linkage and inbreeding, particularly at high selection intensities. Again, the results demonstrate that optimum responses require large populations but if the selection programme is short (n small) then very intense selection may be the optimum procedure.

The development of linkage disequilibria in outcrossed populations

Linkage disequilibria have been recorded in long-term composite cross populations (ALLARD, 1977), and models have described genetic mechanisms which generate them. The outcome of each model is quite specific and dependent upon the specified gene interactions, recombination values, level of outcrossing and the linkage phases in the parent populations. Generally disequilibria were enhanced by close linkage and an increase in the proportion of selfing (ALLARD, JAIN and WORKMAN, 1966; JAIN, 1968; JAIN and ALLARD, 1966); see section 2.5.

Further evidence for the development of linkage disequilibria is reported in models designed to investigate outcrossing populations. These models are particularly relevant to composites which are permitted to respond to selection after controlled intermating has reduced the genetic effects arising from crossing unrelated homozygous parents.

Close linkage promotes states of stable equilibria (BODMER and FELSENSTEIN, 1967; FELDMAN, FRANKLIN and THOMPSON, 1974; KARLIN and FELDMAN, 1970) and partial selfing is also found to enhance stable equilibria (LEWONTIN and KOJIMA, 1960; LEWONTIN, 1964a) as found in outcrossing populations derived directly from intermated homozygous inbreds. LEWONTIN (1964a, 1964b) found that heterotic and optima models of genetic action promoted linkage desequilibria in populations initially at gametic equilibrium. The cumulative effects of adjacent loci were able to maintain disequilibria between distant independent loci.

Different models altered the proportions of coupling and repulsion phase equilibria and their relative frequency in different sectors of linked genes (FRASER, 1967). In general, disequilibria were strongest when the recombination values between adjacent loci were less than 0.1. In addition, JAIN (1968) and HILL and ROBERTSON (1968) found that the phase of disequilibria established in small populations was dependent upon the genetic drift and loss of alleles at particular loci.

When the number of closely linked loci exceed 10 to 20 in multiplicative heterotic models, FRANKLIN and LEWONTIN (1970) found the number of loci became less important than the total map length of chromosome and loci 'crystallised' into supergenes which conferred selective advantage on sections of chromosome rather than individual loci. Similar results were obtained by SVED (1972) but CLEGG (1978) and ASMUSSEN and CLEGG (1981) argued that the 'crystallisation' effect only occurs with specific relationships of selection intensity, recombination values and gene frequencies. In experimental populations of *Drosophila* they found a markedly non-uniform distribution of selective effects along chromosomes. LEWONTIN and HULL (1967) developed a model deomonstrating interactions between blocks of genes. In blocks with loose linkage fixation tended to occur, but with tightly linked blocks, balanced gametic structures developed.

Changes in gametic frequencies caused by bottlenecks through only one small population may require many hundreds of generations to decay if recombination values are small, even though subsequent populations may be large (AVERY and HILL, 1979). Continued propagation in small populations would slow the decline of disequilibria. (HILL, 1977).

In summary, the evidence from theoretical studies strongly suggests that selection in composites will produce significant genetic disequilibria between closely linked loci. Although the mode of interaction of genes will influence the magnitude of the disequilibria it is probable that they could determine the gametic structure on long segments of chromosome. The enhancement of disequilibria by 'bottlenecks' is particularly relevant to composite breeding. If small samples are selected to reconstitute a breeding population, disequilibria will probably be established. Their magnitude would be intensified if the selected sample was permitted to inbreed before reconstituting the composite population.

2.12 The Results of Long-term Selection Experiments

Short term experiments on selection in conjunction with intermating in autogamous species have indicated the potential of this breeding procedure (Section 2.10). The availability of completely effective nuclear male-sterility in wheat (and other autogamous species) now facilitates long-term selection in conjunction with intermating in composites and recurrent selection breeding programmes. Apart from the results of long-term natural selection in barley composites (Section 2.5) there are no examples of long-term selection in outcrossing (or partially outcrossing) populations of autogamous species. However, long term selection studies have been reported with *Zea mays* and *Drosophila melanogaster* and their results may indicate the major effects which could be expected in autogamous species, such as wheat.

The most significant result from long-term selection in both corn and fruitfly has been continuing response to selection for many characters after many generations, ranging from 50 to 90 in different studies, providing that the number of individuals per generation was large (WOODWORTH, LENG and JUGENHEIMER, 1952; LENG; 1961; DUDLEY, 1977; FRANKHAM, JONES AND BARKER, 1968a, b; JONES FRANKHAM and BARKER, 1968; YOO, 1980). Although the responses achieved are usually many times greater than the standard error of the genetic variation in the parent population, simple models of free recombination between a large number of loci (ROBERTSON, 1970a) or of recombination between loci still in intact parental gene sequences (see Section 2.11) are sufficient to explain the continuing response to selection after many generations.

The path of response over generations is usually irregular even in large populations. For example, in corn, selection for low protein for 76 generations had two response phases interrupted by a stable period for 20 generations (DUDLEY, 1977). In fruit fly, YOO (1980) found short periods of more rapid gain in abdominal bristle number in a continual response over 90 generations. Irregularities in response rate possibly reflect stages of release of genetic variation, its exploitation and 'waiting times' before new significant genetic events, such as useful recombinations. YOO (1980) found periods of rapid response were associated with increased phenotypic variance and perturbations in skewness and kutosis, suggesting the influence of major factors in phenotypic expression.

Irregularity of response becomes more pronounced in smaller populations and with high selection intensities (FRANKHAM, JONES and BARKER, 1968a, b; MATHER and HARRISON, 1949). The results in small populations do not correspond with models of theoretical responses to selection with minor genes (GILL, 1965; ROBERTSON, 1960) but tend to resemble responses in models of linked major genes in small populations (FRASER, 1957; FRASER and HANSCHE, 1965; HILL and ROBERTSON, 1966; LATTER, 1965a, b; 1966a, b;). In very small populations, individual replicate lines tend to reach plateaux of response after a few generations (usually of the order of 20) and crosses between these populations can allow a second phase of response which again tends to a plateau after a few generations (MATHER and HARRISON, 1949). From a series of selection experiments with fruitfly, THODAY and BOAM (1961), THODAY, GIBSON and SPICKETT (9164), SPICKETT and THODAY (1966) and THODAY (1977) postulated that irregular responses, plateaux and further responses after crossing were caused by the formation of coupling recombinants between a small number of genetic locations and that these locations (genes or small segments) accounted for most of the response. Furthermore, there was evidence that genes must be exploited in a particular order and that each location had a specific effect.

Other features of long term selection experiments have been the common occurrence of a relatively rapid phase of selection in the first 5 to 10 generations, rapid responses to relaxed or reversed selection and correlated responses in other character not under selection. Rapid initial responses probably reflect the exploitation of independent major genes with high frequency while recombinations and desirable genes at low frequency become the principal determinants of later responses; (see Section2.11). Rapid response to reversed selection, even from plateaued lines, probably indicates that selection responses are dependent upon genetic interactions and linkage relationships which can be rapidly disrupted and decay if selection is not maintained (GRIFFING, 1960). Correlated responses may be undesirable; for example, reduced endosperm size in high oil lines of corn and reduced fertility in selected lines of fruitfly (DUDLEY, 1977, MATHER and HARRISON, 1949). Unfavourable correlated responses may be counteracted by selection indices (MATZINGER, COCKERHAM and WERNSMAN, 1977) or relaxing selection to allow random intermating before recommencing selection (MATHER and HARRISON, 1949).

These studies on long-term selection suggest a number of important implications for long term selection in wheat and other autogamous species. They obviously suggest that long-term selection should be successful, but after a short period (5 to 10 generations) of rapid response a slower long-term response may ensue. Even in large populations with modest selection intensity a regular long-term response may not occur but eventually populations should be obtained which exceed the variation in the initial population. The evidence from long-term selection in small populations or with high selection intensities suggests that the maximum possible gains will not be achieved. However, in practice, it may be rewarding to apply intense selection in a number of composites or families for a few generations and cross selections from the best lines rather than rely upon slower responses in larger populations. Partitioning of a long-term programme will also assist selection against undesirable negative correlations.

In the review of short-term selection (section 2.10) strategies involving alternating cycles of intermating and inbreeding were found more reliable for increasing yield in autogamous species. This conclusion would undoubtedly be sustained in longer term selection. Consequently the progress of long-term selection for yield in a programme with frequent outcrossing would require regular monitoring through testing S_1 and more homozygous inbred derivatives to ensure that the chosen selection strategy leads to impovement in the yield of derived inbreds. There is no evidence on the effectiveness of improving yield in wheat by selecting for plant components in a long-term continuous series of outcrossed generations.

3. EXPERIMENTAL PROGRAMME

3.1 Establishment of the composite population

The 'Cornerstone' nuclear male-sterile stock was initially derived from the cross Federation monosomic 4A x Pitic 62, following γ-irradiation of the pollen of the latter cultivar (DRISCOLL, 1977). Federation was selected because a monosomic 4A stock was available, and Pitic 62 was chosen because of its high general combining ability for yield (DRISCOLL, pers. comm.; ANWAR and ABDUR, 1969; WALTON, 1971).

The composite cross population was established by crossing a 'Cornerstone' stock, Federation monosomic 4A/Pitic 62 (γ-irradiated pollen)//2*Pitic 62 as a female parent (homozygous recessive male-sterile) with seven Australian wheats; Condor, Gamenya, Gamset, Kite, Timgalen, WW-15 and Zenith. 136 F_2 seeds were taken after selfing each of the seven heterozygous (*Msms*) fertile F_1 hybrids, except from the crosses of Condor and Kite which produced only 133 and 27 F_2 seeds respectively. Therefore the parental contributions to the initial genic composition of the composite were Pitic 62:0.44, Gamenya, Gamset, Timgalen, WW15 and Zenith ~~and~~ 0.08, Condor 0.08, Federation 0.06 and Kite 0.02.

The six varieties and the unreleased red-grained germplasm (WW-15) were chosen as a representative sample of Australian wheats which had been widely grown and recognised for particular agronomic qualities or as successful parents in Australian breeding programmes (DRISCOLL, pers. comm.). The pedigrees of the seven parents were delineated by MOSS and WRIGLEY (1974). They are derived from a significant portion of the progenitors of Australian wheats. Federation was bred by Farrer from crosses presumed to involved Purple Straw (from England), Improved Fife (Canadian) and Etawah (Indian) and released in 1901 (MACINDOE and WALKDEN BROWN, 1968). Pitic 62 was bred by CIMMYT, Mexico.

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The 840 F_2 seeds were mechanically mixed and space planted on a 20 cm x 20 cm grid in an isolation block at the Waite Agricultural Research Institute in winter, June, 1976. 691 F_2 plants established and headed. They segregated 531 fertile: 160 male-sterile (x^2 (3:1) = 1.25, p = 0.3 to 0.2) and each plant was individually harvested (DRISCOLL, 1978).

The progenies of the fertile plants were retained as a control population of F_2-derived F_3 families. 100 male-sterile plants were randomly selected and 10 seeds taken from each. The 1,000 seeds were mechanically mixed and sown in an isolation block on a 20 cm x 20 cm grid at the Waite Agricultural Research Institute in summer (January), 1977. This population is designated Random-1977S abbreviated to R77S, to indicate the method of choosing its 100 parent plants, R, the year, 77, and season, S, it was grown. This study was initiated from the R77S population.

3.2 Propagation of the Composite Cross

Propagation of the composite cross commenced in the F_2 population when male-steriles were randomly chosen after cross-pollination by pollen from fertile F_2 plants. From the F_2 and all subsequent generations the composite cross population was maintained through progenies of male-sterile plants only.

Two selection series of the composite cross were propagated: a 'Random' series in which parental male-steriles were chosen randomly in each generation and a 'Selected' series in which the parental male-steriles were selected for height less than 100 cm, and headlength and spikelet number of the longest head on each plant. The two series were commenced by selecting two sets of male-steriles from the R77S population to establish the 'Random 1977 Winter' (R77W) and 'Selected 1977 Winter' (S77W) populations. Random selection only was conducted in the R77W population and subsequent generations of the 'Random' series. In the S77W and subsequent generations of the Selected series male-steriles selection continued for height less than 100 cm and greatest expression of headlength and spikelet number.

This strategy resulted in two parallel series which were propagated until summer 1981 (Figure 1). The generations in each series are described using the notation developed in Section 2.10. For example, the R77W population is the result of an outcross to generate the F_1 (0_1) and one inbreeding (I_1) producing F_2 seed and an outcross in the F_2 followed by random selection of male-sterile parents (0_{1R}). Because there was no selection (other than random choice) of male-steriles in the F_2, one generation of outcrossing with random selection occurs in the derivation of the 'Selected' series.

In the R77S, R77W, R78S, S77W and S78S populations eight characters were scored or measured on each individual plant.

(1) Classification into male-fertile or male-sterile

(2) Height (cm). In the R77S population plants were only classified as tall (>100 cm) or short (<100 cm).

(3) The number of spikes per plant

(4) The length of the longest head (mm) from the base of the lowest spikelet node to the extremity of the glumes at the apex. The awn length was disregarded.

(5) The number of spikelets, including undeveloped basal spikelets, in the longest head.

(6) The number of grains in the longest head

(7) The grain yield of the longest head (g)

(8) The total grain yield of the plant (g)

In the R77S populations only 667 of the 1,000 sown seeds produced seed bearing plants because of losses at establishment and segregation of grass-clumps. They were classified into 410 fertiles and 257 steriles. From the 257 steriles, 100 were chosen randomly as parents of the R77W population and, also from all 257 steriles, the 100 with greatest headlength and spikelet number in the longest head on each plant less than 100 cm tall were selected as parents of the S77W population. Therefore, some steriles from the R77S population were in both sets of 100 parents.

Figure 1: Description of the 'Random' and 'Selected' outcrossing series

	'Random' Series	'Selected' Series
1976 Winter	F2	
	(O_1I_1) ↓	
1977 Summer	R77S	
	$(O_1O_1O_{1R})$ ↓	→
1977 Winter	R77W	S77W
	$(O_1I_1O_{2R})$ ↓	$(O_1I_1O_{1R}O_{1S})$ ↓
1978 Summer	R78S	S78S
	$(O_1I_1O_{3R})$ ↓	$(O_1I_1O_{1R}O_{2S})$ ↓
1978 Winter	R78W	S78W
	$(O_1I_1O_{4R})$ ↓	$(O_1I_1O_{1R}O_{3S})$ ↓
1979 Summer	R79S	S79S
	$(O_1I_1O_{5R})$ ↓	$(O_1I_1O_{1R}O_{4S})$ ↓
1979 Winter	R79W	S79W
	$(O_1I_1O_{6R})$ ↓	$(O_1I_1O_{1R}O_{5S})$ ↓
1980 Summer	R80S	S80S
	$(O_1I_1O_{7R})$ ↓	$(O_1I_1O_{1R}O_{6S})$ ↓
1980 Winter	R80W	S80W
	$(O_1I_1O_{8R})$ ↓	$(O_1I_1O_{1R}O_{7S})$ ↓
1981 Summer	R81S	S81S
	$(O_1I_1O_{9R})$	$(O_1I_1O_{1R}O_{8S})$

The R77W and S77W populations were established by planting 10 progeny from each parent in 100 family rows. The parent plants for the R78S population were one randomly chosen male-sterile from each family row. If there was no sterile in a row, a substitute was selected in the next row sampled. Again 10 progeny from each of the 100 steriles were planted to constitute the R78S population. The parents for the S78S population were selected from the total S77W population of steriles without family restraint, using the same criteria as for selection of the parents of the S77W population from the R77S.

After the 78S generation there was a dichotomy in the programme. Fertile plants were selected from the R78S and S78S populations to commence an inbreeding programme. Also the two composite series were continued, but measurements on individual plants were discontinued because of the demands of other aspects of the experimental programme. The Random series was continued by randomly choosing one sterile from each family row and establishing 100 progeny rows of 10 plants each. The parental steriles of the 'Selected' series were chosen visually from all steriles in each population less than 100 cm tall, and 10 progeny from each of the 100 selected steriles were grown in family rows in the subsequent populations of the 'Selected' series. The 'Random' series was propagated from winter 1977 until summer 1981 at the Northfield Research Laboratories and the 'Selected' series at the Waite Agricultural Research Institute. Both sites are at Adelaide, South Australia.

The 'Summer' generations were sown in January and harvested in late May and the 'Winter' generations were sown in June and harvested in December. The former were irrigated and the latter grew under natural rainfall. All populations in each series from winter 1977 to summer 1981 were established in peat pellets and transplanted as seedlings into a space planted grid with 20 cm spacings within rows and alternate 20 and 30 cm spacings between rows to allow easy access to the populations to distinguish fertile and male-sterile plants. All isolation blocks were fertilized with 20 $g.m^{-2}$ of superphosphate and 10 $g.m^{-2}$ of ammonium nitrate and sprayed with Dachthal (R) to control weeds.

3.3 EXPERIMENT 1: Analysis of the expression of characters of individual plants in the R77S, R77W, S77W and S78S populations

The ratio of fertile to sterile plants

In the F_2 the ratio of fertile to sterile plants did not differ significantly from 3:1 (DRISCOLL, 1978; see Section 3.1). This conforms with the allele for male-sterility, *mscl* (hereafter dengnated *ms*) behaving as a simple recessive with equal effectiveness of *Ms* and *ms* pollen in fertile F_1 plants. The classification of plants in the F_2 and each of the five populations resulting from the first three cycles of outcrossing is presented in Table 1. If transmission of *Ms*-and *ms*-pollen from fertile to male-sterile plants is equally effective the expected ratios of fertiles:steriles are 2:1 in the R77S and 1:1 in all generations thereafter. Ex~~pect~~cept for the F_2, the observed frequencies of fertiles and steriles departed signficantly from the expected ratios.

Differential survival of fertiles and steriles prior to anthesis and differential pollination effectiveness of wind-borne *Ms* and *ms* pollen grains are possible causes of these departures from expected ratios. It is unlikely that differential survival would cause the considerable departures in the R77S and subsequent generations and not in the F_2. Therefore, the more probable explanation for the departures from the expected ratios is diffe~~n~~rential transmission of *Ms* and *ms* pollen from fertiles to male-steriles. Rather than 1:1, a ratio of approximately 3:2 is obtained.

The difference of character expression between fertile and sterile plants.

Introduction

Seven characters were measured on each individual plant in the R77S, R77W, R78S, S77W and S78S populations, (see Section 3.2). That is, all plants produced by the first three cycles of outcrossing within the 'Random' (R) and 'Selected' (S) series were measured.

Table 1: The number and proportion of fertile and sterile plants in the F_2 and first three composite generations in the Random and Selected series.

Population	No. of Plants			χ^2	Probability
	Total	Fertile	Sterile		
F_2	691	531 (0.768)	160 (0.232)	1.35 (3.1)*	0.3 - 0.2
R77S	667	410 (0.615)	257 (0.385)	8.11 (2.1)*	0.01-0.001
R77W	947	569 (0.601)	378 (0.399)	38.52 (1.1)*	0.001
R78S	885	483 (0.546)	402 (0.454)	7.41 (1.1)*	0.01-0.001
S77W	939	576 (0.613)	363 (0.387)	48.32 (1.1)*	0.001
S78S	878	514 (0.585)	364 (0.415)	25.63 (1.1)*	0.001

* Expected ratio if *Ms* and *ms* pollen are equally effective

Three characters, height and the length and number of spikelets in the longest head on each plant, were used to select the male-sterile parents for the 'Selected' propagation series. The number of heads and total grain yield per plant were measured to complete a general morphological description of each plant. The number and yield of grains in the longest head were measured because evidence from analyses of plant components suggest they are probably the most reliable indicators of the breeding value of individual heterozygous plants (see Section 2.7).

Results

The frequency distribution of the seven measured characters on individual fertile and sterile plants in each of the five populations are presented in Figures 2 to 8. The overall mean of each character and its mean in fertiles and steriles in each population are presented in Table 2. The level of significance for the Kolmogorov-Smirnov test for differences between the distributions of fertiles and steriles and the 'F' test for differences between means, where not invalidated by significant departure from normality in the distributions, are presented for each population.

The lower seed-set on male-sterile plants caused extremely significant differences in the three characters dependent upon seed-set; number of grains (GN) and grain yield (GY) in the longest head and the total grain yield per plant (TY).

Plant height (HT), the length of the longest (HL) and number of spikelets on the longest head (SN) were all greater in fertiles in the R77S, R77W where the significant Kolmogorov-Smirnov test probably indicates a difference in distribution rather than mean between fertiles and steriles (Figure 5, S77W). In the R78S and S78S populations neither test indicated any significant difference in plant height, head length or spikelet number between fertiles and male-steriles. The diminution of the differences between fertiles and steriles through successive generations is clearly evident in Figures 2, 4 and 5.

Table 2: The means of seven characters of all plants and the fertiles and steriles in the R77S, R77W, R78S, S77W and S78S composite populations. Parentheses indicate 'F' tests invalidated by non-normality.

Character	Population	Plant Classification			Statistical Test (Fertiles vs. Steriles)	
		Total	Fertiles	Steriles	'F' Test	Kolmogorov Smirnov
Plant Height (HT) (cm)	R77S	-	-	-	-	-
	R77W	95.34	96.32	93.88	**	N.S.
	R78S	81.24	83.01	83.52	N.S.	N.S.
	S77W	101.81	103.73	98.75	***	**
	S78S	86.41	86.88	85.76	N.S.	N.S.
Number of Heads(HN)	R77S	14.21	14.44	12.45	N.S.	N.S.
	R77W	7.18	7.40	6.84	**	*
	R78S	12.43	11.39	13.69	(***)	**
	S77W	7.58	7.85	7.14	(***)	*
	S78S	13.35	13.04	13.78	(N.S.)	N.S.
Head Length(HL) (mm) (longest head)	R77S	99.52	103.97	92.43	***	**
	R77W	110.25	111.55	108.29	**	**
	R78S	93.95	93.21	94.83	N.S.	N.S.
	S77W	115.15	114.51	116.17	N.S.	N.S.
	S78S	109.76	109.37	110.32	N.S.	N.S.
Number of Spikelets (SN) (longest head)	R77S	18.18	18.82	17.17	***	**
	R77W	19.64	19.83	19.35	***	**
	R78S	17.47	17.41	17.55	N.S.	N.S.
	S77W	20.70	20.41	21.16	(***)	**
	S78S	20.19	20.14	20.26	N.S.	N.S.
Number of Grains(GN) (longest head)	R77S	26.97	36.79	11.30	(***)	**
	R77W	39.19	50.80	21.71	(***)	**
	R78S	18.75	29.63	5.68	(***)	**
	S77W	40.90	50.84	25.12	(***)	**
	S78S	25.05	37.34	7.70	(***)	**
Grain Yield(GY) (g) (longest head)	R77S	1.31	1.41	0.37	(***)	**
	R77W	1.50	1.91	0.87	(***)	**
	R78S	0.71	1.10	0.23	(***)	**
	S77W	1.64	2.00	1.07	(***)	**
	S78S	0.94	1.37	0.33	(***)	**
Total Grain Yield (TY) (g)	R77S	20.04	21.60	5.11	(***)	**
	R77W	7.38	9.48	4.22	(***)	**
	R78S	6.93	10.57	2.51	(***)	**
	S77W	8.87	11.25	5.10	(***)	**
	S78S	9.19	13.65	2.90	(***)	**

Figures 2 to 8

The frequency distributions of seven characters of individual plants in the R77S, R77W, R78S, S77W and S78S composite populations

Figure 2: Plant Height

Figure 3: Number of heads per plant

Figure 4: Length of the longest head

Figure 5: Number of spikelets on the longest head

Figure 6: Number of grains in the longest head

Figure 7: Grain yield of the longest head

Figure 8: Total grain yield per plant

X

○ Male sterile

● Male fertile

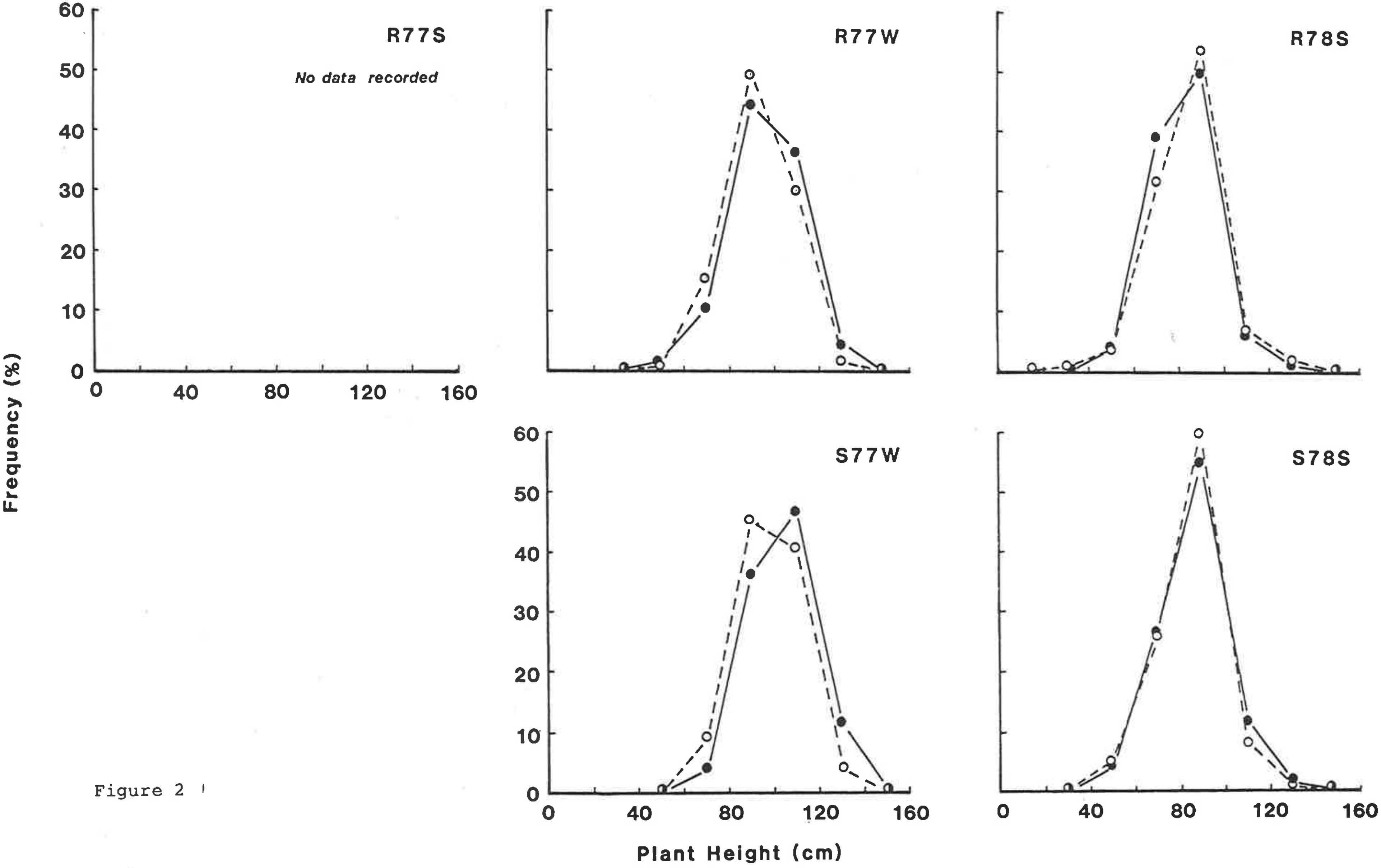

R77S
No data recorded
R77W
R78S
S77W
S78S
Frequency (%)
Plant Height (cm)
0
10
20
30
40
50
60
0
40
80
120
160

Figure 2

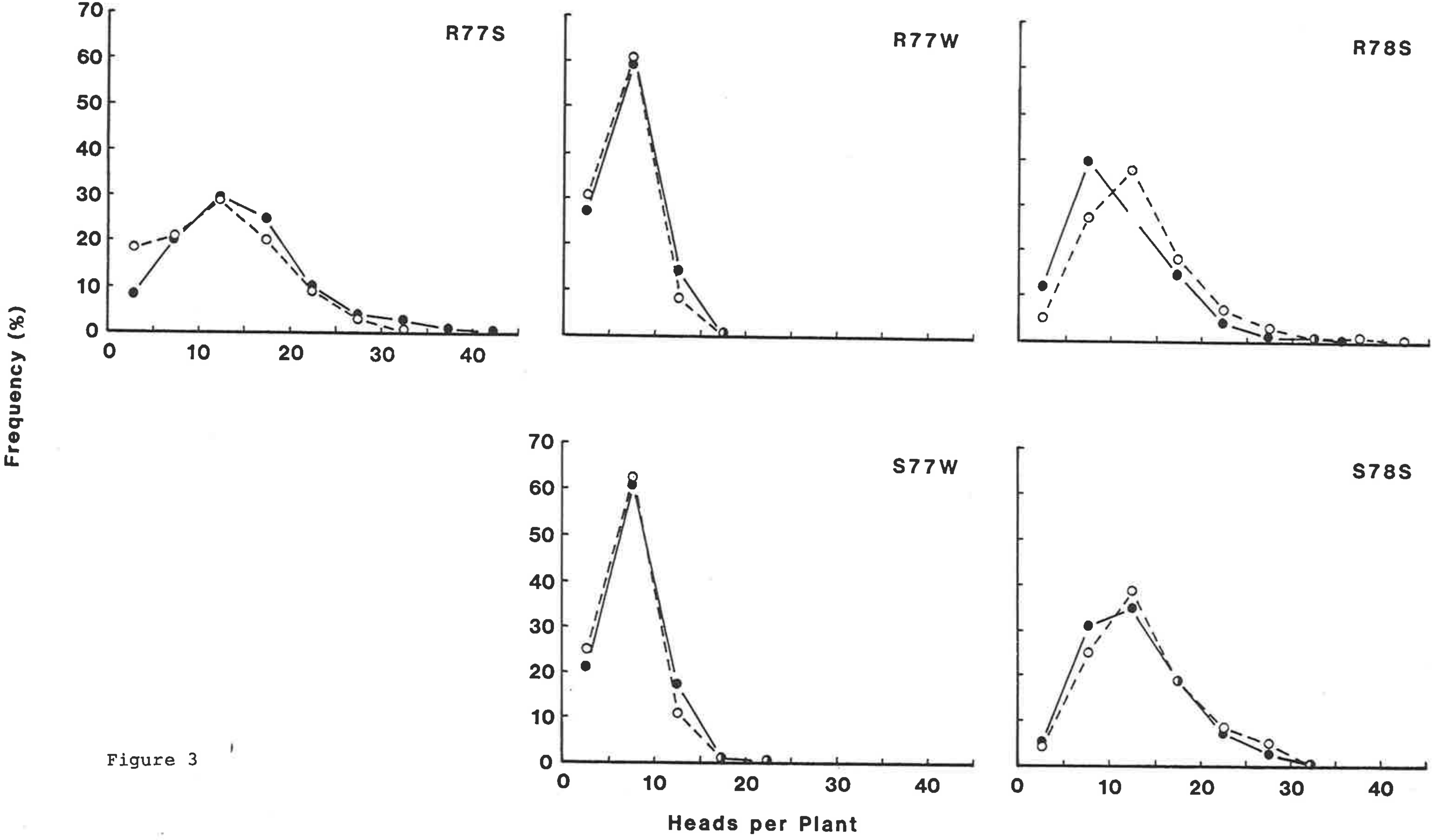

R77S
R77W
R78S
S77W
S78S
Frequency (%)
Heads per Plant
0
10
20
30
40
50
60
70
0
10
20
30
40

Figure 3

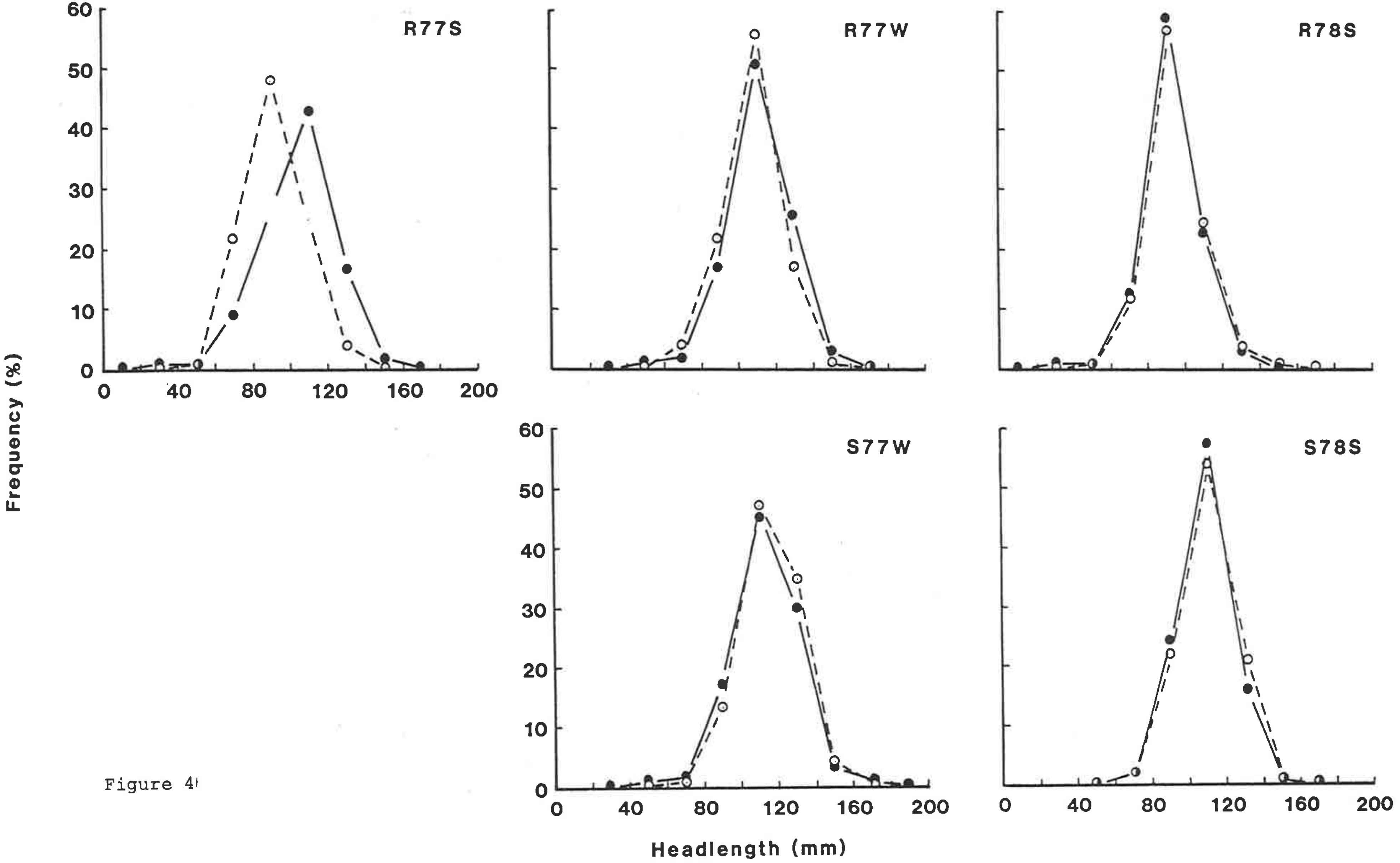

R77S
R77W
R78S
S77W
S78S
Frequency (%)
Headlength (mm)
0
10
20
30
40
50
60
0
40
80
120
160
200

Figure 4

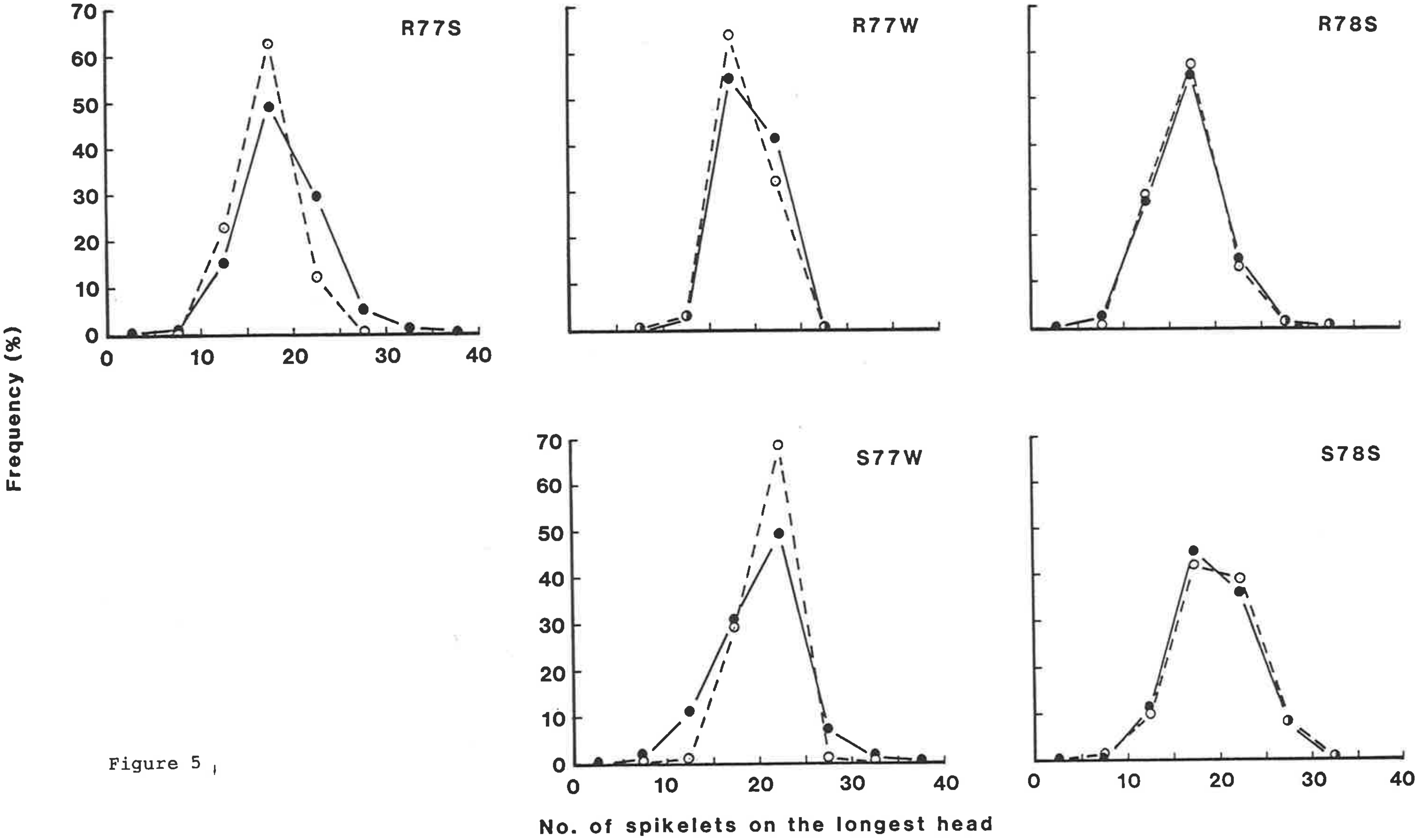

R77S
R77W
R78S
S77W
S78S
70
60
50
40
30
20
10
0
0
10
20
30
40
Frequency (%)
No. of spikelets on the longest head

Figure 5

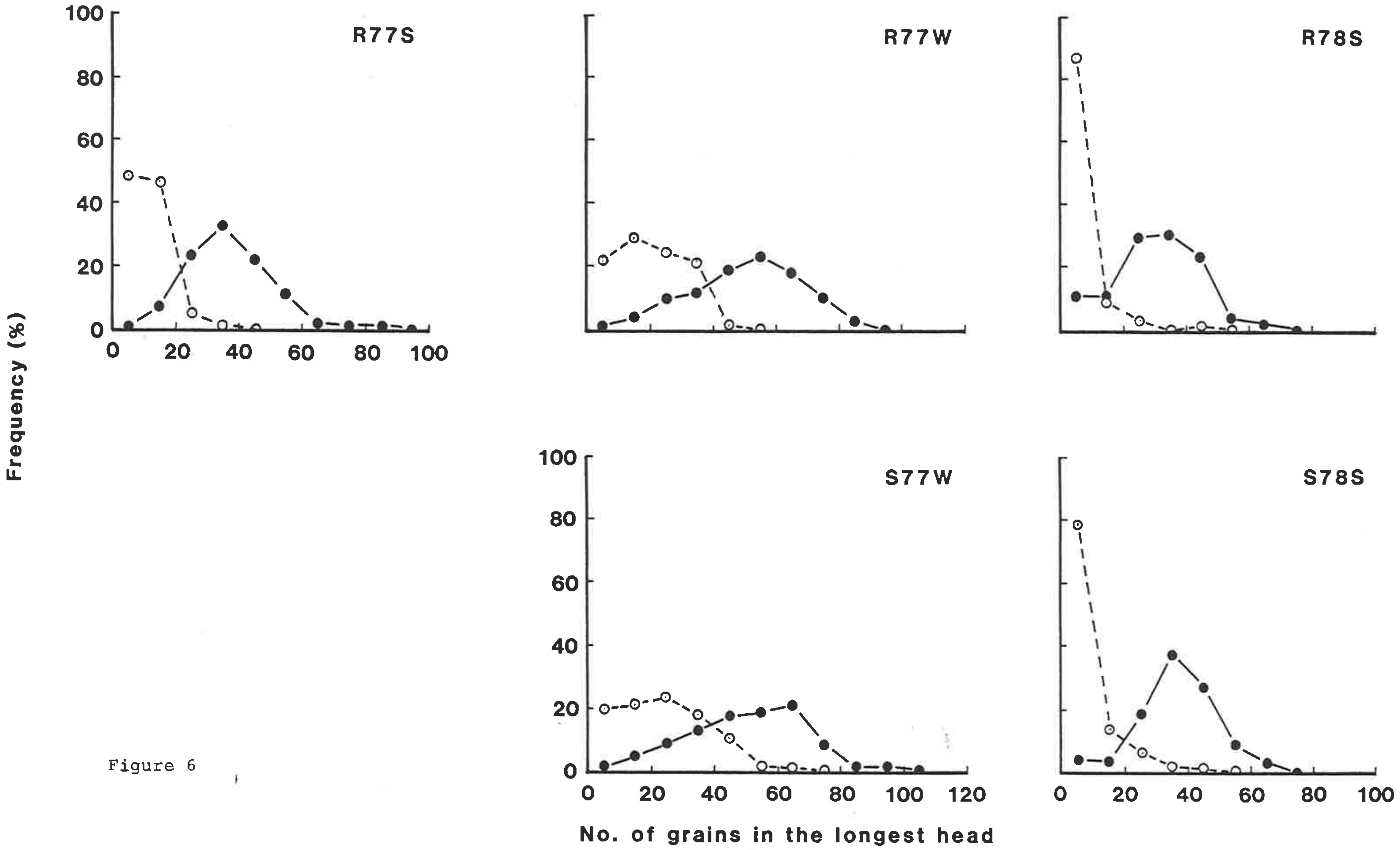

R77S
R77W
R78S
S77W
S78S
Frequency (%)
No. of grains in the longest head
0
20
40
60
80
100
120

Figure 6

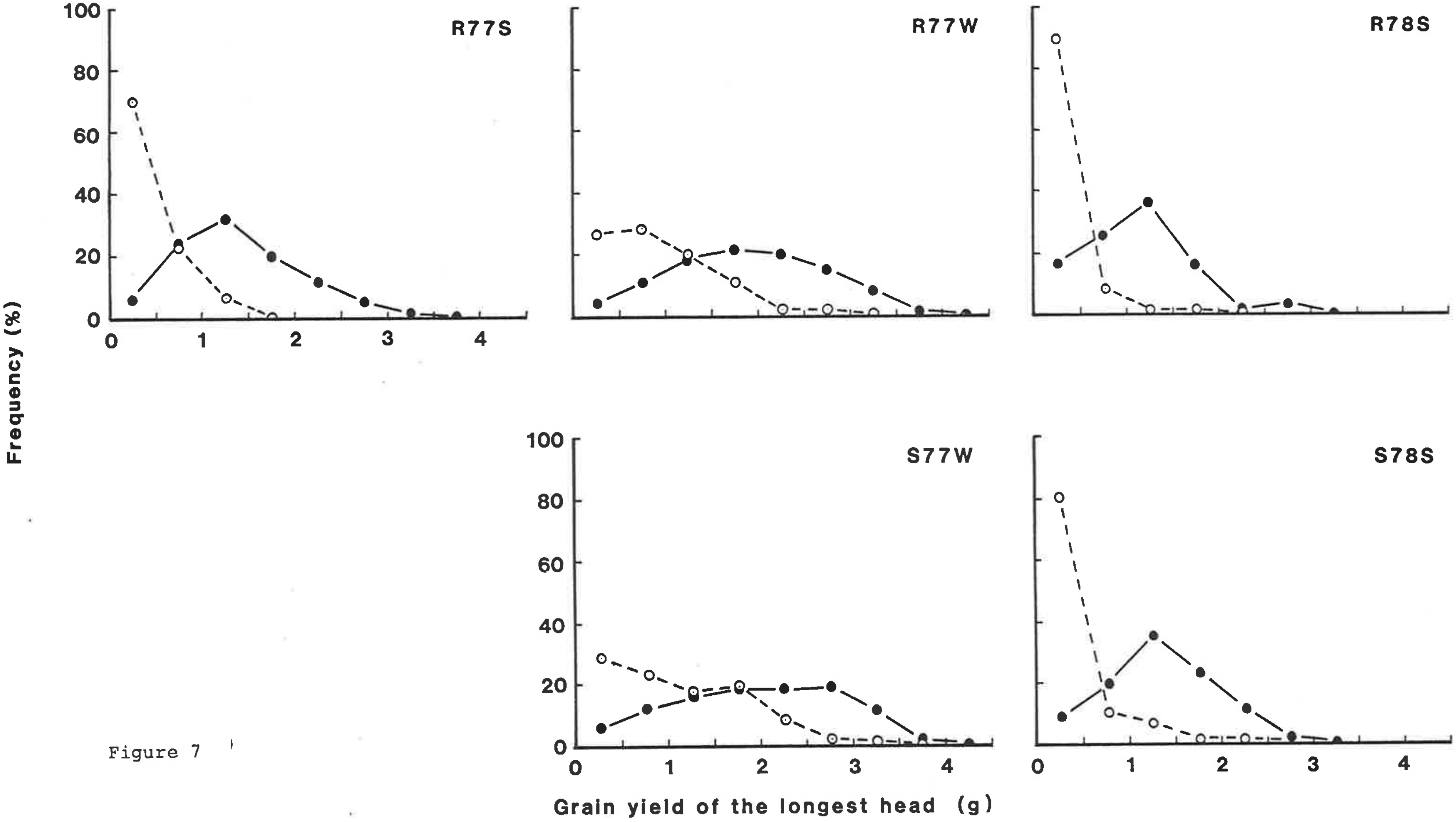

R77S
R77W
R78S
S77W
S78S
100
80
60
40
20
0
0
1
2
3
4
Frequency (%)
Grain yield of the longest head (g)

Figure 7

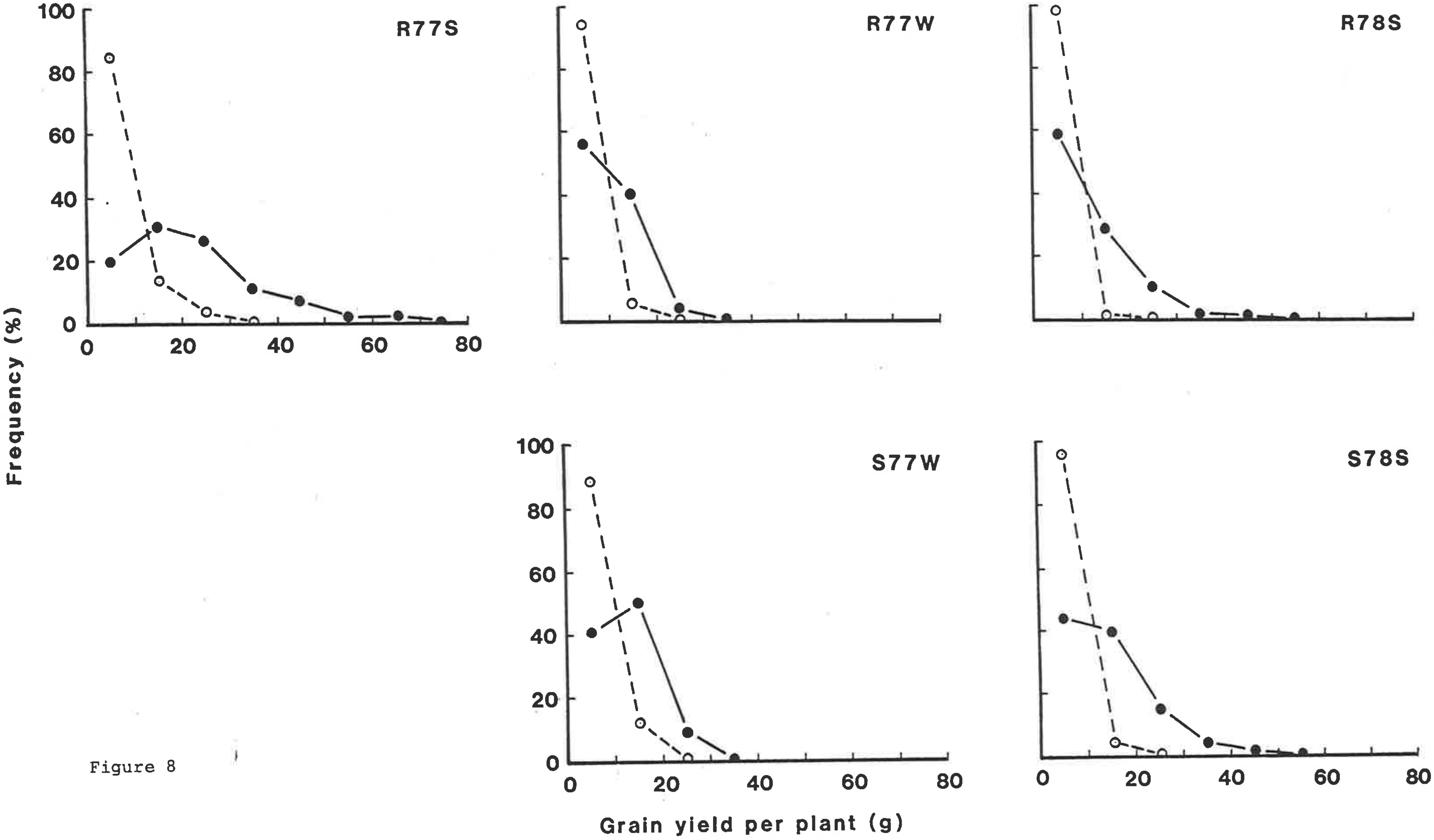

R77S
R77W
R78S
S77W
S78S
100
80
60
40
20
0
0
20
40
60
80
Frequency (%)
Grain yield per plant (g)

Figure 8

Selection for headlength and spikelet number appears to have increased the frequencies of heads longer than 120 mm and heads with more than 20 spikelets in both the S77W and S78S populations relative to the corresponding R77w and R78S. A statistical test of these differences is of little value because the populations were grown in isolation. Nevertheless the populations were sown on the same days and the climatic and edaphic conditions at the two sites (Waite Agricultural Research Institute and Northfield Laboratories) are similar. Therefore, there is a strong likelihood the differences are real.

The trends in number of heads per plant (HN) were erratic in each series (Table 2) but the significant differences between the distributions were small in each population (Figure 3). The effect of season (summer vs winter) was very pronounced.

Although the difference of expression of each character between seasons is confounded with generation and selection strategies the data suggest that summer-grown plants are shorter and have more heads, but the heads are shorter with less spikelets and grains per head, which is reflected in lower grain yield in the longest head. The higher number of heads per plant in summer over-compensated for lower individual fertile head yields and partially compensated for lower seed-set on steriles.

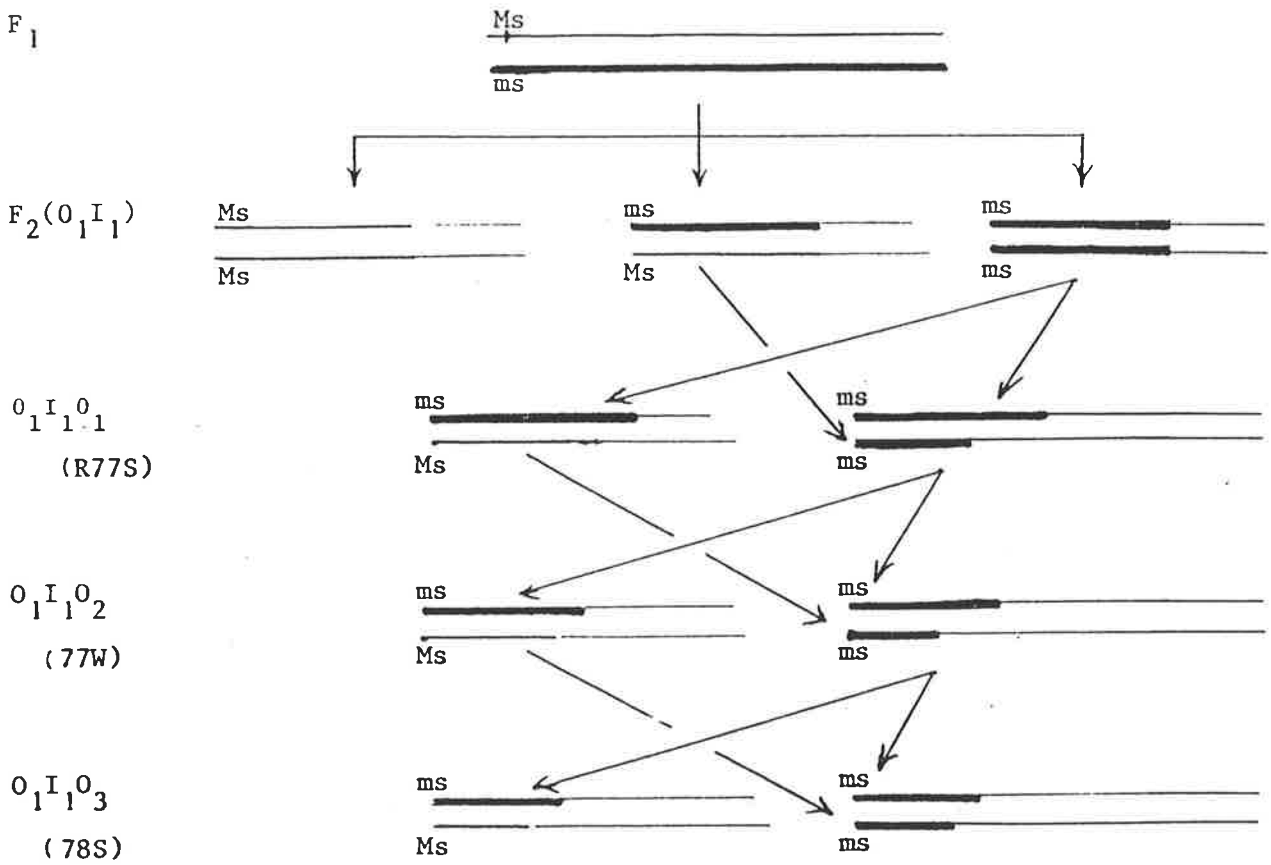
Discussion

The significantly lower seed-set on male-steriles (45% of fertiles in the winter generations and 23% in the summer generations, as judged by seed-set on the longest head) precludes using yield and yield components to select male-sterile parent plants. Consequently characters not dependent upon yield, such as headlength and spikelet number, must be utilised. Therefore, the first determination of the breeding value of an S_0 individual using yield must be delayed until heterozygous fertiles are obtained in the S_1 generation. If seed-set on steriles were equivalent to fertiles as in sorghum (DOGGETT, 1968), 'female choice' selection for yield could be practical. In Experiment 2 (Section 3.4) 'female choice' selection for height, headlength and spikelet number was tested. In Experiment 3 (Section 3.5) the effectiveness of selection in this wheat composite for yield by using components was investigated.

The difference in plant height, headlength and spikelet number between fertiles and steriles in the 77S and 77W generations were probably caused by differences between the genes in each plant class in the vicinity of the *ms* locus. In Figure 9, I have diagrammatically demonstrated the effect of the *Ms* and *ms* alleles on maintaining, in the vicinity of the *ms* locus, heterozygosity in fertiles and homozygosity in male-steriles. The 'Cornerstone' mutant is possibly a terminal deletion on the 4A-chromosome (DRISCOLL, pers. comm.). The heterozygous condition of fertiles results from crossing 'Cornerstone' with seven fertile wheats to produce the F_1. The average length of intact chromosome which remains linked to the *Ms* and *ms* alleles in each generation would be dependent upon the nature and position of the *ms* mutant, the length of chromosome 4A, the population size, the effects of natural and directional selection and the number of generations of propagation (HANSON, 1959c; SVED, 1971; STAM, 1980). It can be assumed that in the F_2 and R77S populations the average length of intact homozygous segment linked to homozygous *ms* in steriles and the region of heterozygous segments in fertiles would be quite long and only reduced significantly after a number of generations of outcrossing. At all loci not linked to *ms* no differences are expected between fertiles and steriles in the frequencies of genes from either 'Cornerstone' or the seven fertile parents. As outcrossing allowed an approach to random assortment near *ms* (disregarding the effects of natural and directional selection) the level of enforced heterosis in fertiles would have been reduced, resulting in no significant differences between fertiles and steriles in the 78S populations.

The significant differences which probably resulted from heterotic effects near the *ms* locus highlight the restriction that linkage to *ms* can impose upon recombination and also emphasises the need to propagate a composite containing a male-sterile through sufficient outcrossing generations to reduce the effect of initial linkage to the *ms* locus.

Figure 9: A diagramatic representation of the expected differences between the intact chromosome segments linked to the *Ms* and *ms* genes in a composite propagated only by outcrossing in each generation



Selection of male-steriles in the R77S and S77W populations shifted the frequency distribution of plant height, head length and spikelet number. The series had diverged after R77S.

A significant contributor to increased headlength and spikelet number may have been the Pitic 62 parent of 'Cornerstone' which contributed approximately 44% of the alleles of the composite. Pitic 62 has a high expression of spikelet number (RAWSON, 1970) and high combining ability for headlength and spikelet number (WALTON, 1971). Chromosome substitution studies indicate a small number of genes control headlength and spikelet number (HALLORAN, 1974). Spikelet number has a moderately high heritability, suggesting the action of only a few genes (SAYED, 1978), and dominant genes control the rate of spikelet initiation (RAHMAN and WILSON, 1977). Consequently a rapid response could be expected and was observed.

The highest expression of spikelet number in this study, 33 in S77W, was comparable to the maximum expression in wheat in the studies of FRIEND (1965), RAWSON (1971), and MOHAPATRA *et al*. (1982). High spikelet number was often associated with a pronounced clustering of spikelets near the apex and the presence of supernumerary spikelets (SCHLEHUBER, 1949) in the basal to middle region of the spike. Each supernumerary spikelet was included in the spikelet number per head.

Although the parents of the composite seldom exceed 24 spikelets per head in the field in southern Australia the results indicate that selection for higher spikelet number would be successful. RAHMAN *et al*. (1977, 1978) and RAHMAN and WILSON (1977) suggest that if the duration and rate of spikelet initiation and the number of double ridges at floral initiation were increased, higher spikelet numbers could be achieved.

Comparison of the mean expression of characters of the selected sets of parents with the populations from which they were selected.

Introduction

Commencing in the R77S, sets of 100 male-steriles were either chosen at random to generate the 'Random' series of populations or selected for height less than 100 cm and head length and spikelet number to generate the 'Selected' series. No data were collected on characters in the F_2 to validate that the 100 F_2 male-steriles chosen as parents of R77S were a true random sample. Comparison of the parents of the R77W and S77W with the R77S population can validate that the parent sample for R77W was random and demonstrate that selection chose a population of parents for S77W with higher mean expression of headlength and spikelet number and possibly a shorter height than the R77S population. Similarly, comparison of the random parent set from R77W and the selected set from S77W with their respective populations would validate that the parents of R78S were a random set of R77W and that the parents of S78S had mean expressions of selected characters significantly different from the mean of S77W. Comparisons of the means of all measured characters of the selected parents with the means of their respective total~~s~~ populations would also indicate any significant correlated responses to selection.

In addition to the sets of male-sterile parents, sets of 100 fertile plants were chosen from the R78S and S78S to initiate an inbreeding programme which will be described in Section 3.7. These sets of fertiles were selected using the same criteria as in selection of male-steriles. That is, in the 'Selected' S78S population fertiles were selected for height, headlength and spikelet number but not for grain number and yield. In the R77S they were chosen randomly. The comparisons of these sets of fertiles with their respective populations is included in this section.

Results

In table 3 the mean expression of each of the seven measured characters: height, head number, total plant yield, and the headlength,

Table 3: The means of seven characters in total composite populations, fertiles, steriles and selected samples of parents.

Population	Character	Classification			Selected sample	Total vs Sample	Class vs Sample
		Total	Fertiles	Steriles			
R77S	HT	–	–	–	–	–	–
	HN	14.21	14.44	12.45	(R)12.52	*	ns
					(D)12.81	*	ns
	HL	99.52	103.97	92.43	(R)95.22	*	ns
					(D)100.71	*	**
	SN	18.18	18.82	17.17	(R)17.66	ns	ns
					(D)18.34	**	**
	GN	26.97	36.79	11.30	(R)12.46	**	ns
					(D)13.41	**	*
	GY	1.31	1.41	0.37	(R) 0.55	**	*
					(D) 0.58	**	*
	TY	20.04	21.60	5.11	(R) 7.65	**	ns
					(D) 7.98	**	*
R77W	HT	95.34	96.32	93.88	(R)92.32	ns	ns
	HN	7.18	7.40	6.84	(R) 7.02	ns	ns
	HL	110.25	111.55	102.29	(R)107.49	*	ns
	SN	19.64	19.83	19.35	(R)19.64	ns	ns
	GN	39.19	50.80	21.71	(R)19.83	**	ns
	GY	1.50	1.91	0.87	(R) 0.75	**	ns
	TY	7.38	9.48	4.22	(R) 3.60	**	ns
R78S	HT	93.24	83.01	83.52	(R)82.91	ns	ns
	HN	12.44	11.39	13.69	(R)12.24	ns	ns
	HL	93.95	93.21	94.83	(R)93.51	ns	ns
	SN	17.47	17.41	17.55	(R)17.65	**	ns
	GN	18.75	29.63	5.68	(R)30.66	**	ns
	GY	0.71	1.10	0.23	(R) 1.12	**	ns
	TY	6.93	10.57	2.51	(R)11.27	**	ns
S77W	HT	101.81	103.73	98.75	(D)95.57	**	**
	HN	7.58	7.85	7.14	(D) 8.37	ns	*
	HL	115.15	114.51	116.17	(D)124.80	**	*
	SN	20.70	20.41	21.16	(D)22.61	**	**
	GN	40.90	50.84	25.12	(D)29.30	**	ns
	GY	1.64	2.00	1.07	(D) 1.16	**	ns
	TY	8.87	11.25	5.10	(D) 5.94	**	ns
S78S	HT	86.41	86.88	85.76	(D)88.23ø	ns	ns
	HN	13.35	13.04	13.78	(D)15.46ø	**	**
	HL	109.76	109.37	110.32	(D)114.62ø	**	**
	SN	20.19	20.14	20.26	(D)21.07ø	**	**
	GN	25.05	37.34	7.70	(D)41.23ø	**	*
	GY	0.94	1.37	0.33	(D) 1.62ø	**	**
	TY	9.19	13.66	2.90	(D)16.58ø	**	**

R - randomly chosen samples
D - directionally selected sets
ø - samples chosen from the fertiles

spikelet number, grain number and yield of the longest head, is presented for parent sets, the total populations, and the fertiles and steriles separately for the R77S, R77W, R78S, S77W and S78S populations.

The mean expressions of characters in the randomly chosen sets in R77S and R77W did not differ significantly from the means of their respective male-sterile populations except for grain yield of the longest head in R77S. This difference may reflect the requirements for male-sterile parents to have at least ten seeds. A corresponding significant difference did not occur for total plant yield (TY-R77S). Consequently the random male-sterile sets of parents were valid random samples. However, they were not valid samples of the total populations, which reflects the significant differences between fertiles and steriles (Table 2). Consequently the male-sterile sets differed significantly from the total populations for head number in R77S and headlength in both R77S and R77W, as well as in characters dependent upon seed-set.

The set of fertiles chosen randomly from R78S was also a valid random sample of the fertiles. Also it did not differ from the total population in any characters independent of seed-set except spikelet number.

The sets of male-steriles selected from R77S and S77W had significantly lower mean height and higher mean headlength and spikelet number than their respective total populations or male-sterile class. (Height was not measured in R77S). Therefore, the parent sets of S77W and S78S differed significantly in the direction of selection for the three selected characters. There were contrasting responses in the unselected characters in these two generations. Directional selection in the R77S did not significantly shift the mean of head number from the male-sterile class mean but did shift the means of seed-set dependent characters (GN, GY and TY). The reverse pattern occurred with selection in the S77W.

The set of fertiles selected from the S78S ~~were~~ was superior to the total population and the fertile class in all characters but height. Therefore, directional selection for headlength and spikelet caused a correlated positive response in seed-set dependent characters and reflects significant correlations which will be discussed in the next section.

Discussion

The lack of significant differences between random sets of parents and their respective class means indicates that the series R77W and R78S was generated through valid random parent sets and that the fertiles chosen from R78S for later inbreeding were also a valid random sample. Selection in the 'Selected' series proceeded through parents which resulted from significant selection for headlength and spikelet number in R77S, S77W andS78S and significant selection for height in S77W.

The difference between fertiles and steriles in the R77S ~~were~~ was of sufficient magnitude to cause significant differences between the randomly selected sample and the total population in head number and headlength. It was only in the R78S, after loss of significant differences between classes (Table 2), that the randomly selected parents were a random sample of the total population. It is of interest that the mean headlength, number of heads and spikelet number of the selected sterile parents from the R77S population was less than the mean of the fertile class, thereby emphasizing the significant differences between fertiles and steriles in that population.

It must be emphasised that the mean expression of characters in the male-sterile parents indicates that only the maternal parent was either randomly or directionally selected. In the 'Random' series the pollen which fertilized the male-steriles was probably not a random sample of equal numbers from each fertile. Consequently any selective difference in pollinator effectiveness of fertiles would have caused genetic shift in the 'Random' series even though the male-steriles were a valid random sample. Similar~~it~~ly in the 'Selected' series, there would have been competition between fertile pollinators. It is unlikely that competition between pollinators would have favoured plants similar to the chosen male-steriles parents in either composite series. Therefore, their progeny would be the outcome of crosses between pollinators with selective advantage and the chosen male-steriles. In each series significant genetic effects would be expected from competition between fertile polllinators. In the 'Selected' series additional effects would be expected from the interaction of natural selection between pollinators and deliberate directional selection within male-steriles. Any significant genetic effects may be indicated by changes in correlations between characters over successive generations.

The correlation between characters in the R77S, R77W, R78S, S77W and S78S populations.

Introduction

The nine parental genotypes of the composite populations are not closely related (Section 3.1). Strong linkage disequilibria would therefore, be expected, particularly in the F_1, F_2 and early generations. Consecutive cycles of intermating could reduce these disequilbria (ALLARD, JAIN and WORKMAN, 1966) and also reduce the magnitudes of correlations between characters (MILLER and RAWLINGS, 1967a) as recombination disrupted the initial parental linkage configurations. Alternatively, natural and directional selection could maintain or intensify the level of disequilibria and correlations between characters (BAL, SUNESON and RAMAGE, 1959).

Results and Discussion

The correlation coefficients between all 21 pairs of the seven characters measured on individual plants in the R77S, R77W, R78S, S77W and S78S populations are presented in Table 4 for all plants in each population and in Tables 5 and 6 for the fertile and sterile classes respectively. The trends in correlations between characters for the fertiles and steriles of each selection strategy, 'Random' and 'Selected', are presented in Figures 10,11, and 12.

Tables 4, 5 and 6

The coefficients of correlation between seven characters and the χ^2 value and degree of significance of a test for homogeneity of the coefficients of all populations in each pair of characters.

The descending order of populations in each cell is R77S, R77W, R78S, S77W and S78S.

All correlations were significant at $P<0.001$ unless indicated. ?

Table 4 : Total populations

Table 5 : Fertile plants

Table 6 : Sterile plants

Table 4

	HT	HN	HL	SN	GN	GY	TY
HT	–	– 0.363 0.523 0.291 0.393	– 0.475 0.585 0.315 0.393	– 0.202 0.492 0.211 0.280	– 0.268 0.157 0.384 0.108	– 0.379 0.225 0.442 0.197	– 0.416 0.363 0.448 0.347
HN	37.66 ***	–	0.233 0.521 0.453 0.306 0.319	0.196 0.342 0.397 0.156 0.232	0.167 0.287 0.029 0.277 0.058	0.147 0.292 0.061 0.236 0.114	0.595 0.605 0.416 0.616 0.454
HL	58.67 ***	551.2 ***	–	0.789 0.656 0.662 0.674 0.580	0.357 0.388 0.190 0.219 0.044	0.280 0.382 0.212 0.200 0.087	0.245 0.442 0.304 0.191 0.177
SN	64.45 ***	40.42 ***	86.51 ***	–	0.272 0.292 0.209 0.153 0.072	0.251 0.223 0.227 0.148 0.069	0.143 0.263 0.292 0.099 0.098
GN	47.42 ***	55.75 ***	74.86 ***	30.29 ***	–	0.785 0.893 0.923 0.861 0.877	0.484 0.755 0.727 0.701 0.722
GY	48.08 ***	33.69 ***	47.87 ***	18.624 ***	103.56 ***	– – –	0.526 0.789 0.764 0.721 0.778
TY	8.43 *	57.16 ***	52.54 ***	31.81 ***	68.75 ***	84.37 ***	–

Table 5

	HT	HN	HL	SN	GN	GY	TY
HT	–	– 0.337 0.532 0.236 0.437	– 0.440 0.548 0.271 0.404	– 0.176 0.436 0.202 0.309	– 0.289 0.330 0.409 0.153	– 0.428 0.423 0.429 0.325	– 0.421 0.543 0.438 0.467
HN	36.34 ***		0.218 0.531 0.459 0.242 0.380	0.171 0.362 0.413 0.109 0.252	0.135 0.389 0.365 0.267 0.228	0.112 0.337 0.371 0.169 0.292	0.621 0.711 0.772 0.671 0.770
HL	30.48 ***	47.30 ***	–	0.799 0.575 0.637 0.707 0.572	0.221 0.498 0.478 0.352 0.203	0.272 0.412 0.481 0.259 0.256	0.229 0.487 0.505 0.242 0.336
SN	26.61 ***	37.82 ***	63.37 ***	–	0.194 0.319 0.439 0.273 0.249	0.246 0.160 0.426 0.216 0.190	0.173 0.265 0.440 0.158 0.205
GN	21.97 ***	20.44 ***	50.54 ***	20.01 ***	–	0.722 0.802 0.842 0.808 0.704	0.373 0.669 0.617 0.593 0.473
GY	5.48 N.S.	23.37 ***	29.01 ***	26.79 ***	43.25 ***	–	0.441 0.717 0.673 0.622 0.629
TY	7.61 N.S.	27.80 ***	47.11 ***	31.65 ***	53.18 ***	46.61 ***	–

Table 6

	HT	HN	HL	SN	GN	GY	TY
HT	–	– 0.395 0.526 0.347 0.336	– 0.524 0.624 0.445 0.385	– 0.224 0.564 0.372 0.241	– 0.284 0.123 0.235 0.062	– 0.356 0.182 0.379 0.039	– 0.485 0.357 0.395 0.246
HN	13.67 **	–	0.286 0.490 0.445 0.457 0.233	0.316 0.291 0.386 0.387 0.208	0.185 0.108 0.018** 0.245 0.099	0.197 0.183 0.070 0.291 0.104	0.576 0.507 0.351 0.603 0.333
HL	22.86 ***	20.64 ***	–	0.722 0.538 0.696 0.612 0.591	0.129 0.292 0.069 0.196 -0.040	-0.005n.s. 0.361 0.088 0.232 -0.019**	0.064 0.387 0.193 0.263 0.037
SN	41.83 ***	10.02 *	21.97 ***	–	0.072 0.220 0.083 0.253 -0.055	-0.131 0.242 0.130 0.267 -0.016*	0.020* 0.175 0.174 0.245 -0.048
GN	12.22 **	10.60 *	24.55 ***	23.07 ***	–	0.846 0.935 0.898 0.853 0.822	0.611 0.624 0.500 0.608 0.695
GY	31.26 ***	11.67 *	34.60 ***	22.34 ***	62.58 ***	–	0.673 0.691 0.581 0.709 0.708
TY	14.65 **	31.79 ***	27.41 ***	18.64 ***	18.24 **	12.92 **	–

Figures 10 to 12

The correlations between seven characters of individual plants in the 77S, 77W and 78S composite generations

HT : Plant height
HN : Number of heads per plant
HL : Length of the longest head
SN : No. of spikelets on the longest head
GN : No. of grains in the longest head
GY : Grain yield of the longest head
TY : Total grain yield per plant

o———o : 'Random fertiles
o------o : 'Random' steriles

●———● : 'Selected' fertiles
●------● : 'Selected' steriles

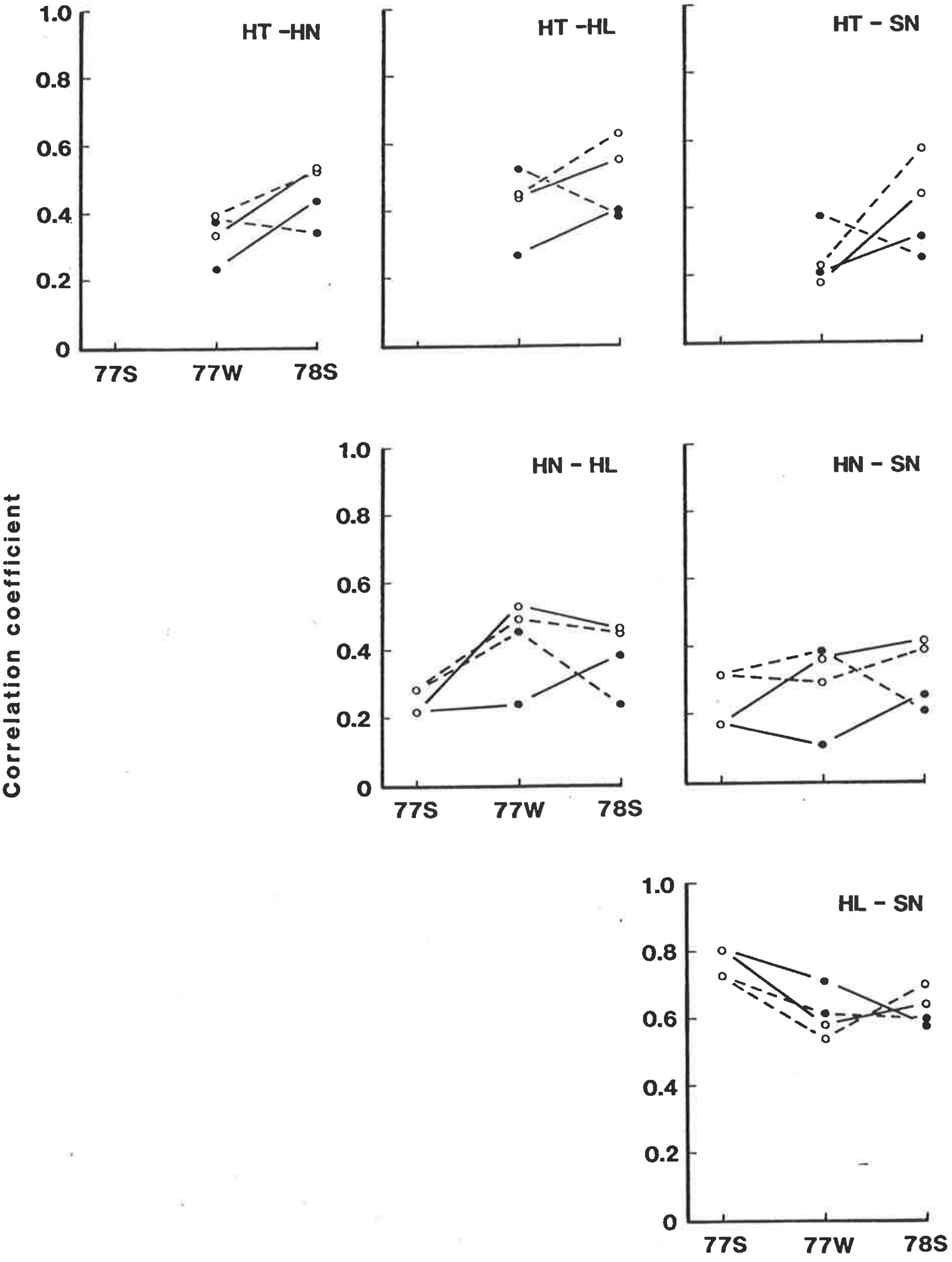

HT -HN
HT -HL
HT - SN
HN - HL
HN - SN
HL - SN
1.0
0.8
0.6
0.4
0.2
0
77S
77W
78S
Correlation coefficient
Generation

Figure 10

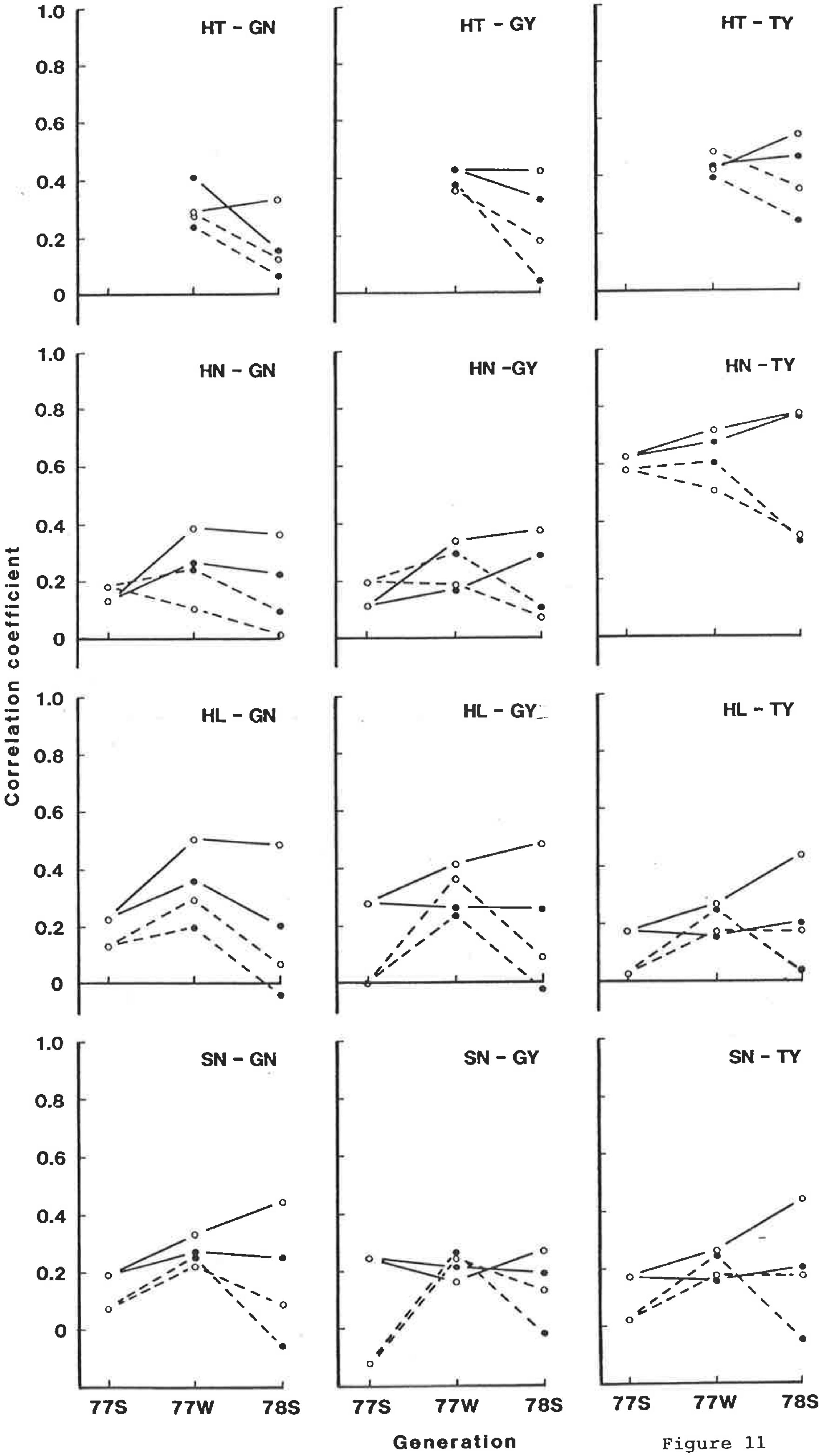
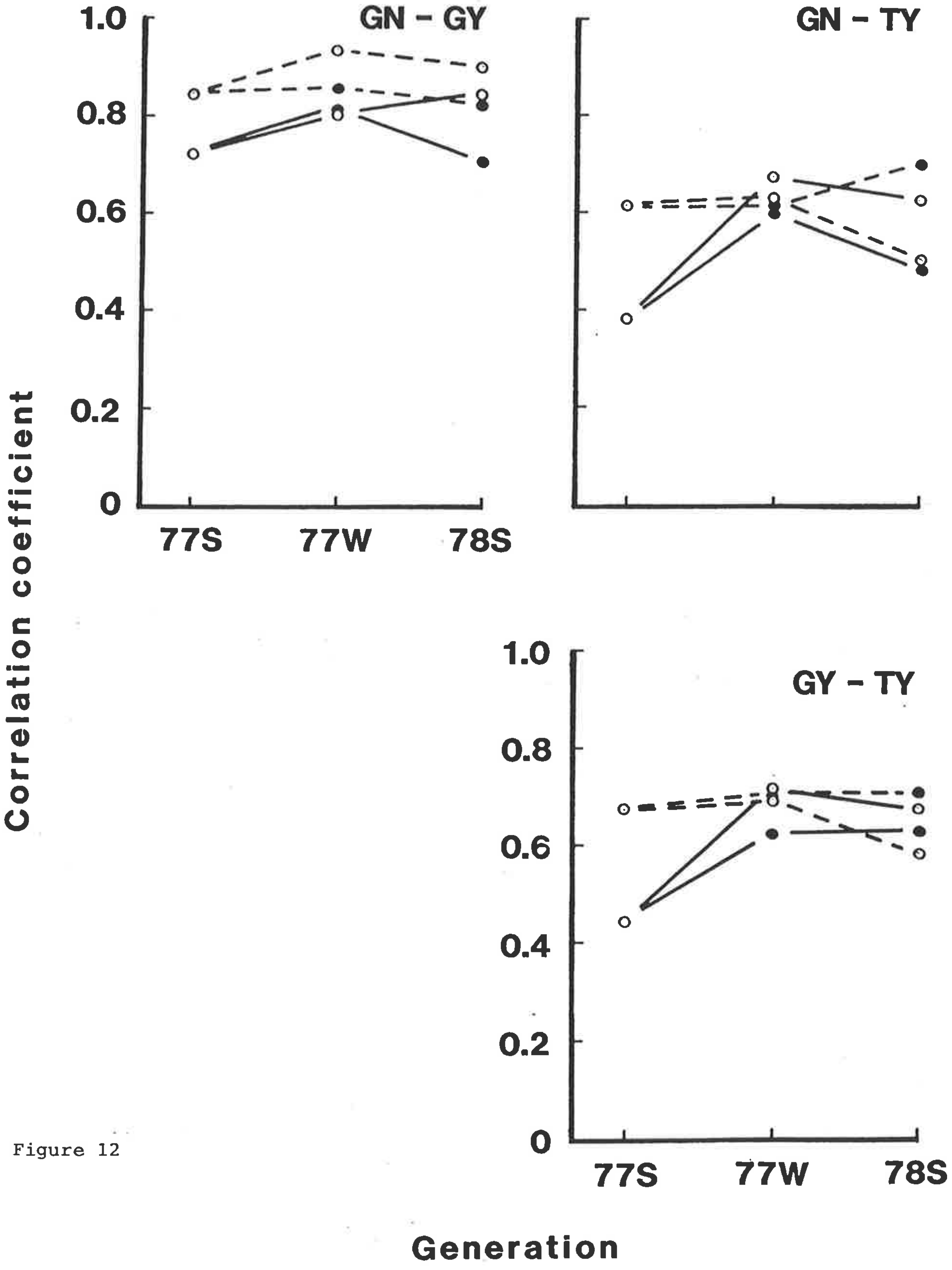

HT - GN
HT - GY
HT - TY
HN - GN
HN -GY
HN - TY
HL - GN
HL - GY
HL - TY
SN - GN
SN - GY
SN - TY
Correlation coefficient
1.0
0.8
0.6
0.4
0.2
0
77S
77W
78S
Generation

Figure 11



GN - GY
GN - TY
GY - TY
1.0
0.8
0.6
0.4
0.2
0
77S
77W
78S
Correlation coefficient
Generation

Figure 12

All individual correlations were significant at $p < 0.001$, except for five indicated by their respective levels of significance in Table 6. Only one correlation, R77S/HL-GY in sterile plants, did not depart significantly from zero. Six correlations were significantly negative (R77S/SN-GY; S78S/HL-GN, HL-GY, SN-GN, SN-GY and SN-TY). All were in sterile plants. The large populations in each class permitted high resolution of the degree of significance of each correlation.

The correlations of each pair of characters from each of the five generations were tested for homogeneity over generations. The X^2 values of each test and their degree of significance are presented for their respective pairs of characters in Tables 4,5 and 6. All tests were significant, indicating that significant shifts in the intensities of associations of characters occurred after the R77S generation. The trends of each association (Figures 10,11 and 12) indicate the very significant shifts in the magnitudes of correlations which caused the lack of homogeneity as the 'Random' and 'Selected' series proceeded from the R77S generation.

Because the seven measured characters are divisible into four which are independent of seed-set, HT, HN, HL and SN and three dependent upon seed-set, GN, GY and TY, the 21 associations can be divided into three groups. The first contains the 6 associations of characters independent of seed-set, HT-HN, HT-HL, HT-SN, HN-HL, HN-SN and HL-SN (figure 10); the second 12 associations between the four characters independent of seed-set and the three dependent upon seed-set (Figure 11) and the third group contains the remaining three associations between seed-set dependent characters (Figure 12). Plant height was not measured in R77S and its correlations could not be calculated.

The trends of correlations in each group of associations tend to be generally similar and therefore, each group will be discussed separately before drawing overall conclusions.

In the first group, the associations of characters independent of seed-set, (Figure 10) there are three dominant features: (1) trends of the 'Random' fertiles and steriles are similar and tend to increase in all associations except HL-SN; (2) the 'Selected' steriles tend to be similar to the random Series from 77S to 77W but diverge to lower values from 77W to 78S; and (3) the 'Selected' fertiles change little from 77S to 77W but increase from 77W to 78S in all associations except HL-SN. The 'Random' and 'Selected' selection strategies had produced distinct sets of trends for each series which tended to be similar for all associations except HL-SN.

Before discussing the possible causes of each set of trends I will review the two selection strategies. The 'Random' and 'Selected' strategies are hierarchical. In the 'Random' strategy male sterile parents were chosen randomly and 10 seeds from each of 100 steriles were used to propagate the series. There was no restriction upon fertile pollinators which were allowed to compete as pollen sources. In the 'Selected' series competition between pollinators was also permitted but the male-steriles were selected for height less than 100 cm and long heads and high spikelet number. Because fertiles were common to each series in R77S the differences between series in 77W would have been due almost entirely to the differences between the two sets of sterile parents chosen from the R77S population. The differences between the series in 78S would have resulted from the accumulated effects of two cycles of selection of steriles and the dissimilar populations of fertiles in R77W and S77W.

Firstly, consider the correlations of characters independent of seed-set in the 'Random' series, in which the only source of changing gene frequencies was competition between fertile pollinators (Figure 10). The intensification of all correlations, except HL-SN in the Random series suggests that strong competition between fertiles ~~was~~ intensif~~ying~~ied the associations between height, head number, headlength, spikelet number. The intensification of these correlations was tending to produce a population of fertiles containing tall, highly-tillered plants with long heads and high spikelet number or short, few-tillered plants with short heads and and low spikelet number. It is particularly interesting that the selective forces intensifying the character-associations did not tend to change their mean expression (Table 2 and Figures 2,3,4 and 5). The intensification of associations probably reflects selection for higher pollinator effectiveness.

DE VRIES (1972, 1973) found the highest concentration of pollen was immediately below a shedding head. Tall, highly-tillered fertile plants with many spikelets per head would be expected to be the most competitive pollinators. They probably produced the largest quantities of pollen per plant and were able to effectively pollinate all steriles in the composite irrespective of their height. The trends of the correlations in steriles of the 'Random' series were similar to those of the fertiles (Figure 10). This suggests there were no interactions between genes determining the competitive ability of fertiles and genes associated with male-sterility. Such interactions probably were prevented from developing because an equal number of seeds (10) were taken from each randomly chosen sterile parent.

In contrast, in the 'Selected' series, where the selected steriles were not a random sample, there was opportunity for interactions to occur between the genes determining competitive ability of fertiles and the genes determining the characters under selection in steriles (height, headlength and spikelet number). Consequently the trends of correlation differed from the 'Random' series. The fertiles had only small increments in correlations (except in HL-SN which decreased) and the trends in steriles were erratic.

The results in the HL-SN were unexpected. Selection for long heads and high spikelet number in steriles less than 100 cm all was unable to prevent a decline in the HL-SN correlation. The effects of competition between fertiles and selection between steriles disrupted the initial strong correlation (0.722 in steriles; 0.799 in fertiles; Tables 5 and 6) but selection for headlength and spikelet number were successful (Figures 4 and 5).

In the second groups of associations (Figure 11) between the four characters independent of seed-set and the three dependent, GN, GY and TY, there is again a general overall pattern. The associations of 'Random' fertiles generally increase. Those in 'Selected' fertiles are more eratic; falling in the three associations of HT (no R77S data available), increasing in HN associations and remaining stable in HL and SN associations. By the 78S generation the associations in fertiles of both series were greater than in the steriles irrespective of selection strategy. In contrast to Figure 10, the 'Random' steriles did not have the same pattern as 'Random' fertiles, but tended to follow the same pattern as 'Selected' steriles. The steriles generally had a pattern tending to values near zero by 78S with varying degrees of fluctuation caused by the 77W generation. There was a marked divergence between steriles and fertiles from 77W to 78S.

These results can again be attributed to the effects of the selection strategies. Grain number in fertiles would be strongly correlated with the number of florets releasing pollen. Therefore, the increasing correlations of HN-GN,HL-GN and SN-GN complement the trends in Figure 10 and indicate that high floret number also increased the competitive advantage of tall highly-tillered fertiles with high numbers of spikelets. Selection amongst steriles had again prevented stronger correlations developing in the fertiles of the 'Selected' series. In the steriles of both selection strategies high seed-set had no selective advantage because ten seeds were taken from each chosen sterile parent, irrespective of their ability to be pollinated. Consequently the correlations in steriles tended to zero in the 78S generation indicating that genes influencing seed-set on steriles were approaching random association with genes affecting height, head number, headlength and spikelet number.

Natural selection amongst fertiles in the R77S (and possibly the F_2, although no data is available) probably caused the general trend for higher correlations in steriles in the 77W generation. However, the tendency to randomness predominated again by the 78S generation.

Figure 12 indicates that correlations between grain number (GN), grain yield of the longest head (GY) and total yield per plant (TY) were high throughout the two series of composites and were not strongly affected by competition between pollinators of the selection strategies.

In summary, the selection strategies had a strong influence on the trends of associations of some characters. In the 'Random' series the characters which conferred selective advantage on fertiles: HT, HL, HL, SN and floret number (reflected in GN, GY and TY) became more strongly associated. The selection strategy in the 'Selected" series tended to disrupt this effect and the changes in 'Selected' fertiles were either smaller or erratic. In steriles the only general increase in magnitude of correlations occurred inthe Random series for characters independent of seed-set (Figure 10). In the 'Selected' series, selection of steriles disrupted this trend. The correlations involving components of seed-set (GN, GY, TY) reflected the lack of opportunity for competition in seed-set between steriles.

If the sterile parents in the 'Random' series had been pollinated by a random sample of fertiles in pair-wise crosses and equal numbers of seeds had been taken from the progeny of each cross for propagation there would have been no opportunity for competition between fertiles. Without selection, all correlations would have probably remained small or tended towards randomness (correlations =0) as genetic equilibrium was approached. The approach to genetic equilibrium using pair-wise random crosses would probably be delayed by a small tendency to assortative matings for flowering time because progeny could not be obtained from pairs of parents with non-overlapping flowering times. (GREGORIUS, 1980a).

The very significant changes in correlations of characters suggest~~s~~ the operation of strong selective forces which intensified genetic disequilibria (ALLARD and HANSCHE, 1964; ALLARD, JAIN and WORKMAN, 1966). The responses were so rapid that they probably caused a significant loss of alleles (JAIN and QUALSET, 1976) and would have reduced the opportunity for recombination of the initial parental genomes. Therefore, it must be concluded that allowing competition between fertile pollinators prevented the movement of the 'Random' population towards genetic equilibria of the initial parental alleles. The main implication of this result for wheat breeding is that the reduction of genetic disequilibria will probably not be achieved in composite crosses. The crossing systems required to achieve that objective, such as random pair-wise crosses, lie outside the conventional definition of composite cross breeding methods.

In contrast to the aim of the 'Random' strategy, in the 'Selected' series selection was consciously imposed upon male-steriles for a morphological type which may increase the likelihood of obtaining high-yielding derivatives from the composite population. Although studies of correlations between yield and yield components indicate that grain yield and grain number in the largest head would be probably the most reliable characters to use for selecting single plants (McNEAL, 1960; McNEAL *et al.*, 1978; McVETTY and EVANS, 1980a; NASS, 1978) they could not be used in this study because seed-set was incomplete on the selected male-steriles. Consequently the 'Selected' selection strategy depended upon an indirect response in yield from selection for short stature (100 cm), long heads and high spikelet number. The data suggest~~s~~ that direct selection for these three characters was successful (Table 3, Figures 4 and 5), but no response was evident in the yield components grain number and grain yield in fertiles (Table 3, Figures 6 and 7). The correlations of headlength and spikelet number with the yield component grain number and grain yield tended to decrease (see Figure 11: HL-GN, HL-GY, SN-GY). Therefore, the 'Selected' strategy shifted the mean expression of the characters under direct selection but it may not have increased the yielding potential of the composite population if this is reliably indicated by grain number and grain yield in the longest head of an individual plant.

~~It is interesting to note that~~ The mean expression of grain number and grain yield in the fertiles selected from the S78S population for height less than 100 cm, long heads and high spikelet number was greater than the mean of the total fertile population in S78S. Therefore, selection of both fertile and sterile parents as an alternative to the 'Selected' strategy may have indirectly increased the expression of grain yield and grain number. If the tallest fertiles were the predominant pollinators in the 'Selected' series, they did not have a beneficial effect upon the expression of grain number and yield even though height was positively correlated with these characters. It is probable that the genetic associations which conferred advantage on the successful pollinators were different from those required for direct selection. Consequently the 'Selected' strategy did not increase the correlations of headlength and spikelet number with grain yield and grain number. The declining correlation of the two characters under selection, headlength and spikelet number (Figure 10: HL-SN) supports the case that strong antagonistic selection forces existed in the 'Selected' series.

A factor which may have strongly influenced the evolution of the 'Selected' series was *Gai/Rht* genes. Although homozygous fertile dwarfs may have been at competitive disadvantage as pollinators a compensating selective advantage may have occurred for heterozygotes. ANWAR and ABDUR (1969) had observed hybrids 131 cm tall between Pitic 62 (a dwarf parent in this study) and tall varieties lacking dwarfing genes. Some of these tall heterozygotes may have expressed the pleiotrophic effects of the dwarfing gene (GALE and LAW, 1977; SYME, 1970). Consequently some tall plants may have had high floret numbers and been very competitive pollinators yet one half of their pollen would not have carried the beneficial dwarfing gene. If most of the selected steriles were homozygous dwarfs (less than 100 cm tall) their progenies would tend to segregate into tall heterozyogotes and shorter homozygotes with a fertility classification dependent upon the *ms* allele carried in their pollen parent. This process would establish a state of balanced polymorphism in which genes lacking the beneficial pleiotropic effects of the *gai/rht* gene could be maintained.

In summary, the patterns of correlations between characters in both selection series indicate that neither selection strategy achieved its intended genetic goal because the pollinating fertiles were allowed to compete freely and introduce a component of strong natural selection. In the 'Random' series this prevented movement towards genetic equilibria and in the 'Selected' series it was probably antagonistic to indirect selection for yield.

3.4 EXPERIMENT 2: The Yield of Bulk Progenies from Successive Generations of the 'Random' and 'Selected' Series.

Introduction

In composites of barley in which outcrossing was low and the progenies of all plants were bulked in each generation slow improvements in yield occurred (ALLARD, 1967; SUNESON and STEVENS, 1953; SUNESON, 1956). However, after this initial phase of natural selection for yield, a stable limit was reached (LOHANI, 1976). When a male-sterility factor was introduced into the composites their yields were not increased even though the male-sterility factor permitted a greater opportunity for outcrossing (JAIN and SUNESON, 1966). In this study the yields of bulked progenies of fertiles from each generation in each series give an opportunity to determine the effectiveness of each selection strategy as a method for improving the mean yield performance of each composite series. Although neither selection strategy permitted direct selection for yield, the responses of spikelet number and headlength to selection in the 'Selected' series and the very significant trends in the correlations of characters in each series have indicated that rapid genetic changes had occurred in each population. Testing the yields of bulk progenies of fertiles from successive generations in each series would indicate if either selection strategy has increased the mean yielding ability of its respective composite.

Preparation of the bulk progenies and experimental design

The seed set on the fertile plants in each generation of each outcrossing series from 1977S to 1980S was bulked into thirteen lines which were designated R77S to R80S for the 'Random' series and S77W to S80S for the 'Selected' series. The only seed excluded from the bulks was that used in Experiments 3 and 5. (Sections 3.5 and 3.7). The excess not required from any plant was returned to the bulk.

The thirteen bulk populations, the nine parents of the composite and two check varieties, Halberd and Warigal were sown in plots in a randomized block design of five replicates at two sites; Charlick Experiment Station, near Strathalbyn and near Saddleworth, South Australia. Each plot contained four rows 3.8 m long with 18 cm spacings between the rows and 25 cm spacings between the outer rows of adjacent plots. The seeding rate was 6.0 $g.m^{-2}$ (60 $kg.ha^{-1}$). The experiments were sown in June and harvested in December 1980.

Results and Discussion

The yields of the thirteen bulks, nine parents and two checks are presented in Table 7. Although the overall means of the sites differed more than twofold, the general patterns of the results were similar at the two sites.

There were no significant differences ~~between~~ among the thirteen bulks within each site and there were no significant regressions of bulk yield on generation in either selection series. Therefore, neither selection series had changed the mean yielding potential of either series and each strategy, particularly the 'Selected' must be regarded as an ineffective method of achieving populations improvement. This result contrasts with the yield improvement reported for barley composites which were propagated through bulks combining the progenies of steriles and fertiles (SUNESON and STEVENS, 1953; JAIN and SUNESON, 1966) and suggests that yield improvement will not occur unless outcrossing and genetic recombination is accompanied by imposed or natural selection for yield. (MILLER and RAWLINGS, 1967b; MATZINGER and WERNSMAN, 1968).

The lack of response in the 'Selected' series indicates that selection of steriles for headlength and the yield component spikelet number, together with height less than 100 cm, while allowing free competition between pollinators is no better than random selection of steriles. The selective forces responsible for the changes in correlations between characters, particularly those which produced higher correlations of spikelet number and grain number with yield, did not have any effect upon population yield.

Table 7: The yield (gm plot^{-1}) of thirteen bulk populations, nine parents and two check varieties at two sites in 1980.

Population	Charlick	Saddleworth
R77S	76	202
R77W	83	239
R78S	78	163
R78W	83	197
R79S	95	180
R79W	76	200
R80S	85	231
S77W	90	244
S78S	92	222
S78W	81	179
S79S	82	271
S79W	80	215
S80S	98	185
Parents		
Federation	118	220
Pitic	85	226
Condor	119	354
Gamenya	108	181
Gammet	20	149
Kite	136	348
Tingalen	96	252
WW-15	113	541
Zenith	208	480
Checks		
Halberd	187	362
Warigal	179	427
Overall Mean	103	258
.05	42	94
LSD .01	55	124
.001	71	158

Because the bulk yields did not differ significantly or have any significant trends at either site, their overall means at each site (84.5 and 209.8) were used to compare bulk yields with the means of the parents (111.4 ad 305.7) and checks (183 and 394.5). In each case the bulks were significantly lower yielding ($p < 0.001$) than either the mean of the parent array or commercial checks.

Because neither strategy increased composite yields after seven cycles of outcrossing other strategies must be adopted to benefit from the considerable recombination o~~r~~f parents which has occurred. One approach may be to propagate the composites as bulks containing the progenies of both fertiles and steriles after a number o~~f~~f generations of outcrossing to allow some natural selection for yield, but this approach also seems ineffective (ALLARD, 1967). A more efficient procedure may be progeny testing individual fertile plants and identifying high-yielding families. These procedures are examined in Sections 3.6 and 3.7.

In summary, bulk progenies of S_0 fertiles from seven cycles of outcrossing in both the 'Random' and 'Selected' series d~~o~~emonstrate that neither strategy effectively increases mean population yield and that the mean yields ~~are~~ were considerably less than the best parents and check commercial varieties. In particular the 'Selected' strategy was ineffective. Therefore, the considerable recombination which occurs in composite breeding strategies involving complete outcrossing in each generation must be exploited by other methods.

3.5 EXPERIMENT 3: The Effectiveness of Indirect Selection for Yield by Selecting for Specific Characters in S_0 Plants.

Introduction

The lack of yield response in the bulked progenies of the 'Selected' composite cross selection strategy may have been caused by two factors (1) the ineffectivenesss of selection of steriles as a method for measuring yield, and (2) outcrossing of the selected steriles with pollen from an unselected set of successful pollinators. Selection for headlength and spikelet number in steriles had shifted their mean expressions in the composite populations (Experiment 1; Figures 4 and 5), but any positive genetic correlation for yield may have been negated by the genetic contribution from the successful pollinators. The lack of yield response in the 'Random' series suggests that competitive advantage for pollination is not correlated with yield improvement.

In this experiment the effectiveness of selection for headlength and spikelet number as an indirect method of improving yield was tested by selecting self-pollinating fertile S_0 plants to avoid the confounding effects of outcrossing. The experiment used the individually measured plants of the 77S, 77W and 78S populations. The method of sampling the populations will be described below.

Four of the seven characters measured on the fertile plants in the composite populations were chosen for this experiment. Headlength and spikelet number were chosen because they were characters used to select steriles in the 'Selected' strategy, and the grain number and yield of the longest head were chosen because they had been generally the most reliable yield components for indirect selection for yield in F_1 and inbreeding wheat populations. The remaining three characters, height, head number and total plant yield were not used because they were generally less reliable in yield component studies. (McNEAL *et al.*, 1978; NASS, 1978; SIKKA *et al.*, 1959). The number of characters which could be studied was also limited by the seed yield of the individual S_0 plants, particularly when one plant was chosen in selected sets for more than one character (see below).

The S_0 plants would be expected to be very heterozygous. They had resulted from two to four outcrosses, including the cornerstone x fertile parent crosses which produced the F_1. BHULLAR, GILL and KHEHRA (1979), PARODI and JOSHI (1970) and SIKKA, JAIN and PARMAR, (1959) had found poor correlations between yield components in the F_1 and the yield of later generations and concluded selection in the F_1 would be ineffective. By analogy, selection between S_0 plants may also be ineffective. However, in composite cross populations the number of S_0 individuals which can be sampled is much greater than a small array of F_1s and the effects of the individual parents and crosses should be reduced because biases from the small number of parental genomes may be removed. Therefore the response in yield to selection of S_0 individuals for yield components and other characters may be more effective than selection between F_1's.

Sampling the Composite Cross Populations

Four sets of twenty one fertile So plants with the highest expression of headlength, spikelet number, grain number and grain yield in the longest head of each plant were identified in the R77S, R77W, R78S, S77W and S78S populations. Each of the four sets from each population was chosen independently and therefore, a selected fertile could occur in each of the four sets. In addition a random set of twenty one fertiles was chosen from each population. In Table 8 the numbers of plants selected in each population for one, two, three or four characters are presented with the expected frequencies of plants for each level of combinations of characters in each population. Significantly higher frequencies than expected with random assortment occurred for combinations of two, three and four characters, which in turn caused significantly lower frequencies of plants selected for only one character and a lower total number of selected individuals in each population than expected. The consistent departure of the HL-SN and GN-GY associations from random expectation reflects the strong correlations of these pairs of characters (Figures 10 and 12). The occurence of thirteen plants in the three-character and three in the four-character level indicates that elite plants with a high phenotypic expression of groups of characters occur much more frequently than expected from random association.

TABLE 8: The number of plants selected for each of four characters or combinations of these characters from the total population of fertiles in each of five composite populations; and the level of significance of the departure of the observed from the expected number of plants shown in parentheses for each level of association for independent assortment of characters.

Character Associations	Population R77S	 R77W	 R78S	 S77W	 S78S
HL	11 N.S.	14 N.S.	7 **	12 N.S.	13 N.S.
SN	11 N.S.	17 N.S.	12 N.S.	13 N.S.	14 N.S.
GN	11 N.S.	11 N.S.	6 **	10 *	10 *
GY	10 N.S.	14 N.S.	7 **	11 N.S.	11 N.S.
	(17.94)	(18.76)	(18.38)	(18.79)	(18.53)
HL-SN	7 ***	4 ***	4 ***	5 ***	2 N.S.
HL-GN	9 N.S.	3 **	2 N.S.	2 N.S.	2 N.S.
HL-GY	1 N.S.	0 N.S.	1 N.S.	0 N.S.	2 N.S.
SN-GN	0 N.S.	0 N.S.	1 N.S.	0 N.S.	1 N.S.
SN-GY	1 N.S.	0 N.S.	1 N.S.	2 N.S.	1 N.S.
GN-GY	8 ***	7 ***	4 ***	7 ***	4 ***
	(0.97)	(0.72)	(0.84)	(0.71)	(0.79)
HL-SN-GN	1 ***	0 N.S.	0 N.S.	1 ***	1 ***
HL-SN-GY	0 N.S.	0 N.S.	0 N.S.	0 N.S.	0 N.S.
HL-GN-GY	0 N.S.	0 N.S.	5 ***	0 N.S.	2 ***
SN-GN-GY	0 N.S.	0 N.S.	1 ***	0 N.S.	2 ***
	(0.05)	(0.03)	(0.04)	(0.03)	(0.03)
HL-SN-GN-GY	1 ***	0 N.S.	2 ***	0 N.S.	0 N.S.
	(0.003)	(0.001)	(0.002)	(0.001)	(0.001)
Fertiles selected	62 N.S.	70 N.S.	53 **	64 N.S.	64 N.S.
	(77.76)	(79.46)	(78.68)	(79.52)	(78.99)
Fertiles sampled	410	569	483	576	514

The range of expression of each character in each selected set of S_0 plants and the mean of each unselected populations of fertiles is presented in Table 9 with a selection differential calculated such:

$$\frac{\text{the lowest value in a selected set - mean of the total population}}{\text{standard deviation of the total population}}$$

The resulting selection differentials assume no normality in each distribution (Figures 4,5,6, and 7). Therefore, the calculated selection differentials must be compared cautiously because of error introduced by non-normality. However, the overall mean selection differential, 1.62, indicates the high selection pressure applied to obtain the selected sets.

Experimental Design

The four sets of twenty one selected fertiles and one set of twenty one randomly chosen fertiles from the R77S, R77W, S77W, R78S and S78S populations constituted twenty-five population x character sets. One individual from each of the twenty five sets was allocated randomly to each of twenty-one replicates to complete a randomized block design with twenty-one blocks. Each plot was a single 3.8 m row sown with 4.5 g of seed. The rows were 0.3 m apart. The experiment was sown at the Charlick Experiment Station in June and harvested in December 1980.

Results and Discussion

The mean yields of S_1 progenies of the S_0 fertiles selected randomly and for headlength (HL), spikelet number (SN), grain number (GN) and grain yield (GY) in the longest head in five composite cross populations are presented in Table 10. There were no significant differences ($p > 0.05$) between any of the twenty-five individual character x population sets of progenies. The mean yields over populations of the selections for spikelet number and grain yield in the longest head were significantly greater than the means of the random and headlength sets. Therefore, selection of S_0 individuals

Table 9: The range of values in each set of selections, the mean expression of each character in their respective populations of fertiles before selection and the selection differential

Character	Population				
	R77S	R77W	R78S	S77W	S78S
H1	130-141[ø]	137-160	129-157	142-180	129-146
	103.97[+]	111.55	93.21	114.51	109.37
	1.40[#]	1.66	2.54	1.61	1.44
SN	25-33	23-25	26-33	27-33	24-29
	18.82	19.83	17.41	20.41	20.14
	1.56	1.69	2.83	1.65	1.05
GN	57-96	78-92	54-70	81-108	47-69
	36.79	50.80	29.63	50.84	37.34
	1.56	1.57	1.75	1.60	0.78
GY	2.2-3.2	3.2-4.0	2.3-2.9	3.6-4.6	2.0-3.
	1.41	1.91	1.10	2.00	1.37
	1.21	1.59	2.07	1.69	1.11

[ø] - the range of values in selected sample

[+] - the mean of the population of fertiles before selection

[#] - the selection differential (see text)

Table 10: The mean yield (g. plot^{-1}) of S_1 progenies of S_o plants selected randomly and for high expression of four characters from five composite populations.

Population	Character					Mean
	RAN	HL	SN	GN	GY	
R77S	102.0	108.8	105.6	106.8	107.8	106.2
R77W	98.8	102.8	113.5	106.8	108.8	106.1
R78S	88.2	89.7	103.8	97.7	102.5	96.4
S77W	99.1	103.3	107.5	101.7	109.0	104.1
S78S	98.5	92.6	106.5	100.4	108.8	101.4
Mean	97.3	99.4	107.4	102.7	107.4	102.8

		Population	Character	Interaction
LSD's	0.050	6.9	6.9	n.s.
	0.010	9.1	9.1	
	0.001	11.7	11.7	

for spikelet number and grain yield in the longest head may increase the mean yield of their progeny in comparison with that of a random sample of S_0 individuals. However, the gain achieved would probably be so small that it would be an ineffective selection procedure for use in wheat breeding. Some individual progeny (unreplicated) were high yielding and suggest that S_1 or S_2 progeny tests of S_0 individuals may identify families which could produce high-yielding inbreds. This avenue for using S_0 derived lines to achieve yield improvement was studied in Experiment 4 (Section 3.6) in which S_2 progenies from the highest yielding S_1 rows in this experiment were compared with the parents of the composite and commercial varieties.

If it is assumed that the genetic potential for yield improvement of steriles with extremely high expression of headlength and spikelet number was similar to that of the sampled S_0 fertiles, then the implications of these results for improving the yield potential of components by selection for these characters in steriles are very discouraging. The results suggest that in the 'Selected' selection strategy there would have been no response to selection for headlength. It is also unlikely that any significant response would have resulted from selection for spikelet number.

The response to the low selection intensity amongst steriles in the 'Selected' composite breeding strategy (100 from 257 to 378, Table 1) would be expected to be less than the 10.4% overall gain over the random sample achieved in this experiment after intense selection (21 fertiles from 410 to 576). In addition the response achieved in this experiment occurred in inbred progenies of S_0 fertiles, but in the 'Selected' composite strategy any genetic gain achieved by selecting steriles would have probably been reduced by the paternal genetic contribution from unselected fertile pollinators.

The small significant overall response to selection for grain yield in the longest head corresponds with the general observation from studies of yield components in inbreeding families that selection for yield per head has a low level of predictability as a selection procedure (DERERA and BHATT, 1972; NASS, 1978; McVETTY and EVANS, 1980a). Heterotic effects in the S_0 individuals probably contributed strongly to their expression of yield components but reduced their value for predicting the yield of their S_1 progenies as found in studies of F_1 and F_2 generations in two-parent wheat crosses (PARODA and JOSHI, 1970; SIKKA, JAIN and PARMAR, 1959).

The general absence of correlations between the expression of S_0 yield components and S_1 yield in the five random samples from the composites (Table 11) also emphasises that selection of morphological characters and yield components to improve yield would be ineffective. Although the overall correlations for headlength and spikelet number were significant, they probably reflected the two significant correlations, HL-R78S and SN-R77S. Of particular interest is the absence of any significant correlations for grain number and grain yield of the longest head and total S_0 plant yield which again corresponds with the poor predictive relationships found between F_1 and F_2 generations.

The lack of large significant responses in S_1 yield after intense selection for headlength and spikelet member in the S_0 and the lack of significant correlations between S_0 expression of plants characters and S_1 yield suggest that the lack of response in bulk composite yields reported in Experiment 2 occurred because the 'Selected' selection strategy was ineffective. Therefore other methods are required to identify those recombinants which may improve yield. The very high yields which were observed in some unreplicated S_1 rows in this experiment suggest that partitioning a composite generated by outcrossing male-steriles into S_0-derived families and yield testing early generation bulks may be an effective procedure.

Table 11: The correlations between seven characters of spaced plants randomly selected from five composite populations and the yields of their progenies

Character	Population					
	R77S	R77W	R78S	S77W	S78S	Overall
HT	[illegible]	0.068	-0.337	-0.156	-0.374	-0.095
HN	0.550	0.428	-0.011	-0.274	-0.204	-0.125
HL	0.418	0.394	0.656**	-0.017	-0.096	0.276**
SN	0.528*	0.291	0.363	0.241	-0.164	0.253*
GN	0.089	0.231	0.311	0.080	0.093	0.112
GY	0.368	0.212	0.230	0.157	0.118	0.199
TY	0.457	0.267	0.036	-0.249	0.111	-0.002

3.6 EXPERIMENT 4: Comparison of the Yields of S_0-derived S_2 Lines with the Parents of the Composite Cross and S_1 and S_2 Bulks derived from Composite Populations.

Introduction

This experiment reports the results of a small explorative study of the possibility of using high-yielding progenies of S_0 plants to select for yield improvement from a composite population produced by a series of enforced outcrossings. Experiment 2 has indicated that selection of outcrossed steriles did not increase the yield of bulk composite populations. Furthermore, Experiment 3 demonstrated that selection within the composites for specific characters of fertile S_0 plants is unlikely to be an effective procedure for improving yield. In Experiment 3 a number of progeny rows were very high yielding. These rows had not been replicated and it was therefore probable that their high yields resulted form variation within the experimental site. Nevertheless, the twelve highest yielding S_1 rows in Experiment 3 were selected to conduct this experiment. Replicated S_2 bulks derived from S_0 plants were compared with bulks derived from the composites, the parents of the composite and check varieties.

The derivations of the experimental entries and experimental design

There were thirty three entries in the experiment:

- The nine parents of the composite cross: Federation, Pitic 62, Condor, Gamenya, Gamset, Kite, Timgalen, WW-15 and Zenith.
- Two check varieties: Lance and Warigal
- Five S_1 bulk populations derived from the R77S, R77W, R77S, S77W and S78S populations in an identical manner to the bulks used in Experiment 2.
- Five S_2 bulk populations obtained by harvesting S_1 plots of the five bulks grown in Experiment 2.
- Twelve S_2 lines derived from high-yielding S_1 progenies in Experiment 3. The S_2 lines, the yields of their S_1 parent rows and the populations from which they were derived were:

S_2 Line No.	Expt. 3 Yield (g. row $^{-1}$)	Parential Population
1	192	R77S-Random
2	188	R78S-GY
3	187	R77S-SN
4	186	R78S-SN
5	184	R77S-GY
6	168	S78S-HL
7	167	R77S-HL
8	166	S77W-HL
9	162	R78S-GN
10	162	R77W-GY
11	161	S78S-Random
12	159	R77S-RN

Each of the thirty three entries was sown in five replicates in a randomized block design at the Charlick Experiment Station in July, 1981. Each plot contained four 3.8 m rows 18 cm apart with 25cm spacing between adjacent plots. The seeding rates was 6 g m^{-2}. The plots were harvested in December, 1981.

Results and Discussion

The yields of the 12 S_2 lines, bulks, parents and checks are presented in Table 12. The yields of S_2 lines contrasts with those of the S_1 and S_2 bulks. Five S_2 lines (4, 5, 7, 9 and 10) were significantly higher yielding than any bulk population. Of these, all except line 4 did not differ significantly from the three highest yielding parents, Condor, Timgalen and Zenith, and three lines (7, 9 and 10) did not significantly differ from the check varieties. Partitioning the composite populations has exposed high yielding S_0-derived families even though the S_1 and S_2 bulk populations had yields similar to the lower-yielding parents.

Table 12: The mean yield of S_2 lines, S_1 and S_2 bulks, and parental and check varieties

POPULATION	YIELD (gm plot^{-1})	
S_2-lines		
1	300	h i j
2	378	d e f g h i j
3	281	i j
4	404	c d e f g
5	405	b c d e f g
6	343	f g h i
7	431	a b c d e f
8	382	d e f g h
9	461	a b c d
10	482	a b c
11	347	f g h i
12	359	f g h i
S_1-Bulks		
R77S	335	g h i
R77W	345	f g h i
R78S	320	g h i j
S77W	376	d e f g h
S78S	329	g h i
S_2-Bulks		
R77S	355	f g h i
R77W	336	g h i
R78S	335	g h i
S77W	367	e f g h i
S78S	346	f g h i
Parents		
Federation	299	h i j
Pitic 62	379	d e f g h
Condor	498	a b
Gamenya	397	c d e f g
Gamset	240	j
Kite	398	c d e f g
Timgalen	430	a b c d e f
WW-15	387	d e f g h
Zenith	448	a b c d e
Mean of Parents	386	
Checks		
Lance	502	a
Warigal	510	a
0.05	72	
l.s.d. 0.01	95	
0.001	121	

The equivalence of yields of the S_1 and S_2 bulks suggests that no significant natural selection for yield occurred in the S_1 bulk. It is probable that after many generations the bulk yield may increase (SUNESON, 1956) but partitioning at the S_0 level has identified high-yielding early generation inbreeding families. Therefore selection amoungst S_0-derived S_2 bulks has extracted from the composite cross those families with high yield potential in two generations. In contrast, the evolutionary concept of utilizing composites could be pursued and after a number of generations of natural selection in a bulk single plant derivatives could be obtained for yield testing. It is probable that these lines would have no greater potential than the S_0 - derived S_2 bulks and they may also still contain significant levels of heterozygosity (ALLARD, 1977).

Therefore this experiment suggests that the most efficient method of exploiting new recombinants produced in composite crosses is to partition the composite into S_0 - derived bulks and test their early generation bulks (S_1 and S_2) for yield. This process is equivalent to early-generation testing between and within two-parent crosses in conventional wheat breeding, which have been shown to be an effective method of identifying inbreeding families with high yield potential (CREGAN and BUSCH, 1977; LUPTON and WHITEHOUSE, 1957).

In conventional breeding emphasis is placed upon selection amongst many F_2 - derived lines within crosses rather than upon selection between a few F_1 - derived bulks of 2-parent crosses (LUPTON, 1961). Because composite crosses can create a very large array of S_0 recombinants from a parent array it would probably be most efficient to impose two stages of selection after a composite cross. In the first stage S_0 - derived S_1 or S_2 bulks could be tested to identify those families (equivalent to F_1 - derived bulks of crosses) with high yield potential. This experiment has demonstrated this would be effective. In the second stage the best S_0 - derived families could be partitioned into S_1 or S_2 families for selection of the highest yielding lines. This would be equivalent to the F_2 - progeny test (LUPTON, 1961). If this proce~~e~~dure had been pursued in the highest yielding S_2 bulks in this experiment it is probable that families higher yielding than the parents and checks may have been identified. In the two stage proce~~e~~dure some S_0 - derivatives containing potentially high-yielding segregants may be discarded but, in general, it would probably be more efficient to select amongst S_1 or S_2 progenies from within the most promising bulks rather than amongst progenies derived from random S_0 parents.

The S_0 - derived bulks will segregate for male-sterility. This presents an opportunity to establish a recurrent selection programme in which S_1 or S_2 progeny testing is alternated with outcrossing as in corn (HORNER, 1968) sorghum (DARRAH, EBERHART and PENNY, 1978) and partially self-fertile pulses (RACHIE and GARDNER, 1975). Residual seed of the best S_1 and S_2 lines could be used to constitute another intermating population from which S_0 individuals could be sampled after one or more generations of outcrossing to commence another cycle of selection. Some S_1- and S_2 - derived lines would be descended from homozygous fertile segregants and could not contribute steriles to the intermating population, while others would be segregating for sterility and therefore outcrossing between lines could occur. Only individuals derived by inbreeding descent in superior S_0 - derived families should be used in recurrent breeding for the derivation of homozygous inbred lines for yield testing.

The proportion of individuals derived only by inbreeding descent in a bulk progeny population from an S_0 plant heterozygous for male-sterility

Given an *Msms* S_0 plant and assuming equal effectiveness of the *Ms* and *ms* gametes during self-fertilization, the expected frequencies of geno-types in the S_1 population are:

MsMs	*Msms*	msms ~~*Msms*~~
0.25	0.5	0.25

Consider firstly the case in which the male-steriles set no seed. The expected proportions of each genotype in the S_2 generation would be:

MsMs	*Msms*	m~~M~~*sms*
(2/3 x 1/4)+(1/3 x 1)	(2/3 x 1/2)	(2/3 x 1/4)
= 3/6	= 2/6	= 1/6

By again partitioning the segregants from the *Msms* indivduals the corresponding frequencies in the S_3 generation are: 7/10; 2/10; 1/10 and in the S_n generation the frequencies would be:

MsMs	*Msms*	*msms*
$\frac{(2^n - 1)}{(2^n + 2)}$	$\frac{2}{(2^n + 2)}$	$\frac{1}{(2^n + 2)}$

Assuming no difference in fitness between the *MsMs* and *Msms* genotypes at each generation, it is seen that the population rapidly approaches homozygosity for male-fertility. For example in the S_4 generation, the frequency of *MsMs* = 5/6 (0.833). It is of interest that the frequencies of homozygotes at loci independent of the *ms* locus in the S_n generation are:

$$\frac{2^n - 1}{2^{(n + 1)}}$$

and the frequency of residual heterozygotes: $1/2^n$

These ratios are the same as $\frac{2^{(x-1)} - 1}{2^{x}}$ for homozygotes and

$\frac{1}{2^{(x-1)}}$ for residual heterozygotes in the F_x generation of inbreeding from F_1 where F_x is equivalent to $S_{(x-1)}$.

In the case where seed is set on male-steriles, the bulk derived from an S_0 heterozygous fertile will contain plants descended entirely by in-breeding from the S_0 and all others will have at least one outcross in their ancestral path from the S_0.

If the ratio of seed set on each genotype in the S_1 is defined as

MsMs		*Msms*		*msms*
1	:	1	:	p

where $p > 0$, the proportion of seed set on the three genotypes in the S_1 is:

$$(Msms): \frac{1}{3+p} \qquad (Msms): \frac{2}{3+p} \qquad (msms): \frac{p}{3+p}$$

The *MsMs* and *Msms* individuals in the S_1 will produce S_2 individuals only by inbreeding, but S_1 *msms* individuals will produce progeny only by outcrossing. If individuals descended from the S_0 only through inbreeding are given the subscript I and those which have at least one outcross in their ancestry from the S_0 are given the subscript 0, then the proportions of $MsMs_I$, $Msms_I$, $msms_I$ in the S_2 descended from the S_0 through S_1 $MsMs_I$ and $Msms_I$ will be

$$\overset{MsMs_I}{\frac{3}{2(3+p)}} \qquad \overset{Msms_I}{\frac{2}{2(3+p)}} \qquad \text{and} \qquad \overset{msms_I}{\frac{1}{2(3+p)}}$$

and the proportions of $Msms_0$ and $msms_0$ in the S_2 derived from outcrossing in the S_1 will be

$$\frac{2p}{3(3+p)} \qquad \text{and} \qquad \frac{p}{3(3+p)} \qquad \text{respectively.}$$

No $MsMs_0$ can result from outcrossing in the S_1. These proportions assume equal effectiveness of *Ms* and *ms* pollen and that p is constant for all steriles. Note that as p approaches 0 the proportions in S_2 approach 3/6 : 2/6 : 1/6 for $MsMs_I$, $Msms_I$ and $msms_I$ as found in the case of no seed-set on steriles ($p = 0$).

In the S_2, $MsMs_I$ will not segregate, $Msms_I$ will segregate producing $msms_I$ in the S_3 ; $MsMs_0$ will inbreed producing $MsMs_0$, $Msms_0$ and $msms_0$ individuals; and $msms_0$ will again outcross. The expected proportions in the S_3 of each genotype in the I and 0 groups is given in Table 13, together with the previously calculated proportions for the S_1 and S_2. Also in Table 13 are the expected proportions of $MsMs_I$, $Msms_I$, $msms_I$ and the sum of the expected proportions of $MsMs_0$, $Msms_0$ and $msms_0$ for the general case, S_n, and the special cases S_n $(p = 0)$, S_n $(p = 1)$ and $S\infty$.

The formulae in Table 13 were used to calculate for given values of n and p for the four expected proportions which are pertinent to bulking from a heterozygous S_0; E $(MsMs_I)$, E $(Msms_I)$, E $(msms_I)$ and E $(MsMs_0 + Msms_0 + msms_0)$ (Table 14). These expected proportions are also presented graphically for selected values of n and p in Figure 13 where R = E $(MsMs_0)$ + E $(Msms_0)$ + E $(msms_0)$.

Table 14 and Figure 13 emphasise the characteristics of populations which are developed by bulking from a heterozygous S_0 individual. Irrespective of the value of p the S_1 proportions of $Msms_I$ and $msms_I$ are 0.5 and 0.25 respectively. E $(Msms_I)$ and E $(msms_I)$ decline with increasing n with only small differences in their frequencies over all values of p.

The greatest differences within $E(Msms_I)$ and $E(msms_I)$ between p = 1.0 and p = 0 occur at n = 2, where

$E(Msms_I)_{p\,=\,0} - E(Msms_I)_{p\,=\,1.0} = 0.083$

and

$E(msms_I)_{p\,=\,0} - E(msms_I)_{p\,=\,1.0} = 0.042.$

These small differences are amplified into large differences in the fixation values of $MsMs_I$ and R.

If one is sampling an S_0 - derived bulk to obtain homozygous fertile families, the critical factors are $E(MsMs_I)$ and $E(MsMs_0)$ in each generation. $MsMs_I$ individuals must occur

Table 13

The expected proportions of $MsMs_I$, $Msms_I$, $msms_I$, $MsMs_0$, $Msms_0$ and $msms_0$ in the bulked progeny of a heterozygous (Msms) S_0 individual in the S_1, S_2, S_3, S_n and S_∞ generations. p is the seed-set on steriles relative to fertiles (see text). The expected proportions $S_{n(p=0)}$ and $S_{n(p=1)}$ are for the special cases of no seed set on steriles, p=0, and equal seed-set on steriles and fertiles, p=1.

Table 13

Generation	$MsMs_I$	$Msms_I$	$msms_I$	$MsMs_0$	$Msms_0$	$msms_0$
S_1	1/4	1/2	1/4			
S_2	$\frac{3}{2(3 + p)}$	$\frac{2}{2(3 + p)}$	$\frac{1}{2(3 + p)}$	0	$\frac{2p}{3(3 + p)}$	$\frac{p}{3(3 + p)}$
S_3	$\frac{7}{2(5 + 3p)}$	$\frac{1}{(5 + 3p)}$	$\frac{1}{2(5 + 3p)}$	$\frac{p}{3(5 + 3p)}$	$\frac{6p\ (5 + p)}{(5 + 3p)(15 + 4p)}$	$\frac{2p\ (15 + 7p)}{3(5 + 3p)(15 + 4p)}$
Sn	$\frac{2^n - 1}{2(2^n+(2^{n-1}-1)(p-1\ )}$	$\frac{1}{2^n+(2^{n-1}-1)(p-1)}$	$\frac{1}{2(2^n+(2^{n-1}-1)(p-1)}$		$\frac{2^n + 2^{n-1}(p - 2) - p}{2^n + (2^{n-1}-1)(p-1)}$	
Sn(p=0)	$\frac{2^{n-1}}{2^n + 2}$	$\frac{2}{2^n + 2}$	$\frac{1}{2^n + 2}$		0	
Sn(p=1)	$\frac{2^n - 1}{2^n + 1}$	$\frac{1}{2^n}$	$\frac{1}{2^n + 1}$		$\frac{2^n - 2^{n-1} - 1}{2^n}$	
S_∞	$\frac{1}{1 + p}$	0	0		$\frac{p}{1 + p}$	

Table 14: The expected values of MsMsI, MsmsI and the residual genotypic groups for specific values of n and p

			0	0.1	0.2	0.333	0.5	1.0
$E(MsMs_I)$	n	1	0.250	0.250	0.250	0.250	0.250	0.250
		2	0.500	0.484	0.469	0.450	0.429	0.375
		3	0.700	0.660	0.625	0.583	0.538	0.438
		5	0.912	0.838	0.775	0.705	0.633	0.484
		10	0.997	0.907	0.831	0.749	0.666	0.499
		∞	1.00	0.909	0.833	0.750	0.667	0.500
$E(Msms_1)$	n							
		1	0.500	0.500	0.500	0.500	0.500	0.500
		2	0.333	0.323	0.313	0.300	0.286	0.250
		3	0.200	0.189	0.179	0.167	0.154	0.125
		5	0.059	0.054	0.050	0.045	0.041	0.031
		10	0.002	0.002	0.002	0.001	0.001	0.001
		∞	0	0	0	0	0	0
$E(msms_0)$	n	1	0.250	0.250	0.250	0.250	0.250	0.250
		2	0.167	0.161	0.156	0.150	0.143	0.125
		3	0.100	0.095	0.089	0.083	0.077	0.063
		5	0.30	0.027	0.025	0.023	0.020	0.016
		10	0.001	0.001	0.001	0.001	0.001	0.001
		∞	0	0	0	0	0	0
$E(MsMs_0 + Msm_0 + msms_0)$								
	n	1	0	0	0	0	0	0
		2	0	0.033	0.063	0.100	0.143	0.250
		3	0	0.056	0.107	0.167	0.231	0.375
		5	0	0.081	0.150	0.227	0.307	0.459
		10	0	0.091	0.166	0.249	0.332	0.499
		∞	0	0.091	0.167	0.250	0.333	0.500

Figure 13

The expected frequencies of fertiles and steriles after n generations of bulking the progeny of a single heterozygous (Msms) parent

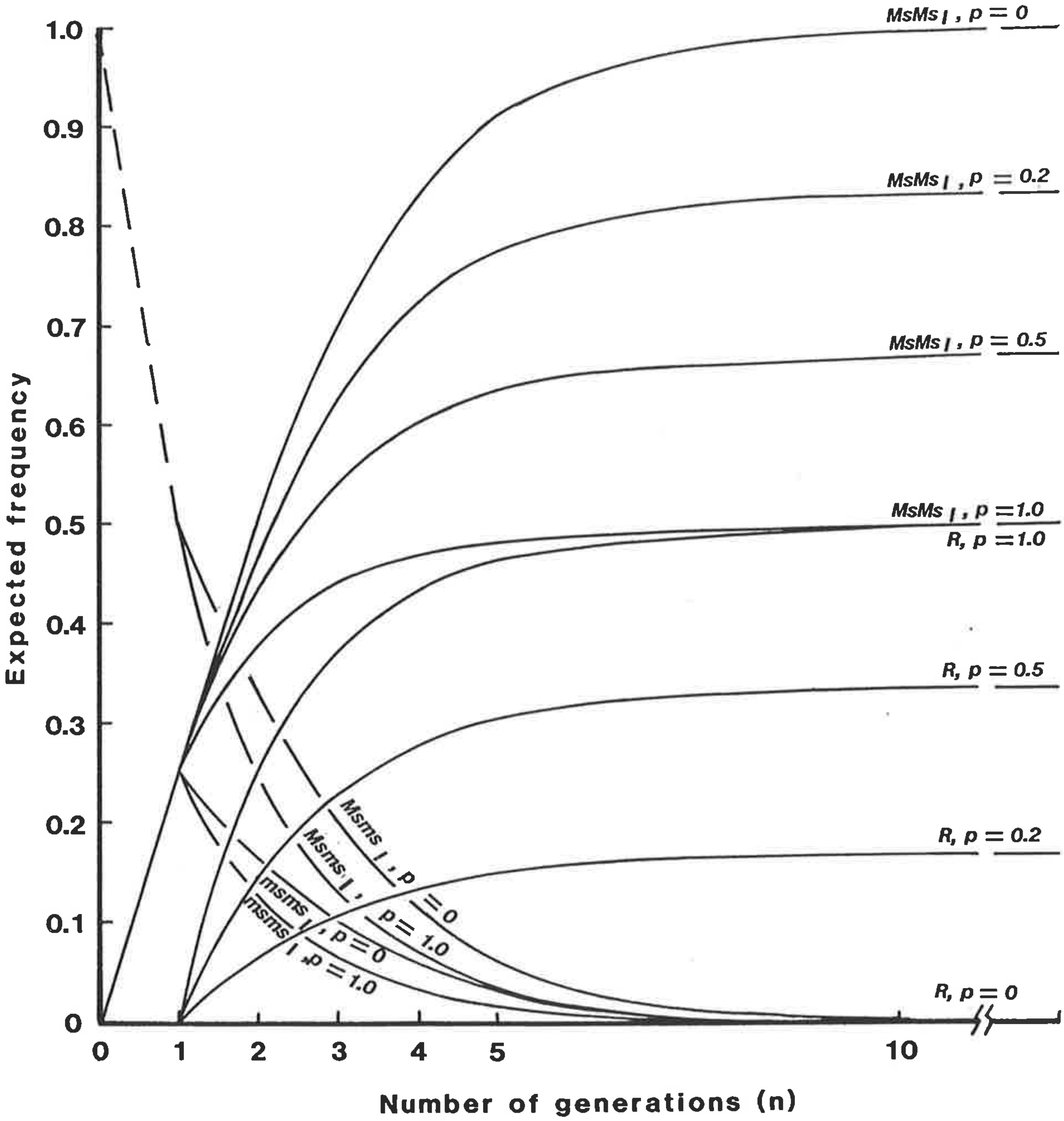
$MsMs_I$: Homozygous fertiles derived by inbreeding only from the initial parent

$Msms_I$: Heterozygous fertiles derived by inbreeding only from the initial parent

$msms_I$: Steriles derived by inbreeding only from the initial parent

R : The total frequency of fertiles and steriles which have at least one outcross in their ancestry

p : : The seedset on steriles expressed as a proportion of the seedset on fertiles



1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Expected frequency
0
1
2
3
4
5
10
Number of generations (n)
MsMs I , p = 0
MsMs I , p = 0.2
MsMs I , p = 0.5
MsMs I , p =1.0
R, p =1.0
R, p = 0.5
R, p = 0.2
R, p = 0
Msms I , p = 0
Msms I , p = 1.0
msms I , p = 0
msms I , p = 1.0

Figure 13

with sufficient frequency for sampling to be an efficient proceedure and $MsMs_0$ individuals must be avoided if only inbred descendants of the S_0 parent of the bulk are required.

As seen in Table 13, no $MsMs_0$ individuals can occur in the S_1 and S_2 and $E(MsMs_I) = 0.25$ in the S_1 and is between 0.375 ($p = 1.0$) and 0.5 ($p = 0$) in the S_2. $MsMs_0$ individuals can occur in the S_3. Therefore sampling of fertiles should be restricted to the S_1 and S_2 to avoid $MsMs_0$ individuals. Steriles in the S_1 and S_2 would not be considered when a sample of fertiles is taken. Therefore the expected proportion of homozygous fertiles descended by inbreeding from the S_0 in a sample of fertiles only in any generation is:

$$\frac{E\ (MsMs_I)}{1 - \quad E(msms_I) + E(msms_0)}$$

which has a value of 0.333 in the S_1 and in the S_2 has a maximum value 0.6 at $p = 0$, and is 0.47 at $p = 1$. Therefore the optimum population to sample to obtain the highest proportion of $MsMs_I$ individuals without contamination by $MsMs_0$ individuals is the S_2. Because S_1 individuals would be expected to retain a higher proportion of desirable genes from the S_0 (SHEBESKI, 1967), greater genetic gain may be achieved by sampling the S_1. However, the proportion of $MsMs_I$ fertiles in the S_1 is lower. Therefore, to retrieve a given number of homozygous fertile families more S_1 - derivatives must be grown than S_2 - derivatives.

It is of interest to note that $Msms_0$ fertiles can occur in the S_2 (Table 13) but their families are eliminated by progeny testing together with those of $Msms_I$ individuals.

If the S_3 were sampled, contamination by progenies of $MsMs_0$ individuals could occur (Table 13). The expected proportion of such families amongst all homozygons fertile families in the S_3 is:

$$\frac{E(MsMs_0)}{E(MsMs_I) + E(MsMs_0)}$$

$$= \frac{2p}{21 + 2p} \qquad \text{(from Table 13)}$$

which has a minimum value of 0 at p = 0 and 0.087 at p = 1. Therefore the proportion of contaminants in the S_3 would be small. In later generations the proportion of contaminants would approach $\frac{p}{1 + p}$ (see Table 13). If p were not near zero the level of contamination would be unacceptably high if a sample containing a high frequency of $MsMs_I$ derivatives were required.

An estimate of p can be obtained from the ratio of grain number in the longest head of fertiles and steriles in the composite populations (Table 2). The ratio ranges from 5.68/29.63 = 0.19 (R78S) to 25.12/50.84 = 0.49 (S77W) with a mean of 0.24. These values were obtained in populations containing from 39% to 45% steriles (Table 1). In S_0 - derived bulks a lower proportion of steriles is expected (Figure 13). Therefore a higher likelihood of pollination would be expected and consequently p may approach 1. It is unlikely that p would exceed 1 because such values could only occur if the mean number of grains set per sterile exceeded that of fertiles within a given S_0 - derived bulk.

This analysis assumes that *Ms* and *ms* pollen are equally effective in outcrossing steriles. The ratio of fertile: sterile in Table 1 suggests that the ratio of *Ms* : *ms* effectiveness is approximately 3:2. A higher frequency of *Ms* pollen would accelerate the approach of an S_0 -derived bulk to fixation and alter the values of $E(MsMs_I)$ but not to such an extent that the general conclusions of this analysis are invalidated.

If a breeder wished to reconstitute the composite cross or an intermating population from the highest yielding S_0 - derived bulks he must ensure that $msms_{\mathrm{I}}$ individuals occur for intermating and that no products of outcrossing to inferior S_0 - derivatives are included. From Table 13 it is seen that only S_1 seed satisfies these requirements. Progeny testing S_2 would not discriminate between $Msms_{\mathrm{I}}$ and $Msms_0$. Therefore residual seed of S_2 fertiles would contribute $msms$ by segregation but violate the requirement for no outcross products. The progeny of homozygous S_2 fertiles could be used to reconstitute the composite provided that a source of $msms_{\mathrm{I}}$ individuals were included.

3.7 EXPERIMENT 5. Comparison of the Yields of Homozygous Fertile F_5 Lines derived from the Composite Populations with F_5 Lines derived from the F_2 Population used to constitute the Composites.

Introduction

The high yielding S_0-derived S_2 bulks in Experiment 4 indicate that enforced outcrossing using 'Cornerstone' male-sterility in composites can generate S_0 recombinants which may have the potential to produce high-yielding inbred progeny.

The S_2 bulks would have been a mixture of individuals derived by two generations of inbreeding only from the S_0 and individuals resulting from outcrossing of male-sterile segregants in the S_1. The outcrosses could have occurred both within and between S_1 rows. Probable heterotic effects in the resultant hybrids may have positively biased the bulk yield. A negative bias would have been expected from incomplete seed-set on the steriles produced by segregation of S_1 *Msms* individuals and *msms* x *Msms* outcrosses in the S_1. Therefore a more accurate assessment of the potential of S_0 individuals requires families which have been derived by inbreeding only from their S_0 parents and do not contain sterile segregants. Although the S_2 (equivalent to F_3) level of inbreeding may be sufficient to identify the most promising families (LUPTON, 1961) only three quarters of all loci would be expected to be homozygous. A greater degree of inbreeding would reduce the residual effects of heterozygosity.

Experiment 4 also did not estimate the efficiency of selection for yield using composites involving outcrossed steriles relative to inbreds derived directly from the set of F_1 parents. The generation of S_0 populations would only be advantageous if they produced higher yielding inbreds than the initial crosses and these occurred at frequencies which could be detected in samples of reasonable size.

In this experiment homozygous fertile $F_3(S_2)$-derived F_5 bulks obtained from S_0 parents sampled from the S78S and R78S composite populations were compared with F_3-derived F_5 bulks sampled directly from the inbred F_2 descendants of the seven initial F_1 crosses between Cornerstone and the seven Australian wheat parents. This comparison allowed a comparison of efficiency of the composite process with conventional inbreeding, and reduced the effects of heterozygosity. The effects of steriles were eliminated by comparing homozygous fertile families from both the composite and F_1 derived populations.

The derivation of homozygous fertile F_5 lines from S_0 and F_2 parent plants

The objective of the derivation programme was to obtain ~~90~~ 3 sets of ~~3~~ 90 F_3 - derived homozyous fertile F_5 sister-lines from each of the following:

(a) 90 homozygous fertile F_2 individuals from the F_2 population used to initiate the composite cross.

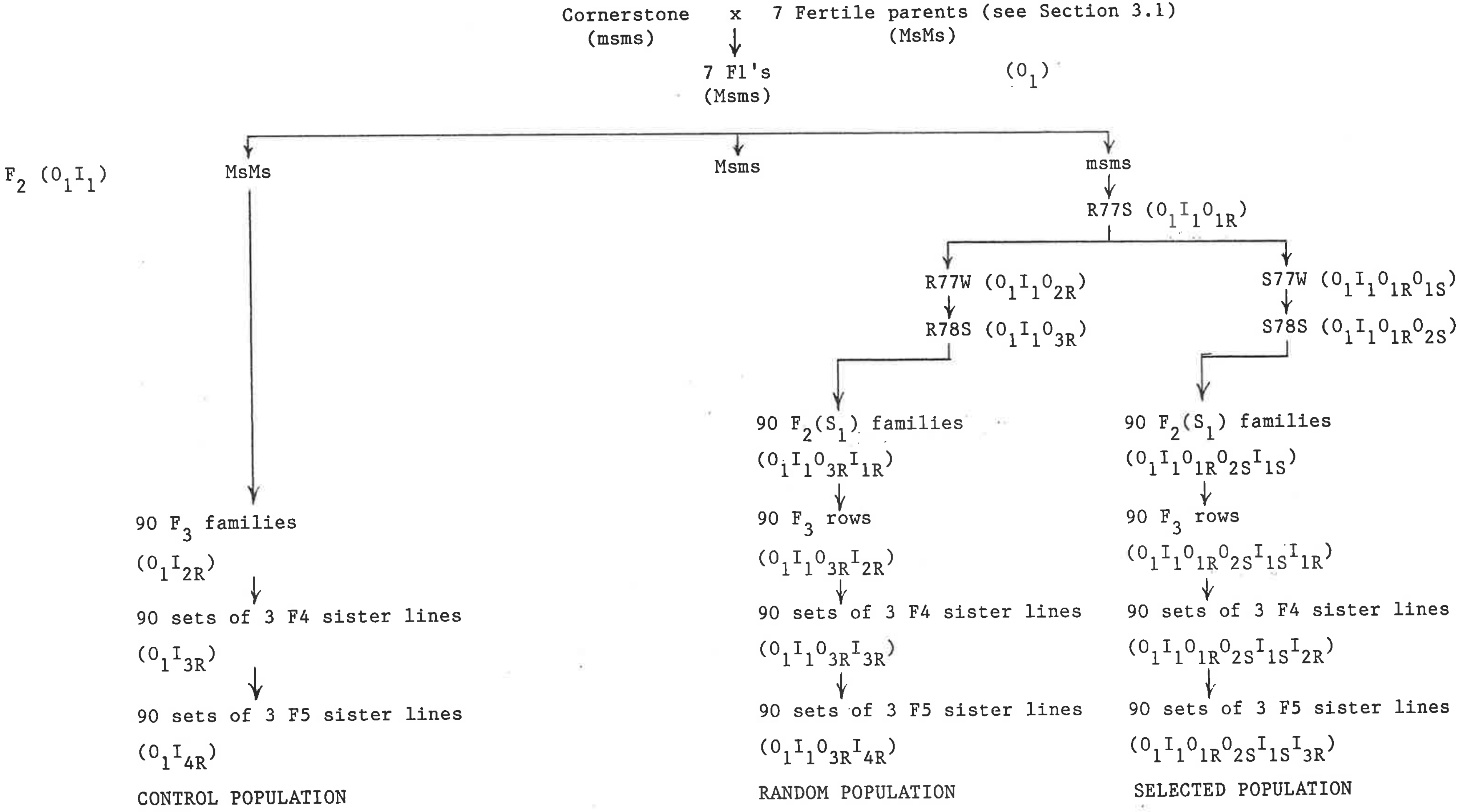
(b) 90 S_0 fertiles randomly chosen from the R78S composite population.

(c) 90 S_0 fertiles selected from the S78S composite population for height less than 100 cm, long headlength and high spikelet number.

The sets of F_5 lines from these sources were designated the 'Control', 'Random' and 'Selected' populations respectively. Each groups of 90 sets of F_5 lines were derived by equivalent random selection during inbreeding to ensure that the 90 sets were random samples of F_3 - derived inbred lines from each of the three populations of 90 parent plants. The derivation of the F_5 lines is presented in a flow diagram in Figure 14 using the 'I' and '0' terminology developed in Section 2.10 to describe breeding histories. The three populations of F_5 lines have hierarchial relationships. The 'Control' is a conventional F_5 (0_1I_{4R}). The 'Random' population involves 3 additional outcrossing cycles. The 'Selected' population

Figure 14

Derivation of the Control, Random and Selected groups of F_5 sister lines from the F_2 and Composite Populations



involved one random outcross, two outcrossings with selection of steriles (to generate S77W and S78S) and selection of the S_0 parents.

Therefore comparing the 'Control' and 'Random' populations test~~s~~ed for the effects of the 3 additional cycles of outcrossing and natural selection which occurred in the 'Random' series of composites, while comparison of the 'Selected' and 'Random' populations tests for the addition effects of selection for morphological characters in the 'Selected' series of composites. The comparison of the 'Control' and 'Selected' populations tests for the effects of both outcrossing and selection during the composite phase.

Three F_5 sister-lines were isolated from each S_0 - or F_2 - derived family so that the three selection strategies; 'Control', 'Random' and 'Selected' could be compared at three sites using a different randomly derived inbred from each parent. (see Experimental Design).

The critical phase in the derivation proce~~e~~dure was to ensure that 90 sets of homozygous families from each of the three selection strategies were retained after selection against sterility.

In the 'Random' and 'Selected' populations each parental S_0 individual was heterozygous fertile. Therefore 3/4 of their S_1 progenies would be fertile but only 1/3 of these S_1 fertile plants would be expected to be homozygous fertile. Therefore to ensure that at least one homozygous fertile S_2 progeny row was detected with a probability near ~~to~~ unity it was necessary to grow an S_1 population sufficiently large that it contained the minimum number of fertiles required for selection between S_2 rows.

The probability p, that at least 1 S_2 (F_3) row in n would be homozygous is given by:

$$(1 - p) = (2/3)^n$$

At n = 10, p has the acceptable value 0.983.

Given that the expected frequency of fertiles in the S_1 (F_2) is 0.75 and that at least 10 $S_1(F_1)$ fertiles must be obtained it is found by summation in the binomial

$$\frac{n!}{r!\ (n-r)!} \quad 0.75^r \quad 0.25^{n-r}$$

that at least 10 fertiles would occur in 20 with 0.996 probability and in 24 with a probability greater than 0.999.

Therefore 24 $S_1(F_2)$ plants were grown from each S_0 progeny and 10 fertiles were selected to grow 10 $S_2(F_3)$ rows. To be certain of detecting a heterozygous $S_2(F_3)$ row with an expected frequency of 1/4 for steriles per row it was found from the relationship

$$(1 - p) = (3/4)^n$$

that the probability of at least 1 sterile in 16 is 0.99 and 1 and 20 is 0.997. Therefore each $S_2(F_3)$ row was sown with at least 30 seeds. If more than one homozygous fertile $S_2(F_3)$ row were found in 10, one was chosen randomly to represent the parental S_0 plant. Plants were randomly chosen in each chosen homozygous S_2 (F_3) row as parents of the 3 F_3 - derived F_5 sister - lines descended from each S_0 parent.

To ensure that 90 sets of F_3 - derived F_5 lines were obtained from each composite, 100 S_0 parent plants were chosen. Homozygous F_3 rows were found in 97 families from the R78S population and 98 from the S78S. 7 and 8 families were randomly discarded from each respectively to leave 90 sets from each composite.

The 'Control' set of F_5 lines was obtained by growing sufficient F_2 - derived F_3 progenies to ensure that a minimum of 90 homozygous families would be detected with a probability near to unity. If it is assumed that 1/3 of the F_2 population were homozygotes, then from the normal distribution approximation of the binomial distribution it is found that at least 352 F_3 progenies must be grown to achieve 100 homozygous families with 0.95 probability. 360 F3 rows were grown. To detect homozygosity in a family it was necessary to grow sufficient F_3 plants per row to detect at least one sterile in a heterozygous row with a probability approaching unity. This is identical to detecting heterozygous S_2 rows. Therefore 20 plants were grown in each F_3 row (with a probability of detection of a heterozygous row being 0.997). 90 homozygous rows were randomly chosen and 3 F_3 plants were chosen randomly within each to produce 3 F_5 sister-lines derived from the F_2 parent of each F_3 row.

The seed from each S_2 or F_3 plant was multiplied in 1979 to produce F_5 seed.

Experiment Design

One sister-line from each set of 3 F_3(or S_2) - derived F_5 sister-lines was allocated to each of three experimental sites. Therefore 90 'Control', 90 'Random' and 90 'Selected' F_5 lines were grown at each site and each line had two sister-lines at the other two sites. In addition to the 3 groups of 90 F_5 lines at each site, the nine parents of the composite cross (Pitic 62, Federation, Condor, Gamenya, Gamset, Kite, Timgalen, WW-15 and Zenith) and three South Australian ~~C~~commercial varieties, Halberd, Lance and Warigal were included. The experimental design was a randomized block with three replicates at each site.

The three experiments were sown in June 1980 at Redbanks, Roseworthy and the Charlick Experiment Station. Each plot was 3.8 m long containing 4 rows 18 cm apart with 25 cm. between adjacent plots. The seeding rate was 60 Kg ha^{-1}. The plots were harvested in December, 1980.

Results and Discussion

The distributions of the yields of the three sets of 90 F_5 lines at each site are presented in Figures 15, 16 and 17 for Redbanks, Roseworthy and Charlick respectively. The yields of the parents and checks are also indicated. The mean, variance, skewness and kurtosis

Figures 15, 16 and 17

The distributions of yields at Redbanks, Roseworthy and Charlick respectively of F_5 lines derived from the Random$^{\circ}$ Selected$^{\bullet}$ and Control$^{\Delta}$ populations. The mean yields of the parental and check varieties are indicated at each site. The codes of the varieties are:

F	Federation
P	Pitic 62
C	Condor
Gy	Gamenya
Ga	Gamset
K	Kite
T	Timgalen
W	WW-15
Z	Zenith
*H	Halberd
*L	Lance
*Wa	Warigal

* check varieties

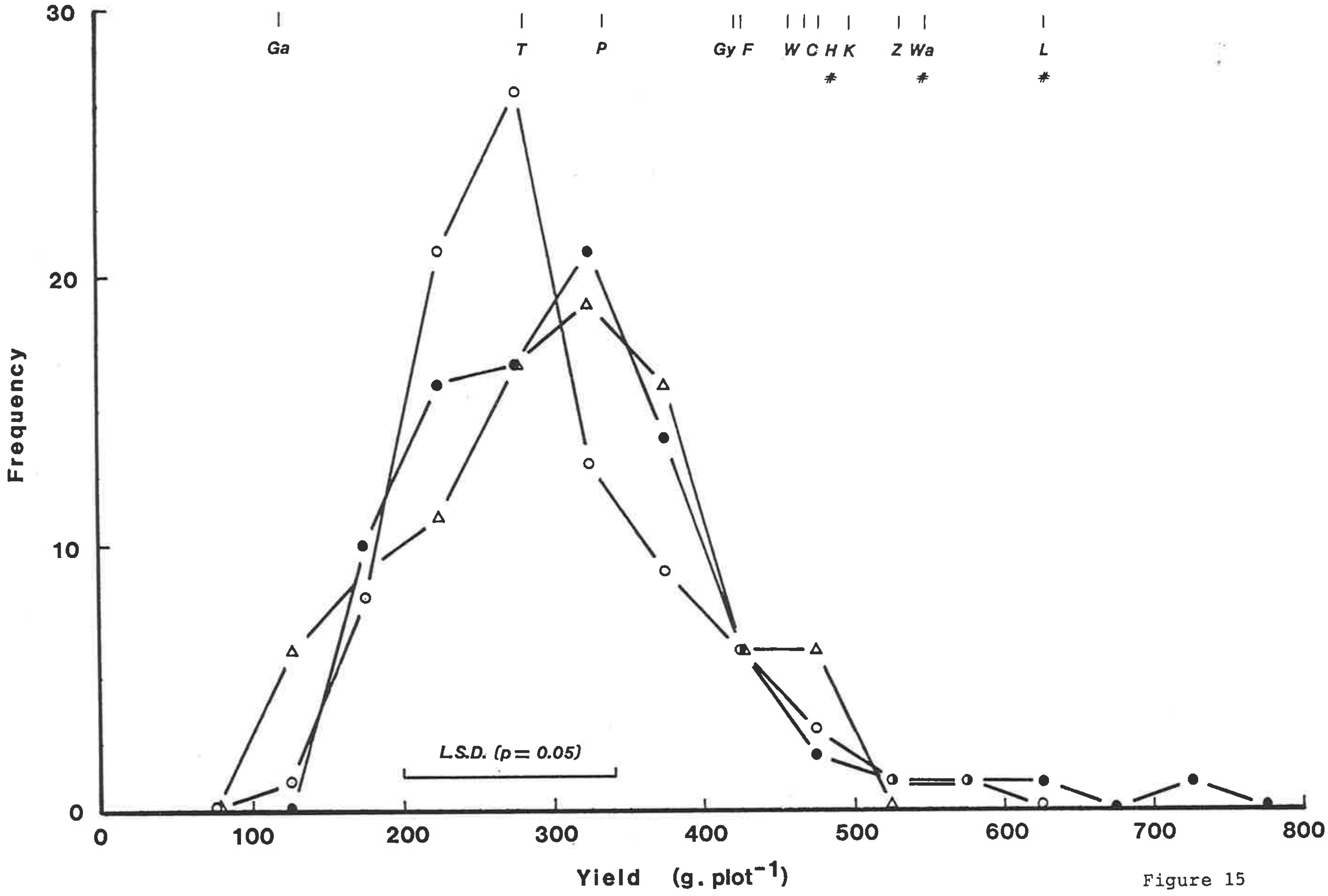

30
20
10
0
Frequency
Ga
T
P
Gy
F
W
C
H
K
Z
Wa
L
#
#
#
L.S.D. (p = 0.05)
0
100
200
300
400
500
600
700
800
Yield (g. plot^{-1})

Figure 15

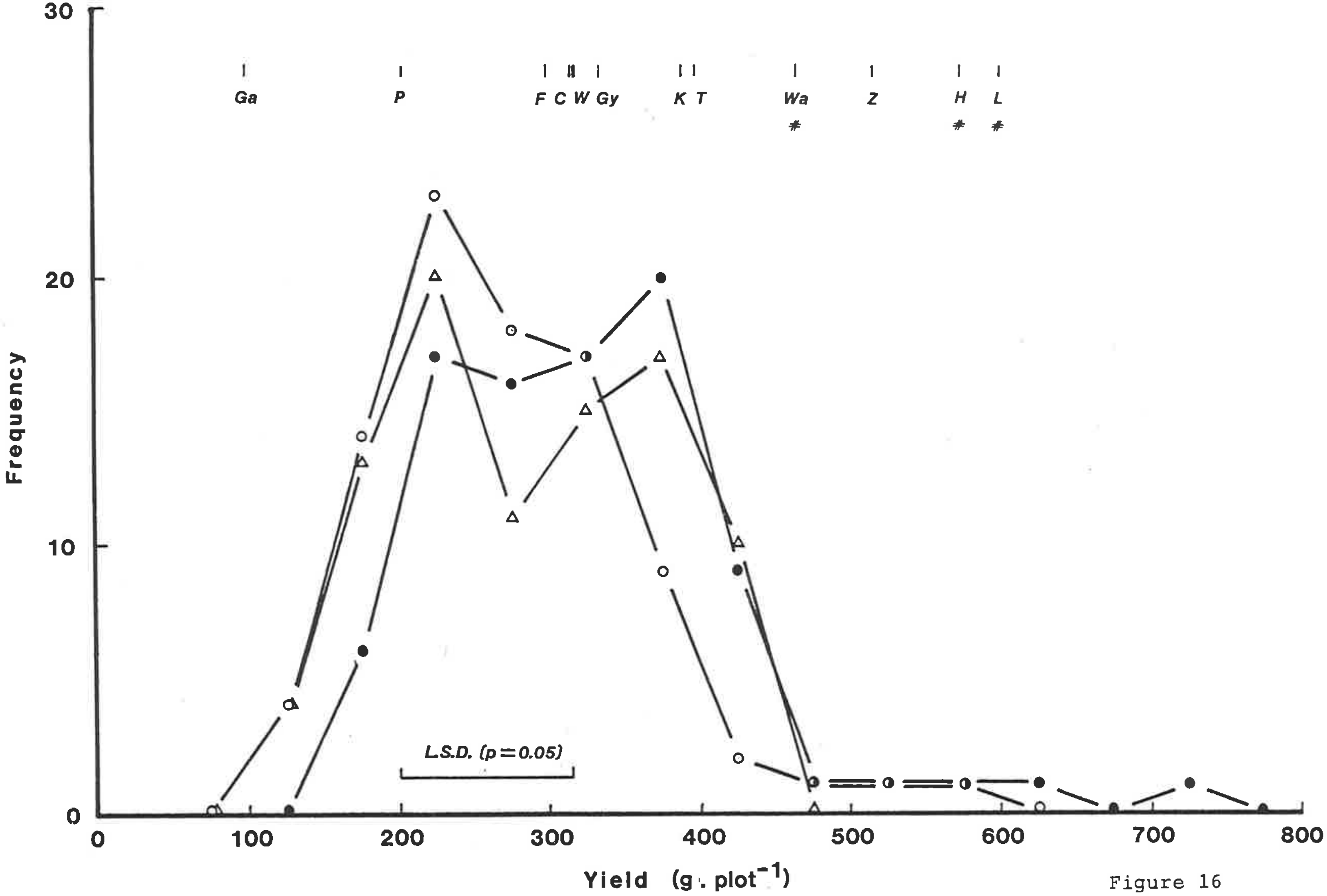

30
20
10
0
Frequency
Ga
P
F C W Gy
K T
Wa
Z
H
L
#
#
#
L.S.D. (p = 0.05)
0
100
200
300
400
500
600
700
800
Yield (g. plot^{-1})

Figure 16

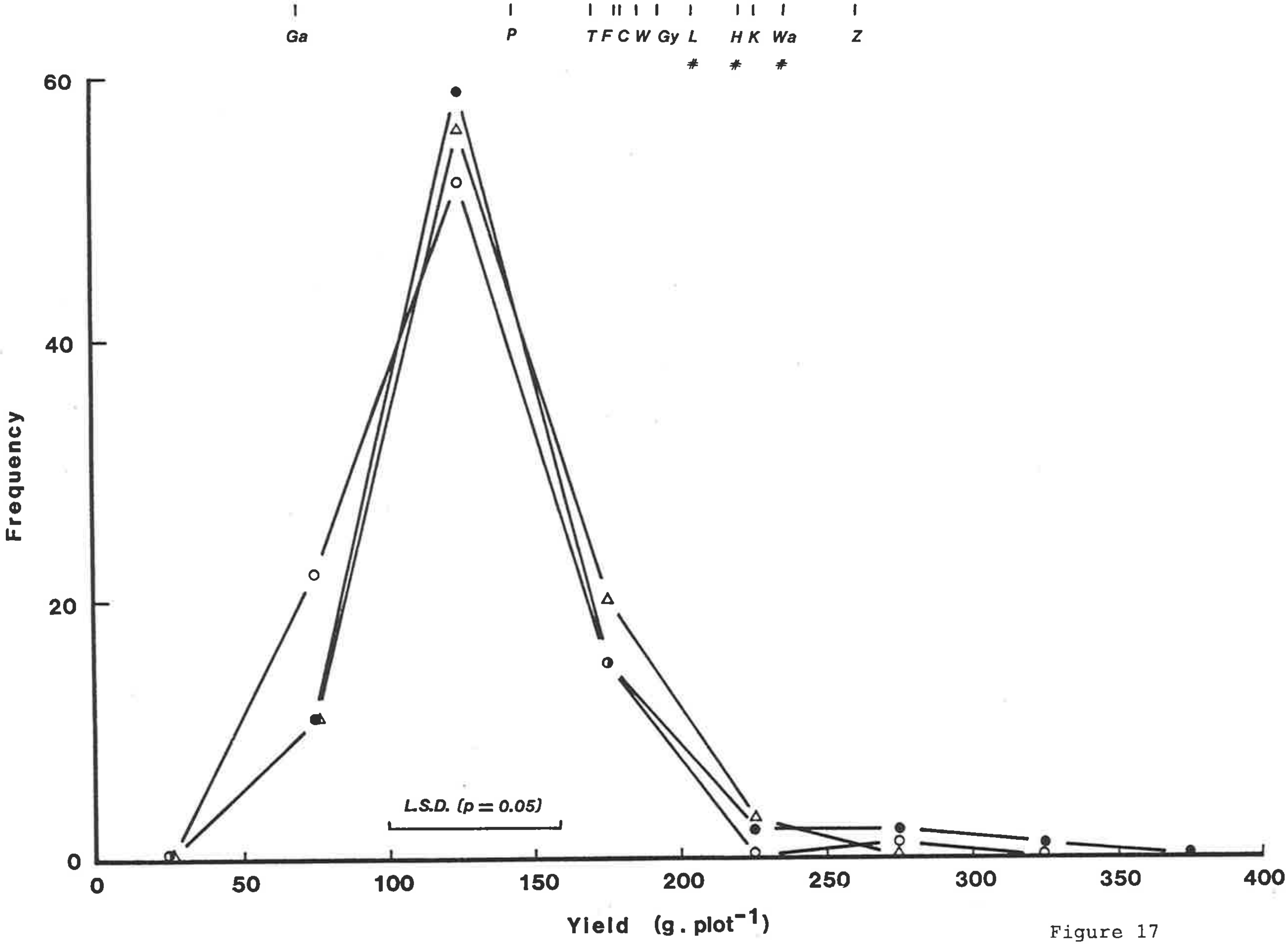

Ga
P
T
F
C
W
Gy
L
H
K
Wa
Z
#
#
#
60
40
20
0
Frequency
L.S.D. (p = 0.05)
0
50
100
150
200
250
300
350
400
Yield (g . plot^{-1})

Figure 17

of each distribution are presented in Table 15.

Significant skewness and kurtosis invalidated parametric tests between the three distributions and parents at each site. The levels of significance of tests between distributions using the non-parametric Kolomogorov-Smirnov test are presented in Table 15.

The results of the Kolmogorov-Smirnov tests for differences between the Control, Random and Selected distributions are inconclusive. At Charlick there were no significant differences and at Redbanks the higher yield of the Selected vs Random was the only significant difference. Only at Roseworthy were the distributions significantly ranked, Selected > Control> Random. The lack of a consistent pattern of ranks suggests that neither of the composite selection strategies significantly changed the mean yield of inbred lines derived from them. A tentative conclusion may be drawn from the significant Random vs Selected comparisons at Redbanks and Roseworthy that the Selected strategy was slightly superior to the Random.

The absence of consistent significant differences between the Selected and Random strategies reflects the lack of differences found between the yields of their respective S_1 and S_2 bulks in Experiments 2 and 4 (Tables 7 and 12). Alternatively, if the small and inconsistent superiority of the Selected over the Random is accepted, it may reflect the response to selection of fertile S_0 parents in the S78S population. The expressions of headlength, spikelet number and yield components were greater in the selected S78S S_0 parent set than in the total population (Table 3). Experiment 4 demonstrated that intense selection for spikelet number slightly increased the mean yield of S_1 lines and, similarly, selection of the S_0 parents for longheadedness and high spikelet number may have slightly increased the mean yield of F_5 lines over those of the Random population.

The range of yields of the parents was consistently greater than the Random and Control at all sites, but less than the range of the Selected lines at Redbanks and Roseworthy. This result again suggests

Table 15: The means (x) variances (σ^2), skewness (s) and kurtosis (k) of the 'Random', 'Selected' and 'Control' F5 populations at three sites and the significance levels of Kolmorgorov-Smirnov tests for differences between F5 populations and distribution of the yield of parental varieties

Population		Site		
		Redbanks	Roseworthy	Charlick
RANDOM (R)	x	302	269	126
	σ^2	11 393	11 268	1 786
	s	0.572**	0.716**	0.817**
	k	0/156 N.S.	2.013**	1.503**
SELECTED (S)	x	313	332	136
	σ^2	16 009	13 241	2 673
	s	0.528**	0.894**	1.489**
	k	0.629*	1.991**	3.83**
CONTROL(C)	x	293	286	133
	σ^2	13 131	10 921	2 019
	s	0.039 N.S.	-0.031 N.S.	0.397**
	k	-0.659**	-0.927**	0.277 N.S.
PARENTS	x	394	318	179
KOLMOGOROV-SMIRNOV TESTS				
R vs S		*	**	N.s.
R vs C		N.S.	*	N.S.
S vs C		N.S.	*	N.S.
R vs Parents		*	**	**
S vs Parents		N.S.	N.S.	*
C vs Parents		*	**	**

the tentative conclusion that the Selected strategy had slightly improved the mean performance of the Selected F_5 lines.

The most obvious aspect of the results is the presence of high yielding 'tails' on the Selected and Random distributions at each site. High-yielding tails did not occur on the Control distributions. In Table 16 the yields of the individual F_5 lines which numerically exceeded the highest yielding control line at each site are presented with the yields of the parents and checks. As a result of the high-yielding tails many Random and Selected F_5 lines did not differ significantly from the highest yielding parents and checks. S34 at Redbanks was significantly higher yielding than any parent and S12 was significantly the highest yielding population at Roseworthy and Charlick. In contrast, the highest yielding Controls did not numerically exceed the highest yielding parent or check at any site.

The high-yielding tails are so consistent that they may be a real effect of the compositing and inbreeding strategies which developed the F5 lines. This could not be tested by analyses of variance or the Kolmogorov-Smirnov test, but a very strong case that they are not the product of experimental error can be developed from probability analysis using the null hypothesis that there are no differences between any F_5 lines at each site. The probability that r Random and s Selected lines would be chosen in a sample of (r + s) lines from all of the 270 F_5 lines at a site before randomly choosing any control line if all had an equal chance of being chosen is:

$$\frac{C_r^{90} \cdot C_s^{90} \cdot C_o^{90}}{C_{(r+s)}^{270}}$$

Table 16: The yields of Random and Selected F_5 lines exceeding the highest yielding Control F_5 line at three sites

Population Family	Redbanks	Roseworthy (gm plot^{-1})	Charlick
R2	497	510	
R6	492		
R26	494		
R67		465	
R75	581	554	266
R77	510		
S12		747	333
S16			219
S19	497	522	295
S24	603		
S27	492		
S29	585	589	268
S30	537		
S34	706	644	240
S60		478	
HIGHEST YIELDING CONTROL LINES			
C62	483		
C66		447	
C83			216
PARENTS			
Federation	426	298	178
Pitic 62	334	204	143
Condor	469	314	180
Gamenya	424	334	195
Gamset	121	97	69
Kite	500	387	227
Timgalen	282	396	171
WW15	461	315	187
Zenith	533	513	262
CHECKS			
Halberd	482	573	221
Lance	631	600	205
Warigal	549	464	237
L.S.D.(0.05)	139	118	58

For example, at Redbanks r = 5 and s = 6 (Table 16) and the probability was 0.0024, while at Roseworthy (r = 3, s = 5) and Charlick (r = 1, s = 5) the probabilities were 0.0082 and 0.0078 respectively. Alternatively, if the distinction between Random and Selected lines which exceed the highest yielding Control is disregarded, the probability becomes:

$$\frac{C^{180}_{(r+s)} \cdot C^{90}_{o}}{C^{270}_{(r+s)}}$$

and the resulting probabilities are: Redbanks, 0.014; Roseworthy, 0.0370; and Charlick, 0.0583. Each analysis of probability suggests that the chance of selecting (r+s) lines before any Control line is so small that it is more probable that the high-yielding tails result from Random and Selected lines which are higher yielding than any Control line.

The occurrence of sister lines in the high-yielding tails (Table 16) *also strengthens the argument that the high-yielding tails were a real effect.* Probability analysis was used to test the null hypothesis that the frequencies of triplet, double and single family lines in the Random and Selected groups which were higher yielding than any Control line occurred with a probability acceptable as random chance.

The probability that x triplets (i.e. x families from all three sites), y doubles (i.e. y families occurring in any 2 sites) and z singles (i.e. z families occurring in 1 site each) would be drawn randomly in a total sample of N = (3x + 2y + z) from a total population of 90 sets of triplets (ie from 90 families of 3 sister lines) is:

$$P_{(x,y,z)} = \frac{C^{90}_{x+y+z} \cdot C^{x+y+z}_{x} \cdot (C^{3}_{3})^{x} \cdot C^{y+z}_{y} \cdot (C^{3}_{2})^{y} \cdot C^{z}_{z} \cdot (C^{3}_{1})^{z}}{C^{270}_{N}}$$

The probabilities from the Random families, i.e. $P_{(1,1,4)}$, and Selected families, i.e. $P_{(3,1,5)}$, were 0.002 and 1.07×10^{-8} respectively. Therefore the particular sets of values of x, y and z for the Random and Selected populations probably were not random because their chance of occurrence was much less than the accepted probability level for the null hypothesis to be valid, 0.05. However, the particular sets of values are only one of many possible combinations in samples of either 9(i.e. (1x3) + (1x2) + (5x1)) or 16 (i.e. (3x3) + (1x2) + (4x1)) drawn randomly from 90 sets of triplets. The above equation for P(x,y,z) can be used to test an alternative null hypothesis that one or more sets of triplets would not occur in samples of 9 and 16 drawn from 90 sets of triplets, i.e. 1 minus the probability of no triplets in samples of 9 and 16. The respective probabilities are 0.0023 and 0.0155 and consequently this null hypothesis must also be rejected. Therefore the occurrence of sets of sister-lines in the high-yielding 'trials' was probably a real effect, which suggests that some S_1 parents had the potential to produce sets of high-yielding F_3 - derived F_5 sister-lines. In contrast, in the 'Control' population no high-yielding tails were evident, which suggests that no Control F_2 parent plant had a genetic potential equivalent to some S_1 parents for producing high-yielding inbreds.

The most obvious explanation for the occurrence of superior S_1 parents is that additional intermating in the composite crosses increased the opportunity for the formation of new recombinants between the parental genotypes. However, the higher frequency of superior S_1 parents from the composites could have resulted from two specific differences between the Control and composite populations.

Firstly, the Control F_2 and composite-derived S_1 parents did not descend from the same exact sets of F_2 plants. The Control population descended from homozygous fertile F_2's while the S_1's were derived from *sterile (msms)* F_2 mothers pollinated by *MsMs* and *Msms* fertiles. Therefore the Control F_2 parents did not carry *ms* and consequently they would have contained a lower frequency of alleles initially linked to *ms* in 'Cornerstone'. This difference in gene frequencies at loci linked to *ms* caused significant morphological differences in the early generations of the composite (Experiment 1, Table 2) and their probable effect on yield cannot be disregarded. If a factor linked to *ms* ~~were~~ was significant then a recombination event would have been required during the composite phase or in the S_o parents to recombine it with the *Ms* allele for transmission into an *MsMs* homozygous S_1 parent. The second difference between the Control F_2 and S_1 parents is their number of contributing parents. Each Control F_2 is derived from Cornerstone and only one Australian ~~W~~wheat parent. In contrast because of the opportunity for outcrossing in the composite generations each S_1 parent would have contained genes contributed by more than one initial Australian wheat parent. They would have still retained an average of one-half Cornerstone genes.

The genetical implications of these differences between the composite and control populations will be discussed later.

The occurrence of sets of high-yielding F_5 (S_4) sister-lines suggests that their respective F_5 (S_2) parents had inherited a factor or factors for high yielding potential from their common S_1 parent. If such factors were rare recombinants formed during outcrossing in the composite phase it is unlikely that they would have been homozygous in S_0 parents of the randomly inbred families. The absence of high-yielding tails containing sister-lines in the Control suggests no factors with equivalent yield potential were created in the F_1 or F_2 generations prior to the composite phase.

Consider a factor which occurs in an S_0 parent and which is inherited as an independent unit without disruption. In the $S_1(F_2)$ the ratio of individuals homozygous, heterozygous and lacking the factor would be 1/4 : 1/2 : 1/4.

All F_3 derived sister-lines descended from S_1 homozygotes would be high yielding. The S_1 heterozygotes would have again segregated 1/4 : 1/2 : 1/4 in the S_2 (F_3). The F_3 homozygotes would produce high-yielding F_5 lines, but the yields of F_5 lines derived from the heterozygous F3 parents would be dependent upon the 'dominance' of the factor and its ability to influence the yield of the F_5 bulk mixture, in which 3/8 homozygotes, 1/4 heterozygotes and 3/8 deficient individuals are expected. If 100% homozygotes are required in an F_3 - derived F_5 bulk for the expression of high yield, then the expected probabilities of 3,2,1, or 0 high - yielding sister lines in the progeny of an initial heterozygous S_0 parent would contain two components:

(a) a probability of 0.25 for triplets descended from homozygous S_1 parents, and

(b) expected probabilities for 3, 2, 1 or 0 sister-lines in the progeny of heterozygous S_1 parents given by

$$1/2 \; [\; C_n^3 \; (1/4)^n \; (3/4)^{3-n}]$$

Therefore the total expected proportions would be:

3 : 0.250 + .008 = 0.258
2 : 0.070
1 : 0.211
0 : 0.461

If the presence of the factor in an F_5 bulk was sufficient for its expression then these proportions would become:

3 : 0.250 + .211 = 0.461
2 : 0.211
1 : 0.070
0 : 0.258

which are derived by transposing 1/4 and 3/4 in the above binomial function.

Therefore a single factor in a heterozyous condition in an S_0 parent would be expected to produce high-yielding triplets of sister-lines with sufficient frequency for them to be frequently detected. This analysis supports the argument that such a factor may have been present in the S_0 parents of the sets of lines found in the high-yielding 'tails' of the 'Selected' and 'Random' populations.

The factor may have been a single gene, but this is unlikely because no 'Control' families expressed equally high yields. It is more probable that the factor in each family was a small segment of linked interacting genes which formed during the composite cross phase and did not segregate frequently during inbreeding. In cases where high yield could result from complex interactions between independent or loosely linked segments of a parental S_0 genome, it is unlikely that the desirable genetic configuration would have been retained during inbreeding and high-yielding lines, in particular sister-lines, would not have occurred. However, the calculated probability of high-yielding sisters caused by one factor is so high that it is probable that two complementary independent factors could have produced some high-yielding sets.

The absence of high-yielding sets of 'Control' sister-lines suggests that the greater opportunity for recombination in the composite crosses increased the frequency in the 'Random' and 'Selected' populations of recombinants which had high-yielding potential.

It is interesting that no low-yielding 'tails' were evident in the 'Random' and 'Selected' populations, but low-yielding sets of sister-lines were present in all three populations. Therefore simply inherited factors may have been causing low yield. The high frequency of low-yielding lines in all populations may have prevented the detection of any differences between populations. However, in the next experiment, in which the extremes of the distributions were analysed in greater detail, no low-yielding tails were evident but the high-yielding tails recurred. This suggests that the composite did not produce S_1 individuals with a lower potential for yield than some of the initial F_1 crosses.

Association in yield between sister-lines were not only confined to the high-yielding 'tails' or some low-yielding families at each site. There were significant tests for rank relationships and correlations of yield between sister lines in all three pairs of sites (Table 17). The tests for rank and correlation of yield were non-significant in only one case, the Control population in the Redbanks-

Table 17: The association between the yields of F_5 sister lines at three sites within each selection strategy.

Association	Population		
	Random	Selected	Control
Redbanks-Roseworthy	ϕ0.277**	0.403**	0.114 N.S.
	+0.380**	0.523**	0.150 N.S.
Redbanks-Charlick	0.208*	0.449**	0.330**
	0.365**	0.555**	0.345**
Ros~~d~~eworthy-Charlick	0.533**	0.449**	0.331**
	0.574**	0.680**	0.306**

ϕ Spearman's Rank Test

\+ Correlation coefficient of yield

Roseworthy pair. The correlation coefficients must be accepted with caution because of non-normality in all the distributions of F_5 lines.

The significant associations of ranks of sister-lines, which is expressed in particular as sets of high-yielding sister-lines, suggests that superior S_1 parents could be detected by yield testing their bulk progeny. This would be equivalent to the successful F_2-progeny method (LUPTON, 1961). It is probable that $S_2(F_3)$ or $S_3(F_4)$ bulks may be as indicative of superior S_1-derived families as the sets of F_5 lines used in this study. Consequently bulks in generations prior to the F_5 could be used to identify those families with the highest potential for producing high-yielding inbred derivatives.

The presence of significant positive skew and positive kurtosis in the Random and Selected populations (Table 15) may indicate significant complementary and epistatic interactions. In computer simulations (SNAPE and RIGGS, 1975; POONI, JINKS and CORNISH, 1977; CHOO and REINBERGS, 1982) these interactions had positive skew and kurtosis in distributions of inbred lines. JINKS and POONI (1981b) also suggested that significant kurtosis would occur if a few genes strongly influenced a distribution of phenotypes and if there were linkage disequilibria in inbreeding populations. Both of these conditions were probably present in the Random and Selected populations. The high-yielding tails and correlations between sister-lines suggest that single genes or small linkage segments were influencing the yields of families. Linkage disequilibria would have been high in the initial parents and possibly enhanced by selection during propagation of the composites (Experiment 1). The lack of significant skew in the control populations at two sites and negative kurtoses suggest less gene interactions than in the distributions derived from the Random and Selected composites. The high-yielding tails may be the extreme expressions of genetic interactions produced by outcrossing and selection in the composite populations and fixed in F_5 inbred lines.

The simultaneous outcrossing and selection which occurred during the composite phases prevents an assessment of the effect of intermating only on the variances of the populations of inbred lines. Therefore it is not possible to test whether intermating only would have changed the magnitudes of the variances (BLISS and GATES, 1968; BOS, 1977; PEDERSON, 1974; STAM, 1977) or whether there would have been no change (NANDA *et al*; 1981; SNAPE, 1978). Intermating may have also disrupted favourable coupling configurations in superior parents (BAILEY and COMSTOCK, 1976), but after recombination, and possibly selection, higher yielding lines were produced from the composites. The significant skews and kurtoses disallow valid comparisons of variances, but appraisal of Figures 15 to 17 suggests that the composite breeding strategies did not appreciably change the variances if the high yielding tails are disregarded. In contrast, JAIN and SUNESON (1966) had found consecutive outcrossings increased the variance of S_0-derived lines in barley.

In summary, this experiment has again emphasised that partitioning the composite populations exposes high-yielding lines. Although intermating had no consistent effect upon the mean performance of populations of inbred derivatives, it caused significant changes to the distribution of yields possibly through interactions. These, in turn, produced the most obvious aspect of the results of this experiment; high-yielding tails on the composite-derived distributions. The high-yielding 'tails' contained a significantly high occurrence of sister-lines, which suggested that relatively simply inherited factors were responsible for the high-yielding families. Such a factor could have been the product of a rare recombination event which was not significantly disrupted during inbreeding. Strong correlation between sister-lines were not only evident in the high-yielding 'tails' but were found in all three groups of sister-lines. Therefore the performance of an inbred is strongly determined at the S_1 (F_2) level of segregation in its ancestry. Consequently, partitioning a composite bulk at the S_1 level and identifying the highest yielding S_2 and S_3 bulks derived from S_1's may be an efficient method of exploiting the recombinants produced by consecutive intercrossings in a composite cross. F_4 or F_5 single plant selections from the highest-yielding bulks could then be progeny tested to identify the highest yielding individual near-homozygous segregants.

Some Specific Genetical Implications of the Procedures used to Establish and Propagate the Control and Composite Populations.

In the preceeding discussion attention was drawn to two aspects of the F_2 population used to establish the control and composite populations which may have had a significant effect upon the outcome of this experiment. Firstly, the homozygous (*MsMs*) fertile parents of the Control population would have contained a higher frequency of genes from the fertile Australian wheat parents at loci closely linked to the *Ms* locus than the heterozygous (*Msms*) and sterile (*msms*) plants. The latter would have contained a higher frequency of 'Cornerstone' genes in the same region. Secondly, each Control F_2 parent was derived from a single cross between 'Cornerstone' and one fertile Australian wheat, but more than one Australian parent contributed to each S_0 selected from the R78S and S78S populations. Therefore the differences between the Control and composite-derived F_5 lines ~~were~~ not only indicat~~ing~~ed the effects of three additional cycles of intermating; they ~~were~~ also indicat~~ing~~ed the effects of permitting association between the genomes of the Australian wheats. Assuming the contribution from each Australian parent to the F_2 parent set of Control lines was proportional to the numbers of F_2 seeds from each initial F_1 cross (Section 3.1.), the 90 Control F_5 lines would have contained expected frequencies of 14.6 lines derived from Gamenya, Gamset, Timgalen, WW-15 and Zenith, 14.2 from Condor and 2.9 from Kite.

In summary, the differences between the Control and composite-derived Random and Selected distributions of yields of F_5 lines were the result of three specific factors: different gene frequencies in the *ms* region; the opportunity for association of the seven Australian wheat genomes; and a greater opportunity for ~~meaningful~~ recombination during three additional cycles of outcrossing during propagation of the composites. Two of these factors; increased association of parental genomes, and additional cycles of intermating are essential elements of the composite breeding proceedure (DRISCOLL, 1981; SUNESON, 1956). Elimination of increased levels of association as outcrossing proceeded would have reverted the procedure from compositing to intermating within crosses only. Nevertheless, the degree of association of parental genomes at the stage when the Control was isolated and additional cycles of intermating commenced probably affected the differences between the Control and composite derived lines. In this experiment the bulk of seven initial F_2 families was arbitarily chosen as the point to sample for a Control. If for example, the seven F_1's had been intermated in a diallel the Control would have contained lines with two Australian parents each and it is probable that recombination in the multiple cross or its succeeding F_2 may have produced higher yielding recombinants.

The different gene frequencies in the *ms* region could have been reduced if backcross sterile derivatives of the fertile parents had been available. The differential effects of genes linked to *Ms* and *ms* cannot be determined. They did cause significant differences in specific characters, particularly in the R77S, and may have also affected yield. The effects of selection during the compositing phase also cannot be determined. They may have been significant, as they were in changing character associations (Experiment 1). They were an integral part of the two compositing procedures chosen in this study and, consequently, probably contributed to the differences between the Control and composite populations.

Another genetical implication of random crossing in the composite procedure is the likelihood that an outcross will occur between two individuals with identical initial parents. In that case, the outcross allows further recombination within that parent set but does not allow association and recombination with other parental genomes. The maximum number of parents which can be associated after N outcrosses is 2^N. Therefore in the composites in this study the first opportunity for all seven parents to asociated occurred in the 1978S populations after three outcrosses. If the small contribution from Kite (Section 3.1) is disregarded, leaving 6 parents, the expected proportions of the composite population in which n of 6 parents are associated are presented in Table 18A. The mean is at n= 4.6. If a larger population of parents had been used only 8 could have formed the highest level of association at N = 3. Therefore large parent sets are futile unless N is increased to achieve the maximum level of association. However, as N increases the number of possible parent combinations at each level of N also increases and therefore the frequency of any given association of parents is small. For example, in this study the expected frequencies of each possible parent association are given in Table 18B. Consequently, in the samples of 90 S_0 individuals taken from the 1978S populations the expected frequencies of each possible combination of parents at each level of association were 5.4×10^{-5}, 1.4×10^{-2}, 0.27, 2.16, 6.75 and 10.3 for n from 1 to 6 respectively, assuming no effect from selection and ignoring the seventh parent. Therefore outcrossing in the composite phase had generated the most frequent associations at the highest values of n and almost eliminated those at n = 1, 2 and 3. If the composite had a larger parent array, associations at n = 7 and 8 could have occurred, but the expected frequency of any given association would have been smaller. Therefore, a larger population would be futile unless a very large S_0 sample were taken to have a high likelihood of obtaining most of all the possible combinations of parents. These results complement HANSON (1959c; 1959d) who concluded that populations larger than 10 or intermating for more than about 4 generations were futile for achieving significantly greater disruption of parental genomes. Therefore the management of this composite was near optimum for achieving both a high level of parent associations which could be retrieved in a sample of 90 and disruption and recombination of the parental genomes.

Table 18

A. The expected proportion of individuals in each composite generation in which N of 6 parents are associated

Generation	N					
	1	2	3	4	5	6
F2	1.000	–	–	–	–	–
1977S	0.167	0.833	–	–	–	–
1977W	$4.6x10^{-3}$	0.162	0.556	0.278	–	–
1978S	$3.6x10^{-6}$	$2.27x10^{-3}$	0.069	0.365	0.450	0.114

B The expected proportion of each possible combination of parents at each level of N.

F2	0.167	–	–	–	–	–
1977S	0.028	0.055	–	–	–	–
1977W	$7.7x10^{-4}$	0.011	0.028	0.019	–	–
1978S	$6.0x10^{-7}$	$1.5x10^{-4}$	0.003	0.024	0.075	0.144

3.8 EXPERIMENT 6: Comparison of the High-and Low-yielding Extremes of F_5 Yield Distributions of Control and Composite-derived Populations

Introduction

The two most prominent aspects of the distributions of F_5 yields in 1980 were high-yielding tails on the Random and Selected distributions and the presence of sister-lines amongst the composite-derived lines which numerically exceeded the highest yielding Control line at each site. It was shown by testing with the null hypothesis that all F_5 line yields were equal that the probabilities of the high-yielding tails and the presence of sister-lines would be extremely low and are more likely to be real effects. However tests of the differences between the distributions could not be used to test the validity of the high-yielding tails. A test for significant differences between samples taken from the high-yielding extremes of each distribution would test for real 'high-yielding tail' effects.

At the low-yield extremes of all distributions there were no apparent 'tails' which suggested that the lowest-yielding lines from each breeding strategy were similar. Again, this could not be tested from comparisons of the total distributions but can be tested by comparing samples of the lowest yielding lines from each distribution.

In this experiment the ten highest and ten lowest yielding lines from the distribution of each breeding strategy at each 1980 site were compared to test for significant differences between the extremities of the distributions and more precisely evaluate the capacities of the breeding strategies to produce either high or low-yielding segregants.

Experimental design

The ten highest yielding and ten lowest yielding lines from the F_5 distribution of each breeding strategy were identified at each site and selected to form high and low selections respectively. The sixty lines identified at each site were compared in a randomized block experimental design with five replicates grown at three sites.

The sites were the same as in 1980: Redbanks, Roseworthy and Charlick. Therefore the selections from each experimental site in 1980 were tested at the same and two additional sites in 1981. The plot dimensions and seeding rates were the same as in 1980. the experiments were sown in June and harvested in December 1981.

Results and Discussion

The mean yields at three sites in 1981 of the sample of ten lines taken from the high and low extremities of each selection strategy at Redbanks, in ~~1980 are presented in Table 19. Tables of the mean yields of identical sets of samples from~~ Roseworthy and Charlick are presented in Tables 19, 20 and 21 respectively. In each table are also presented marginal means for each selection group (High and Low) x selection strategy, each overall mean of selection groups, each strategy averaged over selection groups and site means. The levels of significance of each main effect and interaction are also presented with their relevant values of least significant differences.

The mean yield over three sites, of each line from Redbanks in 1980 are presented in Figures 18A and 18B for the High and Low yielding selection groups respectively. The selection strategy and family number from 1980 are indicated for each line. The mean yields of individual lines selected from Roseworthy and Charlick in 1980 are presented in Figures 19A, 19B, 20A and 20B.

The interaction of the Selection group (High, Low) with Selection Strategy (Random, Selected, Control) is the critical test for differences between the mean yields of the lines which occurred in the extremities of each distribution in 1980. These interactions were significant for selections from Redbanks (Table 19) and Charlick (Table 21) but not for selections from Roseworthy. In the two significant cases the interactions were caused by different patterns of mean yields. In the case of the Redbanks selections (Table 19) High-Selected (H-S) exceeded High-Random (H-R) and High-Control (H-C), which had similar yields (i.e. H-S>H-R = H-C), while in the low selection group Low-Random and Low-Control were similar and both exceeded Low-Selected (i.e. L-R = L-C> L-S). In the Charlick case

Tables 19, 20 and 21

The mean yields in 1981 at three sites of the ten highest and ten lowest yielding lines of the Random, Selected and Control populations in 1980.

Table 19 : Selections from Redbanks, 1980
Table 20 : Selections fro~~M~~m Roseworthy, 1980
Table 21 : Selections from Charlick, 1980

Redbank Selections

Table 19

Selection	Strategy	Site			Mean	Mean
		Redbanks	Roseworthy (gm plot^{-1})	Charlick	(SelxStr)	(Sel)
	Random	361	397	433	397	
High	Selected	458	477	508	481	431
	Control	381	401	460	414	
Mean (High Sel. x Site)		400	425	467		
	Random	294	328	362	328	
Low	Selected	276	307	337	307	318
	Control	290	311	356	319	
Mean (Low Sel. x Site)		287	315	352		

Strategy				Mean (Str)
Random	328	362	398	363
Selected	367	392	423	394
Control	335	356	408	366
Mean (Site)	343	370	409	Grand Mean 374

Levels of Significance and Table of L.S.D's.

		(0.05)	(0.01)	(0.001)
Site	ns	-	-	-
Strategy	***	16	22	33
Selection	***	-	-	20
Strategy x Site	ns	-	-	-
Selection x Site	ns	-	-	-
Selection x Strategy	***	20	27	34
Strategy x Selction x Site	ns	-	-	-

Table 20

Selection (Sel)	Strategy (Str)	Redbanks	Roseworthy (gm plot^{-1})	Charlick	Mean (Sel x Str)	Mean (Sel)
	Random	370	439	477	429	
High	Selected	417	466	500	461	433
	Control	356	412	457	408	
Mean (High Sel x Site)		381	439	478		
	Random	272	330	357	320	
Low	Selected	319	329	352	334	317
	Control	271	292	331	298	
Mean (Low Sel x Site)		288	317	347		
Strategy						Mean
	Random	321	384	417		374
	Selected	368	398	426		397
	Control	314	352	394		353
Mean (Site)						Grand Mean
		334	378	412		375

Levels of Significance and Table of L.S.D's		(0.05)	(0.01)	(0.001)
Site	*	54	-	-
Strategy	***	14	19	24
Selection	***	-	-	19
Strategy x Site	n.s.	-	-	-
Selection x Site	*	50 (Selections between sites) 22 (Selection within site)		
Selection x Strategy	n.s.	-	-	-
Strategy x Selection x Site	n.s.	-	-	-

Table 21

Selection	Strategy	Redbanks	Site Roseworthy (gm plot^{-1})	Charlick	Mean (Sel x Str)	Mean (Sel)
	Random	361	384	442	396	
High	Selected	413	373	407	397	388
	Control	336	369	404	370	
Mean (High Sel x Site)		370	375	418		
	Random	225	263	328	272	
Low	Selected	306	308	329	314	291
	Control	259	264	334	285	
Mean (Low Sel x Site)		263	278	330		
Strategy					Mean (Str)	
	Random	293	323	385	334	
	Selected	359	340	368	356	
	Control	297	316	369	328	
Mean	(Site)				Grand Mean	
		317	327	374	339	

Levels of Significance and Table of L.S.D's

		(0.05)	(0.01)	(0.001)
Site	n.s.	-	-	-
Strategy	**	17	23	-
Selection	***	-	-	24
Strategy x Site		61 (Strategies between sites) 33 (Strategies within sites)		
Selection x Strategy	n.s.	-	-	-
Strategy x Selection x Site	n.s.	-	-	-

Figures 18 to 20

The average yield at three sites in 1981 of the ten highest and ten lowest yielding lines of Control, Random and Selected lines at each of three sites in 1980.

Figure 18A : The highest yielding lines from Redbanks, 1980

Figure 18B : The lowest yielding lines from Redbanks, 1980

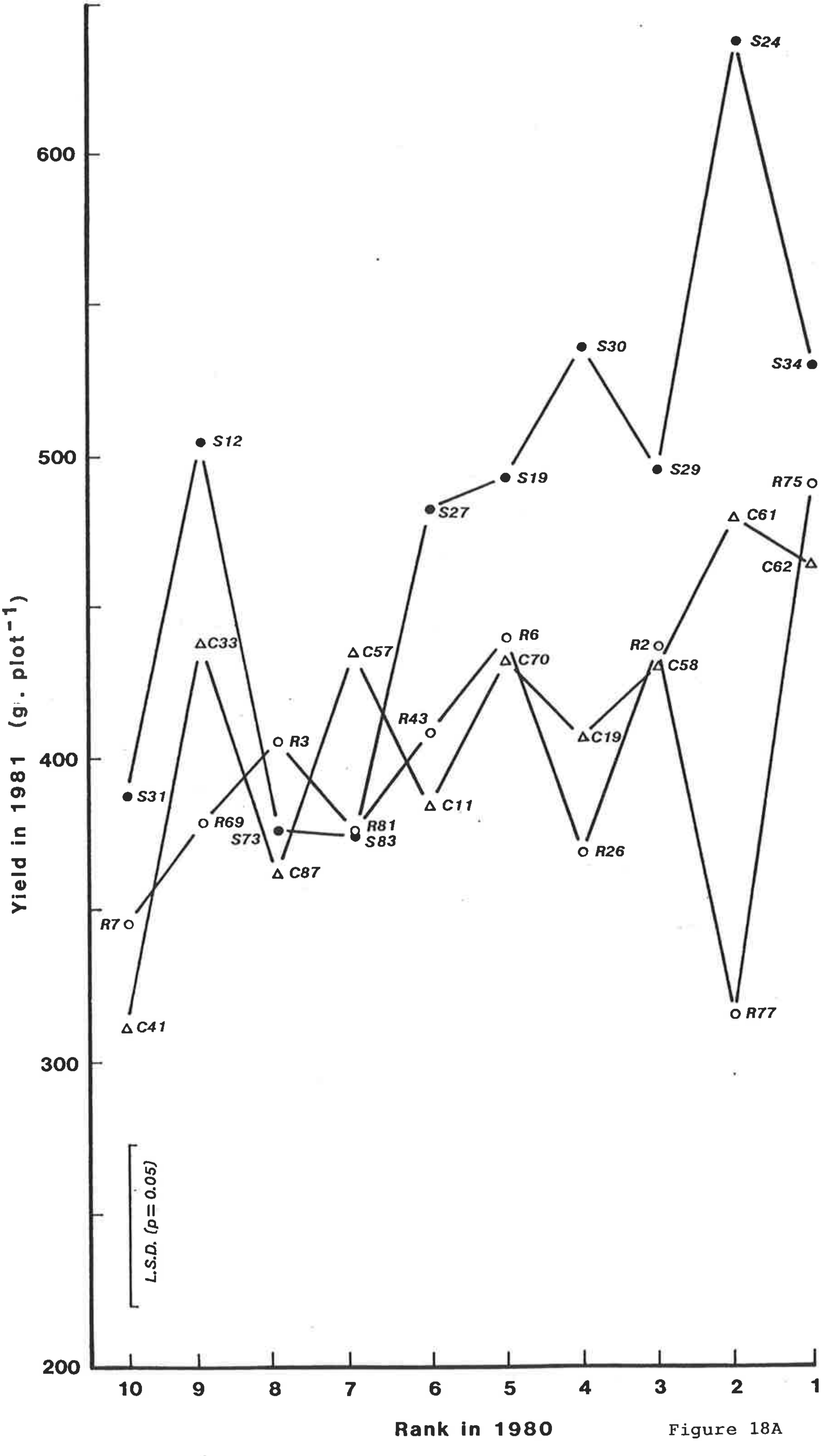
Figure 19A : The highest yielding lines from Roseworthy, 1980

Figure 19B : The lowest yielding lines from Roseworthy, 1980

Figure 20A : The highest yielding lines from Charlick, 1980

Figure 20B : The lowest yielding lines from Charlick, 1980

● Selected
○ Random
△ Control



600
500
400
300
200
Yield in 1981 (g . plot^{-1})
S24
S30
S34
S12
S29
S19
R75
S27
C61
C62
C33
C57
R6
C70
R2
C58
R43
C19
R3
S31
C11
R69
R81
S73
S83
R26
C87
R7
R77
C41
L.S.D. (p = 0.05)
10
9
8
7
6
5
4
3
2
1
Rank in 1980

Figure 18A

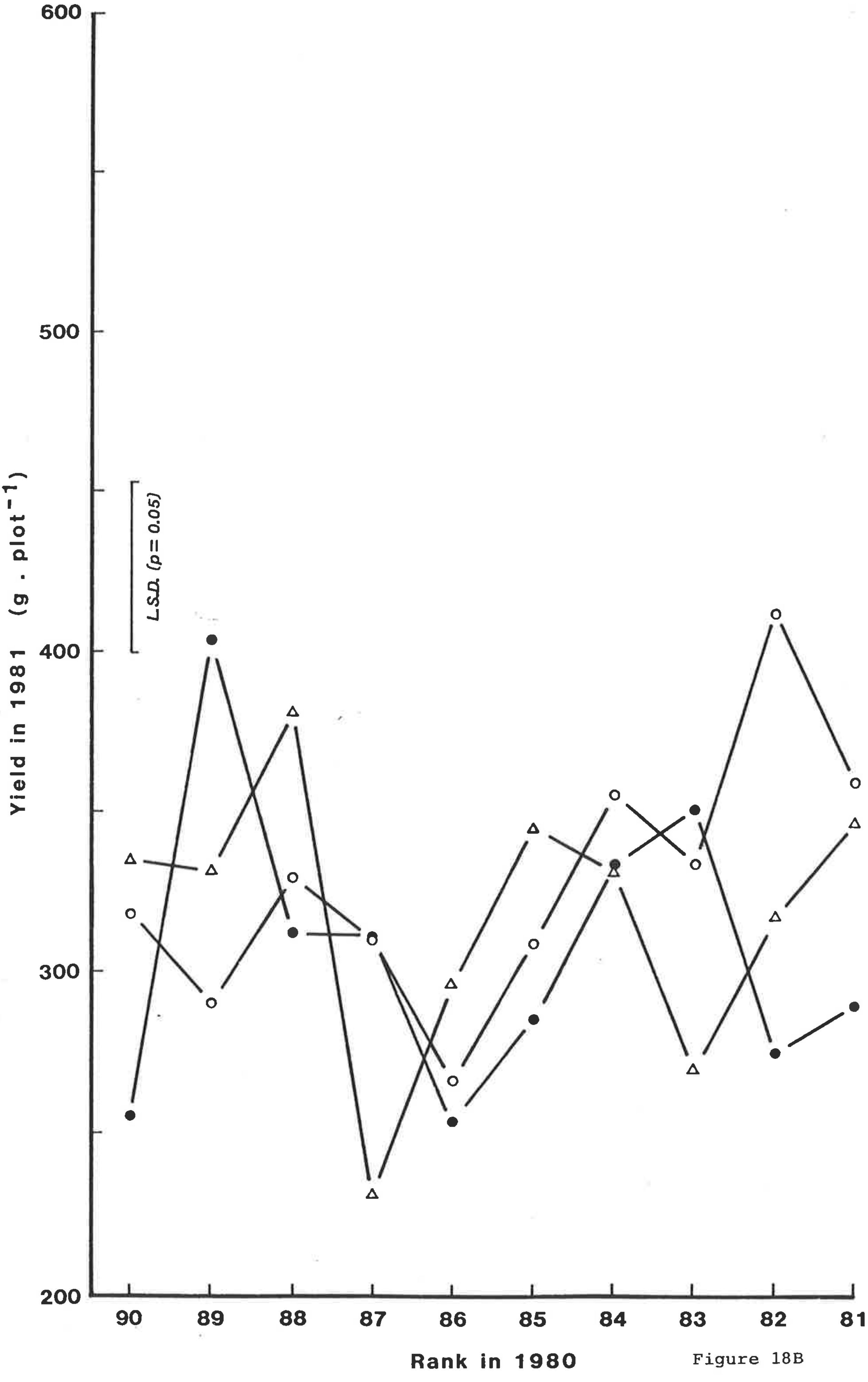

600
500
400
300
200
Yield in 1981 (g . plot^{-1})
L.S.D. (p = 0.05)
90
89
88
87
86
85
84
83
82
81
Rank in 1980

Figure 18B

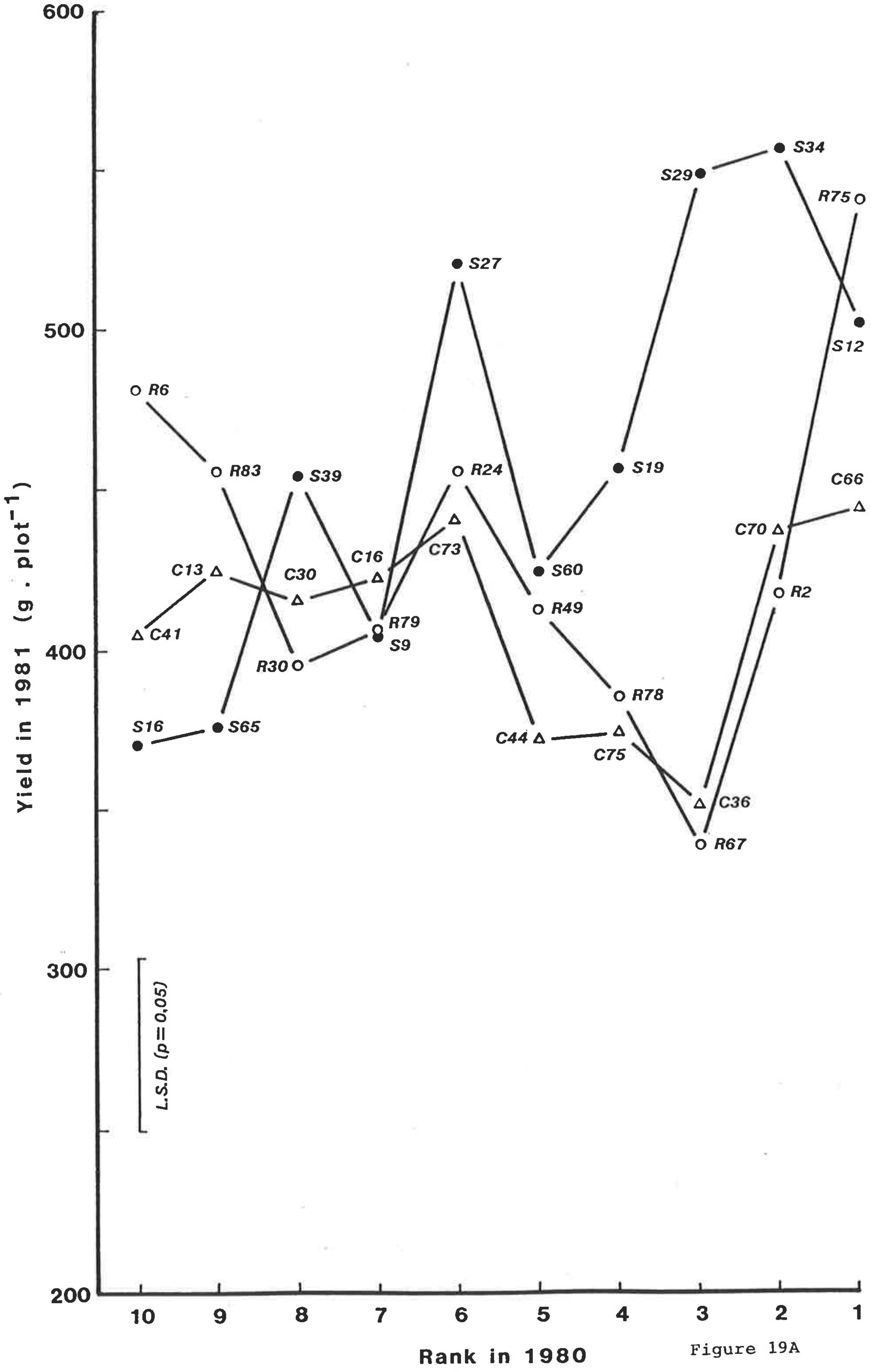

600
500
400
300
200
Yield in 1981 (g . plot^{-1})
Rank in 1980
10
9
8
7
6
5
4
3
2
1
L.S.D. (p=0,05)
R6
R83
S39
C16
C13
C30
C41
R79
S9
R30
S16
S65
S27
R24
C73
S60
R49
C44
C75
S19
R78
S29
S34
R75
S12
C66
C70
R2
C36
R67

Figure 19A

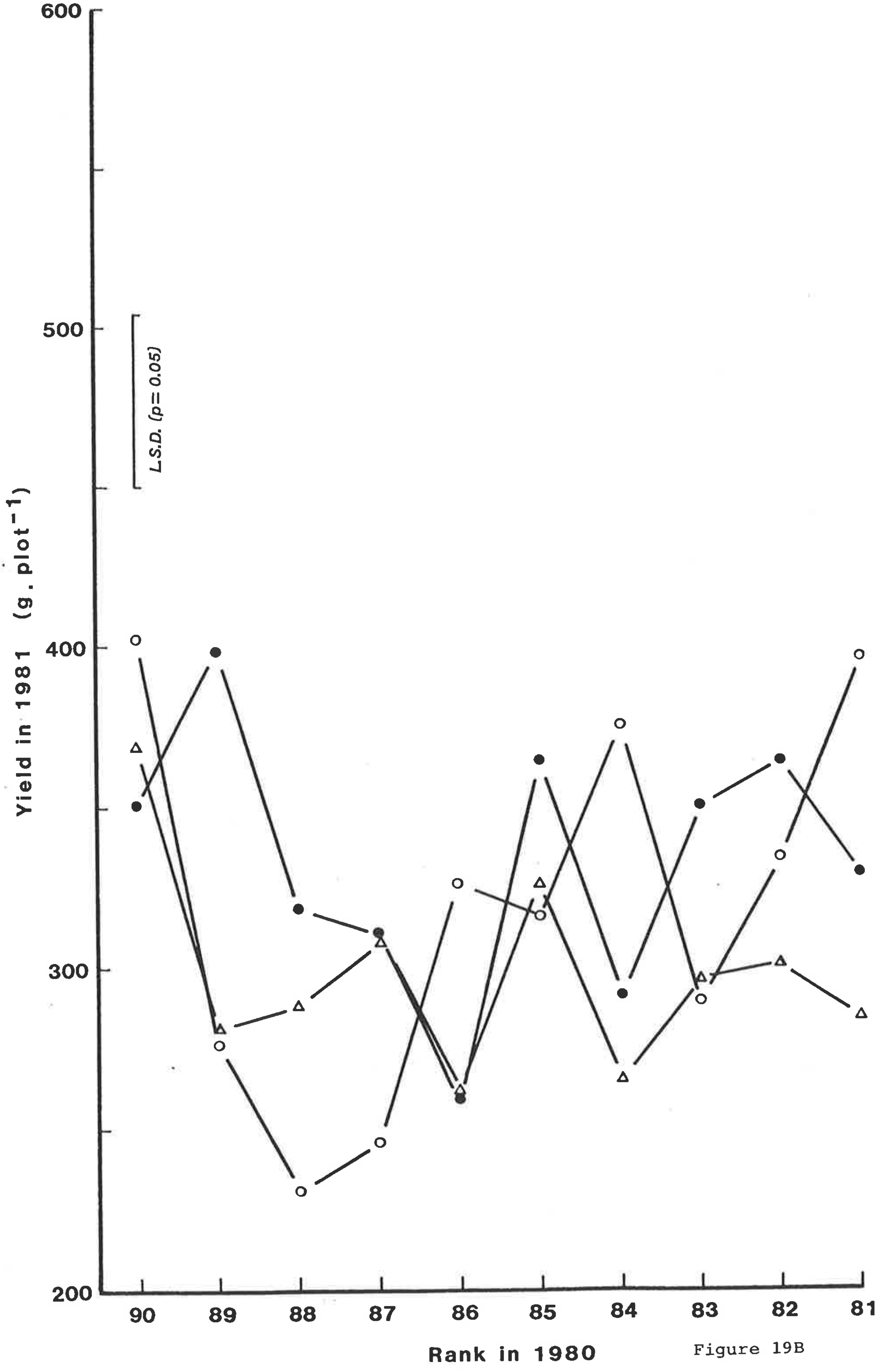

600
500
400
300
200
L.S.D. (p= 0.05)
Yield in 1981 (g . plot⁻¹)
90
89
88
87
86
85
84
83
82
81
Rank in 1980

Figure 19B

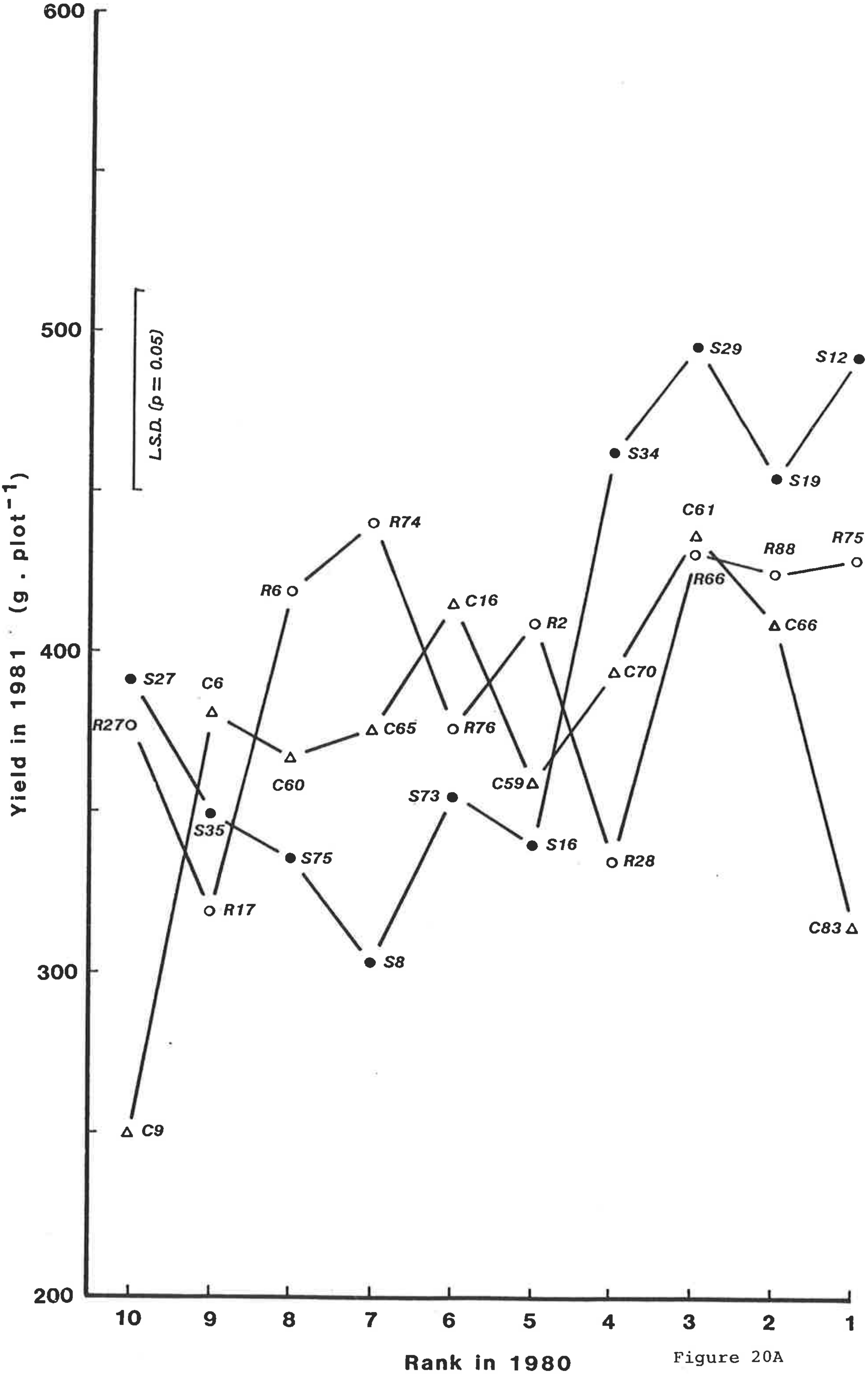

600
500
400
300
200
Yield in 1981 (g . plot^{-1})
L.S.D. (p = 0.05)
10
9
8
7
6
5
4
3
2
1
Rank in 1980
S27
R27
C9
C6
S35
R17
R6
C60
S75
S8
R74
C65
C16
R76
S73
R2
C59
S16
S34
C70
R28
S29
C61
R66
S19
R88
C66
S12
R75
C83

Figure 20A

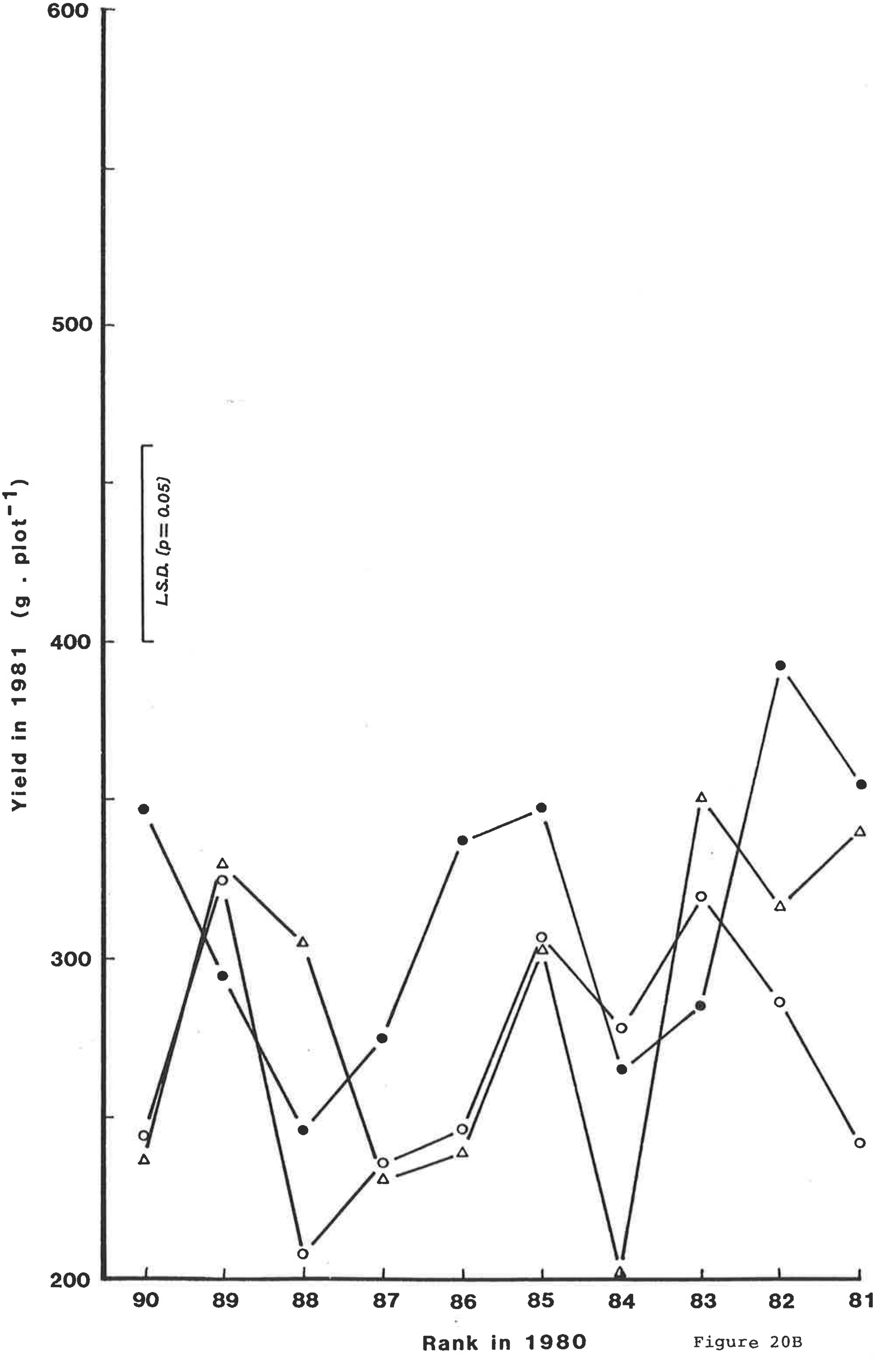

600
500
400
300
200
Yield in 1981 (g . plot^{-1})
L.S.D. (p= 0.05)
90
89
88
87
86
85
84
83
82
81
Rank in 1980

Figure 20B

(Table 21) H-R = H-S> H-C and L-S > L-R = L-C. Although the Selection x Strategy interaction was not significant for the Roseworthy selections (Table 20) the numerical ranking in the High selection groups was H-S> H-R> H-C and for the low selection group L-S >L-R >L-C. Therefore the High-Selected selection group was numerically the highest yielding in the selections from each 1980 site and in two cases they were associated with significant interactions. This result strengthens the case that the high-yielding Selected tails in 1980 were a real effect. Only the High-Random group from Charlick selections could confidently be also classified as a real high-yielding tail effect. The remaining two Random groups from Redbanks and Roseworthy were similar in yield to the Control. The consistent low yield of the Control reflects the lack of any high-yielding lines in 1980. Only one Random family, R75 at Charlick in 1980, was classified as being in a high-yielding group (Table 16) while there were five at Redbanks and three at Roseworthy. However, the high-yielding 'Random' tails at Redbanks and Roseworthy in 1980 were not evident in 1981.

The site effect was only significant for Roseworthy selections (Table 20) and it was involved in a significant Selection x Site interaction caused by a greater difference between the High and Low selection groups at the high yielding site, Charlick, than at the other two sites. The Strategy x Site interaction for Charlick selections (Table 21) was the only other significant interaction. This was caused by the Selected strategy having a higher yield than the Random and Control only at the Redbanks site. The high Selected strategy mean at Redbanks resulted from higher yields in both the High and Low selection groups. These had also contributed strongly to the high mean yields of High-Selected and Low-Selected in their respective selection levels.

The main effects of Strategy and Selection were significant for all three sets of selections from 1980 sites (Tables 19, 20 and 21). They correspond with the very significant differences between the high and low extremes of yield at each site in 1980 (Figures 15, 16 and 17). The Strategy means cannot be used to validly compare the three selection strategies because they only include the highest 10 and lowest 10 yielding lines from each 1980 distribution and do not take into account the other 70 lines in each distribution or the significant non-normality that occurred (Table 15). Therefore the results in Table 15 are the only valid comparisons of selection strategies.

The mean yields over sites of individual lines (Figures 18, 19 and 20) demonstrate how the relative performances of lines contributed to the significant selection and selection x strategy effects in Tables 19, 20 and 21 respectively. The significant selection effects correspond with separation of the High and Low groups although individual lines in each High or Low group do not differ significantly in yield from many lines in the alternate group. Therefore the main performances of the Selection groups have remained significantly different although individual lines have not remained as separated as in 1980. This is expected if the relatively large error, reflected in the size of the 5% L.S.D.'s in 1980, is taken into account.

The consistent high yield of the High-Selected groups in Tables 19, 20 and 21 were caused by a few very high yielding lines in each set of 10 High-Selected lines. Many of these high-yielding lines were amongst those which contributed to the Selected high-yielding 'tails' in 1980 (Table 15). Again there is an obvious contribution from sister-lines to the high yields of the Selected groups, particularly families S12, S19, and S34. The failure of the High-Selected group in Table 20 to produce a significant interaction even though its mean was higher than the Random and control was probably the result of high variation introduced by the low yields of lines S16 and S65 and the range of yield in the Random group (Figure 19A). The similar yields of the Random and Control sets in Figures 18A and 19A correspond with the similar yields of the High-Random and High-Control groups in Tables 19 and 20. The relative ranks of yields of strategies in the High selection groups in Table 21 (H-R = H-S > H-C) resulted from a complex interaction of the individual lines (Figure 20A). Most Random lines were equivalent and no high-yielding set was evident; the high-yielding Selected lines were counter balanced by lower yielding lines, notably S8; and the mean of the Control set was reduced by lines C9 and C83.

The yields of the individual lines emphasises the effect which the arbitary sample size of 10 lines representing the extremities of each distribution had upon the analyses in Tables 19, 20 and 21. If the sample size had been only 4 or 5 the effects of the high yielding Selected lines would have been emphasised more but they would have less reliably estimated the mean performance of the selected sets. In retrospect a sample of 7 or 8 may have been sufficient.

The principal aim of this experiment was to test the validity of the high-yielding tails in 1980. It has shown that these were repeated only for the Selected distributions and that they were caused by a small number of lines amongst which sister-lines are strongly represented. Although the data also suggested small significant non-consistent differences between Strategies in the Low selection group (Tables 19 and 21), Figures 18B, 19B and 20B suggest that these differences may have resulted from variation in the arbitary sample. No consistent difference between strategies occurs at their low-yield extremity. Therefore, apart from the few high-yielding Selected lines, the two composite breeding strategies had failed to significantly and consistently change the range of the distributions of inbred lines from that of the control population.

3.9 EXPERIMENT 7: A Comparison of High-yielding F_5 Lines with their Parents and Checks at Three Sites.

Introduction and Experimental Design

In 1980 the yields of a small number of F_5 lines did not differ significantly from the highest yielding commercial checks and in two cases, S_{12} at Roseworthy and Charlick, significantly exceeded the checks (Figures 15, 16 and 17: Table 16).

While Experiment 6 was designed to test that the high-yielding tails on the Selected and Random were real effects by comparing samples from the F_5 lines only, it was also necessary to test that the relative yielding abilities of the highest yielding F_5's and checks would be repeated. In this experiment the five highest yielding lines from each F_5 distribution in 1980 were compared with the nine parents of the composite and three commercial checks, Halberd, Lance and Warigal, at the three sites used in 1980, Redbanks, Roseworthy and Charlick. The fifteen selections (five Selected, five Random and five Control) from each of the three 1980 sites, Redbanks, Roseworthy and Charlick, were tested in separate trials repeated at those three sites. Therefore there were nine separate trials. Each trial contained 15 F_3-derived F6 lines, nine parents and three checks in five replicates in a randomized block design. The plot dimensions and seeding rates were the same as in Experiments 5 and 6. The plots were sown in June and harvested in December 1981.

Results and discussion

The yield at each site and the mean yields over sites of the selections from Redbanks are presented in Table 22. Their yields at Redbanks in 1980 are also included for comparison. The F_5-derived F_6 bulks are coded with the prefix RB to denote their 1980 site, Redbanks, and they are listed within in each breeding strategy group in the descending order of their 1980 yields. The results from the Roseworthy and Charlick selections, coded RW and CH respectively, are presented in equivalent formats in Tables 23 and 24.

The population x site interaction was not significant in any of the three sets of trials and therefore the mean yields over sites may be validly used to compare the yields of the F_6 bulks with their parents and the checks.

The relationships between the F_6 bulks, parents and checks were similar in each of the three sets of trials. Halberd was consistently the highest yielding check but it was only significantly greater ($p = 0.05$) than Lance in the RB trials and higher yielding than Warigal in the RB and RW trials (Tables 22 and 23). Condor and Zenith were consistently high-yielding parents. Therefore the three checks and the parents Condor and Zenith set the benchmarks in each set of trials for high yielding potential.

Tables 22, 23 and 24

The yields at three sites in 1981 of parental and check varieties and the F6 bulks from the five highest yielding F3-derived lines from each breeding strategy in 1980 at Redbanks (RB), Roseworthy (RW) and Charlick (CH) respectively.

Table 22

Redbanks Selections

Population	Site Redbanks	 Roseworthy (g . plot^{-1})	 Charlick	 Mean	1980 Yield
F6-Bulks					
RB-S 34	454	723	366	514	706
RB-S 24	640	722	402	588	603
RB-S 29	435	568	324	442	585
RB-S 30	510	550	316	459	537
RB-S 19	475	578	242	432	497
RB-R 75	431	505	347	428	581
RB-R 77	272	447	126	282	510
RB-R 2	383	467	296	382	497
RB-R 26	373	431	219	341	494
RB-R 6	484	450	234	389	492
RB-C 62	359	486	305	384	483
RB-C 61	416	500	274	396	480
RB-C 58	395	454	215	355	478
RB-C 19	438	443	279	387	475
RB-C 70	461	552	286	433	468
Parents					
Federation	323	363	141	276	426
Pitic	423	490	222	478	334
Condor	503	566	275	448	469
Gamenya	346	474	224	348	424
Gamset	171	212	134	172	121
Kite	466	516	235	406	500
Timgalen	403	458	187	349	282
WW15	325	541	177	348	461
Zenith	424	595	250	423	533
Checks					
Halberd	470	659	388	506	482
Lance	536	478	294	436	631
Warigal	498	531	269	433	549
Site mean	423	510	260	398	
0.05	98	108	103	59	139
LSD 0.01	129	142	135	78	183
0.001	164	181	172	100	234

Table 23

Roseworthy Selections

Population	Site				1980 Yield
	Redbanks	Roseworthy (g $plot^{-1}$)	Charlick	Mean	
F6-Bulks					
RW-S 12	592	503	517	538	747
RW-S 34	540	639	583	587	644
RW-S 29	508	616	417	514	589
RW-S 19	405	507	294	402	522
RW-S 60	430	418	303	384	478
RW-R 75	506	579	473	519	554
RW-R 2	398	443	375	405	510
RW-R 67	345	320	262	309	405
RW-R 78	376	450	364	397	439
RW-R 49	342	453	323	373	435
RW-C 66	416	503	305	408	447
RW-C 70	370	421	336	376	427
RW-C 36	348	378	291	339	420
RW-C 75	399	362	368	376	417
RW-C 44	352	415	278	348	409
Parents					
Federation	345	400	249	331	298
Pitic	401	519	343	421	204
Condor	477	557	410	481	314
Gamenya	425	495	303	408	334
Gamset	197	267	178	214	97
Kite	524	504	319	449	387
Timgalen	416	413	340	390	396
WW-15	369	567	308	415	315
Zenith	441	587	301	457	513
Checks					
Halberd	498	704	416	539	573
Lance	569	569	388	509	600
Warigal	439	523	408	449	464
Site Mean	423	486	350	420	
LSD 0.05	95	98	103	57	118
LSD 0.01	125	129	136	75	156
LSD 0.001	159	164	173	96	199

Table 24

Charlick Selections

Population	Site				1980 Yield
	Redbanks	Roseworthy (g . plot^{-1})	Charlick	Mean	
F6-Bulks					
CH-S 12	643	554	547	581	333
CH-S 19	405	512	312	410	295
CH-S 29	519	633	520	557	268
CH-S 34	542	649	429	540	240
CH-S 16	299	390	383	357	219
CH-R 75	517	534	528	526	266
CH-R 88	451	464	373	429	198
CH-R 66	377	571	405	451	195
CH-R 28	328	413	337	359	192
CH-R 2	441	511	361	438	188
CH-C 83	300	386	301	329	216
CH-C 66	393	476	331	400	209
CH-C 61	370	425	361	385	204
CH-C 70	452	513	359	441	199
CH-C 59	398	430	305	377	192
Parents					
Federation	378	437	292	369	178
Pitic	424	578	427	477	143
Condor	544	588	408	513	180
Gamenya	342	456	319	372	195
Gamset	224	250	165	213	69
Kite	471	520	422	471	227
Timgalen	416	432	371	407	171
WW-15	401	567	295	421	187
Zenith	437	584	375	465	262
Checks					
Halberd	565	786	420	564	221
Lance	608	519	434	520	205
Warigal	510	605	447	521	237
Site Mean	435	508	379	441	
0.05	98	88	88	53	58
LSD 0.01	129	116	116	69	76
0.001	164	148	147	89	97

In general, the highest yielding F_6 bulks were from the Selected selection strategy. Only one line, RB-S24, was significantly higher yielding (p = 0.01) than Halberd but other Selected lines were equivalent to the benchmark checks and parents, e.g. RB-S34, RB-S29, RB-S19, RW-S12, RW-S34, RW-S29, CH-S12, CH-S29, and CH-S34. As in Experiment 6, there is a frequent occurrence of sisters, particularly of families S12, S29 and S34. In the Random lines only the sister lines of family R75 are equivalent to the checks and high-yielding parents. The remaining Random lines and all Control lines are lower yielding than the highest yielding benchmarks in each set of trials.

This set of trials has confirmed that most of the high-yielding F_5 lines in 1980 have the potential for high yield and in some cases have numerically or significantly exceeded the highest yielding commercial check, Halberd. Some of the lines had also been more consistently high-yielding over two years than the checks and highest yielding parents. In 1980 Lance and Warigal were generally higher yielding than Halberd, Zenith was consistently high yielding and Condor was lower yielding than the checks and some other parents (Figures 15, 16 and 17). Therefore the patterns of benchmark varieties have indicated variety x year interactions while some lines, notably RB-S34, RB-S24, RW-S12, RW-S34, RW-S29, CH-S12, CH-S34 have consistently been either greater than or equivalent to the highest yielding parent or check. Again, note the high frequency of sisters of families S12, S29 and S34. Because these lines are F_3-derived bulks their heterogeneity may contribute to their greater relative stability. It could be postulated that their stability is due to a major factor for yield, generated during the compositing process (see Discussion of Experiment 5), operating in a number of heterogeneous backgrounds to ensure a high mean yield of the lines in the F_5 and F_6.

The results of this set of trials also correspond with the results of Experiment 6 and confirm the presence of a high-yielding Selected 'tail' in each site in 1980. The smaller sample of 5 lines taken from the high-yield extremities of the 1980 distributions have tended to emphasise the high yields of the Selected groups more than in Experiment 6 where some of the samples of 10 reduced the means and introduced increased variation into the selected samples (vide Figure 19A).

This experiment has confirmed that the Selected compositing and selection strategy has successfully produced lines which are equivalent or superior to current commercial varieties.

3.10 EXPERIMENT 8: The Yield and Quality of High Yielding Lines Derived from the Composite Crosses.

Introduction

Experiments 5, 6 and 7 have identified F_5 and F_6 bulks derived from single F_3 (S_2) plants which have been consistently high yielding at one site in 1980 and three sites in 1981. Because these lines had been consistently equal or higher yielding than commerical checks in both years they warranted more extensive yield testing and assessment of their breadmaking quality.

Experimental Design

Eighteen F_3-derived lines were chosen from yield trials in 1980 and 1981. They are listed and described by their 1980 site and family codes in Table 25. All except RB-S12 and the three R75 sister lines were taken from the five highest yielding Selected lines at each 1980 site. RB-S12 was included because it was high yielding in 1981 (Figure 18A). No other Random and no Control lines were chosen.

In 1982 the eighteen chosen lines were tested as F_3-derived F_7 bulks at three sites, the Waite Agricultural Research Institute, Redbanks (used in 1980 and 1981) and McLaren Vale. They were compared with only two varieties of the parent array, Condor and Kite. The other parents were rejected because they were either low yielding (Federation, Gamenya, Gamset, Timgalen, WW-15) or have unacceptable grain characteristics even through they were high yielding in one or both previous years. (Pitic, Zenith). The checks were expanded to

Table 25

The yield (g. plot^{-1}) of eighteen selected F_7 lines, two parents and five check varieties at three sites in 1982.

TABLE 25

POPULATION	WAITE INST.		REDBANKS		MCLAREN VALE		MEAN OVER SITES	
			(gm plot^{-1})					
RB-S34	697	efg	248	bcd	162	cdefg	369	defg
RB-S24	826	abcd	254	bc	192	abc	424	ab
RB-S29	631	fg	112	i	137	fgh	293	i
RB-S30	725	defg	118	i	134	gh	326	ghi
RB-S19	792	abcde	170	efghi	174	bcdef	379	def
RB-S12	778	abcde	263	b	183	abcd	408	bcd
RB-R75	695	efg	158	fghi	147	defgh	333	fghi
RW-S12	770	abcde	198	cdef	134	gh	367	defg
RW-S34	660	fg	236	bcd	154	cdefgh	350	efgh
RW-S29	724	defg	154	fghi	138	efgh	339	efgh
RW-S19	780	abcde	148	fghi	160	cdefg	363	defg
RW-S27	765	bcdef	136	ghi	121	h	341	efgh
RW-R75	661	fg	119	i	134	gh	305	hi
CH-S12	800	abcde	210	bcdef	185	abcd	398	cd
CH-S19	654	fg	125	i	169	cdefg	316	hi
CH-D29	735	cdefg	129	hi	119	h	328	ghi
CH-S34	709	defg	229	bcd	162	cdefg	367	defg
CH-R75	637	g	194	cdefg	137	fgh	323	ghi
Condor	771	abcdef	199	cdef	176	bcde	382	cde
Kite	757	bcdef	189	defgh	178	abcd	375	def
Halberd	661	fg	187	defgh	177	abcd	342	efgh
Lance	811	abcd	211	bcde	175	bcdef	399	cd
Warigal	843	abc	346	a	215	ab	468	a
Aroona	864	ab	270	b	212	ab	449	ab
Bayonet	883	a	172	efghi	172	cdefg	409	bcd
MEAN	745		191		162		366	
0.05	97		53		32		38	
L.S.D. 0.01	127		69		42		50	
0.001	162		88		54		64	

<u>Levels of Significance</u>

Between populations within each site ***

Between sites ***

Between populations over sites ***

Interaction population x site ***

five by the addition of Aroona and Bayonet which had been released during 1980-82.

After the 1982 trials eight more lines were rejected, leaving ten F_8 bulks which are listed in Tables 26A and 26B for comparison in 1983 with the same parents and checks. Trials were sown at four sites in 1983; Redbanks, Charlick, Noarlunga and Palmer.

All the trials in 1982 and 1983 were randomized blocks with five replicates. The plot dimensions and seeding rates were the same as in Experiment 5, 6 and 7. The trials were sown in June and harvested in December in each year.

The grain colour and quality characteristics of each of the 10 F_8 bulks grown in 1983 were determined by H.J. Moss, Bread Research Institute of Australia on seed harvested at Redbanks in December 1983. These determinations were also made for seed harvested from one parent, Condor, and two checks, Halberd and Warigal. The quality characteristics determined were: hectolitre weight, pearling resistance, flour yield, grain protein, maltose content, flour paste viscosity, flour colour, farinograph test (water absorption and development time), extensograph test (resistance and extension), a baking test (volume), and a visual score for bread quality.

Results and Discussion

Table 25 presents the yields of the 18 F_7 bulks, two parents and five checks at three sites, together with their mean yields over sites. The levels of significance between yields are given by Duncan range tests (5% level of significance) and least significant differences. A supplementary table of levels of significance for an overall analysis of variance is included.

The overall analysis indicates a very significant population x site interaction, which invalidates comparisons of the means of populations over sites.

Tables 26A and 26B

The yield (g. plot^{-1}) of ten selected F_8 lines, two parents and five check varieties at four sites in 1983.

TABLE 26A

POPULATION	REDBANKS		CHARLICK		NOARLUNGA		PALMER		MEAN OVER SITES	
					(gm plot^{-1})					
RB-S34	778	abc	869	bc	450	abc	655	ab	688	ab
RB-S24	716	bcd	867	bc	522	a	543	bcd	662	abc
RB-S19	544	ef	750	defg	256	fg	729	a	570	def
RB-S12	472	f	826	bcde	363	bcdef	594	abc	564	def
RW-S12	493	f	867	bc	343	cdefg	586	bc	572	def
RW-S34	862	ab	838	bc	380	bcdef	659	ab	685	ab
RW-S19	552	def	721	efg	141	h	723	a	534	fg
CH-S12	456	f	987	a	289	efg	682	ab	604	cde
CH-S19	570	def	723	efg	126	h	668	ab	522	fg
CH-S34	773	abc	837	bcd	338	cdefg	539	bcd	622	bcd
Condor	545	ef	774	cdef	408	abcde	473	cdef	550	ef
Kite	738	bc	798	cdef	507	a	576	bcd	655	abc
Halberd	698	cde	652	g	223	gh	536	bcde	527	fg
Lance	620	cdef	500	h	321	defg	443	def	471	g
Warigal	569	def	712	fg	415	abcd	403	ef	525	fg
Aroona	916	a	934	ab	373	bcdef	659	ab	721	a
Bayonet	573	def	753	defg	479	ab	349	f	538	efg
MEAN	640		789							
L.S.D. 0.05	144		98		106		120		59	
L.S.D. 0.01	189		128		140		158		78	
L.S.D. 0.001	242		164		179		201		99	

Levels of Significance

Between populations within each site	***
Between populations over sites	***
Between sites	***
Interaction population x site	***

TABLE 26B

POPULATION	SITE REDBANKS		CHARLICK		NOARLUNGA		PALMER		MEAN OVER SITES
RB-S34	804	ab	878	abc	401	bc	659	abc	686
RB-S24	756	abc	893	abc	511	a	577	bcd	684
RB-S19	548	def	778	cde	311	cde	736	a	593
RB-S12	468	f	869	bc	288	def	569	bcd	549
RW-S12	514	ef	894	abc	327	cde	634	abc	592
RW-S34	797	ab	841	bc	402	bc	666	abc	677
RW-S19	629	cde	709	ef	243	ef	675	abc	564
CH-S12	479	f	995	a	327	cde	645	abc	612
CH-S19	567	def	715	def	204	f	700	ab	547
CH-S34	799	ab	837	bcd	337	cde	545	cd	630
Condor	608	def	782	cde	387	bcd	474	de	563
Kite	785	ab	781	cde	479	ab	588	bcd	658
Halberd	689	bcd	647	f	264	ef	550	cd	538
Lance	617	def	471	g	338	cde	460	de	472
Warigal	606	def	708	ef	385	bcd	477	de	544
Aroona	864	a	913	ab	348	cde	598	abcd	681
Bayonet	589	def	783	cde	393	bc	398	e	541
MEAN	645		761		373		591		592
L.S.D. 0.05	125		107		88		122		56
L.S.D. 0.01	164		140		115		160		73
L.S.D. 0.001	209		179		147		205		93

The F_7 lines and varieties can be arbitarily grouped into four classes : six lines which were consistently high-yielding, RB-S24, RB-S12, CH-S12, Lance, Warigal and Aroona; ten which probably caused the significant population x site interaction and were high-yielding in at least on site, RB-S34, RB-S19, RW-S12, RW-S34, RW-S19, CH-S34, Condor, Kite, Halberd and Bayonet; four populations which probably contributed to the population x site interaction but were not high-yielding at any site, RW-S27, CH-S19, CH-S29 and CH-R75; and five consistently low-yielding lines, RB-S29, RB-S30, RB-R75, RW-S29 and RW-R75.

The nine F_7 lines from the first two classes and CH-S19 were chosen for four further yield trials in 1983. The remaining three lines in the third class (RW-S27, CH-S29, and CH-R75) were rejected because they were very tall and had tended to lodge. The results of the four trials in 1983 were analysed in the same manner as those of 1982 (Table 26A). In addition, they were analysed using a 'nearest neighbour' analysis (WILKINSON, ECKERT, HANCOCK and MAYO, 1983) at each site (Table 26B), and the adjusted residual error was used to calculate the Duncan range test values (5% level of signficance) and least significant differences.

Again, a significant population x site interaction occurred which invalidated a comparison of the means of populations over sites (Table 26A). There were only minor differences between the two analyses at each site (compare Tables 26A and 26B). The lines could again be grouped into three of the arbitary classes found in 1982. Six populations were consistently high-yielding RB-S34, RB-S24, RW-S34, CH-S34, Kite and Aroona; one, Lance, was consistently low-yielding and the remaining ten probably contributed to the significant population x site interactions, but were high-yielding in at least one site. Only one line, RB-S24, and one variety, Aroona were consistently high-yielding over all sites in 1982 and 1983.

The occurrence of stripe rust, *Puccinia striiformis*, for the first time in 1983 in this series of experiments probably contributed to the very significant changes in the ranks of the susceptible check varieties, Halberd, Lance, Warigal and Bayonet from 1982 to 1983. A visual rating of the populations for stripe rust resistance at

Charlick is presented in Table 27. Rust may have contributed to the interactive effects in other entries, but it was not the only factor involved. Very significant changes in rank in the F_7 and F_8 lines occurred between 1982 and 1983 even though all were highly tolerant (Table 27). For example, RB-S12 was only the ninth highest Selected line at Redbanks in 1980, fourth highest of Redbanks selections over sites in 1981 (Figure 18A), consistently high-yielding in 1982 but low-yielding at Redbanks in 1983. In contrast, RB-S24 had been consistently high-yielding throughout the four years of trials.

Although selection in 1981 and 1982 had arbitary cut-off levels which may have excluded some lines with promise it is interesting to note that the final set of 10 lines tested in 1983 was composed of three sets of sister-line triplets (families S12, S19 and S34) and the exceptionally stable high-yielding line RB-S24, which did not have high-yielding sister lines included. The sets of triplet sister-lines, which were derived from random F_3 (S_2) sisters in the progeny of a single $F_3(S_1)$ plant, emphasise that an F_2-progeny breeding method (LUPTON, 1961) could be used successfully to isolate high-yielding families from populations generated by enforced outcrossing in composite breeding. In contrast, the line RB-S24, which is derived from a single $F_3(S_2)$ plant, exemplifies that segregants with potential may be lost if an F_1-derived bulk masked their yielding ability. However, the preponderance of sets of sister-lines suggests that F_2-progeny tests, followed by partitioning of the most promising families at the F_3 would be an effective breeding procedure.

Strong family relationships were also found for the quality characteristics of sister-lines (Table 27). MOSS (pers. comm.) found all the S12 lines were very soft wheats (low pearling resistance and maltose content) with weak dough (short farinograph development time and short extensograph extension), which was reflected in a poor baking score and low viscosity. They were light, low protein wheats with only average to good flour colour. Because of a good milling result, Moss suggested CH-S12 "is good as a soft wheat for soft wheat purposes". In contrast to the S12 family, both S19 and S34 were hard to very hard wheats but they differed markedly in dough strength and baking quality. The S19 lines had medium to strong dough and marginal

Table 27

Quality characteristics of ten F_8 lines and three commercial varieties grown at Redbanks, 1983.

TABLE 27

POPULATION	STRIPE RUST TOLERANCE*	GRAIN COLOUR	HECTOLITRE WT. (kg hl^{-1})	PEARLING RESISTANCE	FLOUR YIELD (%)	GRAIN PROTEIN (%)	MALTOSE (mg $100g^{-1}$)	VISCOSITY	COLOUR GRADE	FARINOGRAPH		EXTENSOGRAPH		BAKING TEST	
										Water Absorption (%)	Develop Time (min)	Maximum Resistance	Extension (cm)	Volume (ml)	Score (%)
RB-S12	1	red	72.5	3.3	72	7.9	85	258	-0.5	52.4	1.2	145	15.3	600	52
RW-S12	1	red	71.2	3.1	71	9.0	78	236	-0.6	52.3	1.0	155	17.7	580	50
CH-S12	0-1	red	73.8	3.3	73	8.6	109	247	-0.8	52.9	1.0	130	17.0	580	52
RB-S19	3	white	81.0	5.9	71	8.8	276	282	-1.1	60.6	1.7	200	18.4	600	61
RW-S19	1-2	white	80.2	5.7	73	10.0	234	288	-0.5	59.2	3.5	295	22.1	600	66
CH-S19	2	white	80.0	5.6	72	9.2	267	282	-1.0	59.5	2.5	235	19.8	550	56
RB-S34	0-1	red	78.8	5.0	73	9.8	156	239	-0.5	60.0	2.1	75	18.9	550	51
RW-S34	1	red	80.2	5.2	73	8.9	166	265	-0.5	60.3	1.7	110	15.9	500	46
CH-S34	1	red	79.7	5.0	72	9.1	145	247	-1.1	58.0	2.0	110	18.1	600	56
RB-S24	1	white	78.2	4.1	70	9.1	135	215	-0.7	54.6	2.2	270	20.6	580	57
Condor	1	white	80.0	5.2	72	9.8	154	249	-1.7	58.3	2.7	225	21.1	650	71
Halberd	3	white	83.2	5.5	72	9.1	225	289	-1.0	60.4	2.1	175	16.4	500	40
Warigal	6	white	79.2	5.2	7.1	9.7	228	300	-1.1	60.8	2.6	190	20.0	650	71

* 0 = no symptoms
10 = very susceptible

ø = All data accept the stripe rust score are from H.J. Moss, Bread Research Institute of Australia baking tests while S34 had very weak dough and very poor baking tests. Consequently the S19 lines closely approached acceptable commercial standards. MOSS concluded RW-19 was "the most promising" of all the lines tested, and "next would be CH-S19 on strength if not on baking quality". He considered that RB-S19 had some chance of acceptance for commercial cultivation. The S34 family is unsuitable for normal processing. RB-S24 was also unsuitable for processing because it was a soft wheat with a low flour yield and strong dough.

Grain colour is of particular importance. In Australia, red wheats are not commercially grown. Consequently one of the lines chosen by MOSS, CH-S12 is ineligible for further development in Australia. Of the white lines in family S19, two, RW-S19 and CH-S19, which were considered most promising by Moss are tall. The remaining family, RB-S19, which is a semi-dwarf is being partitioned by single seed selection by DRISCOLL (pers. comm.) for testing of homozygous segregants to determine their suitability as Australian Standard White wheats.

The results of MOSS's quality tests have complemented the observation and conclusion drawn from yield trials. F_2 (S_1-progeny tests will not only identify high-yielding families, but if they were tested for quality characteristics, the between family variance may be much greater than within family variance and those high-yielding families with acceptable profiles for particular grades of wheat could be identified. This experiment suggests that further partitioning at the F_3 (S_2) level would identify the lines with high quality within the most promising families.

It is pertinent to this discussion to add that MOSS commented that he found the combinations of characteristics in this small sample of wheats interesting and unexpected. His comment suggests that not only did the compositing process generate high-yielding recombinants but it may have recombined linked patterns of quality characteristics found in Australian wheats. It may therefore be possible to exploit the recombinations generated in a series of outcrossings to generate and improve quality characteristics while simultaneously generating higher yielding recombinants.

In summary, this experiment has identified in trials at six sites over two years, three families of three sister-lines and one single F_3-derived line which have the potential to be equivalent to the yield of commercial checks. Although selection was arbitary in 1981 and 1982 and no bias was given to sister lines, three sets of sister lines had occurred in the final selections. This result is complemented by similarities in the quality characteristics of the sister-lines and suggests that $F_2(S_1)$-derived lines derived from composites could be tested for yield and quality and the most promising families could be further partitioned to identify high-yielding lines of acceptable quality.

4. GENERAL DISCUSSION

Introduction

The high-yielding S_2 bulks in Experiment 4 (Table 12) and the high-yielding $F_3(S_2)$-derived F_5 to F_8 bulks in Experiments 5 to 8 (Tables 16, 22 to 27) demonstrate that composite crosses propagated only through outcrossed male-steriles can produce S_0 recombinants from which high-yielding inbred families can be derived. The occurrence of these high yielding families at frequencies which allow their detection in samples of moderate size indicates that use of composites involving Cornerstone male-sterility would be an effective wheat breeding procedure.

This conclusion must be prescribed by the physical constraints of this study in which only one initial population and two compositing procedures, the Random and Selected, were used. Composites with different parents and different procedures for propagation and selection may produce different frequencies of high-yielding lines with different relative yields.

A critical analysis of the results suggests other methods for using composite crosses which may be more effective in wheat breeding. The data also presents powerful arguments supporting early-generation selection for yield and quality. It also suggests that recurrent selection involving nuclear male-sterility to facilitate outcrossing would be an effective alternative to pedigree and bulk progeny methods of wheat breeding.

Comparison of the composite procedure of this study with evolutionary composite procedures

The composite procedure of this study differed from the evolutionary composite concepts of SUNESON (1956) in four fundamental aspects. Firstly, the composite was propagated through steriles only, rather than through a bulk of the progenies of all individuals. Consequently, the proportion of male steriles was maintained at approximately 40% in the composites (Table 1) and all individuals resulted from outcrossing in the previous generation. In the evolutionary composites containing a male-sterility factor the proportion of steriles declined because the composites were propagated through bulk seed from fertiles and steriles (JAIN and SUNESON, 1963). Consequently the populations contained predominantly the descendants of inbreeding parents (JAIN, 1961). Secondly, natural selection between the chosen fertile parents was prevented by taking equal numbers of seeds (10) from each sterile. In the evolutionary scheme bulking permitted natural selection for yield. Thirdly, the early generations of the composites were partitioned to detect superior recombinants rather than delaying selection until later generations and relying upon natural selection to increase the frequency of high-yielding genotypes. Fourthly, the array of only 8 parents (7 varieties plus Cornerstone) was smaller than in most of the early composites of SUNESON and STEVEN (1953). They cite examples ranging from 9 to 625 parents. CC XIV was similar to this study. It was based on only 8 adapted parents crossed to a male-sterile (SUNESON, 1956).

These four changes in composite management were made so that the composite cross could maximise the number of meaningful recombination events, exclude natural selection for seed-set, achieve a high degree of association between the parents (Table 18) and identify the superior recombinants quicker than in the evolutionary approach (DRISCOLL, 1981).

Propagation of the composite through steriles which make equal contributions to the next generation is a new development in composite breeding methodology. It is a development of SUNESON'S (1945) proposal to include a male-sterility factor in a composite and propagate it through a bulk of seed from steriles only. Two composites he established involving male-sterility (CC XIV and CC XV) were subsequently propagated by bulking their total progenies which rapidly reduced the proportion of steriles in the population (JAIN and SUNESON, 1963) and permitted natural selection for fitness (SUNESON, 1956). Consequently the composites in this study departed from conventional reliance upon natural selection between seed-bearing parents and depended upon outcrossing to generate useful variation. They retained other features of conventional composites such as a parent set greater than two, a base population generated by crossing the parents, a large number of individuals per generation, propagation through a large parent set (N = 100), and no intervention in cross-pollination.

There is evidence that high-yielding recombinants may have occurred in the early generations of some of the long-term evolutionary barley composites. For example, CC V had high between-family variance for heading time and height in the F_4 (ALLARD and JAIN, 1962). In CC XIV and CC XV high between-family variances for yield and other characters occurred in early generations (JAIN and SUNESON, 1966). None of these samples were compared with a control derived from the initial composite population. Therefore the effectiveness of early generation selection in them could not be estimated.

The capacities of CC's V, XIV and XV to generate a high level of variation in early composite generations suggests that the methods used to establish and propagate those composites could amend or be alternatives to those in this study. CC V was based on a multicross of 31 parents but did not involve male-sterility. It therefore had a high initial level of parental association and, consequently, individuals in early generations would have contained recombinants derived from a high proportion of the parents. However, an expected high proportion of inbreeding would have rapidly decreased the frequency of meaningful recombination events and prevented association of segments of parental genomes fixed in different inbreeding families. If composites involving male-sterility were preceded by multicrossing, the need to outcross for a number of generations to involve all parents in a recombinant (Table 18) would not be necessary. In addition, male-sterile assisted outcrossing could continue to create new association and recombination events between segments of parental genomes. In composites propagated by bulking the progenies of both steriles and fertiles, such as CC XIV and CC XV in which the frequency of steriles was greater than 20% for the first four generations (JAIN and SUNESON, 1963), there may be sufficient opportunities for meaningful recombination events in the early composite generations to generate desirable recombinants. It is probable that these recombinants may occur with frequencies similar to those in composites propagated through steriles only.

Further studies of composites involving male-sterility could compare the control and composite strategies of this study with the following alternative procedures:

(1) Multicrossing the parents or initial F_1's before commencing a composite propagated through male-steriles only.

(2) Bulking the progenies of sterilies and fertiles to propagate the composite. The breeder may arbitrarily choose a minimum frequency of steriles to be maintained. If the frequency fell below this level it would be necessary to select steriles only for a few generations to restore the desired frequency of steriles.

(3) Multicrossing the parents or initial crosses and propagating by bulking the progenies of steriles and fertiles.

The evolutionary composite strategy depends upon natural selection for yield improvement (SUNESON, 1956). The low yield and absence of increasing bulk yield in the first seven generations in this study (Table 7) suggest that the evolutionary method would be ineffective for composites propagated through steriles only. JAIN and SUNESON (1966) had also observed that increased outcrossing decreased the response to natural selection. Therefore the magnitude and any trend of bulk yield in composites propagated through steriles only has little predictive value. Alternatively, the breeder must rely upon the genetic variability which is generated, particularly in early generations.

If a composite containing a sterile factor were propagated by bulking the progenies of steriles and fertiles the bulk yield may increase and exceed commercial checks as in CC XIV (SUNESON, 1956). Therefore it could be argued that bulking and natural selection would be an effective alternative to propagation through steriles only and partitioning in early generations. The bulking strategy is less desirable for three reasons. Firstly, Experiments 4 and 5 have demonstrated that high-yielding families could be identified after one to three generations rather than waiting for a large number of generations before sampling. Secondly, competition during the predominantly inbreeding phase may eliminate or reduce to extremely low frequencies the progenies of the recombinants with the highest yield potential (KHALIFA and QUALSET, 1975). Thirdly, natural selection may reduce between-family variation (JAIN and SUNESON, 1963). Consequently any remaining progeny of the best recombinants may not be detected in samples of reasonable size.

In summary, the success of the composite strategies in this study suggests that the conventional evolutionary composite breeding procedure should be superseded by a composite strategy in which male-sterility is used to enforce outcrossing for a small number of generations to produce a high level of genetic variation between recombinants. Then the recombinants with the highest yield potential should be identified by partitioning the composite into S_0-derived families to avoid their probable loss by competition in a phase of natural selection for population fitness. Evidence from the early generations of specific evolutionary composites suggests that preceding the composite phase with multicrossing to increase the initial level of parental association and relaxing the requirement for propagation through steriles only should be evaluated as alternative propagation procedures.

The effects of parental genotypes and the initial structure of composites on the success of composite breeding.

The parents used on this study were not closely related (MACINDOE and WALKDEN BROWN, 1968). Consequently a high initial level of ~~genetic~~ gametic disequilibrium would have been present (ALLARD, JAIN and WORKMAN, 1966). Also genes in segments with low selective value would have tended to lower frequencies or may have been lost before recombination events could recombine them in segments with greater selective advantage (KARLIN and McGREGOR, 1968; ROBERTSON, 1977). Although the composites were propagated through a reasonably large population (N = 100), the positions of recombination events in the early generations of the composite probably determined the fate of many genes and a specific evolutionary path for the composites (BODMER and PARSONS, 1962; KARLIN, McGREGOR and BODMER, 1967). Consequently the initial pairings of parents may have been critical in the eventual outcomes of the composite crosses. The affects of initial disequilibrium could be reduced if composite were preceded by a number of generations of random intermating or if selection were prevented in the first few generations of the composite. The high levels of disequilibrium would be re-established if unrelated parents were introduced into the composite. Multicrossing prior to the composite would not decrease the initial level of disequilibrium although it would increase the level of association of parental genomes.

In composites containing a male-sterility factor the disequilibria associated with the *ms* loci are a specific factor. The *Ms* and *ms* alleles will tend to carry alleles closely linked to them into fertiles and steriles respectively. This effect probably caused the significant differences between fertiles and steriles in the early generations in this study (Table 2) before they were reduced by recombination events close to the *ms* locus. Disequilibria at the *ms* locus may have contributed to the differences between the Control and composite populations in Experiment 5 (Section 7) because there was less opportunity for recombination in the Control than in composites between the *Ms* alleles of the fertile parents and genes at linked loci in Cornerstone (Figure 9). A composite strategy involving male-sterility could be jeopardised by undesirable linkages with the *ms* locus unless sufficient opportunity is given for their disruption. If the *ms* allele is recombined with more desirable alleles the initial sterile stock should be discarded. It is probable that sterile segregants from high yielding S_0-derived families would be superior sources of sterility.

Some parents with a high breeding value may carry major genes for undesirable characters. For example, in this study WW-15 and possibly Cornerstone (from Pitic 62) carried genes for red grain colour, which occurred in two of the high yielding families which were identified (Table 27). Alternatively some parents may carry desirable major genes such as those for disease resistance and desirable morphological or physiological characters. It would probably be most efficient to select by mass selection S_0 individuals expressing desirable characters controlled by major genes after a few generations of intermating. Only those families containing the desired alleles would then enter yield testing and increase the probability of detecting high-yielding families carrying desired major genes.

In this study the families with undesirable characters, such as red grains, disease susceptibility and lodging, were retained in Experiment 5 because random samples of recombinants were required to compare the breeding strategies. In a practical breeding programme they would have been eliminated at an early inbreeding stage.

The composition of the initial parent set is ~~probably~~ a critical determinant of the outcome of a composite cross. In this study only one parent set was used. Other sets may have produced significantly different outcomes. The low predictive value of the yield of parents in 2-parent crosses (WHITEHOUSE, THOMPSON and DO VALLE RIBEIRO, 1958) will probably also be applicable in composite crosses. Consequently the breeder will probably construct composites in which the frequency of undesirable major characters is not high and most parents have desirable attributes. For example, the fertile parents of this study were all Australian varieties, except WW-15, which was a red-grained, high-yielding breeder's line.

Composites present an opportunity to introduce unadapted parents into ad~~o~~apted populations and test their breeding value (ECKERBIL *et al*, 1977; JENSEN, 1978; SINGH, 1977). They could also be used to attempt to exploit high-yielding adapted parents which have been unsuccessful parents in conventional inbreeding programmes.

The size of the initial parent set is also probably a critical determinant of the outcome of a composite cross involving male-sterile assisted intermating. In this study, Cornerstone and seven parents (the contribution of Kite is so small that six is an acceptable approximation; see Section 3.7) permitted a rapid disruption of parental genomes and detection of recombinants involving a high proportion of the initial parents after only 3 generations of outcrossing (Table 18). HANSON (1959c,d) ~~had~~ show~~n~~ed that parent arrays of greater than 10 were not advantageous for achieved disruption of parental genomes. Also, if the number of parents had been larger, there would have been a greater loss of alleles through genetic drift, particularly if the number of parents had approached the number of chosen parents per cycle (100) (LATTER and NOVITSKI, 1969). The size of the parent ~~sent~~ set in this study was therefore near optimum, even though selection during the composite phase may have reduced the effectiveness of outcrossing and increasing genetic drift.

By definition a composite cross is based on an initial population involving two or more different crosses, which must therefore involve at least three parents. However, it is appropriate at this point to discuss the special limiting case of additional intermating within a two-parent cross. Theoretical and experimental studies have both suggested that random intermating within a single cross will have little advantage (PEDERSON, 1974; BOS, 1977, SNAPE, 1978, NANDA *et al.*, 1981; ALTMAN and BUSCH, 1984), although additional intermating can increase desired genotypic correlations (VERMA *et al.* 1979) and increase the extreme expression of individual characters (RANDHAWAN and GILL, 1978, SINGH and DWIVEDI, 1978). There are many examples of intermating between more than one cross being advantageous for improving yield, increasing expression of individual characters and increasing the frequency of desirable genotypic correlations (MILLER and RAWLINGS, 1967a; MEREDITH and BRIDGES, 1971; HUMPHREY,MATZINGER and COCKERHAM, 1969; HANSON, PROBST and CALDWELL, 1967).

It is unlikely that the S_0 recombinant parents of the high-yielding tails generated by the Random and Selected composites (Figures 15, 16, 17) would have resulted from intermating within only one of the initial crosses between Cornerstone and an Australian wheat. Therefore they are probably the result of meaningful recombination events and associations involving more than two parents. The relative contributions of these two factors to yields exceeding the Control could not be determined in this study. The relative magnitudes of the effects of intermating and the degree of association of parents could be determined by comparing the Control and composite strategies with intermating within single crosses for three cycles. Another strategy which would emphasise association and minimise recombination would be to intercross the seven initial F_1's and then inbreed as in the Control without further cycles of intermating.

The structure of the Control (seven single crosses) was arbitary. In previous composites SUNESON (1956) had used bulks of single crosses (CC11) and multicrosses (CC V). It could be argued that multicrossing is an intrusion between the simple base consisting of single crosses and the composite phase in which intercrossing is uncontrolled. Consequently the Control consisting of seven single crosses was chosen. If the Control had been constructed by intermating the seven single F_1's the opportunity that strategy would have given for association and recombination of the genomes of the seven Australian wheats may have resulted in some higher yielding inbred families in the Control. Any residual superiority of the composite lines would have been the result of additional cycles of intermating within this alternative base population.

The effects of the method of propagation on the outcome of composite crosses.

The trends in correlation in the Random and Selected composites (Figures 10, 11, 12) illustrate the effects which methods of propagation can have upon the outcomes of composite crosses.

The Random strategy (open pollination and propagation through equal numbers of seeds from randomly chosen steriles) was intended to reduce Gametic ~~genetic~~ disequilibria (ALLARD, JAIN and WORKMAN, 1966) and correlations between characters by random intermating (MILLER and RAWLINGS, 1967a; MEREDITH and BRIDGES, 1971). This strategy failed.

The increasing correlations (Figure 10, 11) suggested that strong selective forces were operating, probably through competition between the pollinating fertiles. This process would have probably established and maintained genetic disequilibria (ALLARD and JAIN, 1962; JAIN and ALLARD, 1960, 1966; ALLARD and HANSCHE, 1964). In contrast the correlations involving seed-set on steriles ~~were~~ tend~~ing~~ed towards zero (Figure 11) probably because taking ten seeds from each randomly chosen sterile prevented natural selection for associations of characters which would have enhanced seed-set or yield on steriles.

The major implication of these results is that conventional composite crossing with uncontrolled pollination is likely to produce genetic disequilibria, change initial gene frequencies and reduce the opportunity for recombination between the parents. In addition, undesirable correlations between characters may not be reduced. These effects could be counteracted by pair-crossing randomly chosen fertiles and steriles and taking equal numbers of seeds from each sterile parent. This procedure would contravene the conventional definition of composite crossing which requires uncontrolled pollination. Therefore a more flexible definition of composite breeding is required to permit intervention to achieve random intermating if that is required by the breeder. If the population were reduced to a small number of plants its composite characteristics would be forfeited and the procedure then would be most accurately described as intermating only.

It is probable that the strong selective forces in the Random composite may have reduced the genetic variance and therefore reduced the variance of S_0-derived F_5 lines. The effects of competition between fertile pollinators could be tested by comparing the Random strategy with an equal number of cycles of random pair-wise intermatings of randomly selected fertiles and steriles.

The Selected composite strategy was designed to impose directional selection for three morphological characters, height, headlength and spikelet number, upon an open pollinated population. Selection response for the latter two characters was probably significant (Figures 4 and 5). Selection of both fertilies and steriles would have probably achieved a greater gain (CHOO and KANNENBERG, 1981a), and prevented antagonistic effects of the fertiles pollinators. For example, the lack of response in height (Figure 2) probably was caused by homozygous, (*Rht Rht*) or heterozygous (*Rht rht*) tall plants having selective advantage over short dwarfs.

Again, a more flexible definition of composite breeding is required to encompass selection of both the fertile and sterile parents. Many intermating procedures could be used. For example, either the fertiles or steriles could be selected and the alternate parent be randomly selected for pair-wise crosses. These procedures would probably decrease both the rate of response and decline in variability compared with a procedure involving selection of both parents. However, if a breeder were to intervene in a composite he would most probably be attempting to achieve genetic equilibrium by random crossing or the maximum gain to selection by selection of both fertile and sterile parents.

Intense selection of both parents during propagation of a composite will probably eliminate many desirable genes in unfavourable linkage configurations (LATTER, 1965a, b; 1966a, b; QURESHI, KEMPTHORNE and HAZEL, 1968; ROBERTSON, 1977) and would rapidly reduce genetic variation (CHOO and KANNENBERG, 1981a; YOUNG, 1966). Although less intense selection pressures may achieve equivalent gains in a greater number of generations, during which intermating would have a greater opportunity to disrupt disadvantageous linkages, it is unlikely that moderate selection during intermating would be preferred by breeders because the number of generations required to achieve a response equal to that under intense selection would be unacceptably long (BELLMAN and AHRENS, 1966; MARTIN and COCKERHAM, 1960).

If either natural or directional selection occurs in the initial population of a composite formed by bulking single crosses the contribution of the parents of crosses with selective disadvantage to the next generation will be reduced. This probably occurrred in the initial F_2 population. Therefore the genetic contribution of each Australian parent to the R77S population may have differed significantly from their initial contributions to the F_2 bulk (Section 3.1). In that case, the frequency of two-parent associations in the R77S generation would have been less than expected and this bias would have also reduced the frequencies of higher order associations in later generations. Furthermore, if direct selection for headlength, spikelet number and height had been imposed in the F_2, it is probable that the future contribution from some initial crosses may have been severely reduced or eliminated. Witholding selection until the R77S generation allowed one opportunity for intermating between the single cross families before selection. However, the losses of genes from some parents by the S77W population would have been very high and it is probable that a high proportion of the populations in the Selected series were descended from only a few of the initial parents.

Therefore the breeder must choose the method of propagation of a composite which has the greatest likelihood of generating the genetic structure which he requires in the composite population. Consequently, the definition of composite cross breeding should be expanded to encompass intervention by the breeder into the cross-pollination process. Providing that the population is large and families are not emphasised in preference to the bulk, this modified procedure could be still described as composite breeding.

The genetic evolution of an intensely selected composite will be unique and dependent upon the specific recombinations which are produced. It may therefore be beneficial to the breeder to simultaneously propagate replicated intensively selected populations. The responses in each replicate will be determined by different patterns of recombination and may be dependent upon different genes. After a number of cycles of intense selection further gains may be achieved by creating a new composite composed of selections from two or more replicates. In the new composite intense selection could be again imposed after a number of cycles of random intermating to disrupt the specific linkage relationships generated in each replicate (MATHER and HARRISON, 1949; THODAY and BOAM, 1961).

The effectiveness of selection for yield in composites involving male-sterility.

Indirect selection for yield improvement by selecting individual S_0 sterile parents for yield components and morphological characters was unsuccessful (Table 7). Four factors probably caused this lack of response. Firstly, the expression of the selected characters in S_0 individuals is not consistently correlated with the yields of their progenies (Table 11). This corresponds with similar results in arrays of F_1's (BHULLAR, GILL and KHEHRA, 1979). Secondly, selection of steriles with only partial seed-set precludes selection for the most reiable characters, yield and grain number per spike (McVETTY and EVANS, 1980a; NASS, 1978). Thirdly, selected steriles were outcrossed to unselected fertile pollinators, and fourthly, the selection intensities were low (for example, 38.9% and 27.5% in the R77S and S77W populations respectively). The small response of yield to intense selection for spikelet number in S_0 fertiles (Tables 8, 9 and 10) suggests that intense selection of both the fertile and sterile parents may have produced a small yield response. It is unlikely that the expected genetic gain would be equal to that achieved by partitioning the composite into S_0 derived families.

In the Selected composite there were two phases of selection; firstly, selection of steriles which has been discussed above, and secondly, selection of fertile S_0 parents from the S78S population (Table 3). The effects of these two phases of selection cannot be partitioned in this study. If further experiments compared the Random and Selected strategies with directional selection of S_0 fertiles following random selection of steriles and also with random selection of S_0 fertiles following directional selection of steriles, Then the relative effects of selection of steriles and selection of S_0 fertiles could be estimated by comparing the responses in the distributions of yields of inbred families derived from each of the four strategies.

Nevertheless, it is probable that the selection of fertile S_0 parents was the most significant phase. It has been argued previously that selection of steriles during propagation was probably ineffective. In contrast, selection of S_0 fertiles for height, spikelet number and headlength also selected a sample with higher grain number and yield in the longest head (Table 3) which are two of the most reliable characters for achieving yield improvement by indirect selection of yield components (McNEAL, 1960; NASS, 1978; Table 10). Although heterotic components reduce the effectiveness of selection for yield components in small arrays of F_1's (PARODA and JOSHI, 1970) it is probable that the specific effects of parents and single crosses are reduced in a large S_0 population produced by a series of consecutive outcrossings.

If selection of S_0 fertiles has a significant effect, it may be profitable if further experiments determine the effectiveness of selection for different characters, particularly grain number and yield in the largest or longest head. Also, the effects of intensity of selection of S_0 individuals could be determined because composites have the capacity to generate large S_0 populations from which very small populations of individuals with extreme expression of the selected characters could be selected.

Using selection in early inbreeding generations in conjunction with composites in wheat.

Selection between bulk families derived from early-generation single plant selections is a well-established procedure in 2-parent crosses (BRIGGS and SHEBESKI, 1971; LUPTON, 1961; O'BRIEN, BAKER and EVANS, 1978; SHEBESKI, 1967).

In this study Experiment 4 indicated that S_1 and S_2 bulks can be used to identify high-yielding S_0-derived families (Table 12). Partitioning of S_0 families into sets of 3 S_2-derived sister lines in Experiment 5 supported this conclusion. The significant correlations of yields and ranks between sister-lines (Table 17) suggests that the yields of bulks derived from S_1 plants will indicate those families carrying genetic factors responsible for high yield. Furthermore these factors are probably inherited by a high proportion of the inbred progeny of any S_0 or S_1 plant. This was exemplified by the retrieval of three sets of three sister lines (S12, S19, S34) in the ten highest yielding lines derived from the composite crosses (Tables 22 to 26). The concomitant high degree of similarity of quality factors between sister lines (Table 27) suggests that selection for both yield and quality could be conducted concurrently in S_1 and S_2 bulks. This is of particular importance in families derived from heterozygous fertile S_0 parent plants because partitioning of the families to extract and identify homozygous fertile lines cannot occur later than the S_2 without risking genetic contamination of the selected families by outcrossing (Tables 13, 14; Figure 13). Once bulks derived from homozygous fertiles are obtained, yield and quality determinations can be made in later generations and further partitioning can be delayed until near complete homozygosity (WHAN, RATHJEN and KNIGHT, 1982; KNOTT and KUMAR, 1975). JINKS and POONI (1976, 1981a) had also suggested that superior crosses could usually be identified by the F_2 (S_1) but that superior individual inbreds could only be detected in later inbreeding generations.

Bulk testing in early generations will not indicate the magnitude of variance of yield and quality in subsequent inbreds (LUPTON, 1961; FOWLER and HEYNE, 1955) but it would probably be more efficient to recycle superior families identified at the S_1 and S_2 level into further intermating rather than delay recycling until superior inbreds are identified. Inbred lines could be returned to the intermating programme after they are identified. Although they would not carry the male sterile gene it would be carried at sufficient frequency in S_1 and S_2 bulks to renew cycles of composite propagation through outcrossed steriles.

The integration of composite crosses containing nuclear male-sterility into wheat breeding programs.

The results of this study and the conclusions drawn from them suggest a general framework for the use of composites propagated through nuclear male-sterility in wheat breeding.

The evolutionary method of using composites in which genetic advance relied upon natural selection require an unacceptably large number of generations per cycle of selection. This study found useful recombinants in early generations but also suggested that strong selection pressure in the composite could eliminate desirable recombinants or reduce the chance of detecting them in a reasonable sample of the composite population. Therefore a modified management of composites is proposed in which the conventional concept of composite crosses with uncontrolled cross-pollination is superceded by controlled intermating to enable the breeder to direct the genetic evolution of the composite. For example, he can use random intermating to approach genetic equilibrium and enable parental genomes to have an opportunity to contribute to recombination events. Subsequently, the breeder can intensively select both fertile and sterile parents to achieve maximum genetic gain. In practice, no more than 3 or 4 cycles of random intermating and an equal number of cycles of intense selection may be required to be effective. It may be beneficial to intensively select within replicate composites or replicate subsamples drawn from one randomly intermated composite.

The choice of parents ~~of~~ for composite~~s~~ crosses will remain an arbitary decision of the breeder. However, for theoretical reasons large sets are not advantageous.

A high proportion of major undesirable characters may reduce the frequency of useful recombinants to an unacceptably low level. After a few cycles of random recombination intense selection against undesirable characters could be imposed. Direct intense selection of characters will probably be successful during propagation of composites, but indirect selection for yield will probably not be effective, except for intense selection of S_0 fertiles for the most reliable yield components.

The S_0 populations generated by composite breeding will probably be the most critical in using composites in wheat breeding. Contemporaneous or replicate composites could be selected by comparing the frequencies and magnitude of expression of desirable recombinants in S_0 populations. A small significant response in yield may be achieved by intense selection for yield components in the S_0 prior to generating S_0-derived inbred families. S_0-derived families can be used in early-generation yield tests to identify the most promising sources of superior inbreds. They can also be used as the selection phase of recurrent selection procedures, in which composite crosses could be used as the intermating phase.

Recurrent selection, assisted by male sterility, has been successful in soybean (BRIM and STUBER, 1933; BURTON and BRIM, 1981; KENWORTHY and BRIM, 1979), and sorghum (DOGGETT, 1972; JAN-ORN, GARDNER and ROSS, 1976) and suggested as a general breeding procedure for autogamous species by FREY (1975) and RACHIE and GARDNER (1975). Future research must define the most effective methods for using composite crossing procedures within a recurrent selection programme. Some ways they could be used are (1) short-term intermating populations between inbreeding phases, (2) a method for disrupting unfavourable linkages which occur in selected populations, (3) a method for intermating previously separate paths of selection, (4) populations in which selection could be conducted in outcrossing individuals, and (5) a long-term genetic pool into which selected lines and new parents are added and from which new cycles of selection or new composite sub-populations can be intiated.

This study was based on the recessively inherited Cornerstone male-sterile stock, but dominant nuclear male-steriles have been identified (DENG JINGYANG and GAO ZHONGLI, 1982; MAAN and WILLIAMS, 1984). SORRELLS and FRITZ (1982) proposed a number of breeding strategies in which dominant nuclear male-sterility could be used to increase the frequency of cross pollination. Among their proposals were a scheme similar to the selected strategy of this study and various progeny testing procedures in a framework of recurrent selection. Dominant male-sterility is advantageous for deriving inbred fertile lines from a composite. All fertile S_0 individuals are homozygous fertile and therefore no progeny tests are required to identify homozygotes. However, this is disadvantageous if the breeder wishes to re-establish outcrossing using selection S_0-derived families. Recessive male-sterility permits the transmission of sterility through heterozygous fertiles in an S_0-derived family so that outcrossing can be re-established using steriles which segregate from within selected families. Such sterile segregants cannot occur using dominant male-sterility. Therefore superior S_0 derivatives must be outcrossed to steriles which can be no more closely related than sterile siblings of the fertile S_0 parent.

In the future it is likely that the ease of outcrossing which nuclear male-sterility provides in wheat will enable breeders to use improvement programmes with designs approaching those currently used for predominantly outcrossing species. It is reasonable to postulate that the most exciting period in the domestication of wheat still lies ahead as wheat breeders use genetic male-sterility to increase the frequency of meaningful recombinants beyond that currently achieved by limited crossing and inbreeding. Composite crosses will undoubtedly have a central role in such breeding procedures.

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