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THE EFFECTS OF NATURAL SELECTION ON THE YIELD AND ADAPTATION OF GENOTYPES IN COMPOSITE CROSS POPULATIONS OF BARLEY

by

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PLANT BREEDING

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STATEMENT.

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

SUMMARY.

A study of adaptation was carried out on a random set of 100 lines from each of the F6, F16, and F25 generations of Composite Cross V (CCV) and from each of the F2, F9 and F9DA generations of the Composite Cross XVI (CCXVI) population. The CCXVI generation F9DA differs from the F9 in that it was grown at Davis and Aberdeen in alternate years. The two composite crosses were obtained from Dr. C.A. Suneson. The aim of the present experiment was to measure the yield and adaptation response of individual genotypes that were found in the populations after different generations and to study the association of major agronomic characters and other characters with the individual adaptation responses. Such a study was expected to provide an understanding of the nature of changes in the composite-cross populations and enable an assessment of their suitability as a source of improved breeding material.

A two-replicate randomized block experiment was conducted at Bundaleer, Clinton, Minlaton and Waite Institute in 1967 and [redacted] 1968. These locations provided diverse environments in terms of annual precipitation, fertility, soil type, [redacted], and are in the South Australian cereal belt.

The results were analysed by the analysis of adaptation technique outlined by Finlay and Wilkinson, in which [redacted] the yields of individual genotypes are depicted as a regression on site mean yields. A test for deviation from regression was also made as suggested by Eberhart and Russell. An analysis was carried out both on a logarithmic

scale and a natural scale. ~~From the comparative study~~ It was concluded that the interpretation and the presentation of the result ~~was~~ were simpler on the logarithmic scale. This scale provided a clearer separation of genotypes with various adaptation responses.

The results from [redacted] CCV and CCXVI were analysed separately. Results from CCV forms the major part of this thesis; results considered relevant for the CCXVI population are presented in the last section.

A main finding of the studies on CCV was that there was a progressive shift from F6 to F16 to F25 in the frequency of genotypes with various adaptation response. The F6 generation had a proportion of genotypes which were highly sensitive to change in the environments. Some of these had high yield potential. The F6 also had greater proportion of lines which were specifically adapted to low yielding environments ([redacted]). An absence or a relatively lesser proportion of such lines in the F16 and F25 showed that these lines were eliminated by natural selection. As genotypes with high yield potential, but specific adaptation, are likely to remain in the population for a few generations only, any hoped-for improvement of the population through out-crossing of these genotypes will not be achieved in a composite-cross population. The frequenc~~y~~ies of genotypes with a high yield potential and wide adaptation had increased by F16 and increased still further by F25. The best lines were those which could be included in the 1968 trial only. Their inclusion was restricted to that year because they did not respond to long days of a summer multiplication. The mean yield of the two highest yielding lines from the F6, F16 and F25 generations exceeded the average yield of the two best check varieties (California Coast and C.I. 3576) by 16, 30 and 75 percent (1968 results). All these lines had above average stability (b< 1.0).

Results on days [redacted] to heading showed that the advanced generations had shifted towards earliness. The sensitive genotypes were relatively late; the stable genotypes relatively early; and the generally adapted genotypes tended to be intermediate. Study of days to heading following summer sowing (during seed multiplication) and normal winter sowings showed that genotypes with specific adaptation were long day responsive; the generally adapted genotypes were day neutral. The possibility of the association of genes that govern the day neutral response with high yield potential and adaptability was discussed against a background of results from other crops such as wheat and rice.

Results on shattering showed that the advanced generation populations had improved and were less liable to shatter. Genotypes specifically adapted to poor environments shattered and lodged. These genotypes were thought to be recombinants from the parental varieties which were adapted to a region of poor agricultural practice and low soil fertility. Genotypes with a high yield potential and wide adaptation did not shatter and had a greater straw strength. However in a highly favourable environment (Waite 1968) all [redacted] genotypes lodged. Scores on powdery mildew showed that the generally adapted genotypes had less infection.

Results on morphological characters and the components of yield could not be directly linked with the adaptation response. The results, however, showed that there was a trend for the advanced generations to have a higher ratio of fertile tillers to green tillers [illegible]; more grains per spike; and higher grain weight. The advanced generations had also shifted towards shorter stature.

Results on CCXVI showed that there ~~was~~ were no significant changes from the F2 to the F9 for yield and adaptation. A comparison of results in yield, adaptation, ~~and~~ heading date, and other characters indicated that the CCXVI F2 or F9 and CCV F25 populations were similar. The overall result suggested that the F9DA population was probably inferior. The frequency of genotypes with long day requirements seems to have increased ~~in~~ by the F9DA population. Genotypes from the F2 or F9 which did not respond to long day length in summer, and were included in the 1968 trial only, tended to be superior as in the CCV population; but similar genotypes from F9DA were inferior. The latter genotypes ~~were thought to~~ may have a vernalization requirement and were not day neutral. It was concluded that alternate propagation of bulk material at widely different photoperiodic conditions might not result in day neutral types but that genotypes adapted to a certain day length might be favoured.

The discussion was devoted to a consideration of the nature of changes in the CCV population; the association of agronomical and physiological characters with adaptation responses; aspects of the adaptation analysis technique in relation to the present experiment, and the composite-cross as a breeding technique.

The objectives and validity of measuring adaptation in the presence or absence of specific limiting factors like disease, shattering, etc., were considered. It was suggested that if the results from a trial, where a specific factor is operating, is excluded from the analysis the test for deviation from regression might not be necessary as only large deviations are likely to be significant statistically. The importance of studying the performance of a genotype at each site was emphasized. It was concluded that the parameters, mean yield, regression coefficients, and deviations from regression are only preliminary measures for the rapid comprehension of the performance of a large number of genotypes.

In view of progressive shift in the CCV population and lack of any progress in CCXVI population it was argued that the changes that can be expected in ~~the~~ composite-cross populations are largely determined by the diversity of the base population. The increase in proportion of superior types in the CCV advanced generations was chiefly attributed to an effect of sampling; that is, the loss of inferior types meant that a greater proportion of superior types was present in samples taken at different stages. Since ~~[illegible]~~ CCXVI was constituted from superior lines, the population norm of F2 was close to the optimum for the Davis environment, ~~and~~ hence no improvement occurred. However, the presence of a few exceptional lines in F25 showed that some useful gene combinations have arisen from recombination between the original diverse parents and further segregation.

It was suggested that one could possibly select superior recombinants from a composite-cross population in an earlier generation by screening the material for day-neutral types.

PREFACE.

In cereals, breeding for yield and adaptation is of primary importance. It has been suggested that only a small proportion of genotypes from the total variability within the species is used in ~~the~~ breeding programmes. It would be preferable to use a large number of genotypes with the aim of assembling the useful genes into superior recombinants. It is also desirable to retain the genetic variability in the breeding population to enable further improvement. This is difficult to achieve with the usual pedigree or bulk population methods of breeding.

Composite ~~C~~cross populations or 'mass reservoirs' have been proposed as a suitable method for using a greater proportion of variability, both as a means of deriving superior recombinants as well as the retention of variability. Suneson, on the basis of his work on composite-cross populations of barley, has termed this technique [redacted] 'an evolutionary plant breeding method'. The most critical evidence regarding the long-term improvement in yield in [redacted] composite-cross populations is limited to the publications by Suneson, which apart from pointing out some trends for the population and the yield performance of a few selections from one composite cross, do not furnish results on the nature of changes in the population for yield and adaptation. Use of different control varieties at various stages of the experiment and [redacted] changes in management have cast doubts on some of his interpretations. The method is, however, appealing because of its simplicity and has created interest among plant breeders.

In recent years, following [redacted] studies of adaptation, Finlay has emphasized the possibility of combining high yield with wide adaptation. The performance of Mexican wheat varieties and the result of barley breeding at the Waite Institute suggest that this objective can be achieved.

The present experiment was conducted to study the yield and adaptation of genotypes selected from various generations of Composite Cross V and Composite Cross XVI; and to study the characters which are associated with their individual performance.

REVIEW OF LITERATURE

A. INTRODUCTION

Success in plant breeding requires adequate genetic variability. However, selection reduces variability and limits chances for further improvement. Hybridization is one well-established procedure for increasing the variability on which selection is practiced (Allard 1960).

Although in self-fertilized plants genetic mechanisms exist which confer greater selective advantage on the heterozygote (Rev. Allard *et al*. 1968), homozygosity is approached rapidly in the breeder's population. Calculation of the changes of gene frequencies in an inbreeding population show that lines isolated after 7 to 10 generations of self-fertilization will have achieved homozygosity at most loci even when originally a very large number of genes were segregating, and that most of the intraallelic variation will have been lost through fixation (Williams, 1964). In the improvement of self-fertilized cereals, hybridization and selection form a continuous cycle.

Simmonds (1962) proposed the term 'genetic base' to include the variability of the locally adapted varieties and other genotypes in the breeder's collection. He discussed the advantage of maintaining a broad genetic base. The usual breeding procedure tends to narrow down the genetic base of the self fertilized crops as the ultimate goal in both pedigree and bulk population methods of breeding, is to select a few homozygous lines (Allard 1960). The term conventional method has been used to imply the pedigree and bulk population methods of breeding. (Simmonds 1962, Allard and Hansche 1964).

Frankel (1954) traced the development of wheat improvement in Australia and argued that progress before 1930 was rapid because of the use of wider range of introduced genotypes. Once a certain level of adaptation was achieved, the use of exotic germ plasm by local breeders was slackened. It also became more difficult to combine characters from the exotic parents into the local varieties as their level of adaptation increased. Introductions were mostly utilized as a source of disease resistance which was incorporated by backcrossing, a procedure followed up to the present time. Frankel also pointed out that only a limited number of genotypes were used in ~~the~~ breeding programmes that spanned a period of about 80 years. These constitute the parentage of almost all the Australian wheat varieties. Earlier introductions were made haphazardly and probably did not represent the best genotypes available. The consequence of all this is that the Australian wheats at present have a narrow genetic base or an 'impoverished genetic structure' (Frankel 1954). It is also explicit from Simmond's review that the breeding histories of crop plants elsewhere, especially self fertilized cereals, are similar.

The need to utilize a greater proportion of world germ plasm both for the major genes and for other genes contributing to yield have been emphasized by a number of workers in recent years (Frankel, 1954; Suneson, 1956; Harlan, 1956; Simmonds, 1962; Allard and Hansche, 1964; Finlay, 1963b; etc.) Simmonds (1962) remarked "It seems inconceivable that all the potentially useful combinations should have been assembled in any group of locally adapted stocks. It follows that poorly adapted stocks however uncompromising in intermediate performance must have useful genes and gene combinations to offer the plant breeder. The problem is to isolate them in usable form." The future progress in improving yield and adaptation lies in the judicious use of yet unexploited variability.

Frankel (1954) reported success in producing a wheat variety with much higher yield by making complex crosses involving an adapted variety and exotic parents. His work showed that unadapted introductions can be used to enrich the local genetic base even under a conventional breeding programme. In recent years this step has been emphasized at Waite Agricultural Research Institute in the breeding programme. (Finlay and Wilkinson, 1963; Sparrow, 1966).

Can a better system be adopted which permits even greater use of the variability, cheaply and effectively? Simmonds (1962) ruled out conventional methods on two grounds:

1. That the number of combinations and the size of the population would be too large and the probability of success too low to justify the enormous expenditure of time and effort.
2. That it leads rapidly towards homozygosity and thus reduces the chance of obtaining rare combinations. The cycle of hybridization and selection has to be maintained.

As an alternative Simmonds proposed that a panmictic population, set up on a broad genetic base, might be a cheap and effective means of utilizing unadapted genotypes in combination with local genetic base. He visualized it as 'mass reservoirs' of variability. Advantages attributed to this concept are that:

(1) The population can be maintained at broad genetic base with minimum expense. Actually Simmonds considered it as the best method of maintaining a collection of genetic variability.

(2) Superior lines can be selected from the population and used in the conventional breeding programme.

Similar merits were also pointed out by Suneson (1956) earlier, based on the results from composite-crosses of barley.

In cross-fertilized plants,mass reservoirs can be easily constituted by mixing the seeds of the various genotypes and prop~~o~~agating the bulk in successive years. Such populations have been constituted in cotton (Hutchinson, 1957), and in maize (Swaminathan, 1967). In self-fertilized crops,the closest form to mass reservoirs is known as composite-cross population and was first initiated by Harlan and Martini (1929) in barley. Basically the technique consists of crossing a large number of parents in a number of combinations, mixing the hybrid seeds and prop~~o~~agating the composite bulk under 'natural selection' - apparently indefinitely. The amount of recombination achieved depends on the number and the diversity of the parental genotypes, as well as the number of cyclical crossings. Use of male sterile genotypes enforces more recombinations in the population during the years of prop~~o~~agation. A number of composite-cross populations have been constituted in barley since the original population of Harlan and Martini (Suneson and Stevens, 1953; Suneson, 1956; Suneson and Wiebe, 1960). Composite-cross populations have also been derived in wheat (Suneson *et al*., 1963), lima bean (Allard and Hansche, 1965) and oats (Frey, 1967). Jensen (1962) also proposed an interesting plan for the maintenance of world genetic variability in a composite bulk.

Simmonds (1962) argued that the "..bulk method of handling single crosses and the composite cross type of population,though superficially similar and based on the same assumption as to nature of survivors are in effect quite different : the latter is means of exploring, recombining, and maintaining variability on a scale inaccessible to conventional breeder". Allard and Hansche (1965) pointed out that for mass reservoirs to be of practical value:

(1) It must give rise continuously to new and original variants by segregation and recombination.

(2) Survival in the heterogeneous population must be correlated with agricultural value.

B. NATURAL SELECTION IN POPULATIONS OF SELF FERTILIZED SPECIES.

1. GENERAL CONSIDERATIONS.

Changes brought by natural selection in a population within a few years are exceedingly small and subtle as compared to long term changes that differentiate between species. If the former can be magnified and directed towards producing agronomically more desirable plants it would be of practical importance to plant breeders.

Natural selection can operate in evolution but only if genetic variability exists and different genotypes reproduce at different rates. Stebbins (1950) concluded that the following five processes were the principal contributors to the action of selection. These are: variation in the external environment, mutation (in the broadest sense), genetic recombination, isolation, and, in a small population, the effects of chance variation.

(a) The operation of natural selection.

Lerner (1959) defined natural selection as differential reproduction of genotypes. The reproductive ability of the genotype is measured by the number of progenies produced and is called fitness (Fisher, 1930).

In the absence of sampling error, the composition of a heterogeneous population in each successive generation under natural selection is influenced by the fitness of the genotypes in the previous generation and the percentage of the seeds that survive and reproduce. Thus certain genes and gene complexes will be represented more frequently and others less in each successive generation. Lerner (1959) summed up the relationship between fitness, natural selection, and adaptability: 'adaptation and adaptability simply provide means towards increased fitness, they should be viewed not as causes but consequences of natural selection'. Since fitness of the genotype as a whole is the outcome of natural selection, character associations are often selected rather than single characters (Wright, 1935b; Stebbins, 1959).

There is a difference between natural selection for survival in the natural population and natural selection in the conditions of cultivation. The effectiveness of natural selection in the breeder's population is measured in terms of productivity.

(b) Forms of selections.

Mather (1953) classified the influence of selection into three major forms [redacted]. (1) Directional, (2) Stabilizing, and (3) Disruptive. Selection acts on the phenotype, and only indirectly on the [redacted] genotype, [redacted] through its expressed in the phenotype.

In directional selection, phenotypes towards one extreme of the distribution curve have a selective advantage. Directional selection is a part of artificial selection programme. The intensity of the character can be increased as long as it does not markedly reduce the fitness value of the individual due to correlated changes and as long as heritable variance is available (Mather and Harrison,1949).

Stabilizing selection implies that the individuals close to the population mean i.e.'optimum phenotype' (Wright,1935a)are much fitter than the individuals deviating from it. Stabilizing selection tends to maintain an equilibrium in the population by eliminating individuals from both tails of the distribution curve. The optimum itself can be a moving parameter because of a fluctuating environment (Wright, 1931, 1935b, 1956; Mather, 1953). Under natural selection directional selection occurs only when the optimum lies consistently away from the mean.

Disruptive selection implies that individuals from both tails of the distribution curve are selected. Disruptive selection is also credited with a move to speciation.

(c) Adaptation and adaptability.

Frey (1964) pointed out that the term 'adaptation' may have different meanings under different circumstances and that different mechanisms may be responsible for the adaptation reaction.

In evolutionary studies,adaptation is related to maximum fitness in the existing environment and is synonymous [redacted] with the term fitness and adaptedness (Dobzhansky 1955). Adaptability refers to the genetic mechanism which permits a genotype to adapt to the changed environment. As selection reduces variability, adaptation and adaptability can be antagonistic (Mather 1943). Various genetic systems like polygenic inheritance, linkage, heterozygote advantage etc., may meet requirements for both adaptation and adaptability in a population of cross-fertilized species of plants and animals (Mather, 1943; Darlington and Mather, 1949; Dobzansky 1947; Lerner, 1954, [illegible].) Allard *et al.* (1968) concluded that similar mechanisms operate in populations of self-fertilized species.

In cereal husbandry the criterion of adaptation is the relative performance of selections or varieties and is measured by grain yield (Frey, 1964; Krull *et al.* 1968a). If more than one environment is involved, which is normally the case, adaptation implies relatively high yield in each of the environments and, is indicated by the term 'general adaptation'. The terms, individual buffering, phenotypic stability, developmental homeostatis, or ~~merely~~ homoeostasis have often been used by various workers to indicate the ability of the genotype to perform consistently well in a range of environments. Whether such property of the genotype is due to the basic concepts of homeostasis (see Wardlaw 1965, page 421) or largely due to unrecognized specific adaptations to erratic environmental factors (Simmonds 1962) cannot be easily resolved and is not the main issue in this thesis.

Simmonds (1962) recognized four separable aspects of adaptation which he classified as (1) specific genotypic adaptation, (2) general genotypic adaptation, (3) specific population adaptation, and (4) general population adaptation. In essence, specific adaptation implies superior performance in a particular or a narrow range of environments. General adaptation has already been explained. Both forms of adaptation can be displayed by either individual genotypes or heterogeneous populations and hence the four categories.

More specific definitions and experiments on measurement of adaptation responses will be reviewed later (Page 43). Other relevant aspects will be discussed in conjunction with the results from the present experiment.

2. THE POPULATION STRUCTURE OF SELF FERTILIZED SPECIES.

The genetic structure and the evolutionary potential of self-fertilized plant populations have been reviewed by Stebbins (1950, 1957), which gives an insight into what has been called the traditional view. Stebbins (1957) visualized ~~the~~ populations of self-fertilized species as an array of large numbers of homozygous lines usually isolated from each other reproductively. Occasional outcrossings were expected to occur, resulting in a burst of new recombinants of which only the adapted types remained in the population as additional homozygous lines. Inbreeders were supposed to have evolved such a genetic system for adaptation at the expense of adaptability (also Mather 1953).

Allard et al. (1968) have reviewed more recent works, in light of which the generally held concepts of the dynamics of self-fertilized plant populations need some modification. These works included theoretical studies involving genetic models of increasing complexities, and field studies on cultivated crops, as well as wild species.

A comprehensive review of the theoretical studies is not warranted here. It should also be noticed that controversies exist among authors as to the suitability of certain models or the methods of deriving mathematical theorems (Hayman and Mather, 1953, 1956; Haldane 1956 - to give one example). Some salient points, however, tend to support results from field studies. It has been concluded on the basis of theoretical studies involving single locus models that greater selective value of heterozygotes relative to homozygotes results in the maintenance of genetic variability in the population indefinitely (Hayman and Mather 1953; Workman and Jain, 1966). The effects of linkage and epistasis were introduced in other models (Rev. Allard et/ al. 1968) which suggested that complex inter relationship exists between linkage, epistasis, and selection under inbreeding. In general, linkage and epistasis are expected to result in slow release of variability over a large number of generations even under random mating. This situation is intensified under selfing (Lewontin, 1964a, 1964b; Jain and Allard, 1966).

Hayman's (1953) model has been commonly used for inquiry into field studies. This model assumes genetic change to be [redacted] a function of parameters specifying the amount of selfing versus out-crossing, and the selective value of each genotype at a diallelic locus. Other factors which might influence genotypic frequencies in the populations, i.e. migration, mutation and sampling error which is associated with a finite population size, are assumed to be absent or insignificant in the conditions of the experiment. Based on census data of marked chromosome segments Allard and Workman (1963) outlined methods of estimating actual amount of out-crossing, effective amount of out-crossing, and selective value of the genotype for a diallelic locus.

A certain level of out-crossing occurs in even heavily inbreeding species like subterranean clover (Frankel and Williams, 1958); while [redacted] barley, wheat, lima beans, etc., have a relatively higher out-crossing rate and are typed as 'predominantly self pollinated'. The amount of out-crossing in barley has been observed to be around 1-2% (Jain and Allard 1960). Greater levels of out crossing associated with certain morphological characters have been reported (Suneson and Cox, 1964). The investigations on lima beans (Allard and Workman, 1963; Harding and Tucker, 1964); and in wild oats (Imam and Allard, 1965) showed that the estimated amount of out-crossing varied between populations, seasons, and the marker loci studied. In lima beans it rarely exceeded 5%. Out-crossing in wheat has been a subject of intense interest in recent years and up to 70% seed set in male sterile plants have been reported in special conditions (Review Wilson, 1968).

Some field studies which have provided greater understanding of the dynamics of self pollinated populations will be reviewed here. The study of Jain and Allard (1960), on F3, F5, F6, F13, and F18 generation populations of Composite Cross (CC) V of barley showed that:

(1) The proportion of heterozygotes at a number of marked loci did not decrease at the rate expected from the observed value at out crossing. The ratio suggested a state of equilibrium. It was estimated that the heterozygotes had greater selective advantage than the homozygotes in five [redacted] of eight loci studied.

(2) The selective value of the chromosome segments studied varied, so that the frequency of certain genes increased, others decreased and some approached equilibrium over a period of 18 generations of natural selection. The study of quantitative characters in the same populations (Jain, 1961a; Allard and Jain, 1962) also provided evidence for heterozygote advantage.

Allard and Workman (1963) did a comprehensive study on three lima bean populations from F2 to F11. It was found that advanced generation populations had a higher proportion of heterozygotes than expected under the observed rate of out-crossing. It was estimated that the heterozygotes had greater fitness than either of the heterozygotes and that this was more evident in a poor environment, i.e. the selective value of the genotypes fluctuated between seasons. In general, the homozygotes produced relatively more seeds in a poor season as compared to a favourable season. The selective value for the two homozygotes also fluctuated between seasons and between populations. It should be noted that the conditions in which the experiments were conducted were uniform in regards to irrigation, cultural practices, competition, and even the prevailing meteorological conditions (Allard and Workman 1963). This emphasized that a much wider fluctuation in selective values are likely to occur in a diverse population under rain fed environments.

The work of Imam and Allard (1965) on natural populations of wild oats also showed greater selective value of heterozygotes compared to both the homozygotes for the two loci studied. This was reasoned to account for the amount of within family variability and the extent of between family and between population diversities that were observed in the study.

Harding *et al.* (1966) studied the trend observed in one of the populations of lima bean previously studied by Allard and Workman (1963), which had apparently suggested that the selective value of the heterozygote increased as its frequency decreased in successive generations. A number of populations were artificially constituted by mixing various proportions

(3 to 15%) of early or late generation heterozygotes, with late generation homozygotes. The experiments were designed to test whether the selective advantage of the heterozygotes [redacted] was frequency dependent or due to the changed genetic constitution which might have led to increased fitness. It was concluded that the fitness of the heterozygotes increased as their frequency in the population decreased; and when they were at very low proportion, the heterozygotes produced about three times as many progeny as homozygotes. The relative fitness of the homozygotes and the heterozygotes [redacted] was independent of the generations from which they were derived.

It seems that greater variability, and mechanisms for the retention of variability, exist in populations of predominantly self-pollinated species with broad genetic base - a prerequisite for evolutionary change or success under selection. Allard and Hansche (1964) concluded that such populations differed only in degree from the random mating population and that the recombinational system appeared to permit the formation of new and superior variants for an indefinitely large number of generations. This has led Allard [redacted] to commend 'mass reservoirs' as a valuable aid in plant breeding.

If such a population does not differ much from that of cross pollinated species in the magnitude of recombinations,would it also show rapid directional shift towards the breeder's ideal? Suneson and Ramage (1963) and Jain and Suneson (1966) studied the changes in one composite-cross population of barley in which continuous recombination was achieved for a number of generations by compositing the seeds from only male sterile spikes. The control was the normal sample of the population with originally some proportion of male sterile genotypes whose frequency rapidly declined in advanced generations. Comparisons of the yield performance (Jain and Sunseson 1966) showed that increased recombination did not enhance the rate of improvement of the population as it was actually less productive than the control. It was suggested that the normal rate of out-crossing observable in such populations ~~[illegible]~~ was optimum for adaptive improvement.

It was probably too optimistic to expect improvement solely on the basis of increased recombination. The fact that the value of the parents is more important than the frequency of recombinations for the release of superior segregates, seem to have been often overlooked.

It can be summed up that the population structure of a self-fertilized species is highly complex. The nature of change is largely determined by the chance fluctuation of the environment as well as the selective value of ~~the~~ individual loci. To what extent are the desirable genes likely to be charnelled into superior genotypes in ~~a~~ dynamic populations ~~[illegible]~~ where male contribution (when out-crossing occurs) is from a random genotypic sample? This is assuming that long term recombinations under observed rate of out crossing are effective in breaking up linked blocks of genes. The answer to such question ~~[illegible]~~ depends upon the study of genotypes that are formed and survive in the population over generations; and ~~the~~ studies that predict the kind of combinations that would result in superior segregates.

3. NATURAL SELECTION IN COMPOSITE CROSS POPULATIONS.

(a) Yield and fitness.

Results on the comparison of composite cross populations and simple bulks were first published by Harlan *et*. *al*. (1940) who conducted extensive studies on 378 crosses that resulted from inter-crosses between 28 barley varieties. Each cross was grown as separate bulk and the yield recorded for each generation. The experimental plots consisted of a single 10' nursery row grown at Aberdeen, Idaho. Based on yield records, the crosses were ranked, and three to fifteen selections made from each cross, increasing numbers being selected from higher ranking crosses. The total number selected was 2921. A composite bulk was also constituted by mixing equal amounts of seed from F2 of all crosses and propagated every year. At F8 a total of 2921 lines were also selected from the composite bulk. It was conlcuded on the basis of comparative yield tests that the number of superior lines obtained from the composite bulk compared favourably with that obtained from the individual crosses. Thus growing separate bulks was no more efficient than growing a composite bulk - the latter required less attention. It is also interesting to note that similar number of superior lines survived in a much more competitive condition that might have occurred in the composite bulk.

Suneson (1956) presented results of four composite cross populations of barley. Of these CC II had been grown for 28 generations, CC V and CC XII for fifteen generations and CC XIV for 12 generations. Table 1 summarises Suneson's results. It shows that only the F2 and

Yields of Composite Crosses II, V, XII, and XIV in various generations in comparison with Atlas or Atlas 46

From: Suneson (1956); Agron. J. 48 : p. 189.

Test years	Generation	Acre yield in bushels				
		CC II	CCV	CC XII	CC XIV	Atlas or Atlas 46
1937-38	F3 - F4	58.3	-	-	-	86.2†
1933-34	F7 - F8	71.3	-	-	-	83.8†
1937-40	F11 - F14	72.6	-	-	-	81.7†
1941-46	F15 - F20	75.1	-	-	-	70.8†
1947-50	F21 - F25	53.0	-	-	-	52.3
1951-55	F26 - F29	50.8	-	-	-	49.1
1947-54	F2 - F3	-	42.4**	43.4*	-	51.3
1947-55	F4 - F8	-	41.4*	43.4*	-	49.9
1951-52	F11 - F12	-	50.2	51.8	-	51.6
1953-1955	F13 - F15	-	52.4	54.0	-	54.1
1952-54	F2	-	46.5*	46.8*	-	54.0
1952-54	F12 - F14	-	54.7***	56.7***	-	54.0
1947-54	F2	-	-	-	56.5*	64.2
1947-50	F3	-	-	-	52.6*	59.5
1947-49	F4 - F6	-	-	-	50.2*	62.6
1950-52	F7 - F9	-	-	-	56.0	53.5
1953-55	F10 - F12	-	-	-	51.3	54.1

* Significantly lower yielding than Atlas 46 at 5% level, and ** at 1% level.

*** Significantly higher yielding than F2 for same years at 5% level.

† Yields are for Atlas.

the F12 - F14 populations of CC V and CC XII were grown together in the years of 1952-1954. In both composite populations, the yield of F12 - F14 was significantly higher than that of F2 - an increase of about 8 to 10 bushels/acre. The yields of F12 - F14 had almost equalled or was approaching the yield level of the control, Atlas 46. Since seasonal conditions determine the level of yield, comparison of populations from different generations are more reliable when grown in one trial.

The other comparisons were for populations grown in different years. Atlas or Atlas 46 were grown as control. Relative yield of composite bulk to that of the control was used as an indication of yield improvement over generations, i.e. yield was expressed as percentage of the control. The trends observed from the results were as follows:

(1) The yield of all the composite bulks remained unchanged up to about F6.

(2) Yield improvement occurred from F7 onward. In CC II the yield of the population equalled the yield of the control by F20. Suneson (1963) extended the yield curve of CC II ~~up~~ to F38. Yield values were plotted as percent of Atlas, Atlas 46, Atlas 54, and Atlas 57, at various stages. The figure showed that the yield of the composite bulk had reached the level of about 105% of the control by F27. From F27 to F38 yield seemed to decrease and to plateau at the level of the control. The comparisons with various controls and the paucity of published results make

critical evaluation difficult. Suneson, however, stressed that natural selection was improving the population at a comparable rate to that achieved by back-cross breeding which produced the derivatives of Atlas. The annual performance of CC XII, CC XIV, and CC V (Suneson, 1956) also showed that the yields of those populations were generally approaching the yield of the control. The yield of CC V increased from about 82% in F2 - F6 to about 96% by F15. The yield of CC V up to F24 has been tabulated by Jain and Suneson (1966). The yield of the control (if any) was not given. It was suggested that an annual increment of 32 lbs/acre was achieved.

(3) Suneson (1956) suggested that the composite populations differed in the rate of yield improvement and the number of generations taken to equal or surpass the yield level of the control. Superficial examination of the yield curves would suggest that this is so. Suneson's results will be re-evaluated.

Table 1 showed that the yield of Atlas or its derivatives had steadily declined over the years, i.e. from 86 bushels in the period 1933-34 to 49 bushels in 1951-55. It is conceivable that seasonal fluctuations can account for the change in yield. However, the consistent decrease in yield over the years seems unusual. In an earlier publication (Suneson and Stevens, 1953) the possibility of a yield decline in Atlas was contemplated. The authors did not regard it to be serious. The table showed that Atlas 46 was grown from 1947 onwards. It seemed rather anomalous that the yield of control, from 1947 onward, was drastically reduced to 49-52 bushels/acre while prior to that the yield was about 70-86 bushels. Suneson has remarked that "Recent tests have sought average rather than maximum soil fertility and yield levels". The year of change in management was not mentioned. The exact nature of changes are also unknown. It can only be speculated that probably the change was made in 1947 and that this involved both lowered soil fertility, and relatively greater moisture stress.

The trial of Finlay and Wilkinson (1963) showed (to be reviewed later) that though the yield level of Atlas was above average relative to other varieties, its yield varied from 800 gms/plot in high yielding environment to about 160 gms in low yielding environment, out of the seven environments sampled. In Suneson's trials, the change to a poorer environment would have affected the yield of composite population as well. The yield values for CC II from 1947 onwards as compared to previous values (Table 1) would suggest that this is so. However, the following questions remain unanswered:-

(1) What was the relative decrease in the yield of Atlas 46 as compared to CC II population as a result of the change in management practices?

(2) What would be the actual yield of the composite bulk or the selections derived from it in a better environment?

The other composite-cross populations were grown after 1947 and their comparisons to the control in terms of relative yield can probably be said to be more satisfactory. The initial yield level and the rate of improvement of these populations can hardly be compared with F3 etc., of CC II which was grown from 1933 onwards (i.e. under different conditions).

The yield of the selections derived from the composite bulk is a critical measure of the value of the population and some results are available for CC II (Suneson, 1956). Random selections were made at various generation intervals and yield tests conducted - yield measured as percentage of Atlas or Atlas 46. In F12 none of the selections gave much higher yields than Atlas. Out of 50 F20 selections, one line outyielded Atlas 46 by an average of 37%. The 3 top selections from F24 gave an average of 56% yield increase over Atlas 46. A 56% yield advance is quite substantial progress and it would be intersting to know their adaptation response and some agronomical characteristics of importance. Suneson has, however, predicted that the varieties selected from the composite cross population would have 'maximum assurance of adaptability'. It may occur that the anomalies which were discussed previously in connection with the yield trial of the composite bulk may apply to the evaluation of the selections also as the selections were made and tested in different years and apparently under different management.

Harlan (1956) listed 18 barley varieties, released in the United States or elsewhere, that could be traced directly or by parentage to composite cross populations. These varieties had been selected at different experimental stations (Wiebe and Reid, 1958). Selections were usually made in the early generations of the composite bulk, and about ten years elapsed between the time selections were made and the release of the variety. In what respect they were superior to the varieties that were replaced is not apparent from the published accounts. Selection in populations from planned crosses might also have resulted in improved varieties in the same length of time.

The trend in yield improvement of the composite bulk and increase in proportion of superior types can be expected, as natural selection would operate against inferior types. The critical questions are:-

(1) Did composite cross populations improve to equal or surpass the yield of the control that was apparently the best commercial variety?

(2) Can superior lines be obtained from the composite bulk after a long term natural selection, that are distinctly better than any other available genotypes for yield and adaptability? It is concluded that results published on composite cross populations are not adequate and comprehensive enough to provide definite answers to such questions.

Jain (1961a) and Allard and Jain (1962) conducted experiments to measure yield, fitness and other quantitative and morphological characters in CC V population of barley. It should be noticed that the experimental studies involved individual plants spaced one foot apart between and within rows. Jain (1961a) obtained data on total grain yield and fitness of individual progenies of F4, F7, F14, and F19 generations. The average values were obtained from the bulk of these progenies. The total number of seeds produced per progeny was taken as a measure of fitness, which was computed as total grain yield divided by weight per seed. The estimates obtained were 7940 and 9440 for F4 and F19 generations. Average yields were 307 ~~gms~~ and 394 gm~~s~~, respectively. On the basis of these estimates it was suggested that the population had improved both in fitness and average yield. A strong positive correlation was obtained between the two parameters. Jain also pointed out that the slow rate of progress under natural selection and suggested that artificial selection in the F10 or F15 might be more effective.

Frey (1967) grew composite a population of 250 oat crosses up to F7 without applying selection. Mass selection for larger seed width was carried out on another sample from the F3 to F7. Yield trials of F7 derived lines and the generation by generation study of average seed weight and other characters were conducted on unselected and mass selected populations. The mean yield of the F7 mass selected population was nine percent higher than the control. This was apparently due to effective directional selection for seed width and its positive correlation with seed weight. A strong stabilizing selection for seed width occurred in populations under natural selection, mainly due to selection against heavier seeds. The results on grain yield showed that 37% of lines from the unselected population and 60% of lines from the mass selected population gave higher yields than the highest yielding standard variety. The seven highest yielding lines were derived from the mass selected population.

Frey suggested that the rapid elimination of inferior types by mass selection could have raised the proportion of better lines and increased the chance of obtaining superior lines from limited samples, rather than such lines being products of recombinations within the generations studied. In the unselected population reduction in the frequencies of low seed weight classes did not occur to a significant degree within the generations studied. Whatever the causes, the composite population of oats seem to have given superior lines in fewer generations than the composite populations of barley reviewed previously. In a mass selection study on a sample of CC II population of barley (Suneson and Stevens 1953), selection was effective in increasing the average seed weight. It was implied however, that the mass selected population and the unselected population were similar for yield.

Frey's study is important in that the experiment was well conducted and provided estimates of the rates and nature of changes in the unselected and mass selected populations. For mass selection to be effective the trait under selection should have high heritability and be positively correlated with agronomically important characters. In another study with oat composite bulk (Romero and Frey, 1966) mass selection for shorter plant height was effective and increased yield was obtained.

(b) Changes in genotypic frequencies.

Survival of certain morphological characters in the composite bulks have been studied in detail in CC I, CC II (Suneson and Stevens 1953; Bal *et al*. 1959), and CC V (Jain and Allard, 1960). CC I was grown at ten locations in the U.S.A. for up to 12 years. It was constituted from crosses between the same eleven varieties which were used by Harlan and Martini (1938) in their classic study with mixtures. Annual census of random samples from each location provided estimates for differential survival of genotypes with specific characters. Deficiens, and hooded characters were eliminated at all locations. Two-row types decreased in some locations while in the others it increased. Frequency of smooth awn increased or remained unchanged except in two locations where it showed a slight decrease. Frequency of black seed either decreased or remained unchanged. In another study the decline in frequencies leading to almost extinction of two-rowed, black-seeded, hooded and smooth-awned genotypes were observed in CC II which were grown up to F30 at Davis, California (Suneson and Stevens, 1953; Bal *et al*. 1959). Similar study on CC V (Jain and Allard 1960) showed that black seed and brittle rachis genotypes were almost completely eliminated after about 15 generations of propagation. Increased or unchanged frequencies were observed for [redacted] blue seed, rough awn, long hair, and long awn.

It seems that, though characters like hooded, deficiens and black seed, etc., had definitely low survival value, survival of other characters depended on the overall selection pressure as determined by the environment, and the genetic constitution of the individual plant and the population. Suneson and Stevens, (1953) remarked that the change in frequencies of characters might have been due more to the value of the genotype as a whole rather than the selection pressure on the character itself. Causes for differential survival of some characters [redacted] has been advanced, [redacted] sterility associated with smooth awn, difference in seedling emergence between black seed and normal coloured seeds, etc. (Jain 1961a). Jain concluded that natural selection can improve adaptability by taking various alternative pathways depending on the components of fitness involved in the process.

The studies of Allard and Jain (1962) and Jain (1961a, 1961b) provided estimates of the means and phenotypic variances for heading time, plant height, spike length, spike density, and seed size for different generations of CC V. The results can be summarized as follows:

(1) Spike density was the only character without change in its mean. For other characters the mean shifted as plants with shorter stature, shorter spike, earlier heading, and large seed size increased in frequency.

(2) The variance of all characters decreased as the generations advanced. However, the amount of within family variance for plant height and heading date in F19 was greater than in parental groups. It is hard to tell from the magnitudes of the variance estimates as to whether further changes are likely. Heterozygote advantage was suggested to be the most likely cause for the persistence of variability. Study of frequency distributions suggested that both directional and stabilizing selection operated.

An extensive study of the association of ~~the~~ characters and genetic shift have been done by Bal et al. (1959) on F30 bulk samples of CC II which were maintained at three selection levels between F11 to F19 (Suneson and Stevens, 1953). One sample was unselected, while divergent mass selection for large and small seed size were carried out in two other samples. From F20 onwards mass selection was discontinued. Comparative data for association of 21 different characters for the three populations showed that directional selection for seed size had influenced certain associations while others were unaffected. The estimate of total trait associations between seed weight and the characters was about 10 per cent. Most of the associations were not present in the parents, which suggested that they were the products of natural selection. It was concluded that the genetic contribution from the adapted parents were greater than from non-adapted parents. Some of the characters scored/ [redacted] (auricle colour, lemma colour), [redacted], probably did not have much adaptive value.

A more meaningful study of association of characters has been done by Allard and Jain (1962) on CC V population of barley in which association of metric characters like plant height and heading date with fitness were studied. A two-way frequency table was derived for F19 progenies which showed that genotypes with low fitness occurred in all class values of the other character (i.e. plant height or heading date) but the most fit genotypes were usually intermediate. In another study (Jain and Marshall, 1967) with CC XXI population, an association of intermediate seed size with high fitness was observed.

In artificial selection programmes desirable associations can be selected more intensely and effectively, i.e. association of high yield with dwarf stature (Briggle and Vogel, 1968)/ or early maturity (Frey, 1954); provided adequate genetic variability exists and fitness is not reduced below threshold value due to correlated changes.

4. NATURAL SELECTION IN VARIETAL MIXTURES.

The literature on mixtures in cereals is [redacted] extensive and some of it is helpful in understanding the dynamics of heterogenous populations. Experiments have been conducted (a) To study changes in frequency of genotypes in the mixtures under natural selection, (b) To study competition between genotypes, (c) To investigate the productivity and stability of mixtures as compared to the individual components grown in monoculture. Only the first two objectives [redacted] will be considered. It should be noted that the objectives are not mutually exclusive but differ only in the experimental design and degree of emphasis.

The effectiveness of natural selection in changing the genotypic frequencies has been demonstrated by Harlan and Martini (1938) in their experiment with mixtures of barley. A mixture of equal proportion of seed of eleven barley varieties was constituted and grown at ten widely separated stations in U.S.A. The mixtures were grown for periods ranging from four to twelve years and the population census made annually from samples of seed obtained from each location. The relevant conclusions were as following:

(1) Within a few years of natural selection some varieties were rapidly eliminated from each location or present in very low frequencies.

(2) In a few years one variety dominated the mixture at each location. This leading variety differed among [redacted] the locations.

Two cases were pointed out in which the varieties that dominated in the mixtures were not the ones which were grown in that area. Apparently in other stations the locally adapted types survived and increased.

(3) Some varieties had the ability to persist, in relatively greater proportion or even dominate in more than one location. Others, though dominant in one location, were virtually eliminated from the rest.

This study showed that the survival of particular genotypes in the population was dependent on the environment. It also showed that genotypes might differ in their ability to survive in more than one environment. Theoretical curves for rate of increase or decrease of contrasting types were derived which agreed remarkably with observed frequencies. In general, the rate of increase or decrease in frequency was rapid for the first few years. Many poor competitors persisted in the mixtures in low frequencies till the end of the experiment.

Laude and Swanson (1942) studied 1:1 mixtures of wheat, using the variety Kanred, with each of other two varieties, grown at two stations for nine years. By the end of the experiment Kanred had replaced the other variety at both stations. Kanred was also apparently the locally adapted high yielding variety. However, Laude and Swanson did not rule out the possibility that a more competitive, but less productive genotype might increase in the bulk population under natural selection.

Other works in barley mixtures (Suneson and Wiebe, 1942) and on wheat mixtures (Frankel, 1939; Suneson and Wiebe, 1942) have demonstrated that genotypes which survive and predominate in mixtures are not necessarily the best yielders as known from monoculture yield comparisons. This has been explained in terms of competitive advantage of one genotype over another, and the independence of competitive ability from productivity. Suneson (1949) reported extended results on the mixtures of four barley varieties previously studied by Suneson and Wiebe (1942). The four competing varieties Vaughn, Atlas, Hero, and Club Mauriout, were all adapted commercial varieties and were mixed in equal proportion at the start of the experiment. The varietal ranking on the basis of replicated trials over the years showed that Vaughn outyielded Atlas by about two bushels. Atlas and the other two varieties gave almost similar yields. Yet the final year composition of the mixture showed the proportion of Vaughn and Atlas as 0.4% and 88%, respectively. Workman and Allard (1964) also studied the result of this experiment and concluded that the poorest competitor left 23% fewer progeny on the average than the best competitor. Suneson (1949) had noticed that competitive ability was also apparently independent of desirable characters like disease resistance because Vaughn was known to be ~~fully or relatively~~ more resistant than Atlas to three major leaf diseases of barley. Also in a study with CC II (Suneson and Stevens, 1953) scald resistance was found to be neutral in survival value. However it seems that in severe epidemics, survival of resistant genotypes is paramount as observed on the same population in the succeeding year (Suneson, 1956);

and in wheat mixtures earlier (Klages, 1936). In general, what constitutes competitive ability is highly conjectural and often unexplained (Edward and Allard, 1963; Sakai, 1965). Its complexities in crops and pasture plants have been reviewed by Donald (1963).

It should not be concluded from the results on varietal mixtures, however, that one highly competitive genotype is likely to replace all other genotypes in the heterogenous population after long term natural selection. In these experiments competition was between a few pure lines and thus differed from a natural population or composite bulks. For the same reason, origin of new recombinants due to occassional outcrossing was low, and would have further declined as the population became homogenous rapidly. In some studies the few inter-line hybrids that were formed were apparently removed from the populations (Allard *et*. *al*. 1968). Contrasted to this, Allard et al. described a study on mixture of two pure lines of lima bean in which the out-crossing rate (5%) was higher than the normal rate in wheat or barley; and no attempt was made to maintain the purity of the competing genotypes of the initial mixture. The parents differed for a number of morphological characters. In five to six generations the population comprised of swarms of hybrid forms showing various recombinations of morpholigical traits and quantitative characters. The dynamics of such a population system has already been reviewed.

5. NATURAL SELECTION IN EARLY GENERATION BULK HYBRID POPULATIONS.

The bulk method of breeding self-pollinated crops relies on natural selection to sort out productive adapted types by F6-F7 after which single plant selection is made. In practice, various modifications are also adopted (Allard, 1960). Most of the experiments on simple bulk hybrid populations are conducted to study the combining ability of the parents and the efficiency of the early generation testing [redacted]./ (Harlan et.al., 1940; Immer, 1941; Atkins and Murphy, 1949; Atkins, 1953 etc.). Since the populations were not usually grown for more than 6-7 generations, and also due to different emphasis in experimental set-up, the influence of natural selection in improving the population for yield is hard to ascertain. The shift in mean observed in the first few generations could have been due to changes in dominance and epistasis effects (Grafius et/al. 1952), as well as due to the elimination of inferior types (Frey, 1967).

The work of Adair and Jone (1946) on rice and Taylor and Atkins (1954) on barley populations were specifically planned to demonstrate the influence of natural selection. Adair and Jones divided 20 crosses between 11 rice varieties into three categories (based on grain size) and bulked F2 seeds for each category. Each population was grown in three diverse locations in U.S.A. After eight years of natural selection random samples were studied at one location and it was found that the three environments had moulded the association of characters in the population differently. Directional selection operated for [redacted] heading date and height towards the respective 'optimum' while others remained unchanged. The populations were highly variable for all the characters in all the environments. Yield was not measured.

Taylor and Atkins (1954) grew twenty hybrid populations of barley in four diverse locations in Iowa, from F2 to F4. Yield, maturity, and some other characters were measured. It was conlcuded that the influence of natural selection on yield and maturity was significant and that it varied between locations. However, the experiment seems to have been terminated too early to get any critical measure of changes brought by natural selection, especially on a character like yield.

The influence of natural selection within a few generations has been well domonstrated for characters like heading date and growth habit etc., in barley (Yasuda, 1961, 1963) and rice (Akemine and Kikuchi 1958). Two crosses of barley were grown from F2 to F5 (Yasuda, 1961) at different latitudes in Japan. Selections of plants of various maturity were made at F6 and studied at one station (Yasuda, 1963). Heading dates in the field were recorded. Detailed physiological studies on attributes like winter and spring growth habit, photoperiod response (response of vernalized plants to short day) and 'earliness in narrow sense' (response of vernalized plants to long day) were also conducted in a controlled environment. It was found that late heading types had been selected at the Northernmost location. These were also sensitive to short day length and were of winter growth habit. In the Southernmost location, early to medium early genotypes with spring growth habit dominated. In the Central locations various types survived and the extreme forms were relatively rare. The experiment of Akemine and Kikuchi (1958) on bulk hybrid populations of rice also demonstrated the influence of latitude on heading date. In this case populations from Northern locations were earlier heading while the reverse tendency was observed for populations from Southern locations. The amount of variation also differed with location.

C. BREEDING FOR YIELD AND ADAPTATION

1. IMPROVEMENT OF YIELD.

Frankel (1947) summarized the philosophy of improvement of yield by pointing out that the yield increase could be achieved by either overcoming the limiting factors that affect the genotype or by breeding genotypes with greater yield potential through incorporation of 'productivity genes'. The yield potential of the genotype can be defined as the yield that would be obtained in the absence of limiting factors like disease, etc., and in optimum crop husbandry i.e. adequate moisture, fertility, etc. As long as such potential is not attained due to limiting factors like disease, shattering, lodging, etc., improvement can be achieved by resistance breeding. In the sub-optimum conditions, improvement of external environment or breeding for tolerance to drought etc., would also assist in the better expression of yield potential.

What constitutes 'productivity genes' is not clear ~~out~~ and should not be taken literally. In the literature the influence of productivity genes or yield genes seems to have been implied when high yield is obtained due to success in selection of superior genotypes apparently not associated with resistance breeding (Palmer, 1952, 1953; Whitehouse, 1953).

Donald (1962) posed a question: "Is it possible to breed for increased yield in a positive way - in the sense that the breeders know what plant characters will give increased capacity to exploit the positive components of the environment?" Donald (1968) reviewed a number of works and discussed the attributes of conceptual models of cereal plants in general and of wheat in particular. Such a model was named as an ideotype. Donald suggested that selection of ideotypes might lead to a rapid yield improvement to a much higher level. Theoretically, selection of a plant model aims for the development of a plant with maximum yield potential. The full expression of yield potential of ideotypes will require the environmental conditions for which they are 'tailored'. The development of the ideotype depends on the relevance of various assumptions and successful integration of results that seem to have been obtained in separate studies (Rev. Donald, 1968). Though improvement of yield by this plant model approach might be considered [redacted] one research field to be explored as stressed by Donald and may result in superior genotypes for specific environments, improvement of genotypes for field conditions with the variable environment may yet depend on the so called 'empirical approach' of plant breeding.

The empirical approach centres around studies of values of crosses, efficiency of selection techniques, experimental designs and statistical analysis, ~~etc~~., (Frankel 1947, Bell, 1963).

Selection of genotypes with higher yield potential is difficult because yield is a complex quantitative character governed by polygenes and thus much affected by environment (Mather, 1943; Palmer, 1952). This makes partitioning of genetic and environmental variance from the total variance formidable indeed especially in the earlier phases of selection.

It has been suggested that study of inter-relationship of components might be helpful and even necessary for improvement of yield (Engldow and Wadham, 1923; Frankel, 1947; Grafius, 1956). In cereals like wheat and barley the basic components of yield [redacted] are number of spikes/unit area, number of grains/spike, and average grain weight. Grafius (1956), in a geometrical interpretation, considered yield as a volume with the three principal components as the edges of the enclosed space. This permitted him to derive a number of theorems which he checked against data from barley experiments in the field. It followed that yield could be increased by improving the level of any one component provided the level of expression of the other components remained the same or did not decrease proportionately.

Explanations for heterosis were also forwarded on the basis of component analysis (Grafius, 1956; Williams & Gilbert (1960) and it was proposed that genes for the individual components exist but not for yield itself. Hayman (1960) and Moll et al. (1962) pointed out the complex nature of yield, and the inadequacies of component analysis for either the selection of yield or the explanation of heterosis.

Boice *et al.* (1947) in wheat found with wheat that the efficiency of selection for higher yield was not increased by using yield components instead of yield. Similar conclusions were also arrived at by Nanda (1949) in wheat and Abraham *et. al.* (1954) in rice, in spite of the use of a selection index, that would have involved more detailed attention. (However, the use of a selection index was found to be worthwhile by Robinson et. al. (1951) in corn; Manning (1955) in cotton; and Shanker *et al.* (1963) in pearl millet.) It is interesting to note that all those crops were either cross-pollinating species or mostly cross-pollinating type (e.g. cotton)). Leng (1963) after reevaluation of data of a number of corn inbreds and their hybrids found that widely different combinations of components could lead to approximately the same yield levels. Adams (1963) suggested that compensatory variation amongst components could be explained in terms of developmental plasticity due to intra plant competition and environmental fluctuations. In recent years studies of a large number of wheat crosses have been reported in the literature as a part of hybrid wheat research and all invariably including a detailed component analysis. Apart from providing information as to how yield differed in terms of component interactions for each combination, such analysis did not have much predictive value (Shebeski, 1966). Scorings were mostly done on spaced plants and this further undermined the value of such studies in terms of wider application, as the influence of density on the expression of yield and yield components have been found to be very significant (Leng, 1963; Briggle *et al.*, 1967).

It is concluded that the relationship of yield with the components of yield and their interaction with environment is too complex to generalise as various compensatory mechanisms exist. It can be expected that when a large number of genotypes are tested for yield in one environment, or the same genotype in several environments, the yield measured will be the product of the variable yield components. Finlay (1966) suggested that only yield itself can be the best measure of ? yield. It is likely that in some instances increases in yield above the plateau level might be facilitated by component analysis (Johnson *et/ al*. 1966). If the need to use diverse genetic material is recognized and a large number of crosses studied, quick evaluation of yield and adaptability seem to be the practical alternative.

2. THE GENOTYPE - ENVIRONMENT INTERACTION.

Ranking of the varieties on the basis of a yield test at one location is likely to be different or even a reverse of that of another location. The same is true of ranking for inter annual performance at one location (Immer *et/ al*. 1954; Salmon, 1951). The magnitude of such interactions will of course depend on the extent of differences between the locations and/or the nature of seasonal fluctuations. The camouflaging effect of genotype-environment interaction makes evaluation of selections a formidable task indeed (Comstock and Moll, 1963; Sprague, 1965).

Allard and Bradshaw (1964) recognized two major sources of environmental variation/: (1) predictable and (2) unpredictable. The features of the soil, management practices, and long term seasonal changes [redacted]., were considered [redacted] predictable [redacted] as contrasted to annual rainfall which can be highly unpredictable. Allard and Bradshaw emphasized the complexities and the range of interactions that are likely to occur even between a few genotypes and a few environments. It was calculated that with ten genotypes and ten environments and a single criteria of classification, viz. yield 10^{145} interactions were possible which was larger than the total number of plants that would have ever existed.(on the earth.) Only a few major forms of interactions are of practical importance to the breeder.

In trying to cope with the problem of genotype-environment interaction two approaches are possible (Frankel, 1958):

(1) To subdivide the region on the basis of predictable environmental variation and breed varieties adapted to each specified zone. It requires a large scale breeding programme and may be an impractical proposition for the improvement of field crops.

(2) To select a genotype or constitute a population (mixture or segregating bulk population) that shows minimum genotype-environment interaction.

3. THE MEASURE OF GENOTYPE-ENVIRONMENT INTERACTION AND ADAPTATION.

(a) By the analysis of variance procedure.

Immer *et. al.* (1934) described a method of estimating varietal adaptation by the [redacted] analysis of variance procedure. Yield data were obtained for ten barley varieties grown at six locations for two years. The information sought was as follows:

(1) Whether varieties differed for yielding ability.

(2) Did varieties respond differently in different locations? i.e. an estimate of variety - location interaction, 6^2VL.

(3) Did varieties respond differently in different years? i.e. an estimate of variety - year interaction, 6^2VY.

(4) Whether relative performance of varieties was the same at all stations for both years i.e. an estimate of second order interaction, 6^2VLY.

(5) Measure of differential response of each variety over years and locations i.e. of stability or adaptability.

The objective outlined by Immer et. al. is typical of the kind of information that one would seek in the evaluation of varieties or selections. Partitioning of the different components of the total variation is done by the analysis of variance procedure and appropriate tests of significance conducted, as illustrated by Immer et. al. (1934), and several other workers in recent years (Salmon, 1951; Horner and Frey, 1957; Sandison and Bartlett, 1958; Rasmusson and Lambert, 1961; Schutz et. al. 1967).

The study of Horner and Frey (1957) on results from oat trials showed that 6^2VL decreased as the locations involved became more uniform as expected. It was also found that one location consistently had a large contribution to 6^2VL, the cause of which was not known. Rasmusson and Lambert (1961) analysed results of six varieties of barley grown at eight locations for two years. Partitioning of the variance components showed that 6^2VY, was much larger than 6^2VL, 6^2VYL was about three times larger than 6^2VY and seventy times larger than 6^2VL. The magnitude of 6^2VYL implied important differential response to environment that was not accounted for by either year or location groupings. Schutz et/al. (1967) in [redacted] soybean trials/ conducted at a number of locations in various regions in the U.S.A./ found 6^2VL large enough to suggest that locations could be effectively substituted for years, thus shortening the period of evaluation.

It seems from these results that the magnitude of various interaction components reflected the differences between years or locations or the genotypes sampled for the particular experiment concerned. The genotypes were few and most were adapted varieties. Estimates of interaction variances would have been even greater if a large number of diverse genotypes had been tested. It can be generalised that 6^2VYL is likely to be much greater if diverse locations and fluctuating years are sampled. Partitioning of the variance components, though valuable in general, does not provide an estimate of the relative performance of an individual entry. Immer et/ al. (1934) and Salmon (1951) outlined computational procedure to estimate differential response for each variety. Appropriate calculations of cross differences between various means for each variety, or calculation for each combination of a pair of varieties and statistical test formed the basis of comparison.

A technique to measure stability was described by Plaisted and

Peterson (1959) to analyse a potato varietal trial conducted at several locations within one year. A combined analysis of variance over all locations was computed for each pair of varieties, /n(n-1)/2 pairs for n varieties. This gave an estimate of 6^2VL for each pair. Each variety occurred in n-1 analyses, and an arithmetic mean of the 6^2VL estimate was obtained for each variety. Relatively smaller estimate for mean 6^2VL was taken as measure of greater stability. The reliability of this technique was said to be dependent on the inclusion of control varieties with known performance. Selection of reliable control varieties can itself be difficult, though in this particular experiment this apparently was no problem.

Allard (1961) measured stability and productivity of 10 limabean populations in 16 environments. Stability was evaluated in terms of [redacted] consistency in ranks [redacted] and [redacted] relative magnitude of variances. Rasmusson (1968) also described a somewhat similar procedure for the measure of stability in a few barley populations. Other workers (Frey, 1964; Frey and Maldonado, 1967; Rowe and Andrew, 1964) have partitioned genotype-environments interactions to get an average estimate of stability for various treatments and some comparisons obtained. Low genotype-environment interaction suggested relatively increased stability.

The techniques used by various workers cited above [redacted] provided some measure of relative performance of individual entries.

However, the amount of computation and complexities involved in interpretation make these methods unpractical for the evaluation of more than a few genotypes. Allard and Bradshaw (1964) remarked:

"The development of efficient methods for testing genetically variable populations under a range of environmental conditions represents a problem of great enough importance to justify careful thought and experimentation".

(b) By the analysis of adaptation-regression technique.

The work of Yates and Cochran (1938) will be reviewed as a background to the method of adaptation analysis proposed by Finlay and Wilkinson (1963). Yates and Cochran did a combined analysis of yield results from barley trials of Immer *et al.* (1934) conducted over six locations for two years. Yield results from only five varieties were analysed. The sums of squares in the analysis of variance due to various sources were partitioned further into two groups, i.e. attributable to (a) variety Trebi and (b) the remainder. It was shown that the differential response of Trebi [redacted] contributed most to [redacted] the variety-places interaction. The Variety-places interaction was further partitioned into linear regression and deviations from regression for Trebi and the remaining varieties. Most of the total linear component could be attributed to linear response of Trebi. Regression of mean yield of each variety on the mean yield of all the varieties at each location was calculated and presented graphically to show the differences in varietal performance at various locations. The deviations of Trebi from its regression were greater than that of the other varieties. It was pointed out that "......if the variability of each variety at each centre is the same, apart from the components of the variability accounted for by the regressions, the regressions so obtained will give a correct impression of the results". Obviously the authors were more interested in theoretical requirements for a valid statistical test as they went on to discuss means of inducing homogeneity of error of an analysis using weighted means only to conclude ".....the available rigorous methods of weighting are not of much use in the reduction of the (experimental) results of the type ordinarily met with."

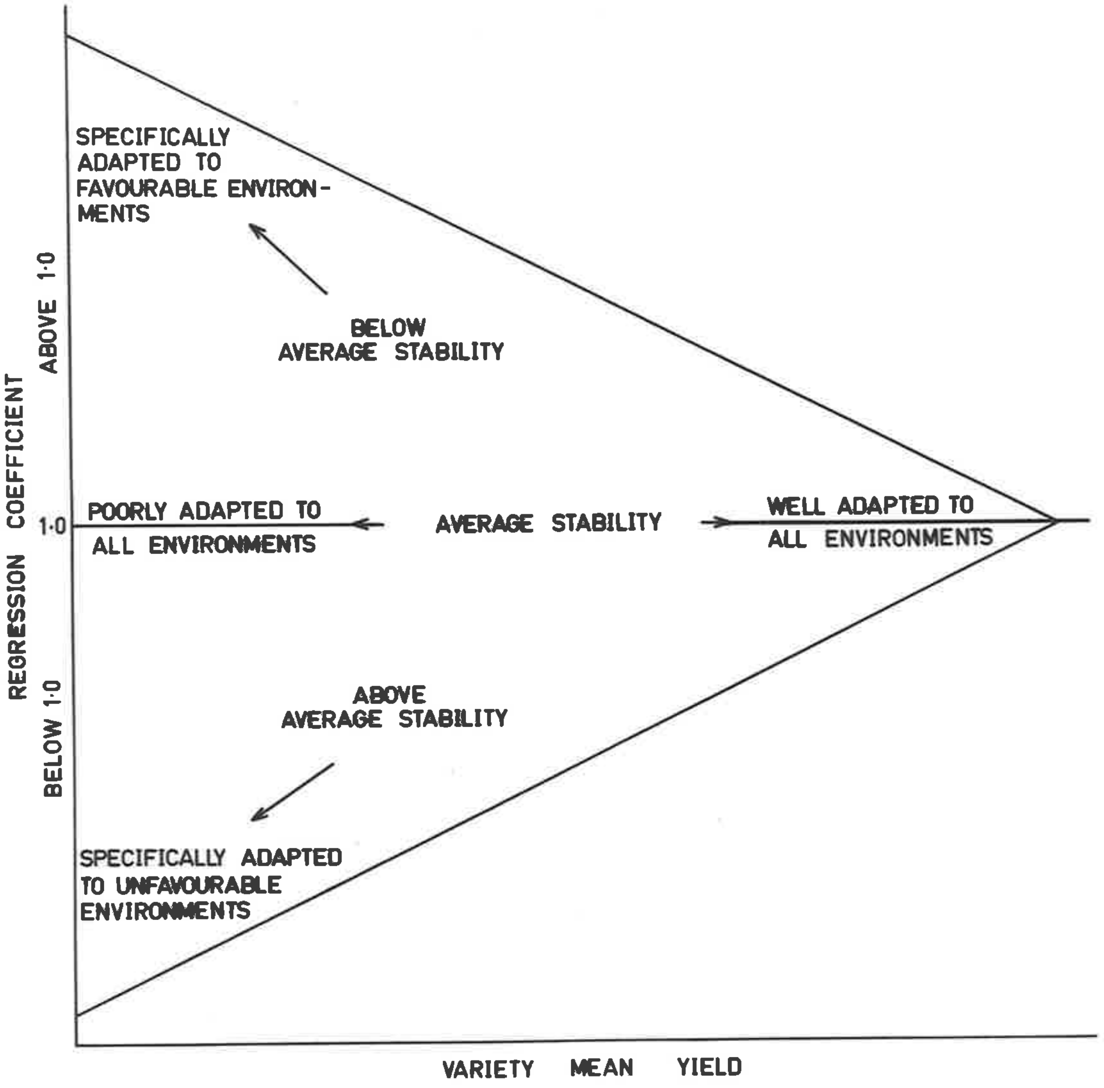
Finlay and Wilkinson (1963) proposed a method for the analysis of adaptation of a large number of genotypes grown in a range of field environments. The regression technique was used for the analysis of the results. However, the concept has been advanced a great deal further than that of Yates and Cochran. Finlay and Wilkinson have described the interpretation of the results in terms of adaptation responses. The adaptation analysis has been used in the study of results from the present experiment and hence will be reviewed in detail.

The study of Finlay and Wilkinson involved the measure of adaptation of 277 barley varieties (a [redacted] sample from a world collection) to a range of South Australian environments, as represented by three sites and from one to three years of trial. A total of seven environments was sampled. The average yield of all the entries at each site in each season was used as measure of the environment. This parameter was called the 'site mean'. A low site mean indicated a poor yielding environment and a high site mean a better yielding environment. Thus a meaningful measure of environment was obtained without measuring the various climatic and edaphic factors and their interactions that constitute the environment. The analysis was carried out on logarithmic transformed values as this induced a high degree of linearity in the regressions of individual yields on site mean. For each entry a linear regression of yield on the respective site mean was computed and used as a measure of varietal adaptation. Mean yield over all sites and seasons (variety mean) was also calculated for each entry. It was shown that the two indices i.e. the regression coefficient 'b', and variety mean together provided a measure of adaptation response of the genotype. These two indices when graphed gave a two dimensional scatter diagram that could be interpreted simply. All the entries in the trial could be compared in the one diagram.

Figure 1 is reproduced from Finlay and Wilkinson's paper and forms the basis for the interpretation of the scatter diagram obtained from the adaptation analysis. The figure is self-explanatory. Finlay and Wilkinson pointed out four major types of adaptation responses as typified by four of the varieties. The following adaptation responses were differentiated; (the variety mean yield in the example is Log 10 gm~~s~~/plot.

(1) General adaptation or adaptability - The genotype would give above average yield in all environments. Such a genotype would have a regression coefficient near to 1.0 and high mean yield. Example: variety Atlas (b = 0.90; var. mean yield = 2.57).

Fig. 1. A generalized interpretation for the adaptation response of a large number of genotypes grown over a range of environments (reproduced from Finlay and Wilkinson 1963, Aust. J. Agric. Res. 14 : p. 748.


REGRESSION COEFFICIENT
ABOVE 1·0
1·0
BELOW 1·0
SPECIFICALLY ADAPTED TO FAVOURABLE ENVIRONMENTS
BELOW AVERAGE STABILITY
POORLY ADAPTED TO ALL ENVIRONMENTS
AVERAGE STABILITY
WELL ADAPTED TO ALL ENVIRONMENTS
ABOVE AVERAGE STABILITY
SPECIFICALLY ADAPTED TO UNFAVOURABLE ENVIRONMENTS
VARIETY MEAN YIELD

(2) Poorly adapted to all environments - Below average yield in all environments. Typified by a regression coefficient near to 1.0 and low mean yield. Example: variety BR 1239. (b = 1.05; var. mean yield 1.85).

(3) Specific adaptation to good environment - Such genotype would have a high yield potential that would be expressed as the environment improved but would suffer greatly in poor environments, i.e. highly sensitive to change in environment. The consequence of this would be a regression coefficient value much greater than 1.0 and a low mean yield. Example: var. Provost (b = 2.13; var. mean yield = 2.05).

(4) Specific adaptation to poor environment - The genotype would give above average yield in a poor environment but would not have an improved yield as the environment bec~~o~~ame favourable, i.e. incapable of responding to a favourable environment. This would result in regression coefficient value considerably below 1.0. Example: var. Bankuti Korai (b = 0.14;var. mean yield = 2.07).

The regression coefficients were suggested to be a good measure of phenotypic stability. Regression coefficient = 1.0 was defined as average stability. The population would have average stability as the average of all the genotypes are plotted against the same value. Thus stability of each genotype could be compared to the population stability. Atlas and BR 1239 showed average stability as b was close to 1.0. Value of b > 1.0 indicated below average stability (Provost); and b< 1.0 indicated above average stability. Absolute stability was defined as b = 0. Bankuti Korai was close to showing absolute stability (b = 0.14).

A number of workers have used adaptation analysis in the study of their results since Finlay and Wilkinson proposed the method. Apart from other experiments on barley (Finlay, 1963b; St. Pierre *et at.*, 1967; Rasmusson, 1968); [redacted] various crops have been studied, e.g. wheat, Johnson *et al.* 1968; Redden, 1968; Jordaan and Laubscher, 1968; Qualset, 1968); maize, (Eberhart and Russell, 1966; Scott, 1967); millet (Atwal and Singh, 1966) and [redacted] Lolium (Breese, 1969). It should be noted that except for Finlay's or Finlay and Wilkinson's; published results on adaptation analysis by other workers are on a natural scale. Of these, the work of Eberhart and Russell (1966) needs to be reviewed.

Eberhart and Russell analysed the results of a maize trial by a method basically the same as that proposed by Finlay and Wilkinson. However they also included deviation from regression as one of the stability parameters. Procedures for the testing of various statistical significances were also outlined. The genotypes in the experiment were a few inbred lines and their diallel crosses ~~etc~~. Mean yield, regression coefficient, and deviation from regression ~~together~~ were used as ~~a~~ measures of adaptation of each entry. The result showed that the regression component of the genotype-environment interaction variance was not very large. The importance of deviation from regression as a stability parameter in such circumstances was emphasized. The small estimate for the linear component of genotype-environment interaction could have been due to similarity of the environments in which the genotypes were tested or due to relatively similar responses of all genotypes or to a combination of both of these factors.

Eberhart and Russell defined a stable variety as one with b = 1.0 and deviation from regression = 0. Breese (1969) suggested deviation from regression alone as a more satisfactory measure of stability. Rowe and Andrew (1964) in their analysis of results from a miaze trial calculated the deviation from the regression for each treatment (various levels of genetic diversity) and used it as a measure of stability.

Relatively lesser magnitude of deviation from regression mean square, was taken as a measure of increased stability.

Measurement of stability by various parameters by different authors has rendered the term 'stability' rather confusing e.g. [redacted] should this be indicated by the regression coefficient or the deviation from the regression, or a combination of both? The various concepts of stability will be discussed later [redacted] in this thesis.

The method of analysis of adaptation as propos[redacted]ed by Finlay and Wilkinson has created considerable interest among workers in several countries as evidenced by the published works. It has been suggested that this method might be used to evaluate the genotypes collected as a part of the International Biological Programme (IBP News, 1967).

4. BREEDING FOR ADAPTABILITY.

Breeding for general adaptation or adaptability should have been considered as a part of review on breeding for increased yield but was postponed until the implications of genotype-environment interactions and its measures were explored. Any attempt to differentiate between breeding for yield and adaptability would be rather abstract in the sense that the latter also deals with the expression of yield. Adaptability implies a consistently high yield in a range of environments.

The first step towards breeding for adaptability is to produce genotypes that are resistant to the limiting factors which are likely to occur in the locations and the seasons to be sampled over the years.

Some of the attributes for high yield and wide adaptation of

Mexican wheat varieties as shown from the results of trials in several countries, (Krull et al., 1967, 1968a, 1968b) were day length insensitivity, non-lodging under high fertility due to dwarf stature, had greater straw strength, and also resistance to certain diseases.

Krull et al. suggested, on the basis of [redacted] their results, that Mexican varieties had greater potential for yield and adaptability than could be explained just in terms of the particular factors mentioned above. According to Borlaug (1968) the Norin 10 x Brevor lines which were used in incorporating the dwarfing genes in the Mexican wheat varieties also introduced [redacted] genes that increased the number of fertile florets per spikelet and the number of tillers per plant.

It is reasonable to expect that genotypes would differ in 'adaptability potential' just as they would differ in yield potential.

The superiority of Mexican wheat varieties for yield and adaptability can be appreciated by considering the results of a few trials in detail. Krull et al. (1968b) reported results of the Second International Spring Wheat Yield Nursery in which 25 varieties, including the best commercial varieties from several countries, were grown at 50 locations in 28 countries. The environments sampled varied in elevation (739 ft below sea level to 7,560 ft above sea level), latitudes (35°S to 61°N), management practices (irrigated and dry land; fertilized and unfertilized) [redacted]. The five varieties with the highest average yield over all locations were the Mexican varieties. This was also evident from one of the earlier trials (Borlaug et al. 1964); the results of which were also analysed by Finlay (1968). The scatter diagram (Finlay, 1968) showed that the five varieties with the highest mean yield and above average stability ($b<1.0$) were all Mexican varieties.

The adaptation studies in barley (Finlay, 1963b, Finlay and Wilkinson, 1963) and results from various wheat trials (reviewed above) have suggested that it is possible to breed genotypes with high yield and wide adaptation. This has added a new dimension to breeding objectives in recent years.

Breeding for higher yield and adaptability involves constituting variability that would provide recombinants with increased yield potential and consistent performance. Identification of such recombinants would obviously involve screening the genotypes against diverse environments and effective selection.

The outcome of superior varieties from the Mexican wheat breeding programme can probably be attributed to the large number of crosses studied as well as the selection method used. In this programme Borlaug and his co-workers studied more than 30,000 wheat crosses through more than 40 generations (Borlaug 1965). Borlaug grew two generations of material each year to accelerate the breeding programme. One generation was grown in a winter nursery at sea level in the North West of Mexico at latitude 27°N, and the other in a summer nursery at 8500ft altitude near Mexico City at latitude 18°N. Some selections were even grown at 9,500ft in Colombia at latitude 4°N. Only the best lines at each location were retained for final selection.

Finlay (1968) pointed out that though such a selection procedure resulted in widely adapted varieties of high yield potential it may also have resulted in the elimination of unstable genotypes. Finlay emphasized the need to retain some of the unstable genotypes with high yield potential. Finlay suggested that yield and adaptability could be improved by crossing generally adapted genotypes with these unstable genotypes. Such objectives have been successfully carried out in barley breeding programmes at the Waite Institute (Sparrow, personal communication).

Growing the experimental material in a range of environments and the adaptation analysis as described by Finlay and Wilkinson (1963) for barley improvement is another way (as contrasted to Borlaug's method) of selecting high yielding genotypes with wide adaptation. The advantage of this method is that it identifies the adaptation response of all the genotypes; selections can be made for use either directly as a variety, or as a parent for further improvement of yield and adaptability.

Finlay (1963b) reported results from a barley experiment involving combining ability analysis for mean yield and stability of yield. The value of the adaptation analysis for such study was pointed out. The analysis was applied to the results of yield values obtained from F2 diallel experiment grown for three years at one site. The annual rainfall in the growing season ranged from 6.67 [redacted] to 15.44 inches. The results indicated that varieties differed in their ability to impart mean yield and stability of yield to their progenies, and that the genetic variation for these characters [redacted] was largely additive. Evidence for independence of high mean yield and stability of yield was obtained and the better parents identified. Finlay (1968) conducted an adaptation analysis on the yield data from a set of diallel crosses of maize from Welhausen's experiments. The yield data were from trials conducted at several locations in Central and South America. The combining ability analysis on the mean yields and b values from an adaptation analysis showed that varieties differed in their ability to impart stability to their progeny.

No attempt was made here to review the works which aim to increase stability by constituting a heterogeneous population involving homozygous lines or varieties or hybrid populations.

(D) CONCLUDING REMARKS.

Relevant works were reviewed to show the influence of natural selection on heterogeneous populations of self fertilized species and to include some of the work on the improvement of yield and adaptation.

Allard and his coworkers concluded that the mechanism for release and maintenance of variability exists in [redacted] population like the composite bulks– a prerequisite for evolutionary change in the population. The [redacted] conclusions were [redacted] based on theoretical and some field studies which provided an estimate of [redacted] variability in the population. While genetic models are valuable tools and can provide working hypothes~~i~~es, prediction of yield improvement in heterogenous populations in fluctuating environments on the basis of models and computer simulated experiments should be regarded with some caution.

The relationship of characters/ for which estimates of variability were obtained/ with yield is not thoroughly understood. However, it seemed to have been implied that the presence of variability in those characters would also indicate variability for yield potential.

The yield improvement in the composite-cross population is mainly confined to the results from a few composite bulks over several generations and the yield performance of selections from one composite cross population. Suneson reported that few high yielding lines were obtained from advanced generations of CCII. Results on the actual frequencies for yields and adaptations of selections from various generations are, however, lacking. It is also desirable to study the association of the more important agronomic characters with such performance.

Since composite-cross populations are expected to improve by natural selection as well as retain genetic variability, measurement of the genotypic value of the constituents of population in terms of yield and adaptation seems more critical. Such a study needs a suitable technique for the measurement of adaptation of a large number of genotypes in the field environment. The analysis of adaptation technique as proposed by Finlay and Wilkinson has recently filled this gap.

EXPERIMENTAL MATERIAL AND PROCEDURES

A. Experimental Material.

A random bulk sample of seeds of F6, F16 and F25 generations of Composite Cross V (CC V); and F2, F9 and F9DA seeds of composite cross XVI (CCXVI) formed the experimental material. These materials were kindly supplied by Dr. C.A. Suneson of Davis, California.

CCV was developed by the late H.V. Harlan from intercrosses among 30 varieties. The resulting F1 plants were crossed in increasing numbers through four successive pairings to give a multiple hybrid stock (Suneson and Stevens, 1953). The parental list and the crossing plan is given in Appendix 1 . Crossing was started in 1937 and the first selfed generation designated as F2 was grown in 1942 at Davis (Allard and Jain, 1962). A comprehensive review of the results from this population was given in the previous chapter.

CCXVI was constituted by Suneson and Stevens in 1953, by 'recurrent random recombinations' between 165 advance generation selections from five of the earlier composite cross populations (Suneson, 1956, 1963) One sample was grown at Davis continuously. Another sample (indicated by the suffix DA to filial generation number) was grown alternately at Davis and Aberdeen, Idaho (Suneson, 1963). Suneson remarked that CCXVI has been the most productive composite cross. As far as I am aware of results of yield trials or other studies on CCXVI have not been published.

A group of 23 varieties including the two South Australian commercial varieties, Prior and Noyep, were also grown. The other varieties were selected to represent the range of adaptation responses as demonstrated in Finlay and Wilkinson's barley trials. 12 varieties were two-row types and 11 six-row. The list of the varieties is given in Appendix 2.

B. Experimental procedures.

1. Seed multiplication.

125 seeds were picked at random from each generation bulk of CCV ([redacted] F6, F16, F25) and CCXVI ([redacted] F2, F9 and F9DA) and grown in pots in the glasshouse in 1965. The plants were numbered and harvested separately. The progeny from each plant was maintained as an individual line~~s~~.

Individual progeny rows were sown in a bird-proof cage (Plate 1.) on 9th February~~,~~ 1966. Regular irrigation and preventive measures against common insects and diseases were carried out to ensure satisfactory growth.

The normal sowing time for barley in South Australia varies from May to July. It was intended to have a one-replicate trial in the same year. Thus it was necessary to break the dormancy of the freshly harvested seeds. The germinability of a number of barley varieties has been investigated at the stages of ripening characterized as 'soft dough' and 'hard dough' by Larson et~~.~~ al. (1936) and Vines (1947). More information on the germination behaviour of cereal grains at different stages of maturity, or after varying periods of after-harvest storage (Harrington and Knowles, 1940; Carpenter and Robert, 1963; Anderson, 1965) and methods of breaking dormancy (Wellington 1956, 1964) were obtained. It was concluded that harvest at the beginning of the 'hard dough' stage and heat treatment of the seeds after initial drying might lead to break in possible dormancy.

Plate 1. Seed multiplication.

A total of 612 lines were either fully ripened or had reached hard dough stage by the middle of July and were harvested. The threshed seeds were heated at a constant temperature of 40° ~~degrees~~ C for three days on an open paper pan (Wellington, 1956, 1964; Hewett, 1958).

A one-replicate trial was sown twice at the Waite Institute (sown on 5/8 and 26/8) and once in a country site as described in the next section. In retrospect it can be considered as another seed multiplication as crop stands in plots were often thin and erratic, especially at the latest sown experiment. This was possibly due to the effect of late sowing as well as variation in the degree of break in dormancy. Yield data from such plots were unreliable.

The remaining lines which could not be sown in the above trials were sown in late October for further seed multiplication (a number of lines were lost by chance during seed multiplication, especially as single plants. Ultimately each generation population had approximately 115 lines).

In 1967, 100 lines were retained at random for each generation from both composite cross populations. It was decided to conduct the trial at four locations with two replications at each. At the proposed seeding rate this required a minimum of 170 ~~grams~~ gm. of seed. 50 lines out of the 600 lines had less than 85 ~~grams~~ gm. of seed precluding even one replication. These lines were sown in seed multiplication block in early June 1967. These lines were included in the 1968 trial.

Seeds of the majority of the lines in the adaptation trial of 1967 were harvested from one site. For some lines seed had to be pooled from different sowings or sites. In the present trial, differences in yield or adaptation that could have been attributed to seed source [redacted] are considered to be hopelessly untraceable and probably insignificant. It should be noted that the 50 lines that were sown in multiplication block in 1967 were sown at the same time as the rest in the experimental block at Waite, so that all the seed sown in the 1968 trial was produced from a single sowing at Waite Institute.

2. Adaptation trial.

The trial was conducted as a two-replicate randomized complete block [redacted] experiment, grown at four locations for two years. In 1967 [redacted] [redacted] 92, 86 and 91 lines (F6, F16 and F25-derived) from CCV population; and 94, 95 and 92 lines (F2, F9 and F9DA-derived) from CCXVI populations were grown. About 8% of the total number of lines were not [redacted] replicated [redacted] due to shortage of seed. A variety was grown in place of the missing second replicates. In the 1968 trial the number of lines were 99, 100 and 100 each for populations in both composite crosses.

It should be pointed out here that two grams of seeds for each line within each generation (i.e. 100 lines) were bulked and also included in the trial. The line mixtures and the 23 varieties were grown in all the trials.

The experiment was designed as a series of sub-blocks consisting of 100 plots, with a 3ft path between sub blocks. The same experimental plan was adopted at all sites in both years, except at the Waite Institute in 1968 when it was sown in sub blocks of 150 plots.

The experimental plot was 10ft long and consisted of 3 rows, 7 inches apart, with a path of 14 inches between plots (Plate 2). Border plots were sown around the perimeter of the experimental area to minimize the border effects.

Sowing was done with the Finlay seeder. The operation of the drill and the seeding procedure etc., has been described by Finlay (1963b). Initially 21 grams of seed was diluted to a suitable constant volume by adding dead seed and drilled to a 13' plot (seed rate ≈ 1 bushel/acre). A 3' path was cleared between sub blocks within a few weeks after germination.

The trials were conducted on farmer's properties near the country townships of Callington (henceforth referred to by the property name Bundaleer), Clinton and Minlaton; and at the Waite Institute, Adelaide. These locations represent diverse regions in terms of annual precipitation, soil type ~~etc~~., and are in the South Australian cereal belt.

Some agronomic and climatological features of the locations are given in Table 2.

Before harvest, one foot at each end of the plot was removed and the rest (i.e. 8') was harvested by a Waite Gravely Harvester. The lodged plots were harvested by sickle and threshed in a stationary thresher.

The grains were further cleaned [redacted] and the yield per plot in grams recorded.

Table 3 summarizes the experimental procedure and the generations at which it was carried out.

Plate 2. Part of the experimental block.

TABLE 2.

Some agronomic and climatological features at the location of the experiments.

Difference	Site of experiments.			
	Bundaleer (B)	Clinton (C)	Minlaton (M)	Waite Institute (W)
Soil type	Sandy mallee	Loamy mallee	Shallow sand overlaying lime stone	Red-brown earth
Normal sowing time	Late May	Mid May	Mid July	Mid June
Annual rainfall inches:*				
1967	5.66	8.45	11.46	12.82
1968	15.56	18.23	23.98	32.28

* Rainfall distribution given in Fig. 2

TABLE 3.

Summary of the experimental procedures and the generations in which it was carried out for CCV and CCXVI populations.

CCV	Seed multiplication and trials	CCXVI
F6, F16, F25	Individual plants in pot (1965)	F2, F9, F9DA
F7, F17, F26	Individual progeny rows (Feb. 1966)	F3, F10, F10DA
F8, F18, F27	Further seed multiplication* (Aug. 1966)	F4, F11, F11DA
F9, F19, F28	Adaptation trial (1967)	F5, F12, F12DA
F10, F20, F29	Adaptation trial (1968)	F6, F13, F13DA

* Some lines multiplied separately in Oct. 1966, and June 1967.

3. Observations on various characters

(a) Scores during seed multiplication 1966.

Observations were made on head characters, [redacted].(two row or six row; husk colour, i.e. yellowish or black); and awn types, [redacted].(smooth, semi-smooth or rough).

A detailed observation on heading date was made on the summer sown (Feb. 9) and one winter sown material (Waite - first sowing). Awn emergence was taken as an indication of heading. The date was recorded if approximately 50% of the plants in the plot showed awn emergence together and the rest did so within four days. This was taken to indicate the homozygosity (for heading) of the plant from which the line was derived. If awn emergence within the plot was sporadic and the spread was more than four days the date of heading of the first and last plants (and also 50% emergence) were noted. This was taken to indicate the heterozygosity of the original plant. Bell (1939) had commented that in a plot (200 to 250 plants) of a pure line barley variety, all normal plants would complete awn emergence within four days.

(b) General scores during adaptation trials in 1967 and 1968.

Unless specified, the following scores were made in both years of the adaptation trials at all sites. Heading date and powdery mildew infestation were scored on first replicate only. Loss of grain and lodging scores were made on both replicates.

Heading date.-

The date when awn emergence was complete for approximately 50% of the plants within a plot was noted as a measure of heading date.

Scoring was done every 3-4 days of the peak time of emergence and every week thereafter. By observing the length of the elongating boot ~~etc~~., it was possible to estimate the probable date of heading. This was confirmed in a subsequent visit.

Lodging.

A score of 0 - 9 was given to indicate the degree of lodging, i.e. from no lodging (0), to 90, degree of lodging (9).

Disease - Powdery mildew.

A score of 0 to 9 was given according to the response (Appendix 3). 0 indicated complete absence of infection and 9 indicated extreme susceptibility.

Loss of grain.

Loss of grain was visually estimated in 1968 when it was noted to be prevalent in some sites. Loss was estimated as percent of the total ears which were lost due to brittle rachis or breakage at or below the collar. For loss due to shattering the extent of shattering and the percent of affected ears were noted. A combined value was calculated to give a single estimate of loss. The term shattering will be used to indicate all forms of loss.

(c) Scores on morphological characters and components of yield of sub-group of CCV populations,

A total of 24, 30 and 29; F6, F16 and F25 derived lines were selected on the basis of the 1967 trial (detail on page 96) and scored for the following characters in the 1968 trials. The 23 varieties were also scored. Scoring was done on both replicates at all sites.

Counts of green tiller numbers and fertile spikes.

A two feet section of the middle row was marked with pegs for sampling. Sampling was done at random except where gaps occurred, when the next section was marked.

The number of green tillers was counted [redacted] 12-14 weeks after sowing. The number of fertile tillers was counted before harvest by counting the ears. This included the ears that had dropped. This was done by counting all the tillers which apparently had ears. Fertile spikes could not be counted at the Waite because of severe lodging.

Height.

Measured in centimetres from the ground level up to the collar of the spike (at the upper level of the canopy).

Leaf measures.

Five tillers were selected at random from the middle row at about heading time. Only tillers which had reached the upper level of the canopy were used. Measurements were made of the length and breadth of the flag leaf and second leaf. Length of flag leaf sheath was also measured.

Spike length.

Five spikes were picked at random from the middle row of the plot. The length was measured from the collar to the tip of the spike excluding awn. In plots where most of the spikes had dropped (only a few cases); spikes were picked from the ground between the rows.

No. of grains/spike.

The spikes from the above were threshed, and the average number of grains/spike obtained.

Thousand grain weight.

Thousand-grain-weight estimate was obtained from the sample harvested from the whole plot.

4. Statistical procedures.

Results from the CCV and CCXVI were analysed separately.

Analysis of variance and adaptation analysis were carried out on the yield values from (a) the 1967 trial (b) the 1968 trial and (c) the combined results from both years. The analyses were carried out on both a natural scale and logarithmic scale. A value of 1.0 was added to yield value of each plot before logarithmic transformation, as some genotypes failed to produce any grain at Clinton in 1967. This result had to be taken into account in the study of the adaptation response and could not be treated as a missing value. Hence the yield values analysed were Log (Y + 1.0).

The procedure of partitioning the total sum of squares; the test of significance of variance mean squares; and the interpretation will be evident from the presentation of results on the analysis of variance. It was concluded from the literature review that such an analysis gives a measure of the average effect of all the entries in the experiment.

The method of analysis of adaptation (Finlay and Wilkinson, 1963) was outlined earlier (page 43). Linear regression of individual yields on respective site means was calculated for each genotype. The mean yield of each genotype over all environments was also calculated.

These two indices together indicate the adaptation response of the genotypes as outlined by Finlay and Wilkinson. Deviation from regression was also obtained for each genotype. An approximate F-test of the deviations from regression was carried out as suggested by Eberhart and Russell (1966) which is:

$F \approx$ Deviation Mean Square/Pooled error

An approximate t-test for difference of individual regression from unity (i.e. population slope) was also performed which is

$t \approx 1 - b/SE\ b$.

The results of such tests will be presented where relevant.

Other analyses and tests are of a routine nature. For the calculation of simple linear regression of individual yield on days to heading, the yield values were transformed ($\sqrt{Y} + 1$).

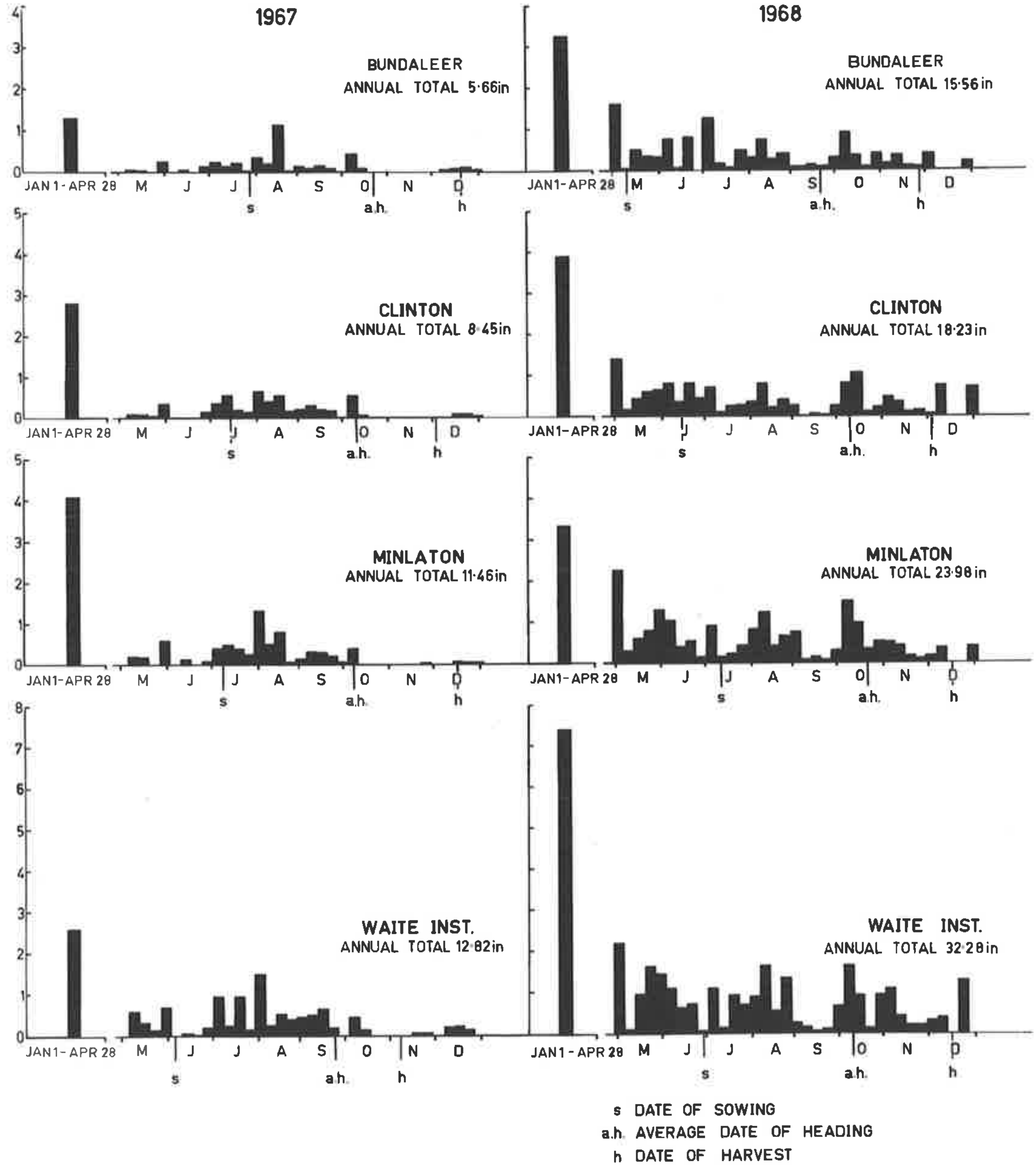
RESULTS.

1. The environment.

The genotypes were grown at four locations, for two years, thus providing a range of eight environments. The term environment is used here to indicate each site in each year. As explained earlier the average yield of all the entries at each environment (i.e. site mean) gave quantitative measure of that environment. Grading of the environment in this manner concedes that it is not possible to account separately for the response of genotypes to all the factors that constitute the field environment. This is especially true when a large number of genotypes is studied. Nevertheless it is possible to examine some of the main climatic factors which might have determined the environmental potential, and its possible effect on site means.

The rainfall and moisture status of the soil, can be considered as probably the most important factor in South Australia. The amount and the incidence of rainfall for the environments sampled in the present trial is given (Figure 2). The annual precipitation value will be quoted here. It should be only taken as a guide to the seasonal conditions in the respective locations in the year of trial. The actual moisture status during the growth of the crop would depend on the moisture reserve from the previous year as well as the rate of absorption and evaporation during the year under consideration. The date of sowing, the average date of heading, and the date of harvest are marked in the figure. The rainfall incidence between any period can be examined.

Fig. 2. The rainfall incidence (in inches) in the locations of the trials.


1967
1968
BUNDALEER
ANNUAL TOTAL 5·66in
BUNDALEER
ANNUAL TOTAL 15·56 in
CLINTON
ANNUAL TOTAL 8·45in
CLINTON
ANNUAL TOTAL 18·23 in
MINLATON
ANNUAL TOTAL 11·46in
MINLATON
ANNUAL TOTAL 23·98 in
WAITE INST.
ANNUAL TOTAL 12·82in
WAITE INST.
ANNUAL TOTAL 32·28 in
JAN 1 - APR 28
M
J
J
A
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O
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D
s
a.h.
h
0
1
2
3
4
5
6
7
8
s DATE OF SOWING
a.h. AVERAGE DATE OF HEADING
h DATE OF HARVEST

In 1967 the total values ranged from 5.66 inches at Clinton to 12.82 inches at Waite. Only Waite had some rainfall after the average date of heading. The cereal growing season in South Australia in 1967 was extremely poor because it was a year of exceptionally low rainfall. In contrast, the 1968 season had above average rainfall. In that year the annual precipitation value ranged from 15.56 inches at Bundaleer to 32.38 inches at Waite. It can be concluded that the amount of rainfall varied widely between locations and between the two years at the same location.

The site mean yields for the different environments are given in Table 4. The range of site means varied on a logarithmic scale from 1.62 at C67 to 2.54 at W68 about a six-fold difference on a natural scale (66 gm~~s~~ to 370 gm~~s~~). Although these environments are also the extremes of annual rainfall, there is in general no close agreement between the site mean yields and rainfall values. Other forms of variation could have affected site mean yield. One simple example is sowing date which varied from year to year depending on 'break of season'. This automatically meant different temperatures and photoperiods at various stages of growth of the genotypes. The differences in soil texture and fertility are other important factors. The genotype-environment interaction that might result from these and other environmental factors are too complex to be accounted for separately.

Site means were also affected by the differential response of the genotypes to various environmental factors that were only manifest in some environments. Loss of grain due to shattering occurred in B68, and to a certain extent in C68 and M68. In favourable growing

TABLE 4.

Site means of yield values for various environments of 1967 and 1968 trials.

Envirorments	Site means		
	Log_{10} gms/plot	gms/plot (antilog)	Bushels/acre
C67	1.62	41	4.1
B67	2.12	131	13.1
B68	2.13	134	13.4
C68	2.29	195	19.5
M67	2.38	239	23.9
W67	2.41	257	25.7
M68	2.41	257	25.7
W68	2.54	338	33.8

conditions (W67, W68) lodging of susceptible genotypes occurred due to luxurious vegetative growth. These conditions were also favourable for the incidence of powdery mildew.

It is concluded that the chance seasonal fluctuations that were sampled were such that the genotypes were tested in a range of environments, and that those environments enabled a measure of the differential response to the selection pressure undergone by the generations of the composite cross.

2. Analysis of variance of yield ~~results~~ - CCV.

Separate analyses were carried out on the yield values from (a) the 1967 trial (b) the 1968 trial and (c) the combined results from both years. Relevant parts of the analysis on both a natural scale and logarithmic scale have been presented in Table 5. Differences in the mean square estimates for 1967 and 1968, and changes resulting from the use of the logarithmic or natural scale are of interest. The mean squares attributable to genotypes were very highly significant in all the analyses. The environment mean square was significant at 0.1% in 1967 and at the 1% level in 1968. The magnitude of the environment mean square in 1967 reflected the extreme range of environments sampled in that year. The replicate mean squares were highly significant in all the analyses. On a natural scale the replicate mean square for 1968 was much higher than for 1967. A detailed study of the results showed this to be due to higher replicate differences at the Waite and Minlaton - the two highest yielding sites. The table shows that the effects of logarithmic transformation on the 1967 and 1968 data were not the same. This was due to the large differences in the frequency distribution of yield values in the poor environment like C67 as contrasted to the favourable environment like W68. There was a negative skewness for the distribution of yields at C67; at W68 it was a positive kurtosis.

The magnitude of the genotype-environment interaction and its components will be considered first on the logarithmic scale. The interaction was highly significant, as were the mean squares attribut-

TABLE 5.

Analysis of variance of the yield values from (A) 1967 trial, (B) 1968 trial and (C) combined results on (1) Log 10 scale and (2) Natural scale.

1. Log 10 scale.

	(A) 1967 results			(B) 1968 results			(C) combined results		
Source	D.F.	MS	VR[(a)]	D.F.	MS	VR	D.F.	MS	VR
Genotypes	294	0.3783	2.68***	324	0.2173	3.67***	294	0.3255	2.61***
Environments	3	79.3000	150.74***	3	18.6700	37.39**	7	48.9960	100.15***
Genotypes x Environments	882	0.1407	4.50***	972	0.0591	2.66***	2058	0.1243	4.62***
Regressions	294	0.3246	6.64***	324	0.0991	2.53***	294	0.3970	5.02***
Deviations from regressions	588	0.0488	1.56***	648	0.0391	1.76***	1764	0.0790	2.93***
Quadratic	294	0.0674	2.22***	324	0.0545	2.29***	294	0.1581	2.50***
Residual	294	0.0302	0.96$^{n.s.}$	324	0.0237	1.06$^{n.s.}$	1470	0.0630	2.35***
Replicates within environments	4	0.5260	16.84***	4	0.4994	22.47***	8	0.4892	18.18***
Error	1176	0.0312		1296	0.0222		2352	0.0269	

2. Natural scale.

	(A) 1967 results			(B) 1968 results			(C) combined results		
Source	D.F.	MS[(b)]	VR[(a)]	D.	MS	VR	D.	MS	VR
Genotypes	294	15.6	3.40***	324	45.2	4.83***	294	34.4	4.02***
Environments	3	5596.0	309.68***	3	4639.9	24.69**	7	5121.0	55.83***
Genotypes x Environments	882	4.8	2.38***	972	9.3	1.93***	2058	8.5	2.60***
Regressions	294	4.5	0.97$^{n.s.}$	324	10.4	1.18*	294	9.1	1.09$^{n.s.}$
Deviations from regressions	588	4.6	2.40***	648	8.8	1.81***	1762	8.4	2.53***
Quadratic	294	3.0	0.48$^{n.s.}$	324	12.5	2.48***	294	8.1	0.95$^{n.s.}$
Residual	294	6.2	3.23***	324	5.0	1.04$^{n.s.}$	1470	8.4	2.58***
Replicates within environments	4	18.0	9.38***	4	187.9	38.83***	8	91.7	27.97***
Error	1176	1.9		1296	4.8		2352	3.2	

(a) Variance ratios: Gen. = $\dfrac{\text{M.S. Gen.}}{\text{M.S. Gen. x Env.}}$; Env. = $\dfrac{\text{M.S. Env.}}{\text{M.S. Rep.}}$; Gen. x Env. = $\dfrac{\text{M.S. Gen. x Env.}}{\text{M.S. Error}}$; Linear regr. = $\dfrac{\text{M.S. Lin. Regr.}}{\text{M.S. Dev. from regr.}}$;

Quad. = $\dfrac{\text{M.S. Quad.}}{\text{M.S. Residual}}$; Rep. = $\dfrac{\text{M.S. Rep.}}{\text{M.S. Error}}$; Dev. from regr. = $\dfrac{\text{M.S. Dev. from regr.}}{\text{M.S. Error}}$;

Residual = $\dfrac{\text{M.S. Residual}}{\text{M.S. Error}}$

(b) M.S. ÷ 1000 (natural scale only).
Level of significance: *(5%); ** (1%); *** (0.1%).

able to linear regressions, suggesting that the genotypes differed in their response to the environments as indicated by their individual regressions of yield against site mean yields. Such differences were more pronounced in the environments of 1967. The percentages of the interaction sums of squares attributable to the linear regressions were 76 and 56 for 1967 and 1968 analyses, respectively. The deviations from regression sum of squares were further partitioned into quadratic and residual components. Quadratic effects were highly significant for both years. Residuals were non-significant. This suggests that a large proportion of the deviation from regression mean squares was due to a curvilinear response of the genotypes. The linear regression model can be considered as an approximate fit for a preliminary examination of the biological response.

Examination of the analyses on a natural scale showed that the interaction variance was highly significant. The linear component of the interaction variance was non-significant in 1967 and significant at the 5% level in 1968. In 1967, deviations from regression were not accounted for by a quadratic term. This was evident in the non significance of the quadratic term and the highly significant variance ratio for the residual effect. In 1968 this was reversed. Loss of grain on a substantial proportion of the genotypes in some sites, but retention of all grain at the Waite site (following lodging), is thought to have resulted in the significant linear regression and a significant quadratic component of the deviations from regression sum of squares.

A comparison of the magnitude of genotype-environment mean squares and its components on the two scales, showed that the logarithmic transformation was highly effective in inducing linearity in the regressions. Finlay and Wilkinson (1963) pointed out a similar advantage of transformation in the analysis of their results.

The results for the two years combined can be understood in view of the interpretations for individual years. All effects were highly significant on a logarithmic scale. On the natural scale the residual component of deviation from regression sum of squares was highly significant. The linear and quadratic components were non-significant.

The experimental error for each site is given in Table 6 for both scales. Bartlett's test for homogeneity of variance (Snedecor and Cochran, 1967) was carried out. The X^2 values (7d.f) obtained were 636 and 587 for the natural and logarithmic scale, The magnitude of X^2 estimates showed that logarithmic transformation was not effective in inducing the homogeneity of error variance in the distribution of yield values obtained in the present experiment. This test was also conducted on the results from the individual years and a similar result obtained.

TABLE 6.

Error mean square of yield values for each site in each year on a natural and $\log_{10}$ scale.

Site and year.	Error mean square~~s~~.	
	Natural scale	Log_{10} scale.
B67	895	.0170
C67	567	.0787
M67	2151	.0163
W67	4084	.0127
B68	3104	.0482
C68	2482	.0145
M68	4394	.0134
W68	8553	.0140

3. Analysis of adaptation of the yield results - CCV.

The results are given on a logarithmic scale. A comparison with the analysis on the natural scale will be presented in section 4.

a. Analysis of 1967 results.

The mean yield and regression coefficient of each genotype for the 1967 seasons have been plotted to give a two dimensional scatter diagram (Fig. 3). The population mean has been marked and from the nature of the adaptation analysis the mean regression coefficient has a value of 1.0. The diagram shows that the mean yields of the majority of the F6 lines were less than the population mean. There were also more lines with b value > 1.0 and a distinct group of genotypes with very high b values (> 2.6) associated with low mean yields (< 1.5), i.e. genotypes which were highly 'sensitive' to differences in the environments. The F16 and F25 generations had relatively more genotypes with high mean yields and regression values close to 1.0. A two-way frequency distribution for mean yield and regression coefficient of each genotype has been derived (Fig. 4) which is a summary of the scatter diagram, meant to facilitate a more thorough examination of shifts in the populations. The x-axis and y-axis have been divided into classes. The number of lines within each class for each generation are enclosed by the respective symbol. The percentage of lines with mean yields greater than the grand mean were 49, 70 and 79 in F6, F16 and F25 generations respectively. The percentage of lines with regression coefficient values > 1.0 were 44, 24 and 19 in the same

Fig. 3. A scatter diagram of the line mean yield and the regression coefficient of genotypes from CCV F6, F16 and F25 generations in the 1967 trials.

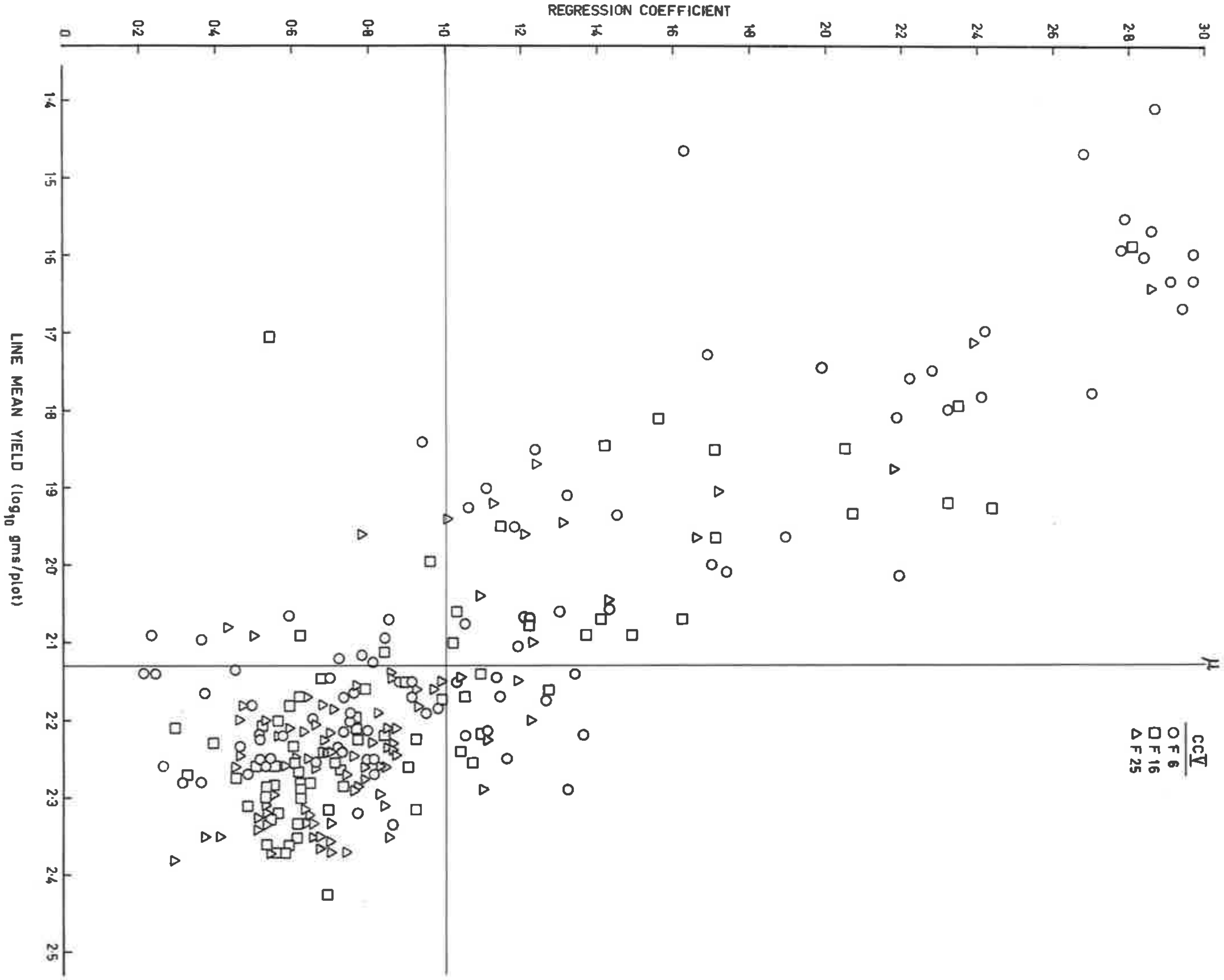
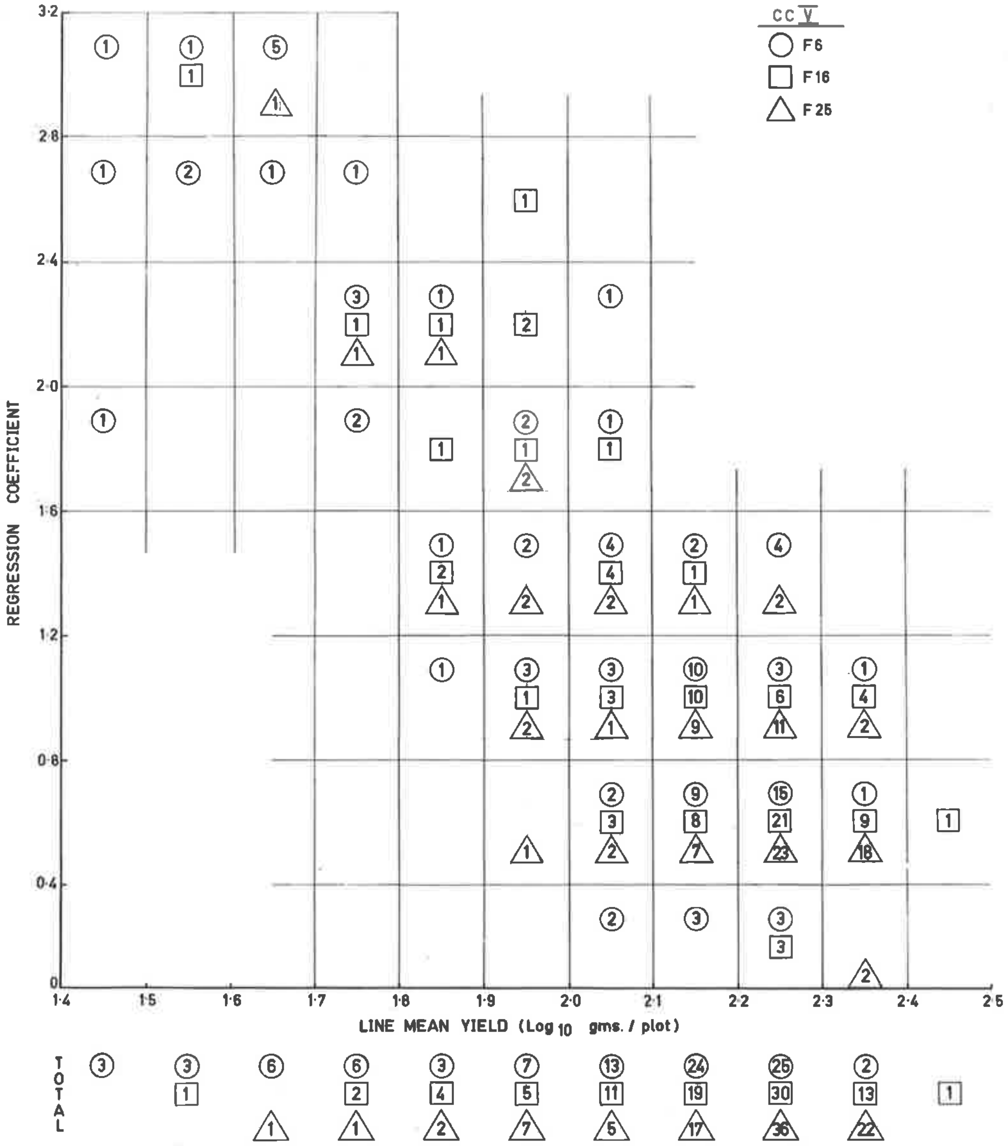

REGRESSION COEFFICIENT
0
0·2
0·4
0·6
0·8
1·0
1·2
1·4
1·6
1·8
2·0
2·2
2·4
2·6
2·8
3·0
LINE MEAN YIELD ($\log_{10}$ gms/plot)
1·4
1·5
1·6
1·7
1·8
1·9
2·0
2·1
2·2
2·3
2·4
2·5
μ
CCV
○ F 6
□ F 16
△ F 25

Fig. 4. The two way frequency of the line mean yields and regression coefficients for the 1967 trials. The numbers within the symbols indicate the number of lines in each class, for each generation.


CC V
F6
F16
F25
REGRESSION COEFFICIENT
3·2
2·8
2·4
2·0
1·6
1·2
0·8
0·4
0
LINE MEAN YIELD (Log10 gms. / plot)
1·4
1·5
1·6
1·7
1·8
1·9
2·0
2·1
2·2
2·3
2·4
2·5
TOTAL

generations. It can be concluded that the F6 generation had a greater proportion of genotypes with low mean yields and below average stability as contrasted to the F16 and F25 generations. Detailed examinations of frequencies in the extreme class intervals show that 11 of the F6 lines were highly sensitive to change in environment as indicated by low mean yield and high regression coefficient values. These genotypes were unstable in the stress environment of C67 and failed to give any yield. Increased yield was obtained at other sites, as the environment improved. The proportion of such extreme genotypes in the F16 and F25 generations was almost nil (1%). It is evident that genotypes which were specifically adapted to high yielding environments were eliminated from composite-cross populations by natural selection.

The figures show that a number of F6 lines with low means were also associated with low regression coefficient values. These lines gave above average yield in C67 but did not show high yield potential in the favourable environment. Such genotypes were stable and were of the kind specifically adapted to low yielding environments.

The frequency distribution in class intervals towards high mean yield showed that 2, 13 and 22 of F6, F16 and F25 lines had mean yields between 2.3 to 2.4. The F25 generation had 9 more lines in this class than the F16 generation suggesting that the population had improved further in the later generation. The regression coefficient values of most of these genotypes ranged from 0.4 to 0.8 indicating that these genotypes had above average stability. However, the line with the mean yield (2.45) was from the F16 generation. It had a regression coefficient value of 0.2. This exceptional performance of an F16 line may be simply a result of sampling.

Tests for significance of the deviation mean squares showed that deviation from the regression of only 8, 4 and 2 lines from F6, F16 and F25 generations were significantly different from zero. This can be considered as a rather small proportion of the total number of entries in the experiment. Of these, nine lines were among the sensitive types. The regression coefficient values of the other five lines were approximately 0.4. Implications of this test will be elaborated later.

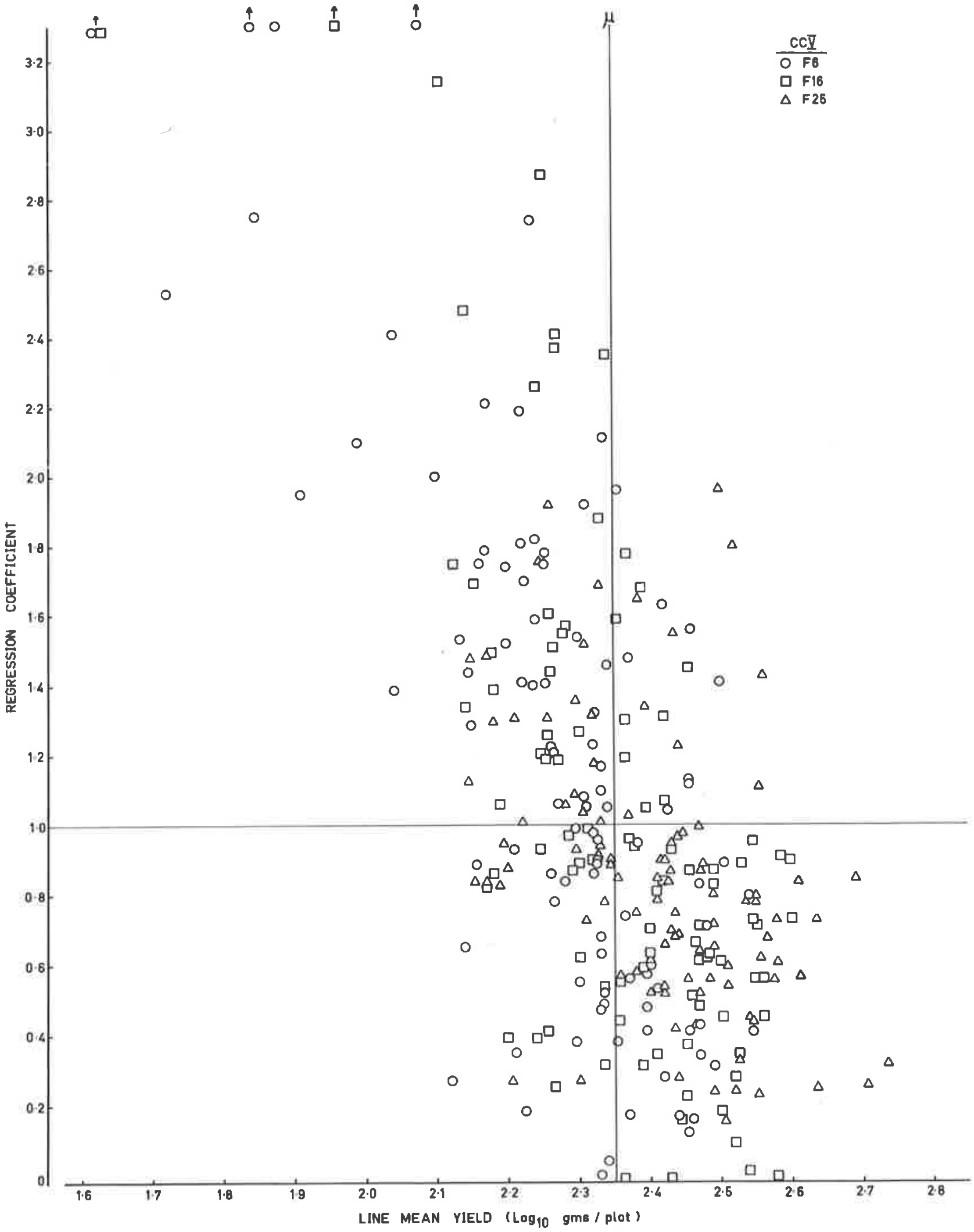
The average yield and regression coefficient for F6, F16 and F25 generation populations were 1.95, b = 1.43; 2.22, b = 0.78; and 2.26, b = 0.70 respectively.

The mean yield and regression coefficient for each generation line mixture was similar to that of the respective population average.

b. Analysis of 1968 results.

The scatter diagram and the two way frequency distribution for line mean yield and regression coefficient are given in Fig. 5, which were derived in the same manner as described previously. Since a different set of environments were sampled in 1968, there was a change in the mean yield and the regression coefficient values. In general, the change in yield was towards increased mean yield for each line. (The regression coefficient values were affected to various degrees.) In general, the genotypes with high mean yield and regression coefficient values < 1.0 in the 1968 environments had similar values in the previous

Fig. 3. A scatter diagram of the line mean yield and the regression coefficient of genotypes from CCV F6, F16 and F25 generations in the 1968 trials.



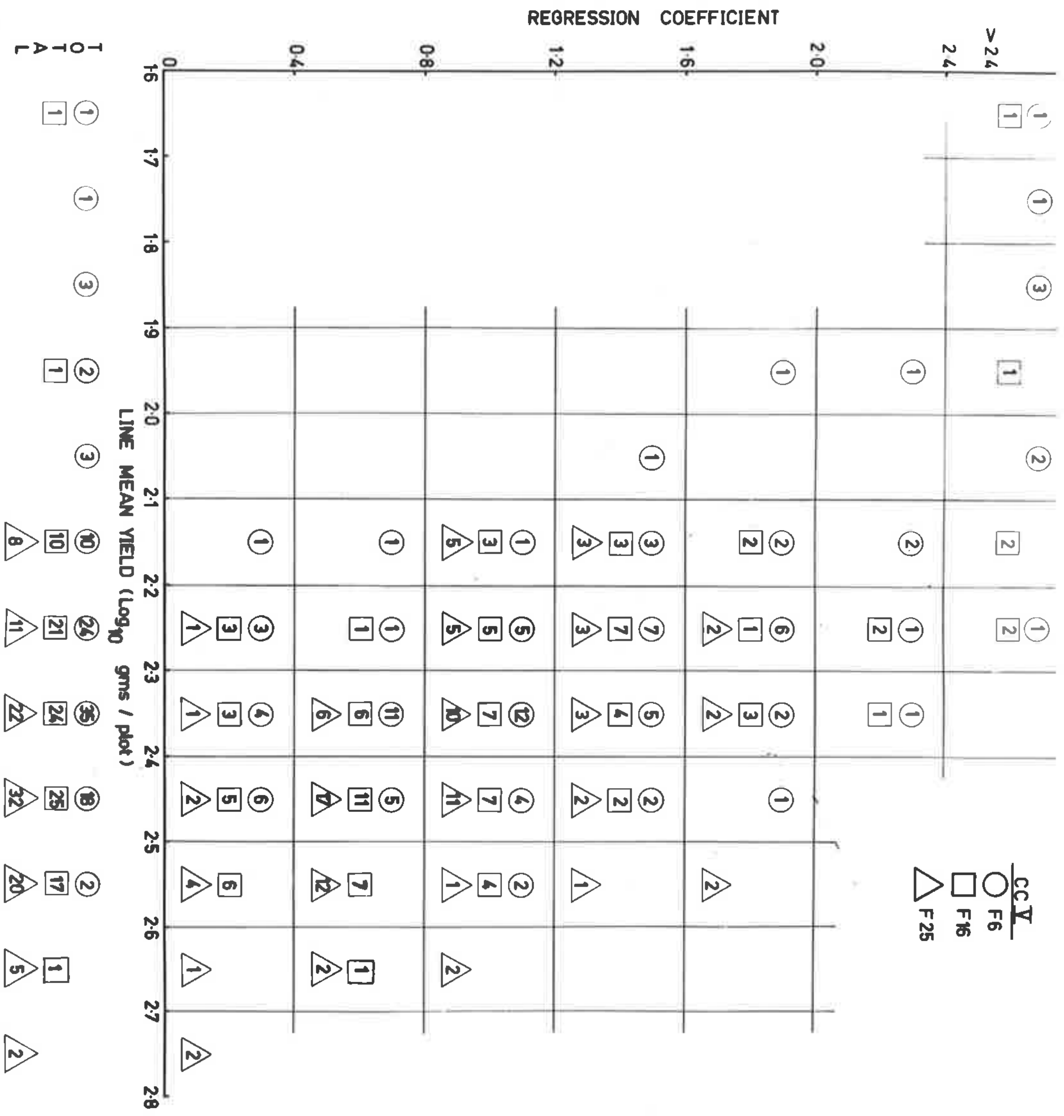
CCV
○ F6
□ F16
△ F25
μ
REGRESSION COEFFICIENT
0
0·2
0·4
0·6
0·8
1·0
1·2
1·4
1·6
1·8
2·0
2·2
2·4
2·6
2·8
3·0
3·2
1·6
1·7
1·8
1·9
2·0
2·1
2·2
2·3
2·4
2·5
2·6
2·7
2·8
LINE MEAN YIELD (Log$_{10}$ gms / plot)

year. The unstable genotypes [redacted] with high b valuesand low mean yieldswere mostly ones which suffered loss of grain through shattering. The extent of the loss of grain largely determined the magnitude of the increase in regression coefficient value and the decrease in mean yield. Though by definition, these lines can be called unstable, the cause for 'unstableness' was quite different from that in the 1967 environments. The unstable genotypes as identified in the previous year were less buffered against a stress environment. This was reflected by their failure to set any seed in C67 and their improvement in other environments. The unstable types in the 1968 environments were mostly those unable to fully retain the grain that had formed. With this difference in mind for the nature of stability in two years, the frequency distribution in the diagram can be examined.

The frequency of lines that exceeded the grand mean for yield were 35, 55 and 72% in F6, F16 and F25 populations,respectively. The F6 generation had a greater proportion of lines with $b > 1.0$ (53%) mostly associated with relatively low mean yield. The proportion of such lines had decreased by the F16 (32%) and F25 (27%). Deviation mean squares were significant for only 8 lines out of all the entries in the experiment.

Inspection of frequencies (Fig. 6) will show that the F16 and F25 generation had 17 and 20 lines in the 2.5 to 2.6 mean yield class. The F6 generation had only 2 lines in the same class. The difference between the F16 and F25 generation was more obvious in the analysis of results from the 1968 trial. There was only one F16 line in the 2.6

Fig. 6. The two way frequency of the line mean yields and regression coefficients for the 1968 trials. The numbers within the symbols indicate the number of lines in each class, for each generation.


REGRESSION COEFFICIENT
>2.4
2.4
2.0
1.6
1.2
0.8
0.4
0
LINE MEAN YIELD (Log10 gms / plot)
1.6
1.7
1.8
1.9
2.0
2.1
2.2
2.3
2.4
2.5
2.6
2.7
2.8
TOTAL
CC V
F6
F16
F25

to 2.7 mean yield class which had five F25 lines. None of the F16 lines exceeded 2.7 mean yield. The two best F25 lines were in the mean yield class of 2.7 to 2.8 (actual values 2.71 and 2.74). On a natural scale the average of these two lines represent a yield of approximately 530 grams/plot (53 bushels/acre). The average yield of the two best lines from F16 and F25 generations were 354 and 394 grams respectively (35 and 39 bushels/acre). Some exceptionally high yielding lines had appeared by F25.

The F25 lines with the highest mean yields were among genotypes which could be included only in the 1968 trial. It may be recalled that 30 lines were added to the experimental material in 1968 (7, 14 and 9 from F6, F16 and F25). The frequency distribution and the percent frequency of these lines for mean yields is given in Table 7 (the same is also given for the rest of the lines). The table shows that the mean yield of most of these lines exceeded 2.4 and that the best lines from each generation tended to be from this group. Most of these lines had above average stability. Results on heading date will suggest that these lines were of day-neutral type.

Figure 6 shows that genotypes with high mean yields also had a greater stability of yield as indicated by low b values. This indication of high stability was the reflection of the ability of these genotypes to yield well and retain grain in the environments where shattering of other genotypes occurred. None of the genotypes shattered at W68 and the genotypes with high yield potential again had above average yield at this environment but the difference from the

TABLE 7.

The frequency and the percent* of lines grown in 1968 trial only (in bracket) and the rest in various mean yield classes.

Generation		Line mean yields.												
		1.6-1.7	1.7-1.8	1.8-1.9	1.9-2.0	2.0-2.1	2.1-2.2	2.2-2.3	2.3-2.4	2.4-2.5	2.5-2.6	2.6-2.7	2.7-2.8	Total
F6	Frequency	1	1	3	2	3	10	23+(1)	33+(2)	15+(3)	1+(1)			92+(7)
	Percent	1	1	3	2	3	11	24,(14)	36,(28)	16,(42)	1,(14)			
F16	Frequency	1			1		10	21	20+(4)	20+(5)	13+(4)	(1)		86+(14)
	Percent	1			1		11	24	23,(28)	23,(35)	15,(28)	(7)		
F25	Frequency						8	9+(2)	21+(1)	31+(1)	18+(2)	4+(1)	(2)	91+(9)
	Percent						9	10,(22)	22,(11)	34,(11)	19,(22)	4,(11)	(22)	

*fractions not given.

site mean was not necessarily as high as that at B68 (on logarithmic scale the difference between the yield value and site mean was actually reduced). The regression coefficients [redacted] of the two best F25 lines were smaller (≈0.4) also because their yields at Waite were less than that at Clinton and Minlaton.

The average yield and regression coefficient for F6, F16 and F25 generation populations were 2.19, b = 1.40; 2.35, b = 1.02; 2.48, b = 0.61. The values for each generation line mixture were similar to that of the respective population average.

e. Combined analysis of 1967 and 1968 results.

The scatter diagram and the two-way frequency distribution from the combined analysis of results from two years are given (Fig. 7 and 8). The distribution of the combined analysis resembles that for 1967 more closely than that for 1968. That the F25 population had a greater proportion of generally adapted lines (as indicated by high mean yields and b values < 1.0) can be seen as noted from the separate analyses.

The way the adaptation indices, especially the regression coefficients, are influenced by the environments sampled, will be examined, not only to assess the nature of genotypic differences, but also to illustrate some aspects of the adaptation analysis.

A comparison of regression coefficient values from the three analyses showed that these values were highly influenced by the environments sampled, and that the nature of change was not the same for the genotypes with different performance. Figures 9, 10 and 12 [redacted] illustrate this point, each has an example of one

Fig. 7. A scatter diagram of the line mean yield and the regression coefficient of the genotypes from CCV F6, F16 and F23 generations for the combined analysis of 1967 and 1968 results.

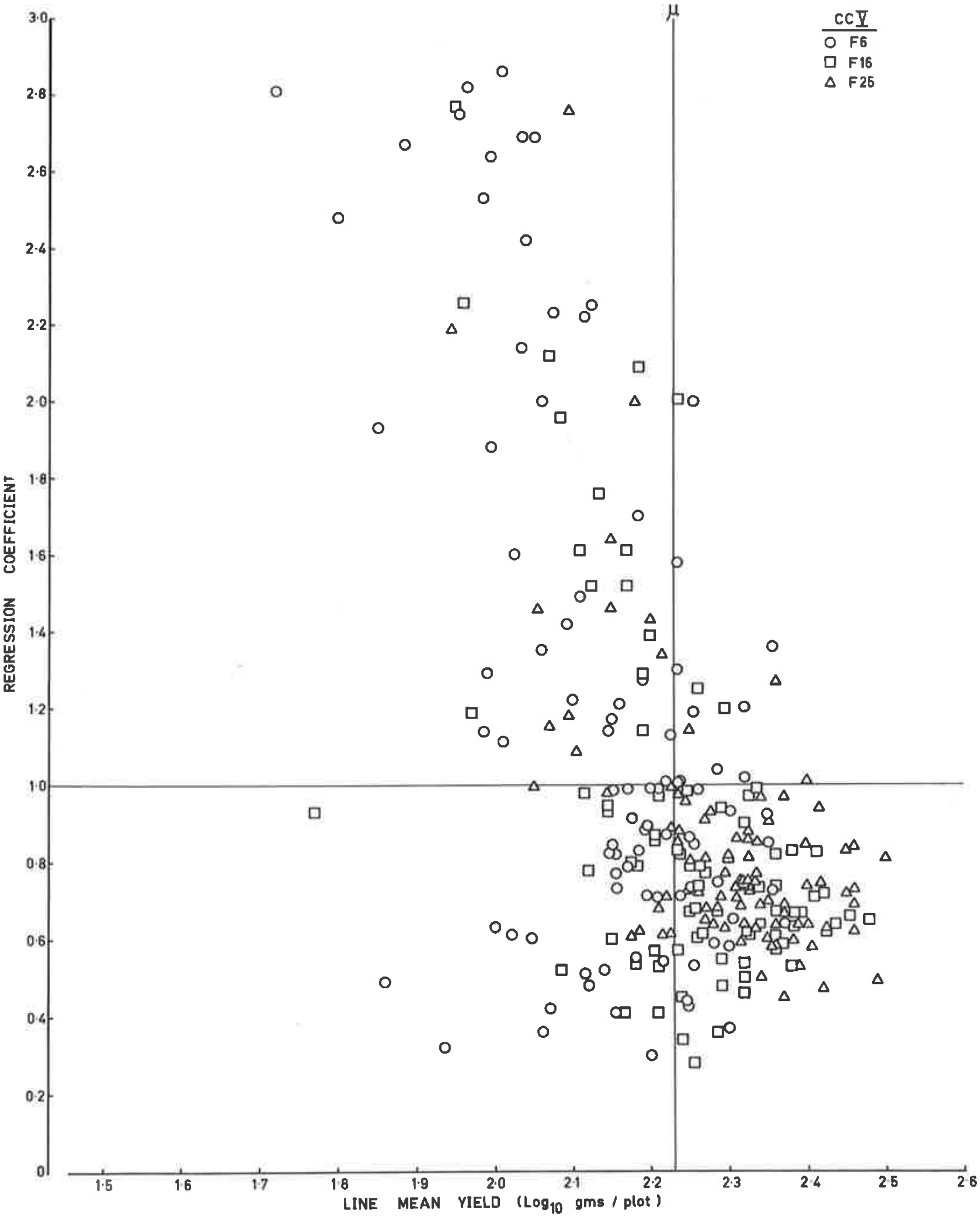
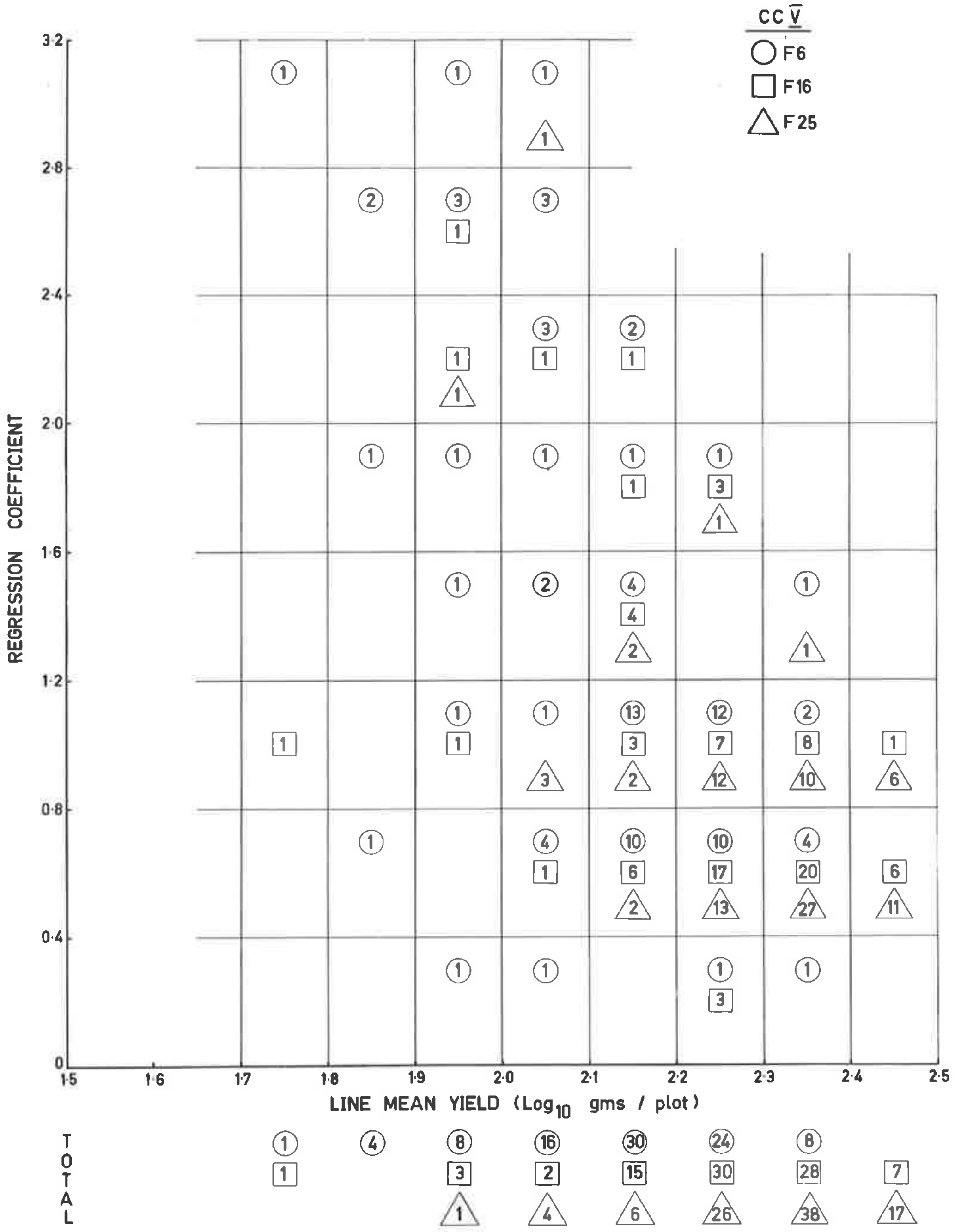

μ
CC V
○ F6
□ F16
△ F25
REGRESSION COEFFICIENT
3·0
2·8
2·6
2·4
2·2
2·0
1·8
1·6
1·4
1·2
1·0
0·8
0·6
0·4
0·2
0
1·5
1·6
1·7
1·8
1·9
2·0
2·1
2·2
2·3
2·4
2·5
2·6
LINE MEAN YIELD (Log10 gms / plot)

Fig. 8. The two way frequency of the line mean yields and regression coefficients for the combined analysis of 1967 and 1968 results. The numbers within the symbols indicate the number of lines in each class, for each generation.


CC V̄
F6
F16
F25
REGRESSION COEFFICIENT
0
0·4
0·8
1·2
1·6
2·0
2·4
2·8
3·2
1·5
1·6
1·7
1·8
1·9
2·0
2·1
2·2
2·3
2·4
2·5
LINE MEAN YIELD (Log10 gms / plot)
TOTAL
1 4 8 16 30 24 8
1 3 2 15 30 28 7
1 4 6 26 38 17

of the following groups:

(1) Genotypes specifically adapted to high yielding environment.

(2) Genotypes specifically adapted to low yielding environment.

(3) Generally adapted genotypes.

The three slopes for the individual genotype have been drawn in the same diagram using a separate set of points for each of two years. All these points were used for the combined regression.

Figure 9 shows that the highly sensitive genotype which was identified in the environments of 1967 had performed well in the high yielding environments of 1968. Though the example given has a regression coefficient value of 1.56, a number of genotypes from group 1 also had b values less than 1.0 associated with high mean yields. These genotypes would have been considered as generally adapted in a set of favourable environments such as those of 1968. The combined analysis indicated the high sensitivity as it included C67 and B67, the two environments with severe moisture stress.

The change in the regression coefficient values of some genotypes in group 2 was most conspicuous (Fig. 10). Basically, these genotypes were specifically adapted to low yielding environments ($b < 1.0$, relatively low mean yield in 1967). Those which shattered less in 1968 seasons had similar values as in the previous year. Others shattered badly in more than one site and high b values were obtained (Fig. 10). In the combined analysis the same genotypes had $b < 1.0$ associated with low mean yield. There was a very large deviation from linearity when all eight points were combined to provide the regression.

Fig. 9. The change in slope of a 'sensitive' genotype in different sets of environments.

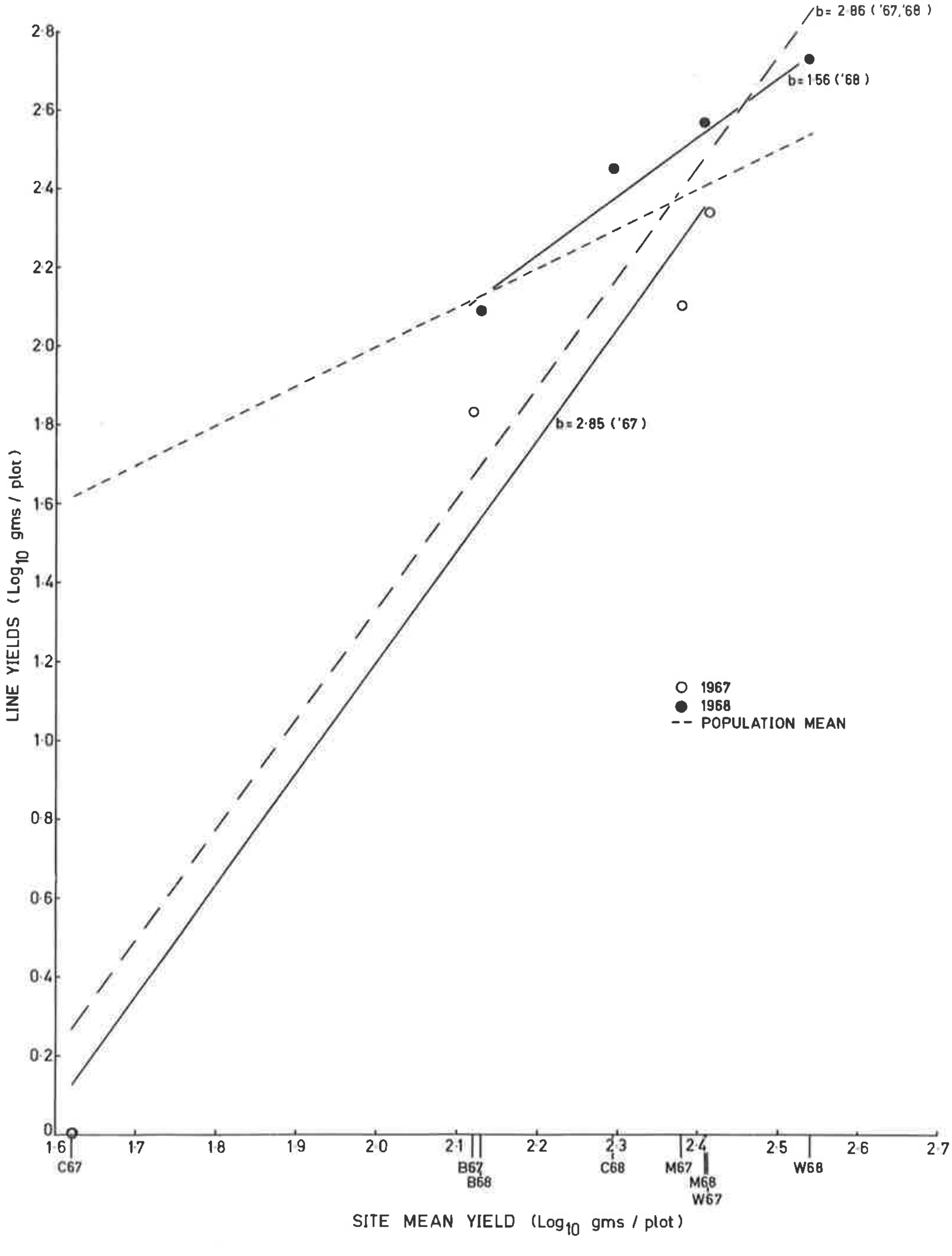
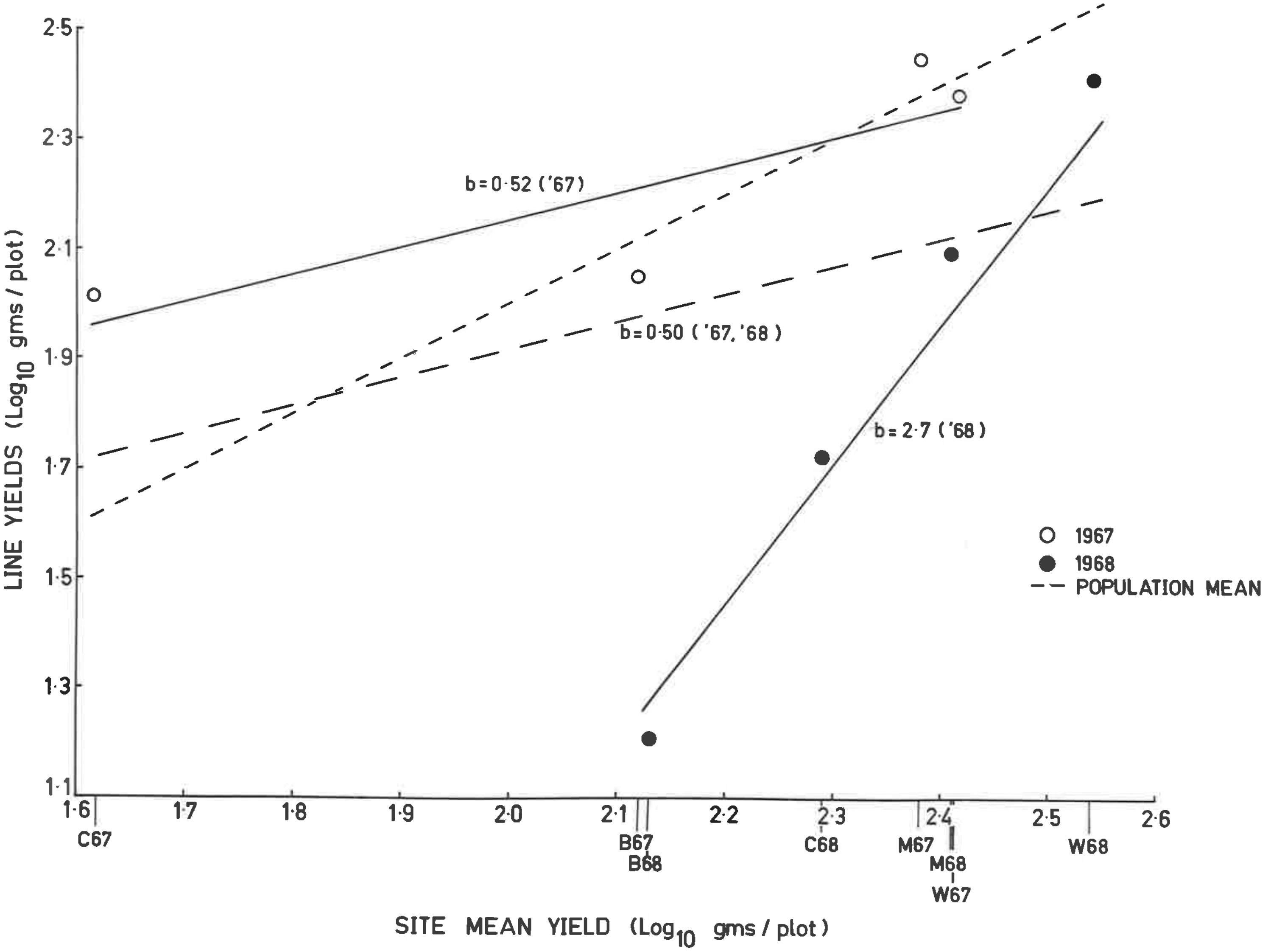

b= 2·86 ('67,'68)
b= 1·56 ('68)
b= 2·85 ('67)
○ 1967
● 1968
-- POPULATION MEAN
LINE YIELDS (Log$_{10}$ gms / plot)
2·8
2·6
2·4
2·2
2·0
1·8
1·6
1·4
1·2
1·0
0·8
0·6
0·4
0·2
0
1·6
1·7
1·8
1·9
2·0
2·1
2·2
2·3
2·4
2·5
2·6
2·7
C67
B67
B68
C68
M67
M68
W67
W68
SITE MEAN YIELD (Log$_{10}$ gms / plot)

Fig. 10. The change in slope of a genotype 'specifically adapted to low yielding environments,' as obtained in different sets of environments.


2·5
2·3
2·1
1·9
1·7
1·5
1·3
1·1
LINE YIELDS (Log$_{10}$ gms / plot)
b = 0·52 ('67)
b = 0·50 ('67, '68)
b = 2·7 ('68)
○ 1967
● 1968
— — POPULATION MEAN
1·6
1·7
1·8
1·9
2·0
2·1
2·2
2·3
2·4
2·5
2·6
C67
B67
B68
C68
M67
M68
W67
W68
SITE MEAN YIELD (Log$_{10}$ gms / plot)

This resulted in a very high deviation mean square.

The numbersof lines in the combined analysis for which Dev. MS were significant were 26, 10 and 5 lines in F6, F16 and F25 populations. All these lines have been plotted (Fig. 11). It showed that genotypes with both high and low regression coefficient values had significant deviations from the fitted slopes. In the present analysis, a b value less than 1.0 cannot always be taken as a measure of increased stability as defined by Finlay and Wilkinson. However, Figure 11 shows that this applies to only a proportion of F6 lines for which the deviations were significant. The number of F16 or F25 lines with b less than 1.0 and significant Dev. MS was almost nil.

Regression coefficient values of generally adapted types (group 3) were similar in all [redacted] three analyses. They had high mean yields with b values less than 1.0 (Fig. 12).

The reliability of performance of generally adapted genotypes [redacted] meansthat they would have been selected on the basis of results from any year that had a similar range of environments to those sampled in this study.

A 't'-test for differences of individual slopes from the population slope was carried out. It will be reported for the combined analyses. The test showed that 38, 35 and 23 lines from F6, F16 and F25 generations had slopes significantly different from 1.0. The significant lines have been plotted (Fig. 13) for all the three generation populations. It showed that the F6 generation had most of the lines which were highly sensitive to a change in environment and that, judged

Fig. 11. The distribution of lines in various generations with Dev. M.S>0. (Combined analysis of 1967 and 1968 results).

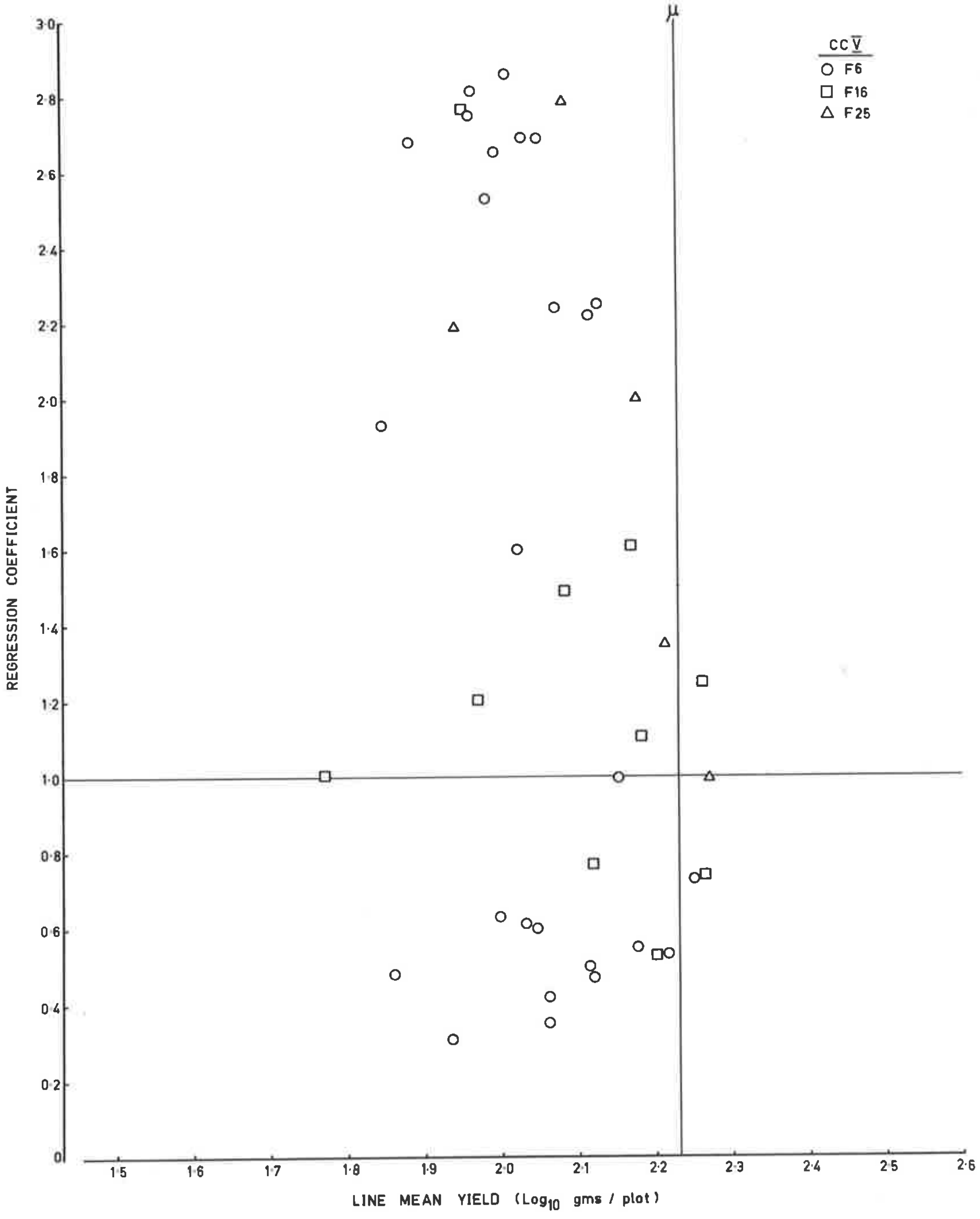
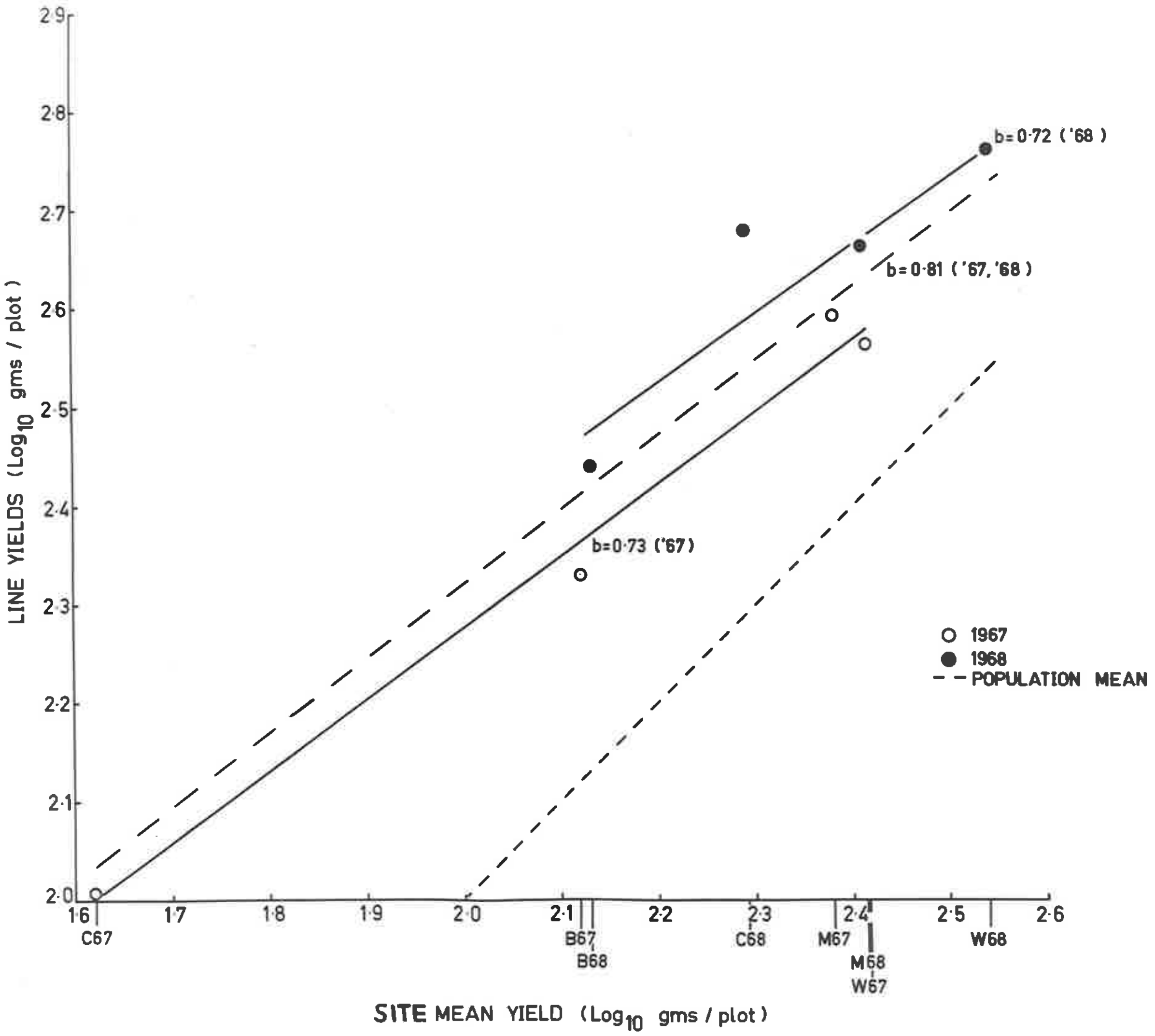
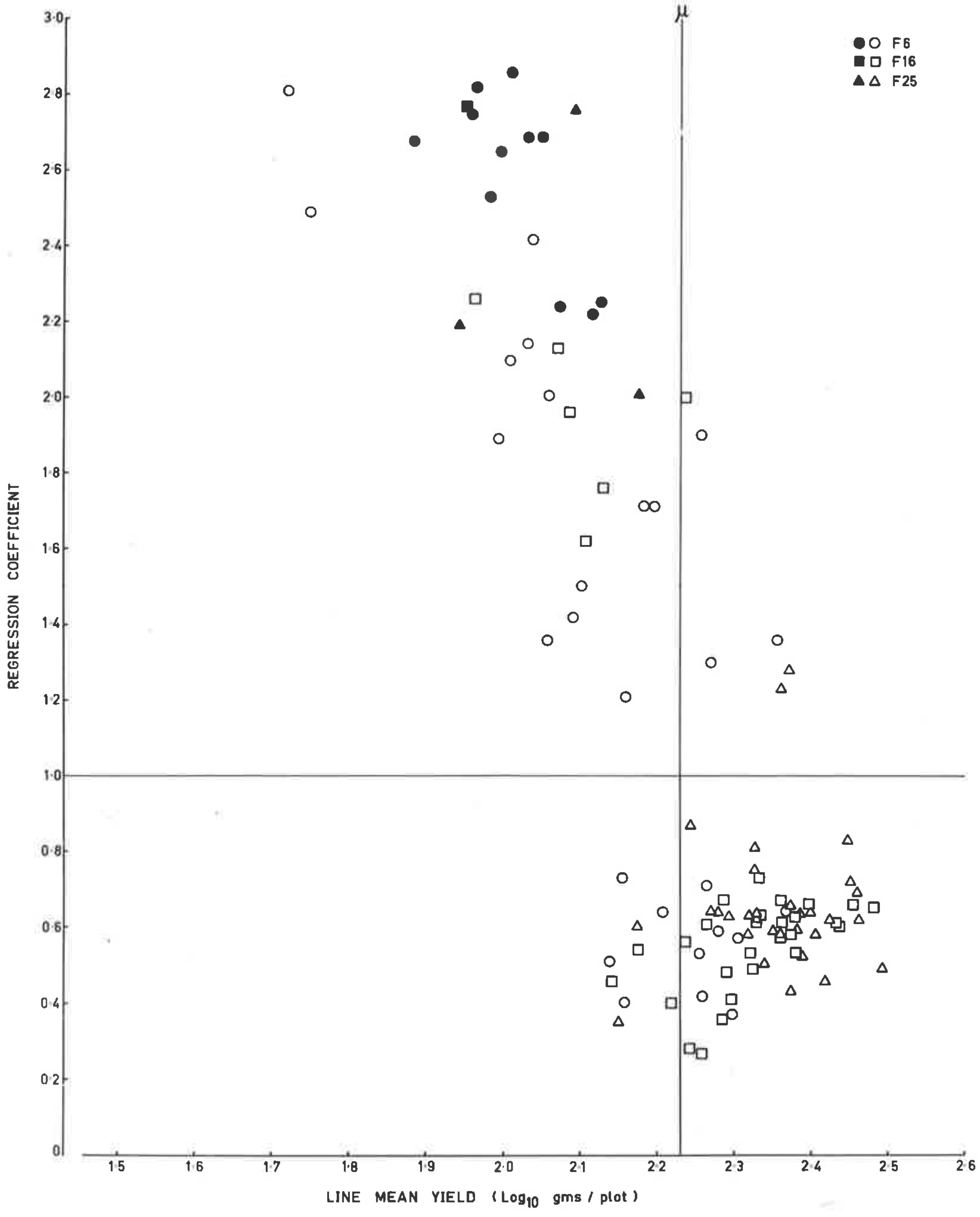

μ
CC $\overline{V}$
○ F6
□ F16
△ F25
REGRESSION COEFFICIENT
3·0
2·8
2·6
2·4
2·2
2·0
1·8
1·6
1·4
1·2
1·0
0·8
0·6
0·4
0·2
0
1·5
1·6
1·7
1·8
1·9
2·0
2·1
2·2
2·3
2·4
2·5
2·6
LINE MEAN YIELD (Log$_{10}$ gms / plot)

Fig. 12. The change in slope of a 'generally adapted' genotype in different sets of environments.



LINE YIELDS (Log10 gms / plot)
2·9
2·8
2·7
2·6
2·5
2·4
2·3
2·2
2·1
2·0
b=0·72 ('68)
b=0·81 ('67,'68)
b=0·73 ('67)
1967
1968
POPULATION MEAN
1·6
1·7
1·8
1·9
2·0
2·1
2·2
2·3
2·4
2·5
2·6
C67
B67
B68
C68
M67
M68
W67
W68
SITE MEAN YIELD (Log10 gms / plot)

Fig. 13. The distribution of lines in various generations for which 't' = 1-b/SEb, were significant, P>0.05% (combined analysis of 1967 and 1968 results). The solid symbol indicates where tests for Dev. M.S were significant.



μ
● ○ F6
■ □ F16
▲ △ F25
REGRESSION COEFFICIENT
3·0
2·8
2·6
2·4
2·2
2·0
1·8
1·6
1·4
1·2
1·0
0·8
0·6
0·4
0·2
0
1·5
1·6
1·7
1·8
1·9
2·0
2·1
2·2
2·3
2·4
2·5
2·6
LINE MEAN YIELD (Log_{10} gms / plot)

by this regression, the rate of improvement of these lines would exceed the rate for the population average. The lines which also had a significant Dev. MS have been marked (as solid symbols). This shows that a number of F6 lines had large deviations from the fitted slope. Most of these genotypes lost little or no grain, and the large Dev. MS reflects their poor performance at C67.

Slopes for most of the F16 and F25 lines were below 1.0 and associated with high mean yield. If individual slopes (< 1.0) are significantly different from the population slope and are associated with high mean yield it might be concluded that these genotypes do not improve (on a log scale) linearly relative to the population average even though they might have given above average yield in all the environments. An explanation for this apparent increase in stability relative to the population average has already been advanced (page 75).

d. Results on varietal performance.

To assess the value of the genotypes from the composite-cross populations in a breeding program it is necessary to compare their performance with commercial varieties or other genotypes of known performance. The performance of some varieties grown in the trial will be considered. Only the superior types are of interest. The mean yields (over eight environments) and regression coefficients for each variety is given in Appendix 2.

The analysis of 1967 results showed that there were six varieties in the same log yield class of 2.3 to 2.4 (b = 0.4 to 0.9) as the best generally adapted types from the advance generation populations. The varieties were C.I. 3576, C.I. 3726, Prior, Noyep (all two-row barleys), California Coast and Sahara (Six row). Prior is a standard commercial variety grown in South Australia, while Noyep is an earlier maturing selection from Prior. This analysis showed that though a greater proportion of advanced generation lines approached the performance of the best generally adapted varieties none were superior in yielding ability.

The analysis of the 1968 results showed that none of the varieties, exceeded a mean yield of 2.5. (There were 7 F25-derived lines which exceeded the mean yield of 2.6). There were five varieties in the mean yield class of 2.4 and 2.5 (b< 1.0). These varieties were C.I. 3576, C.I. 3726, California Coast, Bolivia and Freja. Prior and Noyep which had shown general adaptation in the 1967 environments shattered and had a lower mean yield and higher b value. In view of results from both years it is concluded that varieties C.I. 3576 and California Coast were the best generally adapted varieties in the present trial. These varieties were also among the highest yielding in Finlay and Wilkinson's trial. Regretably [redacted] Atlas and its derivatives, or Vaughn [redacted] were not be grown in this trial. However, Atlas, California Coast and C.I. 3576 had a similar performance in Finlay and Wilkinson's trial. The variety mean yields were 2.57, 2.56 and 2.54 respectively in their analysis. The regression coefficient values for these varieties were 0.8 approximately. C.I. 3576 and C.I. 3726 are both from Northern Egypt. Coast and California Coast are similar and are of North African origin. Coast is likely to have been reselected from California Coast at some stage (Wiebe and Reid, 1958). Atlas, which was used by Suneson as a check variety, is a pure line selection made from Coast. The average yield of California Coast and C.I. 3576 will be used as a basis for comparison with the performance of genotypes from composite-cross populations. The average yield of these two varieties in the 1968 season was 302 grams per plot (30 bushels/acre). The average yields of the two best lines from F6, F16 and F25 generations were 354, 394 and 530 grams respectively (35, 39 and 53 bushels/acre). Indeed there were 7 F25 lines which outyielded the average yield of the two varieties by at least 33%. The yield advantage of the two best F25 lines over the average of the two best varieties is about 75%. It is remarkable that not only the advanced generation populations had some exceptionally high yielding genotypes but also that the F6 generation had a few lines which outyielded the best varieties.

The South Australian commercial varieties like Prior and Noyep, in view of their shattering, cannot be compared with superior lines from the composite cross populations for yielding ability. It should be noted however that Prior and Noyep would not have outyielded California Coast and C.I. 3576 even if these varieties had not shattered. Their performance in the 1967 trial was similar. ~~In~~ From other trials Prior and Noyep are known to have relatively lower mean yield than California Coast and C.I. 3576 (Sparrow, personal communication).

4. Adaptation Analysis of logarithmically transformed data in comparison with natural data.

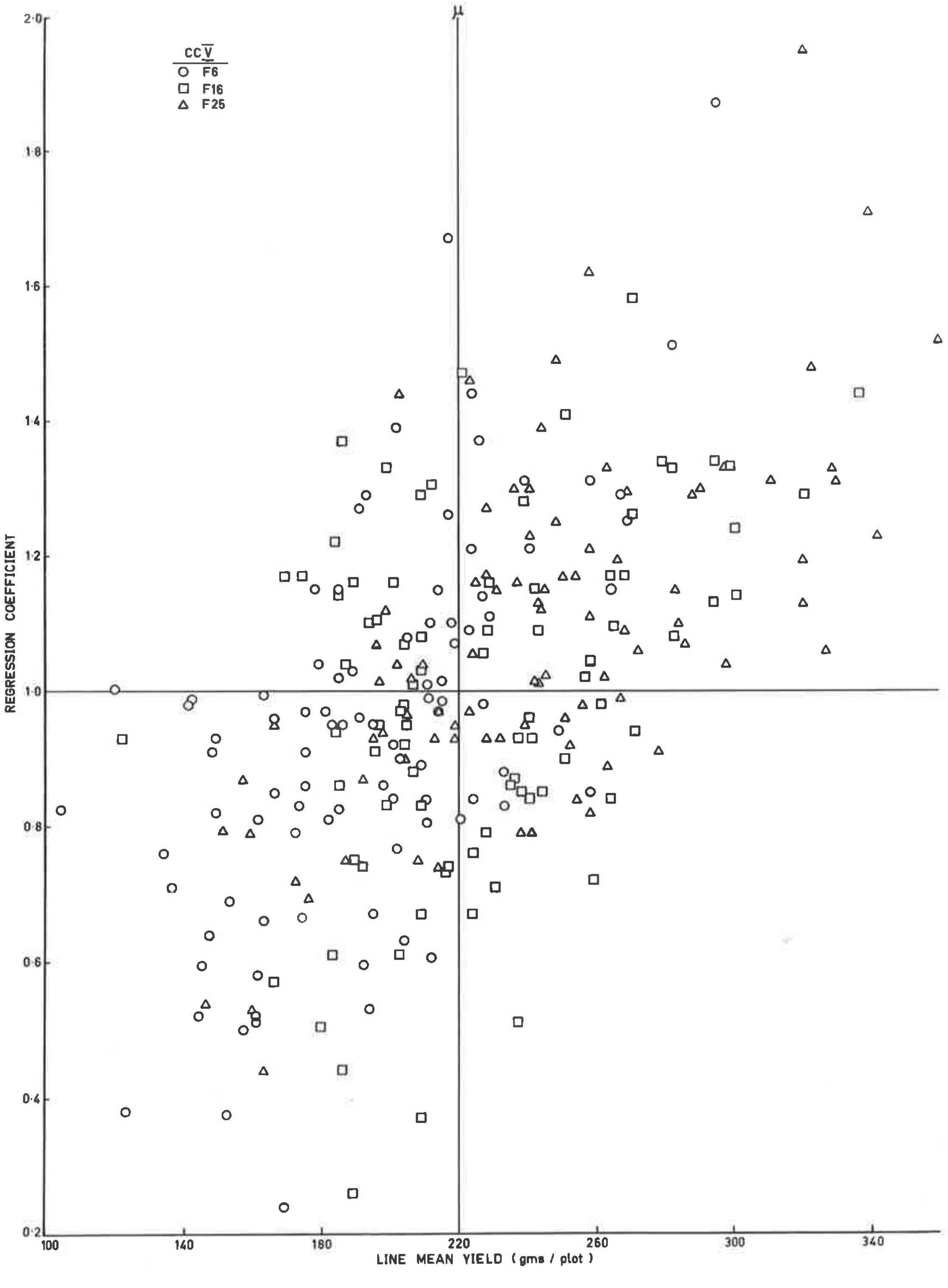
The adaptation analyses of yield were performed on a logarithmic scale in preference to a natural scale because it induced a higher degree of linearity in the regressions.

It will be shown that this simplified the interpretation and presentation of results. The question that can be asked is how truly the indices obtained on a transformed scale measure the biological response of the genotypes over the range of environments. A comparison will be made of the results obtained on the two scales over the 8 environments.

The scatter diagram of the regression coefficient and the line mean yield when calculated on a natural scale (Fig. 14) was different from that obtained on a logarithmic scale (Fig. 7). In the analysis on a natural scale the mean yield and regression coefficient values were positively correlated, i.e. genotypes with higher mean yield tended to have high b-value and vice versa. The correlation coefficient estimates for these two parameters obtained in the two analyses were 0.56 (natural scale and -0.64 (logarithmic scale).

Adaptation indices of genotypes in the three groups previously considered (page 77) are given for both analyses (Table 8). It was found that genotypes with highest mean yields were distinct in both analyses (group 3). On a natural scale the mean yields were >300 grams and b>1.0. On the logarithmic scale the mean yields were greater than 2.4 and b-values ranged from 0.6 to 0.8. It is

Fig. 14. A scatter diagram of the line mean yield and the regression coefficient of genotypes when on a natural scale (combined analysis of 1967 and 1968 results for CCV).


CC$\overline{V}$
F6
F16
F25
μ
REGRESSION COEFFICIENT
2·0
1·8
1·6
1·4
1·2
1·0
0·8
0·6
0·4
0·2
100
140
180
220
260
300
340
LINE MEAN YIELD (gms / plot)

Line mean yields and regression coefficients for genotypes in the three adaptation groups as obtained from Log_{10} scale and natural scale.

Adaptation group	Log_{10} scale				Natural scale		
	Line mean yield Log_{10} gms/plot	b	DEV MS >0	Anti log	Line mean yield gms/plot	b	DEV MS> 0
1. Specifically adapted to high yielding environments.	2.01	2.86^{**}	**	102	218	1.67^{NS}	*
	1.89	2.67^{**}	*	77	150	0.92^{NS}	NS
	2.04	2.69^{**}	**	109	229	0.97^{NS}	**
	1.96	2.75^{**}	*	91	180	1.15^{NS}	NS
2. Specifically adapted to low yielding environments.	2.26	0.41^{**}	NS	182	195	0.52^{*}	NS
	2.25	0.43^{NS}	NS	177	205	0.62^{NS}	NS
	2.16	0.40^{*}	NS	144	162	0.50^{*}	NS
	2.30	0.36^{**}	NS	199	214	0.60^{*}	NS
	2.00	0.62^{NS}	**	100	136	0.70^{NS}	NS
	2.07	0.41^{NS}	**	117	146	0.51^{NS}	*
	1.94	0.59^{NS}	**	87	124	0.37^{NS}	**
	2.05	0.35^{NS}	**	112	163	0.53^{NS}	NS
3. Generally adapted.	2.46	0.65^{*}	NS	288	324	1.31^{NS}	NS
	2.43	0.60^{**}	NS	269	301	1.23^{NS}	NS
	2.44	0.64^{*}	NS	275	304	1.21^{NS}	NS
	2.42	0.71	NS	263	300	1.35^{NS}	NS
	2.47	0.61^{*}	NS	295	329	1.06^{NS}	NS
	2.50	0.80^{NS}	NS	316	366	1.52^{NS}	NS
	2.46	0.71^{*}	NS	288	322	1.23^{NS}	NS
	2.46	0.72^{NS}	NS	288	332	1.33^{NS}	NS

suggested that as far as generally adapted genotypes were concerned it did not matter which scale was used if the purpose was the broad identification of such genotypes. The definition of generally adapted types on the natural scale would be the one with high mean yield and b value > 1.0. Inspection of Fig. 14 will show that the lines in the highest mean yield class were mostly from F25 or F16 generations. The regression coefficient values ranged from 1.0 to 2.0. The scatter diagram showed that genotypes with other forms of adaptation responses were not so distinctly separated as they tended to merge into each other. The sensitive genotypes (those unstable at C67) could be hardly distinguished from the other genotypes. Yet the actual field performance suggested that they were biologically different types. Logarithmic transformation was effective in separating such genotypes and others into major adaptation groups. The scaling effect accentuated the differences and formed a basis for a meaningful interpretation of biological response in the field. The difference between the geometric mean (i.e. antilog of log mean in this case) and the arithmetic mean for genotypes in different adaptation groups needs some comment. Among generally adapted genotypes the geometric means were quite close to the respective arithmetic mean (Table 8). [redacted] Genotypes in group 2, which were stable in both years, had geometric means close to the arithmetic means. [redacted] Those which shattered had greater differences. It was the sensitive genotypes (group 3) that had the greatest difference between geometric means and arithmetic means. Such 'anomalies' arise from the simple mathematical relationship that the geometric mean is equal to the arithmetic mean only when all the values from which these means are derived are the same. The greater the variation in the individual values, the larger the difference between the geometric mean and the arithmetic mean. The difference observed in the table for genotypes in various adaptation groups stemmed from the fact that yield values were relatively more variable for certain groups of genotypes.

5. Results on scores on heading date, shattering, lodging, powdery mildew and spike characters.- CCV.

a. Heading Date.

The number of days from sowing to heading (date of awn emergence on 50% of the plants in a plot) was [redacted] closely associated with the mean yield and regression coefficient values of the genotype. There was also a close relationship between the number of days to heading following a late summer sowing (Feb. 1966), and from normal sowing in winter. These results will be presented together.

The mean and between line variance for each generation population from the summer sown experiment showed that (Table 9) the F16 generation was later in heading than the F6 generation. The means were significantly different. The F25 generation was slightly but not significantly later than F16. The between-line-within-generation variance was greater in the more advanced generations.

The normal sowing time for the trials in 1967 and 1968 ranged from late autumn to mid-winter. The mean number of days to heading for each generation population is given for each sowing time (Table 10). The F16 derived population was significantly earlier than the F6 derived population. The F25 generation was earlier than the F16 but this difference was significant for only two sowings. The shift in mean towards earliness, as noticed in the normal sowing time, is similar to the result of Jain (1961b) who studied the heading dates of F3, F5, F6, F13, F15 and F16 generations of CCV. In Jain's study the difference in mean days to heading between F3 to F18 was 2.44 days, close to that obtained between F6 and F25 in the present study. In both South Australia and Davis, barley is winter sown and the seasons

TABLE 9.

The average days to heading and between lines variance estimates for each generation derived population when sown out of season (9.2.1966)

Generation	Mean	6^2	n
F6	57.52	380.61	99
F16	60.65	430.34	100
F25	60.97	497.72	100

TABLE 10.

The average days to heading for each generation derived population when sown in normal range of seasons.

Site and Year	Sowing Date	Average days to heading			Variance ratio	L.S.D. .05
		F6	F16	F25		
B67	27/7	83.81	82.72	81.13	**	1.02
C67	13/7	88.60	86.72	85.89	**	1.17
M67	6/7	93.72	92.36	91.74	**	1.09
W67	6/6	111.70	110.00	108.50	**	1.31
B68	9/5	135.54	133.69	131.81	**	1.43
C68	12/6	118.71	117.40	116.45	**	1.17
M68	10/7	102.74	101.52	101.12	**	0.99
W68	25/6	106.68	105.16	104.33	**	1.09

are probably similar in terms of day length and temperature etc. The between line within generation variance estimates have been calculated for three sowing dates (Table 11) as they are adequate to illustrate the general trend. C67 was used because it had the lowest site mean. This sowing was also one of the latest. Late heading genotypes suffered greater stress in this environment. Waite had the highest site mean yields in both years. W67 was one of the earliest sown sites. One of the sowings of 1968 ([redacted] W68) was used [redacted] since all the lines were included in this trial. Table 11, when compared with Table 9, showed that the between line within generation variance following normal sowing was much less than following a summer sowing. The estimates for the three-generation populations were similar to each other. It is well established that locally adapted populations of self pollinated and cross-pollinated species with seeming uniformity in heading date reveal a considerable degree of genetic variability when grown under different photoperiodic and temperature conditions; (Review Cooper, 1954; Forster and Vasey, 1935).

The frequency distribution for days to heading in summer and the normal sowing time have been given in Table 12. In the distribution for the summer sowing only 9% of the F6 lines took more than 80 days to heading as contrasted to 17 and 25% of F16 and F25 lines. The dispersed nature of the distribution of the F25 lines suggested that selection pressure was probably not very strong and that different types were favoured in different years in the environment of Davis. This also accounted for the greater estimate of between line variance for the advanced generation population. In general, the F6 generation population responded to

TABLE 11.

Between lines variance estimates for each generation derived population when sown in normal range of seasons.

Sowing date	6^2		
	F6	F16	F25
6.6.67 (W)	21.2	18.3	20.2
25.6.68 (W)	15.8	15.1	12.1
13.7.67 (C)	18.9	14.4	15.6

TABLE 12

Frequency of lines for days taken to heading when sown out of season (summer) and a range of normal sowing times (winter) for each generation derived population.

a. Summer sowing (9.2.66)

No. of days.	Frequency of lines		
	F6	F16	F25
33-36	2	0	11
37-40	11	9	6
41-44	6	8	8
45-48	5	14	9
49-52	21	8	13
53-56	18	6	9
57-60	7	13	8
61-64	9	16	5
65-68	3	6	2
69-72	6	0	2
73-76	1	1	1
77-80	1	2	1
81-90	3	6	10
91-100	4	2	8
>100	2	9	7
n	99	100	100

b. Winter sowing (13.7.67), C.

No. of days	F6	F16	F25
78-81	1	4	11
82-85	22	36	39
86-89	32	27	22
90-93	2	11	14
94-97	13	8	5
98-101	2	-	-
n	92	86	91

TABLE 12 (continued)

c. Winter sowing (6.6.67), W.

No. of days	Frequency of lines		
	F6	F16	F25
97-100	1	4	9
101-104	7	3	6
105-108	11	22	24
109-112	33	32	35
113-116	28	21	17
117-120	12	4	-
n	92	86	91

d. Winter sowing (25.6.68), W.

No. of days	F6	F16	F25
93-96			
97-100	3	8	13
101-104	28	40	48
105-108	41	35	26
109-112	18	12	11
113-116	8	5	2
117-120	1	-	-
n	99	100	100

long day length and headed earlier in contrast to the advanced generation populations. There seemed to be some selection of genotypes [redacted] which did not require long day length and, as will be shown later were possibly [redacted] day neutral types.

The frequency distribution in the normal sowing time showed (Table 12b, c, d) that the F6 generation had a greater proportion of lines that were relatively late heading than the F16 and F25 generations. There was an increase in frequencies of earlier heading types from F6 to F16 and from the F16 to F25. This resulted in an overall shift in mean towards earliness.

The percentage of lines which were noted as heterozygous (based on within plot variation for awn emergence) for days to heading following summer sowing and winter sowing (August, 1966) has been given in Table 13. Within each season the number of heterozygous lines in the three populations were [redacted] similar. As with the between line variability, within line variability was greater in the summer sowing. In this case however, within line variability would have also been reduced because of an advance in generation. (The results from the adaptation trial did not suggest that the lines which were believed to be [redacted] heterozygous were in any way different from the rest for yield and adaptability).

When genotypes are sown out of season, days to heading are governed by sensitivity to photoperiod and vernalization requirements (Bell, 1939; Syme, 1968). In general, days to heading are either decreased or increased depending on whether the material is of a spring or winter type. Various intermediate

TABLE 13.

Percentage of lines recorded as heterozygous when sown in the field environments of 1966 during seed multiplication.

Generation	Summer sowing (9 Feb)		Winter sowing (5 Aug)	
	%	No-scored	%	No.scored.
F6	34	116	19	104
F16	44	111	22	94
F25	42	114	25	102

forms [redacted] also occur. Quantitatively long day plants will come to head early when sown in long days. Short day plants will be late. The day neutral type will be least affected. A cold requirement will mask the response to photoperiod and make all types late if planted in summer. Only controlled physiological experiments (Yasuda, 1961, 1963; Syme, 1968) can accurately differentiate between the various forms of physiological response.

Any interpretation regarding the physiological response of the present experimental population is based on field records and the possible interpretation is thus limited. It does not alter the fact that some change in the population regarding such response was measurable.

It is tentatively concluded that (1) the F6 generation had a greater proportion of lines of the long day type which were highly sensitive to photoperiod. Average day length (sunrise to sunset) in Adelaide for the month of February was about 13 hours and remained above 11 hours until April. Day length was shortest in the months of June-July (about 10 hours) and increasing thereafter (Table 14). Quantitatively long day types headed earlier following a February sowing. The same genotypes when planted in winter were delayed until their day length requirement was met. (2) Genotypes which did not have reduced days to heading in summer were either day neutral or had a cold requirement. Indeed in a composite population like CCV, genotypes with diverse forms of physiological response could be expected to occur.

TABLE 14.

Average day length (from sunrise to sunset) and average temperature (mean of maximum and minimum) for each month in Adelaide.

Month	Day length	Temperature, °F
January	14.2	71.4
February	13.5	71.0
March	12.5	69.0
April	11.5	62.6
May	10.5	57.4
June	9.9	53.2
July	10.0	51.4
August	10.7	52.7
September	11.6	56.2
October	12.7	59.9
November	13.8	64.3
December	14.4	68.2

The number of days to heading following summer and winter sowing have been given for each genotype in various adaptation groups (Table 15). The value for the winter sowing is the average of days to heading from four sowings in 1968. Similar relationships would be obtained if values from one sowing only had been given. The number of Days to heading [redacted] more shortened for all the genotypes ~~as~~ when the date of sowing became [redacted] later in the season. Three categories of genotypes have been compared:

(1) Genotypes specifically adapted to the high yielding environments (i.e. sensitive or unstable). Extreme forms from the F6 generation have been given.

(2) Genotypes specifically adapted to the low yielding environments (i.e. stable). A sample of F6 lines have been given.

(3) Generally adapted genotypes. These are in two groups; those grown in both years, and in the 1968 trial only. As pointed out earlier (page 75) most of the genotypes which were grown in the 1968 trial only had high yield potential and wide adaptation. The two best F25 lines were from this group. These are marked in the table.

The difference in the pair of values for days to heading (summer and winter) for each genotype in various adaptation groups formed the basis of interpretation. It was found that the specifically adapted genotypes were highly sensitive to day length as indicated by the large differences. Those which were specific to a favourable environment were relatively late in winter. Genotypes which were stable (specific to a poor environment) were early. Genotypes in the generally adapted groups showed relatively smaller differences indicating that they were less affected by the change in photoperiod. Such differences were

TABLE 15.

Number of days to heading for genotypes in each adaptation group, when sown in summer, and winter (mean of 1968 values). Each pair of values is for one genotype.

1. Specifically adapted to high yielding environment.		2. Specifically adapted to low yielding environment.		3. Generally adapted.			
				Sown in both years		Sown in 1968 only	
Summer	Winter	Summer	Winter	Summer	Winter	Summer	Winter
F6		**F6**		**F6**		**F6**	
39	124	53	113	65	116	91	114
49	119	48	114	67	109	92	117
50	122	38	116	194	121	90	116
54	115	36	112	61	113	96	116
37	123	40	109				
38	123	52	112	**F16**		**F16**	
42	126	39	107				
50	118	47	112	85	110	108	112
				64	111	114	113
				62	114	116	111
				44	114	90	116
				61	111	89	113
				61	114	84	113
				54	113	117	111
						108	114
						67	114
						106	112
				F25		**F25**	
				96	113	111*	117*
				82	112	117*	118*
				89	112	112	118
				64	117	98	118
				73	111	105	111
				107	112	95	114
				52	112	105	108
				57	114	84	118

* Genotypes which had highest line mean yields and above average stability.

minimal for those genotypes sown only in 1968 indicating that they were of a day neutral type. It is unlikely that their lack of response to long day length following summer sowing was because of winter growth habit. Had this been the case the heading would have been delayed more than that observed in both winter and summer. One of the F6 lines (generally adapted) took 194 days in summer and only 121 days in winter. This is thought to be typical of genotypes with a cold requirement.

Generally adapted genotypes were relatively early in the normal sowing as compared to the specifically adapted (to favourable) genotypes. Days to heading for two sensitive types and two generally adapted types have been plotted (Fig. 15) for all sowing times. The sowing dates are arranged on the Scale as differences in photoperiod will be directly related to sowing date. The figure is self explanatory and supports the results and the interpretations presented above.

Simple linear regression of yield on days to heading was calculated in each generation population at each site in 1967 (Table 16) and 1968 (Table 17). Results for 1967 showed that there were highly significant negative relationships between yields and days to heading at B67, C67, and M67 for all the three generation populations with the exception of F25 at B67. A comparison of regression coefficient estimates for the F6 and F25 derived populations at each site showed that they were in order of C>B>M>W. Comparisons within sites, showed that these estimates were in the order of F6>F16>F25. This pattern was consistent at all sites. The regressions for the populations were significantly

Fig. 15. Days to heading following sowing at different dates for two specifically adapted (sensitive) and two generally adapted genotypes.

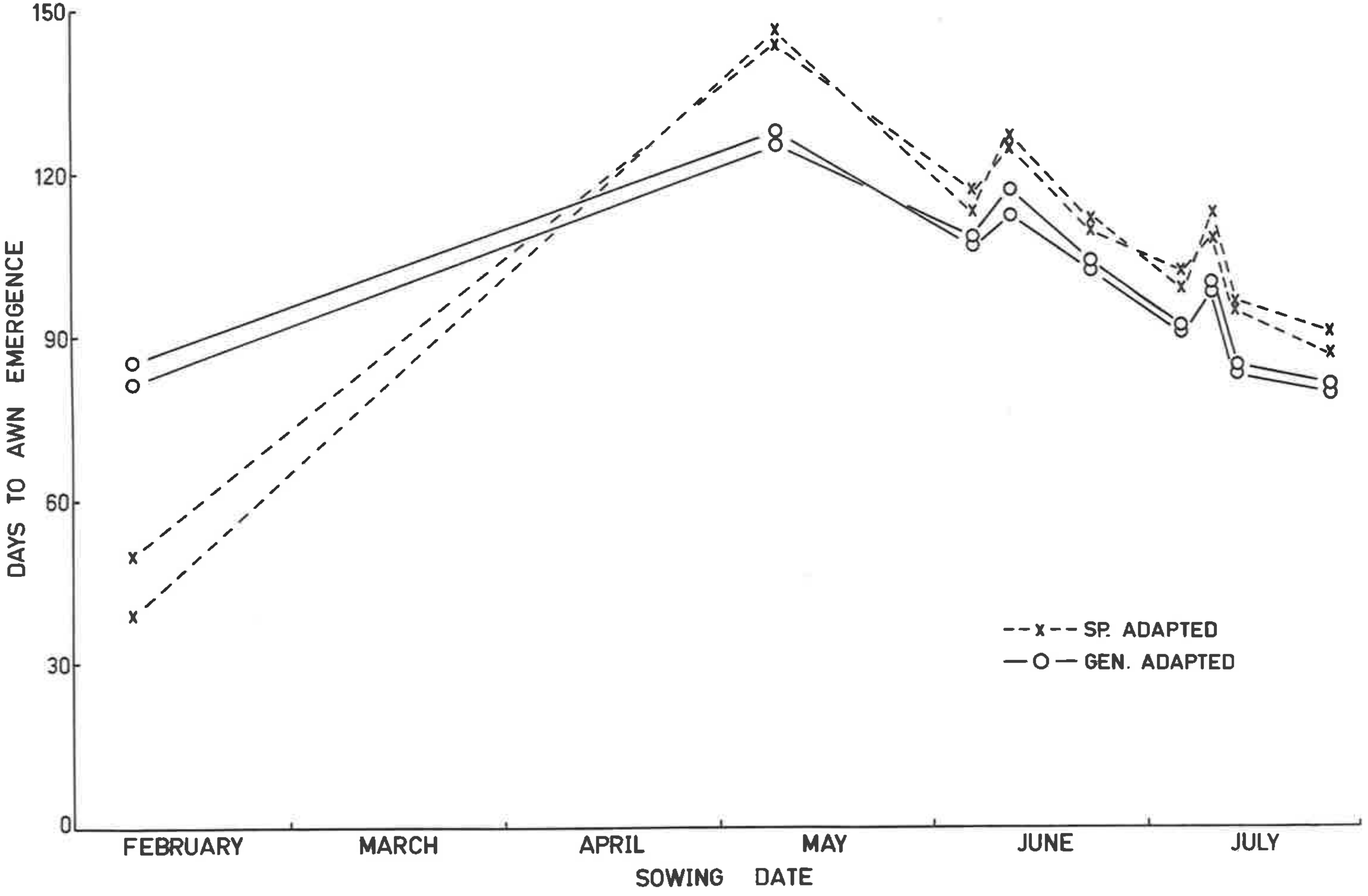

150
120
90
60
30
0
DAYS TO AWN EMERGENCE
FEBRUARY
MARCH
APRIL
MAY
JUNE
JULY
SOWING DATE
--x-- SP. ADAPTED
—O— GEN. ADAPTED

TABLE 16.

The simple linear regression of yield on days to heading for each generation derived population in 1967 environments.

	Bundaleer	Clinton	Minlaton	Waite
F6	-0.064***	-0.256***	-0.048***	-0.019*
F16	-0.033**	-0.135***	-0.031***	-0.009^{NS}
F25	-0.006^{NS}	-0.101***	-0.023***	-0.004^{NS}

TABLE 17.

The simple linear regression of yield on days to heading for each generation derived population in 1968 environments.

	Bundaleer	Clinton	Minlaton	Waite
F6	0.28**	0.30**	0.25**	0.01^{NS}
F16	0.03^{NS}	0.16^{NS}	0.14^{NS}	-0.07^{NS}
F25	0.08^{NS}	0.16^{NS}	-0.004^{NS}	0.06^{NS}

different at Clinton and Bundaleer only. The negative correlation between days to heading and yield is thought to be due to the effect of stress during the critical period between heading and maturation. Since F6 derived lines had a relatively greater proportion of late heading types, regressions of greater slope were obtained for this population at all sites. The estimate was significant even at the Waite site which was relatively the most favourable environment. In Clinton late heading types suffered most, 11 of the F6 derived lines failed to give any yield at all. The effect of drought on such lines was readily observed while scoring for heading date and on subsequent visits to the trial site.

The simple linear regression of yield on days to heading for 1968 environments is given in Table 17. Because of loss of grain in this year (detailed results to follow) an orderly relationship of the type observed in the 1967 season was not expected. A significant positive b value for F6 derived populations was obtained at all sites where loss of grain occurred, indicating that earlier types had lost more grain by shattering than late maturing types. The b values for advance generation populations were non-significant, suggesting that the population had improved for grain holding ability.

b Loss of grain due to shattering.

In 1968, loss of grain occurred at Bundaleer, Clinton and Minlaton in varying degrees. Loss was caused by shattering of ears, brittle rachis, and breakage at or below collar.

The frequency of lines in each generation population and the extent of loss in the three environments has been presented (Table 18). The loss was greatest in B68 and relatively less in C68 and M68 environments. Among the three [redacted] populations the loss was most severe in the F6 and least in F25 generation populations. This was reflected by the number of lines that were affected and the extent of loss. Similar differences between populations were noticed at Clinton and Minlaton but at a lower level of loss.

It was noticed that a substantial proportion of the F6 lines in 0-10% class showed a loss approaching 10%, whereas in the F16 and F25 populations a high proportion of lines were scored as 0 ([redacted] no visible loss) but [redacted] were included in 0-10% class for presentation. More than 90% lines in F16 and F25 derived populations were scored 0 at Minlaton.

Loss of grain at Bundaleer was mostly due to brittle rachis, and breakage at or below the collar. Loss at Clinton and particularly at Minlaton was mostly due to shattering of the ears. The experimental population was apparently subjected to different stresses that affected the grain holding ability of the genotypes to a different degree.

Bundaleer was the earliest sown of all the sites in 1968 and was one month earlier than any other sowing in both years. Clinton was also sown earlier than the other sites. Harvesting was done at the optimum time in terms of maturity of all the plots in the experimental block. Hence the loss of grain does not represent the result of a delayed harvest, but only the wind damage in that season.

It can be concluded from the results on shattering that the

TABLE 18.

Frequency distribution for loss of grain in F_6, F_{16} and F_{25} derived populations, at three locations in 1968.

Extent of loss in percent.	Bundaleer			Clinton			Minlaton		
	F_6	F_{16}	F_{25}	F_6	F_{16}	F_{25}	F_6	F_{16}	F_{25}
0-10	35	46	43	71	83	93	89	96	99
10-20	12	11	18	12	6	3	1	2	1
20-30	16	14	14	8	5	-	3	1	
30-40	8	8	13	5	4	3	0	0	
40-50	8	12	8	1	1	1	2	1	
50-60	4	3	2	1	-		4		
60-70	4	1	1	1	1				
70-80	6	2	1						
80-90	4	1							
90-100	2	2							

advance generation populations had a greater ability to retain ears and grains in the ears. Conversely genotypes which were inferior in this property were eliminated by the 'natural selection' that occurred during the generations of the composite cross population.

c. Lodging and powdery mildew.

The results on lodging and powdery mildew will be presented together for two reasons: (1) the environment where lodging occurred was also favourable for [redacted] powdery mildew, (2) it was difficult to ascertain the effect of both lodging or powdery mildew on yield.

The frequency distribution of lines for lodging and powdery mildew in the W67 environment (Table 19) shows that there was no [redacted] association ~~trend~~ with generation. The advanced generation population did not have a greater resistance to lodging or resistance to powdery mildew, under the field conditions prevailing in the W67 environment. Lodging in cereals is [redacted] likely to occur if the plants grow tall and have profuse growth, which is possible ~~only~~ in favourable environments (i.e. adequate moisture, nutrients). Lodging or powdery mildew did not occur or was insignificant in other environments (excluding W68).

Severe lodging (score approx. six or more) occurred in most of the experimental block in the environment of W68. Plots in other parts of the block did not lodge seriously due to less vegetative growth. This was a reflection of heterogeneity in soil fertility manifested under conditions of adequate moisture. A lodging score under such circumstances could not be used satisfactorily to differentiate between genotypes. Nevertheless, the experiment showed that the material was

TABLE 19.

Frequency of lines for (a) lodging and (b) powdery mildew scores (W67), for each generation derived population.

(a) Lodging.

Score*	Frequency		
	F6	F16	F25
0	17	20	21
1	28	23	31
2	22	23	18
3	8	12	9
4	5	0	1
5	3	2	1
6	5	2	5
7	2	1	1
8	1	1	3
9	1	2	1
n	92	86	91

* 0 = no lodging; 1 = 10 degrees bent, etc.

(b) Powdery mildew

Score*	Frequency		
	F6	F16	F25
0	5	8	3
1	8	13	10
2	27	24	26
3	16	13	18
4	17	18	18
5	9	5	9
6	8	3	4
7	2	1	1
8	–	1	1
9	–	–	1
n	92	86	91

* 0 = no sign of disease. For detail see Appendix 3

unable to stand a rather favourable environment and would lodge heavily. The lodged plots were hand harvested.

The possible influence of lodging and powdery mildew on the yield level of genotypes in the present experiment is hard to gauge. This stems from the fact that [redacted] generally, the lodged plots gave much higher yields than unlodged plots of the same genotypes in a poor environment. Studies on the influence of lodging on barley (Day and Dickson, 1958) and wheat yields (Wiebel and Pendleton, 1964) have shown that the extent of loss was dependent on the growth stage at which lodging occurred and on the severity of lodging. Lodging during heading time and at the milk stage was [redacted] the most critical and a yield reduction of up to 50% was reported (Day and Dickson, 1958) for 90 degrees lodged plots. Lodging in the W68 environment occurred after the 'soft dough' stage for the majority of the genotypes. Depending on the heading date, the genotypes would have been at various stages of grain filling. In general, early types would have suffered less compared to late types. However, this effect, if it occurred, was probably minor.

The reduction in yield due to powdery mildew was probably insignificant. Large and Dolling (1962) described a method of assessing loss in yield attributable to the mildew infection. The score system used in the present experiment (Appendix 3) was for preliminary observations and a score up to five is not suspected to have had much effect on yield. In the detailed study of genotypes in major adaptation groups lodging and powdery mildew score showed some [redacted] association with the general performance of the genotypes. This will be shown in a table presented in the next chapter with the discussion.

d. Results on spike characters.

Evidence for a shift in population over generations was also provided by some scores on spike characters such as awn type and husk colour. The results are given below:

Table 20. Percent of Genotypes.

Generation	Smooth awn	Black husk
F6	24	11
F16	18	5
F25	9	1

Decline in frequency of genotypes with smooth awn (semi-smooth included) and black husk is evident from the table. (Conversely, genotypes with rough awn and yellowish husk had increased). Black husk was almost extinct by F25. Jain's (1961a) study on CCV populations also showed a similar trend. In Jain's study the percent frequency of black husk genotypes at F3 and F18 were 13 and 0, respectively. The percent frequency for smooth awns were 62 and 41 for the same generations. The discrepancy in frequency of smooth-awned genotypes, as noted from the present study and Jain's results is rather puzzling. The awns were examined for smoothness and roughness as described by Wiebe and Reid (1958). A study of the results did not indicate that the genotypic performance for yield and adaptation was in any way associated with these spike characters.

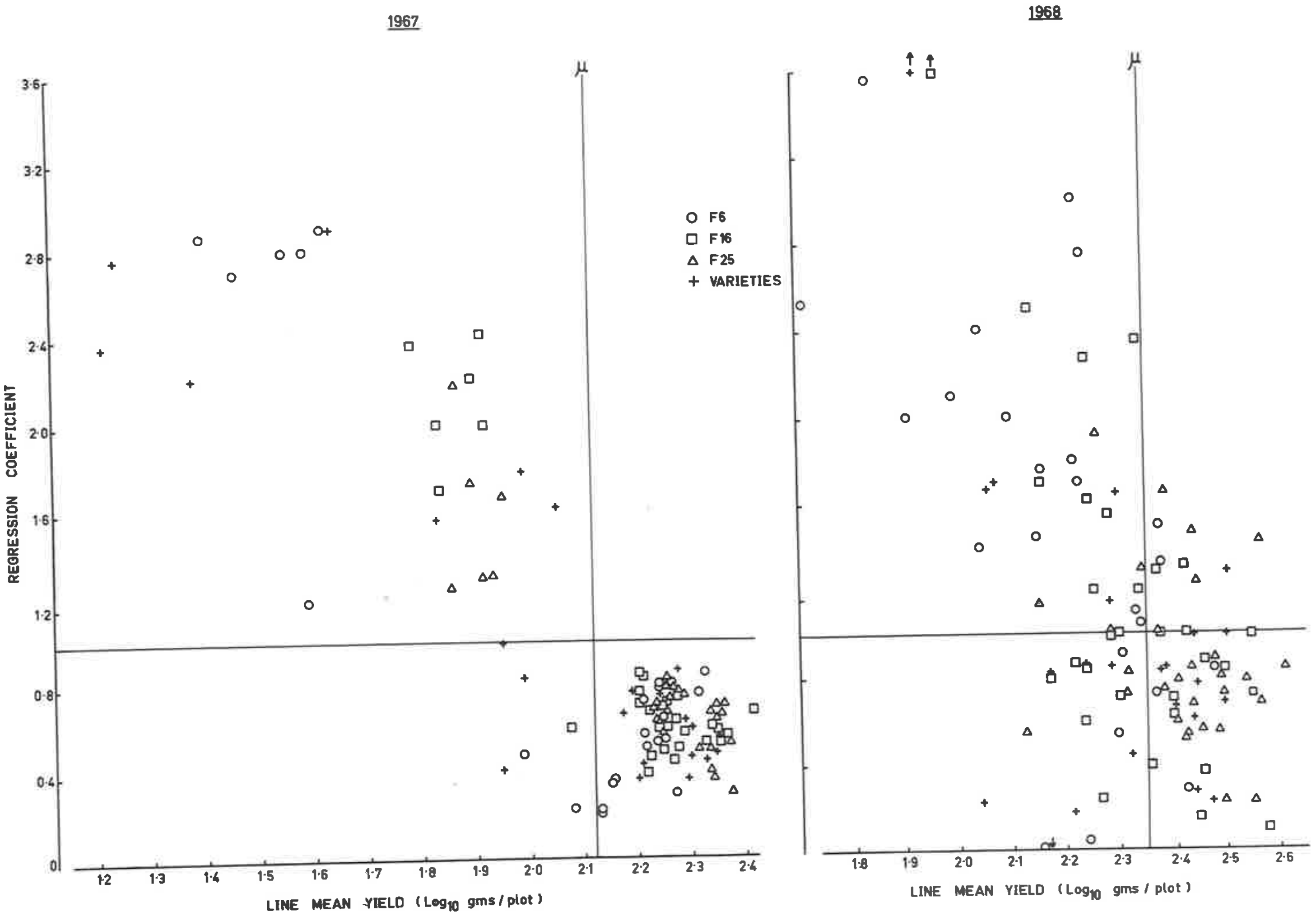
6. Morphological characters and components of yield - CCV.

A total of 24, 30 and 29 lines were selected from the F6, F16 and F25 generations on the basis of the 1967 results and scored for a number of characters in 1968. These lines were randomly selected from among different classes of line mean yields and regression values. The varieties were also scored. The distribution for mean yields and b of the selected lines and the varieties in the two years of the experiment are given (Fig. 16). The nature of the changes in both the mean yields and the regression coefficients for genotypes with different adaptation response and genotypes that shattered has already been elaborated. The chief objective of the detailed scores was to study whether genotypes with various adaptation responses differ in the level of expression of morphological characters and the components of yields in the varying environments. At the conclusion of the experiment it was realised that the results obtained might not reveal such associations due to the following circumstances:

(1) The environments were not very diverse in 1968. In 1968 the sensitive genotypes (as known from the 1967 results) were not very different from the generally adapted types.

(2) Loss of grain due to shattering made it impossible to correlate the scores for the characters with yield. It is obvious that estimates of the components of yield etc., cannot be expected to have any relation with 'yield at harvest' if loss occurs in between. Results on the characters are [redacted] presented, however, as they show some interesting shifts over the generations, and these may account for some of the differences in yield and adaptation observed previously.

Fig. 16. The scatter diagram for a sample of lines from the CCV, and the varieties in two separate years. Detailed scores were made on this material in 1968.


1967
1968
μ
μ
○ F6
□ F16
△ F25
+ VARIETIES
REGRESSION COEFFICIENT
0
0·4
0·8
1·2
1·6
2·0
2·4
2·8
3·2
3·6
1·2
1·3
1·4
1·5
1·6
1·7
1·8
1·9
2·0
2·1
2·2
2·3
2·4
LINE MEAN YIELD (Log$_{10}$ gms / plot)
1·8
1·9
2·0
2·1
2·2
2·3
2·4
2·5
2·6
LINE MEAN YIELD (Log$_{10}$ gms / plot)

The means for each character for each population and the group of varieties are given for each site (Table 21). 12 of the 23 varieties were of the two-row type. CCV populations did not have this character. The varieties were initially selected to represent a range of adaptation response and also included a number of genotypes with low mean yield and low regression coefficient values. Hence the average of the varietal group may not necessarily be an ideal 'control' for comparison with the composite-cross populations. The comparison would have been more useful if they were the parental group of CCV. The following points are of interest:

(1) The difference in the mean of the varietal group and the CCV populations.

(2) The change in means from the F6 to F16 and F25 generations.

An L.S.D. (calculated on the average number of samples) is given for the characters which showed significant differences in the variance ratio tests. At times there were no large differences between the populations although there are between the varieties and the populations.

Spike number.- Significant differences were obtained. The varieties had a greater number of spikes than the F6 generation. There seemed to be a consistent trend for an increased spike number as the generation advanced. The values for the Waite site are missing because of ~~the~~ difficulty of counting in ~~the~~ severely lodged plots.

Grains/spike.- Significant differences were obtained. The varieties had fewer grains than the mean of the lines in the F6 generation. There seemed to be a trend towards increased grain number from F6 to F16. Changes from F16 to F25 were not consistent.

1000-grain weight.- The differences were non-significant. The varieties and the F6 generation means were similar. There was some trend towards an increase in mean from the F16 to F25.

Spike length.- Significant differences were obtained. The varieties had longer spikes than the F6 generation. A trend toward~~s~~ a decrease in spike length from F6 to the later generations was apparent at all sites.

Green tiller No.- The differences were non-significant. The trend in mean showed that the varieties had more tillers than the F6 generation. A trend towards a decrease in tiller number in the advanced generation populations can be observed. A reverse trend was observed for the number of fertile spikes.

Height.- Significant differences were obtained only at Bundaleer. The varieties were shorter than the F6 generation. A trend toward~~s~~ decrease in height from the F6 to F16 and F25 generations can be observed. Height of the F25 population was still greater than that of the varieties.

The table shows that for the three components of yield the superiority of the F25 population over the F6 population was distinct (although not always statistically significant) at all sites. The difference between F6 to F16 to F25 was not clear cut. A larger number ~~of~~ samples would have had to be measured to reduce the experimental error and enable the detection of small differences.

Results of leaf measurements are not presented. Preliminary analysis showed that a large variation can occur in the size of leaves from the same plot or among samples within or between populations. A very much larger number of leaf samples would have to be measured to

TABLE 21.

Average of each character for each generation derived population and the varietal group at each site.

Spike No.

Site	Varieties	F6	F16	F25	Variance ratio	LSD 5%
B	37.2	31.8	32.4	34.1	*	2.8
C	34.3	27.3	30.1	31.1	***	2.5
M	36.9	29.3	30.8	31.2	***	2.4

Grains/spike

Site	Varieties	F6	F16	F25	Variance ratio	LSD 5%
B	30.9	36.8	40.3	37.8	***	3.0
C	30.8	34.2	35.8	38.0	***	3.2
M	31.6	38.2	38.7	38.0	***	3.0
W	37.5	44.3	48.9	46.3	***	3.6

1,000 grain wt,g

Site	Varieties	F6	F16	F25	Variance ratio	LSD 5%
B	39.4	38.6	38.5	39.6	N.S.	
C	42.4	43.1	42.8	45.3	N.S.	
M	44.0	43.7	43.3	46.2	N.S.	
W	42.9	42.2	42.9	44.8	N.S.	

TABLE 21 (continued)

Spike length (cm)

Site	Varieties	F6	F16	F25	Variance ratio	LSD 5%
B	6.79	5.98	5.92	5.24	***	0.34
C	6.86	6.22	5.64	5.71	***	0.37
M	7.23	6.48	6.18	5.91	***	0.34
W	7.69	6.99	6.70	6.16	***	0.39

Tiller No.

Site	Varieties	F6	F16	F25	Variance ratio	LSD 5%
B	83.2	79.7	78.3	76.1	N.S.	
C	71.6	69.6	67.0	66.3	N.S.	
M	78.9	72.8	70.9	67.2	N.S.	
W	91.3	92.6	85.2	86.3	N.S.	

Height, cm

Site	Varieties	F6	F16	F25	Variance ratio	LSD 5%
B	75.0	82.0	79.6	78.0	**	3.0
C	76.5	84.7	82.0	81.9	N.S.	
M	74.9	79.1	78.1	77.4	N.S.	
W	93.6	99.4	100.0	100.2	N.S.	

establish significant and meaningful differences.

The site mean estimates for each [redacted] character (the average of all the genotypes at each site) at Bundaleer, Clinton and Minlaton (Table 22) suggest that different combinations for the components of yield occurred.

In general, the trend for changes in the generation means over locations (Table 21) was similar to the site means for each character, i.e. there is no evidence of population - site interaction.

Some conclusions may be drawn from the results on these detailed scores. The significant differences were chiefly due to the difference between the varietal group and the other material. The varieties had more tillers, more fertile spikes, a lesser number of grains per spike and a longer spike length than the composite-cross populations. This was [redacted] due primarily to the contribution of two-row genotypes in the varietal group. It is interesting to note that the 1000-grain weight of the varieties and the F6 generation were similar in spite of more grains/spike in the latter. The results on the mean height and spike length for the different generation population agree with the results of Jain and Allard (1960) who showed that the stature and spike length decreased in the advanced generations. Though there was a trend towards increased [redacted] number of grains per spike and 1000-grain weight the change was not very distinct. The experiment of Jain and Allard, and Jain (1961a) showed a distinct trend of increase in seed number and grain weight. However, their scores were on spaced plants and from one trial only. Before their results are relevant to the present study

TABLE 22.

Average of all genotypes (i.e. site mean) at each site for each character.

Site	gr/spike	1000 gr.wt.	Spike No.	Spike length	Tiller No.	Height
B	36.7	39.0	33.8	5.98	79.8	78.6
C	34.7	43.4	30.7	6.10	68.6	81.2
M	36.6	44.3	32.0	6.45	72.4	77.6
W	44.0	43.2	-	6.88	88.8	98.3

a more detailed study is necessary to investigate the correlation of estimates obtained from the spaced plants and that obtained at a crop density, especially for characters like seed number and seed weight.

7. Results on composite cross XVI population.

A study of the results on the CCXVI population showed that the population had not changed significantly for adaptation and yield within the generation intervals studied, i.e. F2 and F9 or F9DA (grown at Davis and Aberdeen alternately). Presentation of the results will be confined to (a) an adaptation analysis of yield obtained in eight environments sampled to two years, (b) scores for heading date, shattering etc.

The site means for CCXVI populations are given in Table 23. These means are slightly higher than site means for CCV populations in the same environments (Table 4).

The scatter diagram and frequency distribution diagram for the line mean yield and regression coefficient values are given in Figures 17 and 18. The following conclusions can be drawn from an inspection of these diagrams:

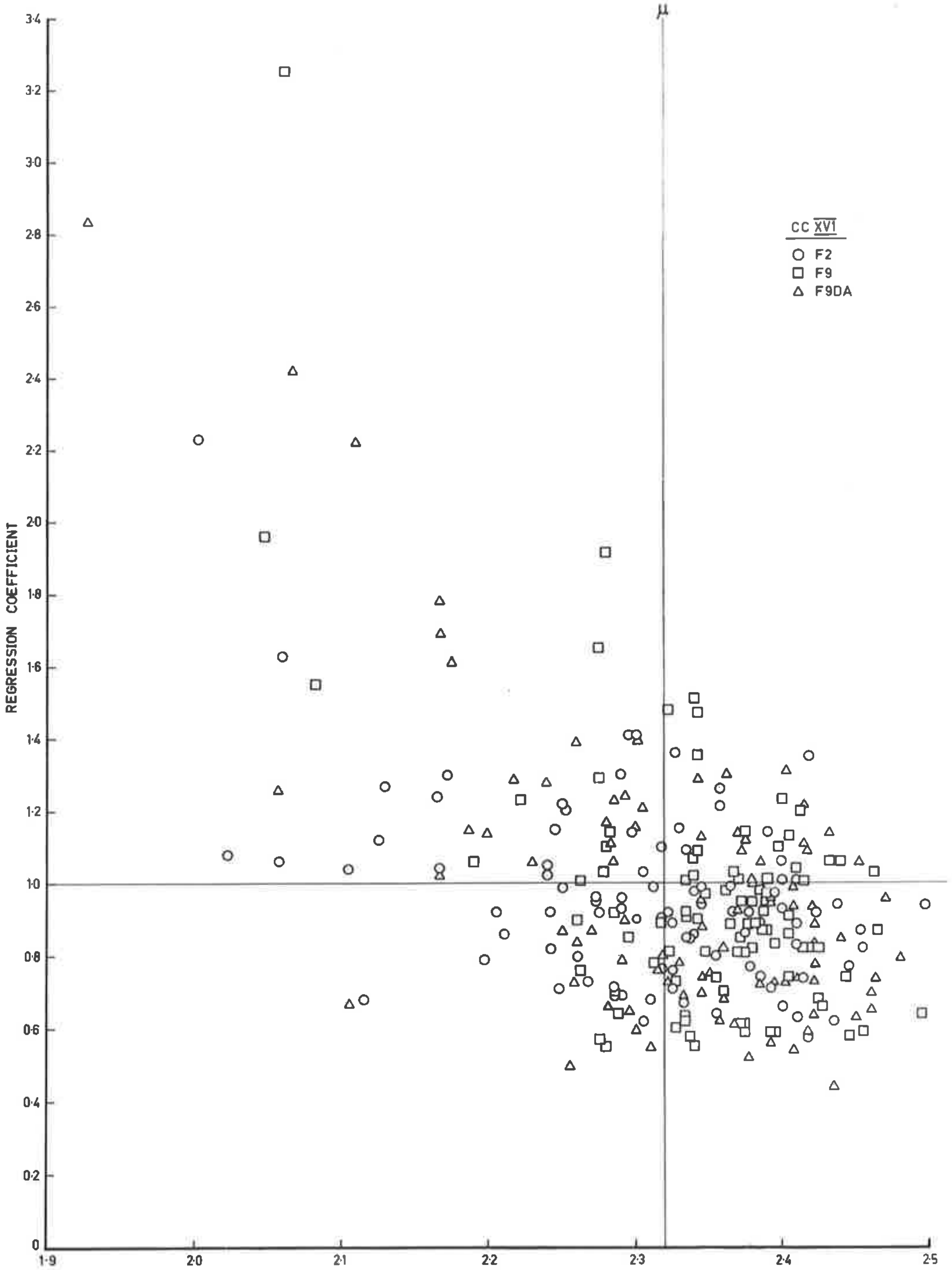
(1) There are no marked differences in the distribution of F2 lines and F9 or F9DA lines. (Fig. 17). Detailed study shows that the number of lines which exceeded the grand mean yield were 51, 74 and 56 for F2, F9 and F9DA populations respectively. The frequency diagram (Fig. 18) shows that the number of lines in the 2.4 to 2.5 mean yield class are 18, 23 and 25 for F2, F9 and F9DA populations.

TABLE 23

Site means of yield values for various environments of 1967 and 1968 trials.

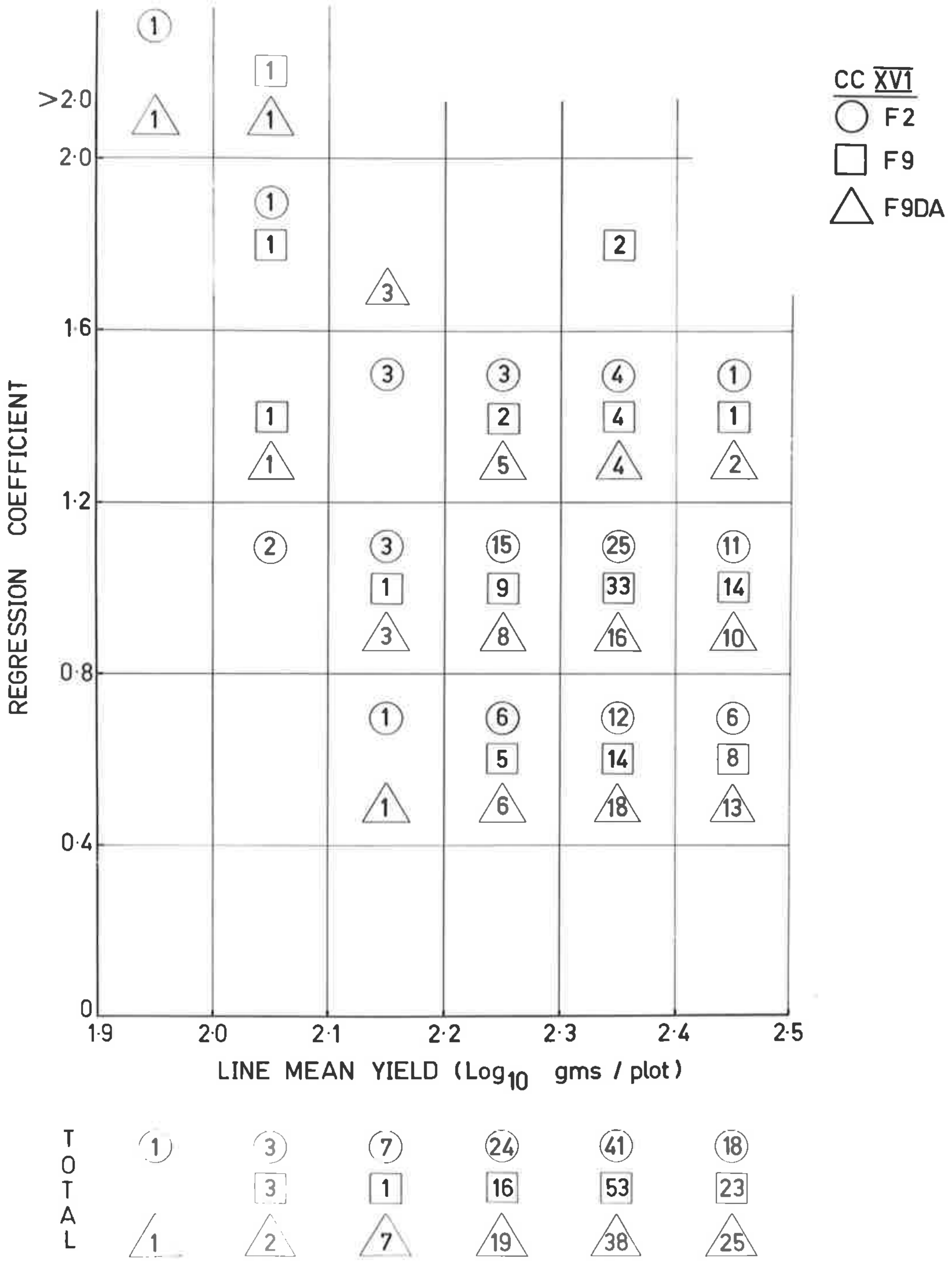
Environments	Site means		
	Log_{10}gms/plot	gms/plot (antilog)	Bushels/acre
C67	1.83	67	6.7
B67	2.19	156	15.6
B68	2.26	182	18.2
C68	2.33	216	21.6
M67	2.40	252	25.2
W67	2.45	283	28.3
M68	2.50	316	31.6
W68	2.62	418	41.8

Fig. 17. A scatter diagram of the line mean yield and the regression coefficient of genotypes from CCXVI F2, F9 and F9DA generations for the combined analysis of 1967 and 1968 results.



μ
CC XVI
○ F2
□ F9
△ F9DA
REGRESSION COEFFICIENT
3·4
3·2
3·0
2·8
2·6
2·4
2·2
2·0
1·8
1·6
1·4
1·2
1·0
0·8
0·6
0·4
0·2
0
1·9
2·0
2·1
2·2
2·3
2·4
2·5
LINE MEAN YIELD (Log$_{10}$ gms / plot)

Fig. 12. The two way frequency of the line mean yields and the regression coefficients. The numbers within the symbols indicate the number of lines in each class for each generation.


CC XV1
F2
F9
F9DA
REGRESSION COEFFICIENT
>2·0
2·0
1·6
1·2
0·8
0·4
0
1·9
2·0
2·1
2·2
2·3
2·4
2·5
LINE MEAN YIELD (Log10 gms / plot)
TOTAL
1
3
7
24
41
18
3
1
16
53
23
1
2
7
19
38
25

(2) The number of lines with regression coefficient values > 1.0 were 32, 35 and 34 for F2, F9 and F9DA populations.

Though the F9 population apparently [redacted] improved slightly as indicated by the greater proportion of lines that exceeded the grand mean; the F9DA population did not seem to be different from the F2. It is concluded however, that the overall similarity between the three populations is more striking than any differences.

Certain features of the CCXVI population are different from the CCV population. For example:

(1) Genotypes of the sensitive type were almost absent from this population. Most of the lines were characterised by regression coefficient values from 0.6 to 1.4.

(2) The frequency distribution of line mean yields (over eight environments) for the populations from CCV and CCXVI are given in Table 24. It shows that frequencies were similar in the CCXVI F2 and CCV F25 population. The highest mean yield class had a few more lines from F9 or F9DA population as contrasted to F25 but none exceeded this class.

The 1967 and 1968 results were studied separately to determine if the conclusions based on the combined analysis were also true for the separate analysis. Results from CCV had shown that most of the exceptionally high yielding lines were from the group of genotypes which could be included in the 1968 trial only. A total of 18 lines from the CCXVI (5, 5 and 8 from F2, F9 and F9DA) were grown in

The frequency of lines for line mean yields (over eight environments) in various generation derived populations in both composite crosses.

	Line mean yields class								
	1.6-1.7	1.7-1.8	1.8-1.9	1.9-2.0	2.0-2.1	2.1-2.2	2.2-2.3	2.3-2.4	2.4-2.5	Total No.
CCV F6		1	4	8	17	30	24	8	-	92
CCV F16		1	-	3	2	15	30	28	7	86
CCV F25				1	4	6	26	37	17	91
CCXVI F2				1	3	7	24	41	18	94
CCXVI F9				-	3	1	16	53	23	95
CC XVI F9DA				1	2	7	19	38	25	92

the 1968 trial only. None exceeded the mean yield of the best F25 derived lines. It was observed that the 5 F2 and the 5 F9 lines tended to give high mean yields (2.40 to 2.72); but the mean yields of the 8 F9DA lines tended to be less than 2.4 and none exceeded 2.5. The group of 8 F9DA lines which were delayed in heading in the summer multiplication (and hence could not be included in the 1967 trial) may have had a cold requirement and been long day types, and thus differed from the day neutral types from the F2 and F9. A detailed study of the days to heading values suggested that this group of genotypes were relatively late in both summer and winter as compared to the day neutral types.

The mean days to heading and variance following a summer sowing (Table 25); the within generation between line variance following winter sowing (Table 26); the percentage of heterozygous lines (Table 27); the mean days to heading in winter sowings (Table 28); and the frequency distribution for various sowing dates (Table 29) are all given. Some conclusions may be drawn:

(1) The mean days to heading of the F9 population was slightly earlier than the F2 population following a summer sowing. Following winter sowings the tendency was reversed and the F9 was consistently later than the F2. The differences were significant for only two sowings (C68, W68). The mean-days-to-heading of F9DA population was later than the F2 populations for all winter sowings. The differences were significant for

five sowings. The frequency distributions for various sowing dates suggest that the F9DA population revealed a greater interaction with environments for days to heading than the F9 population. Attention is drawn to 25.6.68 sowing (Table 29d) which showed a higher proportion of late types in the F9DA as compared to F9. Similar distributions were also noted for the other sowing dates for which the means were significantly different (distributions not given). It seems that alternate sowing at Aberdeen has favoured genotypes which require long days. The shift however is slight. Wheat varieties from this region are relatively late heading in South Australia (Rathjen, personal communication).

(2) The within-generation between-line variance estimates for different sowing times (Table 25, 26) showed the same trend as observed in the CCV populations; that is, a greater variability was revealed when the plants were grown out of season. A higher proportion of F2 lines was scored as heterozygous (Table 27) as compared to F9 or F9DA lines. In winter sowings the percentage was reduced but was still considerably greater in the F2 than in advanced generation populations. The greater proportion of heterozygous lines in the F2 (the progenies of which were scored at F3 and F4) was expected.

TABLE 25.

The mean days to heading and between lines variance estimates for each generation derived population when sown out of season (9.2.1966).

Generation	Mean	σ^2	n
F2	58.85	168.10	99
F9	57.87	321.50	100
F9DA	57.35	254.20	100

TABLE 26.

Between lines variance estimates for each generation derived population when sown in normal range of seasons.

Sowing date	σ^2		
	F2	F9	F9DA
6.6.67 (W)	14.5	11.0	16.1
25.6.68 (W)	8.6	14.2	15.8
13.7.67 (C)	8.5	11.0	10.2

TABLE 27.

Percent of lines recorded as heterozygous in the two environments of 1966, during seed multiplication.

Generation derived	Summer sown (9 Feb.)		Winter sown (5 Aug.)	
	%	No Scored	%	No Scored
F2	74	113	33	101
F9	46	116	18	107
F9DA	53	112	17	104

TABLE 28.

The average days to heading for each generation derived population when sown in normal range of seasons.

Site and Year.	Sowing Date.	Average days to heading.			Variance Ratio	LSD5%
		F2	F9	F9DA		
B67	27/7	80.25	80.44	81.49	*	0.90
C67	13/7	84.78	85.19	85.39	ns	
M67	6/7	90.43	91.31	91.68	*	0.94
W67	6/6	107.31	108.40	107.8	ns	
B68	9/5	129.84	130.81	130.75	ns	
C68	12/6	113.09	114.15	114.31	*	0.93
M68	10/7	95.43	95.87	96.41	*	0.72
W68	25/6	101.86	102.94	103.29	*	0.99

TABLE 29.

Frequency of lines for days taken to heading when sown out of season (summer) and a range of normal sowing times (winter) for each generation derived population.

(a) Summer sowing (9.2.66).

	F2	F9	F9DA
33-36	-	1	4
37-40	4	10	10
41-44	4	8	5
45-48	15	5	4
49-52	10	10	14
53-56	22	21	20
57-60	10	8	9
61-64	8	8	10
65-68	8	4	3
69-72	7	6	8
73-76	5	1	3
77-80	3	1	2
81-90	1	4	4
91-100	1	1	-
>100	1	3	4
n	99	100	100

(b) Winter sowing (13.7.67), C.

	F2	F9	F9DA
78-81	8	7	6
82-85	53	54	51
86-89	26	23	24
90-93	7	9	9
94-97	-	1	2
98-101	-	1	-
n	94	95	92

TABLE 29 (continued)

(c) Winter sowing (6.6.67), W.

	F2	F9	F9DA
97-100	6	1	3
101-104	13	9	15
105-108	34	34	27
109-112	37	41	35
113-116	4	10	11
117-120			1
121-124			
n	94	95	92

(d) Winter sowing (25.6.68), W.

	F2	F9	F9DA
93-96	4	2	1
97-100	20	19	17
101-104	59	57	46
105-108	13	15	24
109-112	3	5	10
113-116		1	1
117-120			
121-124		1	1
125-128			
n	99	100	100

The results on heading behaviour of the CCXVI population may be surprising as the shift in mean for this character was slightly in the reverse direction to that in the CCV populations. A comparison of the distributions for days to heading following various sowing dates and within generation between line variance for CCV populations and CCXVI populations will show that the latter population was more homogeneous from the start.

Comparison of mean days to heading for different generation populations from CCXVI and CCV (Table 28 and Table 10) will show that the CCXVI F2 population mean was earlier than the CCV F6 population mean in all sowings. The difference was about three days in the 1967 seasons and up to 7 days in the 1968 seasons. There was a shift toward lateness in the CCXVI while in CCV it was the reverse. Thus the difference between the CCXVI F9 and CCV F25 was reduced and was mostly of non-significant nature. The CCV population can be expected to have reached the optimum for days to heading after a long-term natural selection in the environment of Davis. From the overall comparison between CCV and CCXVI populations and in view of small shift from the F2 to F9 in CCXVI it is evident that the mean heading days of the CCXVI base population was close to the optimum. Since the CCXVI population was constituted from selections from advanced generations from various composite crosses (presumably grown in Davis) such a result is not surprising.

The estimates for the simple linear regressions of yield on days to heading for various environments (1967) are given in Table 30. The result can be interpreted in a similar manner to

TABLE 30.

The simple linear regression of yield on days to heading for each generation derived population in 1967 environments.

	Bundaleer	Clinton	Minlaton	Waite
F2	-0.078^{***}	-0.122^{***}	$-.012^{ns}$	-0.012^{ns}
F9	-0.011^{ns}	-0.151^{***}	-0.005^{ns}	-0.010^{ns}
F9DA	-0.085^{***}	-0.160^{***}	-0.042^{***}	-0.025^{***}

those for the CCV populations. A point of interest is that the slope for the F9DA is significant at all sites indicating a negative relation between days to heading and yield. The slope for the F2 population is significant at Bundaleer and Clinton; and that of F9 at Clinton only. This again shows the rather similar nature of the F2 and F9 populations and the difference of the F9DA population. Simple linear regressions of yield on days to heading for the 1968 results showed (estimates not given) significant positive relation at the Bundaleer site only for F2 and F9 populations. The relation for F9DA was non significant.

The frequencies for shattering scores in various sites in 1968 are given in Table 31. Though the frequencies in 0 to 10 class is slightly higher (Bundaleer) for F9 or F9DA as contrasted to F2, the overall distribution is not much different. A comparison with the CCV populations (Table 18 and 31) shows that the CCXVI F2 generation population was similar to the CCV F16 generation population and inferior to the F25 population (in view of frequencies in > 60% class) for non-shattering property.

The degree of lodging and powdery mildew infection in CCXVI populations (scored in W67) were similar to that of the CCV populations. There was no difference from F2 to F9 (or F9DA). CCXVI populations lodged as badly as CCV populations in W68. This result suggests that the non-lodging property was probably not one of the criteria used in choosing the material used as parents of the CCXVI population.

TABLE 31.

Frequency distribution for loss of grain in F2, F9 and F9DA derived populations[*] at three locations in 1968.

Extent of loss in %.	Bundaleer			Clinton			Minlaton		
	F2	F9	F9DA	F2	F9	F9DA	F2	F9	F9DA
0-10	52	67	65	82	91	89	98	98	99
10-20	11	10	12	5	3	3	1	2	1
20-30	12	7	8	3	2	2			
30-40	2	3	2	4	2	2			
40-50	7	2	1	2	1	2			
50-60	5	5	4	1	-	1			
60-70	4	2	3	1	-	1			
70-80	3	2	2	1	1				
80-90	2	2	2						
90-100	1	-	1						

[*] 99, 100, and 100 lines in F2, F9 and F9DA populations.

DISCUSSION.

A. The adaptation analysis in relation to the present experiment.

This section of the discussion will be devoted to considering the adaptation analysis and the various concepts of stability on the basis of results from the present and other experiments. Various features of the experiment will also be discussed.

The analysis of yield data showed that the experimental error and the deviations from regression sum of squares of individual genotypes were heterogeneous. This can be considered as corollary of an ~~the~~ experiment [redacted] in which a large number of diverse genotypes are grown in [redacted] diverse environments. Each replicate consisted of more than 300 plots, and covered an area of approximately 0.3 [redacted] acre. Some genotypes showed a greater variation in physiological and morphological characters [redacted] such as days to heading and ability to retain grain. This would also have been so for other characters that might have affected the individual genotypic performance. This automatically resulted in heterogeneity of error from site to site and from one year to another; the two chief contributors to heterogeneity of error being (1) soil heterogeneity and (2) differential response to the environment. Heterogeneity of errors has been reported from even small trials involving a few genotypes (Immer et.al. 1934; Salmon, 1951; Frey, 1964).

Yates (1936) pointed out the problem of conducting a large field experiment and suggested that a pseudo-factorial design would cut down the experimental error arising through soil heterogeneity. Though theoretically such design seems to be useful; the complexities of layout should be weighed against the question, i.e. would such design have substantially reduced the experimental error in a trial of the kind reported here? Previous experiments at the same sites have been conducted as randomized blocks without revealing the need for different designs.

Reduction of heterogeneity of error through analysis of weighted means (Yates and Cochran, 1938) or other forms of transformation (Bartlett, 1947) are some of the theoretical possibilities. The publication of Yates and Cochran pointed out the problems and the difficulties of fulfilling theoretical requirements for the analysis of results from a field trial. It was implied that the induction of homogeneity of error though necessary from a theoretical point of view and possible mathematically, it might often be unpractical for the results of most of the field experiments.

Finlay and Wilkinson used a logarithmic transformation in the analysis of yield values from their experiment as it induced a high degree of linearity of the regressions of individual yields on the site yield means. In their data it also ~~induced~~ a reasonable degree of homogeneity of experimental error. Logarithmic transformation of yield values in the present experiment was not effective in inducing a homogeneity of error. It, however, induced a high degree of linearity and made the interpretation of results more simple. Results on experiments reported by Finlay (1963b, 1968) were all analysed on a logarithmic scale. Other workers have conducted adaptation analysis on natural yield values (Eberhart and Russell, 1966; St. Pierre *et*. *al*. 1967; Johnson *et*. *al*. (1968). Which scale should be used for adaptation analysis? Choice of the scale should be guided by two main considerations (1) that the parameters obtained from the analysis should give a measure of the biological response in the field (2) that it should be simple to interpret.

Some comment on an adaptation analysis on a natural scale is relevant. It was suggested earlier (page 48) that the low range of regression coefficient values (0.7 to 1.3 approximately) found by Eberhart and Russell might have been due to the narrow range of environments that were sampled and also due to lack of diversity of the genotypes in the trial, both contributing to the low genotype-environment interaction. The results of the present experiment when on a natural scale gave a range of regression coefficients that were not as high as that from the analysis of transformed values, in spite of the extreme range of environments and the diversity of the genotype. Indeed the regression coefficient values were reversed in the two analyses, i.e. the sensitive and the generally adapted genotypes tended to have low and high b-values, ~~respectively~~ on the natural scale and high and low b-values on a logarithmic scale, respectively. This change in the regression coefficient values in the two forms of the analyses occurs because [redacted] of the logarithmic transformation [redacted] reduces relatively the variation in yield in the high yielding environments and increases it in the low yielding environments. Under certain instances this induces linearity in the response of the genotypes. Thus a different scatter diagram is obtained from using the two scales. Yet such differences seem to have been overlooked by St. Pierre et. al. (1967) who attempted to fit the triangular configuration obtained by Finlay and Wilkinson to their results analysed on a natural scale.

The diagram of triangular configuration of scatter of points shown by Finlay and Wiliinson (reproduced on page 45) is a generalised version for interpretation of adaptation response and is valid for analysis on logarithmically transformed values. The forms of the scatter diagram will depend on the number and the diversity of the genotypes as well as the variation in the environments.

A comparison of the results of the present experiment on the two scales showed that the analysis on a logarithmic scale gave [redacted] a reliable measure of the adaptation response of the genotypes and was easily interpreted. If the regression coefficient value is the measure of stability, on a natural scale, the genotype with high mean yield and high b value will be called more 'unstable' in that the rate of improvement in yield with change in environment was greater for such genotypes. Genotypes which failed to give yield in the poor yielding environment (C67) would have been called 'stable' as these have relatively smaller b values compared to generally adapted types. To call such genotypes 'stable' is misleading. In a fluctuating environment the ability to give above average yield in all the environments can be considered to be more important than the nature of stability measured by b value per se. On a logarithmic scale the regression coefficient of such genotypes will be close to 1.0 (Finlay and Wilkinson have defined regression coefficient value of 1.0 as average stability). It is obvious that the meaning of stability in the terminology of Finlay and Wilkinson (i.e. on a logarithmic scale) has a special connotation and is not merely a rate of change in yield, as indicated by regression coefficient value alone. It follows that, though the analysis of results on a logarithmic scale might be preferable for presentation of results for reasons outlined previously (page 82), it is necessary to examine the natural yield values of individual genotypes for detailed study.

Rasmusson (1968) commented that the stability which is conferred by homeostasis is of more interest than stability resulting from resistance to diseases. Johnson et al. (1968) used a regression analysis on the yield results of four varieties of wheat from 283 trials (Separate analyses were carried out for other set of varieties also). The trials covered a period of 23 years and were grown at a number of regional stations. Individual trials in which stem rust, insects, birds, hail or winter kill were "the major limiting factors" were excluded. It was argued that "Each (of these factors) has the potential of dominating or masking all other factors of the environment. To have included trials in which these were the major effects on performance would have obscured the measurement of the environment as the end product of many factors". In their study the differences in varietal adaptation were largely determined by the differential response to the stress and non stress environments. It was found that the variety mean yield and the regression coefficient value together gave a good measure of varietal differences for adaptation. Finlay (personal communication) when measuring stability tends to eliminate from his analysis those instances where yield has been affected by disease or other observable limiting factors.

The approach of measuring the stability of the genotypes which might be due to homeostasis apart from resistance to specific causes have a special purpose. The latter such as disease resistance can be identified easily and rectified by known techniques while the former indicates the 'potential' of the genotypes but is harder to assess.

Although disease, lodging, shattering, winter kill etc., are referred to as limiting factors there is no clear demarcation for stress condition which is a complex of factors. The term stress is used to indicate the apparent cumulative effect of drought, the temperature effect, the uptake of nutrients, and other undefined factors.

It follows that in the evaluation of the results from a large number of field trials, the experimenter himself has to decide whether certain trials should be excluded from the analysis. Such decisions are guided by a few basic considerations:

(1) Did some abnormal factor operate in the environment? A factor would be considered abnormal if it was of low frequency at that site in the past.

(2) Even if factors like disease, shattering, winter kill, etc., might be common in some sites the result from such a site might be excluded to assess the genotypic performance in the absence of their effects. This might be useful for deciding on varietal recommendations for other areas.

(3) The magnitude of the experimental error might be another reason for excluding some trials. It is also possible that experimental error might increase if some limiting factor is operating. This appears not to be the case in a drought environment. It is well established that the experimental error tends to be relatively small in a stress environment than in a non stress environment (Salmon, 1951; Frey, 1964) due to unrestricted expression of variability under favourable growing conditions. The influence of soil heterogeneity is also likely to show up when adequate moisture is available.

In the present experiment the differences which were measured in the 1967 environments were apparently free of specific limiting factors such as disease and can be attributed to differences in response to stress or non-stress environments. The 1968 results largely measured differences which could be attributed to variation in grain holding ability. The loss of grain of many of the genotypes 'masked' the 'potential' adaptation response to environmental conditions which prevailed in that year. In the study of population changes reported here, a measure of the differential response of genotypes to the observable factors was [redacted] a necessary part of the adaptation and results from all the sites were analysed. The study of results from various analyses permitted the evaluation of the population differences against different backgrounds.

Tests for significance of the deviation mean square (Eberhart and Russell, 1966) for separate years and over all sites for both years provided some understanding of this test. Theoretically, the use of deviation from regression as one of the stability parameters can be considered to be desirable. It is suggested that the study of the magnitude of deviations at each point and the cause for it should be a subsequent and necessary step in the evaluation of the experimental material. These measures are important for an estimation of the reliability of performance of [redacted] a genotype~~s~~ before its releas[redacted]e as a commercial variety. Breese's (1969) emphasis on deviation as a measure of stability might be appropriate for such a purpose. In the analysis, however, only ~~a~~ large deviations are likely ~~is likley~~ to be significant statistically as was evident from the results of the present experiment. Since site mean is an average of all the genotypes in the trial, regression of each genotype on site mean values is dependent on the performance of other genotypes. This also effects the deviation from the fitted slope. In the present experiment the deviations from regression were highly heterogeneous. The experimental error was also large and heterogeneous. Thus only very large deviations were significant (and mostly in the combined analysis only). This test was not sensitive on natural scale as well, due to similar reasons.

It is concluded that, although the test for deviation mean square (or test for difference of slopes) was not very sensitive and questionable from a statistical point of view, it nevertheless emphasized the population differences (Fig. 12 and ~~Fig~~. 14) in the present study. The test for deviations was useful in separating a number of F6 lines which would have been considered stable from b value alone. It is obvious that if the results from the trials, where a specific factor is operating, [redacted] are not included, the test for deviation might not be important as there would not be a large deviation.

Finally, it is emphasized that in the study of genotypes one should take recognition of individual performance at each site. This would permit the full assessment of the individual genotypes as to its potential for yield and adaptability in the presence or absence of specific causes. Parameters [redacted] such as mean yield, regression coefficients, or deviations from regressions are only preliminary measures for the rapid comprehension of the performance of a large number of genotypes in the trial.

B. Changes in the yield and adaptation of the CCV population and the association of various characters.

A table has been formed (Table 32) to summarize some of the findings on the CCV generations. Results on an illustrative sample of genotypes (grown in both years) are given for each of the three adaptation categories (individual yield values are given in Appendix 4):

(1) Specific adaptation to a high yielding environment.

(2) Specific adaptation to a low yielding environment.

(3) General adaptation.

It was expected on the basis of results of adaptation studies of Finlay and Wilkinson (1963) that genotypes which are specifically adapted to high yielding environments (also called unstable or sensitive) are likely to be eliminated from a heterogeneous population when grown in a fluctuating environment that includes stress conditions. As some of these might have high yield potential and therefore be useful as parents in a breeding programme, it was desirable that such genotypes be identified earlier, in composite cross populations.

The results showed that the F6 generation had a greater proportion of these sensitive genotypes. Absence of highly sensitive types from the F16 and F25 generation showed that such genotypes were at a disadvantage under natural selection and from the results it was evident that these would have been eliminated in a stress environment. A detailed study of the results showed that only a few of the sensitive genotypes from the F6 had a high yield potential. It is emphasized that these genotypes have been tentatively classif-

TABLE 32.

Adaptation indices and associations of major agronomic characters for a sample of genotypes in various adaptation groups as revealed in a different set of environments.

Adaptation group	1966 Results	1967 Results					1968 Results						Combined Analysis		
	Days to heading following summer sowing	Line Mean Yield $\log_{10}$ gms/plot	b	Average† days to heading	Lodging Score (W	Powdery Mildew Score (W67)	Line Mean Yield $\log_{10}$ gms/plot	b	Average† days to heading	Shattering Score			Line Mean Yield $\log_{10}$ gms/plot	b	DEV M.S> 0
										B	C	M			
1. Specifically adapted to high-yielding environments (F6)	39	1.57	2.86	99	0	2	2.46	1.56	124	0	0	0	2.01	2.86^{**}	**
	49	1.56	2.79	99	1	3	2.23	1.70	119	1	0	0	1.89	2.67^{**}	*
	42	1.60	2.78	103	0	6	2.48	0.82	126	0	0	0	2.04	2.69^{**}	**
	54	1.60	2.97	98	1	2	2.33	0.81	117	2	1	0	1.96	2.75^{**}	*
2. Specifically adapted to low-yielding environments (F6)	53	2.23	0.45	92	4	3	2.29	0.37	113	4	0	0	2.26	0.41^{**}	NS
	48	2.28	0.30	90	3	4	2.22	0.18	114	6	1	0	2.25	0.43^{NS}	NS
	38	2.18	0.48	92	1	6	2.12	0.64	116	1	2	2	2.16	0.40^{*}	NS
	36	2.27	0.35	91	7	3	2.34	0.51	112	0	1	0	2.30	0.36^{**}	NS
	40	2.16	0.44	88	8	3	1.88	3.31	109	9	3	3	2.00	0.62^{NS}	**
	52	2.23	0.50	89	4	3	1.91	1.95	112	6	4	5	2.07	0.41^{NS}	**
	39	2.17	0.52	87	5	5	1.74	2.53	107	6	1	1	1.94	0.59^{NS}	**
	47	2.26	0.53	88	6	3	1.84	3.55	112	8	3	2	2.05	0.35^{NS}	*
3. Generally (F16) adapted	62	2.43	0.68	91	1	2	2.49	0.86	114	0	0	0	2.46	0.65^{*}	NS
	64	2.37	0.57	91	0	0	2.49	0.82	113	2	0	0	2.43	0.60^{**}	NS
	61	2.32	0.55	92	2	2	2.56	0.56	111	0	0	0	2.44	0.64^{*}	NS
	61	2.29	0.61	93	0	2	2.55	0.72	114	0	0	0	2.42	0.71	NS
(F25)	96	2.37	0.53	89	0	1	2.57	0.63	113	0	0	0	2.47	0.61^{*}	NS
	82	2.37	0.73	90	0	1	2.64	0.72	112	1	0	0	2.50	0.80^{NS}	NS
	89	2.33	0.64	89	1	1	2.56	0.60	112	0	0	0	2.46	0.71^{*}	NS
	64	2.32	0.62	93	0	1	2.61	0.56	117	0	0	0	2.46	0.72^{NS}	NS

† From four sowings in winter.

ied in group 1 in view of their overall performance in the environment of 1967 and 1968. Their yields at M67 or W67 was lower than that of genotypes in group 2 (Appendix 4). It is likely that a number of these were of the kind poorly adapted to most of the environments. It is possible that genotypes with much higher yield potential but with specific adaptation to a very favourable environment might have been eliminated from the CCV population before the earliest generations sampled in this experiment (i.e. before the F5). It is apparent that any hoped-for yield improvement through out-crossing of these genotypes will not be achieved in a composite cross selection under natural selection because they are eliminated from the populations in a very few generations.

The sensitive genotypes were relatively late in heading and were long day responsive (Table 32). Lodging and shattering scores of these were insignificant. These genotypes might have escaped shattering because of late maturity rather than having the non shattering property per se. However, the fact that they did not lodge suggests that they had strong straw.

The F6 generation also had a greater proportion of lines which were specifically adapted to low yielding environments. They had above average yield in the Clinton trial which had severe moisture stress and was sown late. In W67 (the high yielding environment in 1967) their yield was usually below the population average. Their lodging score was high, indicating weak straw. In the trials of

1968 some of them shattered severely at Bundaleer, Clinton and Minlaton, while others shattered relatively less. Table 32 shows that these genotypes as a group had a much higher lodging and shattering score as compared to genotypes in the other two adaptation groups. A detailed study of the results showed that in the high yielding environment if W68 their yield was much lower than the population average. It is emphasized that this could not have been due to the possible effect of lodging on yield as genotypes from other adaptation groups which also lodged had much higher yield in the same environment. This suggests that these genotypes were inherently low yielding types or stable, i.e. those which are unable to respond to improved environment. Table 32 shows that these genotypes were also relatively earlier heading and day length responsive. These could be the recombinants with greater genotypic contribution from the parental varieties which were adapted to a region of poor agricultural practice, low soil fertility and long day length condition. In rice [redacted], Jennings (1964) noted that the tropical rice varieties which were adapted to poor growing conditions had weak straw and lodged when grown under improved management and failed to give increased yield. These rice varieties were sensitive to day length and were relatively late maturing.

It can be concluded that genotypes which had low yield potential would contribute fewer progeny in a high yielding environment or in years conducive to shattering and would be eliminated from the population. It is evident from the 1968 trial that the advance generations contained fewer genotypes liable to shatter. Elimina~~t~~tion of brittle rachis genotypes from the CCV populations has also been reported by Jain (1961a). [redacted] Natural selection superimposed on conditions of cultivation, [redacted] operated against genotypes which shatter.

It follows that as the genotypes with specific adaptation or those at a disadvantage due to specific causes were eliminated, the proportion of generally adapted genotypes increased in CCV. These genotypes had a high yield potential and wide adaptation. Lodging and shattering scores for generally adapted genotypes were ~~of~~ insignificant [redacted]. However, it should be remembered that in the favourable environment of W68 they lodged. They showed considerable resistance to powdery mildew infection. In general, a greater infection occurred in genotypes from the other groups.

I will now consider the few exceptionally high yielding lines in the F25 generation that were available for growing in 1968. These lines are not represented in Table 32 but they may be considered as belonging to the generally adapted group. Table 15 in the results shows days to heading for generally adapted lines grown in 1968. The generally adapted type tended to be early and had a range of about 9 days in heading. The best F25 lines tended to be late within this range and did not [redacted] shatter[redacted]. In view of the performance of other generally adapted types grown in both years it might be reasonable to predict that these superior F25 lines would have ~~been~~ performed ~~adapted to~~ well in the stress environment of C67 as well. It is also evident from their presence in the population. All of the superior lines were day neutral. They did not respond to long day prevailing during the late summer and came to heading in early winter. Less seeds were obtained from this multiplication probably due to the low fertility in cold weather. Seed multiplication had to be repeated before these lines could be grown in the 1968 trial.

Examination of days to heading after normal winter sowing for all the adaptation groups (Table 32) ~~what~~ shows that the generally adapted genotypes (group 3) were about a week earlier than the sensitive genotypes (group 1) and about two days later than the genotypes with low yield potential (group 2). The table shows that the generally adapted group did not have genotypes with extreme values for days to heading as among genotypes with specific adaptation. Finlay and Wilkinson (1963) also found a range of maturity in the generally adapted group. Genotypes with specific adaptation tended to be late or early. Finlay (1968) suggested that breeding for general adaptation will retain variability in the population. Though the generally adapted genotypes from CCV population tended to be intermediate in days to heading the range of variability in this group cannot be suggested to be larger than in the other adaptation groups. The table shows that there is an overlap in the distribution for days to heading when all the groups are considered together. Finlay (1968) found a range of heading dates extending over three weeks among generally adapted genotypes. His experimental material included the international collection of barley and thus probably contained more variability.

It is important to note that natural selection had selected genotypes which had high yield potential and wide adaptation. This strengthens the soundness of Finlay's emphasis on breeding for high yield and wide adaptation through artificial selection procedures. Studies were reviewed earlier (page 49) which showed that such objectives have been achieved in wheat and barley. These also indicated possibilities for further progress. It also emphasized the importance of adaptation studies covering a range of environments as only such a procedure can identify genotypes with various adaptation responses.

It is also important to note that the genotypes with high yield and wide adaptation from the CCV population headed ~~were~~ relatively earlier than ~~heading (as compared to~~ unstable types~~)~~ and the evidence from days to heading suggest that they were of day neutral type. The Mexican wheat varieties with high yield and wide adaptation are also day neutral (Borlaug, 1965). The wide adaptability of Taiwan rice varieties is believed ~~[illegible]~~ to be based on their relative insensitivity to photoperiod and temperature (Jennings, 1964). One possible advantage of the day neutral character is the lack of interaction with day length associated with different sowing dates or locations.

The generally adapted genotypes were relatively early at all locations in both 1967 and 1968. It can be generalized from the study of Aspinall et. al. (1964) on barley and Chinoy (1962) on wheat, that the earlier types would have an advantage under stress conditions. May and Milthorpe (1962) pointed out that in an area with a Mediterranean climate the most important characteristic for drought resistance of a winter crop is earliness in maturity. The effect of extreme temperature on genotypes which differ in a few days to anthesis has also been suggested to be quite critical in otherwise optimum conditions (Frey and Maldonado 1967). However, the high yield and adaptability of the generally adapted genotypes cannot be attributed to earliness alone as there were also genotypes which were earlier heading but had low yield potential. The latter were usually long day responsive. It is possible that in both CCV of barley and with Mexican wheats the genes that govern the day neutral response are also associated with genes that confer high yield potential and adaptability.

The differential survival of genotypes in a heterogenous population need not be fully accounted for by the interplay of heading behaviour and the fluctuating environment, or the presence of specific characters like shattering, disease, susceptibility to winter kill etc. Nor can the importance of any one character be considered to be mutually exclusive of the other characters. A differential response due to characters less readily observed than heading date or disease can occur and these may be reflected on the yield and fitness of the individual genotype. Laude and Swanson (1942) in their study of a wheat varietal mixture attributed the superiority of the variety Kanred to its capacity to crowd out plants of 'less well adapted' varieties; and to its greater productibity. Lee (1960) reported a study on competition on two barley varieties: Vaughn and Atlas, first described in an earlier study (Suneson, 1949). Vaughn was at a disadvantage in a mixture with Atlas and two other varieties, even though it was superior in yield when sown in monoculture. Lee's study showed that the advantage of Atlas over Vaughn was evident after the jointing stage. From the study of the depth and distribution of the roots of these two varieties an explanation for the greater competitive advantage of Atlas was made. Atlas had a dense mass of roots which was thought to indicate its adaptation to a dry hillside of the Mediterranean region where it originated. Vaughn had long roots and this was considered to indicate its adaptation to alluvial soil of Iraq where it possibly originated. In the mixture, after the onset of stress, Atlas had an advantage over Vaughm. The importance of root distribution for the adaptation of genotypes to a stress environment has been recently emphasized by Hurd (1969).

It can be assumed that the generally adapted genotypes that survived and increased in the composite cross V population might be able to compete more successfully because of its root system or some other characters which conferred on it a high degree of fitness in bith stress environments as well as in improved environments.

What other characters might be associated with the yield and adaptation response of the genotypes? The ratio of fertile tillers to total number of tillers per plant was a character that had increased among genotypes in the later generations. Watson et al. (1958, 1963) showed that high yielding genotypes had a greater proportion of fertile spikes to the total number of tillers, however, Krishnamurthy (1963) reported he had found high yielding varieties with a large number of tillers many of which were senescent. Thorne (1962) and Puckridge (1968) produced evidence for the movement of assimilates from senescent tillers to surviving tillers. The varieties included in these studies formed a narrow range of selected genotypes. Under natural selection, production of fewer tillers, a high proportion of which are fertile, seems to have a selective advantage and to be associated with the generally adapted genotypes. The advanced generation population was also shorter in stature.

Though the importance of shorter stature to avoid lodging is understandable, there is no evidence to suggest that this character as well as characters like tiller number, leaf area etc., were causing the differences in yield and adaptation. They may have been merely linked to more important characters like heading date. In retrospect, the aim of associating morphological characters or components of yield with yield and adaptation is thought to be over ambitious. One would conclude from the relevant literature (Review Langer, 1967) that the results of such studies relating yield and morphological characters are often conflicting.

C. The composite cross technique as a breeding method.

The results obtained from the CCV population confirm some of Suneson's conclusions that the composite cross population will have a greater proportion of superior types in the advanced generations. It also supports his prediction that these genotypes would show greater adaptability. Two other important questions remain to be examined. Will this be true of all the composite cross populations? How long should one grow the composite cross population to derive the greatest benefit and what is the upper limit of the value of the selections that might be obtained? Suneson (1956) suggested that 15 generations of natural selection are desirable, and proposed three alternative procedures:

(1) continued natural selection with prospects for significant gains in yields to accrue 'through a working life time';

(2) cycles of hybrid recombination and natural selection to give a form of recurrent selection; or

(3) conventional selection and evaluation of individual lines from the population (the proportion of well adapted and high yielding lines being a partial function of generations).

As far as I am aware, reports on the yield of selections from composite cross populations are confined to Suneson's brief note on selections from CCII made at the F12, F20 and F24 (reviewed page 21). He found that three exceptionally high yielding lines were obtained from F24. CCII populations have been grown for more than forty generations (Suneson, 1963) but no information is available as to whether better selections were obtained thereafter. Although a yield improvement in the CCV bulk has been reported (Suneson, 1956; Jain and Suneson, 1966) the value of selections from this population were previously unknown.

The present experiment showed that there were exceptionally high yielding lines in the F25 generations which were distinct from the best lines from F16 or F6; and that the yields of the two top lines in the F6, F16 and F25 generations exceeded the average yield of the two best check varieties (California Coast and C.I. 3576) by 16, 30 and 75 per cent (1968 results). The genotypes with high mean yield also had wide adaptation.

The question arises to whether the superior lines found in the F25 were the result of recombinations between genotypes that remained in the population in latter years or was the result due to an effect of sampling; the loss of inferior types would mean that a greater proportion of superior types could be present in samples taken at different stages. The seeds for each generation were a bulk sample from the population.

The aspects of retaining genotypes in a population and the chances for recombination were discussed by Frey (1968) who compared the relative values of single-seed-descent (where seed from each plant is represented) and random systems (i.e. bulk samples) for selecting seeds to propagate bulk hybrid populations of self-fertilized species. In the random bulk system, differential reproductivity of parental plants affects the composition of the subsequent generation. From a theoretical point of view single-seed-descent might be preferable for retaining the genotypes and thereby permitting a greater degree of recombination among various types in the population. It is realised that certain degree of variability will be retained in the compsoite cross populations due to heterozygote advantage and the dynamics of the population of the kind reviewed by Allard et.al. (1968). However, in the sampling system used for propogating the composite ~~compsoite-~~cross population and in view of the sample size (seeds from about 10,000 plants, up to F10; and 5,000 plus thereafter were kept for propogation of CCV - Suneson, personal communication) the original gene pool would have been rapidly narrowed down in each subsequent generation. The loss of genotypes with specific adaptation was also evident from the results on CCV previously considered. It is concluded that the possibility of recombination within the sample retained for propogation might not have been very significant in terms of diversity and under the known rate of out-crossing. However, the crux of the composite cross technique is - would the population have improved had there been more cross pollination? The study by Jain and Suneson (1966) on CCXIV was reviewed on page 15, ~~which~~ suggests that the population in which regular recombination was achieved was actually inferior to the control.

The results on CCXVI is relevant at this juncture. Suneson (1963) commented that CCXVI had the highest level of yield from the beginning among all the composite crosses. CCXVI was constituted from crosses of advance generation selections from various composite crosses. Therefore, its initial high level of yield can be expected. If there had been an improvement in yield from the F2 to F9 generations in the present study of the CCXVI population it might have indicated that further improvement could be expected beyond the F25 generations of CCV. There did not seem to be any significant change from F2 to F9. Suneson's (1956) results on the four composite cross populations (CCII, CCV, CCXVI and CCXIV) also showed that the population did not improve until about the F7 generation. Jain (1961a) commented that this might have been due to the presence of many inferior segregates in the early generations. The same reason is less likely to account for the lack of improvement in CCXVI populations because of superior material that was used in the constitution of this population. More likely is that the population norm of CCXVI is close to the optimum for the Davis environment. This was evident from the similarity of the mean days to heading of the CCXVI F2 or F9 population and that of CCV F25 population and also from the adaptation studies. It suggests that there is a limit beyond which the composite cross population might not improve, and that the changes that can be expected in composite cross populations are largely determined by the diversity in the base population.

In view of the results on CCXVI it is suggested that the change in CCV observed with generations is more likely to be the result of loss of inferior genotypes rather than that of recombinations in later years. It is not known if all the inferior genotypes have been eliminated from CCV by the F25 generation. This could be only determined by growing some of the still later generation Because of stabilizing selection; the moving 'optima' due to fluctuating environment; and the population dynamics of the kind reviewed earlier there will always be range in types retained even in the advance generations. Suneson grew a sample of the CCXVI population alternately at Davis and Aberdeen possibly with hope of getting widely adapted genotypes. The results suggest that this goal has not been achieved, instead genotypes with long day and vernalization requirements have increased in the F9DA population. There was also indication that some superior types might have decreased in frequency from this population (in view of performance of lines included in 1968 trial only).

Barley is grown in spring in Aberdeen and is liberally irrigated. Aberdeen has a short season continental climate (Suneson, 1963) with long day length. It is reasonable to assume that the long day responsive genotypes would have a shortened vegetative period and be adapted to the short growing season. It is likely that the day neutral genotypes by virtue of their being 'day neutral' might not have adjusted to a short season in this instance. It is possible that in the bulk the growth of day length responsive genotypes might have even contributed some competitive advantage over the day neutral types. If a sample of the CCXVI population had been grown constantly at Aberdeen, it would have consisted mostly of long day types.

Borlaug (1965) selected high yielding lines with wide adaptation by propagating two generations a year in Mexico, one in winter at Sonora and the other in summer at Tolucca. Selection was carried out by the pedigree method. [redacted] The varieties that resulted from such selection procedure were also day neutral.

The features of the alternate locations used by Suneson and Borlaug are of interest. By propogating CCXVI population in Aberdeen, Suneson subjected the material to higher latitude (relative to Davis) with day length above 16 hours from sowing to heading. Davis has a day length of about 12 to 13 hours from sowing to heading. Borlaug, on the other hand, grew his summer crop at Tolucca at a lower latitude (relative to Sonora). Day length from sowing to heading at Tolucca is from 12 to 14 hours; at Sonora it is about 12 hours. It is likely that propagation of material at too widely different photoperiodic conditions might not result in a day neutral type but that genotypes adapted to the respective day length requirement might be favoured.

Great care has to be taken in choosing the alternate site and in the timing of the out of season sowing. Consideration has to be given to the day length and the temperature that occur during various growth stages at the place where the material is grown. It might be hazardous to select for yield from plots grown out of season if the effect of these factors are not taken into account.

One significant outcome of the present experiment was the observations which suggested that the lines with high yield potential and wide adaptation were the day neutral types and that these were easily distinguished during summer growing. It might be possible to select some of the best recombinants from the composite cross by screening the population for day neutral types by summer sowing or in a glass house. Only genotypes which did not respond to a long day should be retained for further multiplication and replicated trials. The assumption is that this would permit the screening of a very large proportion of the inferior types which would be slowly eliminated by natural selection in the normal growing season. The sample retained might have genotypes which were similar or better than the best lines obtained in the present experiment from the advanced generations. As a large number could be screened in this way it may be possible to select for superior genotypes when they are in very low frequency in the early generations. Screening should be attempted at about F10. A sample of the population can be propagated without selection for the retention of variability.

Are composite cross or mass reservoirs a useful aid to the plant breeder? Allard and Hansche (1965) emphasized that mass reservoirs are not a substitute for conventional methods of breeding but should be regarded as an additional breeding tool for exploring and recombining a wide range of variability that would otherwise not be utilized. Results from CCV indicate that some useful gene combinations have arisen from recombinations between the original diverse parents. It also shows that genotypes with a high yield potential also have competitive ability and remain in the population. However, the need to wait for 20 to 25 years for natural selection to sort out superior types is a severe handicap. It will only be of use if superior recombinants can be drawn from the populations at an earlier date.

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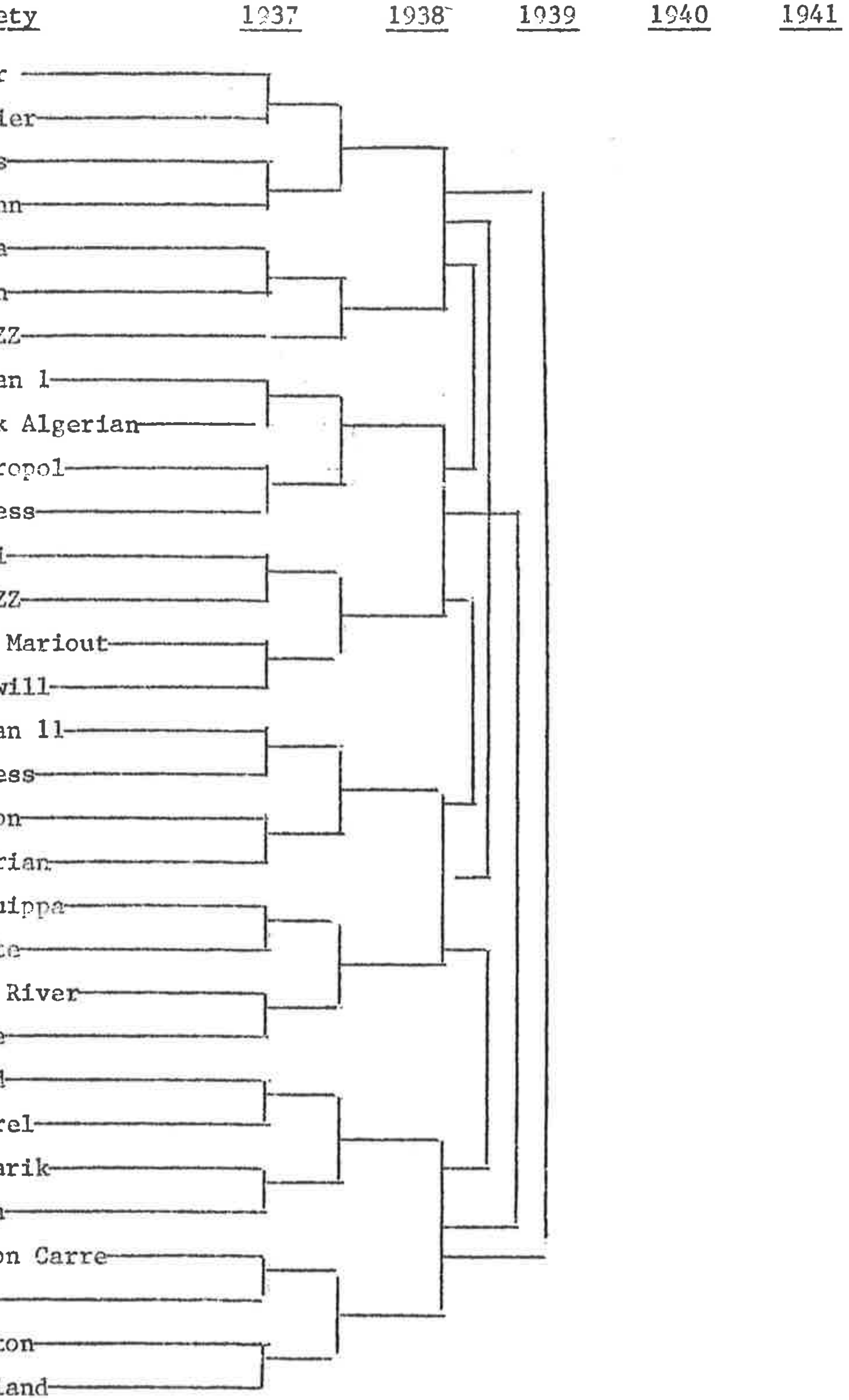
Appendix I.

The crossing plan of CCV, C.I. 6620*

C.I. No.	Variety
975	Baker
2282	Pannier
4118	Atlas
1367	Vaughn
3556	Minia
1311	Flynn
6299	New ZZ
4166	Afghan 1
708	Black Algerian
2103	Stavropol
4019	Lioness
936	Trebi
6298	Old ZZ
261	Club Mariout
6083	Goodwill
4156-2	Afghan 11
4019	Lioness
6109	Velron
1179	Algerian
1256	Arequippa
5888	Rikote
206	Hans River
3290-1	Abate
6265	Ezond
937	Sandrel
3393-1	Bonfarik
3513-1	Parla
3387	Maison Carre
2238	Lion
6626	Coaston
5267	Peatland



	1937	1938	1939	1940	1941
Total No. of Hybrid Seeds produced...............	344	707	577	880	

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* Obtained by courtesy of Dr. Alex. L. Kahler of the Department of Agronomy and Range Science, University of California, Davis.

Appendix 2.

List of the varieties and adaptation indices in the trials of Finlay and Wilkinson and the present experiment.

Varieties.	2 row or 6 row	Adaptation indices in Finlay and Wilkinson's (1963) trial.		Adaptation indices in the present trial (combined analysis of 1967 and 1968 results)	
		Mean yield (Log_{10} gms/plot	Regression coefficient	Mean yield (Log_{10} gms/plot)	Regression coefficient
Bolivia	6	2.50	0.88	2.28	1.43
California Coast	6	2.56	0.93	2.40	0.69
California Mariout	6	2.19	0.44	2.21	0.55
C.I. 3576	2	2.54	0.88	2.39	0.41
C.I. 3726	2	2.50	0.88	2.40	0.70
C.P.I. 18198	2	2.35	0.60	2.26	0.46
C.P.I. 13551	2	2.21	0.82	2.11	1.07
Domen	2	2.14	1.61	2.17	1.10
Freja	2	2.36	1.33	2.23	1.69
Gisborne	2	2.06	1.58	1.88	2.38
Karru	6	2.07	0.12	2.01	0.63
Maraini	6	2.07	1.80	2.22	1.01
Nepal	6	2.03	1.32	1.94	1.50
Noyep	2	-	-	-	-
Peruvian	6	2.55	0.76	2.36	0.84
Peruvian Sezn.	6	2.47	0.59	2.36	0.54
Prior	2	2.40	1.05	2.29	0.43
Proctor	2	2.21	1.54	1.79	2.67
Provost	2	2.02	2.14	1.78	2.91
Sahara	6	2.29	0.41	2.24	0.52
Short Head	6	2.60	0.88	2.32	0.75
Trebi	6	2.25	0.82	2.00	2.68
Volga	2	2.40	1.00	2.24	0.57

Appendix 3.

Score[†] on powdery mildew infection.

Description of response [*]	Symbol	Computer Code
No visible infection but mildew in other adjacent plots	(O)	0
Necrotic brown areas or spots on leaves with no visible mycelium	(VR)	1
Necrotic brown areas or spots on leaves with a trace of visible mycelium	(R)	2
Necrotic brown areas or spots on leaves with abundant mycelium	(MR)	3
Necrotic brown areas or spots on leaves plus a few unrestricted pustules		4
About an equal amount of necrotic brown areas or spots and unrestricted pustules	(M)	5
A few necrotic brown areas or spots among the unrestricted pustules		6
No necrotic brown areas or spots, but with a reduced number of unrestricted pustules	(MS)	7
No necrotic brown areas or spots with many unrestricted pustules	(S)	8
No necrotic brown areas or spots with an abundant number of unrestricted pustules	(VS)	9

[*] According to Moseman

[†] The score system suggested by the "Discussion group on International Standardization, Integration and Mechanization of Crop Data Reporting and Processing. Vienna, 13-17 December, 1965." Kindly provided by Dr. K.W. Finlay.

Appendix 4.

The individual yields (grams/plot)* at each site and year for a sample of genotypes in various adaptation groups†

Adaptation group.	Site and year							
	B67	C67	M67	W67	B68	C68	M68	W68
1. Specifically adapted to high-yielding environments. (F6)	73	0	127	224	124	288	374	537
	72	0	160	145	83	214	257	372
	121	0	88	263	196	292	386	404
	63	0	172	252	112	219	312	310
2. Specifically adapted to low-yielding environments. (F6)	134	113	223	265	179	163	243	232
	154	149	222	280	48	225	304	250
	150	86	250	172	143	101	126	266
	163	132	228	251	222	133	245	318
	83	96	195	231	15	87	121	273
	118	104	325	210	35	58	105	212
	154	107	239	268	34	89	144	232
	115	114	274	102	49	79	112	301
3. Generally adapted (F16)	195	134	438	465	207	360	299	489
	299	122	306	388	218	252	413	440
	196	111	339	282	307	296	414	481
	153	107	279	349	277	271	423	513
(F25)	201	132	304	390	227	541	420	415
	221	102	396	363	305	486	470	582
	247	98	337	291	267	426	449	461
	220	90	229	399	299	394	508	505
Site means (grams/plot)	131	41	239	257	134	195	257	338

* Arithmetic means of two replicates (each of the replicates were transformed for analysis on logarithmic scale.)

† Values are for the genotype given in Table 32; in same order.