THE UNIVERSITY OF ADELAIDE

FACULTY OF AGRICULTURAL SCIENCE

THE INFLUENCE OF INDUCED MUTATION ON THE ADAPTATION OF BARLEY CULTIVARS

by

Abdul Ghafoor Arain, M.Sc.Agri. (Sind)

Thesis submitted for the degree of Doctor of Philosophy
in
Plant Breeding

Department of Agronomy
Waite Agricultural Research Institute
Glen Osmond, South Australia

January, 1973

CONTENTS

SUMMARY

The yield performance of mutagen-treated lines of barley has been compared with that of untreated control lines over a wide range of environments, with the aim of determining the effect of induced mutations on adaptation parameters of barley.

Seeds of five cultivars (Clipper, CI3576, Proctor, Ketch and Prior) having contrasting yields and adaptation characteristics were treated with 0.04M ethyl methanesulphonate (EMS) for 8 hours and populations of M_2-derived treated and control lines were assessed in replicated field trials in the M_4 and M_5 generations.

In 1970 (M_4 generation), the experimental material was grown at four sites in South Australia, covering a wide range of environments. The treated populations of each of the five cultivars gave significantly reduced mean yields and exhibited significant increases in genotypic variance and predicted heritability, compared with the respective control populations. Similarly, the genotypic variances for heading date, plant height and seed weight were significantly increased in the treated populations. The mean heading date of treated lines of each cultivar, was shifted towards lateness irrespective of whether the parent cultivar was 'early' or 'late'. The mean

values for height and seed weight in the treated lines were not significantly altered, except for seed weight of Prior which was significantly reduced.

In 1971, the same treated and control lines of three of these cultivars (Clipper, CI3576 and Proctor) were grown at five sites to test their yield performance across environments in the M_5 generation. Once again the mean yield of the treated lines was reduced below that of controls, except there was evidence of some 'self improvement' in transferring from the M_4 to the M_5 generation. The magnitude of the induced genotypic variance for yield was less than that observed in the M_4, but the heritability values were similar in both generations.

Analyses of variance of yield combined over all sites were carried out separately on the treated and control populations of each cultivar to compare the performance of these populations over sites in the (1) M_4 generation, (2) M_5 generation and (3) M_4 and M_5 generations combined. The control populations of each cultivar did not exhibit genotype X environment (G X E) interaction in any of these analyses, indicating a homogeneity of response across all environments among control lines. In contrast, most of the treated populations showed significant G X E interactions, indicating that the EMS treatment had induced heterogeneity of response across environments among

treated lines. The nature of the significant G X E interactions in treated populations was investigated by partitioning the interaction sum of squares into linear and deviation components using a regression analysis. The G X E variation in the M_4 and M_5 generations taken separately was due mainly to deviations from linear response. However, in the combined analysis, where the number of test environments was increased, both the linear and deviation components were significant with all three cultivars.

An adaptation analysis (Finlay and Wilkinson, 1963; Eberhart and Russell, 1966) was applied to the combined M_4 and M_5 data for each cultivar, to estimate the linear regression coefficient (b) and deviation mean square (S^2d) for each treated and control line, using the mean yield of control lines at each site as the index of environment. The specific effects of EMS-induced mutation on the adaptation characteristics of each cultivar were assessed by comparing the stability parameters (b, S^2d) and mean yield (G) of treated lines with those of control lines, and the following general observations were made:

(1) The average regression slope (β_T) of the treated populations was less than that of the controls ($\beta_C = 1.0$) with each cultivar; this reduction in average slope was attributed to the reduced yield of the treated lines.

(2) With each cultivar there was a strong positive correlation between the b and G values of treated lines.

(3) The treated lines which possessed b values significantly different from the mean of the controls (β_C = 1.0), with few exceptions, had reduced b and associated low yield, showing little yield response in the high-yielding environments.

(4) Some treated lines were more variable (unpredictable) than the controls in their response to changed environmental conditions, as evidenced by their significant S^2d values or larger S.E.(b) compared to controls.

Since most of the EMS-induced changes in stability parameters were associated with low yielding lines an attempt was made to find if low yield was correlated with alterations in other plant characters. Seed sterility, heading date and height were investigated and none of these seemed to be the primary cause of low yield; instead it was concluded that deleterious mutations had occurred in the low yielding lines, leading to reduced vitality and pleiotropic effects on other characters.

STATEMENT OF ORIGINALITY

This thesis contains no material which has been accepted for the award of any degree or diploma in any University. Neither, to the best of my knowledge and belief does this thesis contain any material previously published or written by another person, except when due reference is made in the text.

ACKNOWLEDGEMENTS

I am deeply indebted to my supervisors Dr. K.W. Shepherd and Dr. K.W. Finlay (now of CIMMYT) for suggesting this project and for guidance during the first year of this project. After Dr. K.W. Finlay's departure in 1969, Dr. K.W. Shepherd continued as my sole supervisor. I am extremely grateful to him for help, guidance, and constructive criticism throughout the remaining part of this study.

I sincerely appreciate the advice and interest of Drs. R. Knight, D.H.B. Sparrow and A. Rathjen. Sincere thanks are due to Messrs J. Chigwidden, M. Howe, D. Hatchard, J. Lewis and J. Carrangis who assisted in field operations.

I am very appreciative of the help rendered by Mrs. G. Bishop of the Biometry Department and Mr. R. Lamacraft (now in the CSIRO) for programming and the analyses of the data.

My thanks are due to Miss Angela Trumble who drew the graphs and the figures, and Mr. B. Palk for the photography.

Finally, I am grateful to the Commonwealth Government of Australia for providing a Colombo Plan Fellowship and the Pakistan Atomic Energy Commission for giving me the opportunity to take up this fellowship, and to the personnel of the Australian Commonwealth Department of Education and Science for their help.

INTRODUCTION

Following the discovery of the mutagenic properties of ionizing radiations (Muller, 1927; Stadler, 1928a, b) and chemicals (Auerbach, 1943), numerous attempts have been made to induce beneficial mutations in crop plants. Initially, attention was concentrated on characters determined by major genes, such as disease resistance and short culm and dense ear in cereals. The success of these efforts has been summarized by Gustafsson (1947, 1951). However, in the past seventeen years efforts also have been devoted to the improvement of quantitatively inherited characters controlled by minor genes (or polygenes). The first extensive study was conducted by Gregory (1955) working with peanuts (Arachis hypogaea). He showed that X-irradiation treatment increased the genotypic variance in the M_2 and later generations and shifted the mean of the normal-looking progeny towards reduced yield. Despite this overall reduction in mean yield, he was able to select some treated lines which outyielded the un-irradiated controls.

Since then, many other workers have used mutagens on a range of crop plants to induce genetic variability in quantitative characters. They also have observed negative or positive shifts in the mutated population means. Brock (1965)

reviewed this work and postulated a general hypothesis to account for the behaviour of quantitative characters in a self-fertilizing species after mutagenic treatments. He suggested that "In species which have previously been subjected to breeding and selection, random mutation results in an increase in the variance and a shift in the mean away from the direction of previous selection".

These studies showed that mutagens are effective in generating variability in quantitative characters and that progress could be made from selecting among the variants. However, just as in improvement programmes based on hybridization, the realized selection commonly was less than that predicted from estimates of the genotypic variance of the population from which the selections were made. This discrepancy was ascribed to non-additive genetic effects and to genotype X environment interactions (Brock and Latter, 1961; Aastveit and Gaul, 1967). The genotype X environment interaction component could not be measured in these early mutation studies because tests were conducted in only one environment. However, some recent work of Gaul et al. (1969) has involved the testing of successive generations of M_2-derived families at two locations. Although not specifically designed to estimate genotype X environment interactions, their study revealed that the genotypic variance for yield was inconsistent between generations

and between locations within generations.

In addition to the above studies with micro-mutations, the yield performance of several morphologically and physiologically distinct macro-mutants have been compared with the parent cultivars over a wide range of environments (Gustafsson, 1951; Fröier, 1954; Bogyo et al., 1969). These studies have provided additional evidence of G X E interactions among mutagen-derived material.

The present study is concerned with estimating the magnitude of genotype X environment interactions in material treated with mutagens. The study utilizes statistical methods developed in the last ten years that attempt to specify the nature of genotype X environment interactions.

Plant breeders have long been aware of problems of selection when genotype X environment interactions occur and have tried to develop methods to measure these interactions. At first, the magnitude of the interaction was estimated from the components of variance: (variety X location; variety X year; and variety X location X year) using an analysis of variance method (Immer et al., 1934; Sprague and Federer, 1951; Horner and Frey, 1957). This approach supplied information on the most suitable allocation of replicates, locations and years in variety testing. In addition, some workers evaluated the stability of performance of individual genotypes by estimating the relative magnitudes of

the variance component genotype X environment (σ^2GE) from separate analyses of variance for each genotype in a trial. However, this method did not indicate the nature of the interaction in the manner of more recent analyses.

In the last few years the analysis of variance method has been extended to incorporate a regression analysis of the G X E interactions (Finlay and Wilkinson, 1963; Eberhart and Russell, 1966; Perkins and Jinks, 1968a, b). A simple form of the technique was proposed first in 1938 by Yates and Cochran. With this approach, the genotype X environment sum of squares is partitioned into linear and non-linear components, thus indicating whether the G X E interaction is a linear function of environment or a more complex function. When the genotype response across environments is predominantly linear, the regression coefficient (b) for each genotype provides a measure of its adaptation or phenotypic stability (Finlay and Wilkinson, 1963). On the other hand, when the non-linear (deviation) component is large, a second parameter (S^2d) is required to specify the stability of genotypes (Eberhart and Russell, 1966). These parameters, derived from the regression analysis, have proved useful when interpreting results from a large number of trials in different environments.

In the current project, these methods have been used to study G X E interactions in mutagen-treated material of barley.

An EMS-treatment was applied to five barley cultivars with diverse yield and adaptation patterns and M_2-derived treated and control lines were assessed over a range of environments in the M_4 and M_5 generations.

The specific objectives were:

(1) To measure the genetic variability and heritability of yield in EMS-treated material of each cultivar when grown in different environments and in different generations.

(2) To determine if the treated material of each cultivar exhibits genotype X environment interaction and, if so, to specify the nature of the interaction.

(3) To identify any treated lines which have significantly altered stability (adaptation) parameters for yield, and to resolve whether changes in stability can be associated with changes in morphological or physiological characters.

LITERATURE REVIEW

A. Induced mutations in plants

1. Induced mutations affecting quantitative characters

The importance of so-called minor mutations in evolution was emphasized by Baur (1924) and later by Stubbe and von Wettstein (1941), and Scossiroli (1954). Later, it was realized that these minor mutations might also be important in improving polygenically controlled economic characters in crop plants, and a vast literature now exists on this topic. Herein, no attempt has been made to present a comprehensive review of all work in this field; rather attention has been given to the main effects of mutagens such as shift in mean, induced genetic variability and response to selection for quantitative characters.

The first extensive study involving induction and selection of mutations affecting quantitative characters was conducted by Gregory (1955, 1956) in peanuts (*Arachis hypogaea*). His pioneer work on micro-mutations led to the finding that mutagens induce considerable variability in the background genotype. X-ray irradiation of peanut seeds led to increased genotypic variance in the M_2 and later generation progenies which were not morphological mutants. Although the mean yield of the treated material was considerably reduced as compared with controls, Gregory was able to select high-yielding mutants from the irradiated populations.

Soon after Gregory's (1955, 1956) initial studies, many other authors studied the effects of different irradiation treatments (including X-rays, gamma-rays and neutrons) on yield and other quantitative characters in M_2 and subsequent generations and some of these are listed in Table 1.

These authors observed a significant increase of genetic variability for all quantitative characters among the treated populations and the genotypic variances were increased many-folds as compared with untreated controls. The shift in the mean values for yield was universally reduced among the treated populations in all cases, except Jalil Miah and Yamaguchi (1965) found an increase in yield means of all genotypes, with significant increase in the hybrid. The mean values of all other quantitative characters in the treated populations were significantly altered except the following: plant height and heading date (Oka et al., 1958), maturity, plant height and seed size (Rawlings et al., 1958), flowering time (Daly, 1960), ear density and seed fertility (Jalil Miah and Yamaguchi, 1965), heading date (Gaul, 1965), and flag-leaf length, groat length and groat width (Gonzalez and Frey, 1965).

After these mutagenic treatments the predicted gains from selection and the actual gains obtained were compared for a range of characters by various workers. Papa et al. (1961) checked

Table 1. Studies on induced mutations affecting quantitative characters of different crop species.

Crop/Species	Quantitative characters investigated	Author
Oryza sativa (rice)	Plant height, heading date	Oka *et al.*, 1958
	Plant yield, ear number, ear length, grains per ear, ear density, seed fertility	Jalil Miah and Yamaguchi, 1965
Soja hispida (soybean)	Plant height, maturity, yield and seed size	Rawlings *et al.*, 1958
	Oil content, protein content	Williams and Hanway, 1961
	Yield, maturity, seed size, oil and protein content	Papa *et al.*, 1961
Trifolium subterraneum (subterranean clover)	Flowering time	Brock and Latter, 1961
Avena sativa (oats)	Heading date, plant height and seed size	Krull and Frey, 1961
	Plant height, heading date, no. of branches, seed size, flag-leaf length, groat length, groat width	Gonzalez and Frey, 1965
Triticum aestivum (wheat)	Tiller number, plant height	Bhatia and Swaminathan, 1962
Arabidopsis thaliana	Flowering time	Daly, 1960
	Flowering time, plant weight	Brock, 1965
Hordeum vulgare (barley)	Grain yield, heading date	Gaul, 1965

the validity of gains from selections predicted by Rawlings et al. (1958) and Williams and Hanway (1961) among the treated populations of soybeans. For seed yield, gains from selection were effective in the treated populations of Hawkeye variety, and ineffective in Adams variety. Significant increases in mean yields were achieved from selection in the treated populations of both varieties when compared to their respective population means, but in neither case was the selected population mean better than obtained from selections within controls. In general, selection for maturity, seed size, oil content and protein content was more effective in the treated populations than in the controls.

The predicted heritability of induced genotypic variance for flowering time was reported by Brock and Latter (1961) to be 70% in the M_2 of irradiated populations after excluding morphological mutants as compared with 32% in the controls. The authors further investigated the response to selection in M_3 generation and obtained a realized heritability of 59% in the screened irradiated populations and 34% in the controls. Thus the realized response to selection among the irradiated populations was less than that predicted. They suggested that this discrepancy was due to the following causes:

(i) The occurrence of non-additive genetic effects in M_2 which resulted in an overestimate of the proportion of the total variance available for selection.

(ii) The existence of G X E interaction - Where G X E interaction resulted in a change of ranking of genotypes over years, this would lead to an over-estimation of the predicted advance from selection. On the other hand, a change of scale between season to season contributes to the discrepancy, but the direction of change cannot be specified.

(iii) Inadequate experimental design - The differences between the M_2 family means contain an environmental component, giving a positive bias to the predicted response.

Krull and Frey (1961) measured heritability percentages on both a family and line basis by the standard-unit method for 100-seed weight in three irradiated oat populations (thermal neutron treatment), one each from Clintland variety, Beedee variety and F_2 seeds of Clintland X Beedee in the M_3 generation. Significant heritability values with an average of 16%, 38% and 57% were obtained with the treated populations of Clintland, Beedee and the hybrid respectively, whereas the untreated populations of Clintland and Beedee gave non-significant values. With similar material in rice involving two parents and their F_1 hybrids Jalil Miah and Yamaguchi (1965) obtained heritability values for yield comparable to that obtained by Krull and Frey (1961).

In addition to ionizing radiations, a number of chemical mutagens have also been used for inducing genetic variability of

quantitative characters in various plants. Many authors have compared the relative effectiveness of physical and chemical mutagens. Of the chemical mutagens, ethylmethanesulphonate (EMS) has been used commonly. Abrams and Frey (1964), studied the effects of thermal neutrons (TN), EMS and P^{32} treatments in oats, and found significant genetic variability for all characters among the TN and EMS treated populations. They found a shift in mean values for heading date and plant height, but not seed weight, for all treatments. Similar results were obtained by Brock (1965) who compared the effectiveness of ionizing radiations (TN and gamma rays), with several chemical mutagens (including EMS and DES) in Arabidopsis thaliana. In his experiments TN and gamma rays were as effective as chemical mutagens in inducing genetic variance for flowering time and plant weight in the screened M_2 generation.

In contrast, Gaul et al. (1966) showed EMS to be more effective than X-irradiation for inducing variability of seed yield in barley, giving a ten-fold increase in genotypic variance. The increase of genotypic variance was associated with much reduction of yield means after EMS-treatment. The authors concluded that the action of EMS was equivalent to a "superdose" of ionizing radiation. Similarly, increased effectiveness of EMS has also been reported by Gaul and Aastveit (1966) for plant height,

and Gaul (1967) for yield in barley, and Joshi and Frey (1967) for seed weight in oats.

Brock (1965), in reviewing his own work with subterranean clover and Arabidopsis, and the results of other authors, advanced a general hypothesis to account for the behaviour of quantitative characters in self-fertilizing species after mutagenic treatments. He stated that: "Random mutation would be expected to increase the variance and to shift the mean away from the direction of previous selection. The symmetry of the induced variation and the effectiveness of selection applied to the mutated population would be determined by the intensity of previous selection. Provided that absolute limits had not been reached in the parental genome, a most unlikely occurrence, effective selection responses should be possible in either direction. Characters previously selected for an intermediate mean would be expected to respond with an increase in the variance but no change in the mean. If no selection is applied after induction of mutation, the average effect will be a regression of the mean and a reduction of fitness for all adaptive or previously-selected characters".

However, Frey and his colleagues have observed some significant shifts in mean values of different characters in oats after mutagenic treatments which do not fit Brock's hypothesis. There was a consistent trend for mutagenic treatment to reduce

plant height in all cultivars irrespective of whether they were short or tall (Abrams and Frey, 1964; Gonzalez and Frey, 1965). On the basis of the results of extensive mutation studies on oats carried out at Iowa, Frey (1968) concluded: "The data for Avena indicate that shifts in population means induced by mutagen treatment, which do occur occasionally, are generally unpredictable and are dependent upon specific genotype-trait combinations".

Gaul and Aastveit (1966) set out to test Brock's hypothesis by treating a wheat which had been intensively selected for short culms and one having long culms with EMS and X-rays. They observed that the mutagen-treatments resulted in a significant reduction of the culm length of both varieties among the normal-looking and randomly-selected plants in M_2 and M_3 generations. The authors criticized Brock's hypothesis on the grounds that it does not take account of the deleterious effect of mutations and further that most of the changes of interest to plant breeders, are related to the vitality of the organism. On the basis of their results they suggested an alternative hypothesis to that of Brock's as follows: "By random mutation a change in the mean value of almost any quantitative character of interest for plant breeding is to be expected in a direction associated with reduced vitality, and the alteration of the mean is largely independent of the genotype used for the mutagenic treatment". This loss

of vitality was also observed by Gaul (1965) among the mutagen-derived lines of four genetically different barley cultivars, all of which showed reduction of mean yield in M_3.

Brock (1967a) studied the effects of gamma-rays and TN on flowering time and plant weight among the treated populations of an early flowering race of Arabidopsis thaliana. He found that both mutagens induced visible mutations and genetic variability in the M_2 generation for both characters. However, removal of the visible mutants resulted in greatly reduced magnitude of induced variation in flowering time and plant weight suggesting that most of the induced variability was associated with the morphologically distinct mutants. There was a shift in mean towards late flowering and decreased plant weight in the total M_2 treated population. However, after removing the visible mutants, the shift of mean in flowering was much reduced and the mean plant weight actually exceeded that of the controls.

He observed negative phenotypic and genetic correlations between plant weight and flowering time. Moreover, responses from selection were obtained for both earliness and lateness among the treated populations and the mean plant weight (growth rate) of the late-flowering selections was reduced whereas that of early-flowering selections was increased. On the basis of these and other similar results (Brock 1967b), Brock modified his earlier hypothesis

and suggested that the behaviour of the mean of an unselected character depends not only upon its previous selection history but also upon whether it is genetically correlated with the character being selected.

Gaul and his colleagues have made a comprehensive study of yield performance of mutagen-treated barley cultivars in successive generations following treatment, with and without selection. Gaul (1967), while testing the randomly selected M_2-derived treated families from three varieties of barley in M_3, M_4 and M_5 generations without selection, found shifts in the mean and increases in genotypic variance of yield. However, the genotypic variance from generation to generation was not consistent. The reduction of yield means of the treated material in the M_3 generation varied from 3 to 15% in the different experiments, whereas in the subsequent generations there was a tendency towards a lessening of yield reduction, resulting in 1 to 9% reduction in the M_5 generation. Gaul suggested that this 'self improvement' observed in the successive generations following treatment was due to natural selection occurring within families.

Highly significant correlations for yield between M_3/M_4, M_3/M_5 and M_4/M_5 in the treated families were observed, indicating that selection for yield among the families should be successful.

Recently, Gaul et al. (1969) have published the yield results for M_2-derived treated families of three barley varieties (Wisa, Volla and Haisa II) grown over several generations from M_3 to M_8 and M_9 at two different sites. Beginning in M_4 they partitioned each of Volla and Wisa experiments into sub-experiments (i) without selection, (ii) with positive selection and (iii) with negative selection. The selection was always practised between families and continued through subsequent generations. The treated families showed a "self improvement' for yield, in agreement with Gaul (1967). The authors reported that the yield means of the treated families was similar (99%) to that of controls in the M_8 generation whereas in the M_3 generation, the yield values for Wisa and Volla were 93% and 94% of the controls, respectively. Furthermore, the genotypic variance for yield was not consistent between generations and between locations within generations giving evidence for G X E interaction among the treated families. For example, the M_4 generation of Volla when grown at two different locations showed more than a three-fold difference in the genotypic variance.

Selection in the treated families was much more effective than in the controls and it was possible to select one family (out of 10 families with positive selections) with a yield potential 10% higher and one family (out of 10 families with negative selections) with a yield potential 22% lower than the corresponding controls in

M_8 generation for the Haisa II experiment. This suggests that micro-mutation technique could be used for continuous improvement of newly released varieties.

Several workers have demonstrated that the genetic variability and selection response of quantitative characters in plant populations could be increased by applying a second cycle of mutagen treatment (recurrent or alternate).

Brock (1965, 1966), Jalil and Yamaguchi (1964) and Khadr and Frey (1965) found that the magnitude of the induced variability and responses to selection were considerably smaller than the first mutagen-treatment, suggesting a degree of mutation saturation. On the other hand, Joshi and Frey (1967) and Lawrence (1968) reported approximately equal amounts of induced variation by successive mutagenic treatments.

Recently, Brock and Shaw (1969) have studied the effects of a second cycle of mutagenic treatment on early and late flowering mutants of Arabidopsis thaliana selected from the first mutagenic treatment. They showed that a second cycle of mutagenic treatment was equally effective to that of recombination of newly induced variation for making further progress towards either earliness or lateness.

2. Performance of mutants and their response to different environments

The genotypic variation induced in quantitative characters among the mutagen-derived families has been measured in only one environment per generation in all studies except the work of Gaul and his colleagues (Aastveit and Gaul, 1967; Gaul *et al.*, 1969). Hence there is very little information on the extent of genotype X environment interactions in such material. However, some distinct macro-mutants of different crop plants have been tested in different years and locations, thus making it possible to gauge their response to change in environments.

Mutant forms of plants are generally distinctly inferior to the parent strain, when grown in the environment of their origin. However, in a different environment, some mutants become equal to or even supersede their parents in grain yield or vegetative production. Therefore, it is important for a plant breeder not only to know how a mutant behaves in the original environment suitable to the parent strain but also how it behaves in other environments.

For example, Honing (1923) obtained a spontaneous mutant in tobacco which was a sterile dwarf and it did not flower in the environment of its origin (Indonesia), but when it was grown in the Netherlands it grew much taller and flowered, giving well-developed seeds. Another spontaneous mutant in tobacco flowered

under short day conditions but not under long day conditions (Jones, 1921).

Brücher (1943) isolated a number of mutagen-induced and spontaneous mutants of Antirrhinum majus and he compared their growth with that of the parent strain over a range of environments. Although none of these mutants were superior in performance in their original environments, some of them performed remarkably well under conditions adverse for the parent strain.

After the pioneer work of Stadler on induced mutations in plants, Gustafsson (1947) compared the yield performance of many morphological, physiological and chlorophyll mutants from two commercial varieties of barley, Golden and Maja, with their parents in a range of environments in Sweden. At the original environment (Svalöf), only a few of these mutants produced relatively more yield than their respective parent varieties, when averaged over a number of years. One yellow-green mutant derived from Golden variety showed genotype X environment interaction when tested under different environmental conditions: at its original environment, it yielded 10% less than the parent strain, but in the north of Sweden it yielded 25% more than the parent.

Later Gustafsson and his colleagues studied the performance of some morphologically and physiologically distinct induced mutants from different varieties of barley over a range of environments

including different locations and years, and comparisons of yield were made relative to parent strains. Gustafsson (1951) described one late, tall mutant of Golden variety which produced an average 2.6% more yield than its parent variety for the period of 11 years at one site (Svalöf); under severe drought conditions during early summer at Ultuna Station (700 km north) it produced no less than 10.7% more than the parent when averaged over 7 years. In addition, he tested many erectoides mutants from Golden over many years at four locations and found that erectoides 1 (Ert 1) exhibited genotype X environment interaction: i.e. at Ultuna (60°N) it yielded similarly to its parent variety, whereas at Svalöf (56°N), Ekerum (57°N) and Lännäs (63°N) it produced 1.6%, 1.9% and 2.4% more yield than the parent, respectively.

These workers isolated many erectoides mutations from mutagen-treated populations of Golden, Bonus and Maja varieties of barley especially adapted to Svalöf conditions. Gustafsson (1954) considered that by careful experimentation, the processes of adaptation could be studied by evolving new types suited to a new type of environment. Under different nitrogenous fertilizer treatments, erectoides mutants and their respective parent varieties performed differently. The yield of these mutants increased as the nitrogen dressing increased. One of the erectoides mutants from Bonus (Ert 32) was released as a commercial variety under the name

of "Pallas" in the spring of 1961. It is characterized by improved straw stiffness and responds better than the parents or any other variety to nitrogen dressing, and is thus adapted to fertile soils (Borg, 1959).

Working with morphologically and physiologically distinct mutations from different barley varieties, Frö̈ier (1954) conducted field trials at twelve different locations in Sweden for thirteen years, and found that the mutants were considerably more variable in yield performance than their respective parents over different years at various locations. The response of these mutants varied with soil, latitude and season; most depended on heavy precipitation and optimal humidity for satisfactory development, thus performing best in the more favourable environments and worst in poor environments. On the contrary, Gustafsson (1951), working with seven Maja mutations at Svalö̈f over six years, concluded that mutations performed best during 'bad' years (poor environments) compared with 'better' years. Gelin (1955) produced a high-tillering pea mutant (Strä̈l) from Klö̈ster variety of pea, which yielded 5% more than its parent strain. He reported that Strä̈l yielded considerably more under poor environments, but that its superiority was reduced under better environments (Gelin, 1960).

Gustafsson (1963) discussed the concept that most mutations of diploid plant species are deleterious, leading to decreased viability when homozygous, but becoming positive or neutral in the

heterozygous state. Later Gustafsson (1969) indicated positive mutations do exist in both homozygous and heterozygous states and could be released directly as new varieties or used in further hybridization.

In addition to 'Pallas', an early mutant (early 8) from Bonus barley was released as a commercial variety with the name of 'Mari' in 1962 (Gustafsson, 1963). Mari performed differently when grown in different regions of Sweden. It yielded less in its original environment in the south when compared with its mother strain, but was equally as good as the best two-rowed barley in central Sweden, while in northern Sweden it ripened early, producing a good yield where two-rowed barley could not be grown successfully (Gustafsson et al., 1960).

The sensitivity of response to different photo- and thermo-periods of Mari mutant variety compared with its parental variety Bonus, has been studied by Dormling et al. (1966) and Dormling and Gustafsson (1969) under controlled conditions in the phytotron. They showed that an early flowering form of Mari produced many spikes and performed quite well with regard to kernel production at a photoperiod of 8 hours of light and at low temperatures (10^{o}, 15^{o}C), whereas Bonus failed to produce spikes. This reflects insensitivity of Mari to photo- and thermo-periods and indicates adaptation to extreme conditions.

Furthermore, superiority of Mari over Bonus in kernel weight, percentage protein content and lysine/100 g protein, has also been reported at three different photoperiods at a constant temperature (8, 16 and 24 hours light at 15°C). Though Mari gave a decreased kernel weight at 8 hours photoperiod, percentage protein content actually increased at the same photoperiod (Munck et al., 1969).

In India, Swaminathan induced awned mutants in awnless or apically awnletted varieties of wheat supposedly without altering any other morphological or physiological character. Swaminathan (1965) compared the yield performance of awned mutants with their parent strains after conducting three years of extensive field trials at several irrigated and dryland sites. He indicated that awned mutants produced better yields than their respective parents in low-yielding environments (drylands).

Similar studies of morphologically and physiologically distinct mutants of a variety of Pisum sativum were made by Gottschalk (1966). Stem-forked mutants were tested during the one year in dry and wet environments for yield performance. In contrast to wheat mutants, these pea mutants yielded less under extremely dry conditions when compared with the parent variety, whereas under better conditions they yielded the same or better.

Recently, in order to study genotype X environment

interactions of wheat and rice mutants, Uniform International Trials have been conducted under a wide range of environments (discussed by Sigurbjörnsson, 1968). Promising mutants of durum wheat developed by Professor G.T. Scarascia-Mugnozza in Italy were tested for yield performance and other characters in field trials under FAO Near East Wheat and Barley Improvement Programme in 28 locations in different parts of the world over four years. These mutants were selected on the basis of improved characters such as short straw, resistance to lodging, early maturity, early ripening and better yield. Bogyo et al. (1969) analysed the data from these trials to study the adaptation of these mutants together with Cappelli and Capeiti varieties of durum wheat. The yield performances were also compared with common checks and local varieties at various locations. The data for yield and other quantitative characters were analysed by employing analysis of variance procedure and mean squares due to genotypes X locations (G X L), genotypes X years (G X Y) and genotypes X locations X years (G X L X Y) terms were computed. The authors reported significant interactions for some characters, but non-significant interactions for yield. They claimed that the mutants and varieties were generally adapted over a wide range of environments. However, inspection of the analysis of variance table for yield data (Table 4, page 708) shows that the mean squares for G X L X Y and

G X L interaction terms are significant at 5% and 1% levels when tested against error and G X L X Y terms respectively. Contrary to their interpretation the mutants and varieties performed differently for yield when grown over different locations rather than their yearly variation in a given location.

The authors did not apply a regression analysis to their data, hence no conclusions can be drawn from these studies regarding the stability of individual mutants and the nature of the G X E interactions observed.

3. Biological effects of different mutagens (mutagenic efficiency)

Comparative studies on the biological effects of different doses of EMS and physical mutagens (i.e. X-rays, gamma-rays and neutrons) in cereals have been conducted by several workers. These biological effects were measured in terms of seedling injury, decrease of plant survival, increase in sterility, frequency of chromosome aberrations in meiotic and mitotic cells and frequency of chlorophyll mutations in M_1 and M_2 generations. The highest frequencies of chromosome aberrations and chlorophyll mutations that have been induced by a given dose of EMS and physical mutagens in wheat and barley are summarized in Table 1a. The table indicates that the frequency of chlorophyll mutations based on M_1 spike progenies and M_2 seedlings, were generally greater in the EMS-treated material compared with X-rays and TN treatments.

Table 1a. Frequencies of chromosome aberrations and chlorophyll mutations in barley and wheat induced by treatment of seed with physical mutagens and Ethyl Methanesulphonate - the highest frequencies for each mutagen.

Crop	Variety	Mutagen	Dose (kR)	Conc. mM, % or ppm	Chromosome aberrations/100 cells In mitosis Bridges	Fragments	Total	In meiosis	Mutation frequency Mutations per 100 M_1 plants	Mutants per 100 M_1 spikes	Mutants per 100 M_2 seedlings	M_2 families segregating	
Barley	-	X-rays	10	-	-	-	-	26	-	-	0.8	-	Caldecott, 1959
"	-	"	20	-	-	-	-	19	-	-	1.1	-	"
"	-	"	60	-	18	271	-	29	-	12	1.8	-	Froese-Gertzen et al., 1964
"	-	"	100	-	50	762	-	-	32	17	4.1	-	Konzak et al., 1961
"	Wisa	"	30	-	-	-	-	-	-	-	2.9	-	Gaul et al., 1966
"	-	Thermal neutrons	$12.2x10^{12}$ n/cm^2	-	-	-	-	-	-	15	-	-	Caldecott et al., 1954
"	-	"	$15.5x10^{12}$ n/cm^2	-	-	-	-	88	-	-	-	-	"
"	-	EMS	-	20 mM	4	18	-	1	-	32	6.9	-	Konzak et al., 1965
"	-	EMS	-	40 mM	2	6	-	1	-	37	4.3	-	Froese-Gertzen et al., 1964
"	-	EMS	-	280 ppm	-	-	-	-	-	-	-	88.2	Swaminathan et al., 1962
T. dicoccum	-	EMS	-	280 ppm	-	-	-	-	-	-	-	30.5	"
T. aestivum	Pb0591	EMS	-	280 ppm	-	-	-	-	-	-	-	10.0	"
Barley	-	EMS	-	400 ppm	-	-	27	22	-	-	-	73.2	"
T. dicoccum	-	EMS	-	400 ppm	-	-	18	25	-	-	-	28.1	"
T. aestivum	Pb0591	EMS	-	400 ppm	-	-	44	42	-	-	-	2.2	"
Barley	-	EMS	-	0.06%	-	-	-	42	-	-	-	-	Ramanna and Natarajan, 1965
"	-	EMS	-	0.6%	-	-	-	9	-	-	-	-	"
"	-	EMS	-	0.6%	-	-	-	-	45	57	27.0	-	Moes, 1963
"	Wisa	EMS	-	1.95%	-	-	-	-	-	-	26.9	-	Gaul et al., 1966
"	Volla	EMS	-	2.05%	-	-	-	-	-	-	23.3	-	"

It has been pointed out that EMS is more effective for inducing chlorophyll mutations and more viable mutations per chlorophyll mutation as compared to ionizing radiations (Heslot et al., 1961). Ehrenberg et al. (1961) have compared the M_1 seed sterilities and M_2 mutation rates between ionizing radiation and chemical mutagens in barley. They indicated that neutron and X-rays generally produced up to 8 to 10% chlorophyll mutation, whereas EMS produced a mean rate of almost 50% chlorophyll mutation for 65% M_1 seed sterility in greenhouse tests. Their experiments showed a linear relationship between M_1 sterility and M_2 mutation rate only in the case of EMS treatment. They also observed that the spectrum of chlorophyll mutations varied depending upon the kind of mutagen used with ionizing radiations producing more albina and less viridis as compared with the EMS-treated material. A high frequency as well as a wide spectrum of chlorophyll mutations were observed in EMS-treated diploid barley and tetraploid and hexaploid wheat in M_2 generation (Swaminathan et al., 1962). In hexaploid wheat, several chlorophyll mutations were found in EMS-treated material, but in irradiated material the same mutations were rarely found. On the whole, the authors indicated a higher rate of mutations from EMS-treatment as compared to ionizing radiations in diploid barley.

A comprehensive study on the effects of EMS as compared

to X-rays was reported by Froese-Gertzen et al. (1964). They found that EMS and X-ray treatments gave a comparable reduction in rate of seedling growth and survival. However, more seed sterility was found in the EMS-treated material compared to the irradiated material. EMS induced a high frequency of chlorophyll mutation, correlated with a low frequency of chromosome aberrations (Table 1a). The authors indicated that the efficiency of EMS could be increased by using buffered solutions to reduce the physiological damage caused by hydrolysis products.

Gaul (1967) has compared the mutagenic efficiency of EMS (1.95% for 6 hrs at 24°C) and two doses of X-rays (17 Kr and 40 Kr).

Compared to the 40 Kr X-ray treatment, the EMS treatment produced 16 times more M_1 survival, 4 times more chlorophyll mutations and six-fold increases in genotypic variance for yield. Despite the much greater reduction in yield mean following EMS-treatment, he suggested that the frequency of positive micro-mutations was greater than that obtained from X-irradiation. On the basis of these results it was decided to use EMS as the mutagen in the present study.

B. Yield performance and adaptation in plants

1. Occurrence and measurement of genotype X environment interaction

It is commonly observed that the effects of genotype and environment are not independent and that the relative performance of different genotypes changes in different environments, i.e. there exists a genotype X environment interaction.

Frequently a genotype X environment interaction occurs even when only one factor of environment, such as temperature or fertility level, is varied. Such one factor environments can be accurately described and controlled. However, under those environments, which are subject to unpredictable variation in factors such as temperature, rainfall, insects and disease incidence, interactions are complex and cause a major challenge to the plant breeder attempting to develop improved varieties. Year to year fluctuations cannot be predicted and so the plant breeder should aim to develop varieties suited to the overall environment. Selection of suitable genotypes becomes very difficult because relative performances of different genotypes are not consistent under complex environments.

The problem may be reduced to some extent by stratifying the environment, whereby a region is divided into sub-regions based on macro-environmental factors such as temperature gradients, rainfall distribution and soil types. Improved varieties are

developed for each sub-region but even then the problem cannot be entirely solved since interactions may still occur between genotypes and years and locations within the sub-region.

An alternative approach has been to measure the magnitude of G X E interaction and to select stable genotypes which perform uniformly over the environments in which the crop is grown. Two related procedures have been used to measure these interactions.

(a) The analysis of variance

The first attempt to study the genotype X environment interaction in crop plants was made by Immer et al. (1934), who grew five barley varieties at different locations over several years. The variation was partitioned into components due to varieties, locations, years and appropriate interactions. They measured interactions by calculating the mean squares for variety X location (VL), variety X year (VY) and variety X location X year (VLY) terms. The authors found that all these interactions were significant. They concluded that the relative performance of some varieties varied in different locations, in different years and in some locations in particular years.

Later, Sprague and Federer (1951) used a similar analysis to Immer et al. for measuring genotype X environment interaction of a number of top single and double crosses of corn. They put forward the following mathematical model to explain the main

effects and first-order interactions in the analysis:

$$Y_{ijk} = \mu + G_i + E_j + (GE)_{ij} + R_{jk} + e_{ijk}$$

where

Y_{ijk} = yield of genotype (i) at location (j) and replicate (k)

μ = mean of all genotypes over all locations and replicates (population mean)

G_i = mean effect of genotype (i)

E_j = mean effect at location (j)

$(GE)_{ij}$ = interaction effect of genotype (i) at location (j)

R_{jk} = effect of replicate (k) at location (j)

e_{ijk} = error of genotype (i) at location (j) and in replicate (k)

They calculated the relative magnitudes of error, genotype X location, genotype X year and genotype variance components to study the effects of varying number of genotypes, replications, locations and years on the average genetic advance in corn. The authors used the average ratios of genotype X location variance to error variance and genotype X year variance to error variance as a measure of stability and demonstrated that the yield performance of the double crosses was more stable than that of single crosses.

Comstock and Robinson (1952) extended the above model by including a component for second-order interaction in an analysis

of yield data of F_3 families of Lespedeza over various locations and years. The different estimates of variances due to error (σe^2), genotype X location X year (σ^2VLY), genotype X location (σ^2VL) and genotype X year (σ^2VY) were obtained from the respective mean square expectations of the analysis of variance. The information regarding the first- and second-order interaction was obtained by these workers by testing groups of genotypes at the same locations for more than one year.

In an analysis of segregating populations of soybean, Johnson et al. (1955) have presented different forms of analyses of variance and mean square expectations for data obtained from: (i) several locations in one year, (ii) several years at only one location and (iii) different locations in different years.

These basic models of the analysis of variance have been used by many workers with a wide range of crops, including Hanson et al. (1956) with Lespedeza; Horner and Frey (1957) with oats; Miller et al. (1959, 1962) and Murray and Verhalen (1970) with cotton; Jones et al. (1960) with tobacco; Rasmusson and Lambert (1961) and Rasmusson and Glass (1967) with barley; Gandhi et al. (1964) with wheat; Liang et al. (1966) with wheat, barley and oats; Tyson and Bradner (1967) with flax; and Matzinger (1963) and Schutz and Bernard (1967) with soybean.

These analyses have been useful for deciding the optimum number of replicates, locations and years that should be used in

variety testing programmes. They also indicated if there was any advantage in dividing a particular region into sub-regions for breeding and testing purposes (Horner and Frey, 1957).

One aim of these studies was to determine whether evaluation of potential new cultivars could be achieved by testing the breeding material at an adequate number of locations in just one year. Schulz and Bernard (1967) suggested that low-yielding genotypes could be eliminated by testing strains over ten to fifteen locations in a single year instead of over two or more years. On the other hand various workers such as Jones et al. (1960), Rasmusson and Lambert (1961), Miller et al. (1962), Liang et al. (1966) and Rasmusson and Glass (1967) have observed that the second-order interactions were larger than the first order interactions. Their results indicated that the differential responses of genotypes when grown in a range of environments was not accounted for by either location or year groupings. Thus these authors suggested that the data obtained in one year over locations, or at one location over years, were inadequate for varietal recommendations. In particular, Miller et al. (1962) suggested that the precision of variety evaluation could be improved by increasing the number of test environments over locations and years, rather than by increasing the number of replicates per location.

The major disadvantage of the conventional analysis of variance estimation of G X E interaction is that it considers the average performance of all entries in a trial over a range of environments, and does not specify the response of individual genotypes under these environments. Three alternative approaches have been used to calculate a parameter to indicate the change in yielding ability over a range of environments for individual entries.

(i) Plaisted and Peterson (1959) described a technique to evaluate the yield of individual potato cultivars by testing them at several locations in one year. An estimate of variety X location component of variance (σ^2VL) was obtained from a separate analysis of variance of each pair of cultivars. Further, an arithmetic mean of all these estimates ($\bar{\sigma}^2$VL) was obtained for all pairs of cultivars having one common cultivar. Cultivars giving low values for $\bar{\sigma}^2$VL were considered to be more stable than those giving higher values.

(ii) Allard (1961) and Rasmusson (1968) obtained an estimate of location X year variance component (σ^2LY) by performing a separate analysis of variance involving years, locations and replicates for each entry in the trial.

These two approached are difficult to use when a large number of entries are included in a trial.

(iii) Wricke (1962, 1966) suggested a parameter, termed "ecovalence", as a measure of the relative contribution of individual entries to the overall genotype X environment interaction term.

$$\text{Ecovalence } (W_i) = \sum_{j=1}^{s} [(GE)_{ij}]^2$$

where the parameter can be calculated from the identity

$$W_i = \sum_{j=1}^{s} (\bar{Y}_{ij.} - \bar{Y}_{i..} - \bar{Y}_{.j.} + \bar{Y}_{...})^2$$

where

$\bar{Y}_{ij.}$ is the mean yield of entry (i) at environment (j)

$\bar{Y}_{i..}$ is the mean yield of entry (i) over all environments

$\bar{Y}_{.j.}$ is the mean yield of all entries at environment (j),

and

$\bar{Y}_{...}$ is the mean yield of all entries over all environments.

The relationship between the genotype X environment sum of squares and 'W' parameter is given in the following formula:

$$G \times E \text{ (SS)} = r\Sigma W_i$$

where r is the number of replicates per environment.

The separate interaction variances calculated by Allard (1961) and Rasmusson (1968) and Wricke's 'W' parameter supply useful information about the performance of individual genotypes

across a range of environments and indicate which ones are the most variable. However, they fail to give an adequate account of the response of genotypes to different environments and do not specify the nature of interaction.

(b) Regression analysis (adaptation analysis)

(1) Techniques of analysis

To overcome these limitations of the analysis of variance approach, various attempts have been made to detect and measure the magnitude of genotype X environment interactions by using a regression analysis. Yates and Cochran (1938), in an analysis of the barley yield data of Immer et al. (1934), used a purely statistical technique and partitioned the genotype X environment interaction sum of squares in the analysis of variance into components due to linear regressions and deviations from regression. It was found that the greater part of the interaction sum of squares was accounted for by differences in the linear regressions. The authors proposed that the yield of each variety could be plotted against the mean yield of all varieties at each location and its yield performance could be depicted by a regression line.

Walton (1957), apparently independently of Yates and Cochran, suggested that the yield of the standard variety or the mean yield of all varieties in a trial could be used as a "measure of general productivity". The performance of a variety over the range of

environments was measured by calculating the regression of yield of a variety on the mean yield of all varieties in a trial.

The significance of the regression technique outlined by these workers was not fully recognized until Finlay and Wilkinson (1963) described their adaptation analysis which depends on a regression technique similar to that of Yates and Cochran. Finlay and Wilkinson compared the yields of 277 barley varieties of diverse geographical origin grown at several sites over several seasons. For each variety, the regression of individual yield on the mean yield of all varieties for each site and season (commonly referred to as "site mean yield") was computed. The site mean was regarded as a simple measure of the environment "without the complexities of defining or analysing the interacting edaphic and seasonal factors" and it provided a "numerical grading of sites and seasons".

The authors used logarithmically transformed data in their analysis because it induced (i) a reasonable degree of homogeneity of experimental error, and (ii) a higher degree of linearity in the regressions. They partitioned the genotype X environment interaction into regressions and deviations from regression components similar to the approach of Yates and Cochran and reported that 79% of the interaction variance component was attributable to linear regressions. The deviations from regression

were found to be unimportant. The authors suggested that the linear regression coefficient (b) and variety mean yield over all environments (G) were important measures of the performance of a variety across environments, i.e. its adaptation. They summarized their results by plotting b against mean yield in a two-dimensional scatter diagram.

The use of a log transformation has been criticized by Knight (1970) who stated that the "effect of logarithmic transformation is to minimize genotypic differences at the high values and maximize differences at the low values". He also pointed out that two indices, 'mean' and 'b', are often positively correlated on a natural scale but there is no correlation between these two indices when logarithmically transformed data are used.

Lawrence (1970) reanalyzed portion of Finlay and Wilkinson's data using arithmetic and geometric (logarithmic data) models. He showed that the regression coefficients in these two models are different parameters and the transformation of data to the logarithmic scale did not result in a more homogeneous error. However, linearity of regression was induced in both analyses. Lawrence pointed out that the parameters estimated on a natural scale were more easily interpreted. In addition, Walton (1968) found a high degree of linearity of regressions by using untransformed data. He suggested that "the data need not be

transformed, provided the varieties are compared in small, related groups".

Eberhart and Russell (1966), in an analysis of single crosses and three-way crosses of maize, extended the regression technique used by Finlay and Wilkinson by including a third stability index, deviation mean squares ($S^{2'}d$), in addition to 'mean' and regression coefficient (b). These are defined in the following model.

$$Y_{ij} = x_i + b_i I_j + \delta_{ij}$$

where

Y_{ij} is as defined previously

x_i = the mean of genotype (i) over all environments

b_i = linear regression coefficient of genotype (i) over all environments

I_j = environmental index

$= E_j - \bar{E}$

where

E_j = measure of environment at site (j)

and

$\bar{E}$ = mean of all E_j

δ_{ij} = deviation from regression for genotype (i) at environment (j)

The third stability parameter ($S^{2'}d$) is calculated as follows:

$$S^{2'}d_i = \left[\sum_{j=1}^{s} \delta^2_{ij} \Big/ n-2\right] - S^2_e/r$$

where

n = number of environments

and

S^2_e/r = estimate of pooled error.

Rowe and Andrew (1964) also suggested that the deviation mean square could be used as a measure of stability, but they failed to discuss its importance.

Eberhart and Russell analyzed natural data and found that the sum of squares due to linear regression was not a very large proportion of the genotype X environment interaction and concluded that deviation mean squares was a more important parameter. They obtained large deviations from linear regression for some lines and crosses, and suggested that the deviations might be due to a quadratic response to environments. The data were analyzed using a quadratic model but the deviation mean square was not reduced.

Apart from these purely statistical techniques of adaptation analysis, several workers including Bucio Alanis (1966), and Bucio Alanis and Hill (1966) and Perkins and Jinks (1968a, b) at Birmingham University, Department of Genetics, have developed and used a biometrical-genetical approach to the analysis. Since this

biometrical-genetical approach has not been used in the present study the technique will not be reviewed in detail except the work of Perkins and Jinks (1968a, b) and related studies of others. Perkins and Jinks tried to bridge the gap between the purely statistical and the biometrical-genetical approach using the following mathematical model:

$$Y_{ij} = \mu + D_i + E_j + G_{ij} + e_{ij} \qquad (1)$$

where

Y_{ij} = yield of genotype (i) in environment (j)

μ = mean of all genotypes over all environments (population mean)

D_i = the additive effect of genotype (i)

E_j = the additive effect of environment (j)

G_{ij} = genotype-environment interaction of genotype (i) in environment (j)

e_{ij} = experimental error of genotype (i) in the environment (j)

The genotype X environment interaction was further partitioned into linear and a non-linear component as follows:

$$G_{ij} = \beta_i E_j + \delta_{ij}$$

where

β_i = linear regression coefficient for genotype (i)

and

δ_{ij} = deviation from regression for genotype (i) at environment (j)

The linear regression slope β_i (obtained from regression of Y_{ij} on E_j) is exactly one unit less than the stability parameter, β_{di} (obtained from regression of G_{ij} on E_j), or

$$\beta_i = 1 + \beta_{di}.$$

Thus the above model (1) could be written as:

$$Y_{ij} = \mu + D_i + (1 + \beta_{di})E_j + \delta_{ij} \qquad (2)$$

This regression model of Perkins and Jinks is directly related to that of Eberhart and Russell, as shown below:

$$x_i = \mu + D_i$$

$$b_i = \beta_i = (1 + \beta_{di})$$

and

$$I_j = E_j.$$

In their analysis of final height of inbred lines of Nicotiana, both heterogeneity between regressions (linear) mean squares and remainder (deviation) mean squares were highly significant, which indicated that a significant portion of G X E

interactions was a linear function of the environmental values but there was an equally large portion of the interactions that was not accounted for by linear regressions. They tested the significance of β_i values against the error MS or against the remainder MS and found that 20% of inbred lines (Experiment 1, with equal gene frequencies) had significant β_i values when data were analyzed over 9 environments.

Recently, Freeman and Perkins (1971) have pointed out that the measure of environment used by Yates and Cochran and subsequent workers leads to statistically invalid regressions. They suggested a new model of analysis which was similar to that of Perkins and Jinks (loc. cit.) except that it included an independent assessment of the environment instead of using the mean of all genotypes under test. In the analysis of variance, they partitioned environmental variation into combined regression (linear) and the residual (deviation) mean squares and the genotype X environment interaction into heterogeneity of regression (linear component) and residual (deviation) mean squares. This partitioning of environmental variation provided a check of whether the independent environmental index gave a sufficiently good measure of environment.

They emphasized the need for an independent assessment of environment such as the use of (i) one or more genotypes as standards

to assess the environment, (ii) parental genotypes as standards when testing hybrids or (iii) closely related material in the same environment or replicates of the same material in closely related environments.

Fripp and Caten (1971) and Fripp (1972) carried out studies of genotype X environment interactions of growth rate in Schizophyllum commune by using independent assessments of the environments as suggested by Freeman and Perkins (1971) and also by using mean of all material being tested at each environment (non-independent environmental values).

They found that both indices of environments gave similar results and contrary to Freeman and Perkins, they concluded that the general conclusions drawn from the previous investigations were not invalidated by the use of non-independent environmental values. The regression coefficient and deviations from regression mean squares were referred to as the linear sensitivity and non-linear sensitivity, respectively, in their work. They found that a significant part, but not all, of G X E interactions was accounted for by differences in linear sensitivity.

(2) Adaptation studies

The regression analysis has been used by many workers to investigate yield and adaptation of yield for pure varieties, mixtures and hybrids of different crops by testing over a range of environments. In cereal breeding this analysis has been used to

specify the adaptation characteristics of collections of genotypes and to select stable and high-yielding genotypes for utilization as parents. In addition, several investigations were undertaken to study the comparative performance of different types of populations over environments.

In all of these studies different parameters have been used to define the stability of a genotype or population. Finlay and Wilkinson (1963) used the linear regression coefficient (b) as a measure of phenotypic stability or adaptation of barley varieties to a range of environments. Because the individual variety yields were plotted against the mean of all variety yields, the population mean had a regression coefficient of 1.0. They recognized the following adaptation types.

(i) Average adaptation (average stability)

Varieties having a regression coefficient (b) equal to unity have an average stability and these may exhibit either general adaptation (high mean yield over all environments) or poor adaptation (low mean yield in all environments). They suggested that from the plant breeders' point of view the best variety would be one with high mean yield and b = 1.0.

(ii) Specific adaptation

Varieties having $b < 1.0$ have above-average stability (stable varieties) and are specifically adapted to low-yielding

environments, whereas those having b > 1.0 have below-average stability (unstable varieties) and are specifically adapted to high-yielding environments.

Finlay and Wilkinson's conception of a completely stable variety was one having b = 0.0, whereas Eberhart and Russell, contended that genotypes with b = 1.0 and S^2d = 0 should be classified as stable. The latter definition is more acceptable in plant breeding, because a genotype with high mean yield, unit regression and a small deviation from regression would show an average and consistent increase in yield as the environmental conditions improved. On the other hand, a genotype with b = 0.0 will perform relatively the same over a wide range of environments, with no inherent potential to respond to favourable environments.

Breese (1969) concluded that S^2d (or the standard error of b) was an indication of stability. He adds 'since the linear regression represents very definite and measurable responses to the environment, it is no longer profitable to consider this component of genotype, of the genotype X environment interaction, as a measure of stability in the way described by Finlay and Wilkinson. The term 'stability' should now rather be reserved to describe measurements of unpredictable irregularities in the response to the environment as provided by deviations from regression'.

Sparrow (1969) used the term 'stability' to describe type of response to the environment (i.e. slope of regression line similar to Finlay and Wilkinson) and suggested that S.E.(b) derived from S^2d is the 'reliability' of the response.

The various definitions of 'stable' genotype used by different workers in a range of different crops are summarized in Table 2.

Johnson et al. (1968), Walton (1968) and Joppa et al. (1971) have analyzed yield data of wheat varieties obtained from regional trials conducted over many years at several locations. In the first two studies, the regression coefficient (b) was used as a measure of stability. The main objectives of their studies were to study the yield potential of selected wheat varieties across range of environments and to select for general adaptation. Walton (1968) was able to identify Canadian and Mexican wheat varieties with wide and specific adaptation over a wide range of productivity levels.

Joppa et al. (1971) used the mean squares for deviation from regression (S^2d) and the linear regression coefficient as a measure of stability. Some stable cultivars with small S^2d values were identified in their study. However, other cultivars gave significantly large S^2d values and they found that in many cases these deviations were due to interaction between genotypes and

Table 2. Definition of stable genotype by various authors.

Author	Crop	Material	Definition of stability
Finlay and Wilkinson (1963)	Barley	Varieties	$b = 0.0$
Finlay (1963)	"	Hybrid populations and parent varieties	
Finlay (1968)	Wheat	Varieties	
Johnson *et al.* (1968)	"	"	
Rasmusson (1968)	Barley	Varieties, simple and complex mixtures	
Walton (1968)	Wheat	Varieties	
Perkins and Jinks (1968a, b)	Tobacco	Inbred lines and hybrids	$1 + \beta_{di} = 0.0$
Eberhart and Russell (1966)	Maize	Single- and three-way crosses	$b = 1.0$, $S^{2'}d = 0$
Smith *et al.* (1967)	Soybean	Lines derived from crosses	
Eberhart and Russell (1969)	Maize	Single- and double-crosses	
Reich and Atkins (1970)	Sorghum	Parental lines, F_1 hybrids, parental blends, hybrid blends	
Breese (1968)	*Dactylis glomerata*	Four cultivars and one hybrid	$S^{2'}d = 0$
Joppa *et al.* (1971)	Wheat	Cultivars	
Tai (1971)*	Potato	Varieties and seedlings	$\alpha = -1, \lambda = 1.0$

* The statistics α and λ used by Tai (1971) are related to those of Eberhart and Russell as follows:

$$\hat{\alpha} = b - 1 \quad \text{and} \quad \hat{\lambda} = \frac{\sum_{j}^{s} \delta^2_{ij} \,/\, n\text{-}2 \text{ (Deviation MS)}}{\text{Error MS}/r}$$

where r = no. of replicates.

specific pathogens. In other cases, the causes of large S^2d values were extremely complex and the authors were unable to explain them.

Tai (1971) analyzed the tuber yields of different seedlings and check varieties of potato tested in three regional trials, each covering a range of environments. He used a different statistical procedure from other workers, to estimate the stability parameters, α and λ, which are related to those used by Eberhart and Russell as shown in Table 2. Only a few of the seedlings in the trials showed a linear response to environments and significant deviations from regression were more common. Some high-yielding seedlings were identified but they did not have satisfactory stability as compared with the check varieties.

In addition to the above studies on pure varieties, some workers have compared the performance of different types of populations to determine the most suitable population structure for stabilizing yield across environments. Most of these studies support the contention that hybrids and mixtures of different genotypes are more stable in their performance over a range of environments, than pure varieties. Some results, on the other hand, showed that pure varieties and their simple mixtures were similar in stability and both were somewhat less stable than the hybrids (Rasmusson, 1968).

Reich and Atkins (1970), working with sorghum, studied the stability of yield of parent lines, hybrids, parent blends and hybrid blends, and concluded that hybrid blends were the most stable. Furthermore, it has been shown that segregating groups such as F_2, F_3, first backcross and second backcross generations of maize were more stable in yield performance than the inbreds and F_1 groups of maize when measured by deviation mean squares (Rowe and Andrew, 1964). Similarly, Smith et al. (1967), in their studies of hybrid lines of soybean populations, observed that the pooled deviations from regression for F_5-derived daughter lines were greater than their respective F_2-derived maternal lines in F_6 - F_7 generations over a range of environments. This indicates that a heterogeneous mixture of homozygous genotypes is more stable than the individual component homozygotes.

Qualset (1968) and Jowett (1972), working with different populations of wheat and sorghum, respectively, used the mean and three stability parameters, b, S^2d and W to describe the yield performance of their populations over a range of environments. Qualset (1968) conducted his experiments over only three environments and arrived at the following tentative conclusion: The mixtures were more stable than the hybrids by both S^2d and W parameters, whereas both mixtures and parents were more stable than the hybrids by S^2d parameters. Measured by 'b' parameter

all populations had a similar performance (b ≈ 1.0).

By using logarithmically transformed data, Jowett (1972) indicated that three-way crosses performed more uniformly across environments than single crosses and pure varieties as measured by b, S^2d and W parameters.

Allard and Bradshaw (1964) have distinguished two kinds of buffering leading to stability of performance. Individual buffering refers to a single genotype whose individual members are well buffered over a wide range of environments, whereas population buffering is the property of the population, consisting of a number of genotypes each adapted to a range of environments.

The above results may represent examples where heterozygotes show more individual buffering than the homozygotes and the mixtures show more population buffering.

2. Inheritance of yield stability

It is generally observed when comparing F_2-derived selections from crosses, that some selections seem to have the ability to adapt to a wide range of environments while others do not. A few workers have studied the inheritance of this stability of yield performances.

Bradshaw (1965), in a review of literature on phenotypic plasticity, states that the stability of character can vary from one genotype to another and is genetically determined: this concept was well demonstrated by Williams (1960) who showed that

inbred lines of tomatoes which differed markedly in their stability for a number of characters, transmitted this stability to the F_1 hybrids.

The most extensive study of the inheritance of yield stability has been conducted by Finlay (1963). He found that hybrid populations from diallel crosses of 10 barley cultivars, when grown over a range of natural environments, showed superiority in average yield and stability of yield over their homozygous parents. The cultivar C.I.3576 with a high yield and average stability, was found to have the greatest potential for transmitting high mean yield and increased stability to its progeny. On the other hand, Triple Awned Lemma, which is low yielding and below average stability, transmitted low yield and lack of stability.

Later, in an analysis of data collected by E.J. Wellhausen, Finlay (1968) demonstrated the inheritance of yield stability among the progenies of dent and flint type crosses of maize.

Scott (1967) devised a method to study the inheritance of yield stability in maize. He selected F_2's from different sources showing high, medium and low environmental variance (σ^2E); their test crosses and intercrosses were tested over many sites during the one year. Hybrids between the F_2-derived lines selected for low σ^2E gave progeny which consistently had low b values. However, hybrids between the F_2-derived lines of high

σ^2E from different sources showed an average stability of yield ($b \approx 1.0$).

These results indicate that selections for different levels of yield stability can be made among segregating progenies and thus this character is genetically controlled.

3. Breeding for yield and wide adaptation

An important objective for plant breeders is to produce varieties which have a relatively high yield irrespective of environmental conditions. For example, in South Australia, where climatic features, particularly rainfall, vary markedly from season to season, it is necessary to have varieties with wide adaptation.

Borlaug and his colleagues developed widely adapted varieties of spring wheat in Mexico and Colombia. To accelerate the breeding programme they grew two generations per year; one in winter at sea level at latitude 27°N, and a second in summer at 2600 m altitude at latitude 18°N. Some of the hybrid selections were also grown in summer at 2900 m altitude in Colombia at latitude 4°N.

Borlaug (1965) reported that some of the Mexican and Colombian varieties were top-yielding in all environments when compared with varieties from Canada and northern U.S.A. The environments included locations from 0° to 50° latitude and over

a wide range of longitudes under both irrigated and non-irrigated conditions. He demonstrated that Mexican and Colombian varieties were insensitive to changes in day-length and date of planting, whereas northern U.S.A. and Canadian varieties were extremely sensitive to these changes and therefore could no longer be grown successfully at latitudes of less than 40°.

This superiority in yield and adaptation of some Mexican wheats has further been shown in recent international yield trials conducted over many sites in up to twenty-eight countries (Krull et al., 1968a, b).

In contrast to Mexican workers at CIMMYT, Finlay and co-workers measured the yield and stability of yield by growing sub-samples of each selection in each season over a number of sites in South Australia (Finlay, 1968). Finlay emphasized that his technique is more useful for identifying adaptation types of all lines and for facilitating the selection of lines for release as commercial varieties or for further use in breeding programmes.

Recent experiments at the Waite Institute with cereals, have shown that lines with an increased yield and stability can be obtained from crossing widely adapted genotypes with those specifically adapted to high-yielding environments (Finlay, 1963).

St. Pierre et al. (1967) showed that by growing segregating populations alternately at two different sites, one could select

for wide adaptation. Selections from second to fifth generations of barley were made under low and high yielding sites. During the selection period seed was divided into two lots and planted alternately at the two sites in subsequent years, ultimately providing sixteen selection pathways. The selected strains were tested for their adaptation in the F_7 and F_8 generations by conducting trials at the same two sites (low-yielding and high-yielding) by employing Finlay and Wilkinson's techniques.

The authors concluded that strains selected at the low-yielding site in F_4 possessed greater adaptation than those selected at the high-yielding site. Starting from low-yielding site in F_2, the selected strains grown at alternative sites in successive years possessed the widest adaptation. On the contrary, Frey (1964) showed that selecting oat strains from non-stress (high-yielding) environments provided more chance for obtaining wide adaptation.

Recently, the general adaptation of a number of hard red winter wheat varieties tested in regional nurseries over several environments, was studied by Johnson et al. (1968). After computing the linear regression coefficient (b) of individual entries, the predicted yield of each variety was calculated from the regression equation. The predicted values for each variety were then expressed as percentage of the predicted value for the check variety. By plotting the

percentage yield against the predicted of check variety over a range of environments, the authors were able to select varieties for general or wide adaptation. This technique could be useful to plant breeders for comparing the performance of yield of newly released varieties with the existing commercial variety grown over a large area in the region.

4. Characteristics of plants associated with stability of yield

The environment in the field varies from season to season and locality to locality within a region and much of this variation is uncontrollable. From an evolutionary point of view, Thoday (1953) has indicated that an individual species may react to a variable environment in two ways. First, an individual may have a genotype which provides buffering against environmental variation so that the same adaptive phenotype is produced over a range of environments; second the genotype may produce different phenotypes under different environments, each one particularly adapted to its own environment.

According to Grafius (1956), the stability of yield of a crop plant may be due to inherent characteristics or else it may be due to plasticity of yield components. Plasticity is shown by a genotype when its phenotypic expression, morphological and physiological, is altered by environmental influences. The fitness

of a genotype in varying environments depends on both morphological and physiological characters, and such fitness is the result of the interaction of all the component characters, and their plasticities to environmental variation. Each of these characters, can have its own plasticity and response to environment and maximal fitness can be obtained by plasticity in some characters and stability in others. But if a number of interacting characters are all plastic, the maximal fitness of the organism may be maintained by morphological adjustment (Bradshaw, 1965).

After measuring a number of morphological and physiological characters over a range of environments Finlay and Wilkinson (1963) suggested that maturity is the most significant characteristic associated with stability of yield. In their studies some of the earliest varieties were specifically adapted to a low-yielding environment, whilst the late varieties tended to be specifically adapted to a high-yielding environment. However, they also noticed that a wide range of maturing types were represented in the generally adapted group having very high mean yields.

Borlaug (1965) reported that the wide adaptation of the Mexican wheats was due mainly to their insensitivity to day length. Resistance to rust diseases and to lodging also contributed to their wide adaptation. Recently Lohani (1970), in his studies of composite cross populations of barley, showed that the genotypes with high

yield and wide adaptation under South Australian conditions were those which were resistant to shattering, lodging and powdery mildew.

It has been suggested by many workers that characters such as plant height, tiller number, leaf size, flag leaf area and yield components are important for the selection of widely adapted genotypes. Donald (1963) found that with increasing plant density, yield is maintained relatively 'stable' as the result of an increase of heads per row and a decrease in number of seeds per head, whereas seed weight remains constant. However, in some crops, the yield curves show peak values, falling by 10-40% at very high densities.

Johnson, Schmidt and Mekasha (1966) measured grain yield and its components; number of spikes, kernels per spike and kernel weight among two tall and two short statured wheat varieties under a range of environments. The performance of yield and its components of the short statured varieties were compared with tall variety, 'Pawnee'. They indicated that on average, the short-statured varieties produced more yield than 'Pawnee' because of their consistent increase in number of kernels per spike over these environments.

Roy and Murty (1967) have obtained evidence that bread wheats selected for synchronous tillering have wide adaptation.

The stability of yield and other characters have been measured in different genotypic groups of corn by Rowe and Andrew (1964). They showed that the deviations from regression for non-segregating inbred lines and F_1 groups were significantly larger than for the segregating groups with respect to ear height, plant height and yield. Their results suggest that instability of plant height and ear height characters might have influenced the yield across environments.

It has been suggested that many different combinations of characters interact in different ways to allow plants to produce high and stable yields in a range of environments (Finlay, 1968). He adds further that, "because adaptability is intrinsically a dynamic process, it is likely that the mode and rate of modification of these characters by the plant when grown in a range of environments may be more important than their actual level of expression in each of the environments individually".

Recently, Lawrence (1970) studied the association of various morphological and physiological characters with stability of yield among populations of barley having different yield stabilities. In the stable population, characters such as short stable height, early heading, large grain, high fertile tiller ratio, high harvest index, more heads per plant and large stable flag leaf area were associated with stability of yield. However,

these morphological characters were measured on a sub-sample of only five plants per plot, and such a sample was not very representative because of lack of uniformity of seeding. Lawrence concluded that stability of yield was partly correlated with some morphological and physiological characters but it was difficult to draw any conclusion on the characteristics of a generally adapted 'ideotype' defined by Donald (1968).

MATERIALS AND METHODS

A. Choice of parental cultivars

Cultivars with diverse yield and adaptation pattern were required as parental material for the present study. The adaptation parameters of a large number of two-row barley cultivars, comprising material from Europe, the Mediterranean basin, North America and Australia, have been determined in comprehensive trials conducted over a range of sites and seasons in South Australia by Dr. D.H.B. Sparrow at the Waite Agricultural Research Institute and five cultivars were chosen on the basis of the adaptation performance in his experiments, as follows:

(a) Sparrow (1972) studied the performance of 40 two-row barley cultivars of diverse geographical origin, grown in a four-replicate experiment at each of 15 environments in South Australia. Analysis of data showed a wide range of cultivar performance with respect to "mean yield" and "stability of yield" (Figure 1a).

Three of these cultivars (Proctor, C.I.3576 and Prior) having different geographic origins and exhibiting contrasting yield and stability of yield, were selected for the present study.

(b) Sparrow (unpublished) tested another set of 13 two-row barley cultivars, comprising advanced hybrid lines as well as recently-released cultivars bred at the Waite Institute, in a two-replicate

FIGURE 1

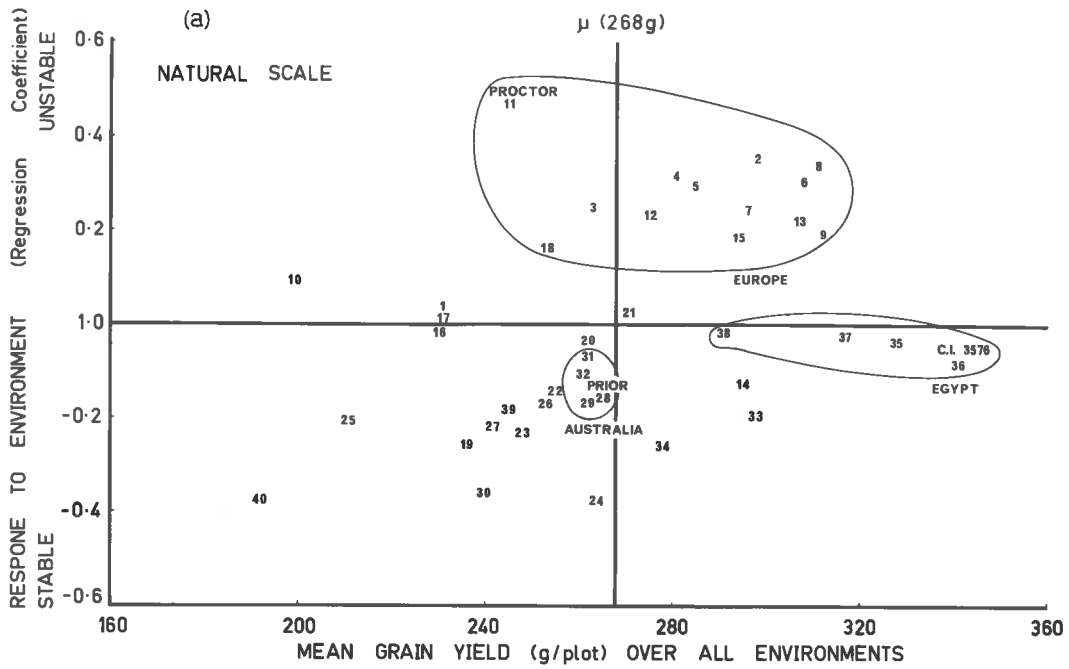
The relation between mean yield over all environments and the stability of yield (regression coefficient) for cultivars from two sources:

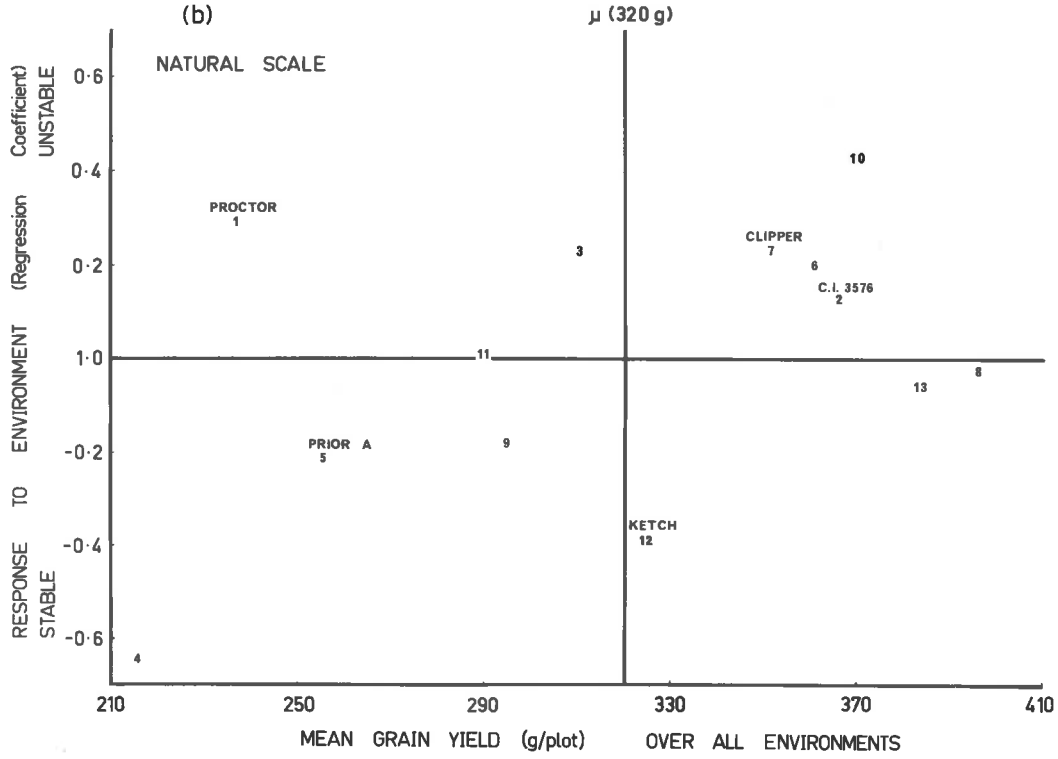
(a) Sparrow (1972)

40 cultivars tested over 15 environments.

(b) Sparrow (unpublished)

13 cultivars tested over 13 environments.


(a)
μ (268g)
NATURAL SCALE
PROCTOR
11
EUROPE
C.I. 3576
36
EGYPT
PRIOR
AUSTRALIA
0·6
0·4
0·2
1·0
-0·2
-0·4
-0·6
160
200
240
280
320
360
RESPONE TO ENVIRONMENT (Regression Coefficient)
UNSTABLE
STABLE
MEAN GRAIN YIELD (g/plot) OVER ALL ENVIRONMENTS


(b)
μ (320 g)
NATURAL SCALE
PROCTOR
1
CLIPPER
7
C.I. 3576
2
PRIOR A
5
KETCH
12
0·6
0·4
0·2
1·0
-0·2
-0·4
-0·6
210
250
290
330
370
410
RESPONSE TO ENVIRONMENT (Regression Coefficient)
UNSTABLE
STABLE
MEAN GRAIN YIELD (g/plot) OVER ALL ENVIRONMENTS

experiment at each of 13 environments. The experiments were conducted in order to select high-yielding cultivars specifically adapted to the different barley growing environments of South Australia (Figure 1b).

The two recently-released cultivars, Ketch and Clipper, which are specifically adapted to low-rainfall and medium to high rainfall areas, respectively, were selected as additional parental material for this project.

The adaptation parameters of these five selected cultivars are given in Table 3, and their origin and agronomic characteristics are described below:

Table 3. Adaptation parameters of cultivars selected for mutation studies.

	Source	Cultivar	Parameters estimated on natural scale		
			Mean yield (g/plot)	b	S.E.(b)
(a)	Sparrow (1972) 40 cultivars tested over 15 environments (Figure 1a)	Proctor	245	1.46	0.14
		C.I.3576	341	0.92	0.25
		Prior	265	0.84	0.15
(b)	Sparrow (unpublished) 13 cultivars tested over 13 environments (Figure 1b)	W.I.2200 (Clipper)	352	1.23	0.13
		W.I.2137 (Ketch)	325	0.61	0.18

(i) Proctor

This cultivar was bred by Dr. G.D.H. Bell at the Plant Breeding Institute, Cambridge, England from a cross between "Abed Kenia X Plumage Archer" and it was released for general cultivation in 1952. It has good malting quality and strong straw but matures late under South Australian conditions. It was introduced into Australia with the international barley collection soon after its release in England. Proctor has below-average stability of yield and is specifically adapted to high rainfall areas with long growing seasons (i.e. high-yielding environments).

(ii) C.I.3576

This cultivar was derived from the progeny of a single spike in the collection of barleys obtained by Dr. H.V. Harlan from the district of Mariut, Egypt, and was introduced to the U.S.A. in 1923. It has not been used commercially but it was included in the U.S.D.A. nursery trials with the name of "Sidi" before it was introduced to Australia in 1949. It is high-yielding, medium in height, and resistant to wind damage, but it has poor malting quality and is susceptible to lodging when grown in highly fertile soils.

C.I.3576 has an average stability associated with above-average yield and is generally adapted to all South Australian barley growing environments.

(iii) Prior (Prior's Chevalier)

This cultivar was selected from Chevalier stock by a South Australian farmer and was first grown commercially about 1904 (Sparrow and Doolette, 1971). It was the standard Australian commercial barley until the advent of Clipper. Prior has medium-early maturity, is tall in height with drooping heads and is susceptible to wind damage and often lodges when grown in highly fertile soils.

It exhibits an average stability associated with an average yield and is adapted to all barley growing regions of South Australia.

(iv) Clipper (W.I.2200)

Clipper was the first barley cultivar produced at the Waite Institute in the programme financed by the Barley Improvement Trust Fund and it was derived from an F_5 plant selection, from the cross "Prior A X Proctor". It was released to registered seed growers in 1968. It is superior in yield and malting quality as compared with Prior. It has an erect head and is resistant to wind damage and lodging. Clipper is adapted to the medium to high rainfall areas of the South Australian barley growing zone (i.e. suited to average to high-yielding environments).

(v) Ketch (W.I.2137)

Ketch was also produced at the Waite Institute, and it was derived from an F_5 plant selection from the cross "Noyep X Lenta".

It was released to registered seed growers for seed multiplication in 1970. It has improved straw strength, yield and grain quality as compared with the "Noyep" parent variety presently grown in low rainfall areas of South Australia. Ketch has above-average stability of yield and it is specifically adapted to barley growing areas in South Australia with low annual rainfall (below 380 mm) and a short growing season.

B. Mutagenic treatment

1. Selection of mutagen and dose rate

EMS (ethylmethanesulphonate) was used as the mutagen in this project for the following reasons:

(i) the frequency of chromosome aberrations observed with EMS-treatment is much less than that with irradiation treatments (Froese-Gertzen et al., 1964).

(ii) EMS induces a high rate of chlorophyll mutations in both M_1 plants and M_2 progenies (Froese-Gertzen et al., 1964).

(iii) EMS has proved to be an effective agent for inducing genetic variability in quantitative characters in crop plants (Gaul et al., 1966).

The EMS treatments used by Nilan et al. (1963), Froese-Gertzen et al. (1964) and Konzak et al. (1965), working with barley, included variations in EMS concentration, soaking time and treatment temperatures. A common treatment consisted

of 0.02 M EMS applied for 5 hours at 30°C, which was quite effective for inducing chlorophyll mutations without drastic effects on spike fertility and plant survival.

A pilot experiment was conducted to determine a suitable mutation treatment for the present study. Four lots of 100 dry seeds (stored in a desiccator to give 8.6% moisture content) of Prior barley were each treated with different doses of EMS for 8 hours at 23°C in the laboratory and were then germinated in Petri dishes (see page 64 for details). The biological response to the various EMS doses was determined by measuring seed germination (%) and average seedling height (cm) 11 days after treatment (Table 4).

Table 4. Response of Prior barley to different concentrations of EMS.

EMS treatment dose	Seed* germination (%)	Average seedling* height (cm)
0.00 M	99	6.92
0.01 M	88	6.25
0.02 M	97	6.31
0.04 M	92	5.78

* Average of 100 seeds per treatment.

The higher EMS concentrations, viz. 0.02 M and 0.04 M, were selected for the seed treatment of parental cultivars as these

doses did not greatly reduce the seed germination and the seedling height as compared with the controls.

2. EMS-treatment of parental cultivars

Homogeneous parental seed is required for mutation studies and usually this would come from single plant multiplication. However such seed was not available for this project, and efforts were made to obtain another source of homogeneous seed.

The seed source of C.I.3576 and Prior had originated from bulking 100 single plants after removing offtypes in the field, whereas Proctor, Clipper and Ketch cultivars originated from single-plant selections. Seed of all five cultivars had been maintained by the Plant Breeding Section at the Waite Institute and constant care was taken to remove offtype plants during their maintenance.

Prior to treatment a sample of 600 dormant seeds from each cultivar was stored in a desiccator over calcium chloride for two weeks until they reached a constant moisture content, which varied from 8.6% to 9.2% depending upon the cultivar.

The mutagen treatment consisted of immersing 200 seeds of each cultivar in 200 mls of freshly prepared unbuffered aqueous solutions of EMS (0.02 M and 0.04 M) in Petri dishes for 8 hours at 23°C. As a control 200 seeds of each cultivar were immersed in distilled water for the same period and at the same temperature. In order to reduce physiological damage, the EMS-treated seeds were

washed with running tap water for one minute immediately after treatment.

C. Production of M_4 seed for field experiments

A schematic outline showing the handling of M_1, M_2 and M_3 generations and the origin of treated and control lines from each cultivar is shown in Figure 2.

Following other workers [Gaul (1964, 1965, 1967); Gaul *et al.* (1966); Abrams and Frey (1964)] and for ease of presentation of results, the first, second and third generations, etc., of both treated and control populations have been designated as M_1, M_2 and M_3 generations, etc. in the present study.

1. M_1 generation

Immediately after EMS-treatment and post-washing the treated and control seeds of each cultivar were germinated in Petri dishes. Subsequently, the seedlings were transplanted into soil in a bird-proof enclosure in the field at 3" X 3"* (7.5 cm X 7.5 cm) spacing during July, 1968. Prior to anthesis, the main spike of each treated and control plant was covered with a glacine bag to

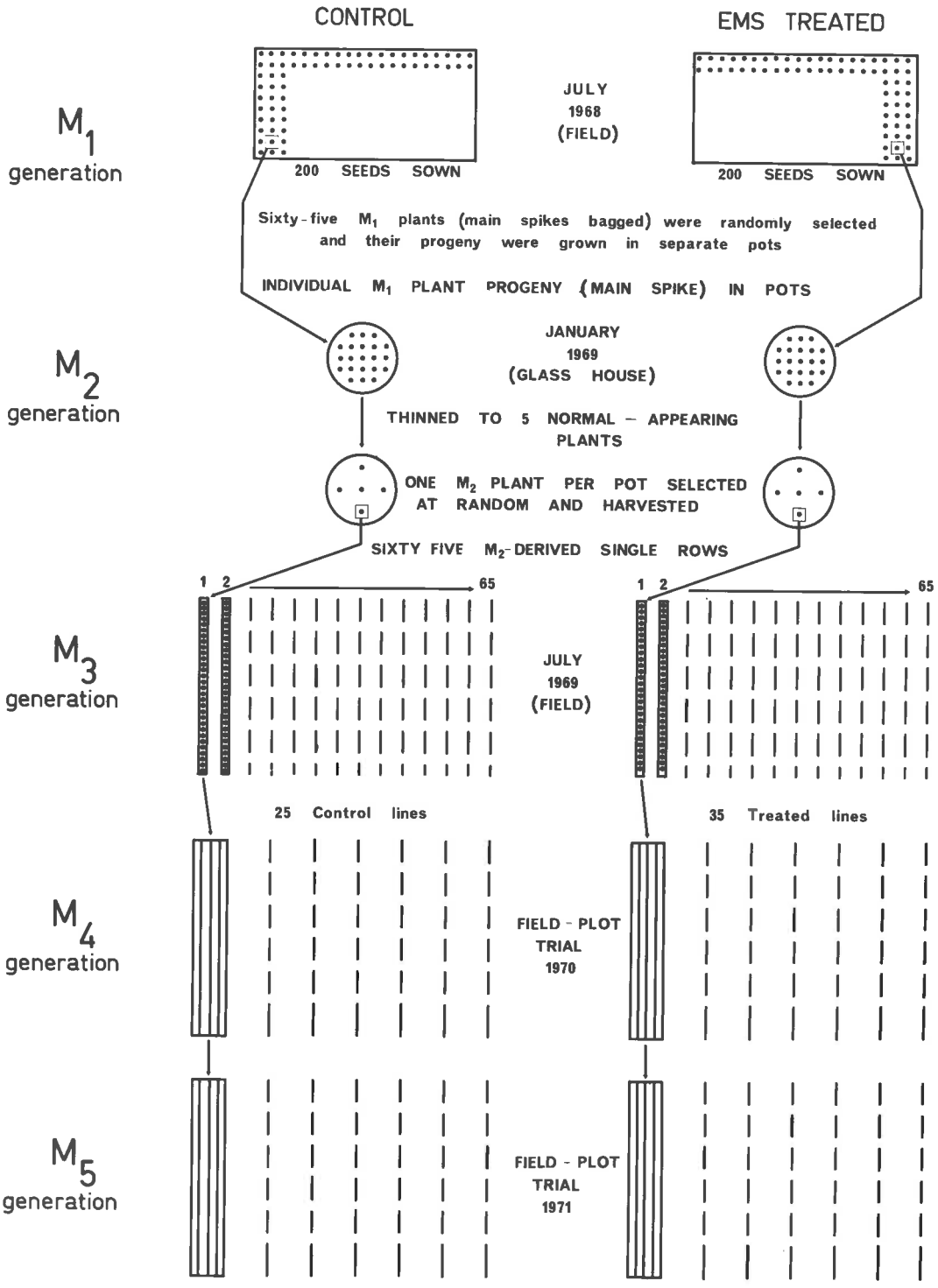
---

* At the beginning of this project the Agronomy Department used British measurements but later the Department changed to the metric system. Hence the early measurements in British units are also given as metric equivalents.

FIGURE 2

Diagram showing the handling of M_1, M_2 and M_3 generations and the origin of treated and control lines of each cultivar and their testing in 1970, 1971.

THE ORIGIN OF M_2-DERIVED LINES OF EACH CULTIVAR AND THEIR TESTING IN 1970, 1971



avoid outcrossing. The 0.04 M EMS-treatment did not result in a drastic decrease in spike fertility when observed visually; hence the M_1 plants from this treatment were carried on further and the 0.02 M treatment material was discarded.

At maturity, the covered main spike of each plant was harvested and threshed individually. In addition, a second uncovered spike from each of 50 random M_1 treated (0.04 M) and control plants per cultivar was harvested to measure the fertility of M_1 plants.

2. M_2 generation

The main spikes were taken from 65 randomly chosen treated (0.04 M) M_1 plants and 65 control M_1 plants, from each cultivar and the seeds from each spike were planted in a 10" (25.5 cm) diameter pot in the glasshouse in January 1969, to raise M_2 plants.

Ten days after planting, the chlorophyll mutation frequency was recorded on the basis of M_1 spike progenies. Any drastic mutant plants were removed and the remainder were then thinned at random to give 5 plants per pot. At maturity, one normal-appearing plant per plot was selected at random and harvested as a source of M_3 seed (Figure 2).

3. M_3 generation

In July, 1969, the M_3 seeds from each of the randomly selected M_2 plants were sown in the field in single rows 10 ft (3.05 m) long. These rows were grown at 14" (0.36 m) spacing

with the aim of obtaining sufficient M_4 seed per M_2-derived line for testing their yield and stability of yield in replicated trials over five sites during 1970.

At maturity, the single rows were harvested and threshed.

D. Field experiments

1. Choice of sites

Since the primary aim of the present study was to measure the effect of random mutation on adaptation parameters of barley, it was essential to select a wide range of sites, in which to test the yield performance of treated and control lines. Five contrasting sites differing in annual rainfall pattern and soil type in the cereal-growing areas of South Australia were selected. The sites chosen were situated near the towns of Monarto South (referred to herein as Bundaleer, the name of the farm), Roseworthy (at the Agricultural College), Minlaton, Adelaide (at the Waite Institute) and Clinton (see Figure 3). The same sites have also been used by barley breeders at the Waite Institute (Finlay and Wilkinson, 1963; Sparrow, 1972).

A brief summary of soil type, normal planting time and annual rainfall for each site is given in Table 5.

FIGURE 3

Annual rainfall map of central districts of South Australia and locations of field-plot trials.

ANNUAL RAINFALL MAP OF CENTRAL DISTRICTS OF SOUTH AUSTRALIA

Average over 100 years to 1966

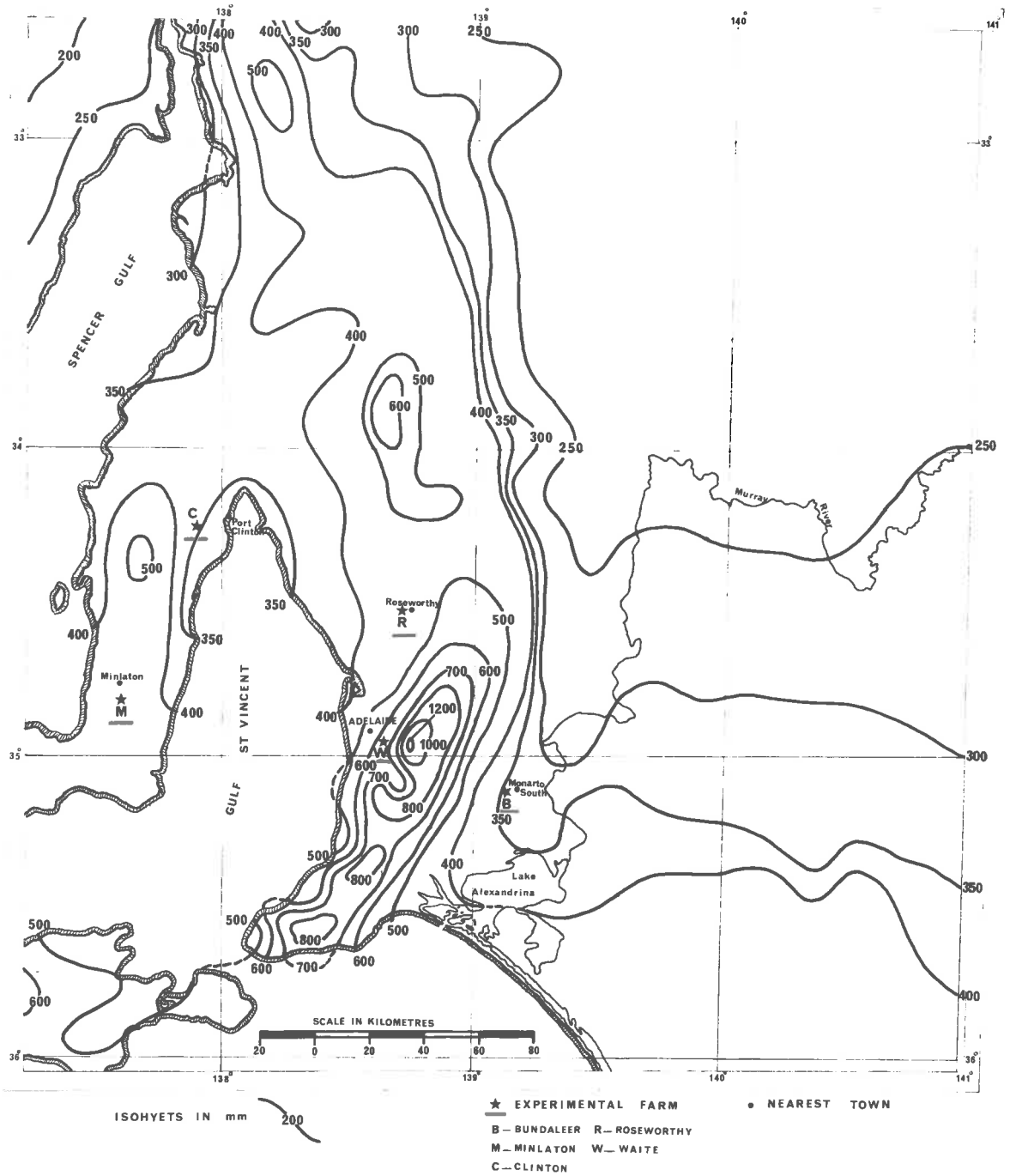


Table 5. Environmental data for experimental sites.

Site characteristic	Experimental site				
	Bundaleer (B)	Roseworthy (R)	Minlaton (M)	Waite (W)	Clinton (C)
Soil type	Sandy mallee	Loamy mallee with free limestone at surface	Shallow sand overlaying limestone	Red brown earth	Loamy mallee
Normal district sowing date	Mid May	Early June	Early to mid June	Late June	Early June
Annual rainfall (mm) (average over 10 years) (1962 - 1971)	336	443	434	639	347

2. Field-plot trials 1970

Because of the large size of the field plots used by the Plant Breeding Section at the Waite Institute, and the limited availability of seed and experimental space, it was not possible to utilize all 65 M_2-derived treated and control lines of each cultivar for testing in a replicated field trial. In order to keep a balance between the need to test a large number of treated lines and to retain a reasonable number of control lines for comparison, a compromise was made. It was decided to include 35 treated and 25 control lines from each of Clipper, C.I.3576, Proctor and Ketch cultivars, with at least 200 gm of M_4 seed, in the field experiments.

Unfortunately, many of the M_3 single rows of Prior did not produce the required quantity of seed for use in field trials. Hence, it was possible to include only 25 treated and 15 control lines of this cultivar in the field experiment.

(a) Experimental layout and planting procedure

The seeds of the M_2-derived treated and control lines were grown in the M_4 generation in a two-replicate randomized block layout at the five selected sites. The experimental layout at each site is shown in Figure 4. The treated and control lines of each cultivar were randomized within a sub-block with two border plots of the parent cultivar separating each sub-block.

The experimental plots were sown with a magazine-loaded cone seeder using 20 gm per plot (67 Kg/ha). The individual plots consisted of four rows 5 m in length and 15 cm apart, with 30 cm space between adjacent plots. Within a month of germination each plot was cut back to a length of 4 m by using the chemical Paraquat (Gramoxone) to produce a pathway (1 m wide) between bays. Border plots of Clipper were sown around the perimeter of each experimental area to minimize edge effects.

(b) Collection of data

No results were obtained from the Clinton site in 1970 since most of the plots were destroyed by field mice soon after germination. Data for yield and other quantitative characters

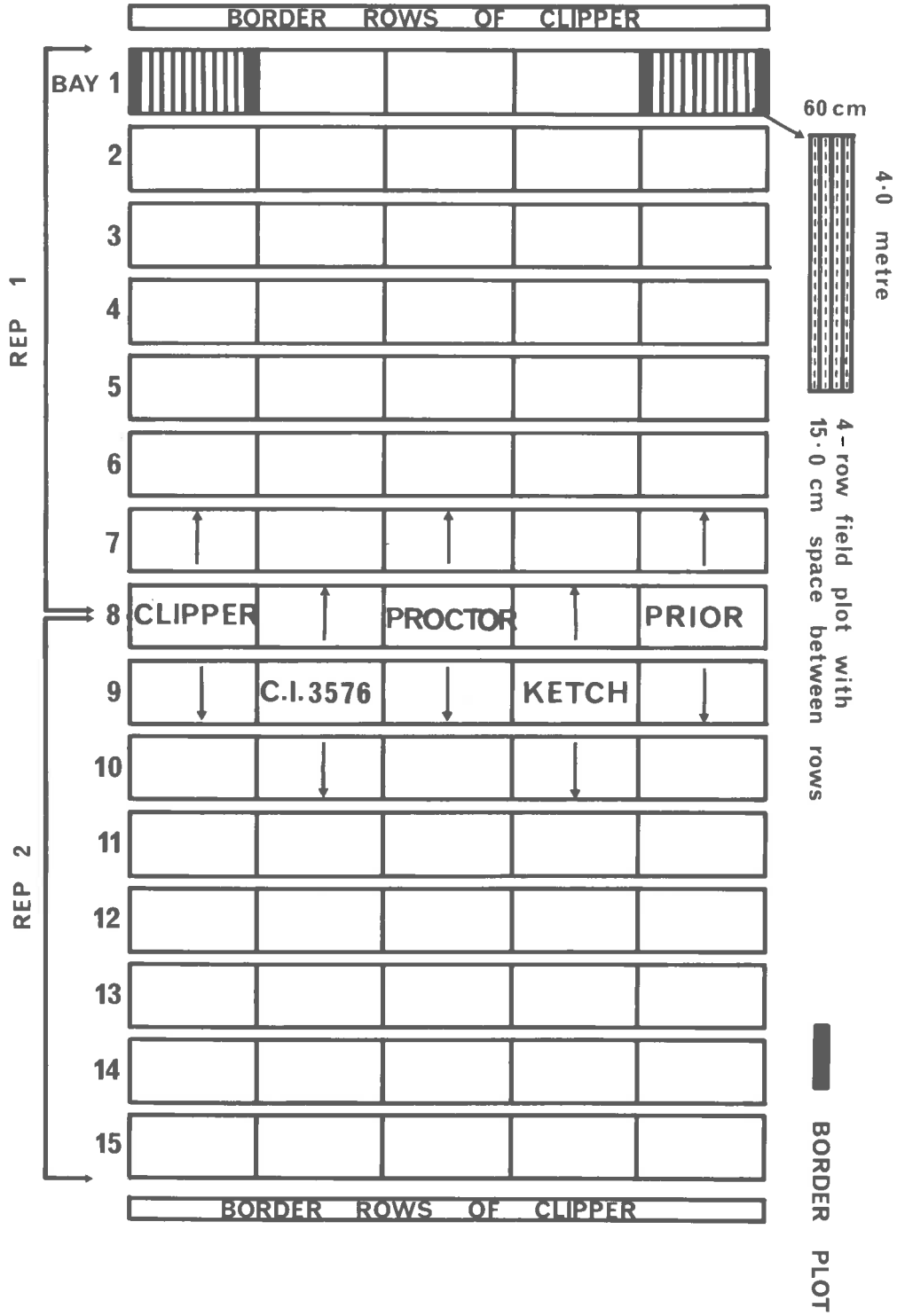
FIGURE 4

Plan of field-plot trials carried out at each site.

Note:

Due to decreased number of Prior lines tested, the Prior sub-block in each replicate was not completely filled.

PLAN OF FIELD-PLOT TRIALS



were recorded for each plot at the remaining four sites: Bundaleer, Roseworthy, Minlaton and Waite.

Heading date. The heading date was scored on a whole plot basis when approximately 50% of tillers in a plot showed at least 2.5 cm awn emergence from the boots. Heading was recorded as the number of days from the date of planting at each site.

Plant height (cm). The mean height of plants in each plot was recorded as the distance from the ground surface to the tips of spikes excluding awns, averaged over 3 plants selected at random within the plot.

Yield. When the plants were mature, 30 cm at each end of the plot was removed and the remainder of the plot (3.40 m) was harvested with a "Waite Gravelly Harvester". The weight of clean grain was recorded in gm/plot.

Seed weight (gm/1000 seed weight). A 15 gm sample of grain was taken from each plot and the number of seeds was counted with an electronic seed counter to give 1000 grain weights.

3. Field-plot trials 1971

(a) Experimental layout and planting procedures

The main field experiments conducted in 1971 consisted of repeating the 1970 field experiments with Clipper, C.I.3576 and Proctor, using M_5 seed instead of M_4 seed; otherwise exactly the same procedures were used as in 1970, with the same randomization

and layout.

In addition, fifteen treated lines from each of Clipper, C.I.3576 and Proctor cultivars contributing most towards genotype X environment interaction as measured by "ecovalence" (W) values and showing differences in mean yield (from low to high), were selected and grown in M_5 generation with two extra replicates (i.e. in addition to two replicates in the main experiments). These selected treated lines were sown at each of the five sites in randomized layout adjacent to their respective main experiments for detailed measurement of their morphological and physiological characters.

(b) Collection of data

Heading date and yield were recorded for all plots grown in 1971, using the same procedures as in 1970.

In addition the following quantitative characters were measured on the 15 selected treated lines of Clipper, C.I.3576 and Proctor cultivars and on 10 randomly selected control lines (included in the main experiment) from each of these cultivars.

Plant height was measured for all plots grown in 1971 similarly to that of 1970 data.

Number of tillers per unit area. Average number of ear-bearing tillers per 30 cm of row was calculated from two 30-cm samples randomly selected from each of the two central rows of each plot. This character was measured on all four replicates of the

selected treated lines and the two replicates of the controls.

Seed sterility was recorded as percentage of sterile florets compared with total number of florets for the randomly chosen spikes. These spikes were sampled from two randomly selected 30 cm lengths of each of two central rows of the plot. This character was measured only on the two replicates of both control and selected treated lines included in the main experiment.

Number of seeds per spike. The mean of the number of seeds per spike was obtained from the ten randomly selected spikes used for seed sterility measurements

E. Statistical analyses

The following statistical procedures were used for the analyses of yield data:

1. A conventional analysis of variance (ANOVA).
2. A regression analysis.

1. An ANOVA was undertaken for:

a) The data for individual sites (environments)

and b) Data combined over all sites (environments).

In the first analysis the residual (error) variances for sites were tested for homogeneity by Bartlett's (1937) X^2 test before combining the data for all sites in the record.

The mean square expectations are given in Table 6.

Table 6. The analyses of variance (ANOVA).

Source of variation	d.f.	Mean square expectations	MS
(a) ANOVA for individual sites (environments)	⁄		
Replicates	r-1	$\sigma^2 e + p\sigma^2 r$	MSR
Lines	p-1	$\sigma^2 e + r\sigma^2 p$	MSP
Residual (error)	(r-1)(p-1)	$\sigma^2 e$	MSE
Total	rp-1		
(b) ANOVA combined over all sites (environments)			
Sites (environments)	s-1	$\sigma^2 e + r\sigma^2 ps + rp\sigma^2 s$	MSS
Replicates within sites	s(r-1)	$\sigma^2 e + ps\sigma^2 r$	MSR
Lines	p-1	$\sigma^2 e + r\sigma^2 ps + rs\sigma^2 p$	MSP
Lines X sites	(p-1)(s-1)	$\sigma^2 e + r\sigma^2 ps$	MSPS
Residual (error)	s(r-1)(p-1)	$\sigma^2 e$	MSE
Total	srp-1		

⁄ s, r and p represent the number of sites, replicates per site and lines respectively.

The mathematical model used for the analysis of variance combined over all sites was:

$$Y_{ijk} = \mu + G_i + E_j + (GE)_{ij} + R_{jk} + e_{ijk} \qquad [1]$$

where

Y_{ijk} = yield of line (i) at site (j) and in replicate (k).

μ = population mean, i.e. mean yield of all lines over all sites and replicates.

G_i = mean genotypic effect of line (i), i = 1, 2, ..., p.

E_j = mean effect of site (j), j = 1, 2, ..., s.

$(GE)_{ij}$ = interaction effect of line (i) at site (j).

R_{jk} = effect of replicate (k) within site (j), k = 1, 2, ..., r.

e_{ijk} = error of line (i) at site (j) and in replicate (k).

Estimates of the variance components $\sigma^2 p$ (genotypic variance due to lines), $\sigma^2 ps$ (line X site interaction variance) and $\sigma^2 e$ (error variance) were obtained by equating the observed and expected mean squares. Such estimates of variances were calculated by using formulae given by Johnson et al. (1955) and Rowe and Andrew (1964).

Heritability (H) in the broad sense is defined as the proportion of genotypic variance to the phenotypic variance and heritabilities were calculated for individual sites and over all sites.

(a) For each individual site the formula of Rawlings et al. (1958) was used.

$$H = \frac{\sigma^2 p}{\sigma^2 ph}$$

where

$\sigma^2 ph = \sigma^2 p + \frac{\sigma^2 e}{r}$ (i.e. phenotypic variance among means of lines)

(b) Heritability for the data combined over all sites was obtained by the method described by Johnson et al. (1955).

$$H = \frac{\sigma^2 p}{\sigma^2 ph}$$

where

$\sigma^2 ph = \sigma^2 p + \frac{\sigma^2 ps}{s} + \frac{\sigma^2 e}{rs}$ (i.e. the phenotypic variance among the means of lines compared in "r" replicates and "s" sites)

The line X site interaction mean squares and an estimate of $\sigma^2 ps$ from the ANOVA combined over all sites were used to assess relative stability of yield of different populations over a range of sites. The ecovalence ('W') parameter, used by Wricke (1962, 1966) as a stability parameter, was calculated from the equation

$$W_i = \sum_{j=1}^{s} [(GE)_{ij}]^2$$

where W_i is the ecovalence for each line and $(GE)_{ij}$ is the interaction term for line (i) at site (j).

This parameter gives a quantitative measure of the change in yield performance of a given line over sites relative to the average

change in performance of all lines over sites.

2. Regression analysis (adaptation analysis)

The statistical approach described by Eberhart and Russell (1966) was used to estimate stability parameters for each line. For each cultivar, an environmental index was calculated from the mean yield of control lines of that cultivar at each site. This index was used to estimate the stability parameters for individual lines of both treated and control groups of the given cultivar. Thus the mean yield of a line in each site was regressed upon the environmental index and the linear regression coefficient (b) and deviations from regression (s^2d) were used as statistics for evaluating the stability of performance of individual line over different sites. The interaction term $(GE)_{ij}$ included in the ANOVA mathematical model [1] was partitioned into two components, viz. the linear response to the environmental effects and deviations from regression as set out in the following equation:

$$(GE)_{ij} = b_i I_j + \delta_{ij} .$$

A quadratic term was included in the regression analysis combined over two years' environments in order to test whether any large deviations from linearity were caused by quadratic response using the following equation:

$$(GE)_{ij} = b_{1i}I_j + b_{2i}I_j^2 + \delta_{ij}$$

I_j, the environmental index, was obtained as a mean of control lines at the environment (j) minus the mean of all environments. Therefore,

$$I_j = E_j - \bar{E}$$

where E_j = measure of environment at site (j)

and $\bar{E}$ = mean of all E_j

Also

$$I_j^2 = E_j^2 - \bar{E^2}$$

where $\bar{E^2}$ = mean of all E_j^2

For the regression analysis, the mathematical model used in the ANOVA [1] was extended to:

$$Y_{ijk} = \mu + G_i + E_j + b_i(E_j - \bar{E}) + \delta_{ij} + R_{jk} + e_{ijk} \qquad [2]$$

when only linear regression was being fitted, or to:

$$Y_{ijk} = \mu + G_i + E_j + b_{1i}(E_j - \bar{E}) + b_{2i}(E_j^2 - \bar{E^2}) + \delta_{ij} + R_{jk} + e_{ijk} \qquad [3]$$

when both linear and quadratic regressions were being fitted.

Where

b_i, b_{1i} are the linear regression coefficients of line (i) over all environments,

b_{2i} = quadratic regression coefficient of line (i) over all environments,

δ_{ij} = deviation from regression of line (i) at environment (j).

The regression analysis models [2] and [3] were also used by Lawrence (1970).

The form of regression analysis used is given in Table 7.

Table 7. Analysis of variance when stability parameters are estimated.

Source of variation	df	MS	VR
Environments (Sites)	s-1	MSS	
Replicates within environments	s(r-1)	MSR	
Lines	p-1	MSP	
Lines X Env. interaction	(p-1)(s-1)	MSPS	
Linear	p-1	MSL	
Quadratic	p-1	MSQ	
Deviation	(p-1)(s-3)	MSD	
Residual (error)	s(p-1)(r-1)	MSE	
Total	spr-1		

Appropriate F-tests of the significance of deviation, linear and quadratic responses, line X environment interaction, lines, replicates and environments were carried out by variance ratios as under:

Variance ratios:

$$\text{Deviation} = \frac{MSD}{MSE},$$

$$\text{Quadratic} = \frac{MSQ}{MSD}$$

$$\text{Linear (a)} = \frac{MSL}{MSD} \quad \text{(if quadratic significant)}$$

$$\text{(b)} = MSL \Big/ \frac{\text{SS for Quadratic + SS for Deviation}}{\text{d.f. for Quadratic + d.f. for Deviation}}$$

(if quadratic non-significant)

$$\text{Lines X Environments} = \frac{MSPS}{MSE}$$

$$\text{Lines} = \frac{MSP}{MSE}$$

$$\text{Replicates} = \frac{MSR}{MSE}$$

$$\text{Environments} = \frac{MSS}{MSE}$$

The mean square for deviation from linear regression (S^2d_i) was calculated as under:

$$S^2d_i = \sum_{j=1}^{s} (\delta^2_{ij})/\text{d.f.}$$

where

δ_{ij} = deviation from regression for line (i) at site (j).

The standard error (b) estimate for line (i) was obtained from:

$$\text{S.E. (b)} = \sqrt{\frac{S^2_{di}}{\sum_{j=1}^{s} (E_j - \bar{E})^2}}$$

Recently, Breese (1969) suggested that S.E. of (b) may be taken as measures of the "stability of response" exhibited by each genotype. Sparrow (1969) used S.E. (b) as a measure of the "reliability" of b.

Estimation of weights

One of the requirements for the analysis of variance combined over all sites is that the residual (error) variances (S_j^2) between sites should be homogeneous. The residual variances obtained from analyses on a natural scale and with all data transformed to a logarithmic scale were tested for homogeneity by Bartlett's (1937) X^2 test. When the data were homogeneous it was legitimate to apply a combined analysis.

Where the residual variances were heterogeneous when analysed on both scales, an alternative method of inducing homogeneity was carried out by performing weighted analyses on a natural scale (Lawrence, 1970). Weighting factors were introduced by using S_j^2 from the unweighted analysis to calculate the appropriate weights for each site.

The steps used for the estimation of weights are set out below:

(i) For site (j), the appropriate weighting factor (w_{sj}) was calculated as:

$$w_{sj} = \frac{1}{s_j^2} \Big/ \frac{1}{NS}\left(\sum_{j=1}^{s} \frac{1}{s_j^2}\right)$$

where

s_j^2 = residual variance for site (j) from unweighted analysis

NS = number of sites

etc.

The reciprocal of residual (error) variance for each site as suggested by Cochran (1937) was used to measure appropriate weighting factor.

(ii) The new weights for each observation in site (j) were introduced into the analysis of variance by using the following formula:

$$w_j' = w_{sj} \times w_j$$

where w_j is previous weight (i.e. 1.0 for unweighted analysis).

RESULTS

A. Effectiveness of EMS-treatment

An early indication of the effectiveness of the EMS treatment independent of its effects on yield was required. The criteria which have been widely used for this purpose are M_1 seed sterility and chlorophyll mutation rate in the M_2 generation, and they were measured in the present study.

1. Seed sterility in M_1 generation

The seed sterility was determined as percentage of sterile florets against the total number of florets per spike. For each cultivar the EMS mutagen induced considerable sterility in the treated material as compared with the respective controls (Table 8).

Table 8. Seed sterility (%) in M_1 spikes of EMS treated and control.

Cultivar	Seed sterility % (average of 50 M_1 spikes)	
	Control	Treated (0.04 M)
Clipper	4.31	21.41
C.I.3576	3.00	25.67
Proctor	21.44	55.50
Ketch	4.69	23.83
Prior	6.12	41.03

However, these values are lower than those reported by some other workers using EMS on barley. For example, seed sterility to the extent of from 67% to 90% at concentrations of 0.02 M to 0.04 M (treatment time 3.5 hr to 5 hr at 30°C) has been reported by Froese-Gertzen et al. (1964). Similarly, Gaul et al. (1966) observed a maximum of 94% sterility in two varieties of barley treated with an approximate dose of 0.16 M (2.0%) EMS for 6 hours at 24°C.

2. Chlorophyll mutations

(a) M_2-generation (Greenhouse)

In the present study, the chlorophyll mutations were classified into different morphological types using the criteria described by Gustafsson (1940) and later modified by Swaminathan et al. (1962) and Gaul (1964). A high frequency as well as a wide spectrum of chlorophyll mutations were found in the EMS-treated material of each of five barley cultivars. In many cases more than one type of chlorophyll mutant was observed in the progeny of a single M_1 spike, as observed by Gaul (1964) and others.

It is difficult to estimate the actual mutation rate after seed treatment because of the multi-cellular nature of the ear primordia in seed and the intervening cell divisions between the induction of mutation in the germ line cell and detection of

mutation in the M_2 plants. Therefore, the frequency of chlorophyll mutation was scored using both M_1 plant progeny (one main spike per plant) and M_2 seedling methods. With the M_2 seedling method, the mutants are referred to the whole M_2 population whereas in the M_1 plant method, mutations are only referred to M_1 plant progenies. The results are given in Table 9, which shows that the highest frequencies of chlorophyll mutations were obtained with the treated material of Proctor and Prior by both M_1 plant (main spike) progeny and M_2 seedlings methods. These percentages are uniformly lower than those reported by Froese-Gertzen et al. (1964), where a mutation frequency of 35.6% - 36.5% in M_1 spikes and 4.3% - 6.4% in M_2 seedlings was observed after EMS treatment (dose of 0.04 M for 3.5 hr to 4.5 hr at 30°C). On the other hand, chlorophyll mutation rates of 12% - 50% per M_1 spike progeny in M_2 generation after EMS treatments (0.08% - 0.33% conc. for 24 hrs) have been reported by Ehrenberg et al. (1965).

Taking the combined results over all cultivars, the 'viridis' and 'albina' mutations were the most frequent with 35.4% and 31.5% respectively. The other most frequent types were 'xantha', 'virido-albina', 'virido-xantha' and 'striata' with 9.9%, 8.3%, 6.1% and 6.6% respectively (Table 9). These results are in agreement with those of other workers using EMS as mutagen (Ehrenberg et al., 1961; Gaul, 1964).

Table 9. Frequency of chlorophyll mutations and spectrum observed in M_2 generation.

Cultivar	Treatment	No. of M_1 plant progenies grown (one main spike per M_1 plant)	No. of M_1 plant progenies segregating for M_2 chlorophyll mutations	%	Spectrum of chlorophyll mutations in M_2								M_2-chlorophyll mutation frequency	
					Albina	Viridis	Xantha	Virido-Albina	Virido-Xantha	Striata	Others	Total	No. of M_2 seedlings studied	M_2 chlorophyll mutants (%)
Clipper	Control	61	Nil	0									1228	0
	0.04M EMS	61	8	13.11	1	8	5	0	0	0	0	14	913	1.53
C.I.3576	Control	61	Nil	0									1069	0
	0.04M EMS	61	14	22.95	5	17	0	3	2	6	0	33	780	4.23
Proctor	Control	62	1	1.61	1							1	865	0.12
	0.04M EMS	62	17	27.42	12	18	6	0	2	2	4	44	660	6.67
Ketch	Control	61	Nil	0	-								1051	0
	0.04M EMS	61	12	19.67	14	4	3	0	0	3	0	24	829	2.90
Prior	Control	61	Nil	0	-		-						1403	0
	0.04M EMS	61	17	27.87	24	17	4	12	7	1	0	65	1025	6.34

(b) M_3 generation (Field planting)

In order to estimate the number of M_2-derived treated lines segregating for chlorophyll mutations, the frequency of chlorophyll mutations was also recorded in M_3 rows. It was observed that 8.3% to 13.3% of M_2-derived treated lines in different cultivars segregated for chlorophyll mutations in M_3 generation. Among the treated lines included in the 1970 field experiments one line from each of Clipper (No. 17), C.I.3576 (No. 3) and Ketch (No. 22) and two lines from each of Proctor (Nos. 12, 13) and Prior (Nos. 1, 14) exhibited segregation for chlorophyll mutations in the M_3 rows.

B. 1970 Field experiments (M_4 generation)

1. Yield data

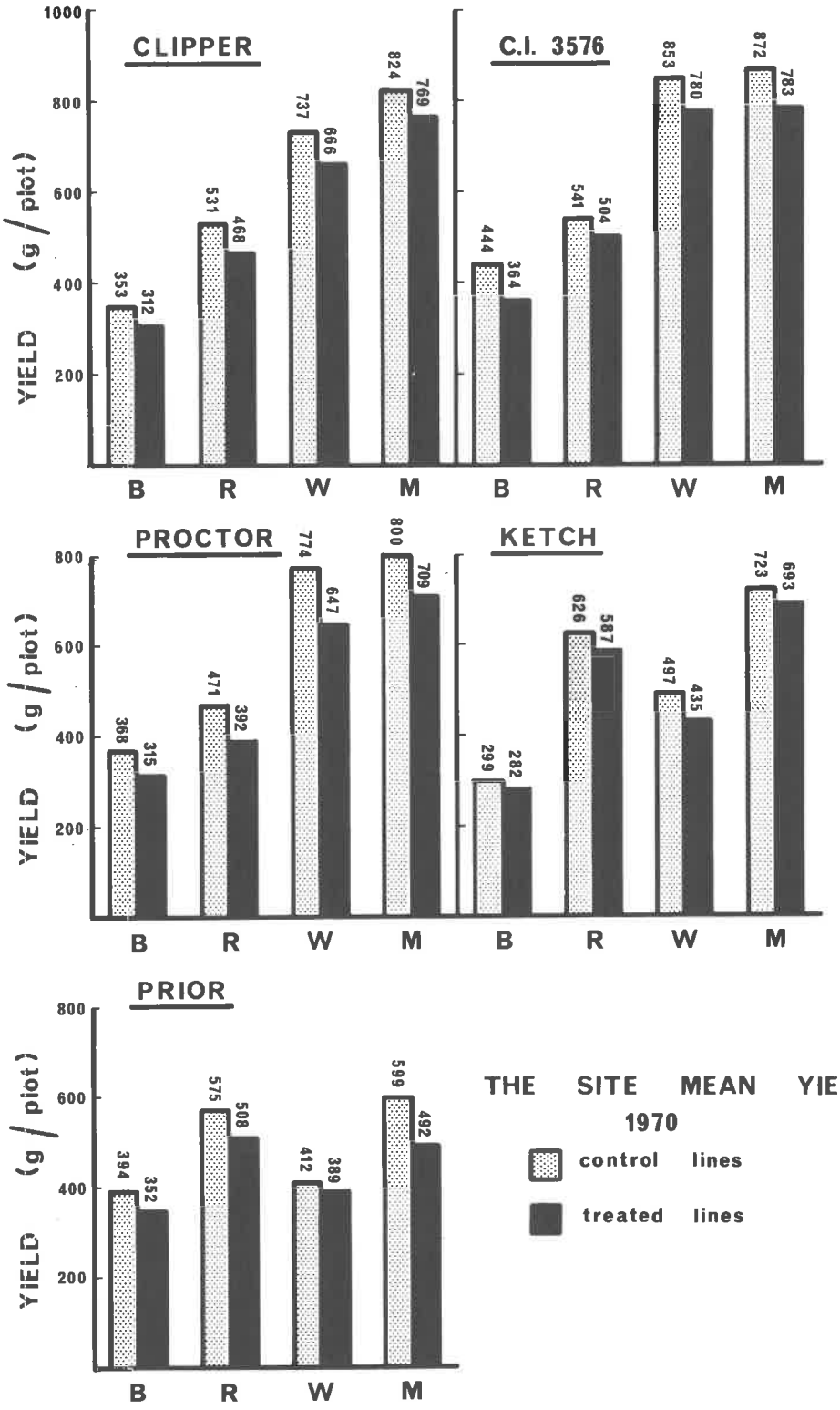
The yields from only four of the five sites planted in 1970 were available for analysis since the plots at Clinton were extensively damaged by mice soon after seed germination.

(a) Site variation

For each cultivar, the mean yield of control lines at each site was used as an estimate of "site mean yield" (environmental index). The sites used in 1970 provided a wide range of environments as shown in Figure 5. For example, the mean yield of all control lines of Clipper at Bundaleer was low (353 g/plot) which indicated a low-yielding environment; on the other hand

FIGURE 5

Mean yields for M_2-derived treated and control lines of each cultivar in M_4 generation at each site, 1970.



THE SITE MEAN YIELDS, 1970

control lines

treated lines

Minlaton (824 g/plot) was considered a high-yielding environment. A similar pattern was observed with the other cultivars (Figure 5).

Besides differences in soil type (see Table 5), another important environmental factor contributing to the variation between sites is annual rainfall. In general, precipitation from April to November is considered effective for plant growth and ultimately yield in the barley growing areas of South Australia. At the time of anthesis (during September to November) rainfall plays a greater role and has a considerable influence on grain formation and yield.

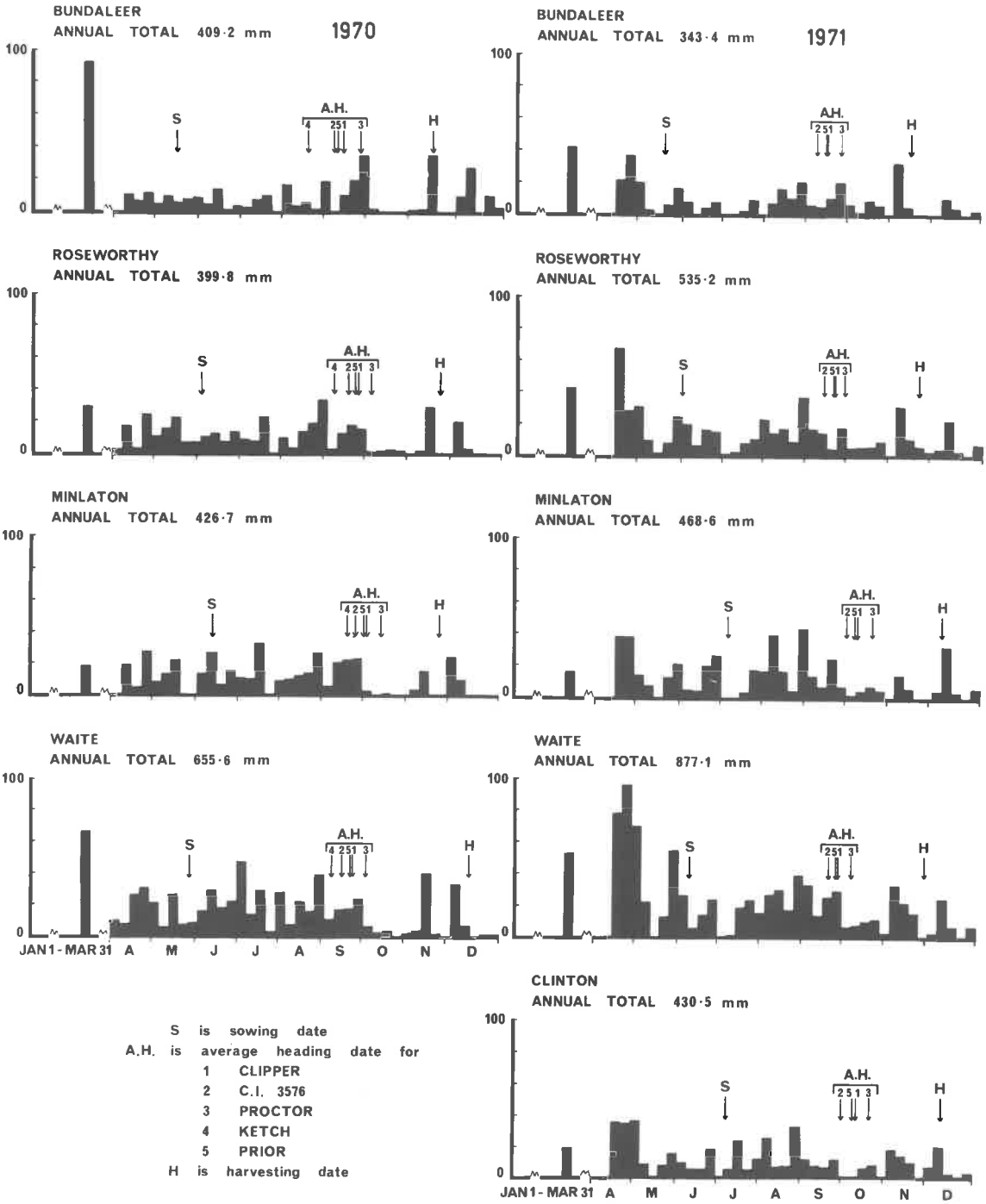
The weekly rainfall (mm) at all sites from April to December 1970 is shown in Figure 6 and a summary of these data is given in Table 10, together with mean yield of all lines of all cultivars at each site.

In general, the sites show an ascending order of effective rainfall from Bundaleer to the Waite Institute. Bundaleer which received minimum effective precipitation produced the lowest overall yield. On the contrary, although the Waite site received maximum effective rainfall, it yielded less than Minlaton (Table 10). In fact the Waite site possessed excessive soil moisture which promoted luxuriant vegetative growth and this resulted in lodging and reduction of yield.

FIGURE 6

Weekly rainfall incidence (mm) during 1970 and 1971 at the experimental sites.

WEEKLY RAINFALL INCIDENCE (mm) IN THE LOCATIONS OF TRIALS



S is sowing date
A.H. is average heading date for
1 CLIPPER
2 C.I. 3576
3 PROCTOR
4 KETCH
5 PRIOR
H is harvesting date

Table 10. Annual total and effective rainfall (mm) and overall mean yields (g/plot) at each site, 1970.

	Sites			
	Bundaleer (B)	Roseworthy (R)	Minlaton (M)	Waite (W)
(a) Rainfall (mm)				
Annual (Total)	409	400	427	656
April - November	267	348	375	551
Sowing - Harvesting	225	242	256	455
(b) Overall Mean Yield (g/plot)				
(Mean of all lines of all cultivars)	348	520	726	619

(b) Analysis of variance for individual sites

Analyses of variance for treated and control lines of each cultivar were carried out separately for each site in order to test whether the control lines were uniform in their performance and to estimate the amount of variability in yield generated by EMS-treatment. Furthermore, the error mean squares for individual sites are required to test for homogeneity of error variance before carrying out a combined analysis over all sites. The estimates of mean squares between lines of treated and control groups along with their respective error mean squares are given in Appendix 1.

The significance of 'between lines' mean squares for control and treated lines of the five cultivars at individual sites are shown in Table 11.

No significant line effects were observed among the control lines from any of the cultivars and thus each group of control lines appeared to be genetically homogeneous with regard to yield. On the contrary, significant line effects were detected among the treated lines at most sites indicating effectiveness of the mutagenic treatment. The only exception to this pattern occurred with Ketch treated lines at Bundaleer and Waite and Prior treated lines at Minlaton, where mean squares between lines were non-significant (Table 11).

Several workers have investigated genotypic variance and heritability estimates for a number of quantitative characters among mutagen-treated populations by conducting experiments at single site (Rawlings et al., 1958; Brock and Latter, 1961; Abrams and Frey, 1964; Jalil Miah and Yamaguchi, 1965). Their studies showed substantial increase of genotypic variance and heritability estimates among the treated material as compared with respective controls for almost all characters.

In the present investigations however, these estimates were calculated by testing material at a number of sites to study the influence of different environments on the expression of

Table 11. Significance level for 'between lines' mean squares at individual sites, 1970.

Cultivar	Sites							
	Bundaleer		Roseworthy		Minlaton		Waite	
	Control	Treated	Control	Treated	Control	Treated	Control	Treated
Clipper	NS	*	NS	***	NS	**	NS	*
C.I.3576	NS	***	NS	*	NS	***	NS	***
Proctor	NS	***	NS	***	NS	**	NS	***
Ketch	NS	NS	NS	**	NS	*	NS	NS
Prior	NS	***	NS	***	NS	NS	NS	**

NS = Non-significant: * = significant at 5%: ** = significant at 1%
*** = significant at .1%.

genotypic component of variance and heritability values. These estimates calculated for each group at each site are presented in Table 12.

It is interesting to note that the magnitude of these estimates among the treated lines of different cultivars varied widely when calculated across range of environments. Among the treated material of these cultivars, the magnitude of induced genotypic variances was small at low-yielding site (Bundaleer) compared with high-yielding site (Minlaton), where with few exceptions a large $\sigma^2 p$ was found (Table 12). Johnson and Frey (1967) also found that genotypic variances among oat cultivars were generally increased under non-stress environmental conditions. In the treated lines of Clipper the heritability values changed from 0.428 at Waite to 0.722 at Roseworthy and for C.I.3576 treated lines varied from 0.410 at Roseworthy to 0.802 at Bundaleer. In other words, about two- to three-fold differences for heritability between sites were observed. This pattern of change in these estimates indicates the unreliability of testing material at one site only.

(c) Analyses of yield data combined over all sites

In order to assess the relative performance of individual treated and control lines, the yield of each line was averaged over all sites to give line mean yields.

Table 12. Estimates of genotypic component of variance ($\sigma^2 p$) and heritability (H) values for treated and control lines of each cultivar at individual sites, 1970.

Cultivar	Estimate	Site							
		Bundaleer		Roseworthy		Minlaton		Waite	
		Control	Treated	Control	Treated	Control	Treated	Control	Treated
Clipper	$\sigma^2 p$	59	1038	0[/]	4774	1494	6998	0	4621
	H	.058	.475	0	.722	.321	.685	0	.428
C.I.3576	$\sigma^2 p$	0	6122	0	3326	1115	1448	95	15303
	H	0	.802	0	.410	.276	.773	.013	.751
Proctor	$\sigma^2 p$	287	1675	1677	4335	773	4692	0	12877
	H	.241	.778	.469	.710	.199	.584	0	.829
Ketch	$\sigma^2 p$	218	252	0	2058	122	2297	0	0
	H	.356	.378	0	.548	.044	.474	0	0
Prior	$\sigma^2 p$	0	2867	0	5650	0	2989	232	5220
	H	0	.841	0	.850	0	.392	.107	.593

[/] The genotypic variance component and heritability estimates were calculated from the mean squares of analyses of variance in each case. Some estimates were found to be negative but theoretically these cannot be negative and they were assumed to be zero.

(i) Mean yield and frequency distributions

The mean yields for treated and control lines of each cultivar are summarized in the frequency distributions shown in Figure 7. A characteristic of the frequency distribution curves is a pronounced shift of the EMS-treated lines away from their respective controls towards lower yield in the M_4 generation.

The mean yields of the treated lines of each cultivar were significantly less than the means of the corresponding control populations in all cases (Table 13). The greater reduction in the treated material of Proctor and Prior is in line with the observed higher frequencies of chlorophyll mutations in these two cultivars (Table 9).

Even though the overall mean yield was reduced, some of the treated lines in Clipper performed similarly to that of the highest yielding control lines and with C.I.3576 three of the treated lines outyielded the highest yielding control line (Figure 7).

(ii) Analyses of variance combined over all sites

Analyses of variance of yield combined over all sites (ANOVA) were carried out to investigate the performance of treated and respective control lines of each cultivar over sites. These analyses were performed separately for the control and treated populations of each cultivar involving lines, sites and replicates

Table 13. The mean yield combined over all sites (g/plot) of treated and respective control populations of barley cultivars in M_4 generation, 1970.

Population	Cultivar				
	Clipper	C.I.3576	Proctor	Ketch	Prior
Control	611	678	603	536	495
Treated	554**	608**	515***	499*	435***
Percentage yield of treated population compared with controls = 100	90.7	89.7	85.4	93.1	87.9

*, ** and *** the mean yield of treated populations significantly reduced from respective controls at 5%, 1% and 0.1% probabilities respectively.

The 't' test for significant differences between treated and control means:

$$t_{[(TDF_1 + TDF_2) - 2]} = \frac{\bar{x}_1 - \bar{x}_2}{\sqrt{s^2\left(\frac{1}{n_1} + \frac{1}{n_2}\right)}}$$

where

$\bar{x}_1$ = mean yield of control population

$\bar{x}_2$ = mean yield of treated population

and $s^2 = \frac{TSS_1 + TSS_2}{TDF_1 + TDF_2}$

where

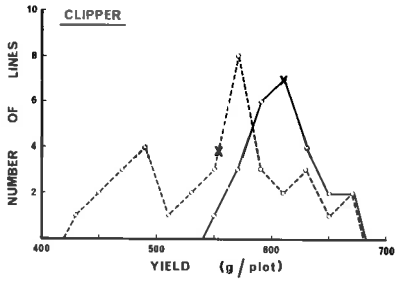
TSS_1 = Total sum of squares of control population

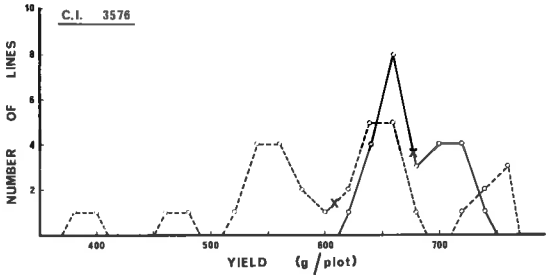
TSS_2 = Total sum of squares of treated population

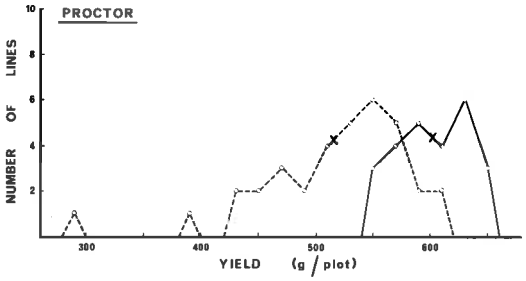
These sum of squares were derived from analysis of variance combined over all sites. And TDF_1 and TDF_2 are total degrees of freedom of control and treated populations, respectively.

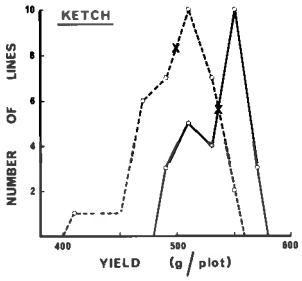
FIGURE 7

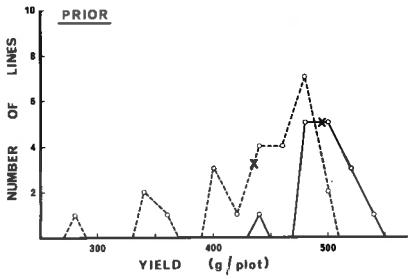
Frequency distributions for yield combined over sites of M_2-derived treated and control lines of five barley cultivars, 1970 (M_4 generation).











	POP. MEANS	
	treat	con
CLIPPER	553·8 ± 12·3	610·6 ± 14·1
C.I. 3576	608·1 ± 13·3	677·9 ± 15·1
PROCTOR	515·3 ± 11·7	603·0 ± 14·5
KETCH	499·3 ± 10·4	536·2 ± 12·5
PRIOR	435·0 ± 8·3	495·4 ± 10·5

FREQUENCY DISTRIBUTIONS FOR YIELD COMBINED OVER ALL SITES, 1970

control lines

treated lines

X population mean

within sites.

In the combined analysis of variance the estimates of error variances from all sites are pooled, and this approach is valid only when the error variances between sites are homogeneous. The pooling of heterogeneous error gives an unreliable estimate of combined error and gives invalid 'F' tests of interaction mean squares (Cochran and Cox, 1964).

However, in the literature many workers have combined yield data over all sites and performed analyses of variance on natural scale without testing for homogeneity of error variances (Comstock and Robinson, 1952; Hanson et al., 1956; Miller et al., 1959; Eberhart and Russell, 1966; Smith et al., 1967; Reich and Atkins, 1970; Tai, 1971).

Finlay and Wilkinson (1963) and Finlay (1963, 1968) used logarithmically transformed data for inducing a reasonable degree of homogeneity of experimental error. On the other hand, Fripp and Caten (1971) transformed data to logarithmic and square root scales in an attempt to induce homogeneity of error variances but these transformations were not successful and they reverted to analyzing the untransformed data on the natural scale. Recently, Lawrence (1970) has utilized a weighted analysis to induce homogeneity of error between sites where other transformations have proved ineffective.

In the present study, therefore, before attempting combined analysis of variance, the error variances on natural scale for sites were tested for heterogeneity by Bartlett's X^2 test in each analysis. Where error variances were significant on natural scale, the data were transformed to logarithmic scale in an attempt to induce homogeneity of error. However, in many cases the error variances between sites remained heterogeneous (Table 14) on the log scale and then a weighted analysis was performed.

Although the unweighted analysis on natural scale is statistically invalid in most cases, it has been commonly used by plant breeders because it is more easily understood in biological terms. Moreover, error variances between sites for the control groups of different cultivars were homogeneous on different scales (Table 14) and there was no common analysis available where both control and treated groups of each cultivar could be compared on the same scale except unweighted analysis on natural scale (approximate analysis).

Hence, in addition to the statistically valid analyses of variance, approximate analyses based on unweighted natural data were included for comparative purposes. These analyses are presented in Tables 15-19.

Table 14. Bartlett's X^2 tests for homogeneity of residual (error) variance over sites for different cultivars, 1970.

Cultivar	Lines	Scale	X^2 values (3 d.f.) Between sites	
Clipper	Control	Natural	21.795	***
		Log_{10}	3.843	NS
	Treated	Natural	27.961	***
		Log_{10}	14.607	**
C.I.3576	Control	Natural	27.380	***
		Log_{10}	40.525	***
	Treated	Natural	15.812	**
		Log_{10}	17.336	***
Proctor	Control	Natural	28.474	***
		Log_{10}	6.226	NS
	Treated	Natural	31.829	***
		Log_{10}	10.604	*
Ketch	Control	Natural	41.233	***
		Log_{10}	27.852	***
	Treated	Natural	54.150	***
		Log_{10}	56.750	***
Prior	Control	Natural	5.536	NS
	Treated	Natural	32.928	***
		Log_{10}	28.899	***

Table 15. Analyses of variance combined over all sites (environments) for yield, components of variances, and heritability values of M_2-derived treated and control lines of CLIPPER in M_4 generation, 1970.

Analysis of Variance	Approximate analysis						Statistically valid analysis					
	Unweighted natural scale						Log_{10} scale unweighted			Natural scale weighted		
Source	Control lines			Treated lines			Control lines			Treated lines		
	df	MS	F	df	MS	F	df	MS	F	df	MS	F
Sites (Env.)	3	2,250,170	390.89***	3	2,913,510	473.39***	3	1.38860	500.67***	3	2,733,560	664.06***
Replicates within sites	4	16,244	2.82*	4	42,933	6.98***	4	.009975	3.60**	4	14,701	3.57**
Lines	24	8048.7	1.40^{NS}	34	33,208	5.40***	24	.003917	1.41^{NS}	34	22,023	5.35***
Lines X Sites interaction	72	5469.2	0.95^{NS}	102	8811.9	1.43*	72	.002778	1.00^{NS}	102	7147.3	1.74**
Linear				34	9115.4	1.05^{NS}				34	9786.2	1.68*
Deviation				68	8660.1	1.41*				68	5827.9	1.42*
Residual	96	5756.6		136	6154.6		96	.002773		136	4116.4	
Variance components												
$\sigma^2 p$		322.44			3049.51							
$\sigma^2 ps$		0.0			1326.65							
$\sigma^2 e$		5756.60			6154.60							
Heritability												
H		0.3094			0.7346							

Table 16. Analyses of variance combined over all sites (environments) for yield, components of variances, and heritability values of M_2-derived treated and control lines of C.I.3576 in M_4 generation, 1970.

Analysis of Variance	Approximate analysis						Statistically valid analysis					
	Unweighted natural scale						Weighted natural scale					
Source	Control lines			Treated lines			Control lines			Treated lines		
	df	MS	F	df	MS	F	df	MS	F	df	MS	F
Sites (Env.)	3	2,350,850	199.08***	3	3,026,750	390.49***	3	2,704,840	412.44***	3	3,197,410	548.61***
Replicates within sites	4	23,533	1.09^{NS}	4	16,181	2.09^{NS}	4	17,507	2.67*	4	17,288	2.97*
Lines	24	9189.5	0.78^{NS}	34	72,795	9.39***	24	6398.2	0.98^{NS}	34	54,772	9.40***
Lines X Sites interaction	72	8708.5	0.74^{NS}	102	10,903	1.41*	72	6265.5	0.96^{NS}	102	9206.5	1.58**
Linear				34	13,467	1.40^{NS}				34	13,832	2.01*
Deviation				68	9620.6	1.24^{NS}				68	6893.5	1.18^{NS}
Residual	96	11,809		136	7751.2		96	6558.1		136	5828.2	
Variance components												
σ^2_p		60.13			7736.50							
σ^2_{ps}		0.0			1575.90							
σ^2_e		11,809.0			7751.20							
Heritability												
H		0.0391			0.8502							

Table 17. Analyses of variance combined over all sites (environments) for yield, components of variance and heritability values of M_2-derived treated and control lines of PROCTOR in M_4 generation, 1970.

Analysis of Variance	Approximate analysis						Statistically valid analysis					
	Unweighted natural scale						Log_{10} scale unweighted			Natural scale weighted		
Source	Control lines			Treated lines			Control lines			Treated lines		
	df	MS	F	df	MS	F	df	MS	F	df	MS	F
Sites (Env.)	3	2,342,650	349.31***	3	2,575,470	627.30***	3	1.3755	435.53***	3	1,819,480	794.99***
Replicates within sites	4	17,419	2.60*	4	50,746	12.36***	4	.005718	1.81^{NS}	4	21,625	9.45***
Lines	24	7906.6	1.18^{NS}	34	35,442	8.63***	24	.004769	1.51^{NS}	34	20,318	8.88***
Lines X Sites interaction	72	5966.7	0.89^{NS}	102	9430.6	2.30***	72	.003197	1.01^{NS}	102	5933.1	2.59***
Linear				34	8877.0	0.91^{NS}				34	7045.2	1.31^{NS}
Deviation				68	9707.4	2.36***				68		2.35***
Residual	96	6706.5		136	4105.6		96	.003158		136	2288.7	
Variance components												
$\sigma^2 p$		242.49			3251.43							
$\sigma^2 ps$		0.0			2662.50							
$\sigma^2 e$		6706.50			4105.60							
Heritability												
H		0.2244			0.7339							

Table 18. Analyses of variance combined over all sites (environments) for yield, components of variances, and heritability values of M_2-derived treated and control lines of KETCH in M_4 generation, 1970.

Analysis of Variance	Approximate analysis						Statistically valid analysis					
	Unweighted natural scale						Weighted natural scale					
Source	Control lines			Treated lines			Control lines			Treated lines		
	df	MS	F	df	MS	F	df	MS	F	df	MS	F
Sites (Env.)	3	1,679,590	240.51***	3	2,245,850	412.67***	3	1,506,010	662.62***	3	2,281,910	1015.00***
Replicates within sites	4	10,503	1.50^{NS}	4	16,186	2.97*	4	4019.1	1.77^{NS}	4	9692.6	4.31**
Lines	24	5221.6	0.75^{NS}	34	7407.5	1.36^{NS}	24	4413.4	1.94*	34	5165.5	2.30**
Lines X Sites interaction	72	4346.6	0.62^{NS}	102	5652.7	1.04^{NS}	72	1376.7	0.61^{NS}	102	2916.7	1.30^{NS}
Residual	96	6983.5		136	5442.3		96	2272.8		136	2248.3	
Variance components												
σ^2_p		109.38			219.35							
σ^2_{ps}		0.0			105.20							
σ^2_e		6983.50			5442.30							
Heritability												
H		0.1113			0.2369							

Table 19. Analyses of variance combined over all sites (environments) for yield, components of variances, and heritability values of M_2-derived treated and control lines of PRIOR in M_4 generation, 1970.

Analysis of variance	Statistically valid analysis			Approximate analysis			Statistically valid analysis		
	Unweighted natural scale/			Unweighted natural scale			Weighted natural scale		
Source	Control lines			Treated lines			Treated lines		
	df	MS	F	df	MS	F	df	MS	F
Sites (Env.)	3	342,454	89.33***	3	293,454	60.10***	3	348,648	145.45***
Replicates within sites	4	35,196	9.23***	4	26,699	5.47***	4	12,803	5.34***
Lines	14	4,029.4	1.06^{NS}	24	23,499	4.81***	24	23,835	9.94***
Lines X Sites interaction	42	3,482.8	0.91^{NS}	72	9,827.6	2.01**	72	5,675.3	2.37***
Linear				24	10,640.0	1.13^{NS}	24	7,501.7	1.58^{NS}
Deviation				48	9,421.6	1.93**	48	4,762.1	1.99**
Residual	56	3,812.2		96	4,882.7		96	2,397.1	
Variance components									
σ^2_p		68.33			1,708.93				
σ^2_{ps}		-			2,472.45				
σ^2_e		3,812.20			4,882.70				
Heritability									
H		0.1254			0.5818				

/ In the case of control lines, unweighted analysis on natural scale is statistically valid as its error variances for sites are homogeneous on natural scale.

Site effects - The mean squares for sites were highly significant for both control and treated lines of each cultivar confirming that there were wide differences between sites in 1970.

Line effects - None of the mean squares attributable to lines were significant among the control lines of each cultivar except with Ketch, where these were significant at 5% level in the valid analysis, but not in the approximate analysis. Thus, there was no evidence of genetic heterogeneity among the control lines of any of the cultivars except possibly with Ketch. It should be noted, however, that Ketch control lines did not show significant heterogeneity within any of the individual sites (Table 11).

On the other hand, highly significant line mean squares occurred among the treated lines from all cultivars. With Ketch the line mean squares were significant in the valid analysis but not in the approximate analysis. Thus the EMS-treatments have generated significant variability in all cultivars but apparently to a lesser extent in Ketch.

Genotype X environment interactions - No significant lines X sites interaction mean squares were obtained among the control lines from each cultivar, indicating that all control lines of each cultivar performed consistently across all sites. In contrast, significant interaction mean squares were observed

with the treated lines of each cultivar except with Ketch. In the valid analyses the levels of significance for the lines X sites interaction terms varied from 0.1% with Prior and Proctor to 1% with Clipper and C.I.3576.

The results obtained with control and treated lines taken together clearly indicate that the EMS treatments have resulted in inducing genetic variability among M_2-derived lines which performed relatively differently when tested over a range of environments, thus showing significant genotype X environment interaction terms in the analyses of variance.

The next question concerns whether the significant G X E interaction terms can be accounted for by linear responses to change in environments or whether they are due partly or wholly to deviations from a linear model. Consequently the lines X sites interactions sum of squares were partitioned into these two components (Tables 15, 16, 17, 19) using the model described earlier (see page 77). In most cases the interaction term was due mainly to deviations from regressions. Thus the deviation component was significant with treated lines of Clipper, Proctor and Prior. Significant linear components occurred only in the valid analyses and then only in treated lines of Clipper and C.I.3576 at the 5% level of significance. This reflects that the differential response to environments of treated lines of

Clipper and C.I.3576 could be explained partly by regression of individual yields on site means as suggested by Finlay and Wilkinson (1963).

The contribution of individual lines to the G X E interaction term is considered later (see page 96).

(iii) Variance components and heritability

The three variance components: $\sigma^2 p$ (genotypic variance due to lines), $\sigma^2 ps$ (lines X sites interaction variance) and $\sigma^2 e$ (error variance) and H (heritability values) were calculated for both control and treated lines of each cultivar from the mean squares of unweighted analyses on natural scale, using the formulae described earlier (see page 74). These estimates are shown in Tables 15-19.

The $\sigma^2 p$ provides a relative magnitude of the genetic variability occurring among lines under varying environmental conditions. The magnitude of $\sigma^2 p$ induced by EMS-treatment among the treated material of each cultivar was several-fold greater than corresponding controls except with Ketch, where it showed only a two-fold increase. The largest $\sigma^2 p$ was obtained with the treated lines of C.I.3576 followed in order by Prior, Proctor, Clipper and Ketch treated lines.

In order to study the differential performance of treated lines over a range of environments, estimates of $\sigma^2 ps$ were calculated.

A high magnitude of σ^2ps is an indication of differential response of lines to change in environment. Relatively large values of σ^2ps were obtained with treated lines of Clipper, C.I.3576, Proctor and Prior cultivars. However, the interaction variances were small in magnitude compared with the σ^2p estimates among the treated lines of all cultivars except Prior, where σ^2ps was slightly greater than σ^2p.

In addition, heritability (H) values estimated over a range of environments for treated lines were compared with corresponding controls in each cultivar. The heritability estimates of the treated lines of each cultivar showed almost the same tendency as the σ^2p. This indicates that greater gains from selection for yield are anticipated among the EMS-treated material of all cultivars than their respective controls.

(iv) Contribution of individual lines to genotype X environment interaction (ecovalence parameter)

After finding significant G X E interaction among the treated lines of Clipper, C.I.3576, Proctor and Prior (Tables 15, 16, 17, 19), the lines contributing most towards these interaction terms, were identified by calculating "ecovalence" (W) values as proposed by Wricke (1962, 1966).

The 'W' values were calculated for both treated and control groups on unweighted natural scale. In addition, these values

were calculated for treated lines using weighted data and 'W' values from both analyses are given in Appendices 2-5. The 'W' values from weighted (natural scale) analyses were much the same as those derived from unweighted (natural scale) analyses, as shown by Spearman's rank correlations (Snedecor and Cochran, 1967) of .978***, .990***, .805***, .991*** in the case of treated lines of Clipper, C.I.3576, Proctor and Prior respectively.

The frequency distributions of the 'W' values calculated from the unweighted analyses on natural scale were plotted so that the performance of the treated lines could be compared with that of controls on a common scale (Figure 8). These 'W' values for the treated lines of each cultivar showed a much wider range of variation as compared with the respective control lines.

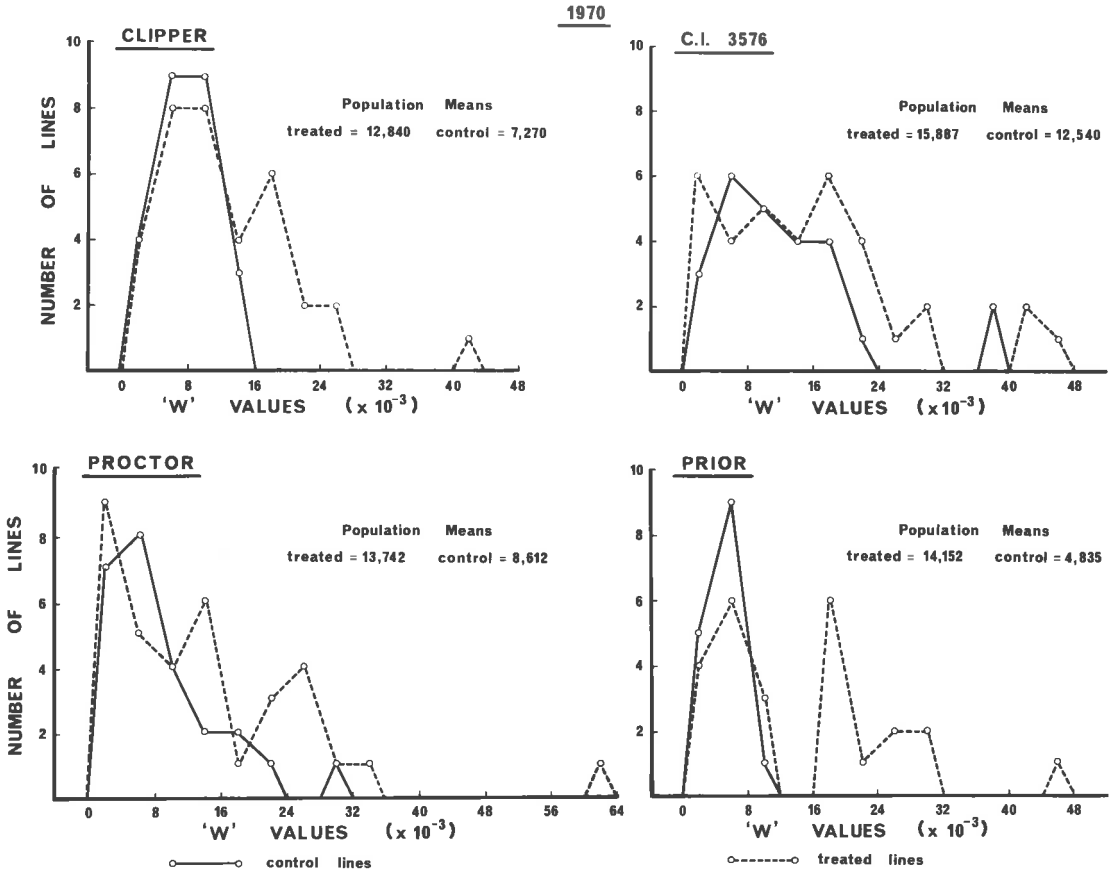
The treated lines of Clipper, C.I.3576 and Proctor with large 'W' values were selected for detailed study in 1971. In addition, to maximize heterogeneity, a few treated lines showing a range of mean yields were also included among the selected groups to give a total of 15 selected lines for each cultivar (see Table 36 for details).

(d) Adaptation studies

The stability parameters, linear regression coefficient and deviation from regression were computed for treated lines of the four barley cultivars which showed significant genotype X environment interaction in the analysis of variance (Tables 15, 16,

FIGURE 8

Frequency distributions of 'W' values for treated and control lines of four barley cultivars, derived from analyses of 1970 data on natural scale.


1970
CLIPPER
Population Means
treated = 12,840 control = 7,270
C.I. 3576
Population Means
treated = 15,887 control = 12,540
PROCTOR
Population Means
treated = 13,742 control = 8,612
PRIOR
Population Means
treated = 14,152 control = 4,835
NUMBER OF LINES
'W' VALUES (x 10⁻³)
control lines
treated lines

17, 19), using the respective control lines as an index of environment.

The average value of the linear regression coefficients (β_T) and S.E. (β_T) for all treated lines of each of four cultivars were calculated in separate analyses using the natural data and weighted data, and these average effects are presented in Table 20.

Table 20 indicates that though the average slope of treated lines was decreased with respect to the controls ($\beta_C = 1.0$) in all the cases, none of these differences were found to be significant.

The linear regression coefficient (b) and deviation mean squares (S^2d) were estimated for each treated line to evaluate its stability of yield over a range of environments. Estimates of the S.E. of (b) which are derived from S^2d values (see page 79) and provide a measure of 'reliability' of b, were also calculated for individual lines. The mean yield (G), b and S.E. (b) of individual treated lines of Clipper, C.I.3576, Proctor and Prior are given in Appendices 6-9. The relationship of mean yield (G) and the stability parameters b and S^2d for each treated line from each of these four cultivars was studied separately by scatter diagrams (Figures 9, 10, 11, 12). For the purpose of comparing the treated lines with respective control lines, b value for individual control line (natural scale) was also calculated by

Table 20. Mean, average slope (β_T) and S.E. (β_T) of the treated lines of four barley cultivars compared with their respective controls (β_C = 1.0 and S.E.(β_C) = 0).

Cultivar	Approximate (unweighted natural scale)				Weighted (natural scale)			
	Mean	β_T	S.E.(β_T)	't'/ test	Mean	β_T	S.E.(β_T)	't' test
Clipper	553.8	0.963	.033	1.10^{NS}	458.2	0.957	.031	1.40^{NS}
C.I.3576	608.1	0.952	.065	0.74^{NS}	517.4	0.982	.059	0.30^{NS}
Proctor	515.3	0.884	.056	2.10^{NS}	396.0	0.865	.042	3.20^{NS}
Prior	435.0	0.699	.111	2.70^{NS}	410.8	0.810	.082	2.31^{NS}

Significant value for t_{n-2} at 5% probability = 4.30 where n = no. of sites.

/ The average slope (β_T) of treated lines of each cultivar was tested for significance against their respective controls (i.e. β_C = 1.0) by 't' test.

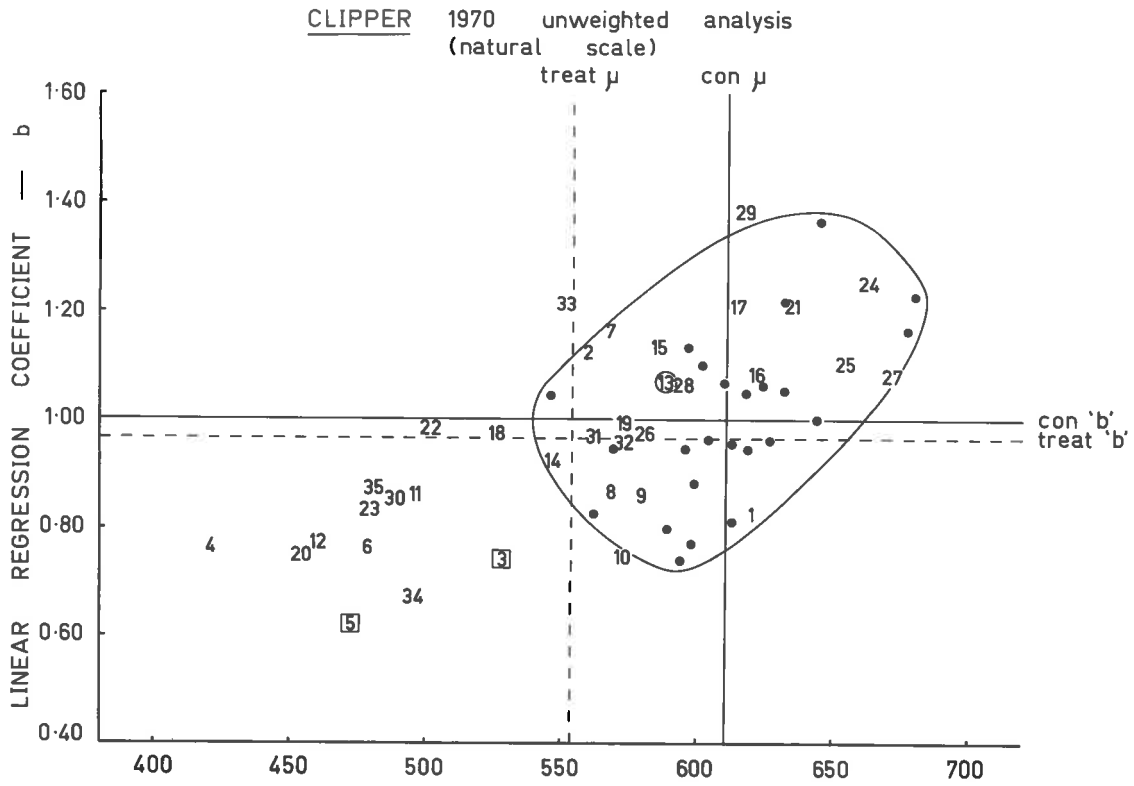
where $t_{n-2} = 1 - \beta_T / \text{S.E.}(\beta_T)$.

FIGURE 9

Scatter diagrams showing relationship of line mean yield (G), linear regression coefficient (b) and significant deviation mean squares (S^2d) for CLIPPER in 1970 experiments.

Upper diagram - analysis of unweighted yield data on natural scale for control and treated lines.

Lower diagram - analysis of weighted yield data on natural scale for treated lines only.


CLIPPER 1970 unweighted analysis
(natural scale)
treat μ
con μ
LINEAR REGRESSION COEFFICIENT — b
1·60
1·40
1·20
1·00
0·80
0·60
0·40
400
450
500
550
600
650
700
con 'b'
treat 'b'

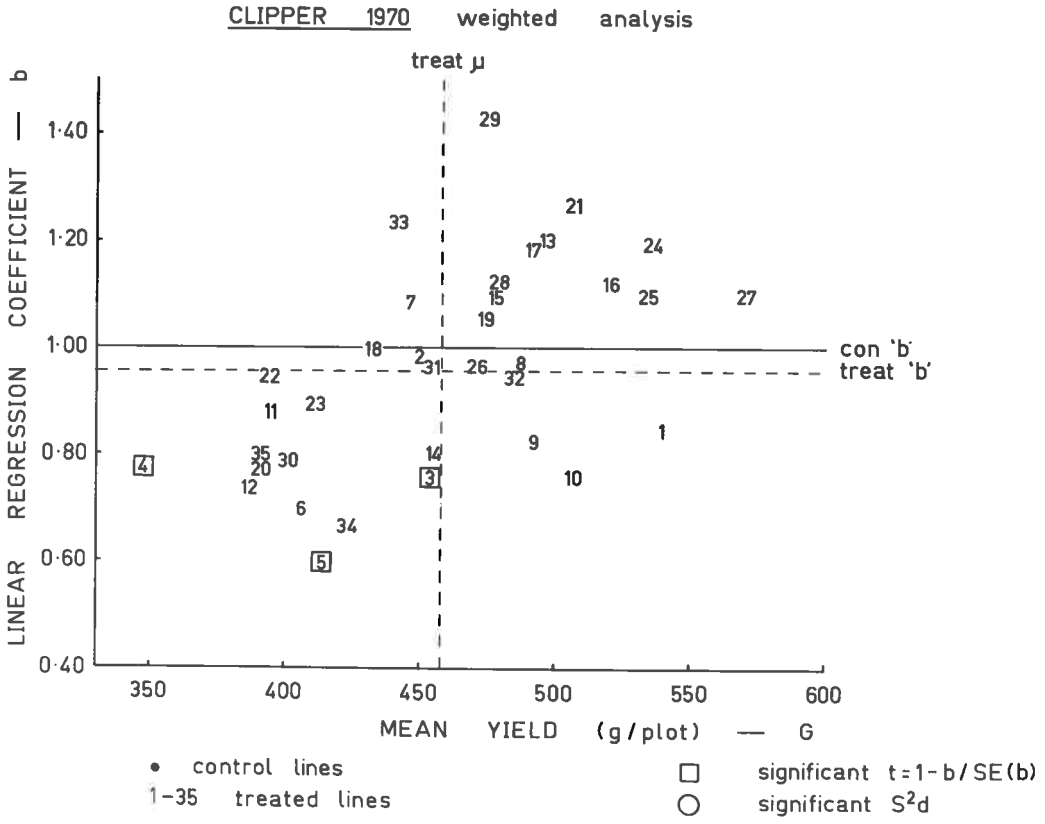
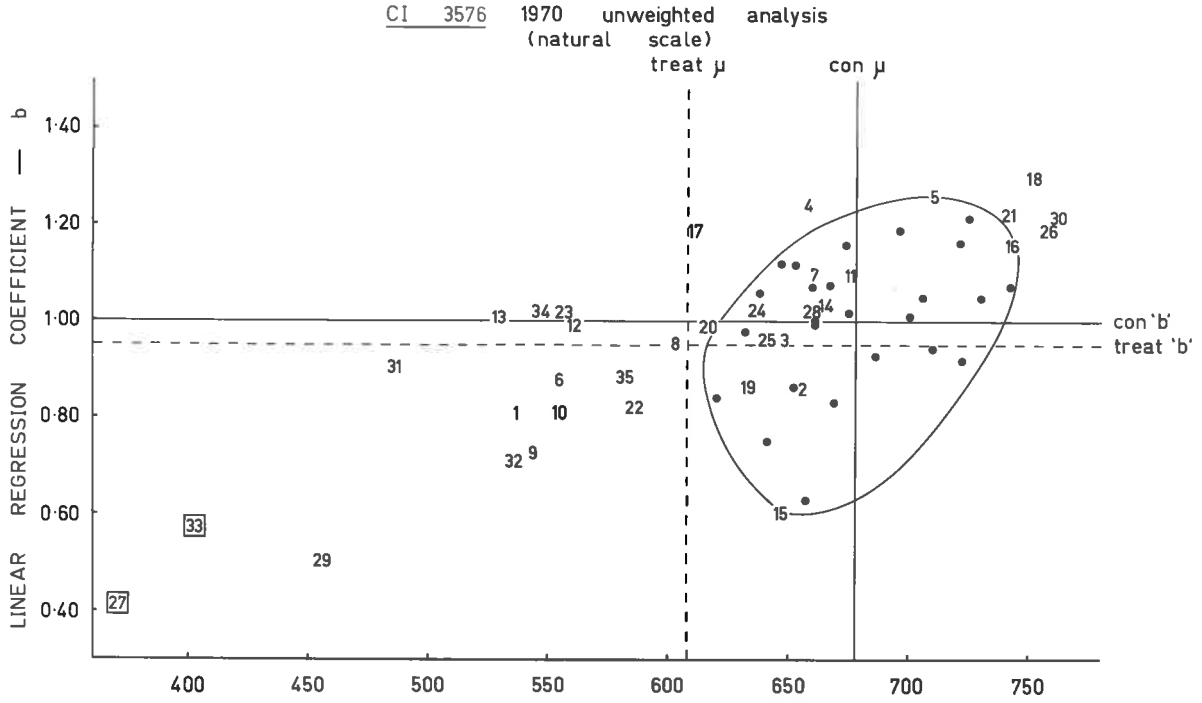

CLIPPER 1970 weighted analysis
treat μ
LINEAR REGRESSION COEFFICIENT — b
1·40
1·20
1·00
0·80
0·60
0·40
350
400
450
500
550
600
MEAN YIELD (g/plot) — G
con 'b'
treat 'b'
• control lines
1-35 treated lines
□ significant t=1-b/SE(b)
○ significant S²d

FIGURE 10

Scatter diagrams showing relationship between line mean yield (G) and linear regression coefficient (b) for C.I.3576 in 1970 experiments.

Upper diagram - analysis of unweighted yield data on natural scale for control and treated lines.

Lower diagram - analysis of weighted yield data on natural scale for control and treated lines.


CI 3576 1970 unweighted analysis
(natural scale)
treat μ
con μ
LINEAR REGRESSION COEFFICIENT — b
1·40
1·20
1·00
0·80
0·60
0·40
con 'b'
treat 'b'
400
450
500
550
600
650
700
750

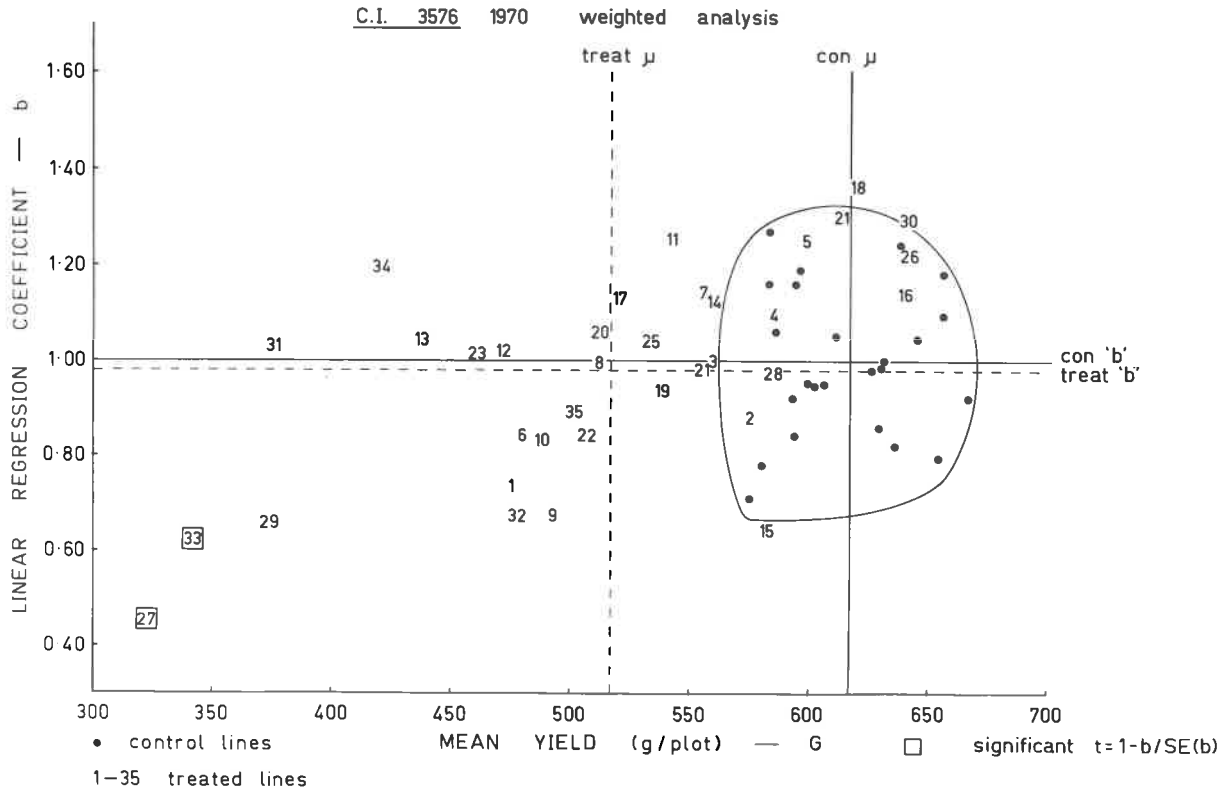
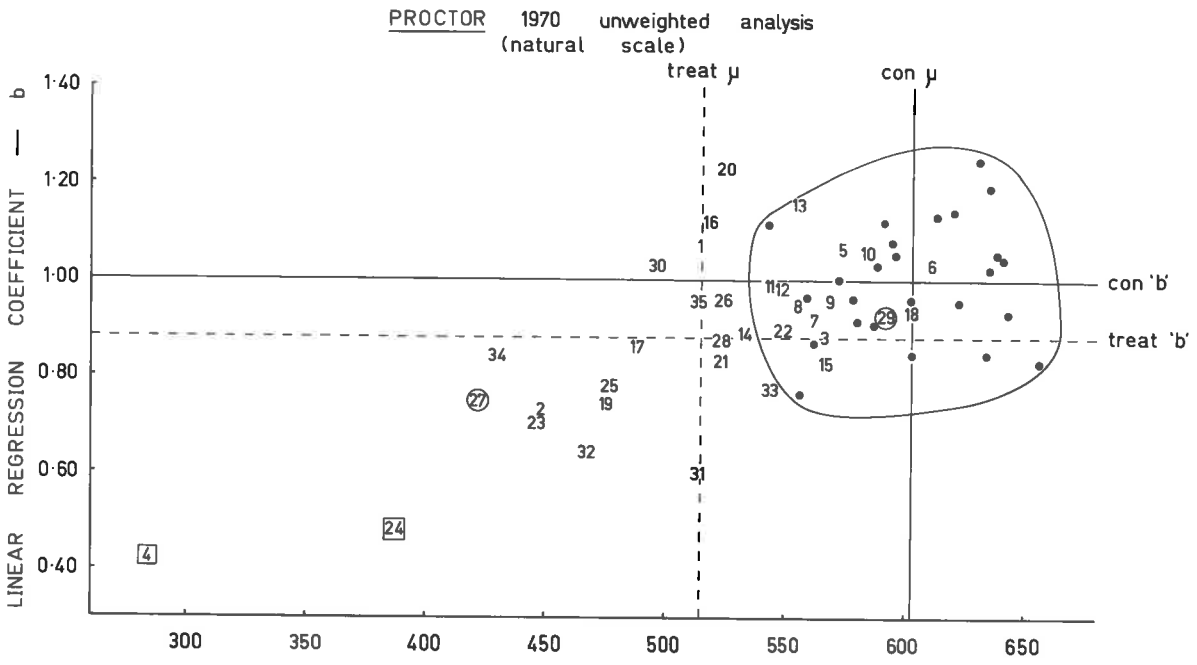

C.I. 3576 1970 weighted analysis
treat μ
con μ
LINEAR REGRESSION COEFFICIENT — b
1·60
1·40
1·20
1·00
0·80
0·60
0 40
con 'b'
treat 'b'
300
350
400
450
500
550
600
650
700
• control lines
MEAN YIELD (g/plot) — G
□ significant t=1-b/SE(b)
1–35 treated lines

FIGURE 11

Scatter diagrams showing relationship of line mean yield (G), linear regression coefficient (b) and significant deviation mean squares (S^2d) for PROCTOR in 1970 experiments.

Upper diagram - analysis of unweighted yield data on natural scale for control and treated lines.

Lower diagram - analysis of weighted yield data on natural scale for treated lines only.


PROCTOR 1970 unweighted analysis
(natural scale)
treat μ
con μ
LINEAR REGRESSION COEFFICIENT — b
1·40
1·20
1·00
0·80
0·60
0·40
con 'b'
treat 'b'
300
350
400
450
500
550
600
650

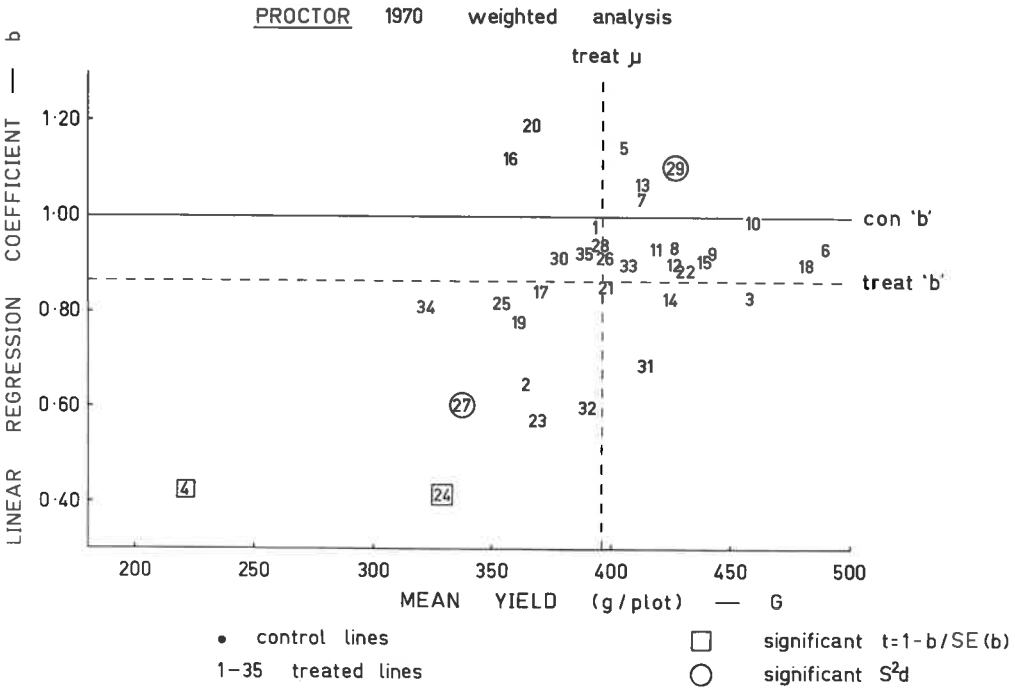
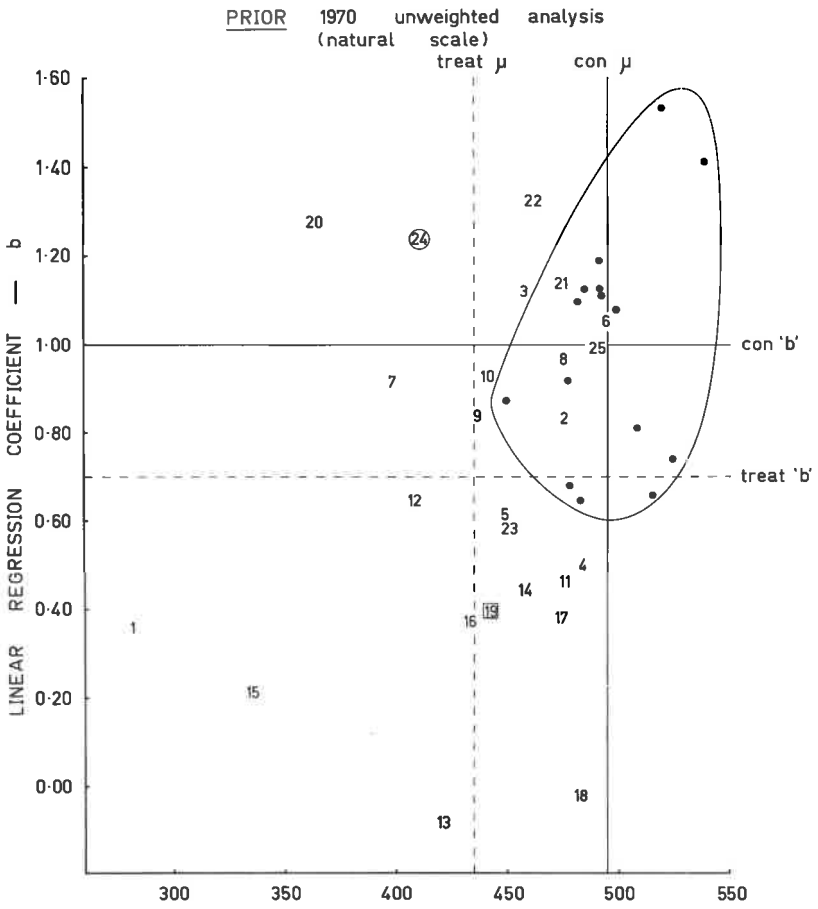

PROCTOR 1970 weighted analysis
treat μ
LINEAR REGRESSION COEFFICIENT — b
1·20
1·00
0·80
0·60
0·40
con 'b'
treat 'b'
200
250
300
350
400
450
500
MEAN YIELD (g/plot) — G
• control lines
1–35 treated lines
□ significant t=1-b/SE(b)
○ significant S²d

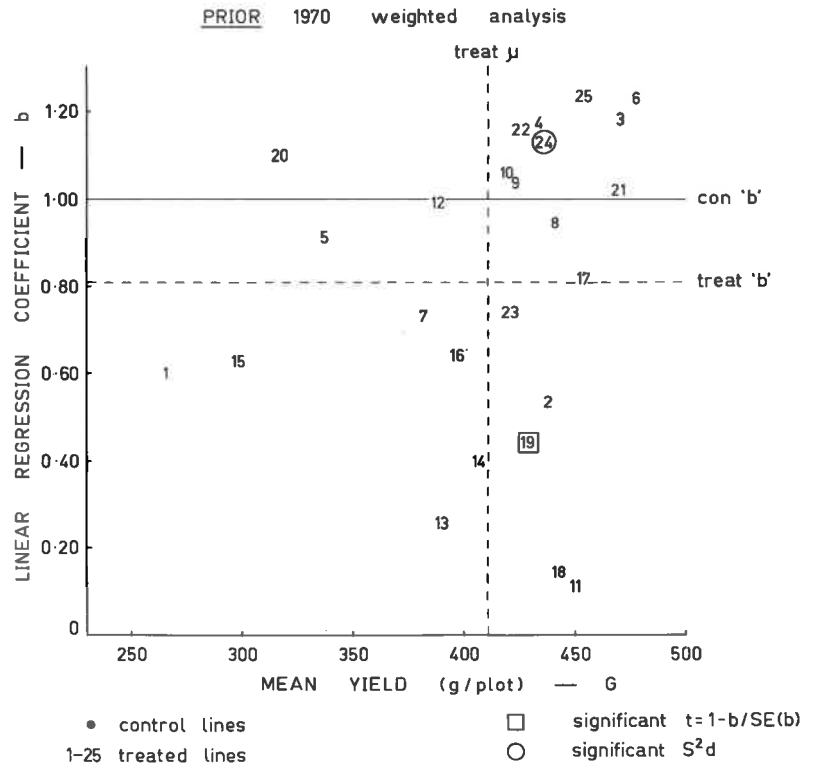
FIGURE 12

Scatter diagrams showing relationship of line mean yield (G), linear regression coefficient (b) and significant deviation mean squares (S^2d) for PRIOR in 1970 experiments.

Upper diagram - analysis of unweighted yield data on natural scale for control and treated lines.

Lower diagram - analysis of weighted yield data on natural scale for treated lines only.


PRIOR 1970 unweighted analysis
(natural scale)
treat μ
con μ
LINEAR REGRESSION COEFFICIENT — b
con 'b'
treat 'b'
1·60
1·40
1·20
1·00
0·80
0·60
0·40
0·20
0·00
300
350
400
450
500
550


PRIOR 1970 weighted analysis
treat μ
LINEAR REGRESSION COEFFICIENT — b
con 'b'
treat 'b'
1·20
1·00
0·80
0·60
0·40
0·20
0
250
300
350
400
450
500
MEAN YIELD (g/plot) — G
control lines
1–25 treated lines
significant t=1-b/SE(b)
significant S²d

using the same environmental index (site mean yield of controls) for each cultivar and these are included in the scatter diagrams.

The significance of the individual 'b' and S^2d values of treated lines was determined as follows:

(i) $$t_{n-2} = \frac{1-b}{S.E.(b)}$$ (significance test for 'b' values)

(ii) $$F = \frac{S^2di}{\sigma^2e}$$ (significance test for S^2d)

where

S^2di = deviation mean squares for line (i)

σ^2e = residual mean squares

Some treated lines had b values significantly different from unity and others had significant deviation mean squares (S^2d) and these are shown in the scatter diagrams.

The majority of the treated lines from each cultivar, except C.I.3576, have b values less than unity on both unweighted (natural scale) and weighted analyses. However, with C.I.3576 the number of lines with $b > 1.0$ is approximately equal to the number with $b < 1.0$.

In both analyses, b and G showed significant positive correlations among all cultivars except Prior (Table 21).

Table 21. Correlation coefficients between G and b for treated lines of different cultivars, 1970.

Cultivar	Unweighted analysis (Natural scale)	Weighted analysis (Natural scale)
Clipper	.7136***	.5467***
C.I.3576	.8026***	.6345***
Proctor	.7054***	.5194**
Prior	.1512^{NS}	.1702^{NS}

** significant at 1% probability

*** significant at 0.1% probability

NS non-significant

This suggested that almost all low-yielding lines have b < 1.0 and vice versa.

The significant b values of the treated lines are associated with low yields in the case of Clipper, C.I.3576 and Proctor, with the exception of line No. 3 of Clipper. Lines Nos. 27 and 29 of Proctor and No. 24 of Prior showed significant S^2d values in the case of their weighted analyses. Such lines were expected with these cultivars since in each case most of the interaction term came from the deviation component rather than the linear component.

Thus a few lines were detected which had stability parameters significantly different from controls. A more detailed consideration of their characteristics is given in the adaptation studies over two years (see page 115).

2. Performance of other quantitative characters over all environments, 1970

In addition to yield three other quantitative characters, namely heading date, plant height and seed weight, were measured on the 1970 field plots to obtain their average performances and the amount of genetic variability induced by EMS when tested over a range of environments. The data for each character were analyzed by analysis of variance combined over all sites using natural scale in all cases. The genotypic variances due to lines ($\sigma^2 p$) were calculated for both control and treated lines of each cultivar from the mean squares in the analysis of variance similar to yield data of 1970. The mean values and genotypic variances for these quantitative characters are presented in Table 22.

(a) Heading date (days)

The frequency distributions for heading date for the treated and control lines of each cultivar are shown in Figure 13.

The control lines of each cultivar exhibited uniform heading over a 2-4 day interval except one control line of Clipper (No. 23C) and Proctor (No. 10C) were 2 days later than the rest of their respective control lines. There was an overall shift towards lateness among the treated lines of all cultivars as shown by the frequency distributions (Figure 13) and significant changes in mean (Table 22), but nevertheless at least one of the

Table 22. Mean values and genotypic variances ($\sigma^2 p$) for heading date, height and seed weight of M_2-derived treated and control lines of the five cultivars grown over four sites in M_4 generation, 1970.

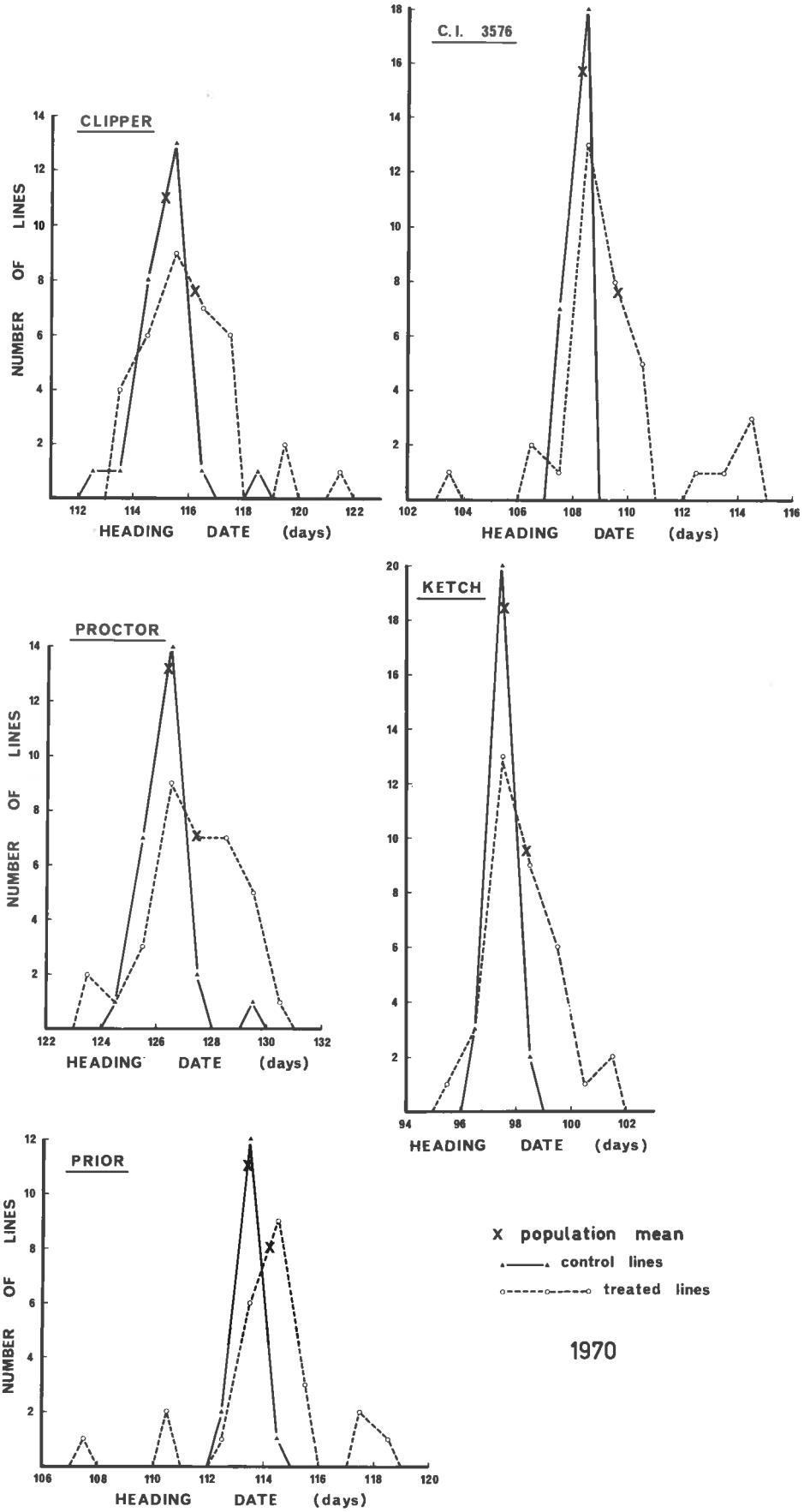
Cultivar	Lines	Heading date (days)		Plant height (cm)		Seed weight (g/100 seeds)	
		Mean value	$\sigma^2 p$	Mean value	$\sigma^2 p$	Mean value	$\sigma^2 p$
Clipper	Control	115.10	1.025	84.16	7.217	40.16	0.206
	Treated	116.18**	2.350	85.59^{NS}	5.231	39.70^{NS}	0.718
C.I.3576	Control	108.26	0.017	84.59	0.339	44.87	0.208
	Treated	109.58***	5.271	83.74^{NS}	11.354	44.50^{NS}	3.206
Proctor	Control	126.38	0.758	80.70	0.0	35.11	0.160
	Treated	127.41**	2.466	80.59^{NS}	2.942	35.54^{NS}	1.159
Ketch	Control	97.59	0.136	87.76	0.064	41.39	0.071
	Treated	98.36*	1.581	87.45^{NS}	1.479	41.23^{NS}	0.543
Prior	Control	113.39	0.078	102.12	0.702	41.86	0.0
	Treated	114.16*	4.499	99.47^{NS}	5.214	40.74**	1.065

* Mean value significantly different at 5% probability
** Mean value significantly different at 1% probability
*** Mean value significantly different at 0.1% probability

't' test used same as for yield data, 1970.

FIGURE 13

Frequency distributions for heading date combined over sites of M_2-derived treated and control lines of five barley cultivars, 1970 (M_4 generation).


CLIPPER
C. I. 3576
PROCTOR
KETCH
PRIOR
NUMBER OF LINES
HEADING DATE (days)
x population mean
control lines
treated lines
1970

treated lines was earlier than the earliest control line in all cultivars except Clipper.

The observed shift to lateness with EMS treated lines of early cultivars such as C.I.3576 and Ketch is in agreement with Brock's hypothesis (1965). However, the shift to lateness which also occurred among the treated material of the medium late and late cultivars Clipper and Proctor, respectively, is in conflict with his hypothesis.

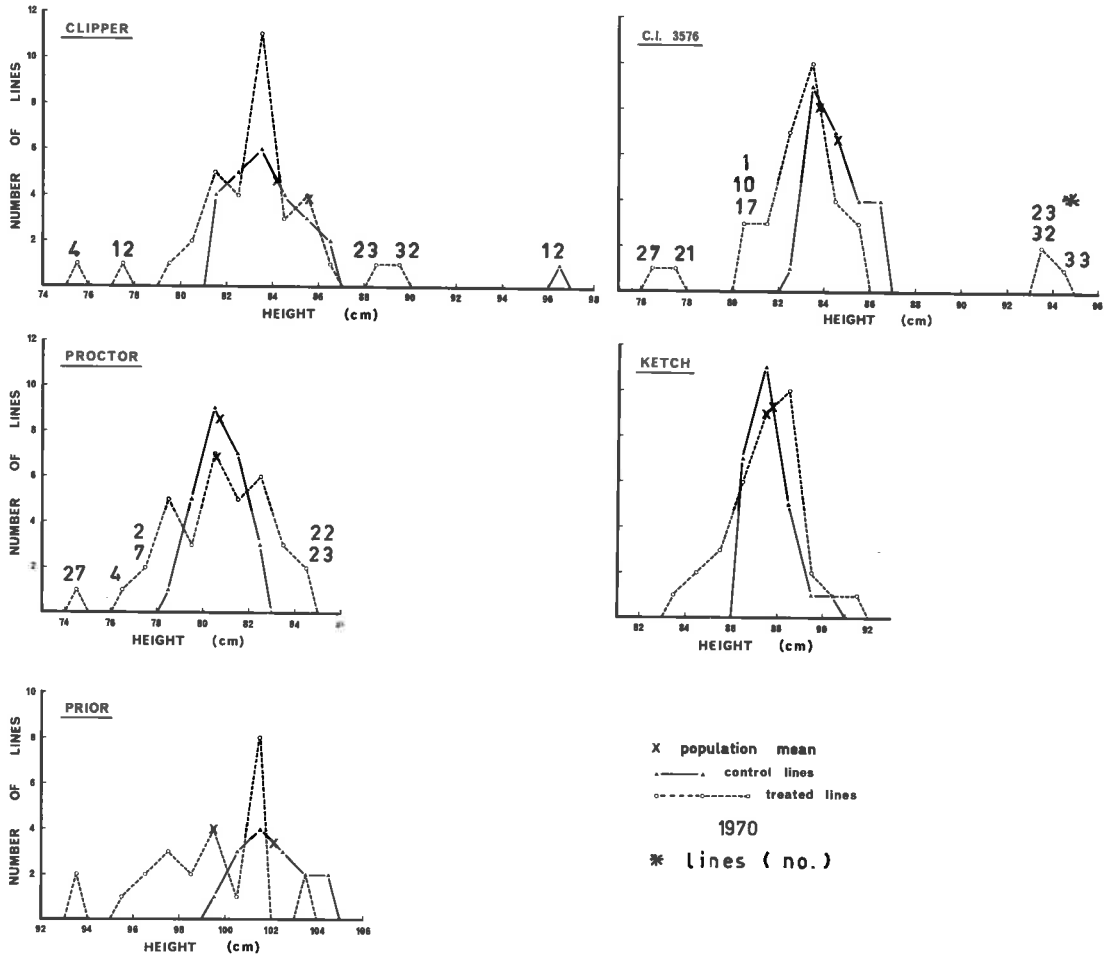
The genotypic variance for heading date was negligible among the control lines of all cultivars except with Clipper and Proctor, where the estimates were increased by the presence of one late line in each cultivar. However, the EMS-treatment resulted in a considerable increase of genotypic variance ($\sigma^2 p$) among all five cultivars as compared with respective controls with the largest increase occurring with C.I.3576 and Prior (Table 22).

(b) Plant height (cm)

The frequency distribution curves for height of treated and control lines are presented in Figure 14. The heights of the control lines were reasonably homogeneous except one line of Clipper (No. 12C) which was clearly much taller than the rest of the controls. As with heading date, the distributions of height among the treated lines were spread over a wide range but there

FIGURE 14

Frequency distributions for height combined over sites of M_2-derived treated and control lines of five barley cultivars, 1970 (M_4 generation).


CLIPPER
NUMBER OF LINES
HEIGHT (cm)
4
12
23 32
12
C.I. 3576
1
10
17
27 21
23
32
33
PROCTOR
2
7
27
4
22
23
KETCH
PRIOR
X population mean
control lines
treated lines
1970
* lines (no.)

was no overall trend to either increased or decreased height except with Prior, where a general decrease in height of treated lines was observed, but this was not significant (Table 22).

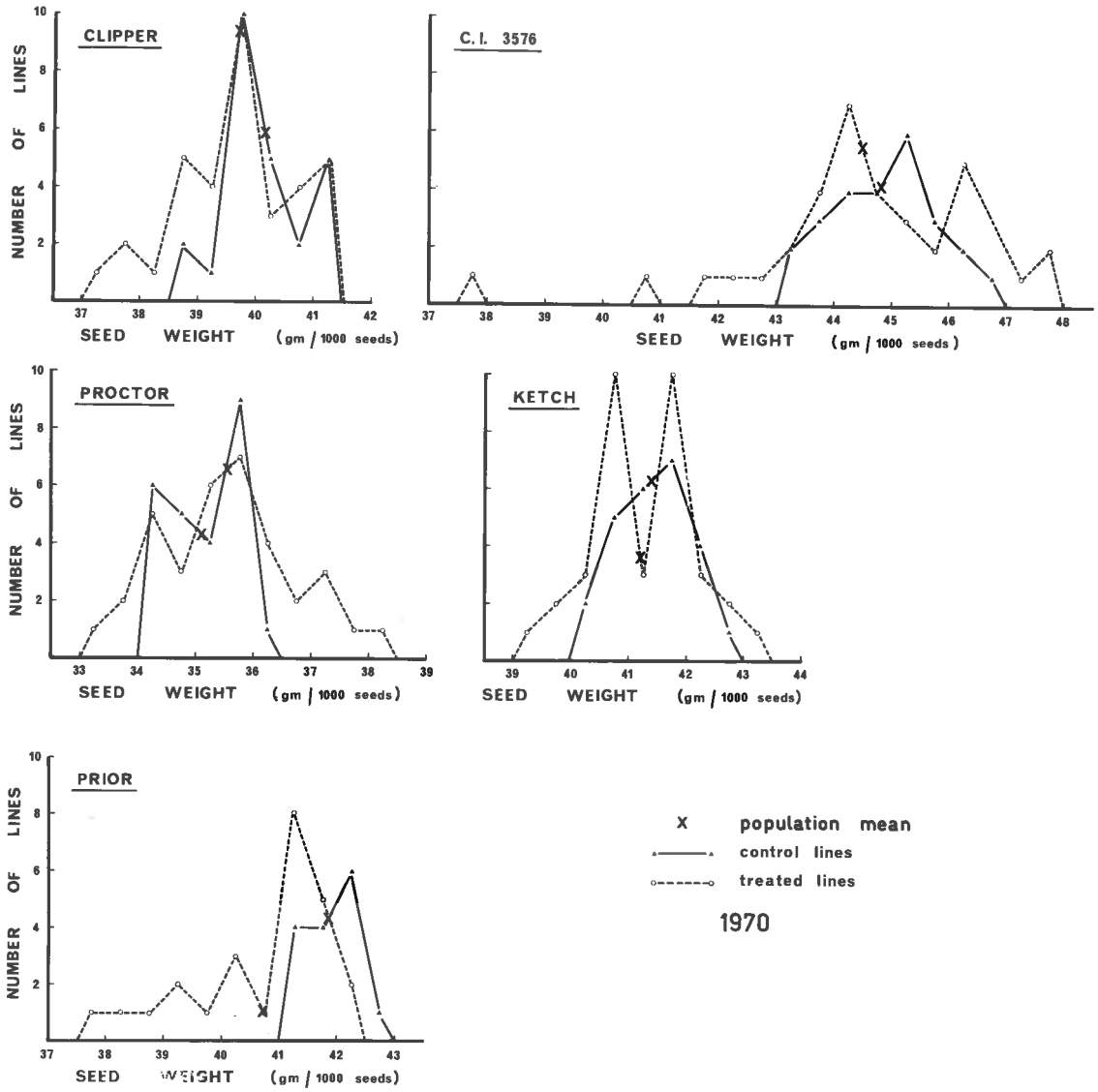
The only substantial genotypic variance (σ^2_p) for height among the control groups was observed with Clipper and apparently this was due mainly to line No. 12C which was 12 cm taller than the mean of the control group. The genotypic variance of the treated lines of the other cultivars greatly exceeded that of respective controls and the most pronounced difference occurred with the C.I.3576 lines (Table 22).

(c) Seed weight (gm/1,000 seeds)

The frequency distributions for seed weight of all cultivars are shown in Figure 15. Except for an increase in spread of seed weight for the treated lines over their respective controls, there was no consistent trend shown over all cultivars. There was an overall trend towards decrease in seed weight among the treated Clipper and Prior lines, whereas spread of seed weight occurred in both directions with C.I.3576, Proctor and Ketch cultivars. The mean value of seed weight was not significantly altered by EMS-treatment in any of the cultivars except Prior (Table 22). The genotypic variances for seed weight were considerably increased in the treated lines of all cultivars compared with the corresponding controls, indicating a substantially greater variability for this character among the treated material.

FIGURE 15

Frequency distributions for seed weight combined over sites of M_2-derived treated and control lines of five barley cultivars, 1970 (M_4 generation).


CLIPPER
C. I. 3576
PROCTOR
KETCH
PRIOR
NUMBER OF LINES
SEED WEIGHT (gm / 1000 seeds)
x population mean
control lines
treated lines
1970

C. 1971 Yield data (M_5 generation)

The M_2-derived treated and control lines of Clipper, C.I.3576, and Proctor grown in M_4 generation in 1970, were grown again in 1971 to test the performance of these lines across environments in the M_5 generation. The treated and control lines of Ketch and Prior were not grown further. The Ketch lines were excluded because the treated lines did not show G X E interaction in 1970 and the Prior lines had to be excluded because of the limitation of experimental space in 1971.

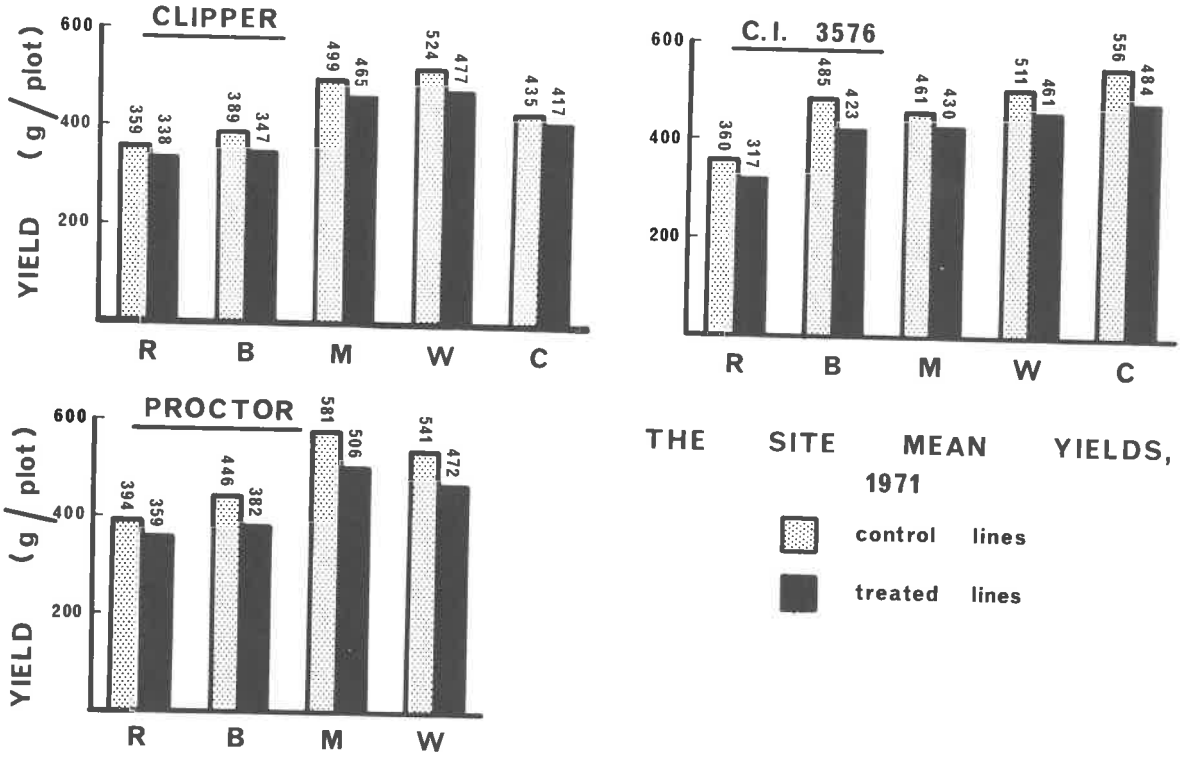
Many plots involving treated lines of Proctor were very badly affected by scald disease (Rhynchosporium secalis) at Clinton. Hence the yield data for Proctor lines at the Clinton site were omitted and analyses were carried out for the remaining four sites.

1. Site variation

The sites at which field trials were grown during 1971, provided a smaller range of environments compared with 1970 as indicated by site means (Figure 16). Roseworthy, with the lowest yields for control lines of each cultivar, indicated a low-yielding environment. On the contrary, the highest-yielding environment for each cultivar occurred at different sites. The difference between the lowest- and highest-yielding environments did not exceed 196 gm/plot in any case, compared to a minimum

FIGURE 16

Mean yields for M_2-derived treated and control lines of each cultivar in M_5 generation at each site, 1971.



THE SITE MEAN YIELDS, 1971

range of 428 gm/plot for these cultivars in 1970 (Figure 5).

The sites used in 1971 also provided a range of variability in rainfall and almost all sites had above-average rainfall. The distribution of precipitation during the 1971 season was different from 1970 as indicated by weekly rainfall (mm) at all sites from April to December (Figure 6). The sites showed an ascending order of effective rainfall from Bundaleer to Waite and the rainfall over different periods is given in Table 23.

Table 23. Annual total and effective rainfall (mm) and overall mean yields (g/plot) at each site, 1971.

	Site				
	Bundaleer (B)	Roseworthy (R)	Minlaton (M)	Waite (W)	Clinton (C)
(a) Rainfall (mm)					
Annual (Total)	343	535	469	877	431
April - November	286	461	410	785	379
Sowing - Harvesting	205	304	260	425	234
(b) Overall Mean Yield (g/plot)					
(Mean of all lines of all cultivars)	412	355	490	498	473

The overall site mean yields follow the trend of effective rainfall except for Roseworthy site which received the second highest

effective rainfall but produced the lowest yield. No obvious reason could be found for this discrepancy. Unexpectedly, the site mean yields in 1971 were generally lower than those in 1970 despite the increased rainfall in 1971.

2. Analyses of variance for individual sites

Analyses of variance for treated and control lines of each of Clipper, C.I.3576 and Proctor cultivars were carried out separately as for the individual sites in 1970 and the results are given in Appendix 10. The significance of "between lines" mean squares at each site are shown in Table 24.

Among the control lines from each cultivar, none of the mean squares between lines was significant except C.I.3576 lines at Roseworthy. It is likely this particular result is a chance deviation since in a total of 34 control comparisons made over the two years at least one of them would be expected to show significance at 5% level by chance. Thus there is no strong evidence for any genetic heterogeneity with respect to yield between any of the control groups.

Although the treated lines of each cultivar showed significant "between lines" mean square at most sites, the level of significance was generally lower than that detected in 1970.

Table 24. Significance levels of 'between lines' mean squares at individual sites, 1971.

Cultivar	Sites									
	Bundaleer		Roseworthy		Minlaton		Waite		Clinton	
	Control	Treated	Control	Treated	Control	Treated	Control	Treated	Control	Treated
Clipper	NS	*	NS	**	NS	*	NS	NS	NS	*
C.I.3576	NS	*	*	NS	NS	***	NS	**	NS	**
Proctor	NS	*	NS	**	NS	NS	NS	*	-/	-

/ Data for Clinton site were omitted as most of the plots were badly affected by scald disease.

3. Analyses of yield data combined over all sites

(a) Mean yield and frequency distributions

The reduction of the yield means (% of control) of the treated lines of Clipper, C.I.3576 and Proctor in M_5 generation is similar to that observed in the M_4 generation except there was a slight improvement in yield with Clipper and Proctor in M_5 (Table 25).

Table 25. The mean yield combined over all sites (g/plot) of treated and respective control populations of different cultivars in M_5 generation (mean yield of treated populations expressed as percent of respective controls observed in M_4 generation, 1970, is also shown).

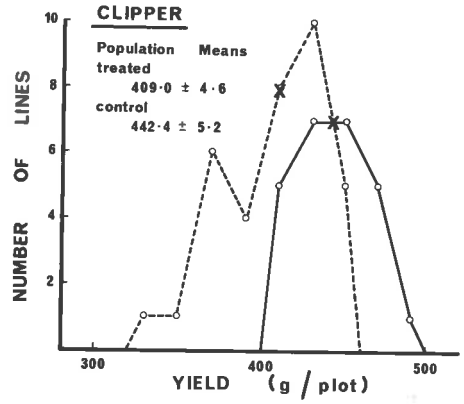
Population	Cultivar		
	Clipper	C.I.3576	Proctor
Control	442	474	491
Treated	409***	422***	430***
Percentage yield of treated population compared with controls = 100	92.5	89.0	87.6
Percentage yield of treated population compared with controls = 100 (M_4 generation)	90.7	89.7	85.4

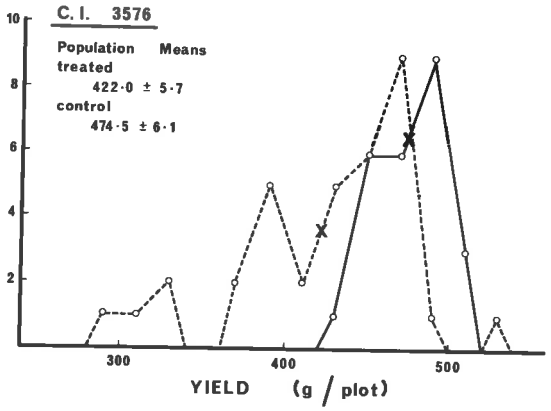
*** The mean yield of treated populations significantly reduced from respective controls at 0.1% probability.

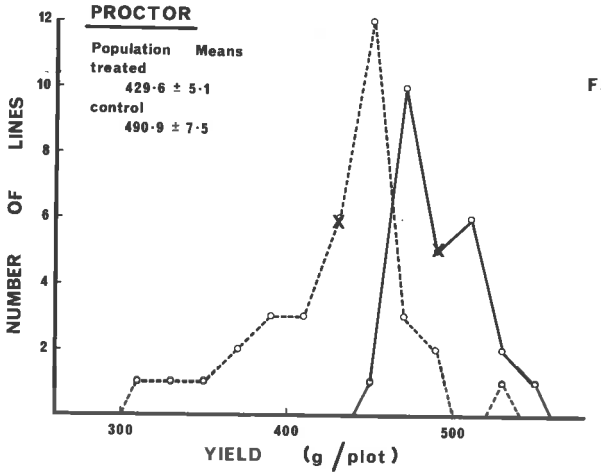
The frequency distributions of mean yields over all sites of these cultivars are shown in Figure 17.

FIGURE 17

Frequency distributions for yield combined over sites of M_2-derived treated and control lines of three barley cultivars, 1971 (M_5 generation).







FREQUENCY DISTRIBUTIONS FOR YIELD COMBINED OVER ALL SITES, 1971

control lines

treated lines

X population mean

The distribution curves of the treated lines of all cultivars showed a similar shift to the left towards lower yield compared with their control groups as in 1970.

(b) Analyses of variance combined over all sites

In order to investigate genotype X environment interaction among the treated and control lines grown in 1971, analyses of variance of yield combined over all sites were performed similar to that of 1970 yield data. The residual (error) variances for sites for each analysis were tested for heterogeneity by Bartlett's X^2 test before combining data for all sites and these variances are presented in Table 26.

Table 26. Bartlett's X^2 test for homogeneity of residual (error) variances for sites, 1971.

Cultivar	No. of sites	Lines	Scale	d.f.	X^2 values between sites
Clipper	5	Control	Natural	4	26.028***
			Log_{10}	4	12.920*
		Treated	Natural	4	27.398***
			Log_{10}	4	9.535*
C.I.3576	5	Control	Natural	4	22.419***
			Log_{10}	4	13.130*
		Treated	Natural	4	7.794 NS
Proctor	4/	Control	Natural	3	16.610***
			Log_{10}	3	5.957 NS
		Treated	Natural	3	20.333***
			Log_{10}	3	4.106 NS

/ Clinton site excluded because of disease incidence.

As in 1970, the mean squares due to sites, lines and lines X sites interactions were obtained by performing analyses on natural scale and also on transformed data, when the residual variances were heterogeneous on the natural scale (Tables 27, 28, 29).

Site effects - The mean squares due to sites were highly significant in all comparisons but the 'F' ratios were smaller than that obtained in 1970. This is expected because of the smaller range of variation between sites in 1971.

Line effects - The mean squares attributable to lines were non-significant among the control lines of Proctor. This indicates that Proctor controls appeared to be homogeneous. On the contrary significant mean squares among the control lines were found with Clipper in both analyses and with C.I.3576 in the valid analysis only. This result with Clipper was quite unexpected because the same control material when it was grown in 1970 and 1971 at 9 individual sites did not show significant line effects. Inspection of plot yields for individual control lines showed that this significant effect with Clipper was mainly due to two lines (Nos. 21C and 24C), which were uniformly the highest yielding control lines across all environments.

Highly significant lines mean squares were obtained among the treated lines from each of these cultivars, indicating that a

Table 27. Analyses of variance combined over all sites (environments) for yield, components of variances, and heritability values of M_2-derived treated and control lines of CLIPPER in M_5 generation, 1971.

Analysis of variance	Approximate analysis						Statistically valid analysis					
	Unweighted natural scale						Weighted natural scale					
Source	Control lines			Treated lines			Control lines			Treated lines		
	df	MS	F	df	MS	F	df	MS	F	df	MS	F
Sites (Env.)	4	225,819	78.41***	4	291,279	103.43***	4	163,199	88.03***	4	235,010	114.61***
Replicates within sites	5	13,537	4.70***	5	20,806	7.39***	5	12,826	6.92***	5	22,813	11.13***
Lines	24	5581.7	1.94*	34	9527.6	3.38***	24	4549.2	2.45**	34	7437.5	3.63***
Lines X Sites interaction	96	2498.1	0.87^{NS}	136	3557.8	1.26^{NS}	96	1959.6	1.06^{NS}	136	2905.2	1.42*
Linear				34	3582.6	1.01^{NS}				34	2665.7	0.89^{NS}
Deviation				102	3549.5	1.26^{NS}				102	2985.0	1.46*
Residual	120	2880.0		170	2816.3		120	1853.9		170	2050.6	
Variance components												
$\sigma^2 p$		308.36			596.98							
$\sigma^2 ps$		0.0			370.75							
$\sigma^2 e$		2880.0			2816.30							
Heritability												
H		0.5171			0.6266							

Table 28. Analyses of variance combined over all sites (environments) for yield, components of variances, heritability values of M_2-derived treated and control lines of C.I 3576 in M_5 generation, 1971.

Analysis of variance	Approximate analysis			Statistically valid analysis					
	Unweighted natural scale			Unweighted natural scale[/]			Weighted natural scale		
Source	Control lines			Treated lines			Control lines		
	df	MS	F	df	MS	F	df	MS	F
Sites (Env.)	4	266,560	62.29***	4	288,651	58.64***	4	317,216	102.14***
Replicates within sites	5	29.950	7.00***	5	30,910	6.28***	5	29,324	9.44***
Lines	24	4,938.5	1.15^{NS}	34	28,196	5.73***	24	5,882.1	1.89*
Lines X Sites interaction	96	4,483.1	1.05^{NS}	136	6,415.6	1.30*	96	3,996.9	1.29^{NS}
Linear				34	5,359.9	0.79^{NS}			
Deviation				102	6,767.4	1.37*			
Residual	120	4,279.5		170	4,922.8		120	3,105.7	
Variance components									
$\sigma^2 p$		45.54			2,178.04				
$\sigma^2 ps$		101.80			746.40				
$\sigma^2 e$		4,279.50			4,922.80				
Heritability									
H		0.0922			0.7725				

/ In the case of treated lines, unweighted analysis on natural scale is statistically valid as its error variances for sites are homogeneous on natural scale.

Table 29. Analyses of variance combined over four sites (environments) for yield, components of variances, heritability values M_2-derived treated and control lines of PROCTOR in M_5 generation, 1971.

Analysis of variance	Approximate analysis						Statistically valid analysis					
	Unweighted natural scale						Unweighted Log_{10} scale					
Source	Control lines			Treated lines			Control lines			Treated lines		
	df	MS	F	df	MS	F	df	MS	F	df	MS	F
Sites (Env.)	3	366,498	60.02***	3	345,788	71.33***	3	.285870	65.33***	3	.344400	80.98***
Replicates within sites	4	24,283	3.98**	4	42,583	8.78***	4	.014525	3.31*	4	.035964	8.46***
Lines	24	5004.2	0.82^{NS}	34	16,470	3.40***	24	.003517	0.80^{NS}	34	.017959	4.22***
Lines X Sites interaction	72	4726.9	0.77^{NS}	102	4865.8	1.00^{NS}	72	.003302	0.75^{NS}	102	.004391	1.03^{NS}
Residual	96	6106.2		136	4847.8		96	.004389		136	.004253	
Variance components												
σ^2_p		34.66			1450.53							
σ^2_{ps}		0.0			9.00							
σ^2_e		6106.20			4847.80							
Heritability												
H		0.0434			0.7046							

considerable amount of genetic variability was still present in the M_5 generation following EMS treatment.

Genotype X environment interactions - Like 1970, none of the lines X sites interactions were significant among the control lines. Significant interaction mean squares were detected among the treated lines of Clipper and C.I.3576 but not with Proctor. In the case of Clipper, significant interaction term was detected only in the valid analysis (Tables 27, 28, 29). The significance levels of these interaction terms are generally lower than those obtained in 1970, probably due to the much narrower range of environments sampled in 1971 compared with the previous year, especially with Proctor where only 4 sites were sampled in 1971.

When the significant lines X sites interaction sum of squares were partitioned into linear and deviation from regression components, only deviation mean squares were significant. The absence of significant linear effects is not unexpected because of the small range of environmental variation between the sites used in 1971.

(c) Variance components and heritability

A considerable amount of EMS-induced genotypic variance ($\sigma^2 p$) was still present among the treated lines in the M_5 generation, but the magnitude was less than that observed in 1970 in the M_4

generation (Tables 27, 28, 29). The maximum induced genotypic variances were obtained in C.I.3576 and Proctor and least with Clipper, where only a two-fold increase over controls was observed in the treated material.

The estimates of σ^2ps among the treated lines of Clipper and C.I.3576 were increased compared with the controls but not to any extent with Proctor (Tables 27, 28, 29). These estimates of σ^2ps were much less than observed in 1970 as expected from the small range of environmental variability occurring at the 1971 sites.

The heritability (H) estimates showed almost the same trend as σ^2p in the M_5 generation. The heritability values showed that a response to selection could be expected among the treated lines of all cultivars. However, the heritability value for Clipper controls was also quite high, due to the variability among the control lines detected in 1971 (see page 109).

D. 1970 + 1971 Yield data (M_4 and M_5 generations)

In a study of the effect of EMS-induced mutation on the adaptation performance of barley it is essential to test material over a wide range of environments. In the present study, it was found that the yields of the treated lines expressed as percentages of the respective controls in M_5 generation were very similar to

that observed in M_4 generation (Table 25), suggesting little 'self improvement' in M_5. Therefore, it was considered legitimate to combine the yield data obtained from M_4 and M_5 generations to give a wider range of test environments. Smith et al. (1967) used a similar approach in their studies of phenotypic stability of F_3-derived lines of different soybean populations, where they combined yield data of F_4 - F_7 generations tested under different environments covered by four years.

1. Analyses of variance combined over all environments

Analyses of variance for yield data combined over all environments (1970 + 1971) were carried out separately for M_2-derived treated and control lines of each cultivar. In each case, the residual (error) variances for environments were tested for heterogeneity by Bartlett's X^2 test similar to the combined analyses over sites of yield data of individual years. Significant heterogeneity of error variances was detected in all cases with both unweighted natural and $\log_{10}$ scales (Table 30), and it was necessary to use weighted (natural scale) data to obtain a valid statistical analysis. However, once again the approximate analyses based on unweighted natural data were included for comparative purposes. These analyses are given in Tables 31, 32 and 33.

Table 30. Bartlett's X^2 tests for homogeneity of residual (error) variances for environments, 1970 + 1971.

Cultivar	No. of Env.	Lines	Scale	d.f.	X^2 values Between environments	
Clipper	9	Control	Natural	8	60.686	***
			Log_{10}	8	17.202	*
		Treated	Natural	8	78.533	***
			Log_{10}	8	31.922	***
C.I.3576	9	Control	Natural	8	77.144	***
			Log_{10}	8	64.559	***
		Treated	Natural	8	31.457	***
			Log_{10}	8	23.649	**
Proctor	8	Control	Natural	7	45.296	***
			Log_{10}	7	14.771	*
		Treated	Natural	7	53.100	***
			Log_{10}	7	19.381	**

Environment effects - The environmental mean squares were very highly significant in all analyses, indicating that the environments used in 1970 and 1971 were highly variable.

Line effects - Mean squares attributable to lines were significant among control groups of Clipper and C.I.3576, but not with Proctor. With C.I.3576, line effects were significant at the 5% level in the valid analysis but were not significant in the approximate analysis. As indicated earlier, the result with C.I.3576 could represent a chance deviation but there is evidence

Table 31. Analyses of variance combined over all environments for yield of M_2-derived treated and control lines of CLIPPER over 2 years (1970 + 1971).

Source	Approximate analysis						Statistically valid analysis					
	Unweighted natural scale						Weighted natural scale					
	Control lines			Treated lines			Control lines			Treated lines		
	df	MS	F	df	MS	F	df	MS	F	df	MS	F
Environments	8	1,346,630	323.83***	8	1,645,810	382.75***	8	702,040	299.10***	8	909,229	344.50***
Replicates within Env.	9	14,740	3.54***	9	30,640	7.13***	9	12,654	5.39***	9	20,501	7.77***
Lines	24	7947.3	1.91**	34	31,995	7.44***	24	5214.2	2.22**	34	18,359	6.96***
Lines X Env. Interaction	192	4010.4	0.96^{NS}	272	6425.9	1.49**	192	2719.6	1.16^{NS}	272	4254.8	1.61***
Linear				34	14,460	2.74***				34	7141.3	1.86**
Quadratic				34	4874.2	0.91^{NS}				34	3670.5	0.95^{NS}
Deviation				204	5345.5	1.24*				204	3871.0	1.47**
Residual	216	4158.5		306	4300		216	2347.1		306	2639.2	

Table 32. Analyses of variance combined over all environments for yield of M_2-derived treated and control lines of C.I.3576 over 2 years (1970 + 1971).

Source	Approximate analysis						Statistically valid analysis					
	Unweighted natural scale						Weighted natural scale					
	Control lines			Treated lines			Control lines			Treated lines		
	df	MS	F	df	MS	F	df	MS	F	df	MS	F
Environments	8	1,589,600	208.45***	8	1,946,520	314.98***	8	1,140,080	281.20***	8	1,411,690	280.97***
Replicates within Env.	9	27,098	3.55***	9	24,364	3.94**	9	26,077	6.43***	9	26,376	5.25***
Lines	24	6401.6	0.84^{NS}	34	81,999	13.27***	24	7111.3	1.75*	34	62,358	12.41***
Lines X Env. Interaction	192	6473.0	0.85^{NS}	272	9670.3	1.56***	192	4626.7	1.14^{NS}	272	7903.6	1.57***
Linear				34	27,442	3.85***				34	18,554	2.91***
Quadratic				34	4108.8	0.54^{NS}				34	4856.3	0.73^{NS}
Deviation				204	7635.3	1.24*				204	6636.4	1.32*
Residual	216	7625.8		306	6179.9		216	4054.3		306	5024.3	

Table 33. Analyses of variance combined over eight environments for yield of M_2-derived treated and control lines of PROCTOR over 2 years (1970 + 1971).

Source	Approximate analysis						Statistically valid analysis					
	Unweighted natural scale						Weighted natural scale					
	Control lines			Treated lines			Control lines			Treated lines		
	df	MS	F	df	MS	F	df	MS	F	df	MS	F
Environments	7	1,340,610	209.26***	7	1,398,760	312.45***	7	969,850	249.94***	7	1,040,120	373.16***
Replicates within Env.	8	20,851	3.25***	8	46,664	10.42***	8	11,877	3.06**	8	24,991	8.97***
Lines	24	6169.6	0.96^{NS}	34	40,746	9.10***	24	5257.7	1.36^{NS}	34	26,751	9.60***
Lines X Env. Interaction	168	5546.0	0.87^{NS}	238	7722.3	1.73***	168	3815.3	0.98^{NS}	238	5612.2	2.01***
Linear				34	12,869	1.87**				34	8893.3	1.76**
Quadratic				34	6126.5	0.87^{NS}				34	6349.5	1.32^{NS}
Deviation				170	7012.2	1.57**				170	4808.5	1.73**
Residual	192	6406.3		272	4476.7		192	3880.3		272	2787.3	

that real heterogeneity exists among the Clipper control lines due mainly to lines 21C and 24C.

On the other hand, the lines mean squares for the treated groups were highly significant with each cultivar in the combined analysis. This is expected in view of the genetic variability detected among the EMS-treated lines in both 1970 and 1971.

Genotype X environment interactions - Once again, no significant lines X environment interaction mean squares were observed among any of the control groups but highly significant interaction mean squares (0.1% level) were found with the treated lines of each cultivar. When the significant lines X environments mean squares were partitioned into variation attributable to linear, quadratic and deviation components of interaction, the linear and deviation components were significant with each cultivar, but none of the quadratic components were significant. It is of interest to note that linear component of the interaction is more pronounced in this analysis involving two years' data than that obtained in the separate analyses of data of 1970 and 1971. The linear mean squares were significant ranging from 1% to 0.1% levels and deviation mean squares were significant from 5% to 1% levels (Table 31, 32, 33). This indicates that the genotypic response to environments in case of treated lines could be only partly accounted for by the regression of individual yields on site means.

From the variance components in the weighted analyses of variance, it was calculated that 35%, 59% and 31% of the genotype X environment variance components in each of Clipper, C.I.3576 and Proctor respectively are attributable to linear regressions, whereas the equivalent figures for the unweighted analyses (natural scale) are 60%, 76% and 37%, respectively indicating a higher linear component with the unweighted scale. Nevertheless it is clear that a large portion of the overall interaction term of each cultivar is due to non-linear response (quadratic and deviation) by both analyses.

2. Adaptation studies

In combined analyses of variance, where the linear regression accounts for most of the genotype X environment interaction (i.e. only linear mean squares are significant), the linear regression coefficients are a convenient measure of the relative sensitivity of genotypes across environments. However, in those analyses, where both linear regression and deviations from regression mean squares are significant, estimates of both b and S^2d are required to specify the relative sensitivity of different genotypes to changes in environment. In these studies, the parameters such as mean yield over all environments, linear regression coefficient (b) and deviation mean squares (S^2d) were estimated to evaluate relative stability of individual treated

lines of Clipper, C.I.3576 and Proctor over a range of environments. The parameters b and S^2d were computed similarly to 1970 analyses by using environmental indices of respective control lines in each case. Furthermore, the standard error of b was also calculated for individual line from S^2d values.

The mean yield over all environments, average value of the linear regression coefficient (β_T) and S.E. (β_T) for all treated lines of each of three cultivars were calculated in separate analyses using natural data and weighted data, and these average effects are given in Table 34.

The difference between the average slope (β_T) of the treated lines of each cultivar and their controls ($\beta_C = 1.0$) was tested for significance using the 't' test, described earlier (Table 20). The average slope (β_T) of treated lines was less than the controls in all cases but the only significant decreases in slope occurred with Proctor lines on both analyses and with Clipper lines when analyzed on a natural scale (unweighted). The reduction of average slope of treated lines (β_T) in each cultivar was due to a scale effect whereby the arithmetic difference between the average yield of treated lines compared with their control means was more pronounced at high-yielding than at low-yielding environments. The possible reason for the more pronounced decrease in average β_T value for Proctor will be given

Table 34. Mean, average slope (β_T) and S.E. (β_T) of treated lines of three barley cultivars compared with their respective controls (β_C = 1.0 and S.E. (β_C) = 0).

Cultivar	No. of environments	Approximate analysis (Unweighted natural scale)				Valid analysis (Weighted natural scale)			
		Mean	β_T	S.E.(β_T)	't' test	Mean	β_T	S.E.(β_T)	't' test
Clipper	9	473.4	.9261	.0293	2.52*	401.6	.9247	.0387	1.94^{NS}
C.I.3576	9	505.2	.9303	.0339	2.06^{NS}	455.0	.9352	.0441	1.47^{NS}
Proctor	8	472.4	.8594	.0354	4.00**	396.9	.8551	.0362	4.00**

* significant at 5% probability

** significant at 1% probability

in the Discussion section.

The mean yield (G), b and S.E. (b) of individual treated lines of Clipper, C.I.3576 and Proctor are given in Appendices 11-13. The relationship of mean yield (G) and other stability parameters such as b and S^2d for each treated line from each cultivar was studied by scatter diagrams (Figures 18, 20, 22). For the purpose of comparing treated lines with respective controls in each cultivar, b for individual control lines was also calculated and are also shown in these diagrams. The significance of b and S^2d for each treated line was examined by appropriate 't' test and 'F' ratio respectively, similar to 1970 results, and the lines showing significant values are indicated in the scatter diagrams. Once again b and G show a significant positive correlation with each cultivar on both analyses (Table 35).

Table 35. Correlation coefficients between b and G for treated lines of different cultivars, 1970 + 1971.

Cultivar	Unweighted analysis (Natural scale)	Weighted analysis (Natural scale)
Clipper	.789***	.722***
C.I.3576	.803***	.727***
Proctor	.711***	.622***

The stability parameters of the individual lines of each cultivar are briefly described below:

(a) Clipper

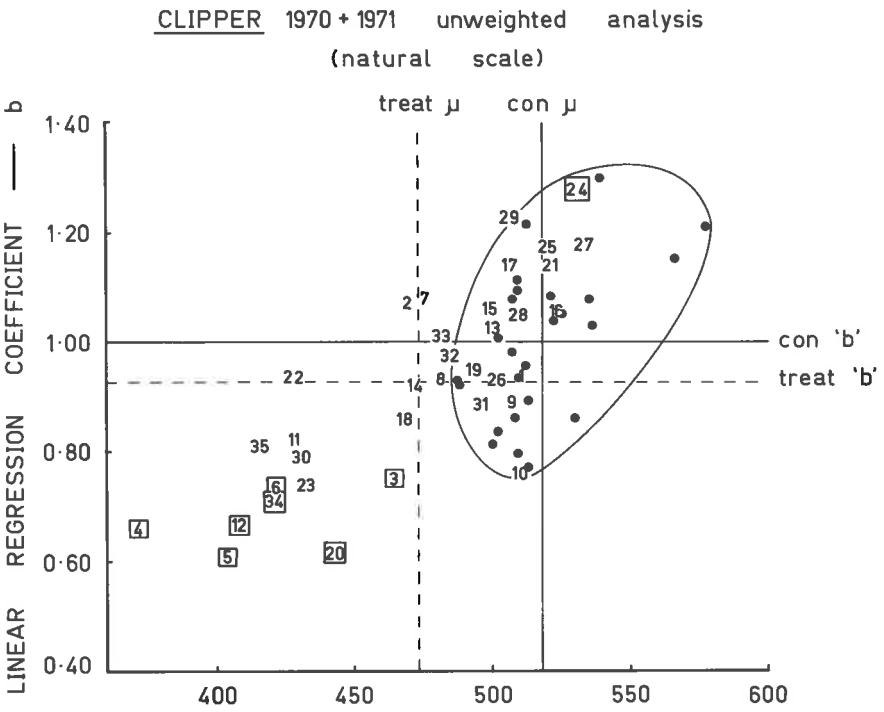
Figure 18 shows that 17% and 23% of treated lines in the case of weighted and unweighted analyses, respectively, have b values less than the control line with the lowest b value, whereas none of the treated lines have b value more than the upper limit of controls. Similarly none of the treated lines show mean yield more than the highest-yielding control line over environments. Six treated lines (Nos. 3, 4, 5, 6, 12 and 34) out of 35 treated lines have b values significantly less than 1.0 by both unweighted and weighted analyses. It is interesting to note that lines Nos. 3, 4 and 5 also possessed b values significantly less than 1.0 when tested in 1970. All of these lines except line No. 3 have low yields (less than Treat μ) and they are relatively stable in performance across the environments sampled in 1970 and 1971, whereas line No. 3 has an average yield (Figure 18). In constrast, line No. 24 yielding more than the average yield (Treat μ), is sensitive to environmental change with b value significantly greater than 1.0 (in the case of unweighted analysis). Even though there is no significant G X E interaction in the control lines of Clipper the same test of significance was applied to the b values of control lines, and it

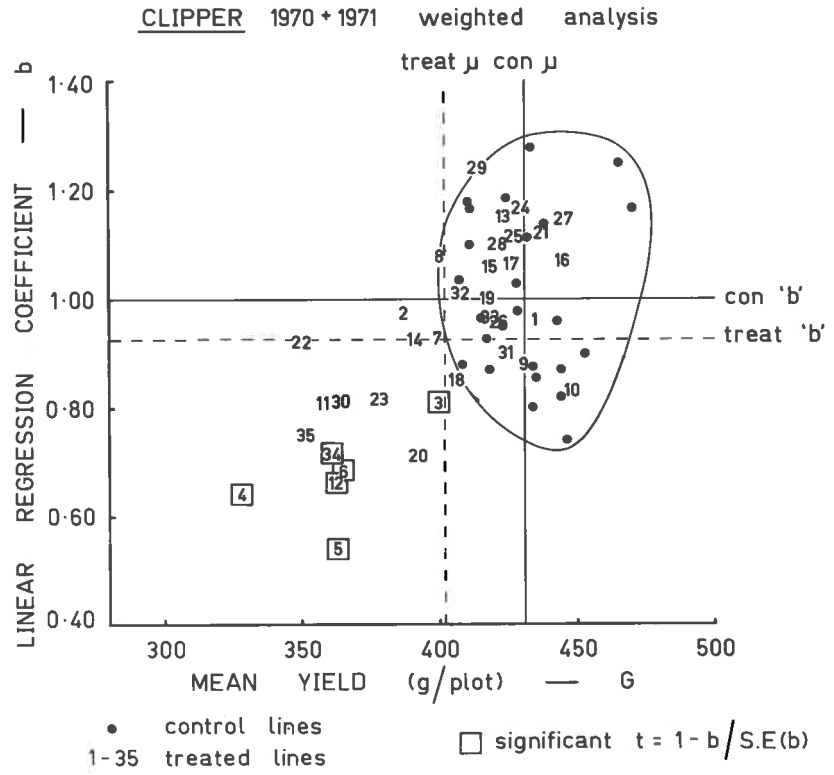
FIGURE 18

Scatter diagrams showing relationship between line mean yield (G) and linear regression coefficient (b) for control and treated lines of CLIPPER, tested over two years (1970 + 1971).

Upper diagram - analysis of unweighted yield data on natural scale.

Lower diagram - analysis of weighted yield data on natural scale.


CLIPPER 1970 + 1971 unweighted analysis
(natural scale)
treat μ
con μ
LINEAR REGRESSION COEFFICIENT — b
1·40
1·20
1·00
0·80
0·60
0·40
con 'b'
treat 'b'
400
450
500
550
600


CLIPPER 1970 + 1971 weighted analysis
treat μ
con μ
LINEAR REGRESSION COEFFICIENT — b
1·40
1·20
1·00
0·80
0·60
0·40
con 'b'
treat 'b'
300
350
400
450
500
MEAN YIELD (g/plot) — G
• control lines
1-35 treated lines
□ significant t = 1 - b/S.E(b)

was found that the line with the highest b value (b = 1.300) was significantly greater than 1.0 at the 5% level. Hence, it is likely that the significant b value of line No. 24 is not due to mutational change.

None of the treated lines has significant S^2d when judged by their appropriate 'F' ratio in both analyses.

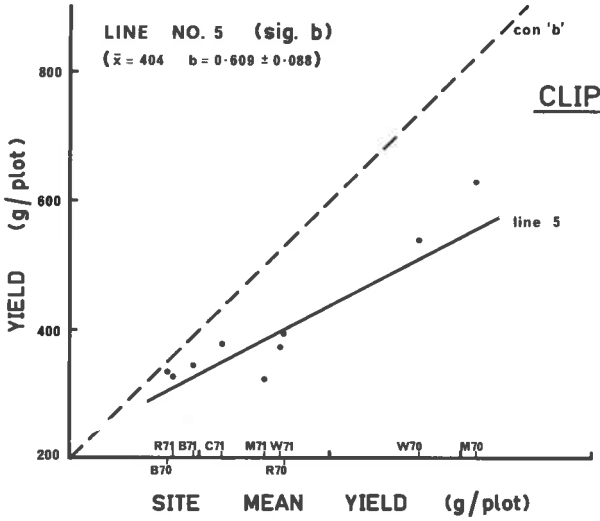
The relation between site mean yield (mean yield of control lines at each site) and the yield of three representative treated lines with different mean yield and b values is shown in Figure 19. Line Nos. 3 and 5 differ with respect to both mean yield and b value (Figure 18) and their performance across environments is accurately described by the regression lines. Thus, lines No. 3 (average-yielding) and No. 5 (low-yielding) gave yields similar to the control means in low-yielding environments and relatively less yield in high-yielding environments. These two lines are relatively stable in performance across environments. In contrast line No. 24 (yielding more than Treat μ) is unstable, giving similar yield to controls in the low-yielding environments, but high yields compared to the controls in the high-yielding environments.

(b) C.I.3576

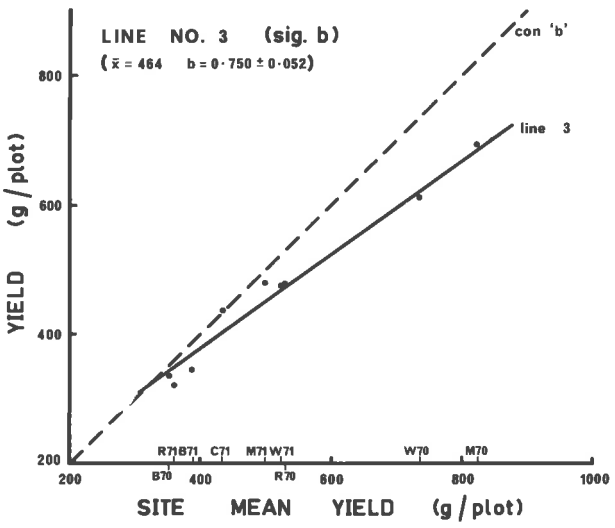
A wide range of G and b values was observed with the treated lines of C.I.3576 (Figure 20). Approximately 20% of the

FIGURE 19

The relation between site mean yield and the yield of three treated lines of Clipper having stability parameters significantly different from controls, over 9 sites (environments).



CLIPPER 1970 + 1971 unweighted analysis (natural scale)



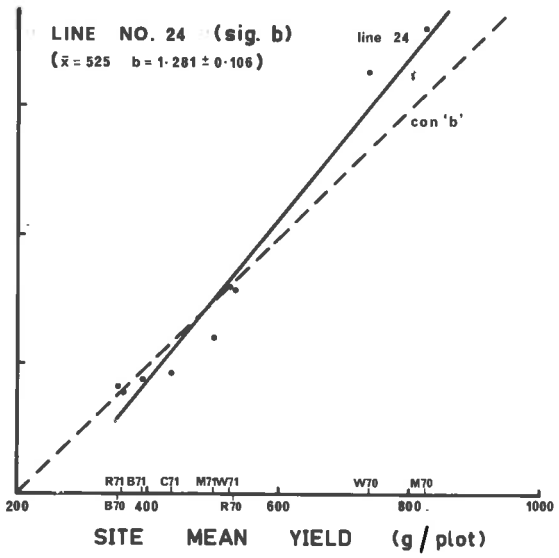
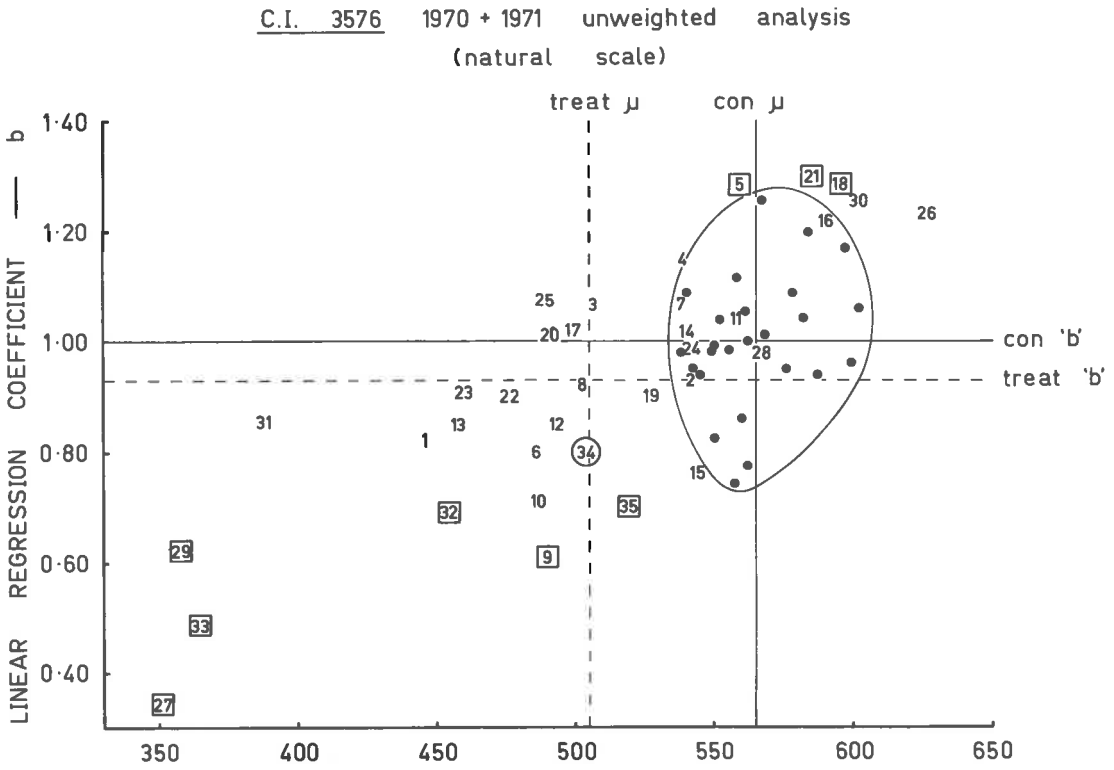


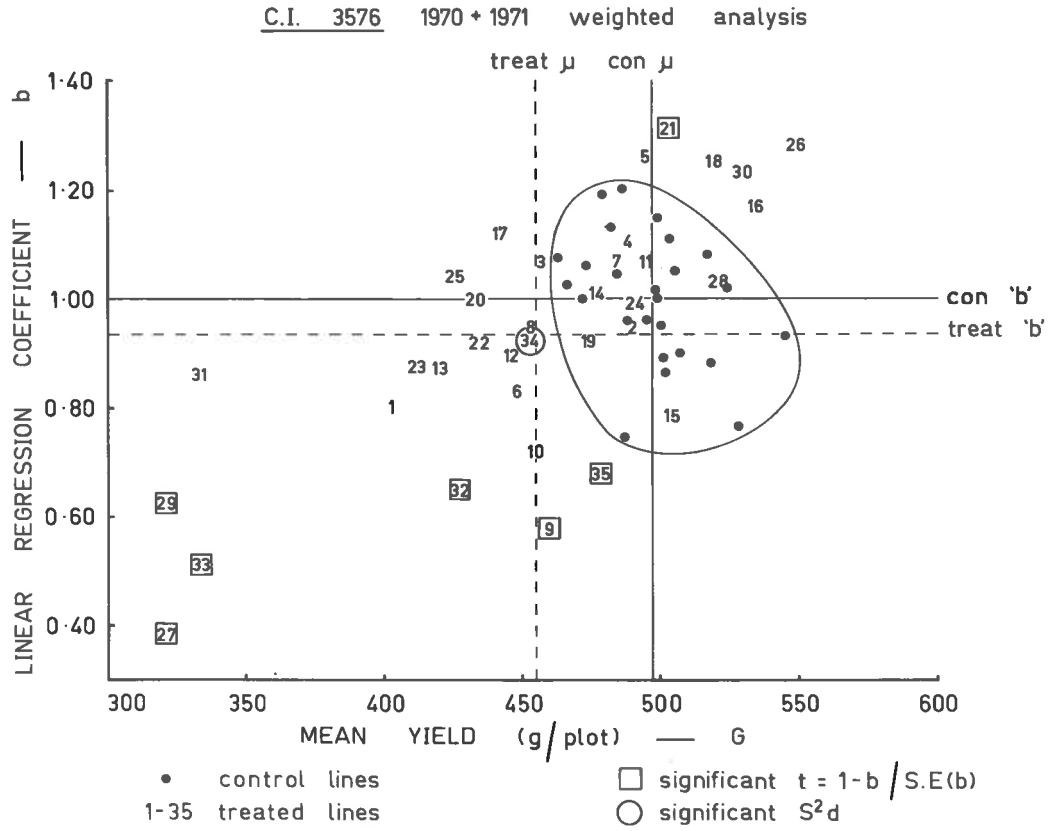
FIGURE 20

Scatter diagrams showing relationship of line mean yield (G), linear regression coefficient (b) and significant deviation mean squares (S^2d) for control and treated lines of C.I.3576, tested over two years (1970 + 1971).

Upper diagram - analysis of unweighted yield data on natural scale.

Lower diagram - analysis of weighted yield data on natural scale.


C.I. 3576 1970 + 1971 unweighted analysis
(natural scale)
treat μ
con μ
LINEAR REGRESSION COEFFICIENT — b
1·40
1·20
1·00
0·80
0·60
0·40
con 'b'
treat 'b'
350
400
450
500
550
600
650


C.I. 3576 1970 + 1971 weighted analysis
treat μ
con μ
LINEAR REGRESSION COEFFICIENT — b
1·40
1·20
1·00
0·80
0·60
0·40
con 'b'
treat 'b'
300
350
400
450
500
550
600
MEAN YIELD (g/plot) — G
• control lines
1-35 treated lines
□ significant t = 1-b / S.E(b)
○ significant S²d

treated lines in each of unweighted and weighted analysis have b values less than the control line with the lowest b value, whereas approximately 8% of the treated lines in the unweighted analysis and 14% in the weighted analysis, have b values more than the upper limit of controls. The treated line No. 26 proved to be the highest yielding line over environments among both treated and control groups, and had b > 1.0 by both analyses, but because of the high S.E. (b), it is not significantly different from 1.0.

Seven treated lines (Nos. 9, 21, 27, 29, 32, 33 and 35) have b values significantly different from slope of 1.0 by both analyses. All of these lines have low b values except line No. 21 where b is greater than 1.0. Line Nos. 27, 29 and 33 all have low yields and they are relatively stable in their yield performance across environments. These lines also showed similar performance in 1970 (Figure 10). On the other hand Line Nos. 9, 32 and 35 with significantly low b values had yields similar to the average yield of treated group (i.e. Treat μ). Line Nos. 5 and 18 yielding more than average yield (Treat μ), are characterized by having b significantly more than 1.0 only in the case of unweighted analysis (Figure 20). It is of some interest to note that whereas three treated lines had significant b values > 1.0 in the analysis of unweighted yield data, only one of the control lines had a b value (b = 1.254) significant at the 5% level, suggesting that these

treated lines may have been altered by mutation treatment. Line No. 34 showed a significant S^2d in both analyses.

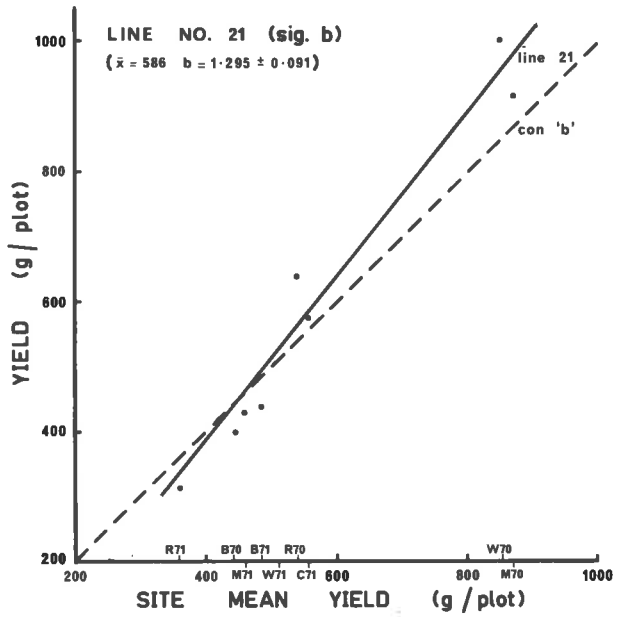
The relation between site mean yield and the yield of four representative treated lines with different mean yield and significantly different stability parameters is illustrated in Figure 21. The low-yielding line Nos. 27 and 29 (with $b < 1.0$) have similar yield over environments but showed different b values. The yield of these lines was slightly lower than the controls mean at low-yielding sites but there was a pronounced decrease in yield relative to the controls, at the high-yielding environments. Line No. 27 was the most stable line, showing very little response to improved environmental conditions. On the contrary, line No. 21 (with $b > 1.0$) produced above-average yield and performed better than the control mean under high-yielding environments.

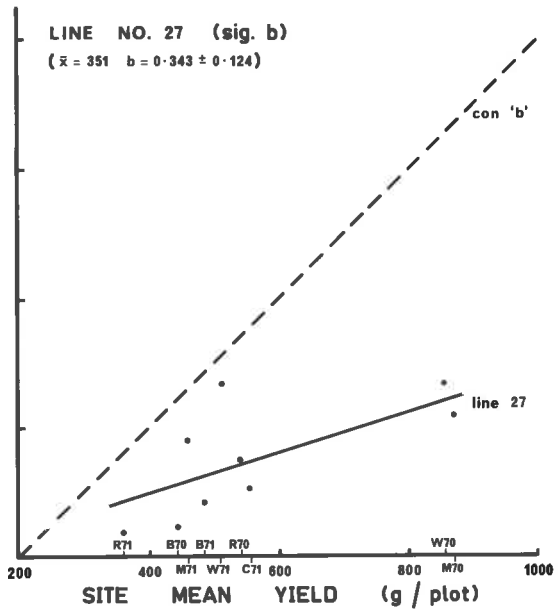
Line No. 34 with significant S^2d provides an example of a different type of G X E interaction. With this line large deviations in yield occurred at B_{70} and M_{71} sites, contributing to the large value of S^2d. At each of these sites the yield of the two replicates was similar and the divergent yields of this line between sites could not be correlated with any specific environmental effects such as disease, insect damage, etc.

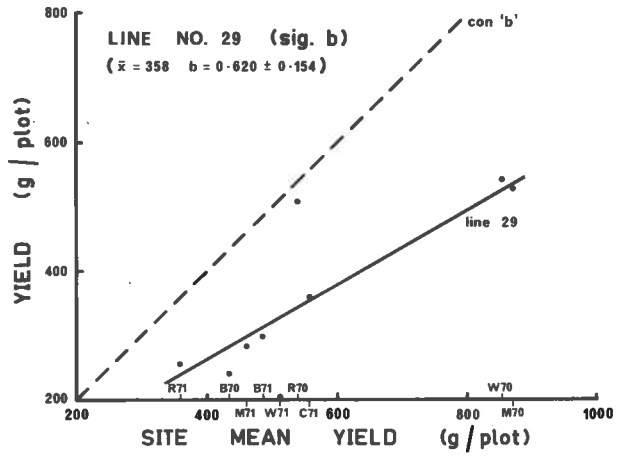
FIGURE 21

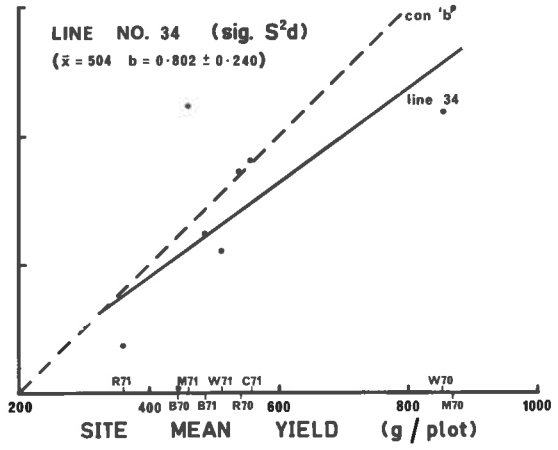
The relation between site mean yield and the yield of four treated lines of C.I.3576 having stability parameters significantly different from controls, over 9 sites (environments).

C.I. 3576 1970 + 1971 unweighted analysis (natural scale)









(c) Proctor

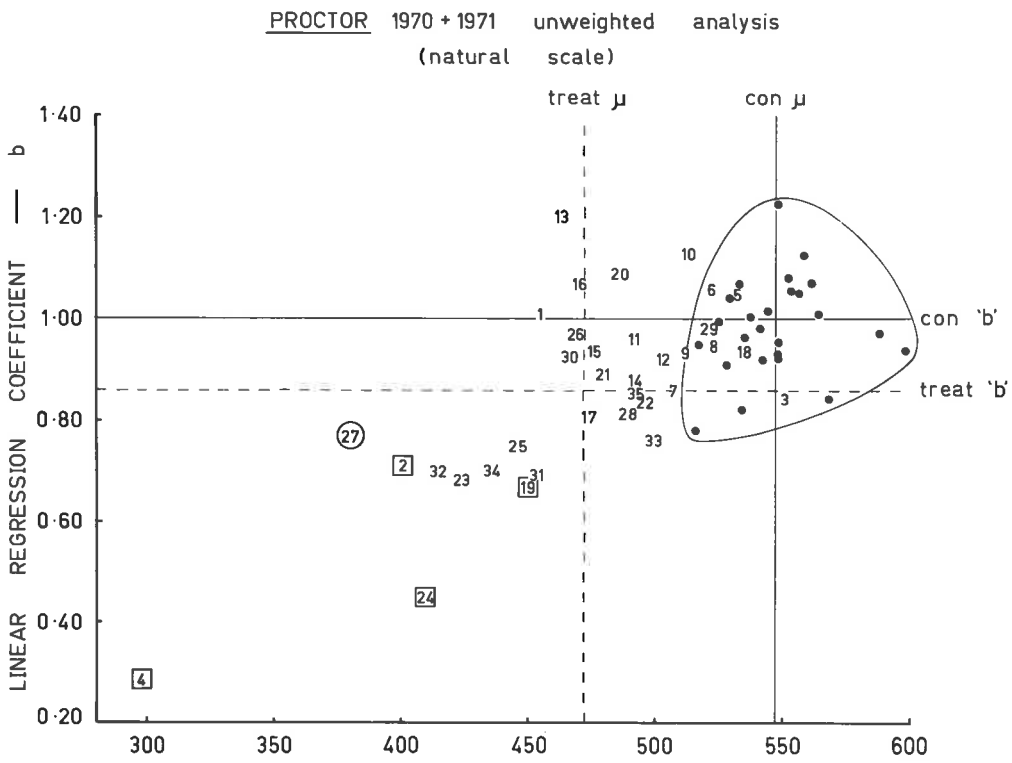
Figure 22 shows that approximately 17% of the treated lines in the weighted analysis and 20% in the unweighted analysis have b values $\geq$ 1.0 but none of these b values are significantly greater than 1.0. About 23% of the treated lines have lower b values compared with control line with the lowest b value in each analysis. Line Nos. 2, 4, 23, 24 and 32 yielding less than the average yield of treated group have b values significantly less than slope of 1.0 in the case of weighted analysis. The three lines (Nos. 2, 4, 24) have significantly lower b values in both weighted and unweighted analyses. In addition, the b value for line No. 19 is significantly reduced (at the 5% level) in the unweighted analysis and it is also close to significance at the 5% level in the weighted analysis. All of these lines with significant b values, except line No. 4, have similar overall yields and are relatively stable in performance across environments. Line No. 4 is the lowest yielding line (Figure 22) and shows maximum stability of yield. Line No. 27 showed a significant S^2d by both analyses and gave low yield. Hence, the two lowest yielding lines No. 4 (with significant $b < 1.0$) and No. 27 (with significant S^2d) are considered the most stable and unstable lines respectively. Line Nos. 4, 24 and 27 also showed similar performance when identified in 1970 environments.

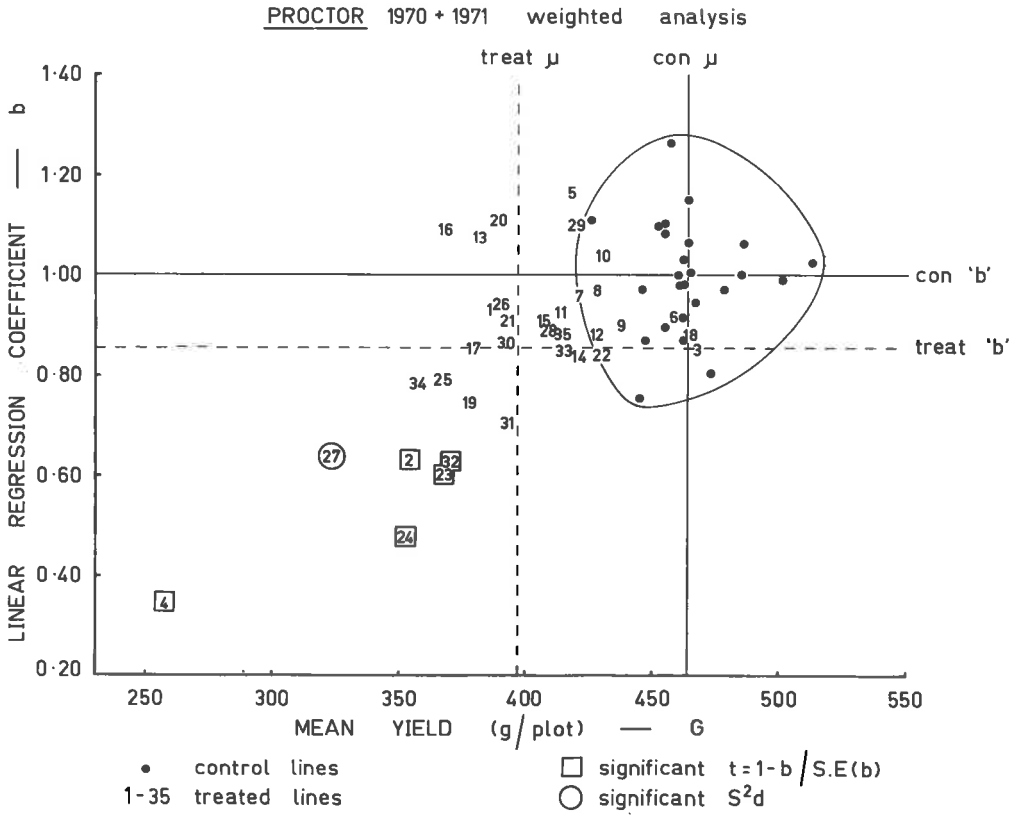
FIGURE 22

Scatter diagrams showing relationship of line mean yield (G), linear regression coefficient (b) and significant deviation mean squares (S^2d) for control and treated lines of PROCTOR, tested over two years (1970 + 1971).

Upper diagram - analysis of unweighted yield data on natural scale.

Lower diagram - analysis of weighted yield data on natural scale.


PROCTOR 1970 + 1971 unweighted analysis
(natural scale)
treat μ
con μ
con 'b'
treat 'b'
LINEAR REGRESSION COEFFICIENT — b
1·40
1·20
1·00
0·80
0·60
0·40
0·20
300
350
400
450
500
550
600


PROCTOR 1970 + 1971 weighted analysis
treat μ
con μ
con 'b'
treat 'b'
LINEAR REGRESSION COEFFICIENT — b
1·40
1·20
1·00
0·80
0·60
0·40
0·20
250
300
350
400
450
500
550
MEAN YIELD (g/plot) — G
• control lines
1-35 treated lines
□ significant t = 1-b / S.E(b)
○ significant S²d

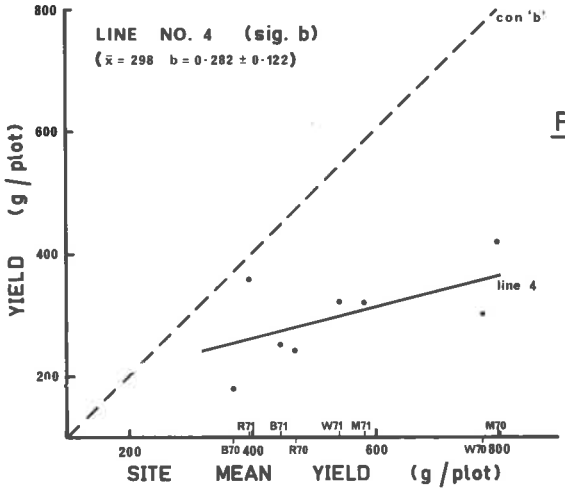
The relation between site mean yield and yield of three representative treated lines with different mean yield and significantly different stability parameters is described in Figure 23. Line No. 4 produced uniformly low-yields at all sites, showing very little or no response to environments as the conditions improved. Another line, No. 24 (yielding less than Treat μ), produced similar or slightly lower yield than the control mean at low-yielding environments and relatively much less at high-yielding environments. Line No. 27 showed significantly large S^2d resulting from large deviations at W_{70} and M_{70} sites. Inspection of individual plot yields at these two sites did not indicate any obvious reason for these deviations as the yield of the two replicates was similar at each of these sites.

E. Selected Lines, 1971

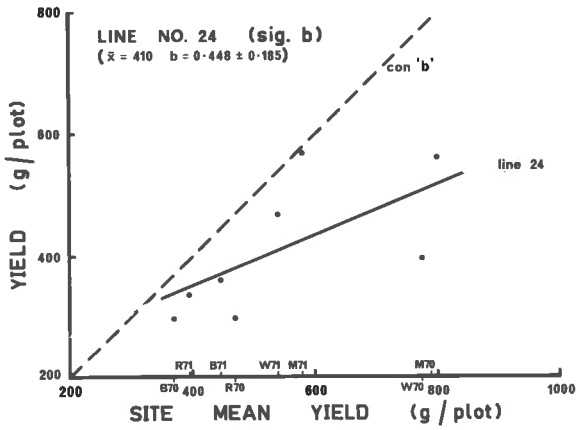
The 15 treated lines of each of Clipper, C.I.3576 and Proctor selected on the basis of high 'W' values and range of mean yields in 1970 (Table 36) were grown in four-replicate trials in 1971 to find whether their yield performance at each site could be correlated with certain plant characters. Thus besides the two replicates included in the main experiments an additional two replicates of each of these lines were sown adjacent to the main experiments to increase the precision of the experiments.

FIGURE 23

The relation between site mean yield and the yield of three treated lines of PROCTOR having stability parameters significantly different from controls, over 8 sites (environments).



PROCTOR 1970 + 1971 unweighted analysis (natural scale)



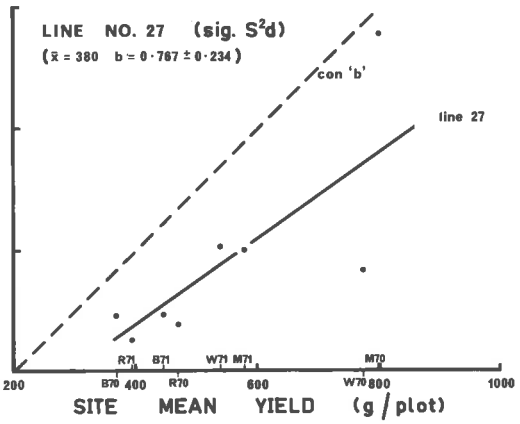


Table 36. Selected treated lines of different cultivars from 1970 field experiments.

Line No.	Mean yield (g/plot)	'W' values ($x10^{-3}$) Unweighted Natural Scale	Selection criteria
(1) CLIPPER			
2	560.3	23.77	large W value
5	472.9	16.37	large W value
7	568.5	16.10	large W value
8	569.4	16.31	large W value
11	496.6	22.92	large W value
17	614.9	9.23	average yield
20	456.5	13.59	low yield
21	635.9	17.33	large W value
23	479.6	24.53	large W value
24	663.3	15.16	large W value, high yield
27	671.9	6.92	high yield
29	617.8	27.53	large W value
31	562.6	11.13	average yield
33	551.8	19.66	large W value
34	496.0	15.70	large W value, low yield
* Line No. 13 of CLIPPER with highest 'W' value (40.77×10^3) was overlooked.			
(2) C.I.3576			
1	536.9	25.63	large W value
4	657.8	46.62	large W value
5	710.9	20.18	large W value
8	602.6	5.56	average yield
10	554.4	29.40	large W value
11	675.6	19.78	large W value
15	647.3	20.39	large W value
17	610.6	16.78	average yield
18	750.8	20.69	large W value, high yield
20	616.8	1.87	average yield
27	371.1	42.17	large W value, low yield
29	455.8	43.57	large W value, low yield
30	761.9	17.93	high yield
33	403.3	20.35	large W value, low yield
34	546.6	31.89	large W value

Table 36 (continued)

Line No.	Mean yield (g/plot)	'W' values ($x10^{-3}$) Unweighted Natural scale	Selection criteria
(3) PROCTOR			
1	515.3	24.76	large W value
4	283.6	32.01	large W value, low yield
6	611.3	6.90	high yield
7	562.4	15.99	average yield
8	555.0	0.81	average yield
10	583.5	27.33	large W value
13	554.9	14.78	average yield
14	533.0	2.65	average yield
15	567.1	20.72	large W value
20	524.8	21.82	large W value
23	446.5	26.49	large W value
24	386.5	29.10	large W value, low yield
27	422.4	60.63	large W value
29	591.9	25.34	large W value, high yield
31	514.9	20.45	large W value

1. Analyses of variance for yield data combined over all sites

To test whether the selected lines of each cultivar exhibited G X E interaction, analyses of variance combined over all sites were carried out by performing both approximate as well as statistically valid analyses. The significance levels of the mean squares attributable to sites, lines and lines X sites interactions are presented in Table 37. Besides significant effects due to sites and lines, the lines X sites interaction mean squares were also significant (5% level) with each cultivar. It should be noted that whereas the whole group of 35 treated lines of Proctor did not show significant interaction when grown in two replicates in 1971 environments (Table 29), the combined effects of selection on the basis of 'W' values and increased replication resulted in a significant interaction.

2. The relationship between plant characters and yield at each site

The main objective of this exercise was to study the relationship of several plant characters with yield among the selected treated lines at each site. Simple correlations between yield and other plant characters were, therefore, computed separately for the selected treated lines (grown in four replicates) and ten randomly selected control lines (grown in two replicates of the main experiments) for comparison, of each of

Table 37. Significance level of mean squares in analyses of variance over sites for selected lines, 1971.

(a) Approximate analyses (Unweighted natural scale)

Source	d.f.	Mean squares for: Clipper (5 sites)	Mean squares for: C.I.3576 (5 sites)	d.f.	Mean squares for: Proctor (4 sites)
Sites	4	***	***	3	***
Reps. within sites	15	**	***	12	***
Lines	14	***	***	14	***
Lines X sites interaction	56	*	*	42	*
Residual	210			168	

(b) Statistically valid analyses (Log_{10} scale)

Source	d.f.	Mean squares for: Clipper (5 sites)	Mean squares for: C.I.3576 (5 sites)	d.f.	Mean squares for: Proctor (4 sites)
Sites	4	***	***	3	***
Reps. within sites	15	***	***	12	***
Lines	14	***	***	14	***
Lines X sites interaction	56	*	*	42	*
Residual	210			168	

Clipper, C.I.3576 and Proctor cultivars at each site during 1971 and these correlations are presented in Tables 38, 39 and 40.

(a) Clipper

There appears to be a negative association between yield and heading date for both treated and control lines at most sites, but these correlations are small and non-significant in most cases (Table 38). Significant positive correlations of yield with height and tiller number were observed among the treated lines at four out of five sites. However, the control lines also show correlations of equal magnitude for these characters at some sites, indicating an environmental rather than a genotypic effect. Because of the unequal number of observations used in the treated and control groups, more emphasis has been given to the magnitude of the correlation coefficients, rather than the significance level, when comparing these two groups.

There is a consistent negative association between the yield and seed sterility of the treated lines, but the correlation was significant at only one site (B_{71}). Furthermore, the control lines showed a negative association of similar magnitude at this particular site, suggesting an environmental effect. Positive associations of small magnitudes between the yield and seed number among the treated lines and variable association of these characters among the control group were observed.

Table 38. Correlation coefficients between yield and other plant characters for CLIPPER at each site for 10 randomly selected control lines and 15 selected treated lines, 1971.

Character	Control lines					Treated lines				
	B_{71}	R_{71}	M_{71}	W_{71}	C_{71}	B_{71}	R_{71}	M_{71}	W_{71}	C_{71}
Yield and:										
Heading date	.3558	-.0684	-.1334	-.2106	-.4890*	-.2813*	.1641	-.1273	-.1938	-.2536*
Height	.6056**	.0353	.5880**	.3936	.4417*	.3694**	-.1129	.7095***	.3788**	.3673**
Tiller No.	-.1844	.1877	.5260*	.2073	.5479*	.5435***	.2709*	.5275***	.4404**	.1819
	n = 20					n = 60				
Yield and:										
Seed sterility	-.3143	.2252	.2193	-.1230	-.1070	-.3760*	-.1342	-.2721	-.0172	-.3391
Seed No./Spike	.5779**	-.2680	.2724	.3428	-.0448	.1133	.0567	.3700*	.2852	.0926
	n = 20					n = 30				

*, **, *** significant at the 5%, 1% and 0.1% levels of probability, respectively.

(b) C.I.3576

Among the treated lines, heading date was negatively correlated with yield at all sites except W_{71} (Table 39). No obvious association of yield with heading date was observed among the controls, except at M_{71}, where a negative but non-significant correlation occurred. A negative association between yield and seed sterility was also found among the treated lines and this was significant at two sites (W_{71}, C_{71}), whereas in the controls a significant negative correlation was found only at one site (C_{71}). The significant negative correlations between yield and seed sterility in both groups at Clinton could have occurred because of the stress environmental conditions which occurred at this site at the time of anthesis. The negative association of yield with both seed sterility and heading date among the treated lines, indicates that the low-yielding lines were usually late in heading and more sterile. With the treated lines, height and seed number showed significant positive correlations with yield at M_{71} and W_{71} sites. A non-significant positive correlation of yield with height was observed at B_{71} and M_{71} sites whereas C_{71} showed a significant negative correlation in the case of control lines.

(c) Proctor

Significant negative correlations between heading date and yield were obtained among the treated lines at all sites except R_{71},

Table 39. Correlation coefficients between yield and other plant characters for C.I.3576 at each site for 10 randomly selected control lines and 15 selected treated lines, 1971.

Character	Control lines					Treated lines				
	B_{71}	R_{71}	M_{71}	W_{71}	C_{71}	B_{71}	R_{71}	M_{71}	W_{71}	C_{71}
Yield and:										
Heading date	-.1013	.0497	-.2802	-.0642	-.0053	-.4343***	-.2507*	-.2391	.1317	-.4068**
Height	.3241	.1230	.3976	.1591	-.6022**	-.0468	.2309	.4071**	.4505***	-.1480
Tiller No.	.3066	.2295	-.0113	.2736	.4438	.0531	.1513	.1743	.1554	.0149
	n = 20					n = 60				
Yield and:										
Seed sterility	.2442	.0198	.1940	.0983	-.4898*	-.3519	-.1256	-.3402	-.5574**	-.4043*
Seed No./Spike	.1279	-.2573	-.1108	-.0659	.0384	.2768	.1011	.4467*	.5152**	-.0702
	n = 20					n = 30				

*, **, *** significant at the 5%, 1% and 0.1% levels of probability, respectively.

Table 40. Correlation coefficients between yield and other plant characters for PROCTOR at each site for 10 randomly selected control lines and 15 selected treated lines, 1971.

Character	Control lines				Treated lines			
	B_{71}	R_{71}	M_{71}	W_{71}	B_{71}	R_{71}	M_{71}	W_{71}
Yield and:								
Heading date	.3278	.2119	.3877	-.0517	-.4077	-.1946	-.4097**	-.4080**
Height	.4747*	.1664	.5931**	.5796**	.4406***	.0684	.6648***	.7735***
Tiller No.	.2535	-.0789	.3634	.8378***	.3288*	.2063	.4669***	.6453***
	n = 20				n = 60			
Yield and:								
Seed sterility	-.2802	-.1202	-.2097	-.5565*	-.1017	-.3284	-.2821	-.4861**
Seed No./Spike	.4749*	-.2217	-.0252	.5620**	.3145	.0159	.4098*	.6006***
	n = 20				n = 30			

*, **, *** significant at the 5%, 1% and 0.1% levels of probability, respectively.

whereas in the case of controls most of these associations were positive but non-significant. Among the treated lines, significant positive correlations of yield with height and tiller number were obtained at all sites except R_{71}. Similar positive correlations between these characters and yield were also found in the control lines at the same sites.

There was a consistent negative association between seed sterility and yield for both treated and control lines, but the correlations were significant only at the W_{71} site. Positive correlations occurred between seed number and yield of treated lines but only two of these correlations were significant. There was no consistent trend of association between these characters among the control group.

It is difficult to interpret these correlations between yield and other characters observed at individual sites for the following reasons:

(i) In some cases, significant correlations were found among both control and treated groups;

(ii) Unequal number of observations for the treated and their respective control groups in each cultivar were used for calculating the correlation coefficients.

However, where the treated lines showed a consistently different pattern of correlations from the controls, this approach gave some

indication of which characters might be associated with the EMS-induced changes in yield of treated lines.

Thus, with treated lines of Clipper, a negative association between the yield and seed sterility was found at most sites, but only one of the correlations was significant. In the case of treated lines of C.I.3576, negative correlations of yield with heading date and seed sterility and positive correlations of the seed number with yield was found at most of the sites. Furthermore, significant negative correlation of yield with heading date was obtained at almost all sites among the treated lines of Proctor.

F. Agronomic characteristics of treated lines having significantly different stability parameters

After detecting treated lines which had significantly different stability parameters in the 1970 + 1971 adaptation studies with Clipper, C.I.3576 and Proctor, an attempt was made to find whether any of these lines differed from the controls with respect to morphological or physiological characters. All available data on other quantitative characters were used, except seed weight. Thus the characters studied included heading date measured on all lines at all sites over two years and plant height measured on all lines at all sites during 1970. Some further limited information was obtained from the measurements (tiller number, seed sterility

and seed number) made on the selected treated and control lines in 1971.

Analyses of variance for these characters were carried out at each site and combined over all sites. Whenever significant line effects occurred, the LSD for difference between the mean of the whole control population and any individual treated line mean was calculated, in order to identify the treated lines showing significant differences from the controls. The results of these analyses for heading date and height for those treated lines which have significantly different stability parameters are given in Tables 41 and 42 respectively. In addition, the other treated lines (with non-significant b and S^2d), which showed the largest deviations from the means of the controls with respect to these characters are included in these tables for comparative purposes.

1. Heading date

As shown in Table 41, highly significant lines mean squares for heading date were observed with all cultivars at all environments except with Clipper at M_{70}.

In interpreting the observed differences between the heading date of individual treated lines and the mean of 25 control lines (Table 41) it is necessary to consider the range of variation in heading date occurring among the individual control lines as well. Inspection of the mean heading date over all environments for

Table 41. Significance levels of lines mean squares in ANOVA for heading date (days) for all lines of CLIPPER, C.I.3576 and PROCTOR and differences of mean values of some treated lines compared with means of respective control populations at each environment and combined over all environments during 1970 and 1971

(1) CLIPPER

Lines	Environments									Over all environments
	B_{70}	R_{70}	M_{70}	W_{70}	B_{71}	R_{71}	M_{71}	W_{71}	C_{71}	
Variance ratios of all 60 lines (25 control + 35 treated)	***	***	NS	***	***	***	***	***	***	***
Mean of 25 control lines	118.9	114.1	111.0	116.5	120.6	112.5	94.9	108.3	95.5	110.3
Treated lines (difference from mean of controls)										
(a) With significant b values										
No. 3	0.6	1.4**	1.0	0.5	0.4	1.0	0.6	0.7	-0.5	0.6
" 4	1.1	0.4	1.0	0	-1.1**	-0.5	1.6**	0.2	0.5	0.3
" 5	7.6**	3.4**	4.0	4.5**	1.9**	2.0**	2.1**	1.7**	1.5**	3.1**
" 6	4.1**	5.4**	4.5	5.0**	4.4**	3.5**	3.6**	3.7**	3.5**	4.1**
" 12	-0.4	-0.6	0.5	0	-0.6	0	0.6	-0.3	-1.5**	0.3
" 20	0.1	0.9	1.0	0.5	0.4	1.0	0.1	-0.3	0.5	0.4
" 24	-2.4*	-0.6	-1.0	-0.5	-1.1**	-2.5**	-0.9	-0.8	1.0	-1.0**
" 34	0.1	1.4**	1.5	0	0.9*	0	-0.4	-0.8	-0.5	0.1
(b) With non-significant b values										
No. 16	-1.4	-1.1*	0	0	-1.4**	-1.0	-1.9**	-1.3*	-1.5**	-1.2**
" 18	4.1**	2.4**	1.0	2.5**	0.9*	2.0**	2.1**	1.2*	1.0	1.9**
" 21	1.1	-2.6**	-0.5	-3.5**	-1.6**	-2.5**	-1.4*	-1.3*	-1.5**	-1.6**
" 30	2.6*	2.4**	2.0	3.0**	2.4**	1.0	2.1**	2.2**	0	1.9**
" 32	8.6**	4.9**	6.0	6.0**	5.4**	5.0**	4.1**	4.7**	3.0**	5.3**
" 33	3.6**	1.9**	1.5	3.0**	1.9**	3.5**	2.6**	2.7**	3.0**	2.6**
" 35	1.6	1.9**	3.0	1.5*	1.4**	2.0**	3.6**	1.7**	1.5**	2.0**
LSD between controls mean and any treated line mean at 5%	2.33	1.03	NS	1.40	0.75	1.52	1.10	1.12	1.04	0.63
LSD between controls mean and any treated line mean at 1%	3.06	1.35	NS	1.84	0.99	2.00	1.44	1.47	1.37	0.83

Table 41 (continued)

(2) C.I.3576

Lines	Environments									Over all environments
	B_{70}	R_{70}	M_{70}	W_{70}	B_{71}	R_{71}	M_{71}	W_{71}	C_{71}	
Variance ratios of all 60 lines (25 control + 35 treated)	***	***	***	***	***	***	***	***	***	***
Mean of 25 control lines	111.9	106.8	103.6	110.8	112.2	106.2	88.3	104.0	87.7	103.5
Treated lines (difference from mean of controls)										
(a) With significant b or S^2d values										
No. 5	1.6	0.7	0.4	0.2	1.8**	0.3	0.7	0.5	0.3	0.7**
" 9	-0.9	0.7	0.4	0.7	-0.2	-0.7	0.2	-1.0*	-0.7	-0.2
" 18	-0.9	0.7	0.4	0.2	-0.2	-0.2	-0.3	-0.5	+0.3	-0.1
" 21	2.6**	1.7**	1.9**	1.2*	2.3**	1.3**	1.7**	2.0**	1.3**	1.8**
" 27	8.1**	6.2**	5.4**	5.2**	6.8**	3.8**	3.2**	3.0**	4.3**	5.1**
" 29	-4.4**	-7.3**	-1.1*	-6.8**	0.3	-2.7**	0.2	-3.0**	-0.7	-2.8**
" 32	5.6**	7.7**	7.4**	6.2**	7.3**	5.3**	5.7**	5.5**	4.8**	6.1**
" 33	5.6**	7.7**	6.4**	6.7**	5.8**	4.3**	4.2**	3.5**	4.3**	5.4**
" 34	1.1	-0.3	0.9	0.7	-1.7**	-0.2	-0.3	-1.0*	-0.2	-0.1
" 35	1.1	0.7	0.4	1.2	-0.2	+0.3	-0.3	0	0.3	0.4*
(b) With non-significant b and S^2d values										
No. 4	2.1*	1.7**	1.9**	2.2**	0.3	0.8	1.2**	1.5**	1.3**	1.4**
" 6	2.1*	2.7**	3.4**	2.2**	2.8**	2.3**	2.7**	3.5**	2.5**	2.7**
" 10	3.1**	2.2**	2.9**	2.2**	0.8	1.3**	0.7	1.5**	0.8	1.7**
" 12	0.6	3.2**	2.4**	1.7**	1.3**	1.3**	0.7	0.5	1.3**	1.4**
" 23	4.1**	5.2**	4.4**	3.7**	4.3**	3.8**	3.7**	3.5**	2.8**	3.9**
" 24	1.9*	-1.8**	-1.1*	-1.3*	-2.2**	-1.2**	-0.8	-2.0**	-0.7	-1.4**
" 31	6.1**	6.2**	4.9**	5.2**	5.3**	4.8**	3.2**	3.5**	3.8**	4.8**
LSD between controls mean and any treated line mean at 5%	1.78	1.05	1.05	1.06	0.96	0.83	0.88	1.00	0.85	0.37
LSD between controls mean and any treated line mean at 1%	2.33	1.37	1.37	1.39	1.25	1.09	1.15	1.31	1.10	0.49

Table 41 (continued)

(3) PROCTOR

Lines	Environments								Over all environments
	B_{70}	R_{70}	M_{70}	W_{70}	B_{71}	R_{71}	M_{71}	W_{71}	
Variance ratios of all 60 lines (25 control + 35 treated)	***	***	***	***	***	***	***	***	***
Mean of 25 control lines	131.1	124.1	122.7	127.7	130.3	121.3	107.7	118.7	123.0
Treated lines (difference from mean of controls)									
(a) With significant b or S^2d values									
No. 2	-2.1*	-0.1	-1.2	-0.2	2.2**	1.2	0.3	0.3	0
" 4	6.4**	3.4**	3.8**	4.3**	3.7**	3.2**	2.3**	2.3**	3.6**
" 19	1.4	-3.1**	-1.2	-7.7**	-0.3	1.2	-0.2	1.2**	-1.2**
" 23	1.4	1.4**	0.8	1.3**	0.2	0.2	0.3	-0.2	0.6**
" 24	2.9**	1.4**	1.3	1.8**	-0.3	-2.3**	-0.2	-0.2	0.5*
" 27	2.9**	3.4**	2.3**	3.8**	4.2**	4.7**	2.8**	3.3**	3.4**
" 32	-0.1	-0.1	-0.2	-0.2	2.2**	-0.3	1.2*	-0.2	0
(b) With non-significant b and S^2d values									
No. 3	-3.1**	-1.6**	-0.7	-2.2**	-0.3	-1.8**	-0.7	-1.7**	-1.6**
" 12	-2.1*	-2.6**	-3.2**	-2.2**	-0.8	-1.8**	-1.7**	-0.2	-1.9**
" 17	3.4**	1.9**	2.3**	2.8**	1.2	2.2**	1.3*	1.3**	2.0**
" 20	6.4**	2.9**	2.8**	2.3**	1.7**	0.7	1.8**	1.3**	2.2**
" 22	4.4**	1.9**	2.3**	2.3**	1.2	2.2**	1.3*	1.3**	2.0**
" 25	6.9*	1.9**	2.3**	2.8**	0.2	0.2	2.8**	-0.2	2.0**
" 28	1.9*	1.9**	2.8**	2.3**	2.7**	2.7**	1.3*	1.3**	2.0**
" 30	0.4	1.9**	2.3**	1.8**	2.2**	1.7**	0.3	1.3**	1.5**
" 34	5.9**	1.9**	1.3	1.8**	1.7**	1.2	1.3*	1.3**	2.0**
LSD between controls mean and any treated line mean at 5%	1.86	1.06	1.36	0.83	1.21	1.35	1.08	0.91	0.44
LSD between controls mean and any treated line mean at 1%	2.43	1.38	1.77	1.09	1.58	1.76	1.41	1.19	0.58

individual control lines revealed the following range of differences from the mean of 25 controls.

Clipper - one early line (-1.5 days) and one late line (2.0 days).

Proctor - one early line (-1.2 days) and one late line (1.8 days).

C.I.3576 - the control lines were highly uniform in heading date with a range from -0.6 to +0.8 days.

It is assumed that any treated lines which have a heading date greatly exceeding the limits of variation shown within controls possess mutational changes for this character.

On this basis, among the treated lines with significant b or S^2d values, line Nos. 5 and 6 of Clipper, Nos. 21, 27, 32 and 33 of C.I.3576 and Nos. 4 and 27 of Proctor have all been clearly altered towards lateness (Table 41). In contrast, only one of these treated lines (No. 29 of C.I.3576) is much earlier than the controls. On the other hand, it should be noted that the heading date of several of the treated lines with significant b and S^2d in each cultivar has not been altered by the mutation treatment.

Many of the other treated lines (with non-significant b and S^2d values) were significantly later than the mean of respective controls at almost all environments (Nos. 32 and 33 of Clipper, Nos. 23 and 31 of C.I.3576), and some others were consistently earlier over these environments (No. 24 of C.I.3576 and No. 12 of

Proctor). Although none of the other treated lines of Proctor are much later than the most extreme control lines (Table 41), it is likely that at least some of the lines exceeding the control in lateness possess a mutational change.

2. Height

Significant lines mean squares for height were found with all cultivars at all sites except with Clipper at R_{70} and with Proctor at M_{70} as indicated in Table 42.

The variation among the individual controls is exhibited in Figure 14. Inspection of the mean height over all sites for individual control lines gave the following range of differences from the mean of 25 controls.

Clipper - two short lines (-2.8 cm), one tall line (2.4 cm) and one extremely tall line (11.9 cm).

C.I.3576 - one short line (-2.1 cm) and one tall line (2.1 cm).

Proctor - one short line (-2.1 cm) and one tall line (2.0 cm).

Inspection of Figure 14 and Table 42 shows that among the treated lines with significant b or S^2d values, line Nos. 4 and 12 of Clipper, Nos. 21 and 27 of C.I.3576, and Nos. 4 and 27 of Proctor are significantly shorter than the controls at most of the sites and over all sites. Similarly lines No. 32 and 33 of C.I.3576 are consistently taller than the controls. Line No. 23 of Proctor was taller than the controls at most sites but

Table 42. Significance levels of lines mean squares in ANOVA for height (cm) for all lines of CLIPPER, C.I.3576 and PROCTOR and differences of mean values of some treated lines compared with means of respective control populations at each site and combined over all sites during 1970.

(1) CLIPPER

Lines		Sites				Over all sites
		B_{70}	R_{70}	M_{70}	W_{70}	
Variance ratios of all 60 lines (25 control + 35 treated)		**	NS	***	***	***
Mean of 25 control lines		56.7	89.5	92.2	98.3	84.2
Treated lines (differences from mean of controls)						
(a) With significant b values	No. 3	-3.2	0.5	-1.7	-1.3	-1.5
	" 4	-0.7	-10.0	-8.2**	-15.8**	-8.7**
	" 5	1.8	-3.0	-0.7	-0.8	-0.7
	" 6	-2.2	3.5	-4.7*	-0.3	-2.7*
	" 12	-4.2*	-4.0	-8.7**	1.7	-6.3**
	" 20	-1.2	-3.0	-2.7	-5.3**	-3.1**
	" 24	-1.7	-0.5	0.3	-0.8	-0.7
	" 34	-0.2	-2.5	-3.7	-2.8	-2.3*
(b) With non-significant b values	No. 23	7.8**	7.0	0.8	0.7	4.0**
	" 27	-3.7	-7.5	-8.2**	1.7	-4.5**
	" 30	-1.7	-1.0	-6.7**	0.2	-2.3*
	" 32	9.8**	-1.5	4.3*	10.7**	5.8**
	" 33	-2.2	-2.5	-3.2	-4.8*	-3.2**
	" 35	-1.7	-5.0	-4.2*	-5.3**	-4.1**
LSD between controls mean and any treated line mean	at 5%	3.82	NS	4.03	3.82	2.26
	at 1%	5.02	NS	5.30	5.02	2.97

Table 42 (continued)

(2) C.I.3576

Lines		Sites				Over all sites
		B_{70}	R_{70}	M_{70}	W_{70}	
Variance ratios of all 60 lines (25 control + 35 treated)		***	*	***	***	***
Mean of 25 control lines		51.4	95.9	95.0	96.1	84.6
Treated lines (difference from mean of controls)						
(a) With significant b or S^2d values	No. 5	-2.9	-1.4	0.5	-2.6	-1.6
	" 9	2.1	2.1	-1.0	1.4	1.1
	" 18	-3.4*	-2.4	-1.5	-2.1	-2.4*
	" 21	-2.9	-5.9*	-7.0**	-12.1**	-7.0**
	" 27	2.1	-10.9*	-13.5**	-10.1**	-8.1**
	" 29	5.6**	1.1	-6.0**	-4.6*	-1.0
	" 32	10.6**	4.1	8.0**	11.4**	8.5**
	" 33	11.1**	4.6	8.5**	14.4**	9.6**
	" 34	-2.9	-1.4	-1.5	-0.6	-1.6
	" 35	-0.9	1.6	3.5	-3.6	0.1
(b) With non-significant b and S^2d values	No. 1	-2.4	-6.9*	-2.5	-2.6	-3.6**
	" 6	0.6	3.1	-0.5	-12.1**	-2.2*
	" 8	-1.4	-1.9	-2.5	-4.1*	-2.5*
	" 10	-1.4	-3.4	-7.0**	-5.1**	-4.2**
	" 17	-0.4	-2.4	-7.0**	-5.1**	-3.7**
	" 23	9.1**	7.6*	10.0**	9.9**	9.2**
	" 31	1.1	-2.9	-5.5*	-4.6*	-3.0**
LSD between controls mean and any treated line mean	at 5%	3.39	4.75	4.39	3.87	2.07
	at 1%	4.46		5.77	5.09	2.70

Table 42 (continued)

(3) PROCTOR

Lines		Sites				Over all sites
		B_{70}	R_{70}	M_{70}	W_{70}	
Variance ratios of all 60 lines (25 control + 35 treated)		**	**	NS	*	***
Mean of 25 control lines		57.7	87.6	83.4	94.1	80.7
Treated lines (differences from mean of controls)						
(a) With significant b or S^2d values	No. 2	0.3	-2.6	-3.9	-4.6*	-2.7*
	" 4	4.8*	-6.6**	-1.9	-13.6*	-4.3**
	" 19	6.8**	3.9	3.6	-4.6*	2.4*
	" 23	9.3**	1.4	4.1	-0.1	3.7**
	" 24	5.3**	-3.1	-2.9	-6.6*	-1.8
	" 27	-2.2	-13.1**	-1.9	-7.1*	-6.1**
	" 32	5.3**	-2.1	1.1	-3.1	0.3
(b) With non-significant b and S^2d values	No. 7	-1.7	-3.1	-2.4	-4.1	-2.8*
	" 9	-0.2	-2.6	-3.9	-3.6	-2.6*
	" 12	1.3	0.4	7.6	0.4	2.4*
	" 14	-1.2	-3.6	-4.9	-0.6	-2.6*
	" 17	5.3**	1.9	0.6	1.9	2.4*
	" 22	5.3**	1.4	5.6	1.9	3.5**
LSD between controls mean and any treated line mean	at 5%	3.67	4.38	NS	4.19	2.28
	at 1%	4.82	5.76	NS		3.00

especially at B_{70}. Lines No. 29 of C.I.3576 and No. 24 of Proctor were very variable in height, being significantly taller at some sites and significantly shorter at the others.

As with heading date, other treated lines (with non-significant b and S^2d values) also showed large differences from the mean of controls with respect to height. Thus lines Nos. 27 and 35 of Clipper, Nos. 10, 17 and 31 of C.I.3576 are generally shorter than the controls whereas lines No. 32 of Clipper, No. 23 of C.I.3576 and No. 22 of Proctor are taller than the controls at most of the sites.

3. Other characters

For seed sterility, tiller number and seed number, analyses of variance were carried out at each site and over all sites on ten selected control lines and only those particular treated lines, which had significant b or S^2d values in the 1970 + 1971 analysis and which were included in the 15 selected lines grown in 1971.

(a) Seed sterility

The data for seed sterility (%) were transformed into arcsin ($\sqrt{\text{seed sterility}/100}$) values and ANOVA were carried out. Whereas line mean squares were significant at all sites for C.I.3576 they were not significant with Clipper and Proctor except at M_{71} and W_{71} sites respectively (Table 43).

Table 43. Significance levels of lines mean squares in ANOVA for seed sterility (arcsin $\sqrt{\text{seed sterility}/100}$) for some lines of CLIPPER, C.I.3576 and PROCTOR and differences of mean values of some selected treated lines (with significant b and S^2d values) compared with means of respective selected control populations at each site and combined over all sites during 1971.

(1) CLIPPER

Lines		Sites					Over all sites
		B_{71}	R_{71}	M_{71}	W_{71}	C_{71}	
Variance ratios of 15 lines (10 control + 5 treated)		NS	NS	*	NS	NS	*
Mean of 10 control lines		.0261	.0177	.0198	.0123	.0298	.0212
Treated lines	No. 5	.0112	-.0041	.0050*	.0067	.0036	.0044*
(difference from control means)	" 20	.0102	.0031	.0020	.0009	-.0060	.0020
(with significant b value and	" 24	.0010	-.0002	-.0038	.0024	.0006	-.0001
included in selected lines)	" 33/	.0001	.0005	.0020	.0062	.0001	.0017
	" 34	.0078	.0047	.0053*	.0007	-.0003	.0036*
LSD at 5% between controls mean and any treated line mean		NS	NS	.0044	NS	NS	.0027

/ Line No. 33 had significant b value in 1971 environments.

Table 43 (continued)

(2) C.I.3576

Lines		Sites					Over all sites
		B_{71}	R_{71}	M_{71}	W_{71}	C_{71}	
Variance ratios of 16 lines (10 controls + 6 treated)		**	**	***	***	*	***
Mean of 10 control lines		.0128	.0193	.0162	.0143	.0208	.0167
Treated lines	No. 5	.0072	.0014	.0029	.0016	-.0043	.0017
(difference from control mean)	" 18	.0014	-.0021	.0050	.0042	.0130*	.0043**
(with significant b or S^2d values	" 27	.0078*	-.0015	-.0019	.0007	-.0025	.0005
and included in selected lines)	" 29	.0128*	.0134*	.0077*	.0217*	.0081	.0127**
	" 33	.0252*	.0184*	.0315*	.0180*	.0186	.0223**
	" 34	.0010	-.0032	-.0025	.0013	-.0007	-.0008
LSD between controls mean and any treated line mean	at 5%	.0073	.0062	.0074	.0058	.0089	.0030
	at 1%	.0096	.0081	.0097	.0076	-	.0039
(3) PROCTOR							
Variance ratios of 14 lines (10 control and 4 treated)		NS	NS	NS	**		*
Mean of 10 control lines		.0384	.0250	.0252	.0341		.0307
Treated lines	No. 4	.0039	.0017	.0054	.0100*		.0052*
(difference from control mean)	" 23	.0025	.0012	.0009	.0115*		.0040*
(with significant b or S^2d values	" 24	.0075	.0023	.0035	.0099		.0040*
and included in selected lines)	" 27	.0062	.0113	.0030	-.0079*		.0000
LSD at 5% level between controls mean and any treated line mean		NS	NS	NS	.0065		.0034

Line Nos. 23 and 33 of C.I.3576 exhibited a marked increase in seed sterility at most sites and over all sites. Some treated lines of Clipper and Proctor also had overall significant differences from controls but these effects were much smaller than those above.

(b) Seed number per spike

A non-significant lines mean squares were obtained for lines of Clipper, C.I.3576 and Proctor at each site. By combining data over all sites, significant line effects (at 5% level) were obtained only for C.I.3576 and Proctor lines. The mean seed number of controls combined over all sites and differences of mean values of some significant treated lines of C.I.3576 and Proctor are given in Table 44.

The treated lines Nos. 29 and 33 of C.I.3576 and No. 4 of Proctor had significantly lower seed number than the corresponding control means. It is interesting to note that all of these lines also had significantly higher seed sterility over all sites (Table 43). Hence, significantly lower seed number in these lines is not unexpected.

(c) Tiller number

Non-significant line effects for lines of each cultivar were observed when data were analyzed for individual sites. Significant line effects (5% level) were found only for C.I.3576 by combining data over all sites. The treated line No. 29 of C.I.3576 had

Table 44. The mean seed number of controls over all sites and difference of overall mean values of some treated lines from respective control means with C.I.3576 and PROCTOR, 1971.

C.I.3576		PROCTOR	
Lines	Mean values over all sites	Lines	Mean value over all sites
Mean of 10 control lines	20.62	Mean of 10 control lines	25.38
Treated lines (difference from control mean)		Treated lines (difference from control mean)	
No. 5	-0.33	No. 4	-3.68*
18	-0.53	23	-1.52
27	0.22	24	-1.11
29	-1.62*	27	0.22
33	-2.20*		
34	0.72		

significantly reduced tiller number (24.6) compared with the control mean (30.0).

4. Overall features

The overall features, including yield, of individual treated lines showing significant and large differences from the controls with respect to stability parameters or other agronomic characters are summarized in Table 45. Only those treated lines which exceed the range of values exhibited by the individual control lines with respect to b, S^2d, heading date or height have been included in the table. Thus for heading date and height emphasis has been given to treated lines which differ from the control means by more than 2 days in heading date or 3 cm in height.

Twelve, sixteen and thirteen of the 35 treated lines of Clipper, C.I.3576 and Proctor, respectively, differ from the controls by the requisite amount for at least one character, and as shown by the yield rank column in Table 45 most of these differences occur in the low-yielding lines. For example, the lowest-yielding lines of each cultivar (rank 1-6) have significantly reduced b (or large S^2d), with two exceptions, and significant differences from the controls in one or more of the other characters measured. The best examples are lines No. 29 and 33 of C.I.3576 and No. 4 of Proctor which are altered in 4 of the 5 characters measured. Obviously

Table 45. Mean yield and yield ranking of treated lines having significant differences from controls mean and exceeding the range shown by individual control lines with respect to stability parameters (b or S^2d) and other plant characters.

Treated line	Difference from mean of controls							
	(25 controls)					(10 controls)		
	Mean Yield		b (S.E.) (1970+1971) Unweighted analysis	Heading date (days) (1970+1971)	Height (cm) (1970)	Seed sterility (arcsin) (1971)	Tiller No. (1971)	Seed No. (1971)
	(g/plot) (1970+1971)	Rank over 35 treated lines						
(1) CLIPPER								
No. 4	-145.3	1	-.336* (.116)	NS	-8.7**			
" 5	-113.7	2	-.391** (.088)	3.1**	NS	.0044* (2.1%)	NS	NS
" 12	-109.1	3	-.332** (.091)	NS	-6.3**			
" 35	-101.6	4	-.192 (.091)	2.0**	-4.1**			
" 34	-96.1	5	-.286** (.078)	NS	[-2.3*] /	.0036* (1.7%)	NS	NS
" 6	-95.3	6	-.269* (.090)	4.1**	[-2.7*]			
" 23	-85.6	10	-.258 (.137)	NS	4.0**			
" 20	-74.4	11	-.385* (.157)	NS	-3.1**	NS	NS	NS
" 3	-53.3	12	-.250** (.052)	NS	NS			
" 33	-35.3	17	+.011 (.125)	2.6**	-3.2**			
" 32	-30.8	19	-.024 (.086)	5.3**	5.8**			
" 27	15.1	35	+.177 (.121)	NS	-4.5**			
(2) C.I.3576								
No. 27	-213.7	1	-.657** (.124)	5.1**	-8.1**	NS	NS	NS
" 29	-206.8	2	-.380* (.154)	-2.8**	NS	.0127** (5.9%)	-5.4*	-1.6*
" 33	-200.3	3	-.515** (.070)	5.4**	9.6**	.0223** (12.4%)	NS	-2.2*
" 31	-175.8	4	-.145 (.093)	4.8**	-3.0**			
" 1	-118.8	5	-.181 (.144)	[0.8**]	-3.6**			
" 32	-109.9	6	-.311* (.121)	6.1**	8.5**			
" 23	-105.2	8	-.092 (.109)	3.9**	9.2**			
" 6	-79.0	9	-.200 (.094)	2.7**	[-2.2*]			
" 10	-78.1	10	-.290 (.140)	[1.7**]	-4.2**			
" 9	-74.5	12	-.389* (.145)	NS	NS			
" 17	-65.7	16	+.018 (.119)	NS	-3.7**			
" 34	-60.5	18	-.198 (.240)*	NS	NS	NS	NS	NS
" 35	-45.2	20	-.294* (.094)	[0.4*]	NS			
" 5	-6.0	29	+.284* (.100)	[0.7**]	NS	NS	NS	NS
" 21	21.4	31	+.295*(.091)	[1.8**]	-7.0**			
" 18	30.5	33	+.286* (.112)	NS	[-2.4*]	.0043** (1.6%)	NS	NS

/ The values in parentheses do not exceed the controls by requisite amount (see Text).

Table 45 (continued)

Treated line	Difference from mean of controls							
	(25 controls)					(10 controls)		
	Mean Yield		b (S.E.) (1970+1971) Unweighted analysis	Heading date (days) (1970+1971)	Height (cm) (1970)	Seed sterility (arcsin) (1971)	Tiller No. (1971)	Seed No. (1971)
	(g/plot) (1970+1971)	Rank over 35 treated lines						
(3) PROCTOR								
No. 4	-249.2	1	-.718** (.122)	3.6**	-4.3**	.0052* (3.1%)	NS	-3.7*
" 27	-167.3	2	-.233 (.234)*	3.4**	-6.1**	NS	NS	NS
" 2	-145.7	3	-.290** (.077)	NS	[-2.7*]			
" 24	-137.3	4	-.552* (.185)	[0.5*]	NS	.0040* (2.6%)	NS	NS
" 32	-131.5	5	-.303≠ (.136)	NS	NS			
" 23	-122.8	6	-.139≠ (.163)	[0.6**]	3.7**	.0040* (2.6%)	NS	NS
" 34	-110.8	7	-.296 (.131)	2.0**	NS			
" 25	-101.3	8	-.251 (.127)	2.0**	NS			
" 19	-96.9	9	-.332* (.093)	[1.2**]	[2.4*]			
" 17	-72.9	16	-.192 (.101)	2.0**	NS			
" 20	-61.1	20	+.089 (.116)	2.2**	NS			
" 28	-57.6	21	-.186 (.112)	2.0**	NS			
" 22	-50.6	25	-.164 (.132)	2.0**	3.5**			

≠ Significant b on weighted analysis only (5% level).

these lines possess a deleterious mutation which has affected some important physiological process, resulting in reduced yield and pleiotropic effects on other characters. It is possible that many of the other low-yielding lines represent similar mutations giving reduced vitality and associated changes in heading date or height or both. It should be noted, however, that line No. 32 of Proctor (Table 45) although low-yielding, does not possess a significant change in heading date or height.

Another line of interest is No. 31 of C.I.3576, which is very low-yielding with associated changes in heading date and height, but its regression coefficient (b) is not much lower than that of the control (Table 45, Figure 20). Thus this line seems to represent an exception to the association between low yield and low b observed with other lines.

In addition to the effects associated with the low-yielding lines, a few of the average-yielding lines also have changed characters relative to the controls. For example, line No. 32 of Clipper is very late and tall yet has yield similar to the mean of the controls thus adding weight to the argument that late heading and tallness are not themselves responsible for low yield.

Line No. 21 of C.I.3576, with high yield, is of special interest because it is the only line of any cultivar to have a significantly increased b value ($b > 1.0$) on both weighted and

unweighted analyses. Since it is also significantly shorter and somewhat later in heading than any control line of C.I.3576, it is likely that its altered performance across environments is due to a mutational change induced by the EMS treatment.

DISCUSSION

Before interpreting the results of the current study it is necessary to review the origin and nature of the experimental material used.

The initial EMS treatments were applied to supposedly homogeneous seed samples of 5 barley cultivars having contrasting yield and adaptation parameters. However it was found later that significant heterogeneity existed in Clipper controls with respect to yield (due mainly to line Nos. 21C and 24C, which were the highest yielding of the controls across all environments), height (line No. 12C, was 12 cm taller than the control mean), and heading date (line No. 23C was 2 days later than the control mean). In addition, there is some evidence of heterogeneity for yield in the control lines of C.I.3576 and Ketch, since in each case significant line mean squares (5% level) were obtained in the weighted analysis of variance. It has been argued earlier that this heterogeneity in C.I.3576 could be due to a chance deviation, but even if real in both cultivars, the variability is not very great since the corresponding analyses of unweighted data did not reveal any heterogeneity. On the other hand Proctor and Prior controls appeared to be homogeneous with respect to all of the characters measured.

The occurrence of heterogeneity in control populations is not uncommon (e.g. see Gaul et al., 1969 and Oka et al., 1958), but where it is present it reduces the precision of measurements on the effects of the mutagen treatment. It is suggested that where accurate estimates of these effects are required, as in the present study, progeny from single plants should be multiplied to provide a homogeneous source of seed.

It is well known that EMS treatment of barley results in considerable seed sterility in the M_1 spikes thus increasing the chance of outcrossing in this generation. In the present work precautions were taken to ensure self-fertilization of M_1 spikes by covering them with glacine bags. Furthermore, the risk of outcrossing in the M_2 generation was minimized by growing M_2 plants in spaced pots in the glasshouse. Thus it is unlikely that any of the increased variability observed in the treated material arose from cross-pollination in M_1 or M_2 generations.

The primary aim of the present study was to measure the effect of micro-mutations on yield performance of EMS treated lines of barley across environments. Hence all obvious deleterious mutants such as dwarfs and steriles were discarded in the M_2 generation and random selections were made from only the normal-appearing M_2 plants grown in pots. Additional selection against deleterious mutations occurred in the M_3 rows where all lines which

did not produce the minimum amount of seed (200 gm) required for field experiments were automatically excluded. Despite these selection procedures, some of the treated lines exhibited discrete differences from the controls with respect to heading date, height and seed weight when grown in field experiments in the M_4 generation.

A major limitation of the current study is the small number of treated lines of each cultivar included in the field experiments. It is well known that there is a low probability of inducing positive mutation for yield following mutagenic treatment, and consequently it is necessary to test very large numbers of treated lines to detect such effects. For example, Gaul and Ulonska (1967) tested the yield performance of 500 M_2-derived treated lines from each of the varieties Volla and Wisa at two sites in the M_4 generation. However they used single-row plots varying from 2.4 m to 3 m in length in their experiments. By using such small plots it is possible to test a much larger number of entries than when large plots are used, but the environmental component of variation is expected to be larger with small plots.

For measuring yield in adaptation experiments large-sized plots are required to obtain a more accurate determination of yield. In the present study, M_2-derived lines were planted in

the 4-row plots used by plant breeders at the Waite Institute and this severely restricted the number of lines that could be tested. To increase the number of treated lines investigated, it was decided to include fewer control lines than treated lines of each cultivar and this resulted in a slight bias towards the treated lines whenever comparisons were made between the range of variability present within treated and control populations.

Other aspects of the experimental approach used are considered in the appropriate parts of the Discussion.

A. The effect of EMS on change in mean and induction of genetic variability

In common with other workers, it was found that EMS treatment of barley cultivars caused a reduction in mean yield and a large increase in genotypic variance for yield. However, unlike all previous workers except Gaul and his colleagues, sub-samples of M_4 and M_5 seed of treated families were tested at several sites, making it possible to assess the effect of different environments and generations on the mean and genotypic variance of the treated populations.

The mean yields (% of controls) of treated lines of each cultivar over sites and generations are given in Table 46. The percentage yield of treated lines of a given cultivar showed

Table 46. Mean yield of treated lines (expressed as percent of respective controls) of different cultivars in M_4 and M_5 generations at individual sites

Rank of site means (mear yield of controls)	Clipper		C.I.3576		Proctor		Ketch	Prior	Average
	M_4	M_5	M_4	M_5	M_4	M_5	M_4	M_4	
1 (High)	93.3	91.0	89.8	87.1	88.6	87.1	95.9	82.1	89.4
2	90.4	93.2	91.4	90.2	83.6	87.3	93.8	88.4	89.8
3	88.1	95.9	93.2	87.2	83.2	85.7	87.5	94.4	89.4
4	88.4	89.2	82.0	93.3	85.6	91.1	94.3	89.3	89.2
5 (Low)	-	94.2	-	88.1	-	-	-	-	91.2
Average	90.1	92.7	89.1	89.2	85.3	87.8	92.9	88.6	

variation between sites within each generation but there was no consistent change with respect to high-yielding and low-yielding sites. However, when M_4 seed was transferred to the M_5 generation there was evidence of some "self-improvement" in two of the three cultivars, as reported by Gaul et al. (1969), but nevertheless the degree of yield improvement was small (2%).

In the M_4 generation, the treated lines showed a significant increase of genotypic variance over the controls at each site and, with few exceptions, the magnitude of the induced genotypic variance was smaller at low-yielding environments and larger at high-yielding environments. This pattern is similar to that found by Johnson and Frey (1967) and Vela-Cardenas and Frey (1972), in their studies of oat cultivars and hybrid-derived progenies, respectively, in stress and non-stress environments.

The heritability estimate, which measures the genetic effects of a character in a given environment and can be used to predict gains from selection, was increased among the treated material at each site. No definite pattern of change in heritability values was observed across environments (Table 12), since the increase in genotypic variance at high-yielding sites was nullified by a corresponding increase in phenotypic variance at these sites. Hence it was not possible to specify any common type of environment for maximizing selection for yield with all

cultivars. This is in contrast to the findings of Frey (1964) and Johnson and Frey (1967) where they concluded that a high-productivity environment was the best for maximizing heritability for grain yield in oats. On the other hand, Gotoh and Osanai (1959a, b) concluded that low-fertility and low-density conditions were the most efficient for selecting high-yielding wheat genotypes.

In the M_5 generation, the magnitude of induced genotypic variance for yield data combined over all sites was generally less than that observed in the M_4 generation. However, the heritability values for the treated lines were similar in both generations suggesting that considerable variability remained in the M_5 generation and that the reduction in induced genotypic variance observed in M_5 was due to the low site mean yields obtained in 1971.

Although all cultivars were given exactly the same EMS treatment, they exhibited different responses with respect to several criteria. The maximum reduction in mean in M_4 generation occurred among the treated lines of Proctor, followed in order by those of Prior, C.I.3576, Clipper and Ketch (Table 46). These results are closely paralleled by the response with respect to M_2 chlorophyll mutation frequency and M_1 seed sterility except in these cases Clipper was less responsive than Ketch (Tables 8

and 9). On the other hand, the magnitude of induced genotypic variance in M_4 did not follow the same trend except that the least amount occurred in Ketch (Tables 15-19). Gaul (1965) has observed that M_1 survival, chlorophyll mutation frequency, reduction of yield mean and increased genotypic variance are closely correlated phenomena and he has used these joint responses to gauge the effectiveness of the mutagen treatment. Therefore, it can be concluded that in the present experiment the EMS treatment was most effective with Proctor and Prior and least effective with Ketch and Clipper. The reasons for these differences are not known but it is possible that the cultivars differ in their seed coat permeability or in the physiological state of the embryo.

The other characters studied, namely heading date, height and seed weight all showed an increase in genotypic variances among the treated populations in M_4 generation except for height of Clipper, where genotypic variance of the control lines was much inflated by the presence of one tall line (No. 12C).

The mean heading date of treated lines in all cultivars was shifted towards lateness. This delay in heading has often been observed in cereals after irradiation and EMS treatments (Abrams and Frey, 1964; Krull and Frey, 1961; Gaul et al., 1966). In the present study, the shift of mean heading date towards

lateness does not fit Brock's (1965) hypothesis since these shifts occurred in EMS treated lines of all 3 cultivars including early, medium-late and late types. On the other hand, it provides support for the hypothesis of Gaul and Aastveit (1965) which states that the change in mean values of quantitative characters occurs in the direction associated with reduced vitality independent of the genotype used. In particular, many of the treated lines of Proctor (which is very late in heading), were 2 days later than the mean of controls and each of these lines had low yield, indicative of reduced vitality.

The mean values for plant height and seed weight in the treated populations were not significantly altered from that of controls except with Prior, where seed weight was significantly reduced. The non-significant shifts in mean values of these characters is in agreement with the findings of Oka et al. (1958) in rice and Rawlings et al. (1958) in soybeans. In the present study, mutations for plant height occurred in both plus and minus directions resulting in no significant shift in the mean value, with all cultivars except Prior. With Prior (the tallest cultivar studied) the treated lines were shifted only towards shortness but the reduction in the mean height was not significant (Fig. 14). The pattern of seed weight changes was similar to that observed for height for all cultivars except Clipper and Prior. The

changes in these two cultivars were towards reduced seed weight, particularly with Prior where the shift in mean was significant and many treated lines had much reduced seed weight. No obvious reason could be found for this different behaviour of Prior.

B. The influence of induced mutation on genotype X environment interaction and adaptation of yield

The influence of induced mutation on adaptation characteristics of different barley cultivars was determined by measuring the yield performance of mutagen-derived populations and their controls across a range of environments.

To obtain meaningful results from such studies it is essential to cover a wide range of test environments. The main environmental factor influencing cereal yields in South Australia is moisture supply (rainfall plus soil moisture), particularly in spring when anthesis occurs and temperatures are rising. Moisture stress in this period can lead to reduced seed setting and in extreme cases total failure of the crop may occur. Consequently the sites used in the present study were selected from different regions of the barley growing areas of South Australia, covering a range of soil types and average annual rainfall incidence.

Spring rainfall was adequate at all sites in 1970 and 1971 and none of the sites suffered moisture stress at the critical flowering period. Nevertheless, there was some association

between site mean yields and the amount of effective rainfall in 1970 and 1971. However, there was no such association between years since the amount of effective rainfall in 1971 was higher than that in 1970 yet the yields were generally lower in 1971. The sites used in 1970 for testing the M_2-derived lines in M_4 generation provided a much wider range of environments than the equivalent tests with the M_5 generation in 1971. The combined results over both generations gave a reasonable range of environments, except there was some clustering of sites in the low-yielding range, especially with C.I.3576 (see Fig. 21).

Individual trials in which disease, mice damage, etc., were the major environmental factors affecting yield, were excluded from the analyses. Similarly, Johnson et al. (1968) excluded those trials from the adaptation analysis in which stem rust, insects, birds, hail or winter kill were the major effects of environment on yield. They argued that each of these factors has the potential for dominating or masking all other factors of the environment. To have included trials involving these major effects would have obscured the measurement of the environment as the end product of many factors.

Combined analyses of variance over all sites were required to investigate the performance of treated as well as respective control lines of each cultivar. As pointed out earlier, the

combined analysis of variance is valid only when the experimental error variance between sites is homogeneous but the error variances were found to be heterogeneous in the present study (Tables 14, 26, 30). Such heterogeneity of error occurs commonly in field experiments and even in small trials with few entries (Immer et al., 1934; Salmon, 1951). This heterogeneity of error has been ascribed to soil heterogeneity and differences between seasons.

Various approaches have been suggested to reduce or eliminate heterogeneity of error. For example, Yates (1936) suggested that a "pseudo-factorial" design could be used to reduce the effects of soil heterogeneity, but this design has not been used widely because of its complexity. Other suggestions include using a weighted analysis (Yates and Cochran, 1938) or transformations of data (Bartlett, 1947). Finlay and Wilkinson (1963) found that a log transformation of data was effective in eliminating heterogeneity of error in their experiments, but such a transformation was not successful in the present study nor in some other analyses (Lawrence, 1970; Fripp and Caten, 1971). Hence the weighting procedure suggested by Yates and Cochran (1938) and used by Lawrence (1970) to analyze yield data of barley varieties, was employed in the present study.

These combined analyses of variance over sites were performed on both unweighted (natural scale) and weighted data.

Herein, emphasis has been given to the results of the weighted analysis where it is the statistically valid procedure. However, since many other workers have employed an unweighted analysis (natural scale) in their studies of adaptation and the results of such an analysis give a measure of actual biological response in the field, the unweighted analysis has also been presented for comparative purposes.

The control lines of each cultivar did not exhibit G X E interaction when the performance was examined over sites within individual years or in the combined analysis over two years. Thus for each cultivar, all control lines behaved consistently across environments and this made it simpler to interpret the effects observed with the treated lines. The treated lines of each cultivar generally showed significant G X E interaction when tested in M_4 and M_5 generations and in combined analyses over both generations. The only exception to this pattern occurred with Ketch in M_4 generation where the induced genotypic variance was low and with Proctor in M_5 when the range of environments sampled was small. It can be concluded therefore that as a result of mutagen-induced genetic variability, the treated lines of each cultivar show a heterogeneity of response across environments.

The main interest in the present study was to determine the nature of the G X E interaction present in the mutagen-derived lines. Consequently the analysis of variance was extended to include a regression analysis similar to that employed by other workers when measuring the adaptation parameters of varieties, mixtures and segregating populations in different crops.

With each cultivar, the assessment of environment (independent variable of the regression analysis) was obtained from the average yield of respective control lines at each site. The use of controls for this purpose represents an independent assessment of environment as recommended by Freeman and Perkins (1971). Furthermore, it is equivalent to their suggestion that parental genotypes could be used as standards for assessing environments for F_2-derived lines from different crosses. In mutation studies, the effect of mutagenic treatment can only be assessed by comparing treated lines with controls. Moreover, it is necessary to use the control means as an environmental index in order to obtain an absolute measure of changes in adaptation parameters among treated lines. For example, if the individual treated lines were regressed on site mean yields of treated lines, instead of the control lines, they would have an

average slope of 1.0 and there would necessarily be an equal distribution of positive and negative deviations from the average slope.

The significant G X E interactions observed among the treated lines in M_4 and M_5 generations were partitioned into linear and non-linear components to find the relative contribution of these two components to the overall interaction term. The G X E interactions observed in these generations, taken separately, were due mainly to deviations from regression, as might be expected because of the small number of environments (sites) included in each year. However, when the number of environments was increased by combining the M_4 and M_5 results, both linear and deviation components became significant.

Although the majority of the G X E variation over two years was due to linear effects with Clipper (60%) and C.I.3576 (76%) in the unweighted analysis, it was much less in the weighted analysis (35% and 59%, respectively). The reason for this difference is not clear since the opposite effect was observed in the 1970 analysis where only the weighted analysis gave significant linear effects. With Proctor, the linear component of G X E was low in both weighted (31%) and unweighted (37%) analyses.

Where the deviation mean square alone is significant there is either no relationship or no simple relationship between G X E interaction and site mean yields and no predictions can be made from the regression analysis. However, where the linear mean square alone is significant, the G X E interaction can be accounted for by the linear regressions, and this has considerable practical value. If both components are significant, the practical usefulness of any predictions will depend on the relative magnitudes of these components. In this regard, Aastveit (1970) has suggested that the G X E interaction among mutagen-derived populations should be considered as experimental error. But this will not be true in those cases where a large portion of the interaction term can be accounted for by linear regressions.

Finlay and Wilkinson (1963) and Fripp and Caten (1971), working with such widely different material as barley and Schizophyllum, respectively, have found that most of the G X E interaction was accounted for by linear regressions on the environmental values. Perkins and Jinks (1968a), working with Nicotiana, found that G X E interaction was made up of approximately equal amounts of the linear and deviation components. Fripp (1972), in further studies with Schizophyllum, used several different methods of assessing the environment and found that

there was a tendency for the linearity of regression to decrease as the assessment material (i.e. material used for environmental index) became more distantly related to the genotypes under study. Nevertheless, even with the most distantly related assessment material the major part of the G X E interaction was still due to linear effects. On the other hand, Eberhart and Russell (1966) and Tai (1971) working with maize and potato, respectively, showed that the major part of G X E variation in their material was due to deviations from regression.

In the present study, a common feature observed in the regression analysis with all cultivars, irrespective of their adaptation type, was a reduction in average slope (β_T) of the treated lines compared with that of the control lines ($\beta_C = 1.0$). Thus with respect to b parameter the treated lines as a group appear to be more stable than the controls across environments. It seems likely, as explained below, that such a reduction of β_T will always occur when the treated and control populations are analyzed on an arithmetic scale.

The average yield of the treated lines was less than that of the controls with each cultivar, and their yield expressed as percentage of controls was relatively constant across sites with no tendency for the percentage yield to decrease at the high-

yielding sites (Table 46). Therefore, the reduction of average slope (β_T) for the treated lines must be due to a scale effect whereby the arithmetic differences between the means of the treated and control populations are amplified at high-yielding sites. On this basis, the more pronounced reduction of average slope observed with the treated lines of Proctor (Table 34) can be related to the greater reduction of percentage yield of these treated lines, which in turn has been ascribed to a more effective EMS treatment. Thus it seems to be merely fortuitous that it was the most unstable cultivar with respect to b parameter (b = 1.46, Table 3), which exhibited the greatest change in average b after EMS treatment.

Turning to the individual treated lines, the b values calculated from the weighted analyses were similar to those obtained from the unweighted analyses, except the S.E.(b) was somewhat larger in the weighted analyses. The b values were found to be positively correlated with the mean yield (G) in both analyses but the magnitude of the correlation was somewhat decreased in the weighted analyses, similar to the finding of Lawrence (1970). These strong positive correlations raise the question of whether b and G are separate attributes of the genotype. Perkins and Jinks (1968a) and Fripp and Caten (1971) also observed a positive correlation between b and G in their analyses of untransformed

data, but they found that the association was not absolute and lines were detected with low yield and high b, and vice versa. The only similar exception observed in the present study is line No. 31 of C.I.3576 which has a b value close to unity despite its very low yield.

In contrast, Finlay and Wilkinson (1963) did not find any correlation between b and G in their analyses of logarithmically-transformed data. Furthermore, Finlay (1963) obtained evidence from a study of combining ability, again using log data, that these indices arelargely independent of each other.

Two types of low-yielding treated lines with significantly reduced b values ($b < 1.0$) were detected in the present study: (i) lines which give more or less similar yield to their respective controls in low-yielding environments and relatively much less in the high-yielding environments; (ii) a few extreme types, which produce uniformly less yield in all environments and show very little or no response to the improved environmental conditions. In other words the latter type seem to be poorly adapted to all environments, and presumably they represent deleterious mutations.

A few high-yielding lines with significantly increased b values ($b > 1.0$) were detected in C.I.3576 and these lines were unstable in performance across environments giving relatively low

yield at the low-yielding environments and higher yield than the control mean at the high-yielding environments. Although positive mutations were not expected in the small number of treated lines included in the present study, line Nos. 21 and 26 of C.I.3576 could possess such changes.

The occurrence of a large deviation component in the G X E interaction of the treated lines suggested that at least some of the treated lines show a more variable response across environments than the controls. One extremely variable treated line with significant S^2d was detected in each of Proctor and C.I.3576. Joppa et al. (1971) detected similar large deviations from linearity in their adaptation studies with wheat genotypes and, in many cases, the deviations could be explained by an interaction between the genotype and specific pathogens. However, no obvious explanation could be found for the large deviations observed in the present study.

Besides lines showing extreme deviations from linearity (significant S^2d), it is of interest to know whether some other treated lines of each cultivar are more variable than the controls across environments. Such treated lines are expected because of the large deviation component of the G X E interaction term especially in the weighted analyses. A crude approach has been

used to identify these lines, simply by comparing the S.E.(b) of treated lines with those of the control lines, in both weighted and unweighted analyses. The number of treated lines of each cultivar which have an S.E.(b) exceeding that of the most extreme control line is given in Table 47.

Table 47. Treated lines with S.E.(b) higher than most extreme control line

Cultivar	No. of treated lines	
	Unweighted analysis	Weighted analysis
Clipper	4	9
C.I.3576	7 /	9 /
Proctor	1 /	4 /

/ Includes one line with significant S^2d.

It is evident from Table 47 that several treated lines of each cultivar are more variable across environments than any of their control lines, especially in the weighted analyses. Some of these lines may have come from the bias introduced by testing more treated lines than control lines, but this effect could not account for the large numbers observed within Clipper and C.I.3576.

The occurrence of treated lines showing large deviations from linear regressions provides support for Brock's (1965) suggestion that random mutations are expected to upset the integrated functioning of genes in a plant leading to reduced phenotypic stability and an increased G X E interaction. Furthermore, Fröier (1954), while testing morphologically and physiologically distinct mutants of barley over a range of environments, observed that the mutants showed increased G X E interaction and were more variable in yield performance across environments as compared with the parent varieties.

In the present study, the treated lines were derived initially from randomly selected M_2 single plants, hence most of them will be heterogeneous in the M_4 generation, consisting of different types of homozygotes and some residual heterozygotes. In the M_5 generation these lines are expected to be equally heterogeneous but to possess fewer heterozygotes. In contrast, the individual control lines are expected to be homogeneous in both generations. Smith et al. (1967), working with hybrid-derived populations of soybeans, found that heterogeneous, homozygous lines were more stable across environments than homogeneous, homozygous lines. Thus if the treated lines in the current material were reselected in M_5 or M_6 to give homozygous lines, they might show even more instability across environments.

C. Association of plant characters with yield and adaptation

The principal effect of EMS treatment observed in the present study was a general reduction in mean of the treated lines as commonly found by other workers. With few exceptions, the significant changes in stability parameters (b or S^2d) were found to be associated with low-yielding lines. Therefore, in attempting to explain the alterations in stability parameters, one needs to find the cause for low yields.

It is well known that EMS induces more seed sterility than irradiation treatments and such an effect will contribute to lower yields. It was not practicable to measure seed sterility on all plots in all environments but the indirect evidence listed below suggests that seed sterility was not a major cause of reduced yield in the present study.

(i) The seed sterility observed in the M_1 spikes was much less than that found by other workers (Gaul et al., 1966; Froese-Gertzen et al., 1964).

(ii) Plants exhibiting high seed sterility were discarded in the M_2 generation.

(iii) The most sterile lines remaining in the M_3 rows would not be expected to produce the required minimum of 200 gm of seed, and hence they would be selected against.

However, direct measurements of seed sterility were made on the 15 selected treated lines in M_5 generation. Although there was a negative association between yield and seed sterility with treated lines of Clipper, C.I.3576 and Proctor at most sites, only a few of these correlations were significant. Furthermore, in the analysis of variance of seed sterility of 10 control and 5 or 6 selected treated lines, many of the treated lines were not significantly different from the controls. The largest amount of sterility detected was in line Nos. 29 and 33 of C.I.3576 which had 5.9% and 12.4% higher seed sterility than the controls, respectively, but this could account for only a small part of their overall yield reduction. Thus, it is concluded that seed sterility was not the major cause of yield reduction in this study.

It was observed that yield was negatively correlated with heading date among the selected treated lines at most of the sites during 1971. Normally heading date has an important influence on barley yields in South Australia, since moisture stress frequently occurs in spring and late cultivars have reduced yield under these conditions. Aspinall *et al.* (1964) in barley, and Chinoy (1962) in wheat, have indicated the advantage of earlier types under stress environments. Furthermore, under Mediterranean type climates, it has been shown that earliness in maturity is the

most important characteristic for drought resistance of a winter crop (May and Milthorpe, 1962).

However, the available evidence suggests that heading date was not the primary cause of low yield in the present experiments. First, stress conditions did not occur at any of the sites used in the field experiments. Second, the late cultivar, Proctor, gave equal or superior yield to the earlier cultivars at most sites in 1970 and 1971. Furthermore, some of the treated lines which were very late in heading gave similar yield to their respective controls, and others which were early, produced low yield.

Generally, the low-yielding treated lines were shorter in height than their controls, but there were many exceptions where the low-yielding lines had increased height. It has been observed that short height is often associated with high mean yield and general adaptation (Borlaug, 1965; Matsuo et al., 1972). Thus the low yield of treated lines cannot be ascribed to height differences.

It appears that none of the characters measured in the present study arethe primary cause of low yield. It seems more likely that some deleterious mutation has occurred in the low-yielding lines affecting an unidentified but important physiological process which leads to reduced vitality and pleiotropic effects

on other characters. On the other hand, with positive changes in performance, the associated character changes are more likely to be causally related to change in performance. In this respect it is interesting to note that line No. 21 of C.I.3576 with b > 1.0 has reduced height and therefore it might be more resistant to lodging than the parent cultivar which frequently lodges under high-fertility conditions.

In view of the discrete differences observed between some treated lines and their controls with respect to several characters, it is necessary to consider whether these changes should be regarded as macro-mutations rather than micro-mutations. Gaul (1965) has emphasised the arbitrary nature of such a distinction, but he has defined micro-mutations as those changes which can be recognized with certainty in a single plant. The treated lines which showed the largest morphological or physiological differences from the controls in the 1970 field experiments were grown in pots in 1971. None of the lines except No. 4 of Proctor could be clearly distinguished from the controls and thus it is concluded that the remaining treated material included in the present study possesses only micro-mutations as defined by Gaul.

D. General conclusions

(1) Significant genotype X environment interaction was induced among the mutagen-derived lines, apparently as a consequence of the EMS-induced genotypic variability. By partitioning the genotype X environment sum of squares into its components it was shown that both the linear and deviation from regression mean squares were significant with all cultivars. Therefore, both linear regression coefficient (b) and deviation mean squares (S^2d) (which is the reliability of the linear response) parameters are required to specify the stability of performance of individual lines in mutagen-treated populations. The linear effects were mainly associated with the low-yielding lines and any deleterious mutation induced by the mutagenic treatment will fall into this category.

Some of the treated lines exhibited a more variable performance across environments than the controls, in support of Brock's (1965) suggestion that random mutations will interfere with the integrated functioning of genes, thereby reducing phenotypic stability.

(2) Because of the general expectation of reduced yield after mutagenic treatment, it can be predicted that all barley cultivars irrespective of their adaptation type will show a decrease in average regression slope when analyzing natural data

on an arithmetic scale, due to a scale effect in the high-yielding environments.

(3) Finally, some suggestions can be made for selecting for wide adaptation among mutagen-treated material. In the M_3 and M_4 generations, the material should be tested at high-yielding environments to identify and eliminate low-yielding lines, which are expected to have low 'b' values and generally give low-yield over all environments.

In the M_5 generation, when reasonable homozygosity has been achieved, one should reselect and test this material after seed increase along with respective controls over a wide range of environments. This is in contrast to the views of Aastveit (1970), who suggested that to select for wide adaptation tests should be conducted over a range of environments, in an early stage of the programme.

BIBLIOGRAPHY

AASTVEIT, K. (1970).
Crop plant characters to be improved by mutation breeding. Yielding ability.
"Manual on Mutation Breeding". Joint FAO/IAEA Tech. Reports series no. 119. IAEA, Vienna, pp. 149-152.

AASTVEIT, K. and GAUL, H. (1967).
Variation and selection of micro-mutants.
Rad. Bot., 7 : 353-361.

ABRAMS, R. and FREY, K.J. (1964).
Variations in quantitative characters of oats (Avena sativa L.) after various mutagen treatments.
Crop Sci., 4 : 163-168.

ALLARD, R.W. (1961).
Relationship between genetic diversity and consistency of performance in different environments.
Crop Sci., 1 : 127-133.

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

ASPINALL, D., NICHOLLS, P.B. and MAY, L.H. (1964).
The effects of soil moisture stress on the growth of barley.
Aust. J. Agric. Res., 15 : 729-745.

AUERBACH, C. (1943).
Drosophila melanogaster: new mutants. Chemically induced mutations and rearrangements.
Dros. Inf. Serv., 17 : 48-50.

BARTLETT, M.S. (1937).
In "Some examples of statistical methods of research in agriculture and applied biology".
J. Roy. Statist. Soc. Suppl., 4 : 121.

BARTLETT, M.S. (1947).
The use of transformations.
Biometrics, 3 : 39-52.

BAUR, E. (1924).
Untersuchungen über das Wesen, die Enstehung und die Vererbung von Rassenunterschieden bei Antirrhinum majus.
Biblio. Genet., 4 : 1-170.

BHATIA, C.R. and SWAMINATHAN, M.S. (1962).
Induced polygenic variability in bread wheat and its bearing on selection procedures.
Z. Pflanzenzücht., 48 : 317-326.

BOGYO, T.P., SCARASCIA-MUGNOZZA, G.T., SIGURBJÖRNSSON, B. and BAGNARA, D. (1969).
Adaptation studies with radiation-induced durum wheat mutants.
"Induced Mutations in Plants". Proc. Symp. Pullman, IAEA/FAO, Vienna, pp. 699-717.

BORG, G. (1959).
Svalöf's original Pallas barley (SV04032), a new 2-row spring barley produced by x-ray treatment of Svalöf's Bonus barley.
Sveriges Utsädesför. tidskr. pp. 72-96.
(English summary, pp. 93-95).

BORLAUG, N.E. (1965).
Wheat, rust and people.
Phytopath., 55 : 1088-1098.

BRADSHAW, A.D. (1965).
Evolutionary significance of phenotypic plasticity in plants.
Advances in Genetics, 13 : 115-155.

BREESE, E.L. (1969).
The measurement and significance of genotype-environment interactions in grasses.
Heredity, 24 : 27-44.

BROCK, R.D. (1965).
Induced mutations affecting quantitative characters.
"The Use of Induced Mutations in Plant Breeding ".
Suppl. Rad. Bot., 5 : 451-464.

BROCK, R.D. (1966).
Second cycle of mutation and selection for quantitative variation in Trifolium subterraneum.
Rad. Bot., 6 : 357-369.

BROCK, R.D. (1967a).
Quantitative variation in Arabidopsis thaliana induced by ionizing radiations.
Rad. Bot., 7 : 193-203.

BROCK, R.D. (1967b).
Induced quantitative variation in Arabidopsis thaliana.
"Induced Mutations and their Utilization".
pp. 263-267. Akademie - Verlag, Berlin, 1967.

BROCK, R.D. and LATTER, B.D.H. (1961).
Radiation induced quantitative variation in subterranean clover.
Proc. Third Australasian Conf. on Rad. Biol., pp. 205-215.

BROCK, R.D. and SHAW, H.F. (1969).
Response to a second cycle of mutagenic treatment in Arabidopsis thaliana.
"Induced Mutations in Plants".
Proc. FAO/IAEA Symp. Nature, Induction and Utilization of Mutations in Plants. Pullman, Wash. IAEA, Vienna, pp. 435-443.

BRÜCHER, H. (1943).
Experimentelle untersuchungen über den Selektionswert künstlich erzengter Mutaten von Antirrhinum majus.
Z. Bot., 39 : 1-47.

BUCIO ALANIS, L. (1966).
Environmental and genotype-environmental components of variability. I. Inbred lines.
Heredity, 21 : 387-397.

BUCIO ALANIS, L. and HILL, J. (1966).
Environmental and genotype-environmental components of variability. II. Heterozygotes.
Heredity, 21 : 399-405.

CALDECOTT, R.S. (1959).
The experimental control of the mutation process.
Proc. First Int. Wheat Genet. Symp., pp. 68-87.

CALDECOTT, R., BEARD, B.H. and GARDNER, C.O. (1954).
Cytogenic effects of x-ray and thermal neutron irradiation on seeds of barley.
Genetics, 39 : 240-259.

CHINOY, J.J. (1962).
Physiology of drought resistance in wheat.
IV. Effect of wilting at different growth and development stages on plant characters determining yield of grain in eight varieties of wheat.
Phyton, 19 : 5-10.

COCHRAN, W.C. (1937).
Problems arising in the analysis of a series of similar experiments.
Jour. Roy. Statist. Soc. Suppl. 4 : 102-118.

COCHRAN, W.G. and COX, G.M. (1964).
In "Experimental Designs". 2nd ed.,
John Wiley & Sons, Inc., New York, pp. 553-555.

COMSTOCK, R.E. and ROBINSON, H.F. (1952).
Genetic parameters, their estimation and significance.
Proc. Sixth Intern. Grasslands Congr., pp. 284-291.

DALY, K. (1960).
The induction of quantitative variability induced by gamma radiation in Arabidopsis thaliana.
Genetics, 45 : 983.

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

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

DORMLING, I. and GUSTAFSSON, Å. (1969).
Phytotron cultivation of early barley mutants.
Theoret. Appl. Genet., 39 : 51-61.

DORMLING, I., GUSTAFSSON, Å., JUNG, H.R. and VON WETTSTEIN, D. (1966).
Phytotron cultivation of Svalöf's Bonus barley, and its mutant Svalöf's Mari.
Hereditas, 56 : 222-237.

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

EBERHART, S.A. and RUSSELL, W.A. (1969).
Yield and stability for a 10-line diallel of single-cross and double-cross maize hybrids.
Crop Sci., 9 : 357-360.

EHRENBERG, L., EKMAN, G., GUSTAFSSON, Å., JANSSON, G. and LUNDQVIST, U. (1965).
Variation in quantitative and biochemical characters in barley after mutagenic treatments.
Suppl. Rad. Bot., 5 : 477-490.

EHRENBERG, L., GUSTAFSSON, Å. and LUNDQVIST, U. (1961).
Viable mutants induced in barley by ionizing radiations and chemical mutagens.
Hereditas, 47 : 243-282.

FINLAY, K.W. (1963).
Adaptation - its measurement and significance in barley breeding.
Proc. 1st Int. Barley Genet. Symp., Wageningen, 1963, pp. 351-359.

FINLAY, K.W. (1968).
The significance of adaptation in wheat breeding.
Proc. 3rd Int. Wheat Genet. Symp., Canberra, 1968.
Ed. K.W. Finlay and K.W. Shepherd, pp. 403-409.

FINLAY, K.W. and WILKINSON, G.N. (1963).
The analysis of adaptation in a plant breeding programme.
Aust. J. Agric. Res., 14 : 742-754.

FREEMAN, G.H. and PERKINS, J.M. (1971).
Environmental and genotype-environmental components of variability. VIII. Relations between genotypes grown in different environments and measures of these environments.
Heredity, 27 : 15-23.

FREY, K.J. (1964).
Adaptation of oat strains selected under stress and non-stress environmental conditions.
Crop Sci., 4 : 55-58.

FREY, K.J. (1968).
Induced variability in diploid and polyploid Avena sp.
"The Present State of Mutation Breeding".
Reprinted from Gamma Field Symposia, No. 7, pp. 41-56.

FRIPP, Y.J. (1972).
Genotype-environmental interactions in Schizophyllum commune.
Heredity, 28 : 223-238.

FRIPP, Y.J. and CATEN, C.E. (1971).
Genotype-environmental interactions in Schizophyllum commune.
Heredity, 27 : 393-407.

FROESE-GERTZEN, E.E., KONZAK, C.F., NILAN, R.A. and HEINER, R.E. (1964).
The effect of ethyl methanesulphonate on the growth response, chromosome structure and mutation rate in barley.
Rad. Bot., 4 : 61-69.

FRÖIER, K. (1954).
Aspects of the agricultural value of certain x-ray mutations produced and tested at the Swedish Seed Association, Svalöf and its branch stations.
Acta Agric. Scand., 4 : 515-543.

GANDHI, S.M., NATHAWAT, K.S. and BHATNAGAR, V.K. (1964).
Variety X environment interaction in wheat varietal tests in Rajasthan.
Indian J. Genet. Pl. Breed., 24 : 36-41.

GAUL, H. (1964).
Mutations in plant breeding.
Rad. Bot., 4 : 155-232.

GAUL, H. (1965).
The concept of macro- and micro-mutations and results on induced micro-mutations in barley.
"The Use of Induced Mutations in Plant Breeding".
Suppl. Rad. Bot., 5 : 407-428.

GAUL, H. (1967).
Studies on populations of micro-mutants in barley and wheat without and with selection.
"Induced Mutations and their Utilization".
Akademie-Verlag, Berlin, 1967, pp. 269-281.

GAUL, H. and AASTVEIT, K. (1966).
Induced variability of culm length in different genotypes of hexaploid wheat following x-irradiation and EMS-treatment.
"Contemporary Agriculture".
Fifth Yugoslav Symp. on Research in Wheat.
Novi Sad, 12-18 VI, 1966, pp. 263-276.

GAUL, H., BENDER, K., ULONSKA, E. and SATO, M. (1966).
EMS-induced genetic variability in barley; the problem of EMS-induced sterility; and a method to increase the efficiency of EMS treatment.
"Mutation in Plant Breeding".
Proc. Panel IAEA/FAO, Vienna, 1966, pp. 63-84.

GAUL, H. and ULONSKA, E. (1967).
Züchterische Bedeutung von Kleinmutationen.
II. Durch Röntgenstrahlen induzierte Variabilität von Kornertrag, Korngrosse und Vegetationslänge bei den Gersten Volla and Wisa.
Z. Pflanzenzücht., 58 : 343-368.

GAUL, H., ULONSKA, E., ZUM WINKEL, C. and BRAKER, G. (1969).
Micro-mutations influencing yield in barley - studies over nine generations.
"Induced Mutations in Plants".
Proc. Symp. IAEA/FAO, Pullman, 1969, pp. 375-398.

GELIN, O. (1955).
Studies on the x-ray mutation Strål pea.
Agr. Hort. Gen., 13 : 183-193.

GELIN, O. (1960).
Breeding problems in field peas.
Agr. Hort. Gen., 18 : 214-218.

GONZALEZ, C. and FREY, K.J. (1965).
Genetic variability in quantitative characters induced by thermal neutron treatment of diploid, tetraploid and hexaploid oat seeds.
Rad. Bot., 5 : 321-335.

GOTOH, K. and OSANAI, S. (1959a).
Efficiency of selection for yield under different densities in a wheat cross.
Jap. J. Breed., 9 : 7-11.

GOTOH, K. and OSANAI, S. (1959b).
Efficiency of selection for yield under different fertilizer levels in a wheat cross.
Jap. J. Breed., 9 : 173-178.

GOTTSCHALK, W. (1966).
The yield capacity of useful mutants. A critical review of a collection of mutant types of Pisum.
"Mutations in Plant Breeding".
Proc. Panel, Joint IAEA/FAO, Vienna, 1966, pp. 85-101.

GRAFIUS, J.E. (1956).
Components of yield in oats: a geometrical interpretation.
Agron. J., 48 : 419-423.

GREGORY, W.C. (1955).
X-ray breeding of peanuts (Arachis hypogea L.).
Agron. J., 47 : 396-399.

GREGORY, W.C. (1956).
The induction of useful mutations in peanut.
Brookhaven Symp. in Biol. (Genetics in Plant Breeding) 9 : 177-190.

GUSTAFSSON, Å. (1940).
The mutation system of the chlorophyll apparatus.
Lunds Univ. Arsskr. (N.F.) Avd., 36 : 1-40.

GUSTAFSSON, Å. (1947).
Mutations in agricultural plants.
Hereditas, 33 : 1-100.

GUSTAFSSON, Å. (1951).
Induction of changes in genes and chromosomes.
II. Mutations, environment and evolution.
Cold Spring Harbor Symp. Quant. Biol., 16 : 263-281.

GUSTAFSSON, Å. (1954).
Mutations, viability and population structure.
Acta Agric. Scand., 4 : 601-632.

GUSTAFSSON, Å. (1963).
Mutations and the concept of viability.
Recent Plant Breeding Research.
Almqvist & Wiksell/John Wiley & Sons, pp. 89-104.

GUSTAFSSON, Å. (1969).
A study on induced mutations in plants. (Introductory address). "Induced Mutations in Plants".
Proc. Symp. Pullman, IAEA/FAO, Vienna, pp. 9-31.

GUSTAFSSON, Å., HAGBERG, A. and LUNDQVIST, U. (1960).
The induction of early mutants in Bonus barley.
Hereditas, 46 : 675-699.

HANSON, C.H., ROBINSON, H.F. and COMSTOCK, R.E. (1956).
Biometrical studies of yield in segregating populations of Korean lespedeza.
Agron. J., 48 : 268-272.

HESLOT, H., FERRARY, R., LEVY, R. and MONARD, C. (1961).
Induction de mutations chez l'orge: Efficacité relative des rayons gamma, du sulfate d'éthyle, du méthane sulfonate d'éthyle et de quelques autres substances.
Effects of Ionizing Radiations on Seeds, IAEA, Vienna, 1961, pp. 243-249.

HONING, I.A. (1923).
Nicotiana deformis n.sp. und die Enzymtheorie der Erblichkeit.
Genetics, 5 : 455-476.

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

IMMER, F.R., HAYES, H.K. and POWERS, L. (1934).
Statistical determination of barley varietal adaptation.
Amer. Soc. Agron. J., 26 : 403-418.

JALIL, M.A. and YAMAGUCHI, H. (1964).
Experiments on the induction of polygenic mutations with successive irradiation in rice.
Phyton, 21 : 149-155.

JALIL, M.A. and YAMAGUCHI, H. (1965).
The variation of quantitative characters in the irradiated progenies of two rice varieties and their hybrid.
Rad. Bot., 5 : 187-196.

JOHNSON, G.R. and FREY, K.J. (1967).
Heritabilities of quantitative attributes of oats (Avena sp.) at varying levels of environmental stress.
Crop Sci., 7 : 43-46.

JOHNSON, H.W., ROBINSON, H.F. and COMSTOCK, R.E. (1955).
Estimates of genetic and environmental variability in soybeans.
Agron. J., 47 : 314-318.

JOHNSON, V.A., SCHMIDT, J.W. and MEKASHA, W. (1966).
Comparison of yield components and agronomic characteristics of four winter wheat varieties differing in plant height.
Agron. J., 58 : 438-441.

JOHNSON, V.A., SHAFER, S.L. and SCHMIDT, J.W. (1968).
Regression analysis of general adaptation in hard red winter wheat (Triticum aestivum L.).
Crop Sci., 8 : 187-191.

JONES, D.F. (1921).
The indeterminate growth factor in tobacco and its effect upon development.
Genetics, 6 : 433-444.

JONES, G.L., MATZINGER, D.F. and COLLINS, W.K. (1960).
A comparison of flue-cured tobacco varieties repeated over location and years with implication on optimum plot allocation.
Agron. J., 52 : 195-199.

JOPPA, L.R., LEBSOCK, K.L. and BUSCH, R.H. (1971).
Yield stability of selected spring wheat cultivars (Triticum aestivum L. em Thell) in the uniform regional nurseries, 1959 to 1968.
Crop Sci., 11 : 238-241.

JOSHI, S.N. and FREY, K.J. (1967).
Genetic variability in oats from recurrent and alternate treatment with physical and chemical mutagens.
Rad. Bot., 7 : 513-520.

JOWETT, D. (1972).
Yield stability parameters for sorghum in East Africa.
Crop Sci., 12 : 314-317.

KHADR, F.H. and FREY, K.J. (1965).
Recurrent irradiation for oat breeding.
Rad. Bot., 5 : 391-402.

KNIGHT, R. (1970).
The measurement and interpretation of genotype-environment interactions.
Euphytica, 19 : 225-235.

KONZAK, C.F., NILAN, R.A., FROESE-GERTZEN, E.E. and FOSTER, R.J. (1965).
Factors affecting the biological action of mutagens.
"Induction of Mutations and the Mutation Process".
Publishing House of Czechoslovak Acad. Sci., Praha, 1965, pp. 1-9.

KONZAK, C.F., NILAN, R.A., LEGAULT, R.R. and HEINER, R.E. (1961).
"Modification of induced genetic damage in seeds".
Effects of Ionizing Radiations on Seeds.
Proc. Symp. Karlsruhe, 1960. IAEA, Vienna, pp. 155-169.

KONZAK, C.F., NILAN, R.A., WAGNER, J. and FOSTER, R.J. (1965).
Efficient chemical mutagenesis.
"The Use of Induced Mutations in Plant Breeding".
Suppl. Rad. Bot., 5 : 49-70.

KRULL, C.F., BORLAUG, N.E., MEZA, C. and NARVAEZ, I. (1968a).
Results of the first International Spring Wheat Yield Nursery, 1964-1965. Res. Bull. No. 8, CIMMYT, Mexico.

KRULL, C.F., CABRERA, A., BORLAUG, N.E. and NARVAEZ, I. (1968b).
Results of the second International Spring Wheat Yield Nursery, 1965-1966. Res. Bull. No. 11, CIMMYT, Mexico.

KRULL, C.F. and FREY, K.J. (1961).
Genetic variability in oats following hybridization and irradiation.
Crop Sci., 1 : 141-146.

LAWRENCE, C.W. (1968).
Radiation induced polygenic mutation in Arabidopsis thaliana. I. Selection for flowering time.
Heredity, 23 : 321-337.

LAWRENCE, P.K. (1970).
Studies in adaptation.
M.Sc. (Agri.) Thesis, University of Adelaide.

LIANG, G.H.L., HEYNE, E.G. and WALTER, T.L. (1966).
Estimates of variety X environment interactions in yield tests of three small grains and their significance on breeding programmes.
Crop Sci., 6 : 135-139.

LOHANI, S. (1970).
The effect of natural selection on the yield and adaptation of genotypes in composite cross populations of barley.
Ph.D. Thesis, University of Adelaide, p. 148.

MATSUO, T., KIKUCHI, F. and KUMAGAI, K. (1972).
Studies on the adaptability of rice. I. Comparative studies on the adaptability of rice varieties tested under different conditions in temperate zone.
Japan. J. Breed., 22 : 83-91.

MATZINGER, D.F. (1963).
Experimental estimates of genetic parameters and their application in self-fertilizing plants.
In "Statistical Genetics and Plant Breeding".
Ed. W.D. Hanson and H.F. Robinson. Nat. Acad. Sci., Nat. Res. Council, pp. 253-279.

MAY, L.H. and MILTHORPE, F.L. (1962).
Drought resistance of crop plants.
(Review). Field Crop Abstr., 15 : 171-179.

MILLER, P.A., ROBINSON, H.F. and POPE, O.A. (1962).
Cotton variety testing: Additional information on variety X environment interactions.
Crop Sci., 2 : 349-352.

MILLER, P.A., WILLIAMS, J.C. and ROBINSON, H.F. (1959).
Variety X environment interaction in cotton variety tests and their implications on testing methods.
Agron. J., 51 : 132-134.

MOES, A. (1963).
Comparison of the effects of x-rays and of ethyl methanesulphonate in barley.
Proc. 1st Int. Barley Genet. Symp., Wageningen, 1963, pp. 82-91.

MULLER, H.J. (1927).
Artificial transmutation of the gene.
Science, 66 : 84-87.

MUNCK, L., KARLSSON, K.E. and HAGBERG, A. (1969).
Selection of a high protein, high lysine variety from World Barley Collection.
Proc. Second Int. Symp. Barley Genetics, Pullman, pp. 544-558.

MURRAY, J.C. and VERHALEN, L.M. (1970).
Genotype by environment interaction study of cotton in Oklahoma.
Crop Sci., 10 : 197-199.

NILAN, R.A., KONZAK, C.F., HEINER, R.E. and FROESE-GERTZEN, E.E. (1963).
Chemical mutagenesis in barley.
Proc. 1st Int. Barley Genet. Symp., Wageningen, 1963, pp. 35-54.

OKA, H.I., HAYASHI, J. and SHIOJIRI, I. (1958).
Induced mutation of polygenes for quantitative characters in rice.
J. Hered., 49 : 11-14.

PAPA, K.E., WILLIAMS, J.H. and HANWAY, D.G. (1961).
Effectiveness of selection for quantitative characters in the third generation following irradiation of soybean seed with x-rays and thermal neutrons.
Crop Sci., 1 : 87-90.

PERKINS, M. JEAN and JINKS, J.L. (1968a).
Environmental and genotype-environmental components of variability. III. Multiple lines and crosses.
Heredity, 23 : 339-356.

PERKINS, M. JEAN and JINKS, J.L. (1968b).
Environmental and genotype-environmental components of variability. IV. Non-linear interaction for multiple inbred lines.
Heredity, 23 : 525-535.

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

QUALSET, C.O. (1968).
Population structure and performance in wheat.
Proc. IIIrd Int. Wheat Genet. Symp. Canberra 1968, Eds. K.W. Finlay and K.W. Shepherd, pp. 397-402.

RAMANNA, M.S. and NATARAJAN, A.T. (1965).
Studies on the relative mutagenic efficiency of alkylating agents under different conditions.
Indian J. Genet. Pl. Breed., 25 : 24-45.

RASMUSSON, D.C. (1968).
Yield and stability of yield of barley populations.
Crop Sci., 8 : 600-602.

RASMUSSON, D.C. and GLASS, R.L. (1967).
Estimates of genetic and environmental variability in barley.
Crop Sci., 7 : 185-188.

RASMUSSON, D.C. and LAMBERT, J.W. (1961).
Variety X environment interaction in barley variety tests.
Crop Sci., 1 : 261-262.

RAWLINGS, J.O., HANWAY, D.G. and GARDNER, C.O. (1958).
Variation in quantitative characters of soybeans after seed irradiation.
Agron. J., 50 : 524-528.

REICH, V.H. and ATKINS, R.E. (1970).
Yield stability of four population types of grain sorghum, Sorghum bicolor (L.) Moench, in different environments.
Crop Sci., 10 : 511-517.

ROWE, P.R. and ANDREW, A.H. (1964).
Phenotypic stability for a systematic series of corn genotypes.
Crop Sci., 4 : 563-567.

ROY, N.N. and MURTY, B.R. (1967).
Response to selection for wide adaptation in bread wheat.
Curr. Sci., 36 : 481.

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

SCHUTZ, W.M. and BERNARD, R.L. (1967).
Genotype X environment in the regional testing of soybean strains.
Crop Sci., 7 : 125-130.

SCOSSIROLI, R.E. (1954).
Artificial selection of a quantitative trait in Drosophila melanogaster under increased mutation rate.
Atti. IX Congr. Int. Genetica Caryologia, Suppl. 2 : 861-864.

SCOTT, G.E. (1967).
Selecting for stability of yield in maize.
Crop Sci., 7 : 549-551.

SIGURBJÖRNSSON, B. (1968).
Induced mutations as a tool for improving world food sources and international co-operation in their use.
Hereditas, 59 : 375-395.

SNEDECOR, G.W. and COCHRAN, W.G. (1967).
Spearman's rank correlations.
In "Statistical Methods" 6th ed., Iowa State University Press, Ames, Iowa, p. 194.

SMITH, R.R., BYTH, D.E., CALDWELL, B.E. and WEBER, C.R. (1967).
Phenotypic stability in soybean populations.
Crop Sci., 7 : 590-592.

SPARROW, D.H.B. (1972).
A study of genotypic differences in the malting quality of barley.
Ph.D. Thesis, University of Adelaide, p. 207.

SPARROW, D.H.B. and DOOLETTE, J. (1971).
Barley in "Cereals in Australia".
Eds. A. Lazenby and E.M. Matheson. Angus and Robertson, Sydney (In press).

SPRAGUE, G.F. and FEDERER, W.T. (1951).
A comparison of variance components in corn yield trials. II. Error, year X variety, location X variety and variety components.
Agron. J., 43 : 535-541.

STADLER, L.J. (1928a).
Mutations in barley induced by x-rays and radium.
Science, 68 : 186-187.

STADLER, L.J. (1928b).
Genetic effects of x-rays in maize.
Proc. Nat. Acad. Sci. U.S., 14 : 69-75.

ST. PIERRE, C.A., KLINK, H.R. and GAUTHIER, F.M. (1967).
Early generation selection under different environments as it influences adaptation of barley.
Can. J. Plant Sci., 47 : 507-517.

STUBBE, H. and VON WETTSTEIN, F. (1941).
Uber die Bedeutung von Klein- und Grossmutationen in der Evolution.
Biol. Zbl., 61 : 265-297.

SWAMINATHAN, M.S. (1965).
A comparison of mutation induction in diploids and polyploids. The use of induced mutations in plant breeding.
Suppl. Rad. Bot., 5 : 619-641.

SWAMINATHAN, M.S., CHOPRA, V.L. and BHASKARAN, S. (1962).
Chromosome aberrations and the frequency and spectrum of mutations induced by ethylmethane sulphonate in barley and wheat.
Indian J. Genet. Pl. Breed., 22 : 192-207.

TAI, G.C.C. (1971).
Genotypic stability analysis and its application to potato regional trials.
Crop Sci., 11 : 184-190.

THODAY, J.M. (1953).
Components of fitness.
Symp. Soc. Exp. Biol., 7 : 96-113.

TYSON, H. and BRADNER, N.R. (1967).
The interaction of variety X environment in flax trials.
Can. J. Plant Sci., 47 : 441-445.

VELA-CARDENAS, M. and FREY, K.J. (1972).
Optimum environment for maximizing heritability and genetic gain from selection.
Iowa State J. Sci., 46 : 381-394.

WALTON, P.D. (1957).
Cotton variety trials in the northern and eastern provinces of Uganda: 1929-55.
Emp. Cott. Grow. Rev., 34 : 99-106.

WALTON, P.D. (1968).
Spring wheat variety trials in the prairie provinces.
Canad. J. Plant Sci., 48 : 601-609.

WILKINSON, G.N. (1961).
Statistical estimates in enzyme kinetics.
Biochem. J., 80 : 324-332.

WILLIAMS, J.H. and HANWAY, D.G. (1961).
Genetic variation in oil and protein content of soybeans induced by seed irradiation.
Crop Sci., 1 : 34-36.

WILLIAMS, W. (1960).
Relative variability of inbred lines and F_1 hybrids in Lycopersicum esculentum.
Genetics, 45 : 1457-1465.

WRICKE, G. (1962).
Uber eine Methode zur Erfassung der ökologischen Streubreite in Feldversuchen.
Z. Pflanzenzucht., 47 : 92-96.

WRICKE, G. (1966).
Über eine biometrische Methode zur Erfassung der ökologischen Anpassung.
Acta Agri. Scand. Suppl., 16 : 98-101.

YATES, F. (1936).
A new method of arranging variety trials involving a large number of varieties.
J. Agric. Sci. Camb., 26 : 424-455.

YATES, F. and COCHRAN, W.G. (1938).
The analysis of groups of experiments.
J. Agric. Sci. Camb., 28 : 556-580.

APPENDIX 1

Analyses of variance for yield data from individual sites for M_2-derived treated and control lines of different cultivars in M_4 generation, 1970.

Cultivar	Site	Variation due to	Control lines			Treated lines		
			d.f.	MS	F	d.f.	MS	F
Clipper	B	Bet. Lines	24	2,058	1.06^{NS}	34	4,370	1.90*
		Residual	17/	1,939		32/	2,295	
	R	Bet. Lines	24	3,641	0.90^{NS}	34	13,220	3.60***
		Residual	24	4,056		34	3,672	
	M	Bet. Lines	24	9,321	1.47^{NS}	34	20,435	3.17**
		Residual	24	6,332		34	6,439	
	W	Bet. Lines	24	8,953	0.81^{NS}	34	21,591	1.75*
		Residual	24	11,082		34	12,348	
C.I.3576	B	Bet. Lines	24	3,042	0.86^{NS}	34	15,266	5.05***
		Residual	20/	3,531		30/	3,022	
	R	Bet. Lines	24	8,808	0.38^{NS}	34	16,739	1.75*
		Residual	24	23,358		34	9,587	
	M	Bet. Lines	24	8,065	1.38^{NS}	34	37,474	4.40***
		Residual	24	5,835		34	8,514	
	W	Bet. Lines	24	15,191	1.01^{NS}	34	40,779	4.01***
		Residual	24	15,002		34	10,173	
Proctor	B	Bet. Lines	24	2,379	1.32^{NS}	34	4,306	4.50***
		Residual	23/	1,806		31/	956	
	R	Bet. Lines	24	7,151	1.88^{NS}	34	12,207	3.45***
		Residual	24	3,796		34	3,536	
	M	Bet. Lines	24	7,785	1.25^{NS}	34	16,080	2.40**
		Residual	24	6,239		34	6,696	
	W	Bet. Lines	24	8,471	0.56^{NS}	34	31,059	5.86***
		Residual	24	15,059		34	5,304	

APPENDIX 1 (continued)

Cultivar	Site	Variation due to	Control lines			Treated lines		
			d.f.	MS	F	d.f.	MS	F
Ketch	B	Bet. Lines	24	1,223	1.55^{NS}	34	1,331	1.61^{NS}
		Residual	22/	788		34	828	
	R	Bet. Lines	24	3,358	0.43^{NS}	34	7,512	2.21**
		Residual	24	7,814		34	3,396	
	M	Bet. Lines	24	5,580	1.05^{NS}	34	9,696	1.90*
		Residual	24	5,336		34	5,102	
	W	Bet. Lines	24	8,050	0.57^{NS}	34	5,826	0.47^{NS}
		Residual	24	14,055		34	12,444	
Prior	B	Bet. Lines	14	1,315	0.80^{NS}	24	6,822	6.27***
		Residual	13/	1,641		24	1,088	
	R	Bet. Lines	14	4,837	0.84^{NS}	24	13,292	6.67***
		Residual	14	5,729		24	1,992	
	M	Bet. Lines	14	3,959	0.98^{NS}	24	15,268	1.64^{NS}
		Residual	14	4,059		24	9,291	
	W	Bet. Lines	14	4,351	1.12^{NS}	24	17,600	2.46**
		Residual	14	3,888		24	7,160	

/ At Bundaleer some plots were damaged by field mice and these were replaced by missing values giving fewer degrees of freedom for residual.

* significant at 5% level

** significant at 1% level

*** significant at 0.1% level

NS Non-significant

APPENDIX 2

Mean (G) and ecovalence (W) values of treated lines of CLIPPER, 1970

Line No.	Mean (g/plot) Natural scale	Ecovalence ($x10^{-3}$)	
		Unweighted analysis (natural scale)	Weighted analysis
1	620.6	3.72	4.60
2	560.3	23.77	24.60
3	529.1	7.02	8.84
4	421.5	6.06	8.01
5	472.9	16.37	21.74
6	479.4	9.36	11.24
7	568.5	16.10	18.91
8	569.4	16.31	17.02
9	579.6	2.99	3.25
10	573.5	11.18	14.55
11	496.6	22.92	23.06
12	457.5	8.33	10.87
13	587.6	40.77	40.79
14	547.3	16.92	16.96
15	585.8	6.87	7.49
16	621.5	8.00	8.13
17	614.9	9.23	12.23
18	526.5	1.43	1.43
19	573.3	7.81	7.87
20	456.5	13.59	17.12
21	635.9	17.33	21.75
22	502.0	10.29	10.87
23	479.6	24.53	27.33
24	663.3	15.16	19.17
25	655.5	13.68	16.33
26	573.0	3.37	3.54
27	671.9	6.92	7.02
28	594.5	11.75	13.39
29	617.8	27.53	36.36
30	482.9	5.84	6.60
31	562.6	11.13	11.73
32	572.0	7.30	7.62
33	551.8	19.66	20.52
34	496.0	15.70	17.66
35	481.9	10.51	10.61

APPENDIX 3

Mean (G) and ecovalence (W) values of treated lines of C.I.3576, 1970

Line No.	Mean (g/plot) Natural scale	Ecovalence ($x10^{-3}$)	
		Unweighted analysis (natural scale)	Weighted analysis
1	536.9	25.63	29.15
2	655.8	1.31	1.69
3	648.9	6.75	6.77
4	657.8	46.62	47.88
5	710.9	20.18	21.94
6	554.5	3.75	4.84
7	661.0	3.76	4.62
8	602.6	5.56	5.56
9	544.4	14.74	21.07
10	554.4	29.40	31.75
11	675.6	19.78	26.73
12	560.1	10.60	10.62
13	529.4	11.49	11.49
14	665.3	15.61	16.66
15	647.3	20.39	23.03
16	742.1	17.32	17.86
17	610.6	16.78	16.79
18	750.8	20.69	27.25
19	633.0	4.74	4.83
20	616.8	1.87	2.53
21	742.1	17.74	23.47
22	586.0	3.28	3.85
23	555.8	8.49	8.57
24	637.4	9.17	9.48
25	641.0	7.84	8.91
26	758.3	13.93	16.45
27	371.1	42.17	49.36
28	661.3	12.99	13.87
29	455.8	43.57	43.92
30	761.9	17.93	21.28
31	486.9	10.37	11.87
32	536.0	18.21	22.54
33	403.3	20.35	24.12
34	546.6	31.89	36.77
35	582.1	1.16	1.64

APPENDIX 4

Mean (G) and ecovalence (W) values of treated lines of PROCTOR, 1970

Line No.	Mean (g/plot) Natural scale	Ecovalence ($x10^{-3}$)	
		Unweighted analysis (Natural scale)	Weighted analysis
1	515.3	24.76	24.81
2	448.4	5.80	10.69
3	567.0	5.21	5.66
4	283.6	32.01	44.72
5	573.5	14.55	24.21
6	611.3	6.90	6.94
7	562.4	15.99	19.92
8	555.0	0.81	1.21
9	568.9	0.94	1.15
10	583.5	27.33	27.44
11	543.5	2.68	2.81
12	548.3	8.51	8.54
13	554.9	14.78	17.06
14	533.0	2.65	3.06
15	567.1	20.72	20.96
16	517.8	18.42	25.31
17	487.5	1.38	1.38
18	602.1	1.29	1.30
19	474.8	5.94	6.06
20	524.8	21.82	27.93
21	523.6	10.59	10.78
22	549.4	4.51	4.51
23	446.5	26.49	33.60
24	386.5	29.10	44.47
25	477.1	15.58	15.64
26	524.4	2.36	2.60
27	422.4	60.63	65.23
28	523.4	8.20	8.71
29	591.9	25.34	34.12
30	497.3	9.34	9.34
31	514.9	20.45	21.97
32	466.8	13.99	21.08
33	543.6	15.22	16.40
34	430.1	2.69	3.19
35	513.8	3.96	4.04

APPENDIX 5

Mean (G) and ecovalence (W) values of treated lines of PRIOR, 1970

Line No.	Mean (g/plot) Natural scale	Ecovalence ($x10^{-3}$)	
		Unweighted analysis (Natural scale)	Weighted analysis
1	281.5	5.07	5.34
2	476.1	16.20	16.99
3	458.0	27.48	32.90
4	484.3	24.91	27.68
5	348.5	4.72	5.35
6	493.5	8.51	8.74
7	399.1	7.70	7.90
8	475.1	4.13	4.52
9	436.9	3.90	4.33
10	440.6	3.52	3.66
11	476.1	21.19	21.20
12	407.6	4.51	4.58
13	421.1	29.73	29.90
14	457.8	17.29	20.05
15	334.5	17.37	17.96
16	433.3	8.05	8.66
17	473.5	10.66	10.75
18	483.0	29.86	30.83
19	441.8	3.39	3.89
20	364.0	18.55	20.58
21	474.9	16.47	17.91
22	461.9	18.80	19.35
23	451.3	1.14	1.26
24	410.5	45.77	55.69
25	491.1	4.87	5.54

APPENDIX 6

Mean (G), b, and S.E.(b) of treated lines of CLIPPER, 1970

Line No.	Mean (g/plot) Natural scale	b		S.E.(b)	
		Unweighted analysis (Natural scale)	Weighted analysis	Unweighted analysis (Natural scale)	Weighted analysis
1	620.6	.823	.846	.071	.067
2	560.3	1.125	.983	.277	.291
3	529.1	.742	.754	.052	.054
4	421.5	.767	.778	.066	.050
5	472.9	.623	.595	.065	.068
6	479.4	.766	.699	.128	.137
7	568.5	1.167	1.085	.201	.158
8	569.4	.873	.973	.240	.213
9	579.6	.865	.826	.086	.072
10	573.5	.751	.755	.142	.100
11	496.6	.864	.877	.286	.230
12	457.5	.771	.736	.117	.115
13	587.6	1.070	1.197	.384	.283
14	547.3	.926	.798	.252	.252
15	585.8	1.137	1.102	.108	.107
16	621.5	1.086	1.119	.153	.105
17	614.9	1.212	1.186	.069	.052
18	526.5	.974	.998	.080	.068
19	573.3	.975	1.051	.174	.188
20	456.5	.757	.775	.175	.118
21	635.9	1.211	1.269	.187	.198
22	502.0	.985	.945	.198	.132
23	479.6	.841	.892	.292	.192
24	663.3	1.253	1.194	.125	.109
25	655.5	1.105	1.100	.205	.154
26	573.0	.969	.967	.117	.080
27	671.9	1.083	1.099	.141	.095
28	594.5	1.066	1.115	.199	.199
29	617.8	1.385	1.426	.122	.133
30	482.9	.854	.788	.130	.142
31	562.6	.972	.962	.206	.152
32	572.0	.967	.944	.168	.140
33	551.8	1.216	1.231	.206	.141
34	496.0	.673	.664	.132	.098
35	481.9	.867	.784	.189	.155

APPENDIX 7

Mean (G), b, and S.E.(b) of treated lines
of C.I.3576, 1970

Line No.	Mean (g/plot) Natural scale	b		S.E.(b)	
		Unweighted analysis (Natural scale)	Weighted analysis	Unweighted analysis (Natural scale)	Weighted analysis
1	536.9	.810	.741	.291	.241
2	655.8	.858	.882	.066	.060
3	648.9	.961	.999	.167	.135
4	657.8	1.242	1.094	.356	.324
5	710.9	1.258	1.248	.169	.138
6	554.5	.879	.843	.121	.107
7	661.0	1.096	1.141	.085	.073
8	602.6	.957	1.004	.154	.125
9	544.4	.729	.676	.177	.161
10	554.4	.812	.830	.313	.252
11	675.6	1.096	1.250	.252	.228
12	560.1	.993	1.021	.202	.163
13	529.4	1.009	1.046	.208	.167
14	665.3	1.033	1.126	.237	.193
15	647.3	.604	.640	.125	.104
16	742.1	1.161	1.142	.208	.169
17	610.6	1.19	1.132	.187	.170
18	750.8	1.303	1.364	.125	.109
19	633.0	.865	.937	.131	.116
20	616.8	.989	1.057	.101	.091
21	742.1	1.224	1.297	.173	.148
22	586.0	.822	.843	.085	.073
23	555.8	1.009	1.016	.180	.145
24	637.4	1.023	.978	.185	.159
25	641.0	.959	1.039	.178	.154
26	758.3	1.192	1.222	.156	.128
27	371.1	.415	.455	.093	.080
28	661.3	1.007	.976	.220	.189
29	455.8	.509	.657	.244	.222
30	761.9	1.221	1.293	.177	.144
31	486.9	.906	1.031	.199	.181
32	536.0	.711	.674	.199	.166
33	403.3	.578	.620	.076	.067
34	546.6	1.019	1.194	.338	.290
35	582.1	.885	.893	.077	.070

APPENDIX 8

Mean (G), b, and S.E.(b) of treated lines of PROCTOR, 1970

Line No.	Mean (g/plot) Natural scale	b		S.E.(b)	
		Unweighted analysis (Natural scale)	Weighted analysis	Unweighted analysis (Natural scale)	Weighted analysis
1	515.3	1.073	.982	.271	.234
2	448.4	.724	.647	.105	.105
3	567.0	.886	.833	.147	.124
4	283.6	.427	.426	.114	.091
5	573.5	1.068	1.145	.195	.193
6	611.3	1.030	.933	.130	.134
7	562.4	.919	1.040	.244	.228
8	555.0	.953	.940	.060	.045
9	568.9	.959	.927	.060	.049
10	583.5	1.061	.990	.291	.237
11	543.5	.989	.934	.084	.079
12	548.3	.983	.898	.169	.135
13	554.9	1.159	1.068	.134	.124
14	533.0	.892	.831	.112	.103
15	567.1	.830	.913	.275	.214
16	517.8	1.123	1.119	.200	.153
17	487.5	.866	.844	.089	.066
18	602.1	.933	.898	.080	.066
19	474.8	.743	.781	.120	.117
20	524.8	1.233	1.189	.141	.115
21	523.6	.834	.855	.199	.164
22	549.4	.898	.888	.138	.101
23	446.5	.705	.574	.285	.227
24	386.5	.485	.415	.165	.125
25	477.1	.782	.818	.231	.195
26	524.4	.960	.919	.093	.070
27	422.4	.749	.603	.458	.341
28	523.4	.879	.934	.180	.145
29	591.9	.923	1.104	.304	.317
30	497.3	1.032	.914	.159	.163
31	514.9	.603	.688	.191	.174
32	466.8	.646	.603	.158	.127
33	543.6	.777	.899	.227	.242
34	430.1	.843	.811	.109	.086
35	513.8	.959	.927	.120	.094

APPENDIX 9

Mean (G), b, and S.E.(b) of treated lines of PRIOR, 1970

Line No.	Mean (g/plot) Natural scale	b		S.E.(b)	
		Unweighted analysis (Natural scale)	Weighted analysis	Unweighted analysis (Natural scale)	Weighted analysis
1	281.5	.361	.603	.171	.126
2	476.1	.835	.536	.489	.352
3	458.0	1.124	1.181	.568	.425
4	484.3	.502	1.176	.597	.454
5	348.5	.617	.915	.279	.200
6	493.5	1.059	1.230	.268	.196
7	399.1	.918	.736	.317	.239
8	475.1	.974	.947	.186	.136
9	436.9	.843	1.039	.243	.176
10	440.6	.930	1.057	.193	.142
11	476.1	.468	.112	.543	.391
12	407.6	.650	.993	.277	.201
13	421.1	-0.081	.257	.376	.289
14	457.8	.448	.402	.483	.350
15	334.5	.214	.630	.385	.295
16	433.3	.377	.645	.279	.214
17	473.5	.386	.823	.350	.254
18	483.0	-0.018	.147	.437	.327
19	441.8	.399	.443	.130	.096
20	364.0	1.278	1.101	.339	.245
21	474.9	1.142	1.019	.393	.302
22	461.9	1.327	1.158	.299	.222
23	451.3	.584	.740	.150	.112
24	410.5	1.240	1.132	.730	.554
25	491.1	.895	1.236	.253	.188

APPENDIX 10

Analyses of variance for yield data from individual sites for M_2-derived treated and control lines of different cultivars in M_5 generation, 1971.

Cultivar	Site	Variation due to	Control lines			Treated lines		
			d.f.	MS	F	d.f.	MS	F
Clipper	B	Bet. Lines	24	2,367	1.57^{NS}	34	2,662	1.84*
		Residual	24	1,510		34	1,449	
	R	Bet. Lines	23≠	2,287	1.82^{NS}	34	2,696	2.36**
		Residual	21≠	1,256		34	1,141	
	M	Bet. Lines	24	4,682	0.81^{NS}	34	6,985	1.91*
		Residual	24	5,775		34	3,649	
	W	Bet. Lines	24	4,989	1.23^{NS}	34	6,721	1.24^{NS}
		Residual	24	4,056		34	5,424	
	C	Bet. Lines	24	1,459	0.66^{NS}	34	4,695	1.94*
		Residual	24	2,197		34	2,418	
C.I.3576	B	Bet. Lines	24	3,751	1.28^{NS}	34	9,014	1.74*
		Residual	24	2,920		34	5,192	
	R	Bet. Lines	24	4,347	2.33*	34	4,399	1.23^{NS}
		Residual	24	1,869		34	3,576	
	M	Bet. Lines	24	5,133	1.86^{NS}	34	11,424	2.84***
		Residual	24	2,753		34	4,022	
	W	Bet. Lines	24	6,054	0.60^{NS}	34	18,487	2.32**
		Residual	24	10,160		34	7,954	
	C	Bet. Lines	24	3,587	0.97^{NS}	34	10,634	2.75**
		Residual	24	3,696		34	3,871	
Proctor	B	Bet. Lines	24	2,341	0.43^{NS}	34	5,199	1.78*
		Residual	24	5,401		34	2,918	
	R	Bet. Lines	24	1,804	1.04^{NS}	34	4,695	2.36**
		Residual	24	1,736		34	1,988	
	M	Bet. Lines	24	4,059	0.51^{NS}	34	7,579	1.09^{NS}
		Residual	24	7,930		34	6,930	
	W	Bet. Lines	24	10,981	1.17^{NS}	34	13,595	1.80*
		Residual	24	9,357		34	7,555	

≠ Reduced d.f. after excluding plots having large gaps.

APPENDIX 11

Mean (G), b, and S.E.(b) of treated lines of CLIPPER, 1970 + 1971

Line No.	Mean (g/plot) Natural scale	b		S.E. (b)	
		Unweighted analysis (Natural scale)	Weighted analysis	Unweighted analysis (Natural scale)	Weighted analysis
1	511.0	.937	.958	.097	.133
2	469.1	1.071	.976	.120	.135
3	464.2	.750	.809	.052	.073
4	372.2	.664	.639	.116	.144
5	403.8	.609	.541	.088	.103
6	422.2	.731	.681	.090	.102
7	474.7	1.077	.927	.122	.154
8	481.1	.937	1.083	.128	.138
9	507.3	.888	.883	.121	.168
10	510.4	.762	.828	.105	.117
11	429.1	.822	.811	.124	.115
12	408.4	.668	.662	.091	.133
13	499.8	1.024	1.149	.168	.147
14	471.6	.918	.927	.137	.188
15	499.3	1.062	1.059	.066	.079
16	523.6	1.055	1.069	.076	.076
17	506.4	1.140	1.065	.117	.127
18	468.3	.858	.854	.076	.115
19	492.7	.948	1.000	.086	.100
20	443.1	.615	.712	.157	.188
21	521.2	1.142	1.121	.145	.171
22	428.3	.935	.922	.096	.093
23	431.9	.742	.814	.137	.113
24	525.3	1.281	1.165	.106	.126
25	520.3	1.175	1.114	.129	.134
26	501.4	.933	.958	.104	.115
27	532.6	1.177	1.145	.121	.157
28	508.7	1.047	1.102	.118	.147
29	505.8	1.262	1.242	.115	.147
30	430.6	.792	.810	.108	.133
31	496.8	.885	.899	.137	.151
32	486.7	.976	1.013	.086	.094
33	482.2	1.011	.965	.125	.151
34	421.4	.714	.716	.078	.086
35	415.9	.808	.750	.091	.095

APPENDIX 12

Mean (G), b, and S.E.(b) of treated lines
of C.I.3576, 1970 + 1971

Line No.	Mean (g/plot) Natural scale	b		S.E.(b)	
		Unweighted analysis (Natural scale)	Weighted analysis	Unweighted analysis (Natural scale)	Weighted analysis
1	446.1	.819	.801	.144	.158
2	541.3	.931	.946	.062	.083
3	507.3	1.067	1.067	.109	.122
4	539.4	1.154	1.106	.163	.176
5	558.9	1.284	1.260	.100	.119
6	485.9	.800	.829	.094	.109
7	538.4	1.071	1.069	.077	.087
8	503.4	.929	.954	.070	.071
9	490.4	.611	.576	.145	.161
10	486.8	.711	.718	.140	.134
11	558.6	1.040	1.064	.135	.154
12	492.5	.848	.895	.125	.137
13	458.2	.853	.873	.145	.167
14	540.2	1.018	1.011	.133	.144
15	544.3	.760	.787	.104	.128
16	589.6	1.214	1.167	.119	.130
17	499.2	1.018	1.120	.119	.131
18	595.4	1.286	1.254	.112	.130
19	526.5	.899	.919	.066	.069
20	490.9	1.014	1.002	.081	.094
21	586.3	1.295	1.313	.091	.094
22	475.9	.904	.918	.118	.146
23	459.7	.908	.875	.109	.124
24	539.8	.984	.991	.098	.109
25	489.1	1.074	1.044	.118	.126
26	626.2	1.231	1.281	.167	.171
27	351.2	.343	.383	.124	.134
28	567.4	.981	1.030	.128	.145
29	358.1	.620	.625	.154	.146
30	601.5	1.255	1.236	.114	.130
31	389.1	.855	.860	.093	.115
32	455.0	.689	.647	.121	.126
33	364.6	.485	.510	.070	.088
34	504.4	.802	.928	.240	.321
35	519.7	.706	.678	.094	.117

APPENDIX 13

Mean (G), b, and S.E.(b) of treated lines of PROCTOR, 1970 + 1971

Line No.	Mean (g/plot) Natural scale	b		S.E.(b)	
		Unweighted analysis (Natural scale)	Weighted analysis	Unweighted analysis (Natural scale)	Weighted analysis
1	454.7	1.010	.933	.156	.145
2	401.2	.710	.630	.077	.084
3	551.1	.844	.851	.185	.149
4	297.7	.282	.345	.122	.171
5	531.7	1.052	1.165	.144	.162
6	522.3	1.062	.915	.134	.149
7	507.1	.861	.959	.160	.164
8	523.4	.951	.976	.171	.128
9	511.6	.936	.898	.074	.062
10	513.2	1.127	1.037	.188	.197
11	493.3	.963	.924	.072	.068
12	503.4	.922	.882	.110	.103
13	463.2	1.203	1.075	.122	.144
14	491.9	.882	.842	.066	.071
15	476.3	.935	.908	.190	.180
16	469.5	1.068	1.093	.105	.099
17	474.0	.808	.851	.101	.092
18	534.8	.937	.880	.095	.092
19	450.0	.668	.744	.093	.109
20	485.8	1.089	1.110	.116	.135
21	479.6	.892	.910	.167	.145
22	496.3	.836	.842	.132	.119
23	424.1	.681	.613	.163	.158
24	409.6	.448	.477	.185	.149
25	445.6	.749	.790	.127	.131
26	468.7	.970	.939	.074	.088
27	379.6	.767	.637	.234	.204
28	489.3	.814	.890	.112	.115
29	521.0	.979	1.100	.171	.183
30	466.6	.927	.865	.122	.137
31	453.8	.694	.707	.131	.134
32	415.4	.697	.625	.136	.133
33	499.8	.759	.849	.141	.164
34	436.1	.704	.786	.131	.145
35	493.4	.854	.884	.127	.128